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CHEMISTRY AND APPLICATIONS OF SIDEROPHORES FROM MARINE MICROORGANISMS: A COMPREHENSIVE REVIEW

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Abstract: Marine microorganisms have evolved sophisticated siderophore systems to thrive in iron-limited oceanic environments. This review highlights the remarkable chemical diversity, biosynthetic pathways, and ecological roles of marine siderophores. It also explores their expanding applications in pharmaceuticals, agriculture, environmental bioremediation, and industry. Advances in analytical technologies and synthetic biology are accelerating the discovery and engineering of these versatile compounds. By integrating insights from chemistry, ecology, and biotechnology, this review provides a roadmap for future research aimed at unlocking the full potential of marine microbial siderophores.

Keywords: Siderophore, Marine microorganisms, Iron acquisition, Biosynthesis, Applications

Introduction:

Iron is vital for most life forms, participating in electron transport, DNA synthesis, and oxygen transport (Andrews et al., 2013). In marine environments, iron exists in scarce, insoluble forms (Boyd & Ellwood, 2010). Marine microbes overcome this through siderophores—high-affinity iron chelators with unique adaptations like halide ions, sulfate esters, and photoreactive groups (Martinez et al., 2017).

Siderophores are small, high-affinity iron chelators produced by microorganisms to scavenge iron from the environment (Miethke & Marahiel, 2007). These molecules possess a high binding constant for iron, enabling them to compete with host iron-binding proteins and sequester iron effectively. By solubilizing and capturing iron, siderophores provide microorganisms with a competitive advantage in iron acquisition (Schwyn & Neilands, 1987; Neilands, 1995).

Siderophores have diverse applications across medicine, agriculture, environment, and industry. They serve as models for novel antibiotics and anticancer agents, biofertilizers that boost plant growth, and biocontrol tools that suppress pathogens. Their metal-chelating ability is harnessed for detoxifying polluted environments and recovering valuable metals. In industry, they find use in cosmetics, food preservation, and eco-friendly metallurgy. These broad applications highlight the growing biotechnological significance of marine siderophores. (Compant et al., 2005; Glick, 2014).

Siderophores:

Iron is an essential nutrient for most living organisms, playing a crucial role in various cellular processes such as respiration, DNA synthesis, and enzyme activity (Andrews et al., 2003). However, iron availability in many environments is often limited due to its low solubility and the presence of iron-binding proteins in host organisms (Miethke & Marahiel, 2007). Microorganisms have evolved sophisticated strategies to acquire iron, and one of the most widespread and effective mechanisms is through the production of siderophores (Neilands, 1995).

Siderophores are small, high-affinity iron chelators produced by microorganisms to scavenge iron from the environment (Miethke & Marahiel, 2007). These molecules possess a high binding constant for iron, enabling them to compete with host iron-binding proteins and sequester iron effectively. Siderophores have a remarkable structural diversity, ranging from small molecules to large peptide-based compounds. They often contain specific functional groups, such as hydroxamates, catechols, or carboxylates, which contribute to their high affinity for iron and ability to form stable complexes (Miethke & Marahiel, 2007).

The basic structure of siderophores consists of a metal-binding motif, which is responsible for chelating the iron atom, and a recognition site that allows specific interactions with receptors or transport systems (Miethke & Marahiel, 2007). The metal-binding motif is typically a functional group or a set of functional groups that coordinate with the iron atom through oxygen, nitrogen, or sulfur atoms. The recognition site, on the other hand, is responsible for the specific recognition and uptake of siderophores by microorganisms.

The structural variations in siderophores contribute to their specificity and effectiveness in iron acquisition. Different microorganisms produce siderophores with distinct structural features, allowing them to target specific iron sources and compete in different environments (Miethke & Marahiel, 2007). The structural diversity of siderophores is a result of evolutionary adaptations and genetic variations in biosynthetic pathways.

Chemical Diversity of Marine Siderophores

Hydroxamate siderophores

Hydroxamate siderophores are a class of siderophores characterized by the presence of hydroxamate functional groups, which act as iron-chelating moieties. These siderophores have a strong affinity for ferric iron (Fe^{3+}) and are produced by various microorganisms as a means to scavenge iron from the environment.

