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ORIGINAL PAPER

Diversity of endophytic bacteria with antimicrobial potential isolated from marine macroalgae from Yacila and Cangrejos beaches, Piura-Peru

Edwin Jorge Vega-Portalatino[1] · Miriam Marleni Rosales-Cuentas[1] · Carmen Tamariz-Angeles[2] · Percy Olivera-Gonzales[2] · Luis Alfredo Espinoza-Espinoza[3] · Luz Arelis Moreno-Quispe[4] · Jube Ciro Portalatino-Zevallos[5]

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Abstract

Endophytic bacteria found in marine macroalgae have been studied for their potential antimicrobial activity, consequently, they could serve as a valuable source of bioactive compounds to control pathogenic bacteria, yeasts, and fungi. Algae endophytic bacteria were isolated from *Caulerpa* sp., *Ulva* sp., *Ahnfeltiopsis* sp., and *Chondracantus chamissoi* from Yacila and Cangrejo Beaches (Piura, Peru). Antimicrobial assays against pathogenic bacteria were evaluated using cross-culture, over-plate, and volatile organic compound tests. Afterward, the minimum inhibitory concentration (MIC) and minimum bactericidal concentration (MBC) of selected crude extracts were determined, also ITS molecular analysis, antifungal activity, and PCR of iturin, fengycin, and surfactin genes were performed for bacteria strains exhibiting better activity. Forty-six algae endophytic bacteria were isolated from algae. Ten strains inhibited gram-positive pathogenic bacteria (*Enterococcus faecalis*, *Staphylococcus epidermidis*, *S. aureus*, and *Listeria monocytogenes*), and 12 inhibited gram-negative bacteria (*Escherichia coli* and *Salmonella enteric* sv *typhimurium*). Bacteria with better activity belong to *Bacillus* sp., *Kluyvera ascorbata*, *Pantoea agglomerans*, *Leclercia adecarboxylata*, and *Enterobacter* sp., which only four showed antifungal activities against *Candida albicans*, *C. tropicalis*, *Colletotrichium* sp., *Fusarium* sp., *Fusarium oxysporum*, and *Alternaria* sp. Furthermore, *K. ascorbata* YAFE21 and *Bacillus* sp. YCFE4 exhibited iturin and fengycin genes. The results indicate that the algae endophytic bacteria found in this study, particularly *K. ascorbata* YAFE21, *Bacillus* sp. YCFR6, *L. adecarboxylata* CUFE2, *Bacillus* sp. YUFE8, *Enterobacter* sp. YAFL1, and *P. agglomerans* YAFL6, could be investigated as potential producers of antimicrobial compounds due to their broad activity against various microorganisms.

Keywords Bacteria · Fungi · Yeasts · Pathogens · Biocontrol · Infections

Vega-Portalatino Edwin Jorge and Rosales-Cuentas Miriam Marleni contributed equally to this work.

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✉ Edwin Jorge Vega-Portalatino
evega@unf.edu.pe

Miriam Marleni Rosales-Cuentas
mrosales@unf.edu.pe

Carmen Tamariz-Angeles
ctamariz@unasam.edu.pe

Percy Olivera-Gonzales
poliverag@unasam.edu.pe

Luis Alfredo Espinoza-Espinoza
lespinozae@unab.edu.pe

Luz Arelis Moreno-Quispe
lmoreno@unf.edu.pe

Jube Ciro Portalatino-Zevallos
jportalatinoz@unasam.edu.pe

[1] Laboratorio de Biotecnología Microbiana, Universidad Nacional de Frontera, Sullana 20100, Peru

[2] Centro de Investigación de la Biodiversidad y Recursos Genéticos de Ancash, Facultad de Ciencias, Universidad Nacional Santiago Antúnez de Mayolo, Huaraz 02001, Peru

[3] Departamento de Ingeniería, Universidad Nacional de Barranca, Barranca 15169, Peru

[4] Faculty of Business Sciences and Tourism, Universidad Nacional de Frontera, Sullana, Piura 20100, Peru

[5] Facultad de Ciencias, Universidad Nacional Santiago Antúnez de Mayolo, Huaraz 02001, Peru

Introduction

Pathogenic microorganisms causing foodborne infections and food spoilage are becoming resistant to common antimicrobials, posing risks to human health and food production and storage (Jakubczyk and Dussart 2020). In this sense, researchers are exploring various sources of antimicrobials to discover new drugs, such as macroalgal endophyte bacteria (Kizhakkekalam and Chakraborty 2020). They have found these microorganisms yield polyphenols, flavonoids, anthocyanins (Carlos et al. 2022), alkaloids, steroids, triterpenoids (Habbu et al. 2016), and lipopeptides (Lam et al. 2021), which could inhibit same pathogenic microorganisms, e.g. *Listeria monocytogenes*, *Staphylococcus aureus*, *Escherichia coli*, *Salmonella typhimurium*, *S. enteritidis*, *S. tiphy*, and *Pseudomonas aeruginosa*, *Saccharomyces cerevisiae*, *Candida albicans*, *Fusarium moniliforme*, *F. cubense*, *Botrytis cinerea*, *Ceratocystis paradoxa*, *Sporisorium scitamineum*, etc. (Jakubczyk and Dussart 2020; Dao-Jun et al. 2020). Among the mechanisms involved in antimicrobial activity, there could be the inhibition or blockage of enzymes, ribosomes, protein synthesis, or DNA synthesis (Carlos et al. 2022), reduction of resistance development, and negative effects on pathogens' morphology and physiology (Vega-portalatino et al. 2023).

Commonly, macroalgae play an important role in the primary production in marine ecosystems, supporting a wide diversity of aquatic organisms including their endophyte microorganisms (Carlos et al. 2022; Kandasamy and Kathirvel 2023). In this sense, Peruvian algae have mainly been studied for their taxonomic classification, but rarely for their biological activities. *Chondracanthus chamissoi* – prevalent endemic red algae – has been considered one of the most abundant species from Peru (Suárez-alarc et al. 2021). It is characterized by its green-blue and reddish membranous, flattened, and irregular branching thallus (Carbajal et al. 2019; Muñoz et al. 2020), but its antimicrobial activity has not been approached yet. However, the ethanolic and methanolic extracts from other species of *Chondracanthus* genus exhibited antibacterial activity against *S. aureus*, *Streptococcus pyogenes*, *L. monocytogenes*, *Salmonella enterica*, *E. faecalis*, *P. aeruginosa*, etc. (Rhimou et al. 2010; Muñoz-Ochoa et al. 2010; Cox et al. 2010). Other macroalgae found on the Peruvian coast belong to *Caulerpa* genus. They are common invasive species, characterized by their long, compact fronds and they grow in shallow waters, colonizing bare sediments, and forming grasslands (Suárez-alarc et al. 2021; Bradley et al. 2021). Their ethanolic extracts inhibited *Klebsiella pneumoniae*, *E. coli*, *P. aeruginosa*, and *Shigella dysenteriae* (María et al. 2023). Similarly, *Ahnfeltiopsis* species that grow on the Peruvian coast exhibit erect, cylindrical, rigid thallus yellowish green to brown or greenish brown darker towards its base with numerous dichotomous branches at the top (Carbajal et al. 2019) (Rodríguez et al. 2018). Ethanolic extract of *Ahnfeltiopsis durvillaei* collected from the Peruvian central coast inhibited *S. aureus* isolated from clinical patients (Magallanes et al. 2003).

