Marine holobionts: a model arena for host–microbe biology, from ecosystem function to biotechnology

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Abstract

Microbial symbioses are the operating system of marine biology. Nearly every macroscopic organism in the ocean exists as a holobiont, the consortium composed of a eukaryotic host and its bacterial, archaeal, microeukaryotic and viral partners. Marine holobionts span a broader range of the metazoan tree of life than likely any other ecological setting on the planet. This breadth makes the marine realm a uniquely informative system to investigate how host-microbe partnerships shape organisms and ecosystems.

In this review, we discuss marine holobionts around three integrative themes. First, marine selective regimes sustain a distinctive phylogenetic and metabolic diversity of holobionts. Second, despite their extraordinary diversity, most of the marine holobionts converge on a single carbon-fixing logic with two complementary branches: photosymbiosis in the photic zone and chemosymbiosis in the aphotic zone, both running through a microbial partner around which the host body is built. Third, each marine model system resolves distinctive mechanisms of host-microbe integration to a depth that no single system could achieve alone. Finally, we discuss the growing biotechnological potential of marine holobionts, including bioactive compounds, industrial enzymes and probiotic interventions. Across all these dimensions, the conservation of marine ecosystems is inseparable from the conservation of marine microbiomes.

Sustainability Statement

This review advances UN Sustainable Development Goal 14 (Life Below Water) by synthesising how marine host–microbe symbioses underpin the function, resilience, and conservation of ocean ecosystems, from coral reefs to deep-sea chemosynthetic communities. By framing the holobiont as a reservoir of beneficial microbes, it informs microbiome-based strategies for coral reef restoration, sustainable aquaculture, and the discovery of marine bioactive compounds and enzymes, including those degrading plastic pollutants. The work additionally contributes to SDG 2 (Zero Hunger), SDG 3 (Good Health and Well-being), SDG 12 (Responsible Consumption and Production), and SDG 13 (Climate Action).

1. Introduction

Life is thought to have originated in the sea (Oparin 1924), and from its earliest microbial forms it has been organized through symbiosis. The two carbon-fixing strategies that transformed the biosphere — chemosynthesis and oxygenic photosynthesis — are ancient bacterial innovations (Schirrmeister et al., 2016; Wernegreen, 2012), and the most consequential evolutionary event in the history of eukaryotes — the acquisition of mitochondria and chloroplasts through endosymbiosis (Martin et al., 2015) — also emerged within marine environments. The ocean is therefore not only where life may have begun; it is where the

partnership between host and microbe first occurred and where such occurrence has been most prolifically diversified.

Endosymbiosis is one of the foundational case of the holobiont concept (Margulis & Fester, 1991), and modern marine environments continue to provide its most spectacular contemporary examples: deep-sea invertebrates that house intracellular chemoautotrophic symbionts in dedicated organs (Hinzke et al., 2019); meiofaunal *Loricifera* reported from permanently anoxic basins and associated with hydrogenosome-like organelles (Danovaro et al., 2010; Neves et al., 2016); jellyfish whose metamorphosis is triggered by a dinoflagellate partner (Jinkerson et al., 2022). These systems are not curiosities. Rather they illustrate how host biology can be profoundly reorganized around a microbial partner, while highlighting the exceptional diversity found in marine environments.

Despite this, marine microbiomes and marine holobionts have only recently begun to be systematically characterized. The Tara Oceans expeditions provided the first oceanographic-scale view of marine microbial diversity (Sunagawa et al., 2015, 2020), and parallel advances in single-cell genomics, multi-omics and gnotobiotic experimentation have begun to resolve the functional contributions of marine microbes to biogeochemical cycles, host physiology, and ecosystem-scale processes (Apprill, 2017; Stévenne et al., 2021). Yet, attention to marine holobionts remains profoundly uneven, with reef-building corals, the bobtail squid-*Vibrio fischeri* pair, sponges, and a handful of deep-sea models accounting for the vast majority of the published literature, while many marine-exclusive phyla remain a near-blank canvas (Boscaro et al., 2022; Holt et al., 2022).

In this review we argue that marine holobiont biology is a uniquely informative arena for understanding the holobiont concept itself. We first outline the selective landscape under which marine holobionts evolved — including the defining abiotic gradients of the ocean, its exceptional phylogenetic breadth, benthic–pelagic connectivity, and habitats actively shaped through microbial metabolism. We examine a central organizing axis of the review: the role of microbial primary production through photosymbiosis in the photic zone and chemosymbiosis in the aphotic zone, both producing ecosystem-engineering holobionts whose ecology and physiology emerge from host-microbe partnership. Next, we survey the model systems in which mechanisms of host-microbe integration have been most deply resolved — from binary specificity in the squid-*Vibrio* pair to bacteria-induced metamorphosis in distantly related phyla. Finally, we examine the translational frontiers that marine holobiont biology, including: coral probiotics, microbiome-aware aquaculture, and the discovery of bioactive compounds and industrial enzymes from marine symbionts.

Box 1: The question of the holobiont

A “holobiont” is a biological unit made by an host organism and all its associated microorganims including bacterial, archaeal, microeukaryotic, viral and other microbial partners that live in and on it; its hologenome is the genomic complement of the holobiont, consisting of both host and microbial genomes (Bordenstein et al., 2024; Bordenstein & Theis, 2015). The concept formalizes a measurable claim: host phenotype is partly an emergent property of the microbial partnership, and the combined action of selection and neutrality on that partnership leaves a signal on host biology that selection on the host genome alone cannot explain.

The holobiont is, first and foremost, a structural unit — host plus microbial partners considered together as the appropriate object of biological description (Bordenstein et al., 2024; Bordenstein & Theis, 2015). From this structural unit, evolutionary processes of multiple kinds operate at multiple biological levels: selection and neutrality, drift and gene flow, microbial recruitment and turnover, all acting variably from the holobiont as a whole through bacterial consortia down to individual genes. Just as gene flow shapes the genetic structure of

populations, microbe flow shapes holobiont structure dynamically and under different combinations of forces in different systems. The empirical programme of holobiont biology is to map where, and at what level, these processes act in any given host-microbe system.

The concept has also prompted a substantive debate about its scope. Douglas & Werren (2016) noted that, if the holobiont is taken to require strict whole-unit coevolution between host and microbiome, many microbial associations — characterised by variable transmission, turnover, and partner opportunism — would not satisfy that criterion (Douglas & Werren, 2016). That observation holds under such a restrictive reading; in current usage, however, the concept is more typically framed as a structural unit on which a mix of selective and neutral processes operates across multiple biological levels. Under this framing, the empirical question becomes not whether the holobiont qualifies as a single-level unit of selection, but where and how, in any given system, the relevant evolutionary forces sit.

The marine record is unusually well-suited to that empirical programme, because the full spectrum of host-microbe coupling is on display in marine systems. Obligate symbiosis in the bobtail squid-*Vibrio fischeri* pair, the photosymbiosis of corals and giant clams with Symbiodiniaceae, the gutless tubeworm *Riftia pachyptila* and its single-strain *Candidatus Endoriftia persephone*, and lucinid clams with their chemosynthetic gammaproteobacteria are all cases in which the host body, life cycle, and metabolism are reorganized around a specific microbial partner that the host cannot survive without. In these systems, treating host and microbe as separate ecological and evolutionary units misses the biology. At the other end of the spectrum, the transient, environmentally driven microbiomes of pelagic teleosts or open-ocean copepods are better described as ecological communities than as holobionts in the strong sense.

In this review, we use the term "holobiont" in its ecological-and-evolutionary sense, recognizing that the strength of the host-microbe coupling varies across systems. Our purpose is not to take a side in the debate over the unit of selection; but rather to recognise that some of the most informative cases of host-microbe integration ever described are marine, and that modern biological tools nowadays allow these systems to be characterised with unprecedented depth.

2. Marine holobionts: a distinct selective and phylogenetic regime

Microbial symbioses are not a garnish on marine biology; they are part of its fundamental operating system (Fig. 1). Nearly every macroscopic organism in the ocean — from the pelagic grazers to the deep-sea cold-seep mussel — exists as a ***holobiont*** (See Box 1), the consortium of a eukaryotic host and its bacterial, archaeal, viral, and unicellular-eukaryotic partners (Apprill, 2017; Bordenstein & Theis, 2015). Although holobiont theory matured largely through terrestrial and coastal model systems, marine environment still forces biology to confront a different set of ecologically and evolutionary constraints. Salinity gradients spanning orders of magnitude, hydrostatic pressure dramatically increasing with depth, three-dimensional light attenuation, dissolved-oxygen heterogeneity, and a planetary circulation that links the abyssal floor to the sunlit surface together create conditions with few terrestrial parallels. Three broad asymmetries emerge from these settings – environmental, phylogenetic and geometric - and together they explain why the marine realm represents a unique arena for symbiosis.

2.1 - The marine selective regime: five abiotic axes that shape holobionts

Abiotic factors in the ocean fluctuate continuously across space and time, and, unlike on land, fluctuate in three dimensions. Five variables dominate the selective landscape experienced by marine holobionts: salinity, temperature, hydrostatic pressure, dissolved oxygen, and light (Abdul Kari, 2025; Fiedler, 2018). Each

structures the biogeography of hosts and shapes the composition and metabolic potential of their associated microbiomes.

Salinity represents one of the most pervasive environmental gradients structuring marine life. While open-ocean values typically oscillate between a relative narrow range (~32 - 37 PSU), marine organism can experience an extraordinary osmotic spectrum extending from freshwater-influenced estuaries to hypersalinic evaporitic basins, and polar sea-ice These osmotic gradients directly sculpt prokaryotic community turnover (DasSarma & DasSarma, 2012) and, through the host, reshape physiology and microbiome assembly: in euryhaline teleosts the gut and skin microbiomes track salinity more strongly than diet (Mkulo et al., 2025), and during Atlantic-salmon smoltification the transition to seawater is accompanied by a profound restructuring of the gut microbiome, with *Aeromonas* declining and *Mycoplasma* dominating (Lokesh & Kiron 2016).

Temperature varies across both latitude and depth (Fiedler, 2018; Shea et al., 1992) and governs the composition and abundance of marine bacterioplankton (Stewart, 2019) and the timing and magnitude of algal blooms (Pistocchi et al., 2011). The Tara Oceans survey of 243 samples across 68 global locations showed that epipelagic community composition is driven by temperature more than by any other environmental or geographic factor (Sunagawa et al., 2015), with diversity rising along the latitudinal gradient up to a thermal threshold beyond which stress reshuffles the assembly toward opportunists and pathogens. Ocean warming now constitutes the single most important driver of holobiont disruption: in reef-building corals, thermal anomalies destabilize the Symbiodiniaceae partnership and reshuffle the bacterial microbiome toward opportunists and pathogens (Maire et al., 2022; Voolstra et al., 2024; Wang et al., 2023). Analogous warming-driven dysbiosis hasow been documented in octocorals (Estaque et al., 2024; Xiang et al., 2022) and kelp forests (Castro et al., 2024).

Hydrostatic pressure represents one of the distinctive environmental gradients of marine ecosystems**.** While most terrestrial organisms experience pressure close to ~1 atm, marine organisms occupy habitats spanning a continuous pressure gradients from the ocean surface to an average depth of 3800 m (381 atm), and life persists even at the 11,000-m hadal maximum (Somero, 1992). Here, piezophiles bacteria of the genera *Psychromonas*, *Moritella*, and *Shewanella* recur in the gut microbiome of hadal fishes and invertebrates (Blanton et al., 2022). These taxa exhibit convergent adaptations to extreme pressures such as elevated unsaturated-fatty-acid content in membrane lipids that preserves membranes fluidity under extreme pressure.

Dissolved oxygen availability depends primarily on temperature, depth, and mixing, and is increasingly modulated by anthropogenic forcing (Lévy et al., 2022; Ito & Deutsch, 2010). Oxygen-minimum and anoxic marine zones (OMZs/AMZs) select for anaerobic and chemolithoautotrophic consortia that underpin an alternative, nitrogen- and sulfur-driven biogeochemistry (Canfield & Kraft, 2022; Ulloa et al., 2012); their expansion under coastal eutrophication and warming (Giomi et al., 2023) propagates through marine holobionts, with cascading consequences for the microbiomes of sessile foundation species that cannot relocate - from the reorganization of coral microbiomes during hypoxic events (Altieri et al., 2017) to the expansion of sediment sulfate-reducers that generate H_2S in the demersal layer (Diaz & Rosenberg, 2008).