One well-known example of a hydroxamate siderophore is desferrioxamine B (DFO-B), produced by various bacteria and fungi. Desferrioxamine B is commonly produced by terrestrial bacteria (Butler.A.et.al, 2000). DFO-B has a cyclic structure with a hydroxamate moiety and serves as a high-affinity iron chelator. It is widely used in clinical settings as a therapeutic agent for iron overload disorders and has been extensively studied for its iron-binding properties (Kontoghiorghes, 2020).

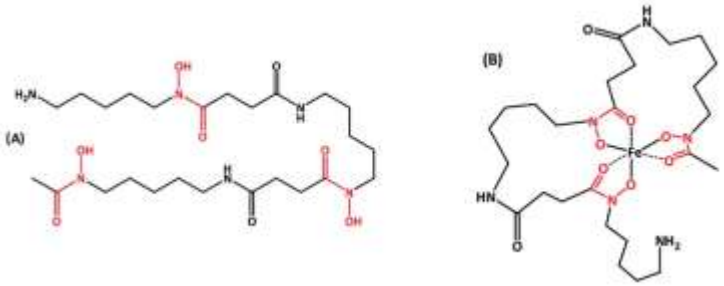

Figure I. Chemical structure of (**A**) deferoxamine B (DFOB) and (**B**) feroxamine B (FOB). Hydroxamic groups, responsible for metal chelation, are evidenced in red (Bellotti.D & Ramelli.M,2019)

The structural diversity of hydroxamate siderophores extends beyond DFO-B. Other hydroxamate siderophores include rhizobactin and yersiniabactin, which are produced by rhizobia and Yersinia species, respectively (O'Brien et al., 2019; Payne, 1994). Deferoxamine mesylate (desferrioxamine) is the best-known example of a medicinal siderophore and the most common one in medical use. DFO has been used for decades to treat iron-overload diseases and remains the current standard for iron-chelation therapy (Hatcher.H.et.al, 2009). These siderophores contribute to the iron acquisition strategies of these microorganisms and play crucial roles in their survival and pathogenesis. Hydroxamate siderophores have been extensively studied due to their importance in microbial iron acquisition and their potential applications in various fields. Understanding their structure, biosynthesis, and mechanisms of iron binding can provide insights into their biological functions and potential therapeutic applications (Miethke & Marahiel, 2007).

Catecholate Siderophores:

Catecholate siderophores constitute a significant class of siderophores produced by microorganisms. These siderophores are characterized by the presence of catechol functional groups in their structures, which are responsible for binding iron ions with high affinity.

One well-known example of a hydroxamate siderophore is enterobactin, which is produced by Enterobacteriaceae and other related Gram-negative bacteria (Crosa & Walsh, 2002). Enterobactin has a trilactone core structure, consisting of three 2,3-dihydroxybenzoic acid (DHB) units connected through ester linkages. Each DHB unit possesses a hydroxamate functional group, which forms a hexadentate iron (III) complex

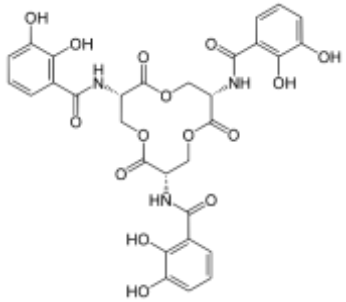

Figure II. Enterobactin (Raymond et al., 2003, Ratledge, 2007; Crosa & Walsh, 2002).

Enterobactin is involved in iron acquisition and is critical for the virulence of certain pathogens, such as *Escherichia coli* and *Salmonella enterica* (Crosa & Walsh, 2002).

Another example of a catecholate siderophore is bacillibactin, produced by various *Bacillus* species. Bacillibactin is a hexapeptide siderophore that contains a catecholate moiety. The catechol group in bacillibactin contributes to its high iron-binding affinity and plays a crucial role in iron uptake by *Bacillus* species (Cendrowski et al., 2004).

Catecholate siderophores play essential roles in microbial iron acquisition and metabolism. The catechol functional groups in these siderophores exhibit a strong affinity for binding iron, allowing microorganisms to scavenge iron from their environments. By chelating iron ions, catecholate siderophores overcome the low solubility and availability of iron, ensuring a sufficient supply of this essential nutrient for microbial growth and survival.