Endophyte microorganisms from the algae species described above have not been reported yet. However, *Ulva lactuca*, which is defined as green algae with rounded lamellar and ovate thallus, lobed, orbicular, or irregular shape, without branching and with undulations (Carbajal et al. 2019; Muñoz et al. 2020; Arakaki et al. 2023) was studied for its endophyte microorganism, so, a sample collected from Someshwar Beach (Mangalore, Dakshina Kannada, Karnataka, India) showed bacterial endophytes with antimicrobial activity against *Enterococcus faecalis*, *Klebsiella pneumoniae*, *Aspergillus* sp., *Candida albicans* (Habbu et al. 2016), *E. coli* and *S. aureus* (Dhanya et al. 2016). These findings suggest that macroalgae and their endophytes may produce a variety of secondary metabolites, potentially leading to the development of new drugs (Stincone et al. 2020). Therefore, isolation of these microorganisms should be a priority (Cochrane and Vederas 2016).

Lipopolypeptides - one type of antimicrobial secondary metabolites- are classified as new antibiotic drugs, they are synthesized by peptide synthases and have D-amino acids linked by a β-hydroxy fatty acid (Wang et al. 2023; Geissler et al. 2019; Fei et al. 2020). They are classified into diverse groups based on their cyclic and linear (non-cyclic) peptides and structure, further, polymyxin B and daptomycin are FDA-approved commercial structures, while others are in various stages of preclinical or clinical trials. (Cochrane and Vederas 2016). Some genes coding lipopolypeptides with antibacterial, antifungal, and antiviral activity are known, e.g. fengycin genes that encode fengincin A, B, and plipastatin (Geissler et al. 2019), iturin genes encoding iturin A-E, bacilomicin D, F, L, mycosubtilin, and mojavencin (Stincone et al. 2020), and surfactin genes for surfactin-C_{11} and surfactin A, B, C (Medeot et al. 2023; Deutsch et al. 2021; Díaz-Castillo et al. 2018). Thus, identifying genes associated with antimicrobial compounds may be crucial as they could encode new natural products (Wang et al. 2023; Muñoz-Silva et al. 2019). Moreover, this information can be used in functional genetic studies to determine the optimal growing conditions (Zamorano et al. 2022; Singh et al. 2021) and to monitor antibiotic yielding during biotechnological production.

Species belonging to *Bacillus*, *Kluyvera*, *Pantoea*, *Leclercia*, and *Enterobacter* isolated from marine macroalgae exhibited antibacterial and antifungal activities (Kizhakkekalam and Chakraborty 2020; Habbu et al. 2016; Dao-Jun et al. 2020; Muñoz et al. 2020; Muñoz-Silva et al.

2019; Zamorano et al. 2022; Singh et al. 2021; Edoamodu and Nwodo 2022; Rangarajan et al. 2015; Gong et al. 2019; Gnanasekaran et al. 2023; Tambekar and Bhutada 2010) and they could be a new source of bioactive compounds as antibiotics, antimicrobials, anticancer, antibiofilm, and antivirals drugs (Gnanasekaran et al. 2023). They could be useful against enteric infections and potential substitutes for medicinal plants (Dhanya et al. 2016; Rani et al. 2021). Hence, they could also be applied as food preservatives to ensure food safety and quality (Arshad and Batool 2017) substituting ineffective and costly antimicrobials (Rani et al. 2021). In addition, they could have industrial and environmental applications (Vega-portalatino et al. 2023). This research aims to study the diversity of endophytic bacteria of marine macroalgae collected from the northern coast of Peru (Yacila and Cangrejos beaches, Piura) and determine their potential as a source of antimicrobials because these algae and their microbial diversity have not been previously investigated. This study could support future research because the findings will open a new approach due to the biotechnological potential and benefits identified in some endophytic bacteria isolated.

Materials and methods

Collection of macroalgae

The most predominant and easily accessible macroalgae (*Caulerpa* sp., *Ahnfeltiopsis* sp., *Ulva* sp., and *C. chamissoi*) were randomly collected from Cangrejo and Yacila beaches (GPS decimal degree: −5.144412, −81.174492 and −5.128802, −81.167577, respectively), Paita, Piura, Peru. Samples without signs of disease or damage were selected. They were externally disinfected with 70° alcohol (Deutsch et al. 2021), put in sterile bags with seawater, and transported to Laboratorio de Biotecnología de la Universidad Nacional de Frontera in a refrigerated container (approx. 4 °C). Taxonomic identification was carried out by the Instituto del Mar del Peru (IMARPE), Paita, Piura-Peru using three samples and the Guide for macroalgae recognition from Callao (Carbajal et al. 2019). Isolation of endophytic bacteria was performed within 24 h of collection.

Isolation of endophytic bacteria

The samples (discs and fronds macroalgae) were washed with tap water to remove external debris. Fragments (1 cm, forty-five) were disinfected with ethanol 70° for 30 s, followed by 2% NaCIO (60 s), and three successive washes (5 min) with sterile distilled water (Rodríguez et al. 2018; Muñoz-Silva et al. 2019). They were placed into sterile vials with Trypticase Soy Broth (TSB, 2 mL) for 5 min (as surface contamination control). Afterward, the samples were transferred to absorbent sterile paper and cut transversely to obtain two pieces, which were placed into sterile vials with Trypticase Soy Agar (TSA) supplemented with nystatin (50 µg/mL). They and their controls were incubated at 25 °C for 2 to 4 days. It was considered bacteria endophyte when its control surface vial did not have bacterial growth, afterward, the bacteria around algae fragments were purified by successive streaking on Petri plates with TSA and culture in TSA-slanted tubes. All axenic bacteria strains were cryopreserved in TSB-glycerol (30%) cryovials (Ulloa-Muñoz et al. 2020).