Finally, **light** is the central limiting resource for primary production in both realms, but in the ocean, it attenuates vertically over tens to hundreds of meters. The photic, dysphotic (twilight) and aphotic zones have set the stage for an eco-evolutionary bifurcation between photosynthetic holobionts — corals, giant clams, anemones, algae — and chemosynthetic ones that inhabit the aphotic realm (Marra et al., 2014; Davies & Smyth, 2025).

2.2 – A taxonomic asymmetry: the ocean holds fewer species but more of the tree of life.

Marine and terrestrial ecosystems differ not only in quantity but in the topology of their biodiversity. An estimated 85–95% of macroscopic species diversity resides on land, driven overwhelmingly by angiosperms and arthropods (Mora et al., 2011; Stork, 2018; Vermeij & Grosberg, 2010). The ocean, by contrast, hosts a minority of species but a disproportionate share of higher taxa: 12–15 of the ~33–35 recognized metazoan phyla are marine-exclusive (Hasebe et al., 2023, WoRMS 2023). Within shared phyla, entire clades are marine-exclusive — mysticete cetaceans, almost all chondrichthyans, and most cephalopod mollusks. While others, such as Porifera and Cnidaria, are not strictly marine-restricted, they are predominantly so. The absolute number of marine species is itself substantial — roughly 2.2 million estimated, of which only ~240,000 are currently catalogued (Mora et al., 2011) — but it is the phylogenetic distribution that matters most, and that distribution is also wildly uneven in scientific attention. Some marine-exclusive phyla, such as Echinodermata, Cnidaria and Ctenophora, are well-characterized hosts. However, most of the marine lineages — including Brachiopoda, Chaetognatha, Cycliophora, Dicyemida, Gnathostomulida, Gnathifera, Hemichordata, Kinorhyncha, Loricifera, Nematomorpha, Orthonectida, Phoronida, Placozoa, and Priapulida — remain a near-blank canvas for symbiosis research (Boscaro et al., 2022; Holt et al., 2022).

The plant kingdom follows the same asymmetric logic. Only ~60 seagrass species colonize the sea (Short et al., 2007), yet seagrass meadows support distinctive rhizosphere microbiomes that can rival the functional richness of any terrestrial soil community (J. Sun et al., 2024). The algal realm, by contrast, is disproportionately marine, with most of the >12,000 Rhodophyta, Chlorophyta and Phaeophyta species marine and each lineage carrying its own symbiotic signature (De Clerck et al., 2013; Guiry, 2024) (Saha et al., 2024).

The prokaryotic dimension is even more unbalanced. The marine pelagic system is globally dominated by the SAR11 clade (Pelagibacterales), with Candidatus Pelagibacter ubique accounting for an estimated 25–50% of surface-ocean bacterioplankton cells (Morris et al. 2002; Zhao et al., 2017), and the proteorhodopsin-based light harvesting they encode (Béjà et al., 2000) couples heterotrophic metabolism to direct solar capture in a way no other open-ocean lineage achieves. Free-living and symbiotic cyanobacteria of the *Prochlorococcus* and *Synechococcus* lineages underwrite roughly half of the planet's primary production (Flombaum et al., 2013; Kuhlisch et al., 2024). These lineages are not merely abundant; they shape the carbon cycle, set the redox chemistry of the ocean surface, and — through phycosphere associations — couple the microbial loop to the metazoan food web (Morris et al. 2002).

Marine environments harbor a remarkable diversity of extremophilic organisms. Life persists at pH <5 (acidophiles) and >9 (alkaliphiles); at 0–20 °C (psychrophiles), 45–80 °C (thermophiles) and >80 °C (hyperthermophiles); at 2.5–5.2 M NaCl (halophiles); at low water activity (xerophiles); and at >35–50 MPa (barophiles / piezophiles) (Veluchamy et al., 2025). Many organisms combine two or more of these axes as polyextremophiles (Saralov, 2019), and although most extremophiles are prokaryotic, a small but ecologically significant proportion are metazoans (Rappaport & Oliverio, 2024).

2.3 - Benthic-pelagic coupling: a distinctive marine geometry for holobionts.

Marine ecology is strongly structured along a vertical axis , with benthic communities on the seafloor being physically and biologically coupled to the pelagic water column above through sinking particulate matter, the marine snow (Turner, 2015), larval dispersal, vertical migration of mesopelagic consumers, and the benthic regeneration of nutrients (Griffiths et al., 2017; Marcus & Boero, 1998). This benthic–pelagic coupling links species with radically different niches and re-routes primary production through food webs in both directions

(Baustian et al., 2014; Ehrnsten et al., 2019). Plankton drive much of ocean's primary production while macrofaunal benthos serves as the system's organic matter reservoir (Ehrnsten et al., 2019) storing a substantial fraction of sinking organic matter (Kuhlisch et al., 2024; Pereira, 2025). The resulting flux of sinking biomass returns carbon to the deep sea on climatically relevant timescales.

For holobiont biology, the key implication of this geometry is that many marine hosts transition between distinct habitat. Complex life cycles are not a marine peculiarity in principle, but they are the rule rather than the exception at sea (Swearer et al., 2019). Scleractinian corals begin life as planktonic larvae before settling on reefs (Harrison, 2011); most teleosts undergo a pelagic larval stage (Downie et al., 2020) and many benthic invertebrates alternate between meroplanktonic and holobenthic phases (Marcus & Boero, 1998). Each life-history stage samples a different microbial environment, and the microbiome is reassembled accordingly (Maritan et al., 2024; Menéndez et al., 2023). The holobiont that leaves the spawn is not the holobiont that reaches maturity and the developmental consequences of that mid-life reassembly remain largely unmapped.

These three asymmetries also explain why the published map of marine holobiont research is so unevenly distributed. Microbiomes modulate host immunity, development, and ecological function (McFall-Ngai et al., 2013), and at oceanographic scale they govern oxygen production, nutrient cycling, and organic-matter turnover (Apprill, 2017; Trevathan-Tackett et al., 2019). Yet attention to marine holobionts is profoundly unequal. Well-studied systems — hermatypic corals (Voolstra et al., 2024), the bobtail squid–*Vibrio fischeri* model (McFall-Ngai et al., 2012; Pipes & Nishiguchi, 2022), deep-sea mussels (Tame et al., 2023), sponges (Schmittmann et al., 2022; Turon et al., 2024) — now account for the vast majority of the published marine microbiome literature, while most marine-exclusive phyla have one or zero primary studies at 16S rRNA gene resolution. Table 1 presents a targeted census of holobiont-relevant literature across marine organisms.

Table 1. Summary of representative marine organisms used in symbiosis research.

Organism	**Phylum**	**Sub-taxa/model**	**Reference**	**Habitat**	**Technique**
Mussel (shallow)	Mollusca	Lucinidae; *Mytilus galloprovincialis.*	(Balbi et al., 2024; Cardini et al., 2019)	Seagrass meadows	16S, isotopes, cultures.
Hermatypic coral	Cnidaria	Scleractinia	(Maire et al., 2022; Voolstra et al., 2024, 2025; Wang et al., 2023)	Coral reef	16S, ITS, Metaomics
Gorgonian coral	Cnidaria	Octocorallia	(Avesani et al., 2025; Estaque et al., 2024; X. Gao et al., 2025; Xiang et al., 2022)	Coral Forest	16S, ITS, Omics
Cold water coral	Cnidaria	*Lophelia pertusa, Madrepora oculata, Desmophyllum*	(Appah et al., 2022; Chapron et al., 2020, 2025; Chemel et al., 2024)	Coral Forest	16S, Metaomics
Seagrass	Magnoliophyta	*Zostera marina, Posidonia oceanica, Cymodocea nodosa*	(Fahimipour et al., 2017; J. Sun et al., 2024)	Seagrass meadows	16S, Inoculation

Sponge	Porifera	*Ianthella basta, Crambe crambe, Theonella swinhoei, Halichondria panicea*.	(Garritano et al., 2023; Peters et al., 2023; Schmittmann et al., 2022; Turon et al., 2024; Webster & Thomas, 2016)	Coral Reef, Sponge Forest	FISH, 16S, Metaomics; Electron Microscopy
Mussel (Deep-sea)	Mollusca	*Bathymodiolus spp.*	(Petersen & Dubilier, 2009; Tame, 2025; Tame et al., 2022, 2023; Ücker et al., 2021)	Deep-sea	FISH, Metaomics, Fluorescence-labelling, Electron Microscopy
Squid	Mollusca	*Euprymna scolopes*	(Kamp et al., 2025; McFall-Ngai et al., 2012; Nyholm & McFall-Ngai, 2021)	Water column	FISH, Electron Microscopy, Omics
Jellyfish	Cnidaria	*Cassiopea* spp., *Aurelia aurita*	(Jinkerson et al., 2022; Ohdera et al., 2018; Weiland-Bräuer et al., 2020)	Water column	16S, Omics, Inoculation
Meiofauna	Multiple phyla	Multiple taxa	(Boscaro et al., 2022; Holt et al., 2022)	Water column, Sediment	16S, 18S
Fish	Chordata	Teleosts	(Blanton et al., 2022; Graziano et al., 2026; Limborg et al., 2018)	Water column, Aquaria	16S, Metaomics
Deep-sea hosts	Annellida/ Mollusca/ Artropoda	*Riftia pachyptila, Ridegia pisceae, Kiwa* spp., *vesicomyid clams, Bathymodiolus*	(Chao et al., 2007; Dubilier et al., 2008; Goffredi et al., 2008; Hinzke et al., 2019)	Deep-sea	SSU rRNA, 16S, Omics, FISH
Mangrove	Rhizophoraceae	*Rhizophora mucronata, Avicennia marina, Sonneratia alba*	(Muwawa et al., 2024; Sujeeth et al., 2026; Wainwright et al., 2023)	Intertidal sediment	ITS, 16S, Metaomics
Salt-marsh halophyte	Plantae (Magnoliophyta)	*Suaeda maritima, Suaeda monoica, Sesuvium portulacastrum*	(Sujeeth et al., 2026)	Intertidal sediment	16S, Omics
Macroalgae/kelp	Chlorophyta/ Ochrophyta/ Heterokontophyta	*Saccharina japonica; Ecklonia radiata; Sargassum lineariforum, Ulva* spp., *Fucus* spp.	(Castro et al., 2024; Saha et al., 2024; J. Zhao et al., 2024)	Macroalgal forest	16S, Metaomics

2.4- Symbiosis shapes marine habitats

Some marine organisms do not merely inhabit ecosystems; they actively create and structure them, often through partnership pivoted on microbial metabolism. Reef-building corals, mangroves, seagrasses, macroalgal forests, salt-marsh halophytes, mussel beds, and — on the deep seafloor — chemosynthetic mats and tubeworm thickets are foundation species whose bodies and associated microbes literally build the three-dimensional architecture in which other marine life evolves (Cardini et al., 2022; Chimienti et al., 2021; Duarte et al., 2022; Mayer-Pinto et al., 2020; Wainwright et al., 2023). The diversity of marine habitats is therefore closely intertwined with the diversity microbial metabolisms that sustain them — sulfur cycling builds the mangrove sediment, sulfide detoxification builds the seagrass meadow, photosymbiosis builds the coral reef, chemolithoautotrophy builds the hydrothermal vent — and protecting these habitats accordingly means conserving their microbiomes alongside their hosts (Corinaldesi et al., 2023). The four habitat clusters that follow provide representative examples of this ecological framework.

