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Antimicrobial and production of hydrolytic enzymes potentials of bacteria and fungi associated with macroalgae and their applications: a review

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Endophytic and epiphytic bacteria and fungi that live in association with macroalgae produce compounds that favor the growth of the host, being in some cases more efficient than those produced by the terrestrial microbiome. This review collects information from articles published in Scopus, ScienceDirect, PubMed, and Wiley Online Library. Articles were organized according to their antimicrobial properties, synthesis of hydrolytic enzymes, production of other bioactive compounds by bacteria and fungi, and their application. The information collected showed that bacteria and fungi associated with macroalgae have the ability to inhibit bacteria, fungi, yeasts, and protozoa that affect aquaculture, public health, and the food industry, reporting that the pyrenocines A, B, E, and S isolated from *Phaeosphaeria* sp. Inhibited pathogenic protozoa. Additionally, other compounds identified as alkaloids, steroids, triterpenoids, and flavonoids could act by altering the morphology and physiology of pathogenic microorganisms, which can be applied in the food, pharmaceutical, paper, chemical, textile, and cosmetic industries. In addition, these microorganisms can synthesize enzymes such as xylanase, amylase, cellulase, pectinase, agarase, lignocellulose, chitinase, gelatinase, asparaginase, glutaminase, and lipase, which can be used to reduce oxidation and enzymatic browning, improve digestibility and functionality of feed, synthesis of chitin oligomers with antimicrobial properties, bioremediation of agricultural residues and industrial effluents, and production of hydrolysates.

KEYWORDS

bioactive compounds, hydrolytic enzymes, bacteria, fungus, yeasts

1 Introduction

Hosts from the marine biome are the most abundant, representing 70% of what exists on the planet (Silva et al., 2020). In addition, there are terrestrial flora, polar vegetation, and tropical forests, which live in association with endophytic microbes (Sarasan et al., 2020), or epiphytic or free-living (Darienko et al., 2021), including bacteria (Deutsch et al., 2021) and fungus (Kjer et al., 2010; Zainee et al., 2021) within the endophytes group (Cha et al., 2021). The most representative within the group of fungus are filamentous Ascomycota (Eurotiales, Capnodiales, Hypocreales, and Pleosporales) as the most numerous (Lucini et al., 2022), basimetric yeasts (Sporidiobolales), and, within the bacteria, Arcobacter, Bacteroidetes, Flavobacteriaceae, Mycoplasma, Labrenzia, Phyllobacteriaceae and Xanthomonadaceae (Hollants et al., 2011).

The presence of bacterial and fungal species as endophytes and epiphytes (Darienko et al., 2021) depends on host conditions such as the growth of the frond, the erect part of variable size and shape with an attachment organ (Pereira, 2021), types of thallus tissues, different heights of the tide, different stages of the life cycle (Bonthond et al., 2022), or the high rate of growth and sporulation of the host (Kamat et al., 2020), as well as geographical differences (Chen et al., 2022), geographic location (Ismail et al., 2016), multiple abiotic parameters (temperature, light, nutrient pollution, salinity, and pH) (Pereira et al., 2017; Deutsch et al., 2021; Wong Chin et al., 2021; Lucini et al., 2022), and anthropomorphic influences (Flewelling et al., 2015) (Figure 1). The latter generates a condition of fragility, favoring the presence of microorganisms in the cell wall, although the endophyte penetration mechanism is unknown (Pereira et al., 2017).

This association and understanding of intercellular chemical signaling pathways between macroalgae and associated bacteria and fungi (Menaa et al., 2020) allows macroalgae to be protected from marine pathogens during the stages of wound repair and from susceptible protoplasts through the production of highly bioactive

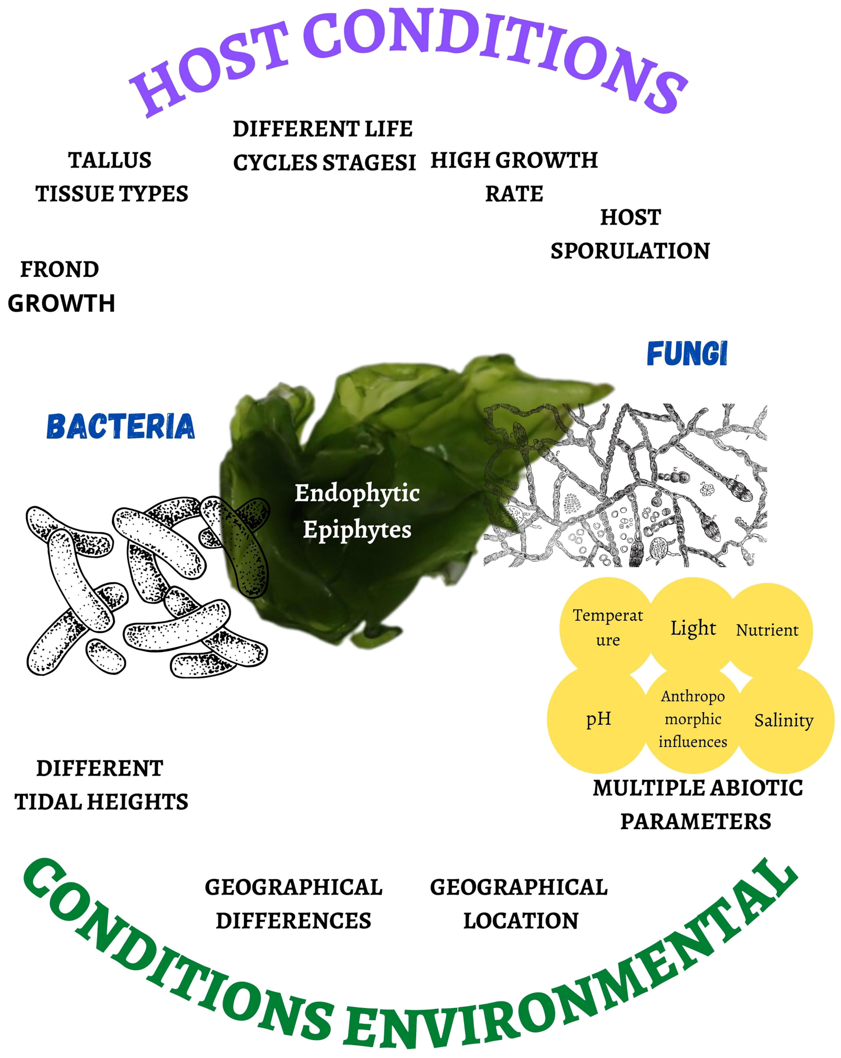

FIGURE 1
Host and environmental conditions that affect the proliferation rate and biodiversity of bacteria and fungi associated with marine macroalgae.

metabolites (Deutsch et al., 2021), such as pyrenocines (Vallet et al., 2018), specific vitamins (Villarreal-Gómez et al., 2010), or others, which also aid to withstand high temperatures and high minerals concentrations (Deutsch et al., 2021). These improve the ability of microalgae to tolerate stress (Gonçalves et al., 2020; Wong Chin et al., 2021), allow the exchange of nutrients *via* photosynthetic pathway (Handayani et al., 2019; Cha et al., 2021), or induce the synthesis of molecules to increase the growth and development of the host macroalgae (Wichard and Beemelmanns, 2018).

