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Review Article

Exploring seaweed-associated microbiota as emerging probiotic candidates for aquaculture

Joshua C. Montefrio[1], Christopher Marlowe A. Caipang[*1,2]

[1]Graduate School, University of the Philippines Visayas, Iloilo City, Philippines.
[2]Division of Biological Sciences, College of Arts and Sciences, University of the Philippines Visayas, Miagao, Iloilo 5023, Philippines.

Abstract: The rapid expansion of aquaculture has intensified the need for sustainable strategies to improve productivity and disease control, particularly amid growing concerns about antibiotic use. Probiotics have emerged as a promising alternative; however, conventional sources, primarily derived from aquatic animal guts, often exhibit inconsistent performance under field conditions. In this context, seaweed-associated microbiota represents a relatively underexplored but potentially valuable source of probiotic candidates. This review synthesizes current knowledge on the diversity and functional traits of seaweed-associated bacteria and evaluates their relevance to probiotic application in aquaculture. Key traits discussed include stress tolerance, antimicrobial activity, competitive exclusion and colonization ability, enzymatic capabilities, and the production of bioactive compounds linked to growth promotion and immunomodulation. Evidence indicates that these bacteria possess adaptive features suited to dynamic marine environments and exhibit multiple functions consistent with established probiotic mechanisms. However, most studies remain trait-specific, with limited *in vivo* validation and insufficient integration of functional assessments. Consequently, there is a need for more comprehensive and systematic evaluation of these microorganisms. Overall, seaweed-associated bacteria present a promising yet underutilized resource, and further research is essential to fully establish their role as next-generation probiotics in sustainable aquaculture systems.

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Introduction

The aquaculture industry has undergone a rapid and significant growth over the past few decades. In the 2024 State of World Fisheries and Aquaculture (SOFIA) report, global aquaculture production increased significantly by 204%, rising from 43 million tons in 2000 to 87.9 million tons in 2022 (FAO, 2024). This marked increase in production has been largely driven by the rapidly growing global population, resulting in a surge in demand for seafood as a sustainable and high-quality source of protein and nutrients (Thilsted et al., 2016; Ahmad et al., 2021; Bjørndal et al., 2023). Combined with the continuing stagnation of the global capture fisheries production and the increasing annual growth rate of the global aquatic animal food consumption, aquaculture production must increasingly rely on the expansion and intensification of its operational systems in order to ensure long-term food security and meet rising economic demands (Béné et al., 2015; Costello et al., 2020; Ahmad et al., 2021).

The adoption of intensified production systems, however, usually necessitates increased stocking densities in farming systems, promoting the emergence of disease outbreaks and spread of infectious pathogens (Aly and Fathi, 2024; Lambert et al., 2024). To remediate this problem, many farming operations resort to chemical inputs, such as antibiotics. While this practice has been adopted for several decades and proven effective in managing bacterial infections and mitigating disease outbreaks, its excessive use and unregulated disposal have raised significant biosecurity and public health concerns (Defoirdt et al., 2011; Lulijwa et al., 2020). Not only

*Correspondence: Christopher Marlowe A. Caipang
E-mail: cacaipang@up.edu.ph
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do antibiotics have bio-accumulative effects in the environment and can disrupt microbial community dynamics, but they can also promote the emergence and spread of antibiotic-resistant bacteria and antibiotic resistance genes (ARGs) (Cabello et al., 2013; Lulijwa et al., 2020). As a result, there has been growing interest in adopting more sustainable management strategies that reduce reliance on antibiotics while maintaining effective disease control in aquaculture systems (Defoirdt et al., 2011; Hoseinifar et al., 2018). Among these approaches, probiotics have emerged as one of the most widely studied and promising alternatives to antibiotics in aquaculture research (Defoirdt et al., 2011; Hoseinifar et al., 2018; Hai, 2015; Mohammed, 2025).

Probiotics are generally defined as beneficial microorganisms that, when administered in adequate amounts, confer health benefits to the host. Traditionally, probiotics have been widely used in humans and terrestrial animals to improve gut health and enhance disease resistance (Markowiak and Śliżewska, 2017; Hoseinifar et al., 2018). More recently, probiotics have been shown to provide multiple benefits in aquaculture systems. Some of the most commonly reported effects are: improvement of growth performance and feed utilization (Hai, 2015; Mugwanya et al., 2022); enhancement of immune responses by stimulating innate defenses, leading to increased resistance against bacterial pathogens (Defoirdt et al., 2011; Hoseinifar et al., 2018); and disease control through competitive exclusion and the production of antimicrobial compounds (Balcázar et al., 2006; Hai, 2015).

Probiotics in aquaculture are mostly isolated from the guts of healthy aquatic animals- such as fish, shrimp, and mollusks as they are already adapted to the host's internal environment and are therefore more likely to survive, colonize, and exert beneficial effects when reintroduced (Hoseinifar et al., 2018). However, several limitations continue to affect their effectiveness, reliability, and long-term viability under field conditions. Several key requirements must be satisfied to be considered effective and sustainable probiotic candidates, which includes: (1) being non-pathogenic; (2) tolerate environmental and physiological stressors such as temperature, salinity, pH, and digestive conditions commonly encountered in aquaculture systems; (3) presence of clear functional properties, such as antagonistic activity against pathogens, competition for nutrients or adhesion sites, production of antimicrobial compounds; and, the capacity to colonize or persist in the host gastrointestinal tract or culture environment (Zorriehzahra et al., 2016; Rahayu et al., 2024; Elsegeny et al., 2025).

In recent years, aquaculture microbiology research has expanded the search for probiotic candidates. Many studies now explore diverse sources in marine environments, including the internal structures of marine animals other than fish and shrimp, surrounding water, sediments, biofilms, and the surfaces of marine organisms. This shift is driven by the need to identify strains naturally adapted to aquatic conditions, thereby increasing their likelihood of survival, colonization, and effective functioning in aquaculture systems (Kesarcodi-Watson et al., 2007; Hai, 2015).

One of the relatively unexplored areas of unconventional potential probiotic candidates in aquaculture is macroalgae or seaweeds. Seaweeds harbor complex communities of epiphytic and endophytic microorganisms, including bacteria, fungi, and microalgae, which play critical roles in seaweeds' overall health, growth, and defense (Egan et al., 2008; Singh and Reddy, 2014). These microbes are known to provide essential functions, including nutrient cycling, morphogenesis, and protection against biofouling and pathogens (Hollants et al., 2013). Many seaweed-associated bacteria produce a wide range of bioactive compounds with proven antibacterial, antioxidant, and antifouling activities, as well as antagonistic effects against pathogens such as *Vibrio* spp., which are among the most common threats in aquaculture (Goecke et al., 2010). The complex association between seaweeds and their associated microbiota, together with the unique physicochemical conditions of the marine environment, suggests that these microorganisms may

possess specialized adaptive traits advantageous for probiotic applications. Despite this, only a limited number of studies have explored the potential of seaweed-associated microorganisms as probiotics in aquaculture. Most studies have instead focused on the use of seaweeds as prebiotic supplements or as fermentation substrates for the production of lactic acid bacteria (LAB)-based probiotics. Thus, this review seeks to synthesize current knowledge on seaweed-associated microbiota and assess their potential as emerging probiotic candidates for aquaculture applications.

Limitations and selection challenges of probiotics in aquaculture

Although gut-derived probiotics from marine animals have gained increasing attention in aquaculture, their performance under field conditions remains inconsistent, with several factors limiting their effectiveness, stability, and long-term applicability. Many bacterial strains show promising probiotic-related traits *in vitro* or in short-term laboratory trials; however, only a limited number consistently meet the stringent requirements needed to function effectively in complex, dynamic aquaculture environments. These limitations have highlighted the need for rigorous selection criteria and have driven interest toward alternative microbial sources that may be better adapted to aquaculture conditions. Below are some of the major limitations that affect the consistent performance and long-term viability of gut-derived probiotics under aquaculture conditions.

***Safety and absence of pathogenicity*:** A fundamental requirement for probiotic application is that candidate microorganisms must be non-pathogenic to humans and other hosts and should not carry virulence factors or transferable antibiotic resistance genes. However, screening studies consistently demonstrate that a substantial proportion of gut-derived isolates fail to meet these safety criteria. Kesarcodi-Watson et al. (2007) reported that bacterial isolates initially identified as potential probiotics exhibited resistance to clinically relevant antibiotics, resulting in their exclusion from further evaluation. Similarly, Kuebutornye et al. (2019) observed that while several *Bacillus* isolates exhibited strong antagonistic activity against *Vibrio* spp., many were resistant to tetracycline or erythromycin, with minimum inhibitory concentrations exceeding established safety thresholds. These findings indicate that antimicrobial activity alone is insufficient for probiotic selection and that biosafety screening remains a major bottleneck in the development of reliable probiotic strains.