Intertidal forest and halophyte marshes

Mangroves are habitats built by the joint metabolism of root-anchored plants and a sulfur-cycling sediment microbiome. Mangrove forests stabilize coasts, nurse larval fish, and rank among the most efficient blue-carbon sinks on Earth (Wainwright et al., 2023). The mangrove sediment is a biogeochemical reactor, and its microbial residents — *Pleurocapsa*, *Tunicatimonas*, *Halomonas*, *Marinomonas*, *Rubrivirga*, *Altererythrobacter*, *Lewinella*, *Erythrobacter* (Wainwright et al., 2023) — drive sulfur, nitrogen and carbon cycling in a habitat that is permanently nutrient-limited and salt-stressed. The Lucinidae clams associated with Rhizophora mangle roots host thiotrophic Gammaproteobacteria that detoxify sulfide and deliver fixed nitrogen to the plant (Lim et al., 2019), constituting a tripartite (plant–animal–bacterium) symbiosis with few terrestrial analogue. Recent metagenomic surveys have begun to resolve the mangrove rhizosphere at functional resolution (Bushra et al., 2024; Muwawa et al., 2024; Sujeeth et al., 2026). Here, fungal partners are emerging as essential and under-studied players in mangrove holobiont health (N. L. Y. Lee et al., 2019).

Salt marshes perform the ecologically complementary role in temperate estuaries. Their sediment-associated bacteria mediate nitrification and denitrification and, in eutrophic and urbanized coastal systems, are the dominant sink for anthropogenic nitrogen (Morris et al., 2023; Wang et al., 2023). Because transitional habitats integrate riverine pollution and coastal eutrophication, the resilience of their microbial communities is a leading indicator of estuarine health.

Seagrass meadows and macroalgal forests

Seagrass meadows can occur astripartite holobionts: the only fully marine angiosperms, the sediment-detoxifying bacteria that allow them to grow, and the lucinid clams that anchor the partnership. Seagrass rhizospheres host sulfate-reducing and sulfur-oxidizing bacterial consortia such as, Desulfobulbaceae, Desulfovibrionaceae, Desulfomonadaceae, Desulfobacteriaceae (Fahimipour et al., 2017) that detoxify sulfide in anoxic sediments. In *Posidonia oceanica* meadows, the architecture is more elaborate: Lucinid clams, their chemoautotrophic sulfur-oxidizing endosymbionts, and the plant itself constitute a tripartite holobiont in which the clams both detoxify the sediment for the seagrass and deliver fixed nitrogen to it (Cardini et al., 2019, 2022). Comparable rhizosphere specificity has now been demonstrated across *Zostera* and *Cymodocea* species (H. Sun et al., 2024; J. Sun et al., 2024). Microbial-based restoration of degraded seagrass meadows — seeding

rhizobacteria to accelerate re-vegetation — has moved from proof of concept to applied protocol (H. Sun et al., 2024).

Macroalgal forests are habitats built on the surface chemistry of the host. They are among the most productive coastal habitats and are now central to blue-carbon accounting (Duarte et al., 2022). Their surfaces harbor dense, species-specific bacterial biofilms whose metabolism co-regulates host growth, chemical defense, and disease susceptibility (Saha et al., 2024). Marine heatwaves and ocean warming destabilize these assemblages and cascade into trophic effects on grazers (Castro et al., 2024). A recently described viral component of the macroalgal holobiont further modulates microbiome equilibrium and the composition of the surrounding water column (J. Zhao et al., 2024). Macroalgal aquaculture is an emerging global industry whose yields will depend on managing these holobionts, not just the host.

Coral reefs and coral forests

Scleractinian (hermatypic) corals are the archetypal marine holobionts and the best studied model system for reef-scale symbiosis. Many of them depend on functional relationships with photosynthetic dinoflagellates of the family Symbiodiniaceae, which are embedded within broader bacterial, archaeal, viral and fungal communities. Together, all these microbial partners contribute to coral physiology, calcification and stress resilience (Dunphy et al., 2019; Voolstra et al., 2024). Heat-driven breakdown of the Symbiodiniaceae association — bleaching — and the parallel reorganization of the bacterial microbiome are the central threats to reef ecosystems globally (Voolstra et al., 2025; Wang et al., 2023). The thermally tolerant members of the coral microbiome remains a major research priority (Maire et al., 2022) and a central opportunity for probiotic, sustainable reef interventions.

Gorgonians and other octocorals can construct complex three-dimensional habitats, particularly in temperate, mesophotic and deep environment (Chimienti et al., 2021). Because these organisms are not dependent on dinoflagellate symbionts, their microbiomes are structurally distinct and are often characterized by a high relative abundance of members of the family Endozoicomonadaceae (Avesani et al., 2025; Xiang et al., 2022). Octocoral microbiomes are also more variable under thermal and anthropogenic stress (Estaque et al., 2024; X. Gao et al., 2025).

Cold-water corals build reef-scale habitats hundreds of meters deep and host their own parallel microbiome literature. *Lophelia*, *Madrepora* and *Desmophyllum* are now the focus of dedicated microbiome studies (Appah et al., 2022; Chapron et al., 2020, 2025; Chemel et al., 2024). Because they live under chronic nutrient limitation and emerging plastic-pollution pressure (Chapron et al., 2025), the cold-water coral microbiome is a sensitive early-warning system for deep-ocean change.

Hydrothermal vents and cold seeps: microbes build the habitat

Deep-sea hydrothermal vents and cold seeps represent some of the most striking examples of ecosystems structured around symbiosis. Chemolithoautotrophic microorganisms — sulfide- and methane-oxidizing bacteria and archaea — fix carbon in the absence of light and support dense, high-biomass animal communities that would otherwise be impossible at these depths (Dick, 2019; Georgieva et al., 2018; Hinzke et al., 2019; Suess, 2018). Giant tubeworms, *Bathymodiolus* mussels, and vesicomyid clams house these chemosynthetic partners in dedicated gill or trophosome tissue; the cellular and immunological choreography of this partnership is now resolved at the level of single-cell phagocytosis and mTOR signaling (Tame, 2025; Tame et al., 2022, 2023). Deep-sea symbioses are the most compact laboratory for one of the central claims of holobiont biology (Bordenstein et al., 2024): host biology is an emergent property of the partnership.

Across these systems, microbes do not merely inhabit ecosystem-forming hosts; they contribute directly to the sustain and habitat shaping. Sulfur detoxification fuels seagrass meadows, carbon fixation fuels reef, chemolithotrophy fuels the vent community, and root-anchored sulfur cycling fuels the mangrove forest. The diversity of marine habitats and the diversity of marine microbiomes are therefore the same biological phenomenon viewed at different scales, and the biodiversity, climate, and food-security stakes rest on the same conceptual foundation: that diversity is the asset, and microbial metabolism is its operating principle. That conceptual foundation is metabolic. The diversity of marine holobionts is not only a diversity of species but also a diversity of metabolic partnerships, in which microbial symbionts mediate the exchange of energy, nutrients, and biochemical functions. Among the most influential of these are carbon-fixing strategies: photosymbiosis in the sunlit upper ocean and chemosymbiosis below it, two forms of symbiotic primary production that have profoundly shaped marine ecosystems. Section 3 develops that bifurcation.

3– Photosymbiosis and chemosymbiosis

3.1 – Two-way solution to the same problem

Every ecosystem on Earth ultimately depends on the fixation of inorganic carbon into biomass against a thermodynamic gradient. The terrestrial answer is overwhelmingly photosynthetic and autonomous — vascular plants and their cyanobacterial ancestors do almost all the work, with mycorrhizal and rhizobial partnerships supplying nutrients on the margins. Marine environments present a different ecological setting. Because photosynthetically active radiation is restricted within the upper few hundred meters but liquid habitat extending several kilometers further (Davies & Smyth, 2025; Marra et al., 2014), and because the upper sunlit layer is itself nutrient-limited (Yellowlees et al., 2008), marine holobionts have converged on two carbon-fixing strategies relying on microbial primary production: photosymbiosis in the photic zone and chemosymbiosis below it (Dick, 2019; Dubilier et al., 2008).

Both strategies are integrative in the holobiont sense. Both host and microbes generate emergent ecological properties that neither could achieve alone – creating foundation systems that support diverse biological communities (Levin et al., 2016; Mayer-Pinto et al., 2020). Both are also threatened by anthropogenic impact. Photsymbiotic systems are particularly vulnerable to ocean warming and acidification, whereas chemosymbiotic systems face growing pressures from deep-sea mining, deoxygenation, and other form of environmental change. This section examines each axis in turn, focusing on two marine systems in which host-microbe integration has been explored most extensively: tropical coral reefs and deep-sea hydrothermal-vent communities.

3.2 – Photosymbiosis: outsourcing photosynthesis to a partner

Photosynthesis is the planet's dominant route for converting solar energy into chemical energy. Consequently, partnership between heterotrophic hosts and phototrophic microorganism have evolved repeatedly across the tree of life wherever light is sufficient available to exploit the primary production. Oxygenic photosynthesis originated in aquatic systems because the substrate it splits - water - is the medium itself (Hohmann-Marriott & Blankenship, 2011). Geochemical and microfossil evidence places oxygenic photosynthesis in cyanobacteria-like ancestors at least 2.7-3 Ga ago (Homann et al., 2015), and from there phototropy has radiated into nearly every photic-zone lineage of life: bacteria, microalgae, macroalgae, seagrasses and the few aquatic angiosperms. Light, however, is not free: it is limited in dose, spectrally narrowed by the water column, and exhausted within ~200 m even in the clearest seas (Davies & Smyth, 2025; K. Gao et al., 2019). For non-

photosynthetic hosts, symbiosis with phototrophic microbes represents a recurrent evolutionary strategy for accessing photosynthetically derived carbon, having evolved independently in at least seven metazoan and protist phyla. In marine systems, the host range spans Porifera, Cnidaria, Platyhelminthes, Mollusca, Foraminifera and Radiolaria, paired across an equally diverse symbiont range that includes Cyanobacteria, dinoflagellates (notably Symbiodiniaceae), Chlorophyta, Rhodophyta, and diatoms (Not et al., 2016).

Cnidaria dominate the photosymbiosis literature. Reef-building corals harbor obligate dinoflagellates of the family *Symbiodiniaceae* (Peixoto, Harkins, et al., 2021; Roik et al., 2024; Voolstra et al., 2024, 2025). The same partnership extends beyond hard corals: the upside-down jellyfish *Cassiopea* (Scyphozoa) *Symbiodinium* acquisition for metamorphic completion (Moffat et al., 2022; Ohdera et al., 2018) and the evolutionary genetics of *Cassiopea* make it one of the few experimentally tractable hosts in which symbiont genotype x temperature interactions can be measured directly (Moffat et al., 2022).

Porifera hosts a comparable diversity of photosymbiotic associations. Most photosymbiotic sponges harbor cyanobacteria, particularly *Candidatus Synechococcus spongiarum*, which can supply more than 50% of the holobiont energetic demand and significantly enhance host fitness and ecological competitiveness, allowing photosynthetic sponges to dominate benthic substrates in some reef systems (Pita et al., 2018; Usher, 2008). The bioeroding family Clionaidae represents a unique case: it associates with Symbiodiniaceae rather than cyanobacteria, making it the only known sponge clade in which symbiont contribution to carbon fixation approaches levels comparable to those observed in corals (Achlatis et al., 2019; Steindler et al. 2002). *Cliona viridis* specifically harbors dinoflagellates of the genus *Gerakladium* (formerly Symbiodinium clade G), from which it receives sufficient photosynthetically derived energy to sustain bioerosion activity within coral reefs. Althougphotosynthesis would theoretically counteract bioerosion by increasing local pH, the symbiosis appears efficient enough to compensate for this limitation, despite the underlying mechanisms remaining only partially understood (Achlatis et al., 2019).

Tunicata provide a distinctive example. Tropical didemnid ascidians associate with the cyanobacterial genus *Prochloron* in an obligate, vertically transmitted partnership, the only known obligate photosymbiosis within Chordata (Kojima & Hirose, 2012). A handful of marine animals can also bypass symbiosis entirely and *steal* the photosynthetic machinery: sacoglossan sea slugs, such as *Elysia spp*., ingest siphonous algae, retain their chloroplasts intact within digestive cells, and continue to drive carbon fixation for days to months without nuclear genes encoding photosynthetic proteins – a phenomenon known as kleptoplasty (Cartaxana et al., 2023; Cruz & Cartaxana, 2022). Functional retention time scales with prey identity (Cartaxana et al., 2023) placing kleptoplasty conceptually between symbiosis proper and predation, and offering a comparative framework against which the costs and benefits of obligate photosymbiosis can be measured. Photosymbiosis is therefore not an idiosyncratic adaptation of a few host lineages but a recurrent evolutionary solution to the marine light economy.