Additionally, microalgae are involved in the degradation of cellulose, lignin, and polymeric organic matter within oxic and anoxic sediments, participating in the carbon cycle in marine environments (Perkins et al., 2021) or degrading chitin as an abundant resource, as it forms part of the shells of marine crustaceans (Venkatachalam et al., 2015), or breaking down proteins. Microalgae also use part of their wide variety of enzymes (Suryanarayanan et al., 2012) and metabolites, which they produce even under adverse conditions (Wong Chin et al., 2021), that are novel and structurally unique (Manomi et al., 2015). These functional properties are more efficient than the terrestrial microbiome (Patyshakuliyeva et al., 2020). It is also known that healthy macroalgae release part of the carbon fixed during photosynthesis as a secretion called mucilage, which is rich in substances of interest that act as an attraction factor for colonizing microorganisms, such as fungi (Teixeira et al., 2019b). However, some of the endophytes and epiphytes are harmful (Aumack et al., 2011).

This great variety of metabolic pathways confers adaptation and survival to the habitat (Bogas et al., 2022), performing an important role in the biological processes of its hosts (Liu et al., 2022b), which can be understood by metaomic technologies (Singh and Reddy, 2016), such as transcriptomic, proteomic, and genomic analysis (Balabanova et al., 2018), in order to have an understanding of the functionality of proteins and enzymes for future applications in different fields of study. These functional properties make macroalgal endophytes a promising new source of biologically active metabolites (Kjer et al., 2010; Espinoza et al., 2021; Cooper and Walker, 2022) and unique in hydrolytic enzymes (Sarasan et al., 2020). They are very important in biotechnological use (Espinoza et al., 2021), by meeting the demands of the pharmaceutical industry (Sarasan et al., 2017). They can also be used to combat infections such as SARS, dengue, and Zika virus (Deshmukh et al., 2018), as new natural antibiotic compounds (Zainee et al., 2021), in anticancer treatments using chrysin production (Kamat et al., 2020), as an apoptotic agent (Sahoo et al., 2021), and they have anti-inflammatory and antioxidant capacities (Teixeira et al., 2019a).

This review discloses the antimicrobial properties of bacteria and fungi associated with marine macroalgae against pathogenic bacteria, fungi, and protozoa or food spoilers. In addition, the production of enzymes such as agarolytic, cellulase, ligninase, chitinase, and others is discussed, as well as their applications.

2 Bacteria associated with macroalgae

2.1 Antimicrobial properties

Currently, the demand for food without synthetic preservatives and the demand for use of natural products has led to studies focusing on different sources that allow food to be preserved from deterioration as part of food safety and quality (Arshad and Batool, 2017). Given this situation, plants are the main source of antimicrobials as part of the terrestrial biome; however, the search for beneficial microorganisms that can produce antibiotics, organic acids, or bacteriocins (Cesa-Luna et al., 2020) are considered untapped reserves of promising biomolecules (Danquah et al., 2022), especially bacteria that are associated with macroalgae as part of the marine biome.

Table 1 summarizes the information that has been reported for the last 7 years, which shows the sampling site, the host macroalgae, the isolated strains, the codes access referring to these sequences, the extracts used, and the microorganisms inhibited. The most important information from the results has been reported, and 50% of the studies were carried out in India and the other 50% in Israel, Egypt, and Morocco.

2.1.1 Bioactive compounds and mechanism of action.

Dhanya et al. (2016), observed that *P. stutzeri* presented a high inhibitory capacity on *S. aureus* and *E. coli*. This inhibitory action may be related to phenol, 3, 5-bis (1, 1-dimethylethyl), which has been evidenced by Abdullah et al. (2011), where this partially lipophilic phenolic compound could cross the cell membrane by passive diffusion, acidifying the cytoplasm, causing alteration of the bacterial membrane, generating the escape of essential intracellular constituents, denaturing the proteins (Campos et al., 2009; Ecevit et al., 2022), and causing cell death (Ecevit et al., 2022) by bacterial lysis (Ochieng et al., 2023). Furthermore, the presence of phenolic compounds synthesized by these endophytic bacteria exerts an inhibitory effect on the biosynthesis of nucleic acids and on their metabolic processes (Flewelling et al., 2015).

Hagaggi and Abdul-Raouf (2022) mentioned that heptacosane and 2-methyloctacosane were the major components detected in *C. thiocycli*, being the first related to antibacterial activity (Magina et al., 2009) and the second to antimicrobial (Res, 2018). Bankeu et al. (2018) showed that heptacosane moderately inhibits ureases that confer pathogenicity to *Helicobacter pylori* (Rego et al., 2018). 2-methyloctacosane, which is a volatile compound (Sharon P. et al., 2021) and a cyclic alkane (Amin et al., 2022) of the octacosane group, could alter membrane permeability, inhibit enzymes, and perturb bacterial morphology, which in some cases can cause irreversible damage by triggering the secretion of proteins and genetic material (Magina et al., 2009).

Kizhakkekalam and Chakraborty (2020) showed that *S. algae* and *B. amyloliquefaciens* inhibited methicillin resistant *S. aureus* (MRSA) and vancomycin resistant *Enterococcus faecalis*, due to the destabilization of the cell membrane permeability (Le and Desbois,

TABLE 1 Bacteria associated with macroalgae and their inhibition capacity against pathogenic microorganisms.