Antibacterial activity

Pathogenic bacteria

Algae endophytic bacteria were evaluated against four gram-positive bacteria (*Enterococcus faecalis* ATCC29212, *Staphylococcus epidermidis* ATCC12228, *Staphylococcus aureus* ATCC25923, and *Listeria monocytogenes* ATCC7644) and three gram-negative bacteria (*Escherichia coli* O157:H7, *E. coli* ATCC10536 and *Salmonella enterica* sv *typhimurium* ATCC14028).

Inoculum preparation

Algae endophytic and pathogenic bacteria were cultured in TSB (5 ml) at 25 or 37 °C for 16 h (Habbu et al. 2016). Afterward, they were centrifuged at 2000 g for 5 min, the pellet was diluted in sterile NaCl (0.8%) at 0.08 optical density at 620 nm, equivalent to approximately 1×10^8 CFU/mL.

Selection of endophytic bacteria

Algae endophytic bacteria (OD_{620}: 0.08) were inoculated-making a cross on Petri dishes with TSA and incubated at 25 °C for 48 h. After, 2 µl fresh culture of pathogenic bacterium (OD_{620}: 0.08) was soaked into a sterile filter paper disk (6 mm) and inoculated on each edge of the previously inoculated plate. Plates were incubated at 25 °C for 96 h. (Deutsch et al. 2021). For negative control, pathogens were cultured on plates without algae endophytic bacteria. Bacterial growth was estimated by comparing the growth of pathogens in the plate with/without endophytic bacteria following this formula Ifo%=[(A-B)/A] *100, where A is the diameter of the pathogen without the endophytic bacteria and B is the diameter of the pathogen when it interacts with the endophytic bacteria. It was considered four levels: 100 to 90% (+++: strong inhibition), 89 to 50% (++: moderate

inhibition), 49 to 8.5% (+: weak inhibition), and 8.5 to 0% (−: no inhibition) (Deutsch et al. 2021).

Over-plate tests (OpT)

Previously, antimicrobial metabolite was produced: 100 µL of algae endophytic bacteria (OD_{620}: 0.08) was inoculated by incorporation into 20 mL of TSA plates and incubated at 25 °C for 10 days. Afterward, the culture was cut into 5 mm disks. For the OpT, 100 µL of pathogenic bacteria (OD_{620}: 0.08) was inoculated by extension in TSA plates, and immediately 3 disks of algae bacteria were added and incubated at 25 °C for 24 h (Carbajal et al. 2019; Fei et al. 2020). TSA without algae endophytic bacteria disks (5 mm) were negative control, and penicillin disks (10 IU) and nystatin were standard antibiotics. Clear halos indicated antibacterial activity and were measured in millimeters (mm).

Volatile Organic compounds Test (VOCt)

One hundred milliliters of algae endophytic bacteria (OD_{620}: 0.08) was inoculated by extension on TSA plates. Parallelly, three filter paper disks (6 mm) with 2 µL of pathogenic bacteria were inoculated on Müller and Hinton agar (MHA) plates. Both bottom plates were put together and sealed with Parafilm. The plate with algae endophytic bacteria was placed on the bottom and the plate with the pathogen was placed on top (Garrido et al. 2020). TSA plates without algae endophytic bacteria were pathogenic bacteria growth control. The growth inhibition of pathogenic bacteria was determined as inhibition percentage: AH% =[(A-B)/A]*100, where A is the diameter of pathogenic bacteria without algae endophytic bacteria; and B is the diameter of pathogenic bacteria when interacting with algae endophytic bacteria.

MIC and MBC test

Three algae endophytic bacteria showing better antimicrobial activity in previous tests were chosen to evaluate minimal inhibition concentration (MIC) following the method described by Tamariz-Angeles et al. (Tamariz-angeles et al. 2023). The endophytic bacteria were grown in TSB (40 mL) at approx. 25 ± 2 °C with orbital agitation at 150 rpm for 10 days. Subsequently, the cultures were centrifuged and then filtered through a Millipore filter with a pore size of 0.22 µm to obtain their extracts containing secondary metabolites. The cell-free extracts were mixed with Müller and Hinton II Broth (MHIIB) at dilutions of 100, 75, 50, 25, and 10% (Sarasan et al. 2020). Immediately, dilutions (100 µL) were transferred to a 96-well microplate and inoculated with 10 µL of fresh pathogenic bacteria (OD_{620}: 0.08). Three replicates and contamination controls were prepared and incubated at 37 °C for 24 h. The growth of pathogenic bacteria was observed using a magnifying glass, and MIC was determined as the minimum concentration of extract that inhibited completely bacterial growth (Tamariz-angeles et al. 2023). To determine the minimum bactericidal concentration (MBC), 10 µL of each well was sub-cultured in MHA plates (extract-free), and incubated at 37 °C for 48 h. The minimum concentration that did not show bacterial growth was considered like MBC (Puškárová et al. 2017).

Molecular taxonomic identification of selected strains

It was performed for bacteria strains with better antibacterial activity. Selected endophytic bacteria were cultured in Luria Bertani Broth (LB), their pellets were recovered by centrifugation and their DNA was extracted by cetyltrimethylammonium bromide (CTAB) method (Díaz-Castillo et al. 2018). Amplification of 16 S rDNA fragments was carried out by PCR using 27 F and 1492R set primers (Díaz-Castillo et al. 2018). Amplicon quality was determined by agarose electrophoresis (1.5%). PCR products were sequenced by the SANGER method in Macrogen (Seul, Korea) with 518 F and 800R set primers. The sequences were edited and assembled with Chromas lite and Cap3 programs. For taxonomic group identification, sequences were aligned with reference sequences from the Genbank using BlastN (https://blast.ncbi.nlm.nih.gov/). According to the taxonomic group, its phylogenetic tree was prepared using ClustralX v.2.1 for aligning, and Mega v.11 with Neighbor-joining, Kimura-2, and 1000 bootstraps algorithms.

Antifungal activity

Endophytic bacteria exhibiting better antibacterial activities were selected for evaluation. Anti-yeast activity was assessed using OpT, VOCt, and MIC methodologies as previously described, while anti-filamentous fungi activity was determined using over-culture (Ulloa-Muñoz et al. 2020); Puškárová et al. 2017).

Anti-candidal activity

Candida albicans ATCC90028 and *C. tropicalis* ATCC750T were used. First, it was performed following OpT and VOCt methods using Papa Dextrose Agar (PDA). Furthermore, the extract with better activities was used to evaluate MIC and MBC against these candida using Potato dextrose broth (PDB) (Tamariz-angeles et al. 2023).