3.3 – Coral Reefs: photosymbiosis as ecosystem engineer

Tropical coral reefs occupy less than 0.1% of the seafloor, yet hosts roughly 30% of described marine multicellular biodiversity, including a quarter of all marine fish species (Bowen et al., 2013; Roberts et al., 2002; Voolstra et al., 2024). Reefs achieve extraordinary levels of productivity and biodiversity in tropical water that are characteristically oligotrophic, with chronically low concentrations of fixed nitrogen and phosphorus that should preclude high-productivity ecosystems (Yellowlees et al., 2008). The resolution of this paradox – Darwin's paradox of the reef – is the holobiont.

Photosynthesis by Symbiodiniaceae inside the coral host translocates fixed carbon directly to host tissue, bypassing the planktonic food web entirely; the coral's nitrogenous waste fertilizes the symbiont in return; and tight internal recycling between partners decouples the holobiont from external nutrient supply (Voolstra et al., 2024; Wall et al., 2020). Reefs are, in other words, what happens when an oligotrophic environment is colonized by an obligate, internally recycling photosymbiotic partnership. This metabolic partnership has consequences at both structural and biogeochemical levels. The first is biophysical: surplus fixed carbon supports rapid calcification, the coral lays down a calcium-carbonate skeleton, and the resulting three-dimensional framework partitions the water columns into hundreds of microhabitats that host the rest of reef diversity (Brandl et al., 2019; Mayer-Pinto et al., 2020; Voolstra et al., 2024). The second is biogeochemical: the holobiont and its associated microbial community produce a chemically distinctive metabolome – sterols, dimethylsulhoniopropionate, vitamins, antimicrobials – that conditions the reef water column and shapes microbial assembly across kilometers (Roach et al., 2017). Reefs do not merely contain microbes; they are built upon microbes.

Beyond Symbiodiniaceae, the bacterial coral microbiome contributes function that is only beginning to be resolved. The dominant taxa - Pseudomonadota (Proteobacteria), Bacteroidota, Bacillota and Cyanobacteriota, with the families Endozoicomonadaceae, Rhodobacteraceae, Vibrionaceae and Alteromonadaceae most abundant – encode antioxidant pathways, secondary metabolites, and nitrogen-cycling functions whose contributions are still being mapped. The genus *Endozoicomonas* was for years assumed to be a near-universal coral mutualist, because several lineages are predicted to contribute vitamins, cofactors, secondary metabolites and antioxidant functions. However, recent comparative genomics has shown that *Endozoicomonas* lineages span the full mtualist-commensalism-opportunism-parasitism spectrum across marine animal hosts (Pogoreutz & Ziegler, 2024). Pathogens – most notably *Vibrio coralliilyticus* – are temperature-amplified, with bleaching and disease outbreaks tightly coupled to thermal anomalies (Balbi et al., 2024; Vezzulli et al., 2013). Microbiome plasticity itself differs between reef-building genera: comparative studies suggest that *Acropora* generally exhibit greater microbiome plasticity than *Pocillopora*, with consequences for bleaching susceptibility and recovery trajectory (Voolstra et al., 2024).

The microeukaryotic and viral compartments are still under-described. Fungi have traditionally been ascribed as pathogens, but their potential diversity hints to a diverse role - including supporting nitrogen fixing bacteria and protecting the host from UV damage through the production of mycosporin-like amino acids (Ainsworth et al., 2017). Many other microeukaryotic taxa have been found in coral reefs - Sagenista, Ciliophora, Colpodellia, Apicomplexa, Dinoflagellata,Chlorophyta and Rhodophyta (Bonacolta et al., 2023). This associated biodiversity can play symbiotic roles to the corals, for example the Chlorophyta *Ostreobium* is capable to exchange nitrogen and carbon to the host even though not being an endosymbiont like Symbiodiniaceae (Bonacolta et al., 2023).

Climate Change remains the dominant threat. Bleaching is now best understood not simply as the loss of a single partner but as the destabilization of a coordinated multipartite metabolism (Grupstra et al., 2024; Voolstra et al., 2024). Consequently identifying the thermally tolerant components of the holobiont – including symbiont haplotypes, bacterial probiotics, microeukaryotic accessory partners – has become a major research in reef science (Maire et al., 2022; Peixoto, Sweet, et al., 2021).

3.4 – Chemosymbiosis: outsourcing carbon fixation in the dark

Photosynthesis is constrained to the photic zone, yet ~75% of the ocean by volume lies below it. Without alternative routes to carbon fixation, primary production in these aphotic environments would be impossible. Deep-sea biology escapes this constraint through two remarkable features. First, chemolithoautotrophy — the fixation of inorganic carbon using energy harvested from inorganic chemical potential rather than light — predates oxygenic photosynthesis and remains widespread; chemoautotrophic bacteria and archaea contribute substantially to global ocean primary production, with conservative estimates placing the dark-ocean microbial biome among the largest on Earth (Pachiadaki et al., 2017; Ricci & Greening, 2024). Second, chemosynthesis is operative wherever reduced inorganic compounds (sulphide, methane, hydrogen, ammonia, iron (II)) meet an oxidant — a condition that is met not only at hydrothermal vents and cold seeps but also in coastal sediments, the rhizosphere of seagrasses, oxygen-minimum zones, and the gut of marine animals. Wherever this redox interface exists, eukaryotes have repeatedly evolved partnerships with chemolithoautotrophic prokaryotes to exploit it (Dubilier et al., 2008; Sogin et al., 2020). Beyond the chemosynthetic interface, organic matter descending through the column water as marine snow supplements but does not replace chemosynthetic primary production (Ricci & Greening, 2024). Indeed chemosynthesis is the more ancient strategy, likely sustained the earliest life on Earth before either anoxygenic or oxygenic photosynthesis (Ricci & Greening, 2024).

The chemoautotrophic toolkit is dominated by sulfur metabolism. Sulfur-oxidizing bacteria (SOB) convert reduced (sulfide, thiosulfate) into more oxidized forms (sulfite, sulfate) and harvest the released electrons for CO_2 fixation (Hu et al., 2018), while sulphate-reducing bacteria (SRB) close the loop in the opposite direction, using sulfate as a terminal electron acceptor under anoxia and regenerating sulfide (Muyzer & Stams, 2008). The persistent vertical separation of these two metabolisms in marine sediments produces a sulfur-cycling microbial reactor that supports a rich array of chemosymbiotic eukaryotic hosts (Dubilier et al., 2008). Within the symbiont-relevant prokaryotes, the phylum Campylobacterota (formerly Epsilonproteobacteria) is ovr-represented as both free-living and symbiotic chemoautotrophs in deep-sea environments. *Sulfurimonas* and the sediment-associated *Sulfurospirillum* oxidize reduced sulfur and contribute to nitrogen and carbon cycling; *Sulfurovum* and *Nitratiruptor* carry the full reductive tricarboxylic-acid (rTCA) cycle for autotrophic CO_2 fixation. Their metabolic flexibility allows them to colonise tubeworm trophosomes, polychaete bodies, snail and shrimp gills, and deep-sea sediments (Nakagawa et al., 2005; Sogin et al., 2021; Van Der Stel & Wösten, 2019).

Methane is the other major reduced substrate. Methanotrophic bacteria of the phyla Pseudomonadota (Gammaproteobacteria, Alphaproteobacteria) and Verrucomicrobia oxidize methane and in many cases enter symbiotic associations with deep-sea invertebrates, plant rhizospheres and salt-marsh sediments (Petersen & Dubilier, 2009; Ponnudurai et al., 2017). On the archaeal side, ammonia-oxidising archaea of the order Nitrososphaerales (formerly Thaumarchaeota) are the dominant nitrogen-cycling associates of marine sponges, where they recycle host nitrogenous waste at high efficiency (Glasl et al., 2025). Methanogenic Methanococci, mostly hydrogenotrophic, span mesophilic to hyperthermophilic regimes, while ANME archaea of the orders Methanomicrobiales and Methanosarcinales perform the reverse pathway — anaerobic oxidation of methane (AOM) — at cold seeps and methane hydrates (Goyal et al., 2016; Timmers et al., 2017).

These metabolic capacities are ecologically relevant when they are recruited into symbiosis. Chemosymbiotic hosts share a common ecological feature: they live in habitats with ample inorganic energy but insufficient bulk organic matter to support a heterotrophic lifestyle (Sogin et al., 2020). The host typically supplies the bacterial partner with stable physicochemical and access to both the reduced substrate and the oxidant; the

symbiont returns fixed carbon, sometimes nitrogen, and detoxification of the reduced compound. The geographic range of these partnerships is broad. In shallow reducing sediments under seagrass meadows and within coral-reef back-reef zones, oligochaetes, nematodes, flatworms, ciliates and lucinid clams host sulfur-oxidising symbionts (Cardini et al., 2019; Sogin et al., 2020). In the deep sea, the canonical models are the giant tubeworm *Riftia pachyptila*, whose trophosome harbors, a single sulfur-oxidising *Candidatus Endoriftia persephone* gammaproteobacterium that fixes CO_2 via the Calvin-Benson and rTCA cycles (Hinzke et al., 2019; Markert et al., 2007; McCowin et al., 2023); the gutless oligochaete *Olavius algarvensis* with up to seven distinct sulfur- and hydrogen-oxidizing symbionts in its body wall (Wippler et al., 2016); and the *Bathymodiolus* mussel lineage, which hosts thiotrophic Thioglobaceae and methanotrophic Methylomonadaceae in dual symbioses across hydrothermal vents, cold seeps and whale falls (Dubilier et al., 2008; Ponnudurai et al., 2017; Ücker et al., 2021).

Photosymbiosis and chemosymbiosis are equivalent in their evolutionary logic — an organism that cannot fix carbon partners with one that can — but they are not equivalent in their phylogenetic distribution: photosymbiosis converges from many host phyla onto a small set of algal symbiont lineages, while chemosymbiosis distributes across many bacterial lineages and a more restricted set of host architectures.

3.5 – Hydrothermal vents and cold seeps: chemosymbiosis as ecosystem engineer

Although biodiversity is generally expected to decline relative to highly productive photic-zone ecosystems such as coral reefs, diverse and structurally complexed habitats persist far below the sunlit ocean, including deep-sea coral forests and sponge grounds; whose associated species remain only partially characterized (Busch et al., 2022; Chapron et al., 2020; Costello & Chaudhary, 2017). At depths where ambient temperature is <4 °C), hydrostatic pressure approaches 400 atm, light is absent, and exported surface productivity is sparse, vent and seep communities sustain biomass densities comparable to the most productive shallow-water ecosystem on Earth (Danovaro et al., 2014; Levin et al., 2016; Tsurumi, 2003). Their metabolic foundation is analogous in form to the reef's — a microbial partner fixes carbon for an animal host that cannot — but the energy source is geological rather than solar.

Hydrothermal vents form when seawater percolates into the basaltic ocean crust, and is heated through contact with hot basaltic rocks. During this process, the fluid becomes chemically reduced, and re-emerges as anoxic, sulfide- and metal-rich fluid that mixes with cold oxic seawater across a redox gradient millimeters wide (Dick, 2019). The plume can be metal-rich (Fe, Mn) supplying the surrounding water with cofactors that themselves shape downstream microbial productivity (Fitzsimmons et al., 2017). Cold seeps are the lower-temperature complement — sites where reduced fluids (sulfide, hydrogen, methane, hydrocarbons) leak from the seafloor more slowly and persistently, and where anaerobic oxidation of methane by archaea is a dominant microbial process (Suess, 2014, 2018). At both vents and seeps, the chemical disequilibrium between the reduced fluid and oxic seawater is the ecosystem's energy currency.

Foundation chemosymbiotic holobionts provide the biological architecture in which the rest of vent community lives. Siboglinid tubeworms - *Riftia pachyptila* with *Cand. Endoriftia persephone* (Hinzke et al., 2019); *Ridgeia piscesae* with its own gammaproteobacterial endosymbiont (Chao et al., 2007) – together with large bivalves such as *Bathymodiolus* mussels and vesicomyid clams form long-lived structural assemblages that persist on the order of decades, even after fluid flow ceases (Govenar & Fisher, 2007; Levin et al., 2016; Murdock et al., 2021). The resulting microbial biomass and metabolic activity sustain grazing, deposit- and suspension-feeding organisms, as well as secondary symbiotic relationships with animal hosts (Govenar & Fisher, 2007; Murdock et al., 2021); the organic carbon produced by chemosynthetic microbes is not confined

to the holobionts themselves but can be exported through benthic–pelagic coupling and trophic transfer within the water column (Levin et al., 2016).