The study of catecholate siderophores is not only important for understanding microbial iron acquisition mechanisms but also has broader implications. These siderophores have been investigated for their involvement in various biological processes, including bacterial pathogenesis, biofilm formation, and host-microbe interactions. Furthermore, catecholate siderophores have attracted attention in the development of therapeutic strategies, such as the design of siderophore-based antibiotics and iron chelators for the treatment of iron-related disorders (Ghssein et al., 2016; Miethke & Marahiel, 2007).

Carboxylate Siderophores:

Carboxylate siderophores represent a significant class of siderophores produced by microorganisms. These siderophores are characterized by the presence of carboxylate functional groups in their structures, which are responsible for chelating iron ions.

One well-known example of a carboxylate siderophore is citrate, which is produced by various microorganisms, including bacteria and fungi. Citrate is a small organic molecule that features three carboxylate groups. It is capable of forming stable complexes with iron ions, enhancing iron solubility and availability for microbial uptake. Citrate has been extensively studied for its role in iron acquisition and metabolism, as well as its broader functions in cellular processes (Chen & Raymond, 2016, Winkelmann G & Drechsel H,1999).

Another example of a carboxylate siderophore is rhizoferrin, produced by various pathogenic fungi. Rhizoferrin is a cyclic trihydroxamate siderophore that contains a carboxylate moiety. The carboxylate group in rhizoferrin contributes to iron chelation and enables efficient iron acquisition by fungal pathogens. Rhizoferrin has been implicated in the virulence and pathogenicity of fungal infections (Drehsel.H,1994).

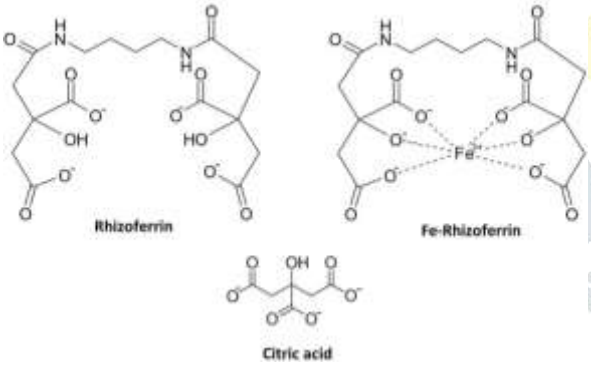

Figure III: Structure of Rhizoferrin (Drehsel.H,1994)

Carboxylate siderophores play crucial roles in microbial iron homeostasis and adaptation to iron-limiting environments. These siderophores enhance iron uptake and utilization by microorganisms by forming stable complexes with iron ions. Carboxylate siderophores are particularly important in environments where iron is scarce or tightly bound to host proteins, as they enable microorganisms to compete for limited iron resources.

The study of carboxylate siderophores has broader implications in various fields, including microbiology, medicine, and biotechnology. Carboxylate siderophores have been investigated for their involvement in microbial pathogenesis, host-microbe interactions, and biofilm formation. Furthermore, these siderophores have attracted attention for their potential applications in iron supplementation therapies, drug delivery systems, and environmental remediation (Miethke & Marahiel, 2007; Loomis et al., 2017).

Novel Marine-Specific Siderophores Recent discoveries include loihichelins from hydrothermal vents (Homann et al., 2019), aquachelins with micelle-forming abilities (Martinez et al., 2017), and synthamide—the first brominated siderophore from sponge symbionts (Elsayed et al., 2020).

Biosynthesis Pathways of Siderophores:

The biosynthesis pathways of siderophores involve a series of enzymatic reactions that lead to the production of these iron-chelating molecules. The biosynthetic pathways can vary depending on the specific type of siderophore and the microorganism producing it. However, there are common elements and enzymatic steps involved in the synthesis of siderophores.

One of the well-studied biosynthetic pathways is the non-ribosomal peptide synthetase (NRPS) pathway, which is responsible for the production of many siderophores, including several types of hydroxamate siderophores. NRPS enzymes are large multi-domain proteins that catalyze the stepwise assembly of siderophore molecules through the incorporation of amino acid building blocks. These enzymes are encoded by gene clusters that contain modules responsible for amino acid activation, elongation, and modification (Crosa, 1997). Examples of siderophores synthesized through NRPS pathways include enterobactin and desferrioxamine B.