Antifungal activity against filamentous fungi

The filamentous fungi used were *Fusarium* sp. H (Tamarizangeles et al. 2023), *F. oxysporum* CTLM12 (Muñoz-Silva et al. 2019), *Alternaria* sp. ATCC20084, and *Colletotrichium* sp. The last strain is a wild fungus isolated from *Persia americana* "avocado" with anthracnosis symptoms. These fungi were cultured in PDA plates at 28 °C for 5 days, subsequently, their mycelium was cut into discs (diameter 5 mm). For the assay, the fresh culture of algae endophytic bacteria (OD_{620}: 0.08) was swabbed in Petri dishes with PDA and immediately 3 discs of mycelium were placed on them. The over-culture plates were incubated at 25 °C for 3 to 5 days. PDA plates without algae endophytic bacteria were used as fungus growth control. The inhibitory capacity was determined from the percentage inhibition of fungi by Ifo%=[(A-B)/A]*100, where A is the diameter of fungus without endophytic bacteria and B is the diameter of fungus when interacting with endophytic bacteria(Ulloa-Muñoz et al. 2020).

Presence of iturin, fengycin, and surfactin genes

Fragments of Iturin C, Fengycin D, and Surfactin A genes were amplified by conventional PCR using previously described set primers (Table 6) (Mora et al. 2011). Amplicons were checked by agarose gel electrophoresis (2%), and DNA bands with the sizes corresponding to described genes in Table 1 were considered positive results.

Statistical analysis

All assays were conducted with 2 or 3 replicates. Mean and standard deviation (SD), ANOVA, and Tukey's test ($\alpha = 0.05$) were analyzed using the Statistical Package for Social Sciences (SPSS) v.23.

Results

Macroalgae collection and isolation of endophytic bacteria

Four macroalgae were collected from each beach (Yacila and Cangrejos), which were identified as *Caulerpa* sp., *Ahnfeltiopsis* sp., *Ulva* sp., and *C. chamissoi* (Fig. 1).

Forty-six algae endophytic bacteria were isolated from all macroalgae collected (Table 2). Thirteen (29.3%) endophytic bacteria corresponded to three macroalgae (*Caulerpa* sp., *Ulva* sp., and *C. chamisoi*) collected from Cangrejos beach, and 33 (71.7%) corresponded to four macroalgae (*Caulerpa* sp., *Ulva* sp., *C. chamisoi*, and *Ahnfeltiopsis* sp.) from Yacila beach. Furthermore, most endophytic bacteria were isolated from algae stipe.

Concerning marine macroalgae phylum, *Chlorophytas* macroalgae (*Caulerpa* sp. and *Ulva* sp.) from Yacila and Cangrejo had 8 (17.4%) and 11 (23.9%) isolated endophytic bacteria strains, respectively. *Rhodophyta* macroalgae (*Ahnfeltiopsis* sp. and *C. chamisoi*) from Yacila and Cangrejo contributed 5 (10.9%) and 22 (47.8%) endophytic bacteria strains, respectively (Fig. 2).

Antibacterial assay

Selection of endophytic bacteria with better antibacterial activity

The antimicrobial activity of 46 endophytic bacteria was evaluated. Results showed that 10 marine endophytic bacteria exhibited strong inhibition against at least 3 of 4 evaluated gram-positive pathogenic bacteria, 30 showed moderate activity, and 6 displayed weak activity (Table 3; Fig. 3). Also, 12 algae endophytic bacteria showed strong inhibitory activity against at least 2 gram-negative pathogenic bacteria, 28 exhibited moderate activity, and 6 displayed weak activities.

Table 1 Oligonucleotide primers used to detect cyclic lipopeptide genes

First	Expression product	Sequence (5′→3′)	Gene	Melting T (oC)	Product size (Ps)
ITUCF	Iturin	GGCTGCTGCAGATGCTTTAT	ituC	60.1	423
ITUCR		TCGCAGATAATCGCAGTGAG			
FENDF	Fengycin	GGCCCGTTCTCTAAATCCAT	fenD	60.1	269
FENDR		GTCATGCTGACGAGAGCAAA			
SRFAF	Surfactin	TCGGGACAGGAAGACATCAT	srfAA	60.4	201
SRFAR		CCACTCAAACGGATAATCCTGA			