***Tolerance to environmental and gastrointestinal stressors*:** Probiotic candidates must withstand physicochemical stresses associated with processing, storage, and application, as well as environmental fluctuations in aquaculture systems, including changes in temperature, salinity, pH, and dissolved oxygen. In addition, feed-administered probiotics must survive gastrointestinal conditions such as low gastric pH and bile exposure. Quantitative assessments have shown that many gut-derived isolates experience substantial losses in viability under these conditions. Studies have reported that exposure to simulated gastric and intestinal environments can significantly reduce the viability of probiotic candidates, thereby limiting their capacity to colonize the host intestine (Hoseinifar et al., 2018; El-Saadony et al., 2021). Furthermore, variability in tolerance to bile salts and other stressors among probiotic strains contributes to inconsistent performance in terms of growth promotion and immune modulation under farming conditions (Balcázar et al., 2006; Golder et al., 2022). Such variability contributes to the inconsistent efficacy of probiotics when applied beyond controlled experimental settings.

***Functional effectiveness and strain-specific performance*:** Functional effectiveness is a central criterion in probiotic selection because probiotics are expected to exert direct or indirect biological effects that suppress pathogens, stabilize microbial communities, and enhance host health in aquaculture systems (Hai, 2015). Core mechanisms underlying these effects include antagonism against pathogens, competition for nutrients or adhesion sites, production of antimicrobial compounds, and modulation of host immune responses. While these mechanisms provide a strong theoretical foundation for probiotic use, their

effectiveness under practical farming conditions is often constrained by ecological, environmental, and host-related factors, leading to highly strain-specific and context-dependent outcomes (Hoseinifar et al., 2018).

Antagonism against pathogens is particularly important because bacterial diseases caused by *Vibrio*, *Aeromonas*, and related genera remain among the primary causes of mortality in fish and shrimp aquaculture (Defoirdt et al., 2011; Austin and Austin, 2016). Probiotic-mediated antagonism can reduce pathogen abundance through inhibitory metabolites or direct microbial competition, and several *in vivo* studies have demonstrated reductions in microbial loads, including *Vibrio* spp., in the gut or rearing water of probiotic-treated shrimp and fish (Ramirez et al., 2021; Gustilatov et al., 2023; Hu et al., 2023). However, this mechanism becomes limiting because antagonistic effects are strongly dependent on probiotic cell density and sustained spatial proximity between probiotics and pathogens. In open or semi-open aquaculture systems, water exchange, dilution, and complex microbial interactions often reduce probiotic-pathogen contact, thereby diminishing antagonistic efficacy under field conditions (Defoirdt et al., 2011).

Competition for nutrients or adhesion sites is another key probiotic mechanism because successful colonization of the gastrointestinal tract can prevent pathogen attachment and proliferation through competitive exclusion (Kesarcodi-Watson et al., 2008; Hoseinifar., 2018). Adhesion to intestinal mucus or epithelial surfaces is therefore commonly used as an indicator of probiotic persistence. This mechanism, however, becomes limiting under aquaculture conditions because poorly or moderately adherent strains are rapidly displaced by resident microbiota once supplementation ceases, particularly in systems characterized by high microbial turnover and continuous environmental exposure (Defoirdt et al., 2011; Hai, 2015; Balcázar et al., 2006). As a result, competitive exclusion is often transient and difficult to maintain without continuous probiotic input.

The production of antimicrobial compounds, including organic acids, bacteriocins, and lipopeptides, is also considered an important probiotic trait because these compounds can directly inhibit pathogen growth (Balcázar et al., 2006; Hai, 2015). However, this mechanism poses limitations in practical aquaculture systems because antimicrobial production is concentration-dependent and sensitive to environmental conditions. Dilution effects, sedimentation, and nutrient limitation frequently prevent probiotics from maintaining the cell densities required to sustain antimicrobial activity, while stressful conditions may downregulate metabolite production (Hai, 2015; Hoseinifar et al., 2018). These constraints reduce the consistency of antimicrobial-mediated pathogen control in field applications.

Modulation of host immune responses is an indirect but important probiotic mechanism, as enhanced innate immunity can increase resistance to infection even in the absence of direct pathogen suppression (Hoseinifar et al., 2018). Probiotic supplementation has been associated with increases in immune parameters, including lysozyme activity, phenoloxidase activity, phagocytic capacity, and immune-related gene expression (El-Saadony et al., 2021; Golder et al., 2022). Nevertheless, immune modulation becomes a limitation because responses are highly strain-, dose-, and host-dependent. Weak or transient immune stimulation may provide little protection, whereas excessive or prolonged activation can impose energetic costs on the host, potentially affecting growth and stress tolerance (Hoseinifar et al., 2018; El-Saadony et al., 2021). These factors limit the predictability and transferability of immune-based probiotic effects across species and production systems.

***Colonization, persistence, and ecological compatibility*:** An additional challenge in probiotic application is the ability of introduced microorganisms to colonize or persist in the host gastrointestinal tract or culture environment long enough to exert sustained benefits. Successful colonization is important because many probiotic mechanisms—such as competitive exclusion, antimicrobial production, and immune modulation—

Table 1. Common bacterial genera isolated from seaweeds.

Bacterial Genus	Seaweed Source(s)	References
Pseudoalteromonas spp.	*Ulva lactuca*, *Ulva australis, Ulva* spp. *Saccharina japonica, Padina pavonica*	Egan et al. (2008); Bernborn et al. (2011); Ling et al. (2022); Kumar et al. (2022); Ismail et al. (2016); Imai et al. (2006)
Vibrio spp.	*Padina pavonica, Mastophora rosea, Gracilaria corticata, Ulva* spp., *Fucus* sp., *Laminaria* sp. *Porphyra* sp., *Undaria* sp., *Saccharina japonica*	Ismail et al. (2016); Karthick et al. (2018); Lu et al. (2023); Kumar et al. (2022); Mahmud et al. (2007); Ma et al. (2023); Imai et al. (2006)
Bacillus spp.	*Padina pavonica, Gracilaria corticata, Ulva lactuca , Ulva* sp., *Sargassum* sp., *Hypnea valentiae, Sargassum wightii, Sargassum myriocystum; Laurenciae papillosa, Gracilaria edulis. Eucheuma cottonii*	Ismail et al. (2016); Karthick et al. (2018); Kumar et al. (2022); Naufal et al. (2025); Vairagkar and Mirza (2021); Chakraborty et al. (2021, 2016); Suji et al. (2024); Trivedi et al. (2010); Suvega and Arunkumar (2019); Indraningrat et al. (2023)
Alteromonas	*Padina pavonica , Ulva* sp., *Ulva prolifera, Sargassum* spp., *Delisea pulchra*, *Gracilaria corticate, Gelidium* sp.	Ismail et al. (2016); Karthick et al. (2018); Kumar et al. (2022); Lv et al. (2025); Imai et al. (2006)
Roseobacter clade	*Grateloupia sp*., *Ulva* spp., *Ulva australis Saccharina* sp., *Cystoseira compressa, Fucus spiralis, Eucheuma okamurai*	Lu et al. (2023); Mancuso et al. (2016); Hahnke et al. (2024); Yin et al. (2022); Breider et al. (2019); Deutsch et al. (2023)
Flavobacterium	*Ulva prolifera*, *Ulva rigida,* red alga, marine algae, *Porphyra*	Supty et al. (2024); Bolinches et al. (1988); Muhammad et al. (2022); Khan et al. (2020); Lavín et al. (2016); Miyashita et al. (2009)

require prolonged presence at sufficient cell densities. However, numerous studies have demonstrated that many probiotics fail to establish stable populations under aquaculture conditions and are rapidly outcompeted by resident microbiota or diluted in open or semi-open systems (Balcázar et al., 2006; Kesarcodi-Watson et al., 2008; Hai, 2015). Han et al. (2021) reported that probiotics generally exhibit transient colonization in the gastrointestinal tract, with their effects on gut microbiota diminishing after supplementation ceases, often returning toward baseline composition. Moreover, Hu et al. (2023) reported that probiotic bacterial counts in rearing water declined to near-background levels within a few days following application, necessitating repeated dosing to maintain measurable effects. Together, these findings indicate that ecological compatibility with both the host and the surrounding culture environment is a critical determinant of probiotic success.

The seaweed microbiome

The composition of bacterial communities associated with seaweeds is enumerated in Table 1. This reveals a consistent dominance of several genera, particularly *Pseudoalteromonas*, *Vibrio*, *Bacillus, Alteromonas*, members of the *Roseobacter* clade, and *Flavobacterium*. Among these, *Pseudoalteromonas* and *Vibrio* appear to be the most frequently reported across multiple studies, reflecting their strong ecological association with macroalgal surfaces (Egan et al., 2008; Ismail et al., 2016; Lu et al., 2023). *Bacillus* spp. are also widely documented, particularly in studies focusing on bioactive compound production and antimicrobial activity (Karthick et al., 2018; Chakraborty et al., 2021).

