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Understanding biofouling and contaminant accretion on submerged marine structures

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Fouling of maritime infrastructure is pervasive due to abundant biological and chemical activity within the oceanic environment. Marine biofilms and their successional growths are prevalent issues in biofouling, but current industrial and research-based analyses often do not provide a holistic view of the fouling biodiversity. Cathodic protection is a longstanding system safeguarding infrastructure from the corrosive marine environment, but limited studies on interactions between biological growth and cathodic activity have been conducted in the context of marine fouling. This review identifies knowledge gaps in the understanding of marine fouling and highlights approaches to better direct development of effective anti-fouling measures.

INTRODUCTION

Fouling is the adhesion of unwanted substances or contaminants onto surfaces and is an operational concern across various areas of industry[1]. Within maritime-based industries, where submerged marine structures are exposed to oceanic waters, the main sources of surface accumulation arise from calcareous deposits due to electrochemical reactions from cathodic protection systems[2] and biocalcifying bacteria[3,4], as well as biological marine growth resulting from the formation of marine biofilms and subsequent settlement of macro-fouling organisms[5,6]. Economic losses in maritime-related industries sustained by fouling issues have necessitated the drive toward the development of effective anti-fouling coatings, with recent advances focusing on non-toxic, environmentally friendly alternatives for modern coatings[7,8]. However, in order to optimize the effectiveness of the repellent mechanisms present in the anti-fouling coatings, a greater understanding of the interactions between fouling agents/ organisms and contact surfaces in a variety of operating scenarios is needed[1].

One of the prominent features seen in the hard fouling of marine structures is the presence of calcareous growths. The calcareous material can be broadly distinguished as either (1) calcareous deposition, which is from scaling due to cathodic protection or the accumulation of carbonates from microbial biomineralization[4] or (2) calcareous organisms, which usually consist of marine invertebrates[9]. Calcareous deposition and marine growth often co-occur on submerged surfaces, and there is a need to understand how the biotic and abiotic sources interact to produce broader countermeasures against marine fouling[10]. This is crucial as there may be potential differences in adhesion dynamics on surfaces with cathodic protection where the formation of the initial conditioning film is calcareous-based[2,4,11], compared to the organic material-based film in typical biofouling successional models[9,12].

Biofilms are also a critical component in marine growth as it forms the foundation of the biofouling community, with the interactions between the substrate/surface, as well as the dynamics between the micro- and macro-fouling organisms being major targets for studies in biofouling control[6]. Biofilms and their associated growths are complex assemblages, with interdisciplinary expertise required to unravel the properties and mechanisms of biofilm formation and propagation[13]. Marine biofilms are responsible for billions of dollars of damage to submerged and underwater structures due to their involvement in biofouling and microbially-influenced corrosion (MIC), but a lack of understanding in how multi-species biofilms develop has hindered the progress of creating effective anti-biofouling controls[14]. The limited models of biofilm formation have not been effective in driving the understanding of the development process in diverse settings, with further experimentation needed to devise anti-growth strategies for in situ multi-species biofilms such as those seen in marine environments[15].

This review discusses fouling on marine surfaces, as well as delving into the processes that drives the formation of biotic and abiotic fouling, from initial submersion into the marine environment, to microbial biofilm development, and through to the settlement of macro-fouling species. The paper will also explore cathodic protection on marine surfaces and how the associated electrochemical processes promote calcareous deposition, as well as what effects they may have on co-occurrent biological growth. The review will also cover the processes of MIC, which is often a consequence of uncontrolled biofouling. We attempt to identify critical interactions between the stages of fouling formation, responses to environmental factors, and the interaction of biodiversity across different kingdoms of life to uncover insights that can help direct strategies for developing effective fouling prevention systems on marine structures.

UNDERSTANDING THE BIODIVERSITY AND BIOLOGICAL ACTIVITY IN MARINE GROWTHS

Ecological insights into biodiversity is the key to addressing biofouling

Marine biofouling is the unwanted attachment and formation of biological marine growth, where organisms across the major kingdoms of life (viruses, archaea, bacterial and eukaryotes) form interconnected communities with entwined ecological and interspecies dynamics (Table 1). The formation of marine

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Table 1. A non-exhaustive list of key sessile (micro)organism groups in marine biofouling communities.

Key fouling groups	Notable biofouling taxa	Issues caused by these biofouling groups
Biofilms[5,6]	Archaea Bacteria Fungi Microalgae (mainly diatoms) Protists	The marine biofilm acts as the foundation on which the subsequent biofouling community is built. The biofilm provides an adhering layer for micro- and macro-fouling organisms alike and has been observed to be critical in the attachment and growth of a variety of sessile marine species.
Biocalcifying microorganisms[55,56,93,94]	Bacterial groups such as Cyanobacteria, sulfate-reducing bacteria, denitrifying bacteria and ureolytic bacteria. Calcareous diatoms	The metabolic processes of these microorganisms can induce precipitation of calcium carbonate in their immediate surrounding leading to scaling and associated issues with hard fouling.
Morphogenesis agents[22,23,25]	Marine invertebrates (Notable bacteria include Pseudoalteromonas luteoviolacea, Cellulophaga lytica, Bacillus aquimaris and Staphylococcus warneri) Algae (Roseovarius sp. MS2 and Maribacter sp. MS6 for the green algae genus Ulva; co-culture containing several Proteobacteria candidates for brown algae Ectocarpus sp.)	Several bacterial species have been observed to be critical for the morphogenesis of marine invertebrate larvae and algal spores into their sessile forms, promoting the propagation of many macro-fouling organisms.
Biofilm-based viruses[34]	Double stranded DNA viruses (Notable examples from Class Caudoviricetes and Class Maveriviricetes)	Biofilm-based viruses have been observed to integrate into bacterial genomes, appearing to provide functional genes for adhesins and polysaccharide metabolism. This integration can potentially increase the biofilm formation capabilities of the host bacteria.
Macro-fouling organisms[9,95–99]	Bivalve molluscs (Phylum Mollusca, Class Bivalvia) Barnacles (Phylum Arthropoda, Class Thecostraca) Bryozoans (Phylum Bryozoa) Calcaerous tubeworms (Phylum Annelida, Class Polychaeta) Hard corals (Phylum Cnidaria, Class Anthozoa, Order Scleractinia) Soft corals (Phylum Cnidaria, Class Anthozoa, Order Alcyonacea) Hydroids (Phylum Cnidaria, Class Hydrozoa) Sea Anemones (Phylum Cnidaria, Class Anthozoa, Order Actiniaria) Ascidians, tunicates and seq squirts (Phylum Chordata, Class Ascidiacea) Marine sponges (Phylum Porifera) Green algae (Division Chlorophyta) Brown algae and kelp (Phylum Gyrista, Class Phaeophyceae) Red algae (Division Rhodophyta)	Uncontrolled growth can lead to increased weight and rugosity of affected structures, compromising structural integrity and efficient operation of traveling vessels. Coverage of vital structural component such as sensors, connectors and moving parts can inhibit the operation of maritime machinery. Increased operational costs due to additional cleaning requirements, as well as increased fuel costs due to drag on maritime vessels.