Sampling site	Host macroalgae	Isolated strains	Access code	Extract solvent	Bioactive compounds: Application	Inhibited microorganisms	Reference
Inhibition of pathogenic bacteria							
Marine and freshwater sources, Israel	*Jania Rubens*	*Bacillus safensis*	NR	SE	NR	*Photobacterium damselae Streptococcus iniae Aeromonas salmonicida*	(Deutsch et al., 2021)
	Laurencia papillosa	*Bacillus safensis*	NR				
		Bacillus safensis	MT186284				
			NR				
	Padina pavonica	*Bacillus pumilus*	MT116792				
			MT186599				
	Gracilaria sp.	*Bacillus safensis*	MT232982				
Mandapam, Gulf of Mannar, India	*Ulva reticulata*	*Pseudomonas stutzeri*	NR	Hexane	phenol, 3, 5-bis (1, 1-dimethylethyl): NT	*Staphylococcus aureus*	(Dhanya et al., 2016)
						Escherichia coli	
Egyptian Red Sea, El Quseir, Egypt	*Cystoseira myrica*	*Catenococcus thiocycli*	OK584768	Methanolics	Heptacosane; 2-methyloctacosane: NT	*Escherichia coli Salmonella typhi Klebsiella pneumoniae Micrococcus luteus Proteus mirabilis*	(Hagaggi and Abdul-Raouf, 2022)
Indian Peninsula and Arabian Sea, India	*Hypnea valentiae*	*Shewanella algae* *Bacillus amyloliquefacien*	MH157093 MH157092	Ethyl acetate	NR	Methicillin resistant *Staphylococcus aureus* (MRSA) Vancomicin resistant *Enterococcus faecalis*	(Kizhakkekalam and Chakraborty, 2020)
Northwestern Atlantic coast of Morocco, southwest of El Jadida, Morocco	*Carpodesmia tamariscifolia*	KC179^{a,b} *Streptomyces albidoflavus*^{c}	NR MW555177	Butanolic^{a} Hexane^{b}	Desferrioxamina B^{c} Desferrioxamina B2^{c}: NT	Methicilin resistant *Staphylococcus* aureus (MRSA)^{b,c} *Acinetobacter baumannii*^{a,c} *Pseudomonas aeruginosa*^{c}	(Katif et al., 2022)
Someshwar beach, located in Mangalore, district of Dakshina Kannada, Karnataka, India	*Ulva lactuca*	*Bacillus subtilis*^{a}	NR	Chloroform Ethyl acetate	Alkaloids^{a} Esteroids^{a,b} Triterpenoids^{a,b} Flavonoids^{a,b}: NT	*Enterococcus faecalis Klebesella pneumoniae*	(Habbu et al., 2016)
		Enterobacter cloacae^{b}	NR				
Inhibition of pathogenic fungi							
Egyptian Red Sea, El Quseir, Egypt	*Cystoseira myrica*	*Catenococcus thiocycli*	OK584768	Ethyl acetate	2-methyloctacosane	*Aspergillus niger Candida albicans*	(Hagaggi and Abdul-Raouf, 2022)
Someshwar beach, located in Mangalore, district of Dakshina Kannada, Karnataka, India	*Ulva lactuca*	*Bacillus subtilis*^{a} *Enterobacter cloacae*^{b}	NR NR	Chloroform Ethyl acetate	Triterpenoids^{a,b} Flavonoids^{a,b} Esteroids^{b}: NT	*Aspergillus niger*^{a} *Aspergillus flavus*^{b} *Candida albicans*^{a,b}	(Habbu et al., 2016)
Inhibition of pathogenic protozoa							
Marine and freshwater sources, Israel	*Jania Rubens*	*Bacillus velezensis*	MT187620	SE	NR	*Saprolegnia parasítica*	(Deutsch et al., 2021)
		Bacillus subtilis	MT192301				
	Bryopsis plumosa	*Bacillus subtilis*	MT187638				
	Pithophora spp.	*Pseudomonas alcaligenes*	MT186697				
	Ulva sp.		MT178235				

(Continued)

TABLE 1 Continued

Sampling site	Host macroalgae	Isolated strains	Access code	Extract solvent	Bioactive compounds: Application	Inhibited microorganisms	Reference
		Bacillus velezensis					
	Enteromorpha ralfsii	*Bacillus subtilis*	MN134034				
		Bacillus pumilus	MT272978				

*NR, Not reported; NE, No extract; NT, Not tested; ^{a,b,c}: Endophytic species related to the solvent, bioactive compound, and pathogen.

2017) because of the presence of polyketides and lipopeptides (Aleti et al., 2015) synthesized from pks-1 and nrps genes (Kizhakkekalam and Chakraborty, 2020). In addition, lipopeptides as antibiotic substances increase the amphipath city of calcium ions forming daptomycin micelles upon interaction with membranes, causing solute secretion in Gram positive bacteria (Gray and Wenzel, 2020).

The inhibition *A. baumannii* and *P. aeruginosa* by *Streptomyces albidoflavus* (Katif et al., 2022) is probably due to a local increase in pluronic micelles on the surface of Gram-negative bacteria, causing an alteration in membrane permeability (Purro et al., 2018), due to the presence of desferrioxamine B and B2 (Katif et al., 2022), a partial structure of butyldiamine that acts as an iron chelator (Purro et al., 2018).

Habbu et al. (2016) demonstrated inhibitory action of *B. subtilis* and *E. cloacae* on *E. faecalis*, *K. pneumoniae*, and *C. albicans*; regarding molds, *B. subtilis* inhibited *Aspergillus niger* and *E. cloacae* inhibited *A. flavus*. Phytochemical investigations of the two endophytes, when fractionated, revealed the presence of alkaloids, steroids, triterpenoids, and flavonoids attributed to antimicrobial activity, although their mechanism of action has not been detailed for each compound identified.

Regardless of the compounds mentioned, endophytic bacteria can produce lytic enzymes (chitinases) or volatile compounds that exert antimicrobial action (Figure 2); these endophytic and pathogenic bacteria can alter the pH and compete with each other for space and nutrients causing indirect inhibition of the pathogen (Ortiz-Ojeda et al., 2020).

2.2 Hydrolytic enzymes

Regarding the potential for polymeric hydrolysis of epiphytic bacteria (*Alteromonas*, *Pseudoalteromonas*, *Psychrobacter*, *Shewanella*, and *Vibrio* sp.; *Brevundimonas*, *Paracoccus*, *Roseomonas*, and *Sphingomonas* sp.; *Bacillus*, *Staphylococcus*, and *Alkalihalobacillus* sp.; *Cellulomonas*, *Cellulosimicrobium*, *Isoptericola*, *Kocuria*, *Micrococcus*, and *Streptomyces* sp.) isolated from macroalgae (*Ulva* sp., *Sargassum polycystum*, *Pterocladia musciformis*, *Dictyota* sp., and *Padina antillarum*) from the central west coast of India, an enzyme activity of 61.3%, 59.7%, 58.8%, and 52.2% on xylan, starch, cellulose, and pectin, respectively, was shown (Kumar et al., 2022).

Additionally, Sánchez Hinojosa et al. (2018) demonstrated that epiphytic bacteria *Cellulophaga* sp., *Colwellia* sp., *Lacinutrix* sp., *Olleya* sp., *Paraglaciecola* sp., *Pseudoalteromonas* sp., and *Winogradskyella* sp. isolated from *Himantothallus grandifolius*, *Pantoneura plocamioides*, and *Plocamium cartilagineum* originating from different parts of the Rey Jorge island, Antarctic Peninsula presented a high agarolytic activity at 20°C; however the isolates *Olleya* sp. and different species of *Pseudoalteromonas* showed the highest activities at low temperature (4°C), demonstrating their potential as biocatalysts for industrial biotechnological applications.