Vagile, mobile holobionts are equally characteristic of vent and seep ecology, and their architecture reveals the same chemosymbiotic logic at smaller spatial scales.

The shrimp *Rimicaris exoculata* forms dense aggregations on black smoker chimney walls, where a chemoautotrophic ectosymbiont community on the gill-cover (Campylobacterota, Gammaproteobacteria, Zetaproteobacteria, Deltaproteobacteria) oxidizes sulfide, iron and methane to feed the host (Cowart et al., 2017; Petersen et al., 2011).

The shallow water hydrothermal crab X*enograpsus testudinatus* hosts gill-associated Epsilonproteobacteria and Gammaproteobacteria that protect that host against sulphide toxicity (Chou et al., 2023). The yeti crab *Kiwa hirsuta* cultivates chemosynthetic episymbionts on its setae and feeds directly upon them (Thurber et al., 2011). The scaly-foot snail *Chrysomallon squamiferum* houses a single sulfur-oxidizing gammaprteobacterial endosymbiont in an enlarged esophageal gland. The endosymbiont is acquired through a mixed horizontal-vertical transmission mode that buffers populations across vent fields with different chemistry (Yin et al., 2023). These mobile and structural holobionts together produce a vent food web that depends almost exclusively on chemosynthetic primary production. As vent fluid declines and a system ages, sulfide-driven biomass collapses but the resulting carbonate or sulfate structure persists, hosting a successional fauna of crustaceans, hagfish, eels and gastropods that may persist for centuries (Cordes et al., 2010). Vent and extreme deep-sea environments are therefore not just biodiversity hotspots and chemosymbiotic at their peak – they leave a chemosymbiotic structural legacy that sustains biodiversity long after the fluid that built them has stopped flowing.

3.6 – The holobiont potential with autotrophy: a zero-mile strategy

The biological output of coral reefs and hydrothermal-vent communities is similar in both scale (high biomass, high biodiversity, structurally complex) and mechanism: a partner microbe fixes inorganic carbon for an animal host that cannot, on a substrate that the partnership itself builds. Although the energy source differs — solar in the photic zone, geochemical in the aphotic one —the holobiont logic behind remains identical. An autotrophic microbe is integrated into the body, life history and ecology of a heterotrophic host, and the result is an emergent metabolic phenotype that the host alone could not produce. In photosymbiotic and chemosymbiotic holobionts alike, secondary functions — diazotrophy by Symbiodiniaceae-associated cyanobacteria (Apprill, 2017), sulfide detoxification by lucinid endosymbionts (Cardini et al., 2019), nitrogen recycling by sponge Nitrososphaerales (Glasl et al., 2025) — extend host metabolism beyond carbon fixation alone (Achlatis et al., 2019; Chou et al., 2023; Sogin et al., 2020).

4 – Marine holobiont models and research

4.1 - Why marine model systems matter for general microbiome science

The diversity of marine holobionts has produced some of the field's cleanest mechanistic dissections of host–microbe symbiosis. The Hawaiian bobtail squid *Euprymna scolopes* and its single luminescent partner *Vibrio fischeri* established agold standard for the binary specificity and horizontal acquisition of a microbial symbiosis. The deep-sea tubeworm *Riftia pachyptila* and the *Bathymodiolus* mussel lineage exposed the molecular logic by which a host's body is rebuilt around a microbial metabolism. The yeti crab *Kiwa hirsuta* showed that the same logic can run through ectosymbiosis rather than endosymbiosis. Sponges

revealed that a single animal lineage can host more than fifty bacterial phyla, including candidate phyla almost entirely restricted to the host. Zebrafish and a few other fish models converted holobiont theory into a translational asset for sustainable aquaculture and vertebrate-relevant immunology. Bacteria-induced metamorphosis demonstrated that microbial partners can write themselves into the developmental program of their host across phyla as distant as cnidarians, annelids and ascidians. Each system below addresses one specific mechanistic question, and together they encompass a breadth of metabolic and developmental processes that no single model could capture alone.

4. 2 - Squid-*Vibrio fischeri*: the textbook for binary specificity and horizontal acquisition

The marine environment offers an iconic example of coevolution in an intimate symbiotic relationship. The hawaiian bobtail squid *Euprymna scolopes* and its single luminescent partner *Vibrio fischeri* provide one of marine biology's clearest demonstration of binary specificity in a microbial symbiosis (McFall-Ngai et al., 2012; Ruby & Lee, 1998).

The squid hosts *V. fischeri* resides inside a dedicated light organ derived from the embryonic hindgut-ink-sac complex; the organ is fully developed in males and is supplemented by an accessory nidamental gland in mature females (Beilinson et al., 2025).

The host uses the bacterial luminescence as nocturnal counter-illumination camouflage, disrupting its own silhouette to evade predators (Nyholm & McFall-Ngai, 2021; Ruby & Lee, 1998).

The specificity of the partnership is the system's most remarkable property, and it is now mechanistically resolved. The squid acquires *V. fischeri* horizontally from the environment within hours of hatching (Ruby & Lee, 1998), and the exclusivity is striking: *V. fischeri* accounts for only 0.1 % of the host environmental bacterioplankton (McFall-Ngai, 2024), yet it is the only colonist the light organ will accept, and if it is absent t the organ remains uncolonized (Nyholm & McFall-Ngai, 2021). Once contact is made, *V. fischeri* cells aggregate along host cilia and induce upregulation of host chitinase, which hydrolyzes the chitin in the mucus and generate a chitobiose gradient that recruits the symbiont chemotactically into the deeper crypts (Kremer et al., 2013). *V. fischeri* strains can dominate individual crypts (Y. Sun et al., 2016), opening the door to questions about strain competition and within-host evolution that no other marine holobiont has yet posed in such direct experimental form. Beyond the light organ, the system provides a second axis for studying horizontal acquisition.

Luminescence itself is regulated by quorum sensing: at low cell density — as in the open water — the lux operon is silent, but once the symbionts are concentrated in the crypts, they luminesce, and the host imposes a circadian rhythm on the signal (McFall-Ngai et al., 2012). The accessory nidamental gland of mature females hosts an additional bacterial community dominated by Alphaproteobacteria and Verrucomicrobia, with Gammaproteobacteria and Flavobacteriia in lower abundances, all acquired from the environment (Kamp et al., 2025). Because the nidamental gland is present only in mature females, whereas the light organ establishes in both sexes from hatching, *E. scolopes* is one of the few systems in which two anatomically distinct horizontal-acquisition symbioses can be studied side by side. Together with its experimental tractability — small body size, captivity-compatible biology and a benthic diurnal habit - these features have made *E. scolopes* the canonical model system for studying horizontal acquisition and developmental microbiology in invertebrates (Nyholm & McFall-Ngai, 2021).

4.3. Chemosynthetic models: from environment to obligate endosymbiosis

Chemosynthetic holobionts are the marine systems in which the host–microbe partnership has been integrated to the deepest physiological level, and the gradient from obligate endosymbiosis to ectosymbiosis offers the most direct evolutionary window onto how that integration is built. Chemosynthetic holobionts are common in marine environments, and several have become canonical mechanistic models (Sogin et al., 2020). Despite all animals living within intimate interactions with microorganisms, the dynamics of host-microbiome interaction remain poorly understood for species that are difficult to sample or neglected in the literature (Ricci & Greening, 2024). In this framework, chemosynthetic holobionts represent a rich and largely under-explored research front.

The giant tubeworm *Riftia pachyptila* is the most emblematic model of chemosynthetic symbiosis. It was the first animal in which chemosynthetic microorganisms were discovered (McCowin et al., 2023). Its association with sulfur-oxidizing bacterial symbionts is so intimate that the host has completely lost its digestive system, relying entirely on symbiont-mediated hydrogen sulfide metabolism for nutrition (Hinzke et al., 2019). Because of this extreme physiological integration, *R. pachyptila* has become a key model for studying host–microbe coevolution, metabolic specialization, and adaptation to deep-sea hydrothermal environments. More broadly, Siboglinidae are important models for investigating the establishment, recruitment, and maintenance of chemosymbiosis, as well as to understand the ecological role of holobionts as foundation species capable of structuring entire vent ecosystems and associated fauna (Bright & Lallier, 2010). In *Riftia*, the host actively supports symbiont metabolism by supplying oxygen, sulphide, and carbon dioxide through highly specialized physiological adaptations: proteomic analyses reveal abundant globins, myohemerythrins, carbonic anhydrases, and V-type ATPases, particularly within the trophosome, where extracellular globins simultaneously bind oxygen and sulfur compounds for delivery to the symbionts (Hinzke et al., 2019). These adaptations highlight the remarkable degree of metabolic integration and coevolution underlying chemosynthetic holobionts.

Bathymodiolus mussels offer a second model of chemosynthetic integration, this time involving two microbial partners. *Bathymodiolus azoricus* harbors Gammaproteobacteria in its gills, establishing symbiosis with both sulfur- and methane-oxidizing microorganisms (Ponnudurai et al., 2017). The *Bathymodiolus* microbiome is characterized by high abundance and low diversity: approximately 2.5 x 10^{12} cells per individual in *B. puteoserpentis* (Piquet et al., 2022), dominated by two Gammaproteobacteria endosymbionts - sulphide-oxidizing (SOX) and methane-oxidizing (MOX) - that live inside the host cell bacteriocytes (Piquet et al., 2022). The genus is plastic in its choice of symbionts, with different species harboring one or both the main partners, making it a promising model for understanding the molecular determinants of symbiont specificity (Piquet et al., 2022). The *Bathymodiolus* "hybrid zone" has resolved a long-standing question about host genetics versus environment in microbiome assembly. *B. puteoserpentis* and *B. Azoricus* form viable hybrid populations across an Atlantic hybrid zone, and Ucker et al. (2021) showed that the microbiome composition in these hybrids is more strongly associated with environmental microbial pools than with host genetic background. The PRR/MAMP innate-immunity machinery of *Bathymodiolus* is also modulated upon *Vibrio* infection (Chen et al., 2019), making the genus a productive model for the molecular pattern recognition that underlies symbiont selection.

Other vent-dwelling chemosynthetic hosts illuminate the ectosymbiotic end of the gradient. The deep-sea yeti crab *Kiwa hirsuta* lives in association with chemosynthetic filamentous bacteria along its setae (Goffredi et al., 2008). The setae-associated microbiome comprises Epsilonproteobacteria, Gammaproteobacteria and

Bacteroidetes, carrying enzymes for the reductive tricarboxylic-acid cycle, sulfite oxidation and dissimilatory sulfate oxidation, useful for carbon fixation and sulphur detoxification (Goffredi et al., 2008). *Kiwa* therefore provides answers to different questions as compared to its sessile counterparts: while *Riftia* and *Bathymodiolus* rely mostly on endosymbionts (Piquet et al., 2022), *Kiwa* (and other chemosynthetic hosts) live with episymbiotic bacteria (Roterman et al., 2013). This difference frames a larger extrapolation: episymbiosis may have been the first evolutionary step toward intracellular endosymbiosis, since even ectosymbiosis already requires specific recognition interactions (Goffredi, 2010).

Specific bacterial lineages map onto either ectosymbiotic or endosymbiotic roles, hinting at evolutionary preferences. The Epsilonproteobacteria family Thiovulgaceae is generally associated as ectosymbiont in *Kiwa* setae and on *Shinkaia crosnieri* and *Rimicaris exoculate*: the Gammaproteobacteria family Thiotrichaceae is also typically ectosymbiotic, on the papillae of the snail *Symmetromphalus regularis* and on *Kiwa sp*. setae (Goffredi, 2010).

Bathymodiolus complicates this picture by hosting both endosymbionts Gammaproteobacteria and ectosymbiotic Campylobacteriota on the gill surface (Y.-T. Lin et al., 2023). These promising animal models live in extreme environments - cold seeps or hydrothermal vents - making sampling logistically demanding (Roterman et al., 2013).