biofouling is generally represented as a layered successional model: (1) organic materials and minerals are adsorbed onto an surface exposed to seawater forming a conditioning film, (2) primary colonizers, usually bacteria, form the biofilm layer enhancing the adherence of subsequent (micro)organisms, (3) the establishment of microfouling communities consisting of microorganisms such as bacteria, microalgae (diatoms and others), and (4) the settlement of macrofoulers such as macroalgae and marine invertebrates[12] (Fig. 1). Although the successional model provides a general outlook on how the biofouling progress occurs, the formation process is more akin to a probabilistic model, where the absence of one layer does not preclude the formation of a subsequent layer[9]. The challenge that lies within studying marine growths for anti-fouling measures is that the biofouling community is an evolving assemblage of diverse (micro)organisms, with a plethora of mechanical, physicochemical and biological interactions that need to be explored to obtain the required insights for developing effective control measures[7,8]. The complexity of the community progression, from the settlement of microbial colonizers to the establishment of macro-fouling organisms means a multifaceted approach is required to encompass the abundance and interactions of species from the marine biofilm to the eventual established biofouling community[8,16]. Although a

holistic approach toward understanding the biodiversity in marine growths is essential to combat biofouling, there have been limited studies that address biofouling communities in its entirety, with our knowledge of core biological mechanisms often derived from studies that focus on model species[6].

Understanding how biofouling communities respond to variations in mechanical and physicochemical interactions is key to developing effective anti-fouling control methods[7,8]. These comprise of slow-release chemical compounds that kill, degrade, or inhibit contact of fouling organisms, or surfaces composed of material engineered to hinder the adhesion of fouling organisms[7,8]. Differences in biofilm community composition when subjected to different anti-fouling coating formulations can provide insight into vulnerable and resistant taxa[17]. The efficacy of individual anti-fouling coatings can be affected by prevailing physicochemical conditions and may vary against different endemic biofouling communities, indicating that anti-fouling systems require site-specific analyses to provide the best results[18,19]. As such, large-scale ecological studies are needed to provide the essential information needed to tailor robust and effective anti-fouling measures for use in specific regions.

Comprehending patterns in micro- and macro-fouling organisms under different stressors can elucidate critical interspecies
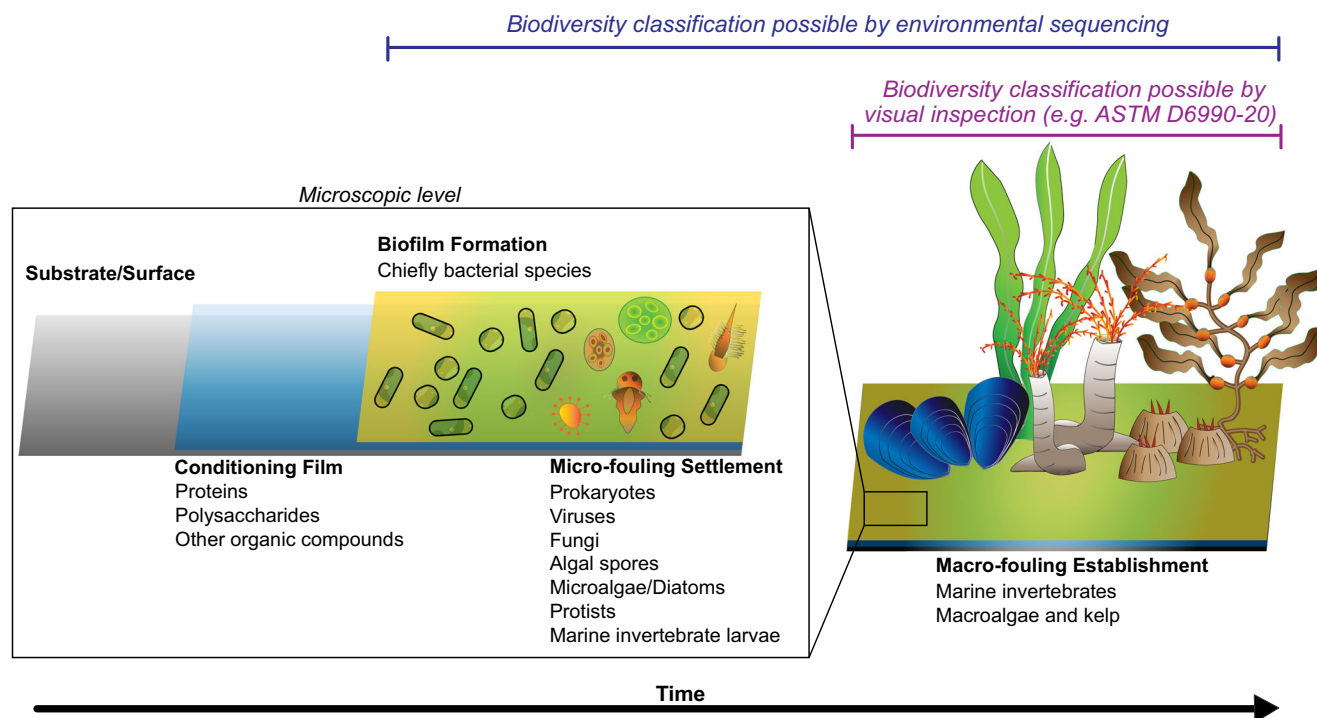
Biological Growths on Subsea Structures