In terms of host distribution, *Ulva* spp. (green algae) and *Sargassum* spp. (brown algae) are among the most frequently studied and reported sources of bacterial isolates, followed by red algae such as *Gracilaria, Gelidium,* and *Porphyra* (Karthick et al., 2018; Kumar et al., 2022; Lu et al., 2023). Brown algae, particularly *Saccharina japonica* and *Padina pavonica*, also host a diverse range of bacterial taxa, including *Pseudoalteromonas, Vibrio,* and *Alteromonas* (Ismail et al., 2016; Ling et al., 2022). Notably, these bacterial genera are not restricted to a single algal group but are distributed across green, brown, and red seaweeds, indicating a broad ecological adaptability and potential functional importance within the seaweed holobiont.

Functionally, as presented in Table 2, many of these seaweed-associated bacterial genera exhibit traits consistent with established probiotic mechanisms in aquaculture systems. Among these, *Bacillus* spp. remain the most extensively validated. For example, supplementation of *Bacillus subtilis* has been shown to significantly improve growth performance, survival, and stress tolerance in fish, with Neissi et al. (2024) reporting enhanced resistance of *Oncorhynchus mykiss* under hypoxic conditions. Similarly, Hu et al. (2023) demonstrated that *Bacillus*-based probiotic formulations improved survival and water quality parameters in *Penaeus vannamei* culture

Table 2. Probiotic functions of seaweed-associated genera.

Bacterial Genus	Documented Probiotic Functions	Supporting Studies
Bacillus spp.	Enhances growth performance, immune response, and survival; improves water quality and modulates microbial communities	Neissi et al. (2024); Hu et al. (2023); Kuebutornye et al. (2019); El-Saadony et al. (2021)
Pseudoalteromonas spp.	Produces antimicrobial compounds; inhibits *Vibrio* spp.; improves host survival and disease resistance; exhibits antibiofilm activity	Gustilatov et al. (2023); Wu et al. (2024); Handayani et al. (2021)
Roseobacter clade (*Phaeobacter*)	Produces antibacterial metabolites (e.g., tropodithietic acid); suppresses *Vibrio* infections; improves larval survival	Sonnenschein et al. (2020); Gram et al. (2015); Grotkjær (2015)
Vibrio spp. (non-pathogenic strains)	Competitive exclusion of pathogens; colonization of host surfaces; improved survival under pathogen challenge	Kesarcodi-Watson et al. (2007); Hossain et al. (2024); Ramirez et al. (2021); Hai (2015)
Alteromonas spp.	Improves larval survival under pathogen challenge; reduces virulence of pathogens through quorum-quenching and microbial interactions	Kesarcodi-Watson et al. (2010); Torres et al. (2019)

systems, alongside shifts in microbial community structure. These consistent findings across studies support the robustness of *Bacillus* as a probiotic candidate in intensive aquaculture environments.

Marine-derived genera such as *Pseudoalteromonas* spp. and members of the *Roseobacter* clade, on the other hand, are more frequently associated with antimicrobial activity against key pathogens. In a biofloc-based shrimp system, *Pseudoalteromonas piscicida* significantly increased the survival of *P. vannamei* following *Vibrio parahaemolyticus* challenge (Gustilatov et al., 2023). Likewise, Wu et al. (2024) reported that *Pseudoalteromonas flavipulchra* not only inhibited multiple *Vibrio* strains but also enhanced microalgal growth, suggesting dual functional roles in aquaculture systems. For *Roseobacter* clade bacteria, particularly *Phaeobacter inhibens*, the production of tropodithietic acid (TDA) has been shown to effectively suppress *Vibrio* pathogens and improve survival rates in marine larvae (Sonnenschein et al., 2020).

Interestingly, even genera that include well-known pathogens, such as *Vibrio*, may harbor strains with beneficial effects. Ramirez et al. (2021) demonstrated that non-pathogenic strains, including *V. diabolicus*, were able to colonize both internal and external surfaces of shrimp larvae and significantly improve survival under *V. parahaemolyticus* challenge. Similarly, Hossain et al. (2024) reported that selected non-pathogenic *Vibrio* strains contributed to disease control in shrimp aquaculture systems, likely through competitive exclusion mechanisms. However, the dual nature of this genus necessitates careful strain-level selection and validation prior to application.

Meanwhile, *Alteromonas* spp. represent a distinct functional strategy. Kesarcodi-Watson et al. (2010) demonstrated that *A. macleodii* improved the survival of hatchery-reared mussel larvae (*Perna canaliculus*) under pathogen pressure. In addition, genomic analyses of *A. stellipolaris* revealed quorum-quenching-related traits that can interfere with pathogen communication systems, potentially reducing virulence expression (Torres et al., 2019). These findings suggest that, rather than directly inhibiting pathogens, some *Alteromonas* strains may act by disrupting pathogenic signaling pathways.

Functional traits of seaweed-associated bacteria and their probiotic potential

***Stress tolerance and environmental adaptation*:** Seaweed-associated bacteria are shaped by some of the most dynamic and stressful marine environments. They are exposed to drastic fluctuations in temperature, salinity, light, and nutrient availability, especially in shallow coastal and intertidal zones. As a result, these microbes tend to develop traits that increase tolerance to a wide range of environmental stressors. These traits are exactly what's needed for probiotics to survive and function in aquaculture systems, making these microbes potential candidates. A summary of the environmental stress adaptation of seaweed-associated bacteria is seen in Table 3.

Several studies have demonstrated tolerance of epiphytic microbes on macroalgae to environmental stressors. For instance, environmental studies show that bacterial communities associated with seaweeds remain stable under pronounced environmental fluctuations, such as shifts in temperature and salinity across intertidal zones and salinity gradients from

marine to brackish waters (Van Der Loos et al., 2022; Nahor et al., 2024). More direct experimental evidence further supports their tolerance, with several isolates, particularly from genera such as *Bacillus*, *Pseudomonas*, and *Vibrio*, demonstrating the ability to grow across a wide temperature range (approximately 0-45°C) while maintaining viability under saline conditions (Saha et al., 2024). Likewise, seaweed-associated lactic acid bacteria have been shown to tolerate elevated salinity levels up to ~7.1% NaCl, with evidence of adaptive improvement under prolonged exposure (Papadopoulou et al., 2023). In terms of pH tolerance, isolates from seaweeds have been reported to grow across broad pH ranges (approximately pH 4–10), demonstrating strong acid–alkaline adaptability (Ibrahim et al., 2015). For example, specific seaweed-derived bacteria, such as *Phycicoccus jejuensis*, exhibit growth across pH 5.1-10.1, further supporting their physiological flexibility (Lee, 2006).

Despite this strong body of evidence on general environmental tolerance, a notable gap remains in the literature. Specifically, very few studies have directly evaluated the tolerance of seaweed-associated bacteria to digestive enzymes, such as pepsin, trypsin, or pancreatin. While traits such as pH and salinity tolerance are often used as indirect indicators of probiotic potential, they do not fully confirm these bacteria's ability to survive and function in the gastrointestinal tract of aquatic animals. This highlights an important limitation in current research and underscores the need for more targeted studies.

***Antimicrobial and antagonistic activity*:** Seaweed-associated bacteria also play an important role in surface defense. Seaweed thalli are constantly exposed to fouling organisms and opportunistic microbes, and many associated bacteria produce antimicrobial compounds that inhibit the settlement and growth of competitors and pathogens (Goecke et al., 2010). These defensive functions are directly relevant to probiotic use, as they are particularly important in mitigating disease outbreaks and controlling pathogen spread in aquaculture.

Among these, *Bacillus velezensis* isolated from marine macroalgae has been shown to inhibit multidrug-resistant pathogens such as *Staphylococcus aureus* and *Pseudomonas aeruginosa*, with relatively large inhibition zones and low minimum inhibitory concentrations (Chakraborty et al., 2021). The same strain also produces siderophores and bioactive compounds with higher antibacterial activity than some conventional antibiotics, indicating its strong antagonistic capacity. Similar observations have been reported for other seaweed-associated bacteria, in which members of Firmicutes and Gammaproteobacteria, including *Bacillus* and *Pseudoalteromonas*, exhibit measurable inhibitory activity against drug-resistant strains (Kizhakkekalam and Chakraborty, 2020). In addition, several studies have identified specific compounds responsible for these antagonistic effects. For example, seaweed-derived *Bacillus* spp. have been found to produce lichenicidin, a two-peptide bacteriocin with strong activity against Gram-positive bacteria (Prieto et al., 2012). Likewise, *B. subtilis* associated with *Sargassum myriocystum* produces O-heterocyclic compounds that show antibacterial activity against human pathogens (Chakraborty et al., 2017). Antagonistic activity is not limited to laboratory assays but is also evident in natural host systems. In seaweeds affected by bleaching disease, *Vibrio alginolyticus* X-2 has been shown to reduce disease progression by suppressing pathogenic microorganisms, thereby improving host conditions (Ma et al., 2023). These findings show that seaweed-associated bacteria inhibit competing microorganisms through diverse mechanistic pathways, supporting their role in host defense and potential probiotic applications (Egan et al., 2013; Hollants et al., 2013). Table 4 presents the summary of the antimicrobial and antagonistic activity of seaweed-associated bacteria.