2.3 Production of other bioactive compounds

In another study, Harikrishnan et al. (2021) identified compounds such as 1H-Indole, 3-ethyl-2-(2-pyridyl)-, 2H-Benzo (d,E)isoquinoline-1,3(1H,3H)-dione, 2-(2-acetoxyethyl)- 6-(4-morpholyl)-, arsenic acid, tris(trimethylsilyl), ester, Thiocarbamic acid, N,N-dimethyl,S-1,3-diphenyl-2-butenyl-ester, Phenol, 2,5-bis (1,1- dimethylethyl)- and Tris(tert-butyldimethylsiloxy)arsane from *Pichia kudriavzevii*, *Cystobasidium minutum*, *Grammothele fuligo*, *Candida railenensis*, and *Rigidoporus vinctus* isolated from macroalgae *Chaetomorpha*, *Rhizoclonium*, *Undaria*, *Ulva*, and *Enteromorpha*. Even though the bioactivity of these compounds is unknown, it could be related to their antibacterial activity and antioxidant capacity.

3 Fungi associated with macroalgae

3.1 Antimicrobial properties

Resistance to antimicrobial compounds by pathogenic microbes has had a major impact on food production worldwide, boosting a constant need for new discoveries, where marine fungi have been identified as a novel source of natural fungal products (Jakubczyk and Dussart, 2020). However, their synthesis on a commercial scale must be achieved by improving the potentiality of the strain, optimizing growth conditions, and incorporating omic techniques, to be offered as suitable substitutes for ineffective and expensive antimicrobials (Rani et al., 2021).

Table 2 compiles information from the last 10 years including the sampling site, host macroalgae, isolated strains, codes access referring to these sequences, extract used, and microorganisms

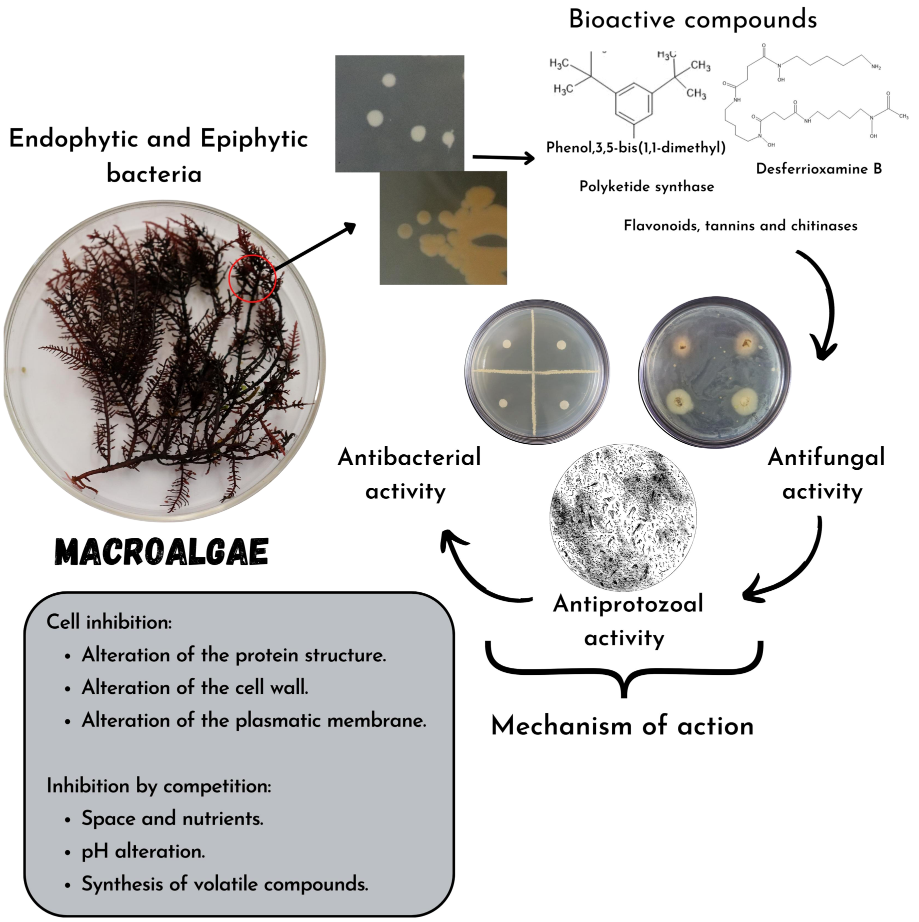

FIGURE 2
Mechanisms of action of bioactive compounds synthesized by bacteria associated with macroalgae and their inhibition capacity in pathogenic bacteria, fungi, and protozoa or food spoiler.

inhibited from the main reported results. It can be observed that 33.3% of the studies were carried out in India, followed by Indonesia (22%) and other countries such as Malaysia, Brazil, Canada, Scotland and France. Green macroalgae were collected in the highest proportion for isolation, and the presence of associated fungi of the species was identified.

3.1.1 Bioactive compounds and mechanism of action

E. coli, *S. aureus*, *P. aeruginosa*, *X. campestris*, *B. subtilis*, and *B. megaterium* were inhibited by *C. globosum* and *A. unguis*, and some compounds such as azelaic acid, azetidine, and the furo-pyrans were identified in *A. unguis* (Kamat et al., 2020). In another study, azelaic acid showed antibiotic action on *Propionibacterium acnes* (Park et al., 2018); however, its mechanisms of action at the cellular level are unknown. Azitidine, as an antibacterial compound, could cause inhibitory action on protein synthesis and bacterial 50S RNA target molecules (O'Dowd et al., 2008). Furo-pyrans could act by binding to the phosphate group (negative ions) of the phospholipids of the membrane and cell wall, causing an inhibition of lysosomal phospholipase activities due to its neutralization of negative charges (Magesh et al., 2004).

Harikrishnan et al. (2021) showed that *P. aeruginosa* was inhibited from ethyl acetate extracts of *Cystobasidium minutum*, *Candida railenensis*, *Rigidoporus vinctus*, *Grammothele fuligo*, and *Pichia kudriavzevii*, in which Phenol, 2,4-bis(1,1-dimethylethyl)- may be one of the causes of the decrease in reactive oxygen species (ROS) by pumping intracellular protons, acidifying the medium and causing the inhibition of pathogens (Romero-Correa et al., 2014). It could also act, hindering the production of biofilms (Padmavathi et al., 2014) by a bacterial signaling pathway that controls physiological mechanisms called *quorum sensing* (Samanta et al., 2011). In addition, silicic acid (diethyl bis(trimethylsilyl) ester) identified by Harikrishnan et al. (2021) in a phospholipid compound could act by interacting with the negatively charged compounds of the membranes of pathogenic microbes, altering their permeability and inhibiting their cell wall, nucleic acids, proteins, and enzymes (Abd El Baky et al., 2014); while with arsenous acid (tris(trimethylsilyl) ester) and butylated hydroxytoluene identified by Harikrishnan et al. (2021), an inhibitory mechanism at the cellular level is not reported.

S. aureus and *Klebsiella pneumoniaea* were inhibited by *Penicillium waksmanii*, *Acremonium implicatum*, and *Xylaria* sp. Cytochalasin D identified in *Xylaria* sp. (De Felício et al., 2015)

TABLE 2 Fungi associated with macroalgae and their inhibition capacity against pathogenic microorganisms.