Biodiversity classification possible by environmental sequencing

Biodiversity classification possible by visual inspection (e.g. ASTM D6990-20)

Microscopic level

Substrate/Surface

Biofilm Formation
Chiefly bacterial species

Conditioning Film
Proteins
Polysaccharides
Other organic compounds

Micro-fouling Settlement
Prokaryotes
Viruses
Fungi
Algal spores
Microalgae/Diatoms
Protists
Marine invertebrate larvae

Macro-fouling Establishment
Marine invertebrates
Macroalgae and kelp

Time

Fig. 1   Representation of biofouling community progression. A simplified process of the successional model detailing development of the biological growth. Visual inspection of biofouling can only reliably identify macro-fouling organisms, whereas sequencing of DNA and RNA from environmental samples can provide detail on all biodiversity.

interactions[20]. Marine biofilms are vital for the settlement and morphogenesis of macro-fouling organisms[20,21], with model studies showing extracellular phage-like structures or vesicles from specific bacterial strains inducing morphogenesis in marine invertebrates[21,22], whereas in brown and green algae a co-culture of different strains is required for morphogenic development[23–25] (Fig. 2). This symbiotic relationship appears to be supported in model testing of anti-fouling measures. A study that investigated different cementitious materials for biofouling prevention discovered that surfaces with biofilms containing lower total cell counts also saw reduction in respective total biomass of macro-fouling organisms[26]. Similarly, a study on *Shewanella marisflavi* biofilm formation and mussel settlement showed that enzymatic inhibition of total bacterial protein count reduced both the cell count of the bacterial population, as well as the settlement of the mussels[27]. Taken together, a holistic approach in surveying biodiversity appears necessary to further discern the potential symbiotic associations between the micro- and macro-fouling organisms driving the settlement and succession of the biofouling community.

Environmental DNA and RNA data can provide wider insights into fouling biodiversity

Advances in sequencing technology and molecular microbiology have provided remarkable progress in exploring the marine microbiome, with various large-scale studies driving increased understanding of biodiversity and biological activity that exists in our oceans[28–31]. Environmental sequencing is an approach that captures DNA and RNA data directly from a habitat or biome of interest, with the subsequent sequence data generated enabling the characterization of the taxonomic profile, as well as the metabolic capacity of the living communities within in its entirety. The all-encompassing informational platform that can be delivered by environmental sequencing is well-suited for the study of

marine growths, where sampling of this interconnected ecosystem can provide information for all micro- and macro-organisms present, alongside other contextual data and testing methods to better characterize the biofouling community (Fig. 1). In contrast, the standard industry practice for evaluating marine coating systems for resistance against biofouling ASTM D6990-20, relies purely visual inspection and comparison of testing surfaces which in its nature limits the investigation to visible macro-fouling species.

Although environmental sequencing has the potential to reveal the biodiversity of an ecosystem in its entirety, the approach has unfortunately been relatively limited in scope for marine growths and biofouling communities. Even though environmental sequencing has provided an enormous bank of data for planktonic marine microorganisms, this does not properly represent that biodiversity that is present within sessile marine growths such as biofilms, which has shown to contain taxa and functions not observed within seawater sampling data[32]. Due to microbial biofilms species being critical colonizers that drive the rest of the biofouling community, sequencing studies have focused mainly on microbial communities[33]. As a result, the investigation of larger multi-cellular organisms using molecular techniques has been neglected in biofouling studies, with more data generation needed to understand the diversity of macrofoulers by building and expanding the vital databases needed for proper characterization[33]. Similarly, marine viruses discovered in biofilm populations did not match those in online databases derived from oceanic surveys, again showing a clear delineation between planktonic and sessile populations[34]. These marine biofilm viruses appeared to integrate with the microbial genomes in functions related to adhesion and polysaccharide metabolism, meaning that viruses endemic to this niche may contribute to biofilm formation capabilities of their host[34]. As such, the need to characterize biodiversity within marine growths in their entirety is crucial for unraveling the interspecies
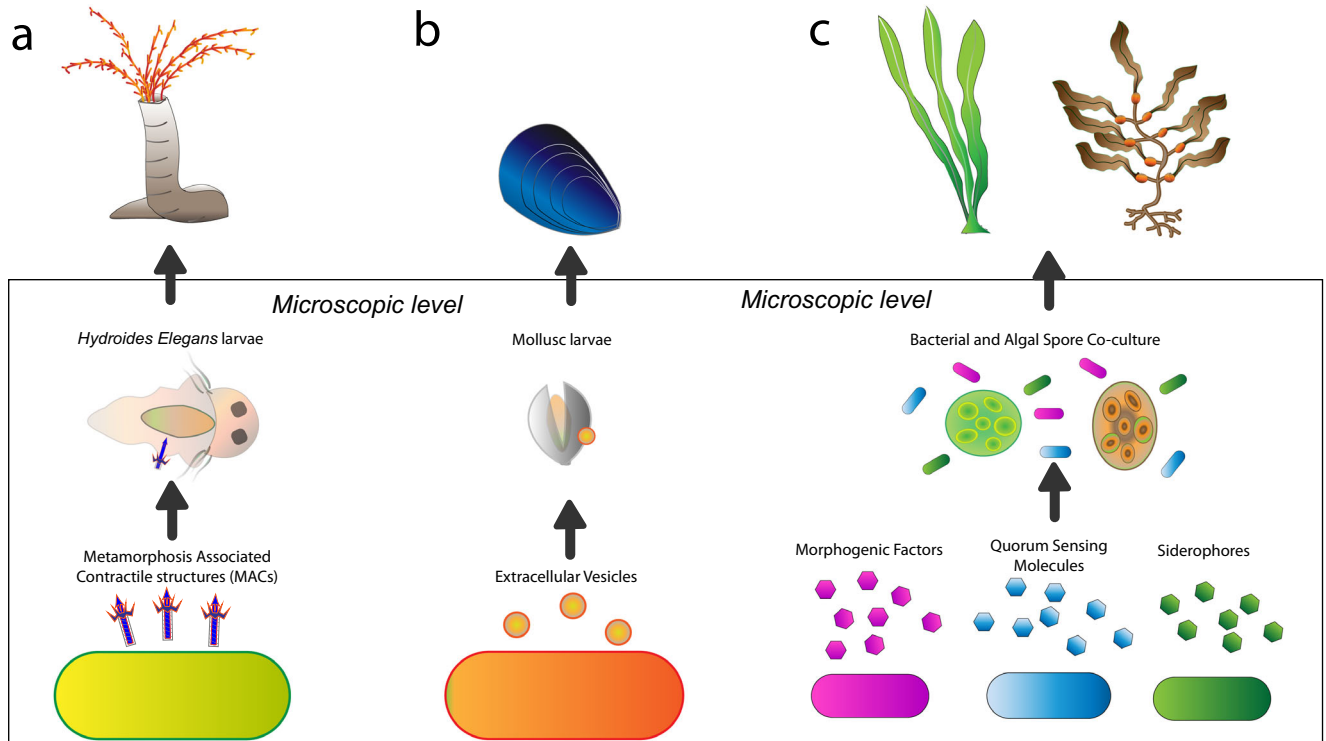
Fig. 2 Bacterial induced morphogenesis of macro-fouling organisms. a Metamorphosis-associated contractile structures produced by Pseudoalteromonas luteoviolacea have been demonstrated to induce metamorphosis in the *Hydroides elegans* larvae. **b** Similarly, extracellular vesicles from bacteria are purported to induce metamorphosis in other species of marine invertebrates. **c** In comparison, spores from green and brown algae require co-culture conditions with multiple strains of bacteria to undergo metamorphosis, with a variety of signaling molecules purported as the drivers that induce metamorphosis.