***Competitive exclusion and colonization ability*:** Competitive exclusion and colonization ability are fundamental ecological traits that enable seaweed-associated bacteria to establish, persist, and regulate microbial communities on algal surfaces. Seaweeds provide a nutrient-rich yet competitive habitat in which microbial colonizers must rapidly attach, form

Table 3. Environmental stress adaptation of seaweed-associated bacteria.

Seaweed Host	Bacterial Isolate	Stressor	Key Evidence	Reference
Mixed intertidal seaweeds	Epiphytic bacterial communities	Salt + Temperature (indirect)	Persistence in intertidal environments with fluctuating temperature and salinity indicates environmental tolerance	Nahor et al. (2024)
Ulva spp.	Seaweed-associated bacterial communities	Salt (indirect)	Communities maintained across marine to brackish salinity gradient, indicating halotolerance	Van Der Loos et al. (2022)
Fucus serratus, *Palmaria palmata*, *Ulva* spp.	*Vibrio parahaemolyticus*, *V. alginolyticus*, *V. vulnificus*	Temperature (direct)	Increased abundance at 20 °C vs 16 °C, demonstrating thermotolerance	Wilson and Saha (2025)
Ulva, *Sargassum*, *Padina*	*Bacillus*, *Pseudomonas*, *Vibrio* spp.	Salt + Temperature (direct)	Isolates grew across wide temperature range (~0–45 °C) and tolerated saline conditions	Saha et al. (2024)
Alaria esculenta substrate	*Lactobacillus plantarum*, *Enterococcus faecium*, *Pediococcus pentosaceus*	Salt (direct)	Growth up to ~7.1% NaCl, with increased tolerance after adaptive evolution	Papadopoulou et al. (2023)
Mixed seaweeds (Alexandria coastline)	*Pseudomonas*, *Vibrio*, *Flavobacterium* spp.	pH (direct)	Isolates showed growth across broad pH range (~4–10), indicating strong acid–alkaline tolerance	Ibrahim et al. (2015)
Unspecified seaweed species	*Phycicoccus jejuensis*	pH (direct)	Growth range reported at pH 5.1–10.1, indicating wide tolerance	Lee (2006)

Table 4. Antimicrobial and antagonistic activity of seaweed-associated bacteria.

Seaweed Host	Bacterial Isolate	Bioactive Compounds / Mechanism	Target Pathogen(s)	Key Findings	Reference
Marine macroalgae (unspecified)	*Bacillus velezensis*	Siderophores (iron-chelating compounds)	MDR pathogens (*Staphylococcus aureus*, *Pseudomonas aeruginosa*)	Strong antimicrobial activity via siderophore-mediated iron deprivation, inhibiting drug-resistant pathogens	Chakraborty et al. (2021)
Marine macroalgae (various spp.)	Firmicutes & Gammaproteobacteria	Secondary metabolites (not fully characterized)	Multidrug-resistant bacteria	Exhibited broad-spectrum antibacterial activity against MDR pathogens	Kizhakkekalam and Chakraborty (2020)
Saccharina japonica (bleaching disease host)	*Vibrio alginolyticus* X-2	Antagonistic metabolites; probiotic interaction	Seaweed bleaching pathogens	Reduced disease and improved host health via protective antagonism	Ma et al. (2023b)
Marine macroalgae (various spp.)	*Bacillus* spp.	Bacteriocin (lichenicidin)	Gram-positive bacteria	Identified lichenicidin production, a potent antimicrobial peptide	Prieto et al. (2012)
Sargassum myriocystum	*Bacillus subtilis*	O-heterocyclic compounds	Human pathogenic bacteria	Discovered novel antibacterial compounds with strong inhibitory effects	Chakraborty et al. (2017)
Gracilaria edulis	Mixed probiotic bacteria	Antibacterial proteins	Marine pathogens	Promoted host growth and produced antibacterial proteins (dual probiotic-antagonistic role)	Suvega and Arunkumar (2019)
Microalgal-associated system	*Pseudoalteromonas flavipulchra*	Antimicrobial metabolites	*Vibrio* spp.	Demonstrated strong antagonism against Vibrio pathogens and probiotic potential	Wu et al. (2024)
Eucheuma cottonii	*Bacillus cereus* SMPRL-2	Secondary metabolites (antibacterial, antifungal)	Bacteria and fungi	Exhibited broad-spectrum antibacterial and antifungal activity	Indraningrat et al. (2023)

stable associations, and effectively exclude competing or potentially harmful microorganisms. In this context, colonization is not merely a passive process but involves active mechanisms such as adhesion, biofilm formation, and chemical interference, which collectively contribute to persistence and community structuring (Saha and Weinberger, 2019). Table 5 summarizes the functional traits of seaweed-associated bacteria involved in surface colonization, biofilm formation, and competitive exclusion.

Experimental evidence from seaweed-associated systems demonstrates that early colonization and biofilm formation play a central role in establishing dominance on host surfaces. For instance, epiphytic bacteria associated with *Ulva australis* rapidly attach to algal surfaces and form structured biofilms, leading to the dominance of specific strains that outcompete less-adapted colonizers (Rao et al., 2006). This rapid surface colonization limits available space and resources, thereby restricting the establishment of subsequent microorganisms and promoting the formation of stable microbial communities. In addition to physical occupation, chemical-mediated interactions further reinforce competitive exclusion among seaweed-associated bacteria. Yasim et al. (2022) demonstrated that isolates exhibited both antibacterial activity and inhibition of quorum sensing (QS), as evidenced by suppression of violacein production in *Chromobacterium violaceum* without affecting bacterial growth. Similarly, Muthukrishnan et al. (2023) reported that bacteria associated with *Gracilaria changii* significantly reduced biofilm biomass and disrupted QS-regulated behaviors in *Pseudomonas aeruginosa*, highlighting the role of chemical interference in preventing the establishment of competing microbes. Beyond direct antagonism, colonization by resident microbiota can confer resistance against secondary settlement. Surfaces of *Ulva reticulata* with established bacterial communities showed significantly reduced settlement of fouling organisms compared to sterile controls, indicating effective colonization resistance through space occupation and surface-mediated exclusion (Dobretsov and Qian, 2002). Collectively, these findings demonstrate that competitive exclusion in seaweed-associated bacteria is a multifactorial process involving rapid colonization, biofilm-mediated persistence, and both physical and chemical interference mechanisms (Saha and Weinberger, 2019).

Enzymatic activity: It is a key functional trait enabling seaweed-associated bacteria to utilize complex algal substrates and maintain stable associations on host surfaces. Marine macroalgae contain structurally diverse polysaccharides, including alginate, agar, carrageenan, and cellulose, that require specialized hydrolytic enzymes for degradation. Consequently, epiphytic bacteria typically possess a wide range of extracellular enzymes that support nutrient acquisition and ecological fitness within the seaweed holobiont (Saha and Weinberger, 2019). Table 6 summarizes the enzymatic activities of seaweed-associated bacteria and their functional roles in substrate degradation.

Experimental studies consistently show that these bacteria are not limited to a single enzymatic function but instead exhibit a broad, integrated capacity to degrade multiple substrates. For example, isolates reported by Kumar et al. (2022) produced agarase, alginate lyase, cellulase, and protease within the same system, allowing simultaneous breakdown of major seaweed polymers. This multifunctionality is further reflected in the work of Gu et al. (2021), where a single enzyme exhibited activity on agar, carrageenan, cellulose, and alginate, while Sun et al. (2020) demonstrated that combining alginate lyase and cellulase enhanced hydrolysis of *Laminaria japonica*, thereby emphasizing cooperative degradation. Alongside these broad-spectrum activities, more specialized enzymes such as carrageenase (Li et al., 2022) and dual agarase–alginate lyase systems (Lavin et al., 2016) highlight adaptation to specific substrates, whereas the presence of proteases and lipases (González et al., 2021; Saravanan et al., 2024) extends this capacity to non-polysaccharide components associated with algal surfaces.

This level of enzymatic versatility has clear implications for probiotic potential. Bacteria capable of breaking down complex polysaccharides, proteins,

Table 5. Functional traits of seaweed-associated bacteria involved in surface colonization, biofilm formation, and competitive exclusion.