However, chemosymbiosis is not restricted to extreme environments. Many chemosynthetic hosts and model organisms also occur in shallow-water anoxic or hypoxic sediments, where sulfur compounds, are abundant (Sogin et al., 2020).

The gutless oligochaete *Olavius algarvensis* is a tractable model for shallow-water chemosymbiotic worms: it lives in an obligate symbiosis with several bacteria species, including sulphate-reducing Deltaproteobacteria that supply sulphide and sulphide-oxidizing symbionts Gammaproteobacteria that provide energy (Dubilier et al., 2001). These bacteria are extracellular endosymbionts, living between the cuticle and the epidermis of the host (Wippler et al., 2016). Among shallow-water bivalves, lucinid clams from seagrass-meadow sediment host chemosymbionts that provide nutrients to the clams while contributing to the health of the surrounding meadow (Cardini et al., 2019, 2022).

The recurrence of analogous chemosymbioses in phylogenetically unrelated hosts from contrasting habitats suggests that environmental chemistry (reduced compounds and redox potential) may be a stronger determinant of symbiotic assembly than host phylogeny alone (Ruehland & Dubilier, 2010).

4.4 - Sponges: discovery science from a deep-time symbiosis

Sponges may represent the longest-running natural experiment in animal-microbe symbiosis, and the densest source of bioactive compounds the marine biosphere has produced. Porifera are among the most ancient animal taxa. with 8.000 recognized species distributed from shallow waters to the deep-sea floor (Busch et al., 2022; Webster & Thomas, 2016). They play a major role in benthic communities - occupying large portions of the substrate, providing habitats for other organisms, and contributing to benthic–pelagic coupling - and as passive filter feeders, they process large volumes of water, driving nutrient recycling of carbon, nitrogen and phosphorus and selecting the free-living environmental microbiome (Lurgi et al., 2019; Pita et al., 2018; Webster & Thomas, 2016). Sponges host microbial communities of remarkable density and diversity, with associated cells reaching more than 30% of the holobiont biomass and spanning bacteria, archaea, algae, fungi and viruses (Glasl et al., 2025; Webster & Thomas, 2016).

Sponges are among the best marine model systems for holobiont studies because their microbial associations have been characterized in unusual depth. Sponges are routinely classified by holobiont parameters: High

Microbial Abundance (HMA) when associated microbial density reaches ~10^9 cells/cm^3, and Low Microbial Abundance (LMA) when density is ~ 10^5 - 10^6 cells/cm^3 (Webster & Thomas, 2016). The HMA / LMA dichotomy is reflected by microbial community composition as well as in density: HMA sponges are typically enriched with Chloroflexi, Acidobacteria and Poribacteria, whereas LMA sponges are enriched in Proteobacteria and Cyanobacteria. This classification is now widely used, although the processes driving such dichotomy remain unresolved (Pita et al., 2018). Whereas the human gut microbiome is species-diverse, the sponge holobiont is phylum-diverse, harboring more than 50 phyla or candidate phyla. Among the represented lineages are Gammaproteobacteria, Alphaproteobacteria, Actinobacteria, Chloroflexi, Nitrospirae, Cyanobacteria and Nitrososphaeria (formerly Thaumarchaeota) (Webster & Thomas, 2016); making sponges a complementary holobiont model to canonical systems.

Two candidate phyla illustrate the depth of sponge–microbe coevolution. The candidate phylum Poribacteria is almost exclusively associated with sponges associated, supporting the hypothesis of intimate and long-term relationship (Kamke et al., 2014); the candidate phylum Tectomicrobia is another sponge-associated lineage, now central to natural-product discovery (Peters et al., 2023).

The functional diversity of the sponge microbiome is supported by the host's e substructure - pores, channels, choanocyte chambers and pinacoderm provide distinct microenvironments that support different symbiotic niches (Webster & Thomas, 2016). This intimacy extends to the species level: C*andidatus Synechococcus spongiarum* is an intimate photosymbiont thought to be one of the oldest symbiotic relationships in the animal kingdom (Slaby & Hentschel, 2017), and in sponges the host species is generally a reliable indicator of the associated microbial community (Lurgi et al., 2019).

Sponges also establish chemolithoautotrophic symbioses for nutrient supply, with the principal group of microorganism involved being ammonia-oxidizing archaea (AOA) (Glasl et al., 2025). AOA , particularly in the family Nitrosopumilaceae, contribute to organic-matter supply via the 3-hydroxypropionate/4-hydroxybutyrate cycle and represent the only sponge symbiont group capable of oxidizing ammonia, making them crucial to the sponge-microbe partnership (Robbins et al., 2021). This contribution is particularly pronounced in in deep sea sponges (Garritano et al., 2023).

At the ecosystem scale, sponges assimilate most dissolved organic matter (DOM) and convert it into particulate organic matter (POM), making it available to other organisms and supporting nutrient cycling in reef ecosystems. The holobiont perspective helps understanding this process by linking the microbial metabolism within the host to broader ecosystem-level the recycling of organic matter(Pita et al., 2018).

The richness of the sponge holobiont is also the basis of its pharmacological importance. Sponges produce a wide range of secondary metabolites that protect them from predators and epibionts, compensating for the lack of escape defense typical of sessile invertebrates (Rohde et al., 2015). These chemical defenses are a major contributor to the evolutionary and ecological success of sponges. Importantly many of these compounds are actually produced by the associated microbiome - including group B vitamins and a wide range of secondary metabolites (Webster & Thomas, 2016).

The sponge *Theonella swinhoei* hosts *Candidatus Entotheonella factor,* a microbe with an exceptional range of biosynthetic capacity – probably encoding e amino acids alongside numerous bioactive or toxic compounds (Lackner et al., 2017). *Entotheonella* belongs to Tectomicrobia, the candidate phylum that is now central to natural-product discovery in the sponge microbiome (Peters et al., 2023).

4.5 – Vertebrate and fish models: extending holobiont theory to sustainability

Marine vertebrates harbor highly diverse microbial communities and exhibit pronounced tissue specificity, with distinct microbial assemblages associated with different host organs and body surfaces. These microbiomes can encode up to ten times more genetic information than the host genome and are tightly regulated by the innate immune system (Beilinson et al., 2025; Colston & Jackson, 2016; Lescak & Milligan-Myhre, 2017). Because marine vertebrates rapidly respond to environmental disturbances, both hosts and their associated microbiota can serve as sensitive bioindicators of ecosystem change (Apprill, 2017).

Among vertebrates, ray-finned fish (Actinopterygii) provide one of the most informative systems to study holobiont biology. They represent the most numerous class within the subphylum Vertebrata, accounting for nearly 50% of vertebrate diversity with more than 30,000 described species (Colston & Jackson, 2016; Egerton et al., 2018). Fish holobiont research therefore provides an important framework for understanding vertebrate host–microbe interactions more broadly, including mechanisms potentially relevant to other vertebrates (Colston & Jackson, 2016; Lescak & Milligan-Myhre, 2017). Fish microbiomes are also among the best characterized in vertebrates, partly because of their ecological, commercial, and aquaculture relevance (Colston & Jackson, 2016): they include bacteria, archaea, fungi, protists, and viruses, with bacteria dominating the intestinal microbiome (Egerton et al., 2018). The fish gut microbiome is the most extensively studied, given its central role in digestion, nutrient absorption, synthesis of essential compounds, antimicrobial peptides, bacteriocins, and immune regulation function (Singh et al., 2025).

Several fish species have become canonical experimental models for microbiome research. The zebrafish (*Danio rerio*) is among the best-established vertebrate models in developmental biology, genetics, neuroscience, and host–microbe interaction studies. Its microbiome changes dynamically throughout ontogenesis, and the possibility of generating gnotobiotic individuals allows highly controlled investigations of microbial transmission and host interactions (Robinson et al., 2018; Soares et al., 2019). A key advantage is its external fertilization (the greatly preponderant form of reproduction in Teleosts) which permits the production and maintenance of microbially sterile zygotes and resulting offspring under highly controlled conditions, facilitating experimental manipulation of microbiome assembly. Moreover, zebrafish offer the major experimental advantages typical of “the” animal model, including rapid development, small body size, high reproductive output, and ease of microbiome sampling under controlled laboratory conditions (Lescak & Milligan-Myhre, 2017). The guppy (*Poecilia reticulata*), widely used in ecology and behavioral evolution studies: provides a complementary perspective. Whereas externally fertilizing models are particularly powerful for studying microbiome assembly under controlled conditions, the guppy's internal fertilization allows investigation of processes that are difficult to address in externally fertilizing species, including reproductive microbiomes characterization, mate-mediated microbial exchange, and potential routes of vertical inheritance. By reducing the direct environmental exposure associated with external gamete release, this reproductive strategy offers a valuable framework for disentangling host-associated microbial transmission from environmental acquisition(Graziano et al., 2026; Soares et al., 2019).

Fish microbiome research is also increasingly relevant for sustainable aquaculture. Driven by the growing global demand for fish products, fish microbiome research now informs the design of aquaculture systems in which the gut microbiome is recognized as a key factor in immune development, nutrient assimilation, and disease resistance (Sundaray et al., 2026). In this context, integrative approaches combining metagenomics, pathway reconstruction, and microbial network analyses are becoming standard tools for understanding the functional capacities of fish microbiomes (Betiku et al., 2023; Sundaray et al., 2026). Functional

characterization at the species level is equally important: for example, *Cetobacterium somerae* has been shown to provide vitamin B12 to tilapia and carp species (Qi et al., 2023).

High-density aquaculture systems can favor the proliferation of opportunistic pathogens, particularly species of the genus *Vibrio*, including *V. anguillarum*, *V. splendidus*, and *V. logei* (Reid et al., 2009). To reduce antibiotic overuse in aquaculture, probiotic-based strategies are increasingly explored as sustainable alternatives, with lactic acid bacteria emerging among the most promising candidates for improving fish and shellfish health (Mariom et al., 2026). Beyond aquaculture, fish-associated microbiomes also represent a potentially valuable source of bioactive compounds and natural products. Although vertebrates have historically been less explored than invertebrates in bioprospecting, fish-associated microbes, particularly Actinobacteria, are known producers of secondary metabolites such as sebastenoic acid, highlighting fish holobionts as reservoirs of microbial and metabolic diversity (Colston & Jackson, 2016; Sanchez et al., 2012).

4.6 – Bacteria-induced metamorphosis: a non-taxonomic phenomenon-model

Beyond organism-level models, the marine environment provides phenomenon-level models. With marine animals typically exhibiting complex multiphase life cycles, with a larval stage and an adult stage separated by an obligatory metamorphic transition (Swearer et al., 2019). The microbiome is known to change across the life cycle (Maritan et al., 2024), and in marine environments can be the actual trigger for the transition between stages — a class of holobiont mechanism that has now been resolved across multiple phyla. The sponge *Crambe crambe* shifts its associated microbiome along its life stages, through adult, brooded larvae, free living larvae and settled juveniles, with a constant presence of *Candidatus Beroebacter blanensis* through every stage; consistent with vertical transmission and a stable core microbiome (Turon et al., 2024).

The upside-down jellyfish *Cassiopea* spp., lives in association with the family Symbiodiniaceae. In *Cassiopea*, acquisition of Symbiodiniaceae is required for strobilation and successful medusa phase (Jinkerson et al., 2022). In normal condition, the symbionts are required for the transition from the polyp to medusa: the polyp acquires the symbionts orally, and in the absence of the symbiont no strobilation occurs. The symbionts are pivotal for producing secondary metabolites that can induce host metamorphosis; making the symbiosis essential to the developmental program (Ohdera et al., 2018). In addition, the settlement of *Cassiopea* larvae depends on bacterial biofilms – particularly those containing *Vibrio* - that supply the cue for the metamorphic transition.