Sampling site	Host macroalgae	Isolated strains	Access code	Extract solvent	Bioactive compounds: Application	Inhibited microorganisms	Reference
Inhibition of pathogenic bacteria							
Rocky coastline of Konkan and Goa, India	*Chaetomorpha* sp.	*Chaetomium globosum*[a]	MH645800.1	Ethyl acetate	Azelaic acid, azetidine and furo-pyrans[e]: NT	*Escherichia coli*[a,b,c,d,e] *Staphylococcus aureus*[b,c,d] *Pseudomona aeruginosa*[a,b,c,d,e] *Xantomonas campestris*[a,b,c,d,e] *Bacillus subtilis*[b,c,d] *Bacillus megaterium*[b,c,d]	(Kamat et al., 2020)
	Chaetomorpha sp.	*Aspergillus unguis*	MH654996[b]				
			MH654997[c]				
			MH655006[d]				
			MH655000[e]				
Nirvana beach, Padang, West Sumatra, Indonesia	*Padina* sp.	*Trichoderma harzianum*[a]	NR	Ethyl acetate	NR	*Escherichia coli*[a] *Staphylococcus aureus*[a]	(Handayani et al., 2019)
Kovalam coast, Trivandrum, Kerala, India	*Sargassum wightii* *Caulerpa peltata*	*Aspergillus flavus*[a]	MH469530	Raw fungal extract	NR	*Escherichia coli*[a,b,c,d,e] *Edwardsiella tarda*[a,b,c,d,e] *Pseudomonas aeruginosa*[a,b,c,d,e] *Aeromonas hydrophila*[a,b,c,d,e] *Vibrio cholera*[a,b,c,d,e] *Vibrio parahaemolyticus*[a,b,c,d,e] *Vibrio alginolyticus*[a,b,c,d,e] *Vibrio harveyi*[a,b,c,d,e] *Vibrio proteolyticcus*[a,b,c,d,e] *Bacillus cereus*[c,d,e] *Staphylococcus aureus*[c,d,e]	(Sarasan et al., 2020)
	Sargassum wightii *Dictyota dichotoma* *Halymenia venusta* *Grateloupia lithophila*	*Penicillium chrysogenum*[b]	MH469504				
	Hypnea musiformis	*Aspergillus terreus*[c]	MH469513				
	Chaetomorpha antennina	*Aspergillus versicolor*[d]	MH469523 MH469532				
	Sargassum wightii *Hypnea musiformis*	*Hortea werneckii*[e]	MH469501				
Munambam beach, Cochin and Varkala beach, Trivandrum, Kerala, India	*Rhizoclonium*	*Cystobasidium minutum*[a]	MT372471	Ethyl acetate	Phenol, 2,4-bis(1,1-dimethylethyl)-; Arsenous acid, tris(trimethylsilyl) ester; silicic acid, diethyl bis(trimethylsil) ester and butylated hydroxytoluene [a,c,c,d,e]: NT	*Pseudomona aeruginosa*[a,b,c,d]	(Harikrishnan et al., 2021)
	Ulva	*Candida railenensis*[b]	MK920215				
	Enteromorpha	*Rigidoporus vinctus*[c]	MK920214				
	Undaria	*Grammothele fuligo*[d]	MT372472				
	Chaetomorpha	*Pichia kudriavzevii*[e]	MT372473				
Johor coast (Pulau Merambong, Nusajaya, Tanjung Dato, and Tanjung Lompa), Malaysia	*Sargassum polycystum*	*Trichoderma viride*[a]	NR	NE	NR	*Staphylococcus aureus*[a,b] *Shigella* sp.[a,b] *Escherichia coli* [a,b] *Serratia marcescens* [a,b] *Salmonella typhi* [a,b] *Klebsiella pneumoniae* [a]	(Zainee et al., 2021)
	Ulva Lactuca	*Pythium* sp.[b]					

(Continued)

TABLE 2 Continued

Sampling site	Host macroalgae	Isolated strains	Access code	Extract solvent	Bioactive compounds: Application	Inhibited microorganisms	Reference
Rocky coastlines of Praia Dura, Ubatuba, São Paulo, Brazil	*Bostrychia tenella*	*Penicillium waksmanii*[a] *Acremonium implicatum*[b] *Xylaria* sp.[c]	NR	n-hexane fraction	Cytochalasin D[c]: NT	*Staphylococcus aureus*[a,b,c] *Klebsiella pneumoniae*[a,c]	(De Felício et al., 2015)
L'Etete, New Brunswick, Canada	*Devaleraea ramentacea*	*Aureobasidium pullulans*[a]	NR	Methanol	NR	*Staphylococcus aureus*[a,b,c,d,e,f] *Pseudomonas aeruginosa*[a]	(Flewelling et al., 2013)
		Botrytis sp.[b]	NR				
	Palmaria palmata	*Penicillium crustosum*[c]	KF572147				
		Botrytis sp.[d]	NR				
	Polysiphonia lanosa	*Botryotinia fuckeliana*[e]	KF572148				
	Ascophyllum nodosum	*Aspergillus* sp.[f]	NR				
Indonesia	*Euchema* sp.	*Aspergillus elegans*	NR	Ethyl acetate	(+)-Epi-Epoformin: NT	*Escherichia coli* *Staphylococcus aureus* *Bacillus subtilis*	(Rajamani et al., 2019)
Inhibition of pathogenic fungi							
Nirvana beach, Padang, West Sumatra, Indonesia	*Padina* sp.	*Trichoderma harzianum*	NR NT9	Ethyl acetate	NR	*Candida albicans*	(Handayani et al., 2019)
Kovalam coast, Trivandrum, Kerala, India	*Hypnea musiformis*	*Aspergillus terreus*	MH469513	Fungal crude extract	NR	*Aspergillus fumigatus* *A. flavus* *Candida albicans* *C. tropicalis* *C. duobushaemulonii*	(Sarasan et al., 2020)
	Chaetomorpha antennina	*Aspergillus versicolor*	MH469523 MH469532				
	Sargassum wightii and *Hypnea musiformis*	*Hortea werneckii*	MH469501				
Rocky coastlines of Praia Dura, Ubatuba, São Paulo, Brazil	*Bostrychia tenella*	*Penicillium waksmanii*[a] *Penicillium decaturense*[b]	NR	n-hexane[a] Ethyl acetate[b]	NR	*Cladosporium cladosporioide*[a,b] *Cladosporium sphaerospermum*[a,b]	(De Felício et al., 2015)
L'Etete, New Brunswick, Canadá	*Devaleraea ramentacea*	*Penicillium decumbens*	KF572138	Methanol	NR	*Candida albicans*	(Flewelling et al., 2013)
Inhibition of pathogenic protozoa							
Scotland and France	*Ascophyllum nodosum* *Pelvetia canaliculata* *Laminaria digitata* *Saccharina latissima*	*Penicillium janczewskii*[a] *Phaeosphaeria* sp.[b] *Chaetomium globosum*[c] *Chaetomium globosum*[d] *Phoma exigua*[e] *Paradendryphiella arenaria*[f]	MH397623-MH397663	Ethyl acetate	Pyrenocines (A y B), (S) and (E)[b]	*Eurychasma dicksonii*[a,b,c,d,e,f] *Anisolpidium ectocarpii*[a,b,c,d,e] *Maullinia ectocarpii*[a,b,c,d,e]	(Vallet et al., 2018)