Seaweed host	Bacterial isolate	Competitive mechanism	Targeted pathogen / Epibiont	Key findings	Reference
Various seaweeds (Pulau Bidong)	*Bacillus*, *Kocuria*, *Exiguobacterium*, *Vibrio* spp.	Antibacterial activity; QS inhibition (AHL interference)	*Chromobacterium violaceum* CV026; marine bacteria	Violacein assay showed QS inhibition without affecting bacterial growth, while agar diffusion assays confirmed antagonistic activity against marine isolates	Yasim et al. (2022)
Ulva spp.	*Epibacterium ulvae* DSM 24752T	Secondary metabolite-mediated competition; colonization potential	Not tested	Genome analysis revealed biosynthetic clusters for indigoidine and genes linked to surface attachment, indicating potential for antimicrobial competition and persistent colonization	Breider et al. (2019)
Gracilaria changii	Mixed associated bacterial isolates	Anti-biofilm activity; QS inhibition	*Pseudomonas aeruginosa*, *Chromobacterium violaceum*	Crystal violet assays showed reduced biofilm biomass, while violacein inhibition assays confirmed disruption of QS-regulated behaviors	Muthukrishnan et al. (2023)
Ulva australis	*Pseudoalteromonas*, *Roseobacter* spp.	Surface colonization; biofilm formation; competition	Surface-associated bacteria	Rapid attachment to algal surfaces followed by biofilm formation led to dominance of specific strains and exclusion of less competitive colonizers	Rao et al. (2006)
Ulva reticulata	Natural epiphytic bacterial community	Anti-settlement activity; colonization resistance	Marine foulers (bacteria, larvae)	Bacteria-associated surfaces significantly reduced settlement of fouling organisms compared to sterile controls, indicating inhibition of secondary colonization	Dobretsov and Qian (2002)

Table 6. Enzymatic activity of seaweed-associated bacteria and their functional roles in substrate degradation.

Seaweed host	Bacterial isolate	Enzyme(s) produced	Substrate / Target compound	Key findings	Reference
Marine macroalgae (various)	Mixed epiphytic bacteria	Agarase, alginate lyase, cellulase, protease	Agar, alginate, cellulose, proteins	Multiple isolates exhibited polymer-degrading activity across agar, alginate, cellulose, and protein substrates	Kumar et al. (2022)
Porphyra decomposing fronds	*Flavobacterium* sp.	Agarase, alginate lyase	Agar, alginate	Isolate demonstrated dual enzymatic activity capable of degrading both agar and alginate	Lavin et al. (2016)
Laminaria japonica	*Pseudoalteromonas* sp. (enzyme source)	Alginate lyase, cellulase	Alginate, cellulose	Combined enzymes achieved a high hydrolysis efficiency of seaweed biomass through synergistic degradation of alginate and cellulose	Sun et al. (2020)
Marine macroalgae (various bacteria)	Alkalophilic bacterial isolate	α-amylase with agarase, carrageenase, cellulase, alginate lyase activities	Starch, agar, carrageenan, cellulose, alginate	Multifunctional enzyme showed activity across multiple seaweed polysaccharides under alkaline conditions	Gu et al. (2021)
Marine macroalgae (various)	Mixed associated bacteria	Cellulase, agarase, protease, lipase	Cellulose, agar, proteins, lipids	Isolates displayed diverse enzymatic profiles targeting both polysaccharide and non-polysaccharide substrates	Saravanan et al. (2024)
Antarctic macroalgae	Associated bacterial isolate (Car1383)	Carrageenase	κ-carrageenan	Enzyme exhibited high activity and specificity toward κ-carrageenan	Li et al. (2022
Ulva lactuca	*Bacillus altitudinis* strain 19_A	Protease, lipase, esterase, carbohydrate-degrading enzymes	Proteins, lipids, polysaccharides	Genome analysis identified multiple enzyme systems involved in degradation of proteins, lipids, and polysaccharides	González et al. (2021)

and lipids can enhance nutrient availability within host-associated environments, particularly in aquaculture systems where feed efficiency is critical (Ringø et al., 2010). By facilitating the degradation of otherwise indigestible compounds, these microbes can complement host digestion and improve nutrient utilization (Balcázar et al., 2006). At the same time, the ability to metabolize a wide range of substrates supports their persistence and activity within dynamic microbial communities, allowing them to remain functionally relevant over time (Saha and Weinberger, 2019).

Growth promotion and immunomodulatory effects: Growth promotion and immunomodulatory effects are key traits expected of probiotic bacteria, yet direct evidence for these functions in seaweed-associated bacteria remains limited. Only a few studies have explicitly demonstrated such effects. For example, Sathishkumar et al. (2024) showed that exopolysaccharides from a seaweed-associated *Bacillus megaterium* stimulated immune responses, including macrophage activation and cytokine production. In a similar context, Hu et al. (2023) reported improved survival and overall condition in *Penaeus vannamei* following administration of a *Bacillus* probiotic, reflecting outcomes commonly associated with enhanced immune status and microbial balance. More consistent evidence comes from algal host systems, where bacteria play a direct role in growth and development. Ghaderiardakani et al. (2017) demonstrated that specific bacterial partners are required for normal morphogenesis in *Ulva*, while Gemin et al. (2019) and Suvega and Arunkumar (2019) reported increased biomass in *Ulva clathrata* and *Gracilaria edulis*, respectively, following bacterial association. These findings suggest that seaweed-associated bacteria can actively regulate host growth, rather than simply coexist on the surface.

At the same time, much of the current evidence remains indirect. Seaweed-associated bacteria are known to produce bioactive compounds such as exopolysaccharides, antimicrobial proteins, and secondary metabolites, many of which are involved in host defense and physiological regulation. These compounds can function as signaling molecules or immune elicitors, capable of activating defense-related pathways and enhancing resistance to stress or infection (McKenna et al., 2025). In addition, bioactive metabolites derived from seaweeds and their associated microbiota have been shown to improve immune responses, antioxidant status, and disease resistance in aquatic organisms (Siddik et al., 2023). Even when immune parameters are not directly measured, these functional traits point toward downstream benefits for host health. While direct studies remain relatively scarce, the available evidence indicates a clear potential for seaweed-associated bacteria to influence host growth and immune responses. Their combined traits highlight a promising but underexplored area that warrants further investigation through targeted *in vivo* and functional studies.

Challenges and future directions

Despite the growing interest in alternative probiotic sources, research on seaweed-associated bacteria remains relatively underdeveloped compared to other marine or gut-derived systems. As noted earlier, most studies have focused on using seaweeds as prebiotic supplements or fermentation substrates for lactic acid bacteria (LAB) rather than directly investigating the associated microbiota as probiotic candidates. While many studies report promising functional traits, particularly antimicrobial activity, these are often assessed in isolation and are rarely linked to actual probiotic performance *in vivo*.

More importantly, even among commonly reported traits, there is a clear lack of comprehensive functional validation. Although seaweed-associated bacteria have shown potential in areas such as stress tolerance, competitive exclusion, colonization, and bioactive compound production, these traits are not consistently evaluated with standardized assays. For example, tolerance to gastrointestinal conditions (e.g., bile salts, digestive enzymes) is rarely tested, despite being a fundamental requirement for probiotic survival. Similarly, while competitive exclusion and colonization ability are often inferred from antimicrobial or biofilm studies, direct evidence

demonstrating stable persistence in host systems remains limited. The same pattern is observed for growth promotion and immunomodulatory effects, where only a few studies have been conducted *in vivo* or immune-based assessments, leaving much of the evidence indirect or inferred. This lack of integrated testing makes it difficult to determine whether these bacteria can reliably function as probiotics under real-world conditions (Kesarcodi-Watson et al., 2007).

Another key challenge lies in the lack of integrated functional validation. Many studies report traits such as antagonism, enzyme production, or biofilm formation, but few assess how these traits translate into host-level outcomes, such as improved growth, immune response, or disease resistance. As seen in conventional probiotic research, strain performance is highly context-dependent and influenced by host species, environmental conditions, and microbial interactions (Kesarcodi-Watson et al., 2007). Without *in vivo* validation, it remains difficult to determine whether seaweed-associated bacteria can consistently meet the requirements of effective probiotics in aquaculture systems.

Moving forward, there is a clear need to actively explore seaweed-associated microbiota as a distinct and valuable source of probiotic candidates. Future studies should prioritize not only the identification of these microbes but also the systematic evaluation of their functional traits using integrated and host-relevant approaches. This includes combining *in vitro* screening with *in vivo* validation, and using omics-based tools to better understand their interactions within the host and surrounding environment. Given their demonstrated ecological adaptability and metabolic versatility, seaweed-associated bacteria remain a promising but underexplored resource. Addressing these gaps will be essential to fully establish their role as next-generation probiotics in sustainable aquaculture systems.

Conclusion

Seaweed-associated bacteria represent a diverse and functionally rich microbial group with considerable potential for probiotic application in aquaculture. Across the different functional traits discussed—ranging from stress tolerance and antimicrobial activity to enzymatic capability, colonization ability, and bioactive compound production—these bacteria consistently demonstrate characteristics that align with established probiotic criteria. In particular, their adaptation to dynamic marine environments and their close association with host surfaces suggest a strong capacity for persistence and functional activity under aquaculture conditions. Despite these promising traits, research on seaweed-associated bacteria remains largely fragmented and trait-specific, with few studies directly linking these properties to host-level outcomes, including growth promotion, immune modulation, and disease resistance. This highlights a critical gap between identifying functional potential and validating probiotic efficacy. Future research that integrates multiple functional assays with *in vivo* validation will be essential to bridge this gap. With more targeted and systematic investigation, seaweed-associated bacteria could emerge as a valuable and sustainable source of next-generation probiotics for aquaculture systems.