and interkingdom interactions between the biofouling (micro) organisms, and how this cooperation contributes toward community proliferation.

Aside from limitations in the scope of multi-kingdom biodiversity, biogeographical data for sessile marine growth also remains limited. The focus has been on marine biofilms due to their importance in propagating further marine growth but known studies have been relegated to a few regions mainly in the Atlantic coast of the US, the European Coastline and coastal waters around East Asia[9,32,34]. As the efficacy of anti-fouling coatings have been observed to be site-dependant[18,19], biogeographical community data can help identify predominant biofouling species, as well as the prevailing ecological conditions in regions of interest, to better direct strategies for targeted anti-growth measures.

How genetic information can help unravel the processes behind biofouling

Marine biofilms are critical targets for biofouling prevention as they have been established to be a fundamental component in marine growth that promotes the adhesion of successional (micro) organisms[9,26,27,35]. Environmental sequence data allowed researchers to peek into the biofilm communications network through the comparisons of signal transduction genes across different microbial communities, giving insights into how signaling molecules enable the formation and settlement of biofilm communities[36,37]. In situ experiments have been performed to study the effects of zinc-[38] and copper-based[39] surfaces, materials known to have anti-microbial properties, on its effects against the marine biofilm microbial communities. An abundance of heavy metal resistance genes, transposases and genes that regulate the composition of extracellular polymeric substances suggest that microbial communities within marine biofilms have the capability

to adapt to and disperse genetic countermeasures against toxic agents. Adhesion dynamics of initial surfaces colonizers has also been explored with metagenomics, demonstrating a wide array of genes that are involved in motility, attachment, secretion systems and quorum sensing that are critical to biofilm formation[40]. The environmental sequencing approach has been critical in understanding the bioprocesses that drive biofilm development and how they contribute to the resilient properties associated with biofilms.

Genetic information can also help elucidate the bioprocesses and interspecies interactions that drive the growth and settlement of the macro-fouling organisms that build upon the initial biofilm. The CA enzyme is core for regulating carbonate biomineralization in marine invertebrates[41] and can be used to quantify calcareous macrofoulers such as mussels[42] and tube-worms[43], as well as biocalcifying bacteria[44] to estimate the rate of biological-based hard fouling. In a similar vein, bacterial components that induce morphogenesis in the planktonic forms of marine invertebrates into their mature sessile forms present valuable genetic targets for further investigation[22]. A model example are the metamorphosis-associated contractile structures discovered in *Pseudoalteromonas luteoviolacea* thought to be responsible for inducing the metamorphosis of *Hydroides elegans* from its larval form[45]. The genes related to this structure were found to be more abundant and diverse in marine biofilms compared to seawater, and that the highly diverse gene clusters found in biofilm-related species is likely due to gene transfer between different microbial taxa[46]. By surveying genetic markers of interest, we can uncover candidates to monitor for the progression and growth of biofouling communities, enabling the development of more focused and targeted preventative measures against key taxa.
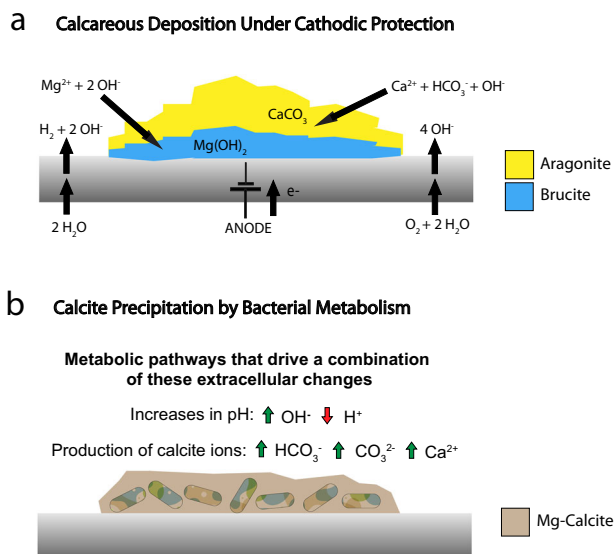
Fig. 3 Visualization of calcareous deposition on marine surfaces. a Electrochemical reactions on surfaces protected by cathodic protection are typically aragonite and brucite. **b** Biomineralization from biocalcifying bacteria form calcite containing traces of magnesium.