*NR, Not reported; NE, No extract; NT, Not tested; [a,b,c,d,e,f], Endophytic species related to the solvent, bioactive compound, and pathogen.

probably intervenes in the transduction of signals by the protein tyrosine kinase, and it can affect the actin filaments that form part of the structure of the bacterial cytoskeleton (Akeda et al., 1997) and a decrease in DNA synthesis (Rubtsova et al., 1998). In another study, this compound can inhibit the polymerization of the formed actin contractile rings to be formed on the fungal wall (Gabriel et al., 1998).

Rajamani et al. (2019) showed that *A. elegans* inhibited *E. coli*, *S. aureus*, and *B. subtilis*, possibly due to chemical modifications in its structure, synthesizing biocompatibility derivatives such as antimicrobial properties, causing a reduction in the formation of biofilms, and generating susceptibility to antibiotics (Roscetto et al., 2020), due to (+)-Epi-Epoformin identified by Rajamani et al. (2019). Additionally, this compound inhibits the germination of *Puccinia* sp. and *Uromyces* sp., preventing its penetration into the host (Barilli et al., 2017).

Vallet et al. (2018) showed that pyrenocin A and B; E; and S compounds from *C. globosum* inhibited *E. dicksonii*, *A. ectocarpii*, and *M. ectocarpii*; *E. dicksonii* and *M. ectocarpii*; and *E. dicksonii* and *A. ectocarpii*, respectively. Pyrenokines A and B cause an apoptotic process without permeabilization of the plasma membrane, generating a depolarization of the mitochondrial electrochemical gradient (Chan-Bacab et al., 2021). Regarding pyrenocines E and S, their inhibitory mechanism is not clear.

It has been shown that the production of some antifungal compounds were effective when these strains were co-cultivated with marine bacteria (Cueto et al., 2001). Although bioactive compounds are now being sought to act solely as antifungal agents without any detrimental effect on bacteria (or vice versa), they could become a promising source of specific antimicrobial substances (Sarasan et al., 2020) (Figure 3).

Moreover, it was found that a high percentage of fungi associated with macroalgae have the ability to inhibit pathogenic microbes; however there were genera that did not have the expected effect, possibly because these pathogens were resistant due to modifications of the target site, enzymatic activation, or decreased intracellular drug accumulations (Mathan et al., 2013). Even though there are more reports of studies on fungi associated with macroalgae, the mechanisms of action at cellular level of the identified bioactive compounds are still not clear.

It is likely that antimicrobial mechanisms associated to endophytic organisms could be linked to an inhibition of cell wall synthesis, alteration of plasma membrane function (Xu et al., 2019; Hashem et al., 2022), disruption of mitochondrial function (Xu et al., 2019), interference with nucleic acid or protein synthesis, or induction of oxidative stress, highlighting that each mechanism may depend on the synthesized metabolite (Tijith K. et al., 2019) (Figure 4).

3.2 Hydrolytic enzymes

3.2.1 Cellulolytic activity

Aspergillus proliferans, *Epicoccum sorghinum*, *Cladosporium* sp., *Penicillium corylophilum*, *Penicillium* sp., *Penicillium fagi*, and *Mucor circinelloides* originating from *Ecklonia radiata* had a high degradation of cellulose a week after being evaluated; for *Truncospora tephropora* the degradation only occurred in the third week, decreasing its activity after 6 weeks under oxic conditions (Perkins et al., 2021). Sarasan et al. (2021) also reported that of the 133 endophytic fungi evaluated and isolated from different algae (*Sargassum wightii*, *Caulerpa peltata*, *U. fasciata*, *Dictyota dichotoma*, *Halymenia venusta*, *Hypnea musiformis*, *Grateloupia lithophila*, *Enteromorpha compressa*, *Ceramium diaphanum*, *Padina tetrastromatica*, and *Chaetomorpha antennina*), only 37.6% of the endophytes presented cellulolytic activity.

In spite of its wide application in the paper industry, waste plant matter degradation (Balabanova et al., 2018), and the food industry (Kumar et al., 2018), is it is clear that marine fungi have a low cellulolytic capacity (Balabanova et al., 2018) (Patyshakuliyeva et al., 2020) compared to terrestrial strains, possibly due to the 2–10% content in cellulose and hemicellulose in seaweed (Balabanova et al., 2018).

3.2.2 Lignin degradation

E. sorghinum, *Cladosporium* sp., *T. tephropora*, *Ganoderma sessile*, and *Pleurotus ostreatus* isolated from *E. radiata* showed high degradation of lignin in the third week of evaluation under oxic conditions. However, *M. circinelloides* is one of the endophytes that produce more lignin-degrading enzymes under anoxic conditions (Perkins et al., 2021).

3.2.3 Chitinases production

Chitin (N-acetyl-D-glucosamine repeating units linked to β (1→4)) is the second most abundant biopolymer in nature, constituting part of insects, crustaceans, and fungi (Suryanarayanan et al., 2012). Venkatachalam et al. (2015) found that endophytic fungi *Aspergillus nidulans*, *Penicillium* sp., and *Penicillium* sp. isolated from macroalgae *Halymenia* sp., *Halimeda macroloba*, and *Caulerpa scalpelliformis* produced enzymes that acted on chitin and three chitosan substrates (56%, 38%, or 1.6% degree of acetylation) (Venkatachalam et al., 2015).

Similarly, Sarasan et al. (2021), found that 14% of endophytes isolated from different algae (*Sargassum wightii*, *Caulerpa peltata*, *Ulva fasciata*, *Dictyota dichotoma*, *Halymenia venusta*, *Hypnea musiformis*, *Grateloupia lithophila*, *Enteromorpha compressa*, *Ceramium diaphanum*, *Padina tetrastromatica*, and *Chaetomorpha antennina*) degraded chitin, with *Aspergillus nonius* standing out from the 133 endophytic fungi evaluated.