Another important biosynthetic pathway is the polyketide synthase (PKS) pathway, which is involved in the synthesis of siderophores such as mycobactin and erythrobactin. PKS enzymes are responsible for the iterative condensation and modification of acyl-CoA building blocks to generate the siderophore backbone. These enzymes are also encoded by gene clusters that contain various domains for substrate loading, chain extension, and modification (Quadri, 2000).

In addition to NRPS and PKS pathways, other biosynthetic pathways have been identified for specific siderophores. For example, the biosynthesis of catecholate siderophores such as enterobactin involves enzymes encoded by the ent genes, which are responsible for the production and transport of these siderophores in enteric bacteria (Miethke & Marahiel, 2007).

Understanding the biosynthesis pathways of siderophores is essential for unravelling their functional roles, regulation, and potential applications. By studying these pathways, researchers can gain insights into the mechanisms underlying siderophore production and explore ways to manipulate or engineer these pathways for various purposes, including the development of novel antimicrobial agents or strategies for iron sequestration in industrial and environmental applications.

Ecological Roles in Marine Environments

Iron Acquisition Strategies Siderophores solubilize Fe^{3+} from oxides, making it bioavailable. They shuttle iron through diffusion and can even pirate iron chelated by other species' siderophores (Kraemer et al., 2015). Marine microorganisms have evolved siderophore systems to thrive in iron-limited waters. These iron acquisition mechanisms include producing structurally diverse siderophores tailored to specific environmental conditions. Siderophores are critical for supporting microbial growth, survival, and primary productivity in iron-poor marine environments.

Microbial Interactions Siderophores act as chemical weapons and communication signals. They mediate competition—such as *Vibrio* species outcompeting neighbors—and cooperation, as in coral-associated bacteria providing iron to algal symbionts (Martinez et al., 2017). They also structure microbial communities by determining which organisms can thrive based on iron acquisition abilities.

Biogeochemical Cycling Marine siderophores play a pivotal role in iron cycling, facilitating its uptake by phytoplankton and thus influencing primary production. By supporting phytoplankton, they indirectly affect carbon sequestration through enhanced biological pump activity and marine snow formation (Boyd & Ellwood, 2010). This siderophore-mediated iron cycling connects microbial activity to global carbon and nutrient fluxes.

Applications of siderophores in various fields

Pharmaceutical Applications

Marine siderophores have emerged as promising candidates for pharmaceutical development due to their unique iron-chelating capabilities and structural diversity. A landmark example is *cefiderocol*, an FDA-approved siderophore-cephalosporin conjugate that exploits the bacterial iron uptake pathway—known as the "Trojan horse" strategy—to deliver antibiotics into resistant Gram-negative bacteria, overcoming outer membrane permeability barriers (Ito & Butler, 2005). Beyond antibacterial applications, marine siderophores are being investigated as potential anticancer agents. Tumor cells exhibit high iron demands for rapid proliferation, and siderophores can limit iron bioavailability, inducing iron deprivation and suppressing tumor growth (Baars et al., 2018). Additionally, iron chelation disrupts iron-dependent enzymes critical for DNA synthesis and cell cycle progression in cancer cells. Marine-derived siderophores, with their novel photoreactive and halogenated structures, also show antiviral potential by interfering with viral replication processes that rely on iron. Furthermore, they are being explored for the treatment of iron overload disorders such as hemochromatosis and thalassemia, where selective iron removal is essential to prevent organ damage. The combination of targeted iron chelation and favourable pharmacokinetics makes marine siderophores attractive scaffolds for next-generation therapeutics addressing antimicrobial resistance, cancer, and metabolic iron disorders (Hatcher.H.et.al, 2009).