The marine annelid *Hydroides elegans* provides the most molecularly resolved case of bacterial induction of metamorphosis. Larval settlement requires contact with a biofilm of *Pseudoalteromonas luteoviolacea*, and the inductive cue is not a soluble signal but a physical injection device — the Metamorphosis-Associated Contractile structures (MACs), arrays of phage-tail-like injection complexes that deliver the proteinaceous effector Mif1 (Metamorphosis-Inducing Factor 1) into the larva (Ericson et al., 2019; Shikuma et al., 2014, 2016). This molecule activates a p38 / JNK MAPK cascade in the larva and a parallel DAG / PKC cascade that together drive the morphological transition from swimming larva to settled tube-dwelling adult (Malter et al., 2022; Shikuma et al., 2016). The bacterial side is genetically tractable: *P. luteoviolacea* carries a second metamorphogenic factor, tetrabromopyrrole, in addition to the MACs system (Alker et al., 2020), and the same MACs machinery induces metamorphosis in other settling marine invertebrates such as corals and tubeworms (Shikuma et al., 2014). *Hydroides* therefore offers something rare in holobiont biology: a metamorphic inductive cue whose molecular mechanism is resolved on both the bacterial and the host side, and whose evolutionary conservation across phyla is now testable.

In general, many marine taxonomic groups, in phylogenetically distant lineages, undergo metamorphosis, and microbial communities are increasingly recognized as important regulators in this transition, documented in metazoans such as Sponges, Cnidarians, Ascidians, Annelida and Bryozoa (Weiland-Brauer et al. 2020). This makes these organisms crucial not only for developmental biology, but also for understanding how microbiomes are assembled, transmitted, and reshaped across major life-history transition. By moving between pelagic and benthic environments, they provide natural systems in which to investigate interactions between host-associated and environmental microbial communities, as well as the role of benthic-pelagic couple in microbial transmission across habitats.

Taken together, the marine model systems described above share a property that makes them disproportionately useful to general microbiome biology: each has resolved one mechanism — binary specificity, episymbiosis-to-endosymbiosis, candidate-phylum diversity, vertebrate translatability, bacterial induction of host development — to a degree that other systems have not. These mechanistic resolutions are not endpoints; they are the design principles for the applied programme that Section 5 develops in detail.

4.7 - Corals as a translational model: from microbiome diagnostics to probiotic design

Corals occupy a relevant position among marine holobiont models because they are the system in which the holobiont theory has been most directly translated into intervention. The cnidarian host integrates Symbiodiniaceae, bacteria, archaea, fungi and viruses across distinct anatomical compartments - mucus, tissues, skeleton, and the gastrovascular cavity – into a multipartite consortium whose stability is essential for calcification, nutrient cycling and stress resilience (Ainsworth et al., 2017; Peixoto et al., 2017; Webster & Reusch, 2017).

Among coral-associated bacteria, *Endozoicomonas* is one of the most ubiquitous coral-associated bacterial genus and its abundance mirrors host health, declining under thermal stress, bleaching and turbidity (Pogoreutz & Ziegler, 2024; Ruiz-Toquica et al., 2025). *Vibrio,* by contrast, expands under stress and has been linked to disease in both gorgonians and scleratinians, with recent evidence suggests that fluctuation range of *Vibrio*, rather than its presence alone, is the more reliable environmental indicator (Munn, 2015; Rubio-Portillo et al., 2014; Vezzulli et al., 2010). Together, *Endozoicomonas* and *Vibrio* genera may provide a useful diagnostic axis for detecting shifts in coral holobiont state.

Heat stress further reveals that microbiome shifts under perturbation can reflect either dysbiosis or microbiome plasticity as an acclimatory mechanism (Baldassarre et al., 2022; MacKnight et al., 2021; Ruiz-Toquica et al., 2025). Because coral species differ in microbial dynamics and thermal sensitivity (Voolstra & Ziegler, 2020), microbiome composition and stability are increasingly considered functional mediators of coral resilience, not as passive readouts. From this diagnostic foundation the field has built one of the most concrete translational programme in marine microbiology: the Beneficial Microorganisms for Corals (BMCs) framework formalizes the use of probiotic consortia to enhance host resistance (Peixoto et al., 2017), and the experimental dissection of BMC interventions has shown that probiotic inoculation can mitigate heat-stress mortality and restructure the microbiome toward more resilient states (De Breuyn et al., 2025).

Corals therefore illustrate how marine holobiont research can move from microbiome diagnostic to experimental intervention – a chain that we address in Section 5.1.

5 - Applications and Perspectives

So far, we have discussed how marine holobiont diversity is inherently multidimensional, shaped by host morphology and spatial structure, abiotic constraints, phylogenetic history, and evolutionary processes.

Beyond advancing our fundamental understanding of symbiosis, however, marine holobiont research also offers substantial opportunities for ecological monitoring, conservation, and biotechnological development. This final section focuses on three major application areas in which marine holobiont biology is already informing practice: probiotic interventions for coral and aquaculture health, the development of microbiome-aware aquaculture approaches more broadly, and blue biotechnology, including the discovery of novel bioactive compounds.

5.1 Probiotics: from the coral probiotic hypothesis to applied microbiome design

The translational programme of marine microbiology began with a hypothesis. The Coral Probiotics Hypothesis (Reshef et al., 2006) proposed that manipulating the coral-associated microbiome could enhance resistance to pathogens and prevent disease — one of the earliest explicit proposal to manipulate a marine host-associated microbiome for health benefits. Two decades later, that hypothesis has matured into a defined applied framework: the Beneficial Microorganisms for Corals "BMCs" (Peixoto et al., 2017), which specifies the criteria a microbial probiotic candidate must satisfy to be considered for coral inoculation. The experimental demonstration that BMC inoculation can mitigate heat-stress mortality and restructure the coral microbiome toward resilience-associated states (Delgadillo-Ordoñez et al., 2024) and that a single inoculation hours before a thermal anomaly can prevent acute bleaching mortality (De Breuyn et al., 2025) has turned the hypothesis into a working protocol. Identifying candidate beneficial bacteria is now an active comparative-genomics programme. *Halomonas*, *Pseudoalteromonas* and *Bacillus* are recurrent in benign coral microbiomes and correlate with the relative increase of other beneficial taxa, such as *Ruegeria* and *Limosilactobacillus*, and with the decline of *Vibrio*; in *Stylophora pistillata*, *Galaxea fascicularis* and *Pocillopora verrucosa* (Delgadillo-Ordoñez et al., 2024). In *Pocillopora damicornis*, a BMC consortium of *Pseudoalteromonas*, *Cobetia* and *Halomonas* mitigates the effects of *Vibrio coralliilyticus* under thermal stress while preserving host calcification (Moradi et al., 2023; Rosado et al., 2019).

Beyond their direct antagonism toward pathogens, beneficial bacteria provide vitamins, cofactors and secondary metabolites that support host physiology, and they can also detoxify chemical pollutants – making them a multi-axis intervention against the converging causes of bleaching (Silva et al., 2021).

The two remaining bottlenecks are practical. First, BMC trials have been largely conducted in mesocosm conditions where probiotic cells interact closely with mucus and tissue; in the open ocean, dilution constraints have pushed delivery technologies such as cell immobilization in clay zeolite, chitin, agar, alginate, carrageenan and synthetic polymers (Bouabidi et al., 2019) or via food carriers - *Artemia salina* has been used to deliver sulfated galactans as immune stimulants to the aquaculture shrimp *Penaeus vannamei* (Rudtanatip et al., 2019), and analogous strategies are now being designed for reef restoration and aquaculture facilities (Peixoto, Sweet, et al., 2021). Second, the field-level conservation for BMC depends on the economic stakes: coral reefs support cumulative ecosystem services in the hundreds of billions USD per year (Costanza et al., 2014), justifying sustained investment in conservation and restoration (Duarte Rosado et al., 2025). Probiotic interventions extend well beyond reefs. In aquaculture, where the global demand for marine and aquatic products continue to rise (Mariom et al., 2026), microbiome-aware approaches areincreasingly being explored as alternatives for routine antibiotic prophylaxis.

Lactic Acid Bacteria "LAB" are the most studied candidate class, along with *Bacillus* and other genera such as *Aeromonas*, *Alteromonas*, *Arthrobacter*, *Bifidobacterium*, *Clostridium*, *Paenibacillus*, *Phaeobacter*, *Pseud*

oalteromonas, *Pseudomonas*, *Rhodosporidium*, *Roseobacter*, *Streptomyces*, *Vibrio*, and microalgae (*Tetraselmis*) and yeast (*Debaryomyces*, *Phaffia* and *Saccharomyces*) (Ringø et al., 2020).

Lactococcus lactis improves growth and immune response in the freshwater prawn *Macrobrachium rosembergii* (Kader et al., 2021); in the sea water shrimps *Penaeus vannamei*, dietary supplementation with *Weissella cibaria* and *Saccharomyces cerevisiae* increases growth, hemocyte counts and resistance to *Vibrio parahaemolyticus* (Kanjan et al., 2025). LAB are naturally present in the gut of marine fishes across Labridae, Sparidae, Congridae, Scorpaenidae, Triglidae, and Balistidae and they exhibit antimicrobial activity against known fish pathogens such as *Vibrio anguillarum* and A*eromnas salmonicida* through bacteriocin and hydrogen peroxide production and other prevent proliferation compounds (Alonso et al., 2019; Ringø et al., 2018). At the larval stage, *Lactobacillus rhamnonus* stabilizes the zebrafish gut microbiome and improves lipid metabolism (Falcinelli et al., 2015).

Lactic Acid Bacteria are, therefore the most broadly applicable and extensively studied probiotic candidates currently available for finfish aquaculture.

5.2 – Microbiome aquaculture: from species inventory to multi-omic management

Sustainable aquaculture is the second front on which marine holobiont biology has produced applied tools, and probiotic supplementation is only one of them. Microbiome-aware aquaculture spans diet design, multi-omic monitoring, the identification of resident and core microbiomes as biomarkers of host health, and the management of species with complex life cycles whose holobiont reassembles between developmental stages. Conceptually, the shift mirrors that already occurring in basic research: a fish is not a digestive tract that happens to host microbes, but rather an holobiont, in which host performance and microbial function are tightly intertwined and where growth, immunity and product quality cannot be optimized separately from the microbial consortium. To disentangle this complexity, studies increasingly combine genomic, metagenomic, metatranscriptomic, and epigenomic approaches, providing a more integrated view of host-microbe interaction (Limborg et al., 2018), and environmental, dietary and host-genetic determinants of microbiome composition are increasingly resolved at the species level (Bozzi et al., 2021).

Teleosts alone comprise more than 28.000 species but only a small fraction have been characterized microbiologically, mostly limited to aquaculture targets and laboratory models organisms (Scheifler et al., 2022). Atlantic salmon (*Salmo salar*) and the Rainbow trout (*Onchorynchus mykiss)* are now among the best-studied (Afewerki et al., 2023).

In *Salmo salar*, Tenacibaculosis (caused by *Tenacibaculum* infection) and *Aliivibrio* opportunistic infections are well-characterized pathologies, while the genus *Mycoplasma* is positively associated with the salmon health status (Bozzi et al., 2021); dietary supplementation with fermented kelp *Saccharina latissima* preserves the dominance of *Mycoplasma*, *Photobacterium* and *Brevinema* and is associated with improved host condition (Rasmussen et al., 2025).

For anadromous species like *Salmo salar*, the holobiont undergoes substantial assembly during smoltification, a fish transition from freshwater to seawater. Identifying the core resident microbiome that persists across this transition has therefore become an important objective in microbiome aware aquaculture management (Afewerki et al., 2023; Katirtzoglou et al., 2024).

Tissue-specific microbiomes deserve specific attention. Skin and gill microbiomes are the first barrier against pathogen invasion and environmental stressors, and host-microbe dynamics in those compartments are central to disease management in *Sparus aurata* and *Dicentrarchus labrax* (Rosado et al., 2019). Beyond their

immunological role, reproductive-tract microbiomes are emerging as functional determinants of fitness and inheritance (Graziano et al., 2026), with consequences for breeding programs.
Together, these studies suggest that future aquaculture may increasingly focus on promoting beneficial resident microbiomes through diet, breeding, and system design, rather than treating microbial communities as passive by-products of culture conditions.