3.2.4 Other enzymes

Of the five magroalgae sampled (*Sargassum* sp., *U. fasciata*, *Caulerpa* sp., *Hypnea valentiae*, and *H. venusta*), 29 endophytic fungi were isolated from the Vizhinjam coast, Kerala, India, varying for each algal host, verifying that 90% of all fungal isolates presented amylolytic capacity, 86% lipolytic, 69% gelatinase and asparaginase action, and 62% glutaminase (Manomi et al., 2015). In addition, Sarasan et al. (2021) isolated 133 endophytic fungi from 11 macroalgae (*S. wightii*, *C. peltata*, *U. fasciata*, *D. dichotoma*, and *H. venusta* from the coast of Kovalam, Trivandrum, India, and *H. musiformis*, *G. lithophila*, *E. compressa*, *C. diaphanum*, *P. tetrastromatica*, and *C/antennina* from Palakkulam Beach, Calicut, Kerala, India), in which 89.5% have amylolytic activity, 79% gelatinous activity, and 88% lipolytic activity.

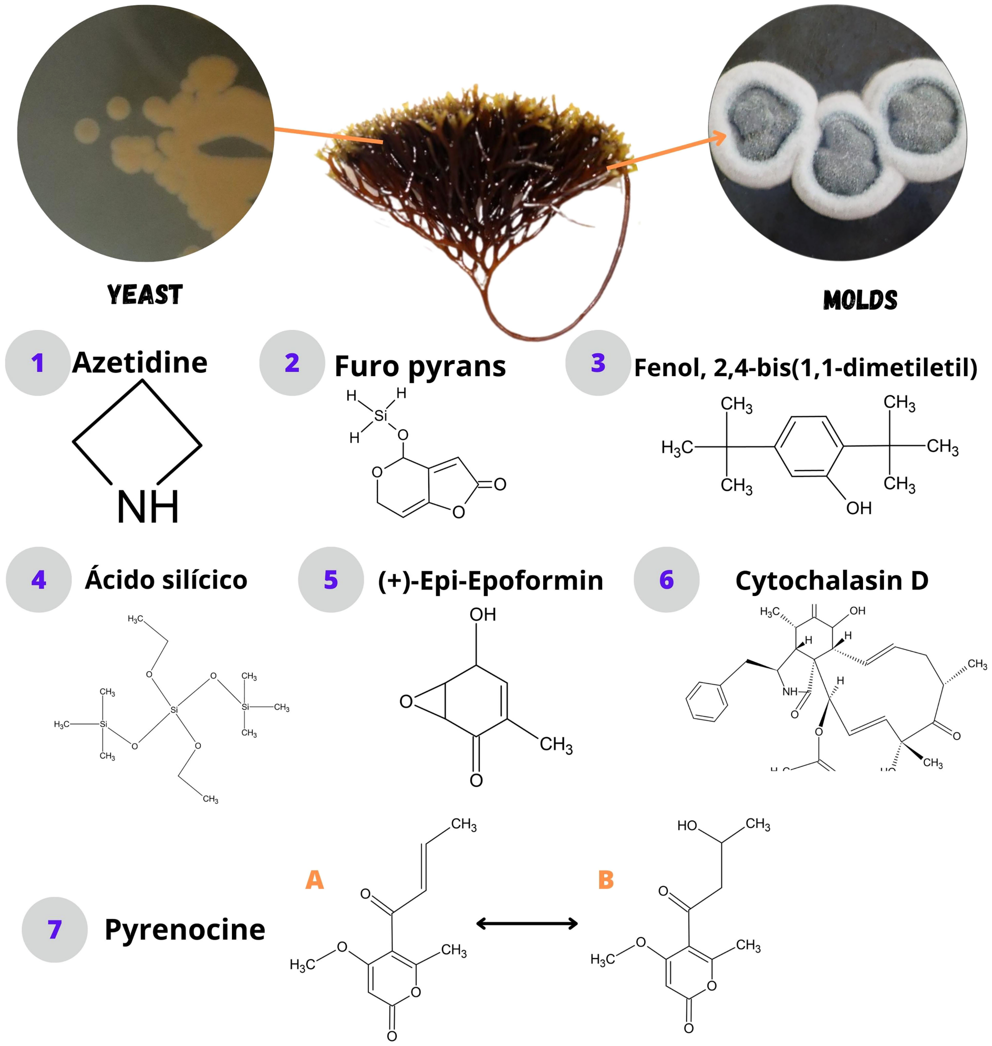

FIGURE 3
Bioactive compounds synthesized by fungi associated with macroalgae.

In addition, Patyshakuliyeva et al. (2020), showed that *Epicoccum nigrum*, *Penicillium brevicompactum*, and *Trichoderma paraviridescens* isolated from *Fucus vesiculosus* from the Scheveningen Beach (the Netherlands), had a higher xylanase production, but *T. paraviridescens* had endoglucanase, xylanase, and glucosidase activities after 120 hours.

3.3 Production of other bioactive compounds

Teixeira et al. (2019b) showed in the mycelia of endophytic fungus *A. flavus*, *Penicillium echinulatum*, *Penicillium purpurogenum*, and *Microascus croci* isolated from macroalgae *Ascoseira mirabilis*, *Adenocystis utricularis*, *Phaeurus antarcticus*, and *Desmarestia anceps* the presence of palmitic, linoleic, oleic, and stearic acids. Squalene and ergosterol (ergosta-5,7,9(11) and 22-tetraen-3β-ol) concentrations of about 16% were obtained in *P. echinulatum*.

Some bacteria like *Bacillus pumilus* and *Bacillus licheniformis* isolated from *Gracilaria dura* produced 445.5 and 335 μgmL^{-1} of indole acetic acid (IAA) and 12.51 and 10.14 mM mL^{-1} of ammonia, demonstrating that these compounds induced the growth of new buds in *G. dura* (Singh et al., 2011) and can be used to improve the production of macroalgae of biotechnological interest.

4 Application of antimicrobials and hydrolytic enzymes produced by bacteria and fungi associated with macroalgae

4.1 Antimicrobial application

Bioactive compounds synthesized by bacteria and fungi associated with macroalgae with antimicrobial potential against pathogens and food spoilers can be applied in the food industry