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References

Ahmad A., Abdullah S.R.S., Hasan H.A., Othman A.R., Ismail N. (2021). Aquaculture industry: Supply and demand, best practices, effluent and its current issues and treatment technology. Journal of Environmental Management, 287: 112271.

Aly S.M., Fathi M. (2024). Advancing aquaculture biosecurity: a scientometric analysis and future outlook for disease prevention and environmental sustainability. Aquaculture International, 32(7): 8763-8789.

Austin B., Austin D.A. (2016). Bacterial fish pathogens. https://doi.org/10.1007/978-3-319-32674-0

Balcazar J., Blas I., Ruizzarzuela I., Cunningham D., Vendrell D., Muzquiz J. (2006). The role of probiotics in aquaculture. Veterinary Microbiology, 114(3-4):

173-186.

Béné C., Barange M., Subasinghe R., Pinstrup-Andersen P., Merino G., Hemre G., Williams M. (2015). Feeding 9 billion by 2050 – Putting fish back on the menu. Food Security, 7(2): 261-274.

Bernbom N., Ng Y.Y., Kjelleberg S., Harder T., Gram L. (2011). Marine bacteria from Danish coastal waters show antifouling activity against the marine fouling bacterium *Pseudoalteromonas* sp. Strain S91 and zoospores of the green alga *Ulva australis* independent of bacteriocidal activity. Applied and Environmental Microbiology, 77(24): 8557-8567.

Bjørndal T., Dey M., Tusvik A. (2023). Economic analysis of the contributions of aquaculture to future food security. Aquaculture, 578: 740071.

Bolinches J., Lemos M.L., Barja J.L. (1988). Population dynamics of heterotrophic bacterial communities associated with *Fucus vesiculosus* and *Ulva rigida* in an estuary. Microbial Ecology, 15(3): 345-357.

Breider S., Sehar S., Berger M., Thomas T., Brinkhoff T., Egan S. (2019a). Genome sequence of *Epibacterium ulvae* strain DSM 24752T, an indigoidine-producing, macroalga-associated member of the marine Roseobacter group. Environmental Microbiome, 14(1): 4.

Cabello F.C., Godfrey H.P., Tomova A., Ivanova L., Dölz H., Millanao A., Buschmann A.H. (2013). Antimicrobial use in aquaculture re-examined: its relevance to antimicrobial resistance and to animal and human health. Environmental Microbiology, 15(7): 1917-1942.

Chakraborty K., Francis A., Chakraborty R.D., Asharaf S., Kizhakkekalam V.K., Paulose S.K. (2021). Marine macroalga-associated heterotrophic *Bacillus velezensis*: a novel antimicrobial agent with siderophore mode of action against drug-resistant nosocomial pathogens. Archives of Microbiology, 203(9): 5561-5575.

Chakraborty K., Kizhakkekalam V.K., Joy M., Chakraborty R.D. (2021). Novel amylomacins from seaweed-associated *Bacillus amyloliquefaciens* as prospective antimicrobial leads attenuating resistant bacteria. World Journal of Microbiology and Biotechnology, 37(12): 200.

Chakraborty K., Thilakan B., Chakraborty R.D., Raola V.K., Joy M. (2017). O-heterocyclic derivatives with antibacterial properties from marine bacterium *Bacillus subtilis* associated with seaweed, *Sargassum myriocystum*. Applied Microbiology and Biotechnology, 101(2): 569-583.

Chakraborty K., Thilakan B., Raola V.K., Joy M. (2016). Antibacterial polyketides from *Bacillus amyloliquefaciens* associated with edible red seaweed *Laurenciae papillosa*. Food Chemistry, 218: 427-434.

Costello C., Cao L., Gelcich S., Cisneros-Mata M.Á., Free C.M., Froehlich H.E., Golden C.D., Ishimura G., Maier J., Macadam-Somer I., Mangin T., Melnychuk M.C., Miyahara M., De Moor C.L., Naylor, R., Nøstbakken L., Ojea E., O'Reilly E., Parma A.M., . . . Lubchenco J. (2020). The future of food from the sea. Nature, 588(7836): 95-100.

Defoirdt T., Sorgeloos P., Bossier P. (2011). Alternatives to antibiotics for the control of bacterial disease in aquaculture. Current Opinion in Microbiology, 14(3): 251-258.

Deutsch Y., Ofek-Lalzar M., Borenstein M., Berman-Frank I., Ezra D. (2023). Re-introduction of a bioactive bacterial endophyte back to its seaweed (*Ulva* sp.) host, influences the host's microbiome. Frontiers in Marine Science, 10. https://doi.org/10.3389/fmars.2023.1099478

Dobretsov S.V., Qian P. (2002). Effect of bacteria associated with the green alga *Ulva reticulata* on marine micro- and macrofouling. Biofouling, 18(3): 217-228.

Egan S., Thomas T., Kjelleberg S. (2008). Unlocking the diversity and biotechnological potential of marine surface associated microbial communities. Current Opinion in Microbiology, 11(3): 219-225.

Elsegeny S.R., Radwan F.S., Elshamy Y.M., Amer S.M., Mohamed R.A., Shokrak N.M., Abdella B. (2025). A comprehensive overview of probiotics in aquaculture: from efficacy evaluation to diverse applications. Annals of Microbiology, 75(1). https://doi.org/10.1186/s13213-25-01825-7

El-Saadony M.T., Alagawany M., Patra A.K., Kar I., Tiwari R., Dawood M.A., Dhama K., Abdel-Latif H.M. (2021). The functionality of probiotics in aquaculture: An overview. Fish and Shellfish Immunology, 117: 36-52.

FAO. (2024). The state of world fisheries and aquaculture 2024 – Blue Transformation in Action. https://doi.org/10.4060/cd0683en

Gemin M., Peña-Rodríguez A., Quiroz-Guzmán E., Magallón-Servín P., Barajas-Sandoval D., Elizondo-González R. (2019). Growth-promoting bacteria for the green seaweed *Ulva clathrata*. Aquaculture Research, 50(12): 3741-3748.

Ghaderiardakani F., Coates J.C., Wichard T. (2017). Bacteria-induced morphogenesis of Ulva intestinalis and *Ulva mutabilis* (Chlorophyta): a contribution to the lottery theory. FEMS Microbiology Ecology, 93(8). https://doi.org/10.1093/femsec/fix094

Goecke F., Labes A., Wiese J., Imhoff J. (2010). Chemical interactions between marine macroalgae and bacteria. Marine Ecology Progress Series, 409: 267-299.

Golder H.M., Simon A.A.S., Santigosa E., De Ondarza M., Lean I.J. (2022). Effects of probiotic interventions on production efficiency, survival rate, and immune responses of shrimp: A meta-analysis and meta-regression. Aquaculture, 552: 737973.

González N.B.C., Castaño D.M., Lara J.S.M. (2021). Genome sequence of the epiphytic bacteria *Bacillus altitudinis* strain 19_A, isolated from the marine macroalga *Ulva lactuca*. Biotechnology Reports, 30: e00634.

Gram L., Rasmussen B.B., Wemheuer B., Bernbom N., Ng Y.Y., Porsby C.H., Breider S., Brinkhoff T. (2015). *Phaeobacter inhibens* from the Roseobacter clade has an environmental niche as a surface colonizer in harbors. Systematic and Applied Microbiology, 38(7): 483-493.

Grtokjaer T. (2015). Roseobacter-clade bacteria as probiotics in marine larvaeculture. PhD Dissertation, Technical University of Denmark.

Gu X., Fu L., Pan A., Gui Y., Zhang Q., Li J. (2021). Multifunctional alkalophilic α-amylase with diverse raw seaweed degrading activities. AMB Express, 11(1): 139.

Gustilatov M., Widanarni W., Ekasari J., Julyantoro, P.G.S., Waturangi D.E. (2023). Biofloc system supplemented by *Pseudoalteromonas piscicida* 1Ub protects the Pacific white shrimp *Penaeus vannamei* from *Vibrio parahaemolyticus* infection. Aquaculture and Fisheries, 9(6): 967-974.

Hahnke S., Berger M., Schlingloff A., Athale I., Wolf J., Neumann-Schaal M., Adenaya A., Poehlein A., Daniel R., Petersen J., Brinkhoff T. (2024). *Roseobacter fucihabitans* sp. nov., isolated from the brown alga Fucus spiralis. International Journal of Systematic and Evolutionary Microbiology, 74(6).

Hai N. (2015). The use of probiotics in aquaculture. Journal of Applied Microbiology, 119(4): 917-935.

Han S., Lu Y., Xie J., Fei Y., Zheng G., Wang Z., Liu J., Lv L., Ling Z., Berglund B., Yao M., Li L. (2021). Probiotic gastrointestinal transit and colonization after oral administration: A long journey. Frontiers in Cellular and Infection Microbiology, 11: 609722.

Handayani D.P., Isnansetyo A., Istiqomah I., Jumina J. (2021). Anti- Vibrio activity of *Pseudoalteromonas xiamenensis* STKMTI.2, a new potential vibriosis biocontrol bacterium in marine aquaculture. Aquaculture Research, 53(5): 1800-1813.