5.3 - Blue technology: the diversity of marine holobionts as a chemical and enzymatic reservoir.
Marine biotechnology rests on a single empirical observation: marine holobionts are metabolically asymmetric, and that asymmetry has been a productive source of novel compounds since the field's beginning. Host bodies produce compounds, microbial symbionts produce compounds, and many of the most interesting molecules are the joint product of the partnership. The ocean hosts more than two million estimated species (Mora et al., 2011), each potentially a complex holobiont, and high genetic diversity translates directly into chemical diversity (Sigwart et al., 2021).
The aquatic literature already includes some of biotechnology's foundational discoveries: green fluorescent protein from the jellyfish *Aequorea victoria*; the hemolymph of *Limulus polyphemus* is rich in bioactive compounds, Taq polymerase from the thermophile *Thermus aquaticus*, which made the polymerase chain reaction possible (Sigwart et al., 2021; Svendsen et al., 2017); and the nucleosides spongouridine and spongothymidine from the sponge *Tectitethya* ('An Overview of the Marine Natural Products in Clinical Trials and on the Market', 2015), which gave rise to the antiviral and antitumor drugs ARA-A, ARA-C and indirectly acyclovir.
The first contemporary front is the bioactive output of sessile marine invertebrates. Sponges, cnidarians, bryozoans and tunicates produce a rich repertoire of compounds for chemical defense – a strategy compensating for their lack of escape mechanisms (Rohde et al., 2015) and many of these molecules are actually produced by associated microbial symbionts (Lopanik, 2014).
Thiocoralline, a depsipetide with antibacterial and antitumor activity, was isolated from the marine actinomycete *Micromonospora* that lives in soft corals (Romero et al., 1997); *Micromonospora* is recurrent in coral holobionts of the genera *Palythoa*, *Favia*, *Porites* and *Acropora* and across coastal sediments and mangrove rhizospheres (Hirsch & Valdés, 2010; Kanchanasin et al., 2024). It produces mycosporine-like amino acids (MAAs), natural filters of UV lights with antioxidant, anti-inflammatory and anti-ageing properties (Van De Water et al., 2022). Furthermore, the most known coral symbionts, Symbiodinium spp. produce active diterpenes in the soft coral *Pseudopterogoria* (Lopanik, 2014). Beyond corals, the bryozoan *Bugula neritina* hosts the gammaproteobacterial *symbiont Candidatus Endobugula sertula*, which biosynthesises bryostatin, a macrolide that protects larvae from predators and is in clinical trials as an anticancer agent (Lopanik, 2014).
The second front is the sponge holobiont specifically, which has emerged as the field's richest pharmacological reservoir (Webster & Thomas, 2016). *Candidatus Entotheonella factor* - within the candidate phylum Tectomicrobia - produces most of the polyketides and peptides previously attributed to its sponge host *Theonella swinhoei* (Peters et al., 2023; Pita et al., 2018).
The freshwater sponge *Spongilla lacustris* hosts up to forty bacterial genera including *Bacillus* and *Streptomyces*, the latter producing siderophores such as, nocardamine, coelichelin and other host-protective products (Graffius et al., 2023).

Across the genera *Haliclona*, *Aplysina* and *Dendrilla*, sponge holobionts are productive sources of carbohydrate-active enzymes (CAZymes), peptidases, esterases, lipases, halogenases, proteases and chitinases (De Oliveira et al., 2020), making them an enzyme-discovery platform as well as a small-molecule one.

The third front is the bioactive output of animal toxins, many of which are produced or sequestered by the host microbiome rather than by the animal itself. Tetrodotoxin (TTX) is the textbook case. The blue-ringed octopus *Hapalochlaena spp*. concentrates TTX produced by environmental bacteria of the genera *Bacillus*, *Micrococcus*, *Acinetobacter*, *Aeromonas*, *Alcaligenes*, *Alteromonas*, *Flavobacterium*, *Moraxella*, *Pseudomonas* and *Vibrio* (Whitelaw et al., 2019); the common Mediterranean octopus *Octopus vulgaris* retains saxitoxin from dinoflagellate-contaminated bivalves in its digestive glands (Lopes et al., 2014). TTX also occurs in vertebrates: the pufferfish *Takifugu rubripes* and other tetraodontiformes concentrate the toxin, and within the genus *Takifugu* different species harbor different microbial producers — *Vibrio alginolyticus*T. vermicularis, *Pseudomonas spp*. in *T. poecilonotus* skin, *Microbacterium arabinogalactanolyticum* in *T. alboplumbeus* ovary, *Serratia marcescens* in *Chelonodon patoca* skin (Pratheepa & Vasconcelos, 2013; Simidu et al., 1990). The diversity of TTX producers across hosts is itself a window onto the holobiont basis of animal venoms, with direct implications for sodium-channel-targeting neuropharmacology (Narahashi, 2001). Sea snail cone toxins are the other paradigmatic frontier: ziconotide, derived from the venom of *Conus magus*, is now a clinical treatment for chronic pain (J. Lin et al., 2024).

The fourth front is the enzymatic output of marine extremophiles. Acidophiles, alkaliphiles, thermophiles, psychrophiles, halophiles and barophiles produce catalysts that operate under industrial conditions where mesophilic enzymes fail (Ferrer et al., 2019; Ye et al., 2023).

Polar environment microbes encode polymer-degrading enzymes that have direct relevance to plastic biodegradation under low temperature conditions (Urbanek et al., 2018).

Across all four fronts, omics methodologies — metagenomics, metatranscriptomics, single-cell genomics — are the universal tool for converting the diversity of marine holobionts into characterized biocatalysts (Barone et al., 2014; H. S. Lee et al., 2010; Wiederkehr et al., 2026). Because the marine microbial fraction that has been sequenced and functionally characterized is still a small minority of the predicted diversity (Wiederkehr et al., 2026), much remains to be discovered.

Conclusions

From the coral reef that exists only as a holobiont under oligotrophy, to the vent tubeworm whose digestive system has been replaced by a sulfide-oxidizing bacterium, to the squid whose light organ refuses any colonist that is not *Vibrio fischeri*, marine systems show that the holobiont concept is not just a theoretical framework but a biological phenomenon that can be observed, measured and experimentally manipulated. We identify three main priorities for the field. First, the uneven taxonomic coverage of marine holobiont research remains a major knowledge gap that warrants broader phylogenetic sampling (Section 2.2 and Table 1): the phyla that occupies fewer than one primary 16S study per phylum cannot remain largely unexplored from symbiosis perspective, because the conceptual reach of holobiont biology is limited by the taxa actually sampled. Second, the applied programme outlined in this review — coral probiotics, microbiome-aware aquaculture, blue biotechnology — should be evaluated with the same scientific standard as the basic research that fed it; the framework Beneficial Microorganisms for Corals (Peixoto et al., 2017) and its experimental dissection (De Breuyn et al., 2025) are an early but instructive example. Third, the conservation case for marine ecosystems is, in the era of holobiont biology, also a conservation case for marine microbiomes (Corinaldesi et al., 2023).

On all three priorities, marine microbiology is increasingly moving beyond cataloguing diversity toward understanding the mechanisms and applications emerging from host-microbe interactions.

What the marine record makes clear is that the diversity of marine holobionts represents a vast and still incompletely explored resource of evolutionary, ecological, and applied potential. Continued exploration of this diversity promises to deepen our mechanistic understanding of host-microbe interactions while expanding opportunities for conservation, aquaculture and biotechnology.

Glossary

Aphotic zone: The deepest region of the oceanic realm, where sunlight does not penetrate.

Acidophiles: Organisms capable of surviving and thriving in acidic environments.

Algal blooms: Rapid proliferations of phytoplankton populations that lead to the formation of dense accumulations in aquatic ecosystems.

Alkaliphiles: Organisms capable of surviving and thriving in alkaline environments.

Bacterioplankton: The bacterial component of the planktonic community.

Barophiles / Piezophiles: Organisms adapted to survive and thrive under high hydrostatic pressure, typically in deep-sea environments.

Benthic–pelagic coupling: The exchange of energy, matter, and organisms between the benthic environment and the pelagic water column, often mediated through trophic interactions and larval dispersal.

Benthos: Aquatic organisms that live in close association with the bottom of a water body for all or part of their life cycle. These organisms may be sessile or vagile.

Chemolithoautotrophic: A metabolic strategy based on the oxidation of inorganic compounds to obtain energy for primary production.

Chemosymbiosis: A symbiotic association between a eukaryotic host and one or more chemosynthetic microorganisms.

Chemosymbiont: A chemosynthetic microorganism that provides energy and organic compounds to its host through chemosynthesis.

Dysphotic zone: The oceanic zone below the photic layer, where only a faint amount of light penetrates.

Dissolved Organic Matter (DOM): Organic matter dissolved and suspended within the water column.

Dysbiosis: An imbalance in the composition and relative abundance of microbial communities, often associated with pathological conditions.

Ectosymbiosis / Episymbiosis: A symbiotic relationship in which one organism lives on the external surface or tissues of another organism.

Endosymbiosis: A symbiotic relationship in which one organism lives intracellularly within another organism.

Epipelagic zone: The uppermost region of the pelagic realm located within the photic zone, generally extending from the surface to approximately 200 m depth.

Eukaryotes: Uni- or multicellular organisms characterized by the presence of membrane-bound nuclei and organelles. Eukaryotes are thought to have originated through endosymbiotic events.

Euryhaline: Referring to organisms capable of tolerating a broad range of salinity conditions.

Eutrophication: The enrichment of aquatic systems with nutrients, particularly nitrogen and phosphorus, often resulting in oxygen depletion.

Extremophiles: Organisms capable of surviving and thriving under extreme environmental conditions.

Hadal zone: The deepest region of the marine environment, corresponding to oceanic trenches below approximately 6000 m depth.

Halophiles: Organisms capable of surviving and thriving in environments with high salt concentrations.

Hologenome: The collective genetic material of a host organism and its associated microbial communities.

Holobenthos: Organisms that spend their entire life cycle within the benthic environment and lack a planktonic larval stage.

Holobiont: A functional ecological and evolutionary entity composed of a eukaryotic host and its associated microbial communities.

Hydrothermal vents: Deep-sea environments characterized by the emission of geothermally heated fluids enriched in metals and inorganic compounds.

Hypoxic: Referring to environments characterized by low oxygen concentrations.

Kleptoplasty: The retention and functional use of plastids acquired through ingestion from other organisms.

Marine snow: Aggregates of organic matter produced in upper aquatic layers that sink through the water column, supplying organic carbon to deeper environments.

Meroplankton: Organisms that spend only part of their life cycle within the planktonic environment.

Mesopelagic zone: The pelagic region located below the epipelagic zone, generally extending from approximately 200 m to 1000 m depth.

Particulate Organic Matter (POM): Organic particles suspended within the water column.

Pelagos: Aquatic organisms that live suspended within the water column for all or part of their life cycle.

Photic zone: The upper layer of the ocean where sufficient sunlight penetrates to support photosynthesis, generally extending to approximately 200 m depth.

Photosymbiosis: A symbiotic association between a eukaryotic host and one or more photosynthetic microorganisms.

Photosymbiont: A photosynthetic microorganism that provides energy and organic compounds to its host through photosynthesis.

Picoplankton: The smallest planktonic fraction, generally comprising organisms 0.2 - 200 µm in size.

Practical Salinity Unit (PSU): A dimensionless unit used to express salinity based on the electrical conductivity of seawater; numerically 1 PSU is approximately equivalent to 1 g of dissolved salts per Kg of seawater.

Prokaryotes: Unicellular organisms lacking membrane-bound nuclei and organelles, with genetic material dispersed within the cytoplasm. This group includes Bacteria and Archaea.

Psychrophiles: Organisms capable of surviving and thriving at low temperatures.

Hermatypic corals: Reef-building hard corals belonging to the subclass Hexacorallia (typically the order Scleractinia) that establish symbioses with dinoflagellates, contributing to coral reef formation.

Sessile: Referring to aquatic organisms permanently attached to the substrate and incapable of active movement.

Symbiosis: A close and persistent association between two or more organisms, which may be mutualistic, commensalistic, or parasitic.

Thermophiles: Organisms capable of surviving and thriving at high temperatures.

Hyperthermophiles: Organisms adapted to survive and thrive at extremely high temperatures, exceeding those tolerated by thermophiles.

Vagile: Referring to benthic organisms capable of movement through walking, crawling, or swimming near the substrate.

Xerophiles: Organisms capable of surviving and thriving in environments with very low water availability.

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Author contributions
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Conflicts of interest
None declared.

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Data availability
All relevant data are contained within this manuscript.

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