ACCRETION OF CALCAREOUS DEPOSITION ON MARINE SURFACES

Cathodic protection driven deposition

Cathodic protection is a long-utilized system in the maritime industry to protect metallic surfaces immersed in seawater from corrosion by causing an electrical gradient between the protected surface and an anode, with the return path for the current through the seawater acting as an electrolyte. This results in the protected surface being held at a negative potential, where reduction occurs, thereby preventing the effects of corrosion. The applied potential can be provided by an anode with a higher reduction potential (galvanic system) or from a DC voltage source (impressed current system)[2]. Calcareous deposition can occur on surfaces protected by either galvanic or impressed current cathodic protection systems[2].

The accretion of calcareous deposits occurs due to a series of electrochemical reactions between the cathodically protected surface and the anode[2] (Fig. 3a). At the protected metal surface dissolved oxygen molecules are reduced to hydroxyl ions and at higher potential water is reduced to hydroxyl ions and hydrogen gas. The production of hydroxyl ions from these reduction reactions raises the pH of the interface between the metal and the surrounding water. Dissolved carbon dioxide in the surrounding seawater with raised pH will be converted to carbonate ions, causing the solubility product of magnesium hydroxide, as well as calcium and magnesium carbonates to be exceeded, which results in precipitation onto the cathodically protected surface.

Calcareous polymorph formation on cathodically protected surfaces

Initially, the high levels of hydroxyl ions react with magnesium to form magnesium hydroxide preferentially, and as the hydroxyl ions levels are reduced through precipitation, so does the pH level in the immediate area, therefore changing the preferred reaction to calcium carbonate formation[47]. Although if dissolved oxygen is still present at the metal surface or the metal potential is held sufficiently negative for water reduction to occur, the hydroxyl ion concentration depleted by precipitation will be replaced. The initial layer of magnesium hydroxide forms as brucite, which has a

gelatinous and porous nature[48,49]. Subsequent layers of calcareous deposit are calcium carbonate-based polymorphs, including magnesium calcium carbonate in the form of dolomite, and pure calcium carbonate polymorphs (in order of stability): anhydrous calcite, aragonite, hydrated forms of hydrocalcite, ikaite, vaterite and amorphous calcium carbonate (ACC)[2]. The formation of ACC occurs when calcium carbonate is saturated in solution, but this form is unstable and converts rapidly to anhydrous forms[50]. When Ca/Mg ratios are greater than 1:3, hydrocalcite formation may occur[51], and whilst it is considered a metastable polymorph, the presence of hydrocalcite has been observed after 12 months on cathodically protected steel in contact with seawater and marine sediments[52]. Ikaite can form at 0 °C but decomposes to an anhydrous form at 25 °C[50]. Aragonite appears to be the most common calcium carbonate polymorph seen in marine deposition, occurring when the Mg/Ca ratios are roughly 5:1 as adsorbed magnesium ions inhibit the growth of calcite and promotes the formation of aragonite, with aragonite being the most preferential form of calcium carbonate that occurs in seawater greater than 6 °C[53].

Bacterial carbonate biomineralization

The formation of calcite can also be due to bacterial action (Table 2), and is referred to as microbially-induced calcite precipitation (MICP)[54]. MICP occurs in a similar process to electrochemical reactions on cathodically protected surfaces whereby reactions raising the surrounding pH in environments with carbonates available provide conditions favorable for calcareous deposition to occur[4] (Fig. 3b). Due to the high precipitation potential and the extensive range of ureolytic bacteria across various environments, the urease and carbonic anhydrase (CA) based metabolic pathway is the most extensively studied form of MICP[4,55,56]. The ubiquity and relatively low complexity of the urease/CA metabolism has made it the model process for recent MICP studies on cathodically protected surfaces[3,4,57]. However, a recent study found that marine bacterial strains isolated from cathodically protected surfaces that tested positive for CA and negative for urease production was still able to undergo MICP in the absence of urea[3]. This suggests CA may be critical in other MICP pathways, and that there is a need to expand past urease hydrolysis as the model for MICP, particularly in studies on subsea fouling.

Interactions between inorganic calcareous deposition and biological marine growth

As cathodic protection is a long-time and essential component of marine structures[2], there is a need to understand the co-occurrent interactions that inevitably occur between electrochemical and microbial deposition[4], as well as the settlement of subsequent biofouling communities on submerged infrastructure[10,58]. Within the marine environment, only a handful of marine biocalcifying bacterial strains from genera *Bhargavaea, Epibacterium, Planococcus, Pseudidiomarina, Pseudoalteromonas,* and *Virgibacillus* have been isolated from calcareous deposits formed from cathodic protection[3,57]. Additionally, studies on the interactions between MICP and electrochemical calcareous deposition, particularly within the natural marine environments is currently limited to model studies[4]. Biocalcifying *Pseudoalteromonas* and *Virgibacillus* species tested in an artificial seawater model showed that impressed current from cathodic protection systems had no appreciable effect on bacterial growth, metabolic activity, or carbonate production[4]. In addition, the model testing found that bacterial activity appeared to change the preferential formation of calcareous deposits on cathodically protected surfaces, favouring the formation of magnesium-containing calcites and impeded the formation of aragonite and brucite[4]. Despite the common co-occurrence in maritime structures, the combined effects of

Table 2. Overview of bacterial metabolic processes that facilitate carbonate precipitation.