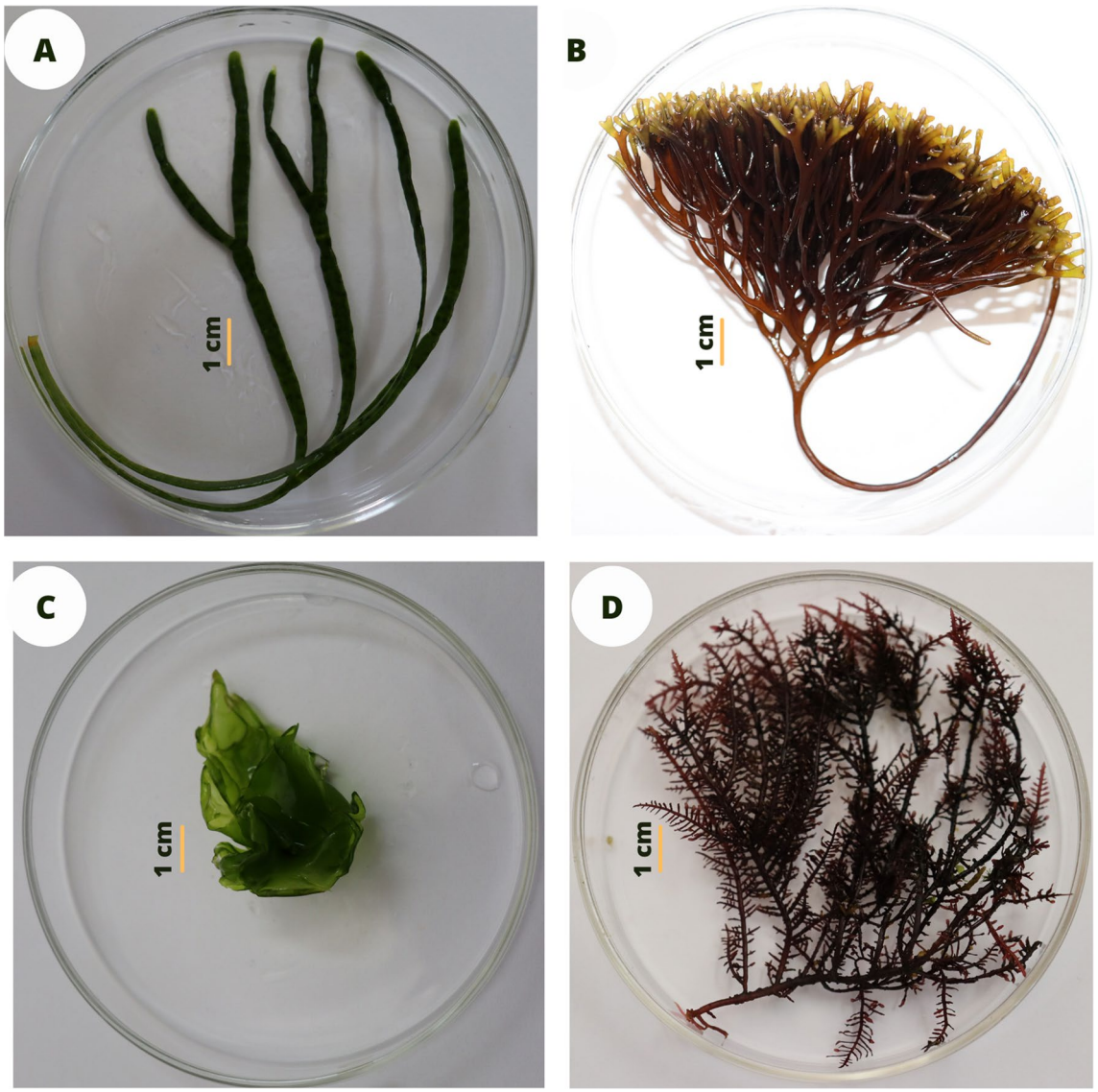

Fig. 1 Marine macroalgae collected at Yacila and Cangrejo beaches. **A** *Caulerpa* sp. **B** *Ahnfeltiopsis* sp. **C** *Ulva* sp. **D** *Chondracantus chamissoi*

OpT, VOC, and MIC tests

Ten selected endophytic bacterial strains were tested using OpT and VOCt against gram-positive pathogens (Table 4). YAFL9 showed higher antibacterial activity against *E. faecalis* by VOCt, but by OpT methodology no algae endophytic strains inhibited this pathogen. Furthermore, YAFE21 showed strong inhibitory activity against *S. epidermidis* by OpT, like YCFE1 and YCFR6 by VOCt. YAFL6 exhibited strong inhibition activity against *S. aureus* by OpT, but YCFE1 and YCFR6 strains showed better results by VOCt. Only YAFE21 inhibited *L. monocytogenes* by OpT, but YCFE4 and YAFE21 showed higher inhibitory activity by VOCt.

Regarding the antibacterial activity against gram-negative pathogenic bacteria, 12 endophytic bacteria were selected for OpT and VOC tests (Table 5). CUFE2 showed higher inhibitory activity against *E. coli* O157:H7 by OpT, also, YCFR5, YUFE8, and CUFE2 showed higher activity by VOCt. Furthermore, YAFL1 reached a higher inhibitory activity against *E. coli* ATCC10536 by OpT, and YCFE4, CUFE2, YUFE8, YCFEP3, and YCFR5 were more active by VOCt. Likewise, YAFL1 inhibited *S. enterica* cv *typhimurium* by OpT and YAFL6 VOCt.

According to these results, three algae endophytic bacteria were selected for MIC and MBC assays: YCFE4, which exhibited antibacterial activity against four gram-positive pathogens; CUFE2 and YAFL6, which showed antibacterial activity against three gram-negative pathogens tested. The extracts obtained showed variable concentrations corresponding to 5.662 mg/ml (CUFE2 and YAFL6) and 6.52 mg/ml (YCFE4) at maximum concentration for each

Table 2 Endophytic bacteria isolated from different marine macroalgae from Cangrejos and Yacila beaches, Piura - Peru

Collection site	Phylum	Species	Algae parts		Codes	Number of fragments	Number of isolated algae endophytic bacteria
Cangrejo Beach	*Chlorophyta*	*Caulerpa* sp.	Fixing disc		CCDF	15	2
			Fronda	Stipite	CCFE	15	1
				Lamina	CCFL	15	0
		Ulva sp.	Fronda	Stipite	CUFE	15	4
				Lamina	CUFL	30	1
	Rhodophyta	*Ahnfeltiopsis* sp.	Fronda	Stipite	CAFÉ	30	0
				Lamina	CAFL	15	0
		Chondracantus chamissoi	Fronda	Main shaft	CCFEP	30	0
				Branching	CCFR	15	5
Yacila Beach	*Chlorophyta*	*Caulerpa* sp.	Fixing disc		YCDF	15	0
			Fronda	Stipite	YCFE	15	5
				Lamina	YCFL	15	3
		Ulva sp.	Fronda	Stipite	YUFE	30	3
				Lamina	YUFL	15	0
	Rhodophyta	*Ahnfeltiopsis* sp.	Fronda	Stipite	YAFE	15	8
				Lamina	YAFL	30	5
		Chondracantus chamissoi	Fronda	Main shaft	YCFEP	30	2
				Branching	YCFR	15	7

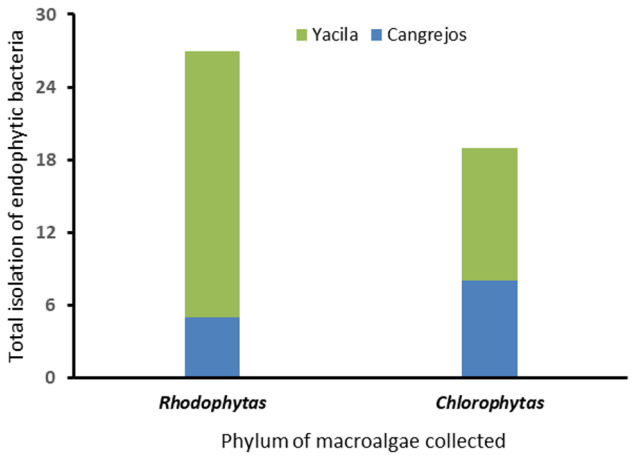

Fig. 2 Total number of endophytic algae bacteria isolated according to phylum *Rhodophytas* (*Ahnfeltiopsis* sp. and *C. chamisoi*), and *Chlorophytas* (*Caulerpa* sp. and *Ulva* sp.)

bacterial strain. Extract of CUFE2 (5.662 mg/ml, 100%) inhibited *Escherichia coli* O157:H7 and *Escherichia coli* ATCC10536, then, this concentration corresponds to MIC. Furthermore, this extract exhibited bactericidal activity against *Escherichia coli* ATCC10536 (100%) (Fig. 4C).