Hollants J., Leliaert F., De Clerck O., Willems A. (2013). What we can learn from sushi: a review on seaweed-bacterial associations. FEMS Microbiology Ecology, 83(1): 1-16.

Hoseinifar S.H., Sun Y., Wang A., Zhou Z. (2018). Probiotics as means of diseases control in aquaculture, a review of current knowledge and future perspectives. Frontiers in Microbiology, 9: 2429.

Hossain M.M.M., Tanni L.N., Rahman M.A., Farjana N., Moon R.S., Tonni N.Z., Mekat M.R., Mojumdar S., Rahman N., Sen B.K., Rojoni S.A., Rubayea U., Saha P.K. (2024). Bacteriophage and non-pathogenic *Vibrio* to control diseases in shrimp aquaculture. Comparative Immunology Reports, 6: 200126.

Hu X., Xu Y., Su H., Xu W., Wen G., Xu C., Yang K., Zhang S., Cao Y. (2023). Effect of a *Bacillus* probiotic compound on *Penaeus vannamei* survival, water quality, and microbial communities. Fishes, 8(7): 362.

Ibrahim H.A., Beltagy E.A., El-Din N.G.S., Zokm G.M.E., El-Sikaily A.M., Abu-Elela G.M. (2015). Seaweeds agarophytes and associated epiphytic bacteria along Alexandria coastline, Egypt, with emphasis on the evaluation and extraction of agar and agarose. Revista De Biología Marina Y Oceanografía, 50(3): 545-561.

Imai I., Fujimaru D., Nishigaki T., Kurosaki M., Sugita H. (2006). Algicidal bacteria isolated from the surface of seaweeds from the coast of Osaka Bay in the Seto Inland Sea, Japan. African Journal of Marine Science, 28(2): 319-323.

Indraningrat A.A.G., Purnami P.P.C.P., Aryastuti A.A.S. A., Wijaya M.D., Horng J.T. (2023). Antibacterial, antifungal and antioxidant activities of *Bacillus cereus* SMPRL-2 isolated from seaweeds *Eucheuma cottonii*. IOP Conference Series Earth and Environmental Science, 1271(1): 012066.

Ismail A., Ktari L., Ahmed M., Bolhuis H., Boudabbous A., Stal L.J., Cretoiu M.S., Bour M.E. (2016). Antimicrobial activities of bacteria associated with the brown alga *Padina pavonica*. Frontiers in Microbiology, 7: 1072.

Karthick P., Mohanraju R. (2018). Antimicrobial potential

of epiphytic bacteria associated with seaweeds of Little Andaman, India. Frontiers in Microbiology, 9: 611.

Kesarcodi-Watson A., Kaspar H., Lategan M. J., Gibson L. (2007). Probiotics in aquaculture: The need, principles and mechanisms of action and screening processes. Aquaculture, 274(1): 1-14.

Kesarcodi-Watson A., Kaspar H., Lategan M.J., Gibson L. (2010). *Alteromonas macleodii* 0444 and *Neptunomonas* sp. 0536, two novel probiotics for hatchery-reared Greenshell mussel larvae, *Perna canaliculus*. Aquaculture, 309(1-4): 49-55.

Khan I., Debnath S.C., Yan C., Chen C., Xu Y., Wang W., Yu Y., Zheng D., Xu J., Wang P. (2020). *Flavobacterium ajazii* sp. nov., isolated from seaweed of Gouqi Island, China. Current Microbiology, 77(10): 2925-2932.

Kizhakkekalam V.K., Chakraborty K. (2020). Marine macroalgae-associated heterotrophic Firmicutes and Gamma-proteobacteria: Prospective anti-infective agents against multidrug resistant pathogens. Archives of Microbiology, 202(4): 905-920.

Kuebutornye F.K., Abarike E.D., Lu Y. (2019). A review on the application of Bacillus as probiotics in aquaculture. Fish and Shellfish Immunology, 87: 820-828.

Kumar P., Verma A., Sundharam S.S., Ojha A.K., Krishnamurthi S. (2022). Exploring diversity and polymer degrading potential of epiphytic bacteria isolated from marine macroalgae. Microorganisms, 10(12): 2513.

Lambert H., Cornish A., Waley D. (2024). The value of regulating stocking densities in aquaculture must not be dismissed: a reply to Saraiva et al. 2022. Frontiers in Veterinary Science, 10: 1335667.

Lavín P., Atala C., Gallardo-Cerda J., Gonzalez-Aravena M., De La Iglesia R., Oses R., Torres-Díaz C., Trefault N., Molina-Montenegro M.A., Laughinghouse H.D., IV. (2016). Isolation and characterization of an Antarctic *Flavobacterium* strain with agarase and alginate lyase activities. Polish Polar Research, 37(3): 403-419.

Lee S.D. (2006). *Phycicoccus jejuensis* gen. nov., sp. nov., an actinomycete isolated from seaweed. International Journal of Systematic and Evolutionary Microbiology, 56(10): 2369-2373.

Li J., Gu X., Zhang Q., Fu L., Tan J., Zhao L. (2022). Biochemical characterization of a carrageenase, CAR1383, derived from associated bacteria of Antarctic macroalgae. Frontiers in Microbiology, 13: 851182.

Ling F., Egan S., Zhuang Y., Chang L., Xiao L., Yang Q., Wang G. (2022). Epimicrobiome shifts with bleaching disease progression in the brown seaweed *Saccharina japonica*. Frontiers in Marine Science, 9. https://doi.org/10.3389/fmars.2022.865224

Lu D., Wang F., Amann R.I., Teeling H., Du Z. (2023). Epiphytic common core bacteria in the microbiomes of co-located green (*Ulva*), brown (*Saccharina*) and red (*Grateloupia, Gelidium*) macroalgae. Microbiome, 11(1): 126.

Lulijwa R., Rupia E.J., Alfaro A.C. (2020). Antibiotic use in aquaculture, policies and regulation, health and environmental risks: A review of the top 15 major producers. Reviews in Aquaculture, 12(2): 640-663.

Lv X., Zhao J., Jiang P. (2025). *Alteromonas algae* sp. nov. and *Alteromonas ulvae* sp. nov., isolated from the seaweed *Ulva prolifera* dominating green tides in the Yellow Sea. International Journal of Systematic and Evolutionary Microbiology, 75(10). https://doi.org/10.1099/ijsem.0.006925

Ma M., Zhuang Y., Chang L., Xiao L., Lin Q., Qiu Q., Chen D., Egan S., Wang G. (2023). Naturally occurring beneficial bacteria *Vibrio alginolyticus* X-2 protects seaweed from bleaching disease. mBio, 14(4): e0006523.

Mahmud Z.H., Neogi S.B., Kassu A., Wada T., Islam M.S., Nair G.B., Ota F. (2007). Seaweeds as a reservoir for diverse Vibrio parahaemolyticus populations in Japan. International Journal of Food Microbiology, 118(1): 92-96.

Mancuso F.P., D'Hondt S., Willems A., Airoldi L., De Clerck O. (2016). Diversity and temporal dynamics of the epiphytic bacterial communities associated with the canopy-forming seaweed *Cystoseira compressa* (Esper) Gerloff and Nizamuddin. Frontiers in Microbiology, 7: 476.

Markowiak P., Śliżewska K. (2017). Effects of probiotics, prebiotics, and synbiotics on human health. Nutrients, 9(9): 1021.

McKenna S., Da Silva Pereira E.H., For A. (2025). Seaweed-associated microbes as a novel source of crop agrochemicals. Frontiers in Marine Science, 12. https://doi.org/10.3389/fmars.2025.1629196

Miyashita M., Fujimura S., Nakagawa Y., Nishizawa M., Tomizuka N., Nakagawa T., Nakagawa J. (2009). *Flavobacterium algicola* sp. nov., isolated from marine

algae. International Journal of Systematic and Evolutionary Microbiology, 60(2): 344-348.

Mugwanya M., Dawood M.A.O., Kimera F., Sewilam H. (2022). Updating the role of probiotics, prebiotics, and synbiotics for tilapia aquaculture as leading candidates for food sustainability: A Review. Probiotics and Antimicrobial Proteins, 14(1): 130-157.

Mohammed E.A.H., Ahmed A.E.M., Kovács B., Pál K. (2025). The Significance of probiotics in aquaculture: A review of research trend and latest scientific findings. Antibiotics, 14(3): 242.

Muhammad N., Han H.L., Lee Y., Ko J., Nguyen T.T.H., Kim S. (2022). *Flavobacterium litorale* sp. nov., isolated from red alga. International Journal of Systematic and Evolutionary Microbiology, 72(8). https://doi.org/10.1099/ijsem.0.005458

Muthukrishnan S., Muthar N.I., Zakaria M.H., Rukayadi Y., Natrah I. (2023). Anti-biofilm and Anti-quorum Sensing Activities of the Red Seaweed, *Gracilaria changii* and its Associated Bacteria. Journal of Applied Phycology, 35(5): 2555-2566.