Metabolic process	Known bacterial groups/candidates	Metabolic enzymes	How the metabolic process induces precipitation
Urea hydrolysis[55,56]	Ureolytic bacteria	Urease, Carbonic anhydrase	The process behind urea hydrolysis releases ammonium, bicarbonate, and hydroxyl ions. This synergistically acts with carbonic anhydrase which catalyzes the reversible reaction of water and carbon dioxide into carbonic acid. Both processes result in a net increase in pH and increasing levels of bicarbonate, driving carbonate precipitation.
Methane oxidation[56,100]	Methanogens	Methane monooxygenase	In anaerobic conditions, methane oxidation results in bicarbonate which in the presence of calcium ions precipitates into calcium carbonate.
Denitrification[56,100]	Nitrate-reducing bacteria	Nitrate reductase	Denitrification induces carbonate precipitation through the production of carbon dioxide and hydroxyl ions, as well as the consumption of hydrogen ions in the metabolic process. The increase in pH and levels of carbon dioxide in the presence of calcium ions drive the precipitation of calcium carbonate.
Sulfate reduction[55,56]	Sulfate-reducing bacteria	Dissimilatory sulfite reductase	The processes that reduce sulfate into sulfide also oxidizes organic carbon into carbonate, as well as consuming hydrogen ions increasing the favorability of carbonate precipitation. In addition, sulfate-reducing bacteria are known to degrade carboxylic acids with calcium complexation, releasing calcium ions into the surrounding environment, further driving the precipitation of calcium carbonates.
Photosynthesis[56,100]	Cyanobacteria	RuBisCO; Carbonic anhydrase	In photosynthetic microorganisms, carbonates ions diffuse into the cell and is converted by carbonic to carbon dioxide and hydroxyl ions, whereby the carbon dioxide is converted into organic compounds by RuBisCO and the hydroxyl ions diffuse out of the cell. To maintain pH levels in the cell, antiporters exchange intracellular calcium ions for extracellular hydrogen ions. These combined processes result in an increase in pH and calcium ions in the surrounding environment, promoting the precipitation of calcium carbonate.
Ammonification[56,101]	Alcanivorax borkumensis, Myxococcus xanthus	Urease, Nitrite reductase, Putative enzymes comprised of deaminases, hydratases, peptidases, and proteases	This process includes urea hydrolysis, as well as parts of the denitrification pathways in nitrogen metabolism. In an alternative denitrification pathway, nitrite undergoes dissimilatory nitrate reduction to ammonium via nitrite reductase. Alternatively, proteins and amino acids are broken down by a variety of enzymes, whereby ammonium and sometimes carbon dioxide is released as a byproduct. Like urea hydrolysis and denitrification, a resultant net increase in pH and bicarbonate production drives favorability toward precipitation of carbonate compounds.
Fatty acid catabolism[56,102]	Bacillus subtilis	Putative flavoproteins	B. subtilis is an ureolytic bacteria that has been observed to precipitate calcite (a polymorph of calcium carbonate) in the absence of urea. A likely enzymatic candidate was a putative heterodimeric flavoprotein associated with fatty acid metabolism. A study showed calcite precipitation in the wild type, but not in knockout strains when the associated flavoprotein gene was modified.

impressed current cathodic protection and microbial activity on calcareous deposition requires further investigation.

Another vital area for understanding fouling mechanics is the interaction between marine growth involved in biofouling and their settlement on cathodically protected marine surfaces. A study by Zhang et al.[10] found that calcareous deposits provided favorable conditions for microbial attachments due to the strong adsorption of bioadhesives to calcium carbonate. In comparison, it was more advantageous for macro-fouling organisms to adhere directly to the surface substrate as they are more susceptible to hydrological scouring by adhering to the calcareous deposits instead[10]. On cathodically protected surfaces, the accretion of calcareous deposits appeared to take priority over the biofilm formation, with deposition progressing even after the biofilm has been established[10]. Another study by Erdogan and Swain[58] explored impressed current cathodic protected and non-protected steel panels exposed to the intermittent tide, completely immersed in seawater, and half buried in marine sediment. The study found that the panels that were only intermittently exposed to seawater developed fouling rapidly during a period of high tides, demonstrating the effects of moving seawater in promoting biofouling[58]. The protected panels formed stable

biofouling communities compared to the non-protected panels which had denser biofouling along the edges, likely due to the cathodic potential occurring close to the edges, with the buried non-protected panel developing the quickest biofouling growth likely due to the largest observed cathodic area[58]. This may be the result of increased pH leading to carbonate ion production from cathodic activity[2]. As carbonate availability is vital for the development of marine invertebrates, the increased carbonate concentrations in these areas may have created favorable conditions for these organisms to propagate[59,60].

The effects of calcareous deposition on structural operations

The deposition of calcareous layers improves the corrosion resistance of surfaces under cathodic protection by forming an insulating layer against corrosive agents in the marine environment, as well as reducing the current demand needed to maintain the protective effect[47]. Similarly, bacterial carbonate biomineralization was also demonstrated to mitigate the effects of corrosion on carbon steel, albeit in small scale model testing[61]. However, the protective nature depends on the coverage provided by calcareous deposit—brucite for example is too porous and allows free electrolyte diffusion[49], whereas calcium carbonate provides the best coverage with the aragonite polymorph performing better as an insulating layer compared to calcite[62]. Although calcareous deposition may afford some benefits in corrosion protection and structural reinforcement, its presence may introduce structural and operation issues typical of hard fouling, such as interfering with heat exchange surfaces, impediment of moving parts, and the obstruction of components such as sensors, connecters, and interfaces[1,9]. More research is needed across different environmental marine settings into the adhesion mechanics/dynamics and composition of calcareous deposits formed under cathodic protection, along with whether the observed protective effects is maintained in the long term, and how biological activity interacts with or influences the formation of calcareous material[11,47].