Molecular taxonomic identification

Nine marine endophytic bacteria were selected for molecular taxonomic analysis. Four bacterial strains belonged to genus *Bacillus* (YCFR5, YCFR6, YUFE8, and YCFE4) (Fig. 5A). Likewise, five gram-negative strains belonged to four genera: *Kluyvera ascorbata* (YAFE21 and YAFL9), *Pantoea agglomerans* (YAFL6), *Leclercia adecarboxylata* (CUFE2), *Enterobacter* sp. (YAFL1) (Fig. 5B). These results indicate that the most representative genus was *Bacillus*, followed by *Kluyvera.*

Antifungal activity of algae endophytic bacteria

Anticandidal activity

Nine endophytic bacteria were selected to evaluate their inhibitory activity against yeasts finding that YAFL1, YAFL6, CUFE2, YUFE8, and YCFR6 showed strong inhibitory activity against at least 1 pathogenic yeast by the cross-culture method (Table 6).

Five algae endophytic bacteria were selected for OpT (Figs. 6 and 7). *Bacillus* sp. YUFE8 exhibited higher inhibitory activity against *C. albicans*, while the inhibitory activity against *C. tropicalis* was low. Furthermore, YAFL6 and CUFE2 exhibited strong inhibitory activity against *C. albicans* ATCC90028 and *C. tropicalis*, respectively by VOCt method. However, MIC and MBC of CUFE2 (5.662 mg/ml), YAFL6 (5.662 mg/ml), and YCFE4 (6.52 mg/ml) crude extracts did not show inhibitory activity against both evaluated *Candida*.

Antifungal activity against filamentous fungi

Nine algae endophytic bacteria were evaluated (Figs. 8 and 9). *Enterobacter* sp. YAFL1 and *P. agglomerans* YAFL6

Table 3 Antibacterial activity of algae endophytic bacteria against pathogenic gram-positive and gram-negative bacteria by the cross-culture methodology

Sample	Algae endophytic bacteria	Gram-positive bacteria				Gram-negative bacteria		
		Ef	Se	Sa	Lm	EcOH	EcAT	Sety
Caulerpa sp.	CCDF3	++	++	+++	+	+++	++	++
	CCDF5	+	+++	++	+	+++	++	++
	CCFE1	+	+++	++	++	++	++	++
	YCFE13	–	+++	+++	+	+++	+++	+
	YCFE6	++	++	++	++	++	+++	+
	YCFE1	++	+++	+++	+++	++	++	–
	YCFE4	+++	+++	++	+++	+++	+++	++
	YCFE8	+++	++	++	++	+++	+++	++
	YCFL2	+	++	+++	++	++	++	++
	YCFL1	+	++	+++	++	+++	++	++
	YCFL11	+	+	++	++	++	++	++
Ahnfeltiopsis sp.	YAFE2	+	+	+	–	++	+++	–
	YAFE11	–	–	+++	++	+	++	++
	YAFE30	+++	+	++	++	++	+++	++
	YAFE21	+++	++	+++	+++	–	++	+++
	YAFE10	+	++	+++	+++	++	++	+++
	YAFE7	++	+	++	++	–	+	++
	YAFE13	+	++	++	+	++	++	+++
	YAFE12	++	++	+	++	++	+	++
	YAFL1	+	+++	+++	+++	+++	+++	++
	YAFL6	+++	+	+++	+++	+++	++	+++
	YAFL9	+++	++	+++	+++	+	++	+
	YAFL3	+++	++	+++	++	+	–	++
	YAFL5	+++	++	–	+	+	++	+++
Ulva sp.	CUFE2	+	+	+++	+++	++	+++	+++
	CUFE6	+	+++	++	++	–	+	++
	CUFE11	–	–	+++	+++	+++	++	+++
	CUFE13	–	+++	+++	++	++	++	++
	CUFL2	+++	+	+++	+++	+	+	++
	YUFE6	+	++	+	+++	++	++	+++
	YUFE8	+++	++	+++	++	+++	+++	++
	YUFE20	+++	+++	++	++	–	++	++
Chondracantus chamisoi	CCFR3	++	++	++	+	++	++	++
	CCFR10	+++	+++	+++	+	++	++	++
	CCFR11	+++	+++	++	++	+++	++	++
	CCFR12	+	+++	+++	++	++	+++	+++
	CCFR4	+++	+++	++	+	++	–	+
	YCFEP3	+	++	++	+	+++	++	+++
	YCFEP10	+++	+++	++	–	+++	+	++
	YCFR1	+++	++	+++	++	++	+++	++
	YCFR14	++	+++	+++	+++	+	+++	+++
	YCFR4	++	+++	+++	++	++	++	+++
	YCFR5	++	++	+++	+++	+++	+++	+++
	YCFR3	–	++	+	–	++	++	++
	YCFR12	++	+++	+++	–	+++	+	++
	YCFR6	+++	+++	++	+++	++	+++	++

Ef: Enterococcus faecalis ATCC29212, Se: Staphylococcus epidermidis ATCC12228, Sa: Staphylococcus aureus ATCC25923 and Lm: Listeria monocytogenes ATCC7644, EcOH: Escherichia coli O157:H7, EcAT: Escherichia coli ATCC10536 and Sety: Salmonella enterica sv typhimurium ATCC14028. Inhibition compared to control: (+++) strong inhibition (≥ 90–100%), (++) moderate inhibition (≥ 50–89%), (+) weak inhibition (≥ 8.5 to 49%), (-) no inhibition (0%)