Agricultural Uses

The agricultural sector is increasingly turning to siderophore-producing marine bacteria as sustainable biofertilizers and biocontrol agents. These microorganisms enhance plant growth by mobilizing insoluble iron in alkaline and calcareous soils, where iron deficiency commonly limits crop productivity (Kraemer et al., 2015). By producing high-affinity siderophores, marine bacteria such as *Vibrio* and *Halomonas* spp. chelate Fe^{3+} and facilitate its uptake by plant roots, thereby alleviating chlorosis and boosting photosynthesis. Moreover, their competitive iron sequestration abilities suppress soilborne phytopathogens, including *Fusarium*, *Pythium*, and *Rhizoctonia* species, which depend on iron for infection and colonization. This dual role of iron mobilization and pathogen suppression positions marine siderophores as eco-friendly alternatives to chemical fertilizers and pesticides. Field trials have demonstrated improved yields in cereals, legumes, and vegetables when inoculated with siderophore-producing strains (Compant et al., 2005). Additionally, marine siderophores stimulate beneficial rhizosphere microbiota and modulate plant hormone signalling pathways, further enhancing nutrient uptake and stress resilience. With growing concerns over soil degradation and agrochemical pollution, integrating marine-derived siderophores into integrated pest management and organic farming systems represents a promising frontier for sustainable agriculture.

Environmental Bioremediation

Siderophores from marine microorganisms hold significant promise for environmental cleanup through their ability to chelate and mobilize toxic heavy metals. Their high affinity for metals such as arsenic, cadmium, lead, and mercury enables detoxification in contaminated soils, sediments, and aquatic systems (Homann et al., 2019). By forming stable siderophore-metal complexes, these compounds prevent metal bioaccumulation in food chains and facilitate microbial-mediated sequestration and removal. In marine

oil spill scenarios, siderophores have shown the ability to enhance hydrocarbon degradation by supplying bioavailable iron to oil-degrading bacteria, thereby boosting their metabolic activity. This was notably observed during the Deepwater Horizon spill, where iron limitation was a bottleneck for hydrocarbon biodegradation. Furthermore, siderophores can mobilize metals from mine tailings and industrial waste, enabling phytoremediation and microbial remediation of mining-impacted sites. Emerging applications include their integration into permeable reactive barriers and bioreactors for in situ treatment of contaminated groundwater. Their specificity, biodegradability, and effectiveness in trace metal binding make marine siderophores valuable tools for advancing green remediation technologies that restore polluted ecosystems while minimizing secondary environmental impacts.

Industrial Applications

The industrial potential of marine siderophores is rapidly expanding across sectors such as cosmetics, food preservation, metallurgy, and water treatment. In cosmetics, siderophores act as natural anti-aging agents by chelating iron, which catalyzes the formation of harmful reactive oxygen species responsible for oxidative skin damage and aging (Martinez et al., 2017). Their antioxidant properties are harnessed in skincare formulations targeting wrinkle prevention and skin brightening. In the food industry, marine siderophores inhibit spoilage and pathogenic microbes by depriving them of essential iron, extending shelf life and enhancing food safety. They also enable sustainable extraction and recycling of critical raw materials, such as rare earth elements and precious metals, from seawater, mining effluents, and electronic waste (Kraemer et al., 2015). This bioleaching process leverages the metal-binding selectivity of siderophores to recover valuable metals with minimal environmental impact. Additionally, siderophores are incorporated into industrial water treatment systems to prevent iron-fouling, scaling, and biofilm formation, thereby improving process efficiency. In green metallurgy, siderophores serve as selective chelating agents for metal recovery from low-grade ores, supporting the development of cleaner extraction technologies. Their application further extends to biosensors for detecting bioavailable iron, diagnostic kits for microbial infections, and biodegradable chelators replacing synthetic agents in industrial cleaning and processing. (Martinez et al., 2017, Winkelmann G & Drechsel H,1999). Collectively, these innovations position marine siderophores as versatile biochemicals driving the transition to greener, more sustainable industrial practices.

Conclusion:

Marine siderophores represent a remarkable evolutionary solution to iron scarcity in the world's oceans, characterized by unique chemical diversity and ecological versatility. Beyond their fundamental role in iron acquisition, they orchestrate complex microbial interactions and drive key processes in global biogeochemical cycling, such as carbon sequestration and nutrient fluxes. Recent breakthroughs in analytical chemistry, genomics, and synthetic biology are rapidly expanding our understanding of these molecules, paving the way for their application in diverse fields. From next-generation antibiotics and anticancer agents to sustainable agriculture, green metallurgy, environmental cleanup, and industrial biotechnology, marine siderophores are emerging as valuable tools for addressing 21st-century challenges. Realizing their full potential will require integrated, multidisciplinary research efforts to overcome current challenges in cultivation, detection, and scalable production.

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