The effect of coatings in cathodic protection systems

Cathodic protection is seldom used alone to protect marine structures from corrosion, with coatings used in tandem to improve the longevity and effectiveness of the protective system[63,64]. The coatings also serve to prevent the build-up of fouling material, such as calcareous deposition or biofouling, with a study showing a large reduction in fouling on panels with anti-fouling coatings compared to uncoated panels, regardless of whether the surfaces had galvanic or impressed current cathodic protection[11]. Zinc based coatings have been trialed as a more environmentally friendly alternative, with these coatings appearing to inhibit the formation of calcareous scales through the elimination of brucite and the promotion of hydrated forms of calcium carbonate over aragonite, likely due to the release of zinc cations interfering with the formation process[65]. As the crystal structure of calcareous deposits are influenced by the availability and adsorption of ions[47], the exploration of different chelation approaches may be useful in combating the development of inorganic scale.

MICROBIALLY INFLUENCED CORROSION—A COMMON CONSEQUENCE OF BIOFILM FORMATION

Beyond enabling the build-up of biological growth on submerged surfaces, the growth of microorganisms and their associated biofilms also increases the risk of MIC in marine environments, where corrosion of submerged surfaces occur because of microbial metabolic and physiological activity[14,66,67]. MIC can be broadly classified as 1) metabolite MIC where surfaces are affected directly by corrosive metabolites, and 2) extracellular electron
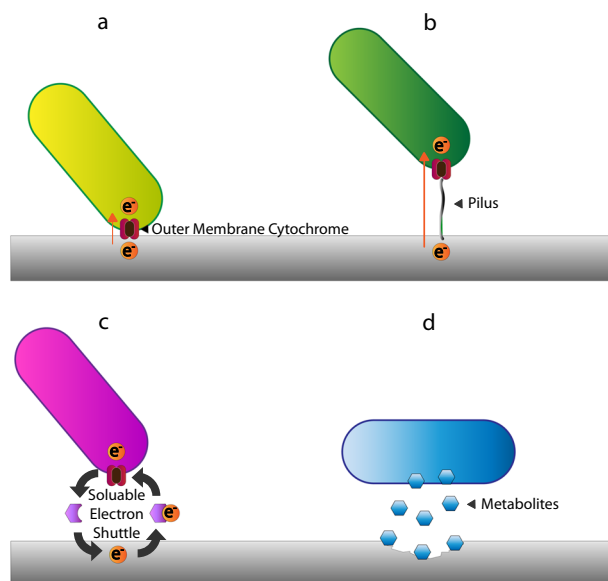

Fig. 4 Visualization of microbially induced corrosion (MIC) by bacteria. Extracellular electron transfer MIC occurs when outer membrane cytochromes scavenge electrons from a surface via (**a**) direct contact, (**b**) conductive pili or (**c**) delivery through soluble electron shuttles. **d** Metabolite MIC occurs when corrosive bacterial metabolic products or their derivatives degrade a surface.

transfer MIC (EET-MIC) where erosion is caused by microbial cathodic action[14,68] (Fig. 4). On metallic structures EET-MIC is considered the more prevalent form of biocorrosion[14]. Microbial electrochemical activity occurs either through direct microbial contact, through conductive pili, or via mediated electron transfer where soluble electron shuttle molecules (with examples being flavins, melanin, phenazines, and quinines) transfer electrons from the metallic substrates to the microbial cell[69,70]. *Shewanella*[71] and *Geobacter*[72] spp. have been the model species for direct EET-MIC, with corrosion occurring via outer membrane cytochromes, which are purported to act as channels that contact and exchange electrons from extracellular sources. *Shewanella* have also demonstrated the ability to use H_2-[71] and riboflavin-mediated[73] electron transfer, indicating that extensive forms of biocorrosion can be present within a single genus. Marine *Pseudomonas aeruginosa* strains have shown to perform mediated electron transfer via phenazine-1-carboxamide[74], with a gene expression study demonstrating the rates that the molecule is secreted influences the rate of corrosion observed on steel surfaces[75]. Although headway has been made in this field, current studies have been relegated to a few model species meaning the understanding of multi-species EET-MIC is still in its infancy[70].

Sulfate-reducing bacteria (SRB) are a biofouling group that is associated with metabolite MIC through the reduction of sulfates into corrosive sulfides, as well as EET-MIC via H_2-mediated electron transfer[68]. SRBs are also involved in biofilm formation and have been shown to be key players in promoting biofouling and structural obstruction issues[76]. In addition, when sulfate reduction occurs, hydrogen ions, hydrogen sulfide, and bicarbonate is produced leading to carbonate precipitation[77], with sessile SRB observed to have key roles in the precipitation of carbonates in lithifying communities[78]. Cathodically protected surfaces that have SRB attachment has been observed to require higher current demands in order to maintain adequate levels of corrosion prevention, potentially driving up operating costs[79]. As SRB are major promoters of carbonate scaling and corrosion, and the establishment of SRB populations can interfere with cathodic current loads, they are prime candidates for developing targeted
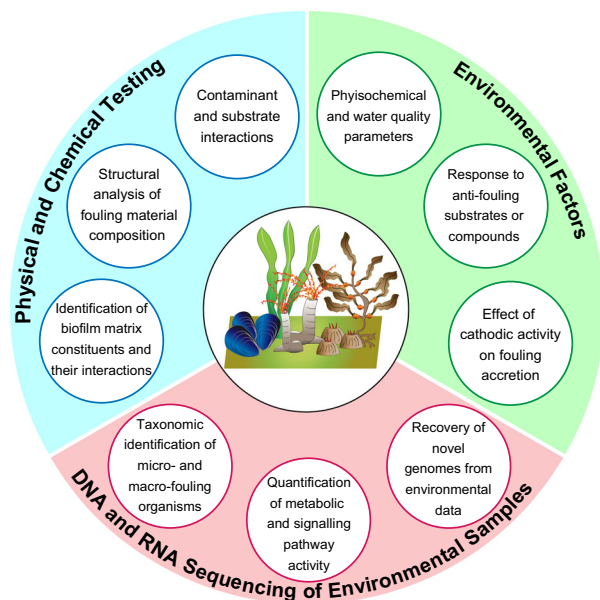
Fig. 5 Holistic measures required for effective research of marine fouling. Interdisciplinary expertise is vital to investigate the different aspects that drive fouling and to decipher the plethora of interactions within the entwined systems.

preventative measures toward, due to being both biofouling and biocorrosion agents. More studies are required to understand how microbial communities establish on catholically protected surfaces, and how biofouling and MIC interact with the electrochemical processes present in these vital protective systems within the marine environment[79].