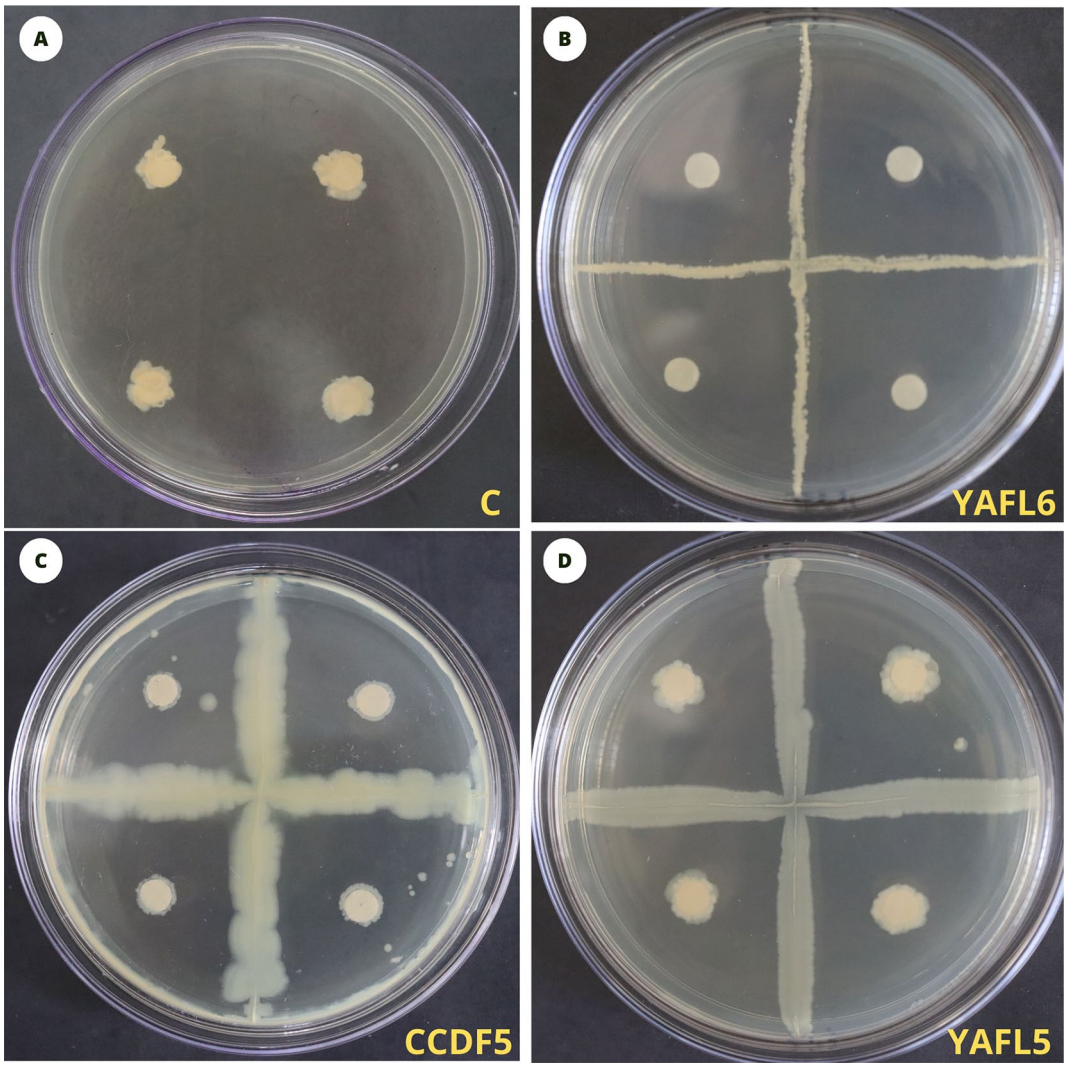

Fig. 3 Antibacterial cross-culture assay of algae endophytic bacteria. **A** *Staphylococcus aureus* growth control, **B** YAFL6 exhibited strong inhibition against *S.aureus*, **C** CCDF5 showed moderate inhibition against *S.aaureus*, **D** YAFL5 without inhibitory effect

Table 4 Antibacterial activity of selected algae endophytic bacteria against gram-positive pathogenic bacteria by OpT and VOC tests

Sample	Algae endophytic bacteria	Ef		Se		Sa		Lm	
		OpT	VOCt	OpT	VOCt	OpT	VOCt	OpT	VOCt
Caulerpa sp.	YCFE1	–	$42.9 \pm 0.0^{c, d}$	–	100.0 ± 0.0^{a}	–	100.0 ± 0.0^{a}	–	28.6 ± 0.0^{c}
	YCFE4	–	76.2 ± 8.2^{b}	–	87.5 ± 0.0^{b}	13.3 ± 0.6^{c}	–	–	100.0 ± 0.0^{a}
Ahnfeltiopsis sp.	YAFE21	–	57.1 ± 0.0^{c}	3.3 ± 0.6^{b}	37.5 ± 0.0^{e}	–	–	2.7 ± 0.6^{b}	100.0 ± 0.0^{a}
	YAFL1	–	$19.1 \pm 8.2^{e, f}$	–	12.5 ± 0.0^{g}	9.3 ± 0.6^{d}	$26.7 \pm 11.5^{d, e}$	–	–
	YAFL6	–	$4.8 \pm 8.2^{f, g}$	–	50.0 ± 0.0^{d}	23.3 ± 0.6^{b}	$53.3 \pm 11.5^{b, c}$	–	–
	YAFL9	–	100.0 ± 0.0^{a}	–	66.7 ± 7.2^{c}	–	$40.0 \pm 0.0^{c, d}$	–	28.6 ± 0.0^{c}
Ulva sp.	CUFE2	–	$28.6 \pm 0.0^{d, e}$	–	25.0 ± 0.0^{f}	7.0 ± 0.00^{e}	–	–	–
C. chamissoi	CCFR10	–	$28.6 \pm 0.0^{d, e}$	–	$58.3 \pm 7.2^{c, d}$	–	$13.3 \pm 11.5^{e, f}$	–	85.7 ± 0.0^{b}
	YCFR14	–	23.8 ± 8.2^{e}	–	25.0 ± 0.0^{f}	1.0 ± 0.0^{f}	60.0 ± 0.0^{b}	–	19.5 ± 8.2^{d}
	YCFR6	–	$28.6 \pm 0.0^{d, e}$	–	100.0 ± 0.0^{a}	–	100.0 ± 0.0^{a}	–	28.6 ± 0.0^{c}
Penicillin (mm)		19.0 ± 0.0	–	11.7 ± 0.6^{a}	–	35.0 ± 0.0^{a}	–	24.7 ± 0.6^{a}	–

OpT: inhibition halo by over plate test (mm), VOCs: volatile organic compounds (percentage inhibition), Ef: *Enterococcus faecalis* ATCC29212, Se: *Staphylococcus epidermidis* ATCC12228, Sa: *Staphylococcus aureus* ATCC25923 and Lm: *Listeria monocytogenes* ATCC7644. (-) No inhibitory activity. Letters indicate groups with significant differences according to Tukey's statistical test ($P < 0.05$). Values represent the mean of three blocks ± SD

Table 5 Antibacterial activity of selected algae endophytic bacteria against gram-negative pathogenic bacteria by OpT and VOC tests