Nahor O., Israel Á., Barger N., Rubin-Blum M., Luzzatto-Knaan T. (2024). Epiphytic microbiome associated with intertidal seaweeds in the Mediterranean Sea: comparative analysis of bacterial communities across seaweed phyla. Scientific Reports, 14(1): 18631.

Naufal M., Zunuraen S., Latifah L.A., Septiana N.I., Nababan Y.I., Purbiantoro W., Chasanah E., Fahrurrozi F. (2025). Abiotic stress responses of a seaweed-associated *Bacillus*: Implications for coastal aquaculture ecosystems. Thalassas an International Journal of Marine Sciences, 41(4): https://doi.org/ 10.1007/s41208-025-01008-w

Neissi A., Zahed H.M., Roshan R. (2024). Probiotic performance of *B. subtilis* MS. 45 improves aquaculture of rainbow trout *Oncorhynchus mykiss* during acute hypoxia stress. Scientific Reports, 14(1): 3720.

Papadopoulou E., De Evgrafov M.C.R., Kalea A., Tsapekos P., Angelidaki I. (2023). Adaptive laboratory evolution to hypersaline conditions of lactic acid bacteria isolated from seaweed. New Biotechnology, 75: 21-30.

Prieto M.L., O'Sullivan L., Tan S.P., McLoughlin P., Hughes H., O'Connor P.M., Cotter P.D., Lawlor P.G., Gardiner G.E. (2012). Assessment of the Bacteriocinogenic potential of marine bacteria reveals lichenicidin production by seaweed-derived *Bacillus* spp. Marine Drugs, 10(10): 2280-2299.

Rahayu S., Amoah K., Huang Y., Cai J., Wang B., Shija V.M., Jin X., Anokyewaa M.A., Jiang M. (2024). Probiotics application in aquaculture: its potential effects, current status in China and future prospects. Frontiers in Marine Science, 11. https://doi.org /10.3389/fmars.2024.1455905

Ramirez M., Domínguez-Borbor C., Salazar L., Debut A., Vizuete K., Sonnenholzner S., Alexis F., Rodríguez J. (2021). The probiotics *Vibrio diabolicus* (Ili), *Vibrio hepatarius* (P62), and *Bacillus cereus* sensu stricto (P64) colonize internal and external surfaces of *Penaeus vannamei* shrimp larvae and protect it against *Vibrio parahaemolyticus*. Aquaculture, 549: 737826.

Rao D., Webb J.S., Kjelleberg S. (2006). Microbial colonization and competition on the marine alga *Ulva australis*. Applied and Environmental Microbiology, 72(8): 5547-5555.

Ringø E., Olsen R., Gifstad T., Dalmo R., Amlund H., Hemre G., Bakke A. (2010). Prebiotics in aquaculture: a review. Aquaculture Nutrition, 16(2): 117-136.

Saha M., Weinberger F. (2019). Microbial "gardening" by a seaweed holobiont: Surface metabolites attract protective and deter pathogenic epibacterial settlement. Journal of Ecology, 107(5): 2255-2265.

Saha S., Kumar S.H., Nayak B.B., Lekshmi M. (2024). Isolation, characterization and molecular identification of bacteria associated with green and brown seaweeds. Microbiology Research Journal International, 34(11): 60-71.

Saravanan P., Chatterjee A., Kiran K.J., Bhowmick G.D., Sappati P.K., Nagarajan V. (2024). Exploring seaweed-associated marine microbes: Growth impacts and enzymatic potential for sustainable resource utilization. Indian Journal of Microbiology, 64(2): 593-602.

Sathishkumar R., Thirumalaikumar E., Rajeswari M.V., Arun J., Vimal S., Babu M.M., Citarasu T. (2022). Extraction, statistical optimization, and immunomodulatory activity of exopolysaccharide from seaweed-associated *Bacillus megaterium* DSKPDF CMST3. Biomass Conversion and Biorefinery. https://doi.org/10.1007/s13399-021-02180-8

Sawabe T., Makino H., Tatsumi M., Nakano K., Tajima K., Iqbal M.M., Yumoto I., Ezura Y., Christen R. (1998). *Pseudoalteromonas bacteriolytica* sp. nov., a marine bacterium that is the causative agent of red spot disease of *Laminaria japonica*. International Journal of Systematic Bacteriology, 48(3): 769-774.

Sedgwick H., Gibson G., Adams J., Wijeyesekera A.

(2025). Seaweed-derived bioactives: Gut microbiota targeted interventions for immune function. Journal of Functional Foods, 125: 106696.

Siddik M.A.B., Francis P., Rohani M.F., Azam M.S., Mock T.S., Francis D.S. (2023). Seaweed and seaweed-based functional metabolites as potential modulators of growth, immune and antioxidant responses, and gut microbiota in fish. Antioxidants, 12(12): 2066.

Singh R.P., Reddy C. (2014). Seaweed-microbial interactions: key functions of seaweed-associated bacteria. FEMS Microbiology Ecology, 88(2): 213-230.

Sonnenschein E.C., Jimenez G., Castex M., Gram L. (2020). The Roseobacter-Group bacterium phaeobacter as a safe probiotic solution for aquaculture. Applied and Environmental Microbiology, 87(5): e0258120.

Suji H.A., Manikandan K., Sudha A., Muthukumar A., Jeyalakshmi C., Charumathi M., Rajesh M., Raj T.S. (2024). Whole genome sequence of seaweed endophyte *Bacillus halotolerans* strain AUPP for antagonistic activity against *Fusarium incarnatum* causing chilli fruit rot. Scientific Reports, 14(1): 31881.

Sun C., Zhou J., Duan G., Yu X. (2020). Hydrolyzing Laminaria japonica with a combination of microbial alginate lyase and cellulase. Bioresource Technology, 311: 123548.

Supty M.S.A., Jahan K., Lee J., Choi K. (2024). Epiphytic bacterial community analysis of *Ulva prolifera* in Garorim and Muan Bays, Republic of Korea. Microorganisms, 12(6): 1142.

Suvega T., Arunkumar K. (2019a). Probiotic bacteria promote the growth of associating host (red seaweed, G*racilaria edulis*) also synthesize antibacterial protein. Biocatalysis and Agricultural Biotechnology, 19: 101136.

Thilsted S.H., Thorne-Lyman A., Webb P., Bogard J.R., Subasinghe R., Phillips M.J., Allison E.H. (2016). Sustaining healthy diets: The role of capture fisheries and aquaculture for improving nutrition in the post-2015 era. Food Policy, 61: 126-131.

Torres M., Hong K., Chong T., Reina, J.C., Chan K., Dessaux Y., Llamas I. (2019). Genomic analyses of two *Alteromonas stellipolaris* strains reveal traits with potential biotechnological applications. Scientific Reports, 9(1): 1215.

Trivedi N., Gupta V., Kumar M., Kumari P., Reddy C.R.K., Jha B. (2010). An alkali-halotolerant cellulase from *Bacillus flexus* isolated from green seaweed *Ulva lactuca*. Carbohydrate Polymers, 83(2): 891-897.

Vairagkar U., Mirza Y. (2021). Antagonistic activity of antimicrobial metabolites produced from seaweed-associated *Bacillus amyloliquefaciens* MTCC 10456 Against *Malassezia* spp. Probiotics and Antimicrobial Proteins, 13(4): 1228-1237.

Van Der Loos L.M., D'hondt S., Engelen A.H., Pavia H., Toth G.B., Willems A., Weinberger F., De Clerck O., Steinhagen S. (2022). Salinity and host drive *Ulva*-associated bacterial communities across the Atlantic–Baltic Sea gradient. Molecular Ecology, 32(23): 6260-6277.

Wilson S., Saha M. (2025). Warmer oceans will increase abundance of human pathogens on seaweeds. Phycology, 5(3): 38.

Wu M., Xu Y., Shao M., Wang Z., Cao J., Xu J. (2024). *Pseudoalteromonas flavipulchra* as a dual-functional probiotic for aquaculture: enhancing microalgae growth and antagonizing *Vibrio* pathogens. Frontiers in Marine Science, 11. https://doi.org/10.3389/fmars.2024.1492142

Yasim S.N.M., Omar N.S., Iehata S., Ikhsan N.F.M., Wahid M.E.A., Emilia S.N. (2022). Anti-Bacterial and Anti-Quorum Sensing Potential of Seaweed-Associated Bacteria from Pulau Bidong, East Coast of Peninsular Malaysia. https://li01.tci-thaijo.org/index.php/JFE/article/view/255343

Yin Q., Zhu F., Tang H., Chen X., Liu X., Tang L., Li X. (2022). Complete genome sequence of marine Roseobacter lineage member *Ruegeria* sp. YS9 with five plasmids isolated from red algae. Marine Genomics, 67: 100997.

Zorriehzahra M.J., Delshad S.T., Adel M., Tiwari R., Karthik K., Dhama K., Lazado C.C. (2016). Probiotics as beneficial microbes in aquaculture: an update on their multiple modes of action: A review. Veterinary Quarterly, 36(4): 228-241.