HOW INTERDISCIPLINARY APPROACHES DRIVES EFFECTIVE RESEARCH TOWARD FOULING SOLUTIONS

A requirement for addressing marine fouling, whether the origin is biotic, abiotic, or a combination of both, requires the understanding how environmental factors influence the formation and composition of the resultant contaminants. To enable solution-driven research in marine fouling studies, whereby scientific data can be applied to industrial applications, an array of techniques and instruments that can characterize the species or substrates of interest that comprise the accumulated materials is required. In a dynamic environment such as the ocean, where biological activity and raw chemistry are abundant, a holistic approach is needed to understand the mechanisms behind the core drivers of marine fouling (Fig. 5).

Abiotic and biotic factors influence the composition of fouling material

Both calcareous deposition and biofilms have similarities whereby both forms of fouling are akin to a "second skin" for marine structures. Understanding the composition of these fouling matrixes is vital in elucidating the mechanical and physical properties in both calcareous deposits[2] and the extracellular polymeric substances that constitute biofilms[80]. In calcium carbonates, the stability, solubility, and resistance to shear forces is dependent on the polymorph and morphology of the deposited type[2,81,82]. As the structure of calcium carbonate can be modified by the introduction of inorganic salts[47,65] or from biological activity[4,11], additives or coatings could be used to facilitate the formation of more amenable forms that are easier to remove or cause less impediment. Analysis of interactions with carbonate polymorphs from biotic and abiotic sources are also essential to

understanding key connections between fouling and the marine environment, such as how in co-occurrent calcareous deposition from cathodic protection and biocalcifying bacteria interact[4], preferences of (micro)organism attachment to calcareous surfaces[10], as well as solubility and adhesion of different polymorphs to submerged surfaces[83] provides vital information needed to assess and combat hard fouling. The ability to discern and link biological and enviro-chemical activity is an important step to successfully develop effective research toward the prevention of calcareous deposition on marine structures.

The defining property of a biofilm ecosystem is the extracellular matrix that encompasses the whole living structure. This matrix is a dynamic structure, constantly being degraded and rebuilt by microbial activity, and untangling this dynamic through analyses of structural composition, and identifying the contributors from the microbial community is vital for establishing strategies in developing anti-biofouling measures[80]. A deeper understanding of how environmental conditions influence the biofilm matrix, such as differences in protein/polysaccharide ratios in extracellular polymeric substance compositions[84], recruitment of macro-fouling species[85], factors that influence adhesion properties[86], how extracellular DNA interacts with other extracellular matrix components[87], and the how the underlying microbial biodiversity responds to environmental stressors[88] can help unravel the mechanisms that provide the resiliency and pervasiveness found in marine biofilms. Reconciling biological activity from cornerstone taxa to the physical constituents that forms the biofilm network provides a holistic approach to discovering how biofilm formation occurs in differing marine conditions, which in turn can direct strategies for improving biofouling prevention systems.

Ecological factors influencing the biodiversity in marine growth

A plethora of environmental variables such as physicochemical conditions, spatiotemporal dynamics, light and UV levels, tides and hydrodynamic conditions can vastly influence the microbial community present in the marine biofilm, as well as the successive macro-invertebrate community that subsequently settle upon them[6,35,89]. Arguably the greatest ecological driver of concern is oceanic warming and acidification due to climate change and its potential effects on biofouling communities[90]. Lowered pH levels have been observed to inhibit the calcification of calcareous invertebrates[91], but there is still limited information on how oceanic acidification affects the settlement process of marine invertebrates[92]. Current studies have suggested that conditions associated with oceanic warming and acidification is likely to negatively affect anti-fouling measures due to alterations in the composition of micro- and macro-fouling communities, and from physicochemical changes in operating conditions reducing the effectiveness of current preventative systems[90]. The sweeping changes brought on by global warming affects all life under the sea, thus more studies that encompass the complete micro- and macro-organism biodiversity of marine biofilm/growth ecosystems are needed to comprehend the extent of these massive ecological shifts on biofouling communities.

The drivers behind marine fouling are multilayered, both literally and figuratively, with various environmental and biological sources entwined in propagating the accretion of unwanted material on vital subsea structures. However, as studies unravel each step of the fouling process, we begin to understand how the accretion of materials occur, as well as the mechanisms behind the establishment and proliferation of biological growth, revealing critical interactions that can be exploited to halt or inhibit the progression of fouling activity. Using a stepwise approach, we need to delve into the genetic

aspects of biodiversity that mediate the various mechanisms responsible for biofouling, as well as the bioprocesses and critical components that enable the seemingly cooperative resiliency seen in these fouling communities. There is also a need to expand understanding of calcareous deposition under cathodic protection beyond the scope of physical chemistry, and to understand that within the natural marine environment where biological activity is abound, there will be a need to consider how (micro)organisms interact with this long used protective system. Fouling in submerged structures pose complex problems across many maritime industries that requires multidisciplinary cooperation to address, and an approach that reconciles genetic analysis and physical/chemical testing may provide the insights needed to produce a solution to this pervasive issue.

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AUTHOR CONTRIBUTIONS

P.K. and P.V. conceptualized the review. P.V. wrote the manuscript with contributions from P.K. and A.M. All authors read the manuscript and approved the content.

COMPETING INTERESTS

The authors declare no competing interests.

ADDITIONAL INFORMATION

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