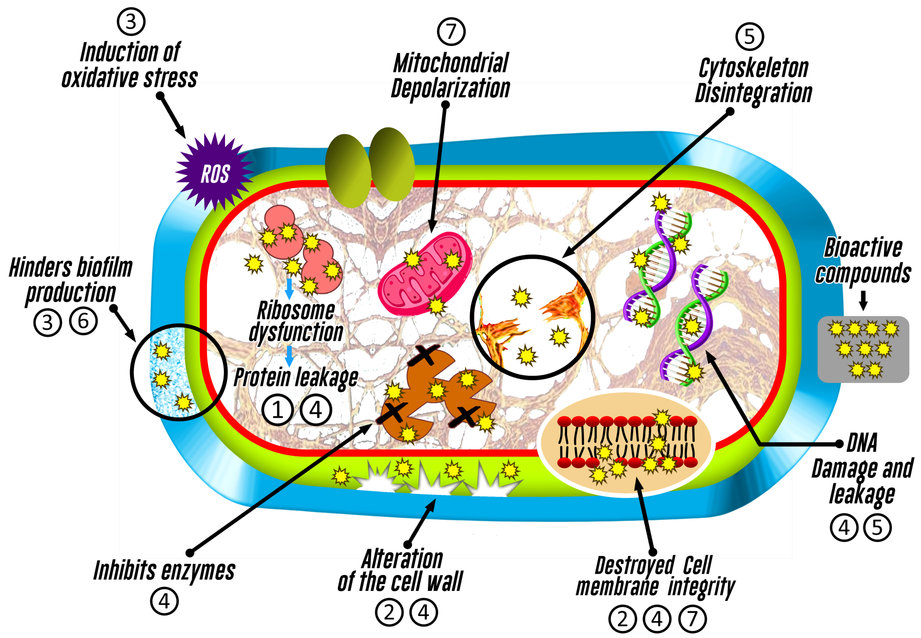

FIGURE 4
Inhibitory action mechanisms of bioactive compounds identified in fungi associated with macroalgae on pathogenic microorganisms. The numbering represents the bioactive compound (1: Azetidine; 2: Furo-pyrans; 3: Phenol, 2,4-bis(1,1-dimethylethyl)-; 4: Silicic acid; 5: (+)-Epi-Epoformin; 6: Cytochalasin D; and 7: Pyrenocine).

as preservatives for perishable foods (Yong et al., 2007; Bouarab-Chibane et al., 2019; Rani et al., 2021), selection of starter cultures in fermentation processes (Sánchez-Maldonado et al., 2011), disinfectant active compounds (Soni and Brightwell, 2022), water treatment, and pulp processing. In other fields, bioactive compounds can replace synthetic drugs in the treatment of infectious diseases (Danquah et al., 2022) and be used in paper manufacturing, mastics, adhesives, and as disinfectants for textiles, plastics, and cosmetics (Farr et al., 2003).

4.2 Hydrolytic enzyme application

Cellulase, together with hemicelluloses and pectinases, is an important group of enzymes, where its application in food increases its quality and antioxidants (Kumar et al., 2018), and reduces browning (Sims and Bates, 1994), rancidity, and residuality (Kumar et al., 2018). Furthermore, the use of cellulases allows polymers to be degraded, reducing their effect during the baking process, as they are in their pure form, or reducing yield during juice production.

Commercial animal feed can also be prepared using cellulase enzymes, due to their low digestion in some mammals and birds (Kumar et al., 2018), and farmers can use the enzymes as supplements (Liu and Kokare, 2017). In addition, cellulase enzymes present a potential utility in biorefineries, where certain estuaries and mangroves with a rich lignocellulosic biomass constitute a feeding zone for cellulose digesters (Barzkar and Sohail, 2020). Additionally, Trivedi et al. (2016) mentioned that microbial cellulases have demonstrated their efficiency in the conversion of cellulosic plant biomass into fermentable sugar, presenting great bioenergetic potential. Ligninase from these marine microbes may be suitable for bioremediation of effluents from the paper industry (Sarasan et al., 2021) due to its ability to degrade lignocellulosic biomass into fermentable sugars (Suryanarayanan et al., 2012) and could be used in the biofuels field (Bonugli-Santos et al., 2015).

Chitin deacetylases and chitosanases could be used to remodel natural chitin or chitosans and can be adapted according to needs (Suryanarayanan et al., 2012) such as functional foods and nutraceuticals for humans or in the preservation of foods from agriculture and livestock (Zhang et al., 2022). In addition, they allow the biodegradation of chitinous waste, reducing environmental risks and generating products of industrial value (Tamadoni Jahromi and Barzkar, 2018).

Although Patyshakuliyeva et al. (2020) evidenced the presence of endoglucanases, xylanases, and glucosidases in *T. paraviridescens*, the knowledge of the enzymes involved in algal carbon sources (laminaria, alginate, and carrageenan) is still scarce. These results show that amylolytic activities are enzymatic processes that allow the formation of very specific products compared to chemical modifications (hard conditions and a greater number of by-products), providing various starch products with multiple uses for the food industry and with good biochemical characteristics for industrial processes (Farias et al., 2021). Similarly, amylases and gelatinases are enzymes that hydrolyze gelatin into smaller oligopeptides, being important for the production of hydrolysates that could be applied in the production of various foods (desserts and candies) and non-foods (cosmetics) (Mekonnen et al., 2022). Likewise, lipolytic activity mediated by lipases is important, as it allows the degradation of oleaginous substances used in the food industry, releasing fatty acids as health protectors from edible oil converting themselves into good additives of functional food products (Kotogán et al., 2022).

Asparaginases may be an alternative source for anticancer enzyme production (Hatamzadeh et al., 2020) by converting asparagine into aspartic acid, reducing the presence of acrylamide produced at high temperatures in starchy foods and maintaining sensory quality (Xu et al., 2016) and as a source of therapeutic enzymes by being part of functional foods. Regarding glutaminase, it is an enzyme that could improve functional properties such as solubility, emulsification, and foaming properties, and flavor, and could reduce allergenicity. The redesign of protein foods could improve their process performance and consumer acceptance (Liu et al., 2022a).

5 Conclusion

Bacteria and fungi associated with macroalgae have the ability to inhibit pathogenic bacteria, fungi, yeasts, and protozoa that affect aquaculture, public health, and the food industry. Pyrenocins A, B, E, and S obtained and fractionated from *Phaeosphaeria* sp. inhibited pathogenic protozoa. Other compounds, such as phenol, 3, 5-bis (1, 1-dimethylethyl), heptacosane, 2-methyloctacosane, polyketides, lipopeptides, desferrioxamine B and B2, azelaic acid, azitidine, furopyrans, phenol, 2,4-bis(1,1-dimethylethyl)-, silicic acid, cytochalasin D, and (+)-Epi-Epoformin, were only identified, and the mechanisms of action of each compound have not been reported yet, except pyrenocines A and B, which demonstrated inhibitory action. These compounds found in living organisms act by altering the membrane and wall cells, inhibiting and denaturing proteins and enzymes, damaging genetic material, decreasing reactive oxygen species (ROS), and altering the actin filaments of the cytoskeleton, causing mitochondrial electrochemical depolarization or hindering biofilms production.

Independent of antimicrobial activity, the associated microorganisms can synthesize hydrolytic enzymes such as xylanase, amylase, cellulase, pectinase, agarase, lignocellulase, chitinase, gelatinase, asparaginase, glutaminase, and lipase that can be used to reduce enzymatic oxidation and browning, improve digestibility, functionality, and food preservation. Likewise, they could be used for the bioremediation of agricultural waste, industrial effluents, or production of hydrolysates.

Author contributions

EV-P and MR-C conceived, designed, and wrote the original draft of the manuscript. JV-M and NA-T edited, reviewed, and proposed amendments to the manuscript. LE-E, LM-Q and HC-S supervised, reviewed, and critically commented on and edited the manuscript. All authors contributed to the manuscript and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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