Sample	Algae endophytic bacteria	EcOH		EcAT		Sety	
		OpT	VOCt	OpT	VOCt	OpT	VOCt
Caulerpa sp.	YCFE13	–	$53.3 \pm 5.8^{b, c}$	–	$40.0 \pm 0.0^{b, c}$	–	–
	YCFE4	–	$40.0 \pm 0.0^{d, e}$	8.7 ± 0.6^{c}	$46.7 \pm 5.8^{a, b}$	–	–
	YCFE8	–	$23.3 \pm 5.8^{f, g}$	–	–	–	25.0 ± 0.0^{b}
Ahnfeltiopsis sp.	YAFL1	–	$53.3 \pm 5.8^{b, c}$	10.3 ± 0.6^{b}	–	9.7 ± 0.6^{b}	25.0 ± 0.0^{b}
	YAFL6	2.0 ± 0.0^{d}	–	8.7 ± 0.6^{c}	23.3 ± 5.8^{e}	7.7 ± 0.6^{c}	45.8 ± 7.2^{a}
Ulva sp.	CUFE2	18.3 ± 0.6^{b}	$60.0 \pm 0.0^{a, b}$	1.3 ± 0.6^{d}	53.3 ± 5.8^{a}	–	4.17 ± 7.2^{c}
	CUFE11	–	$30.0 \pm 0.0^{e, f}$	–	$30.0 \pm 0.0^{d, e}$	–	4.17 ± 7.2^{c}
	YUFE8	11.7 ± 0.6^{c}	$60.0 \pm 0.0^{a, b}$	–	50.0 ± 0.0^{a}	–	–
C. chamissoi	CCFR12	–	16.7 ± 5.8^{g}	–	10.0 ± 0.0^{f}	–	–
	YCFEP3	–	$23.3 \pm 5.8^{f, g}$	–	50.0 ± 0.0^{a}	–	4.17 ± 7.2^{c}
	YCFR14	–	$46.7 \pm 5.8^{c, d}$	–	$33.3 \pm 5.8^{c, d}$	–	–
	YCFR5	–	66.7 ± 5.8^{a}	–	50.0 ± 0.0^{a}	–	4.17 ± 7.2^{c}
Penicillin (mm)		23.0 ± 0.6^{a}	–	16.67 ± 0.6^{a}	–	12.0 ± 0.0^{a}	–

OpT: inhibition halo by over plate methodology (mm), VOCt: volatile organic compounds (percentage of inhibition), EcOH: *Escherichia coli* O157:H7, EcAT: *Escherichia coli* ATCC10536 and Sety: *Salmonella enterica* sv *typhimurium* ATCC14028. (-) No inhibitory activity. Letters indicate groups with significant differences according to Tukey's statistical test ($P < 0.05$). Values represent the mean of three blocks ± SD

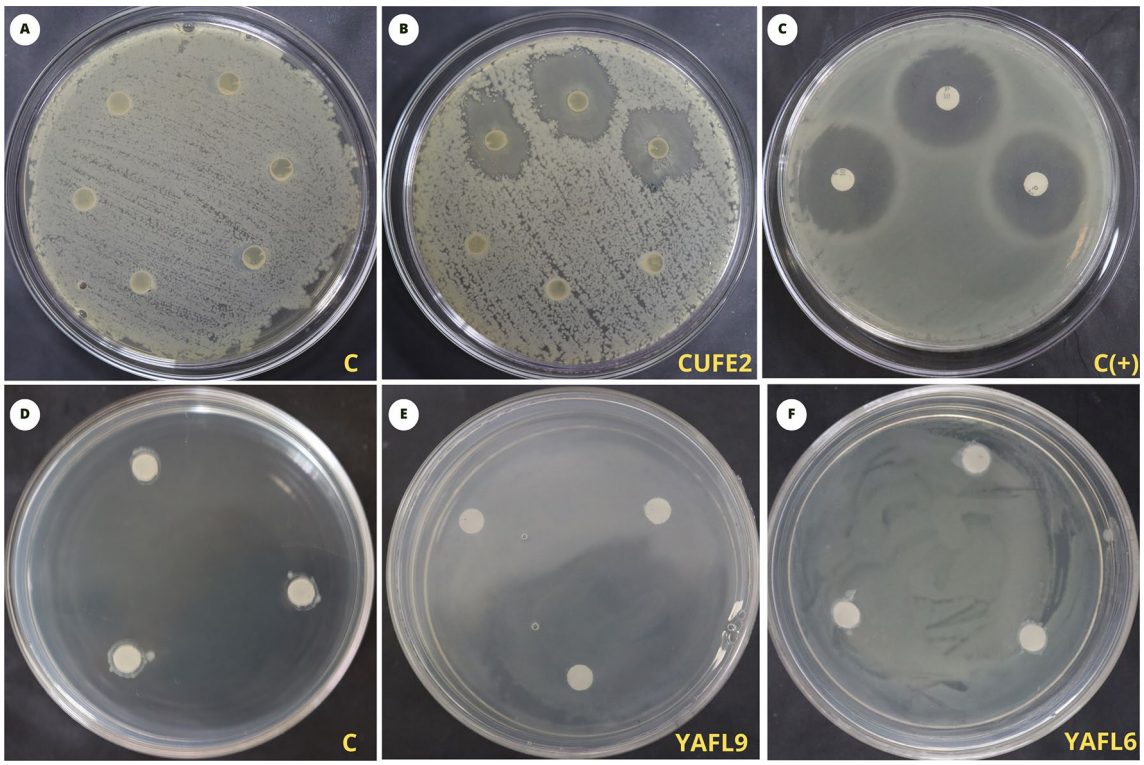

Fig. 4 Antibacterial activity by OpT and DpT of selected algae endophytic bacteria. Inhibitory assay against *Escherichia coli* O157:H7 by OpT: **A** growth control without the marine endophytic bacteria, **B** inhibitory action of CUFE2 (top) and lack of activity of bacterial strain YAFL6 (bottom), **C** activity of penicillin 10 IU discs. Inhibitory assay against *Enterococcus faecalis* by VOCt: **D** growth control without marine endophytic bacteria, **E** antibacterial activity of YAFL9, and **F** YAFL6 without antibacterial activity

inhibited completely *Colletotrichium* sp. and *F. oxysporum* CTLM12. Also, *P. agglomerans* YAFL6, *Bacillus* sp. YCFR6, and *Bacillus* sp. YUFE8 exhibited complete inhibition activity against *Fusarium* sp. H, similarly *Bacillus* sp. YUFE8 inhibited 100% *Alternaria* sp. ATCC20084.

Detection of iturin, fengycin, and surfactin genes

Iturin gene was detected in *K. ascorbata* YAFE21 with a length of 423 base pairs (bp) corresponding to iturin C fragment. Further, fengycin gene was detected in *Bacillus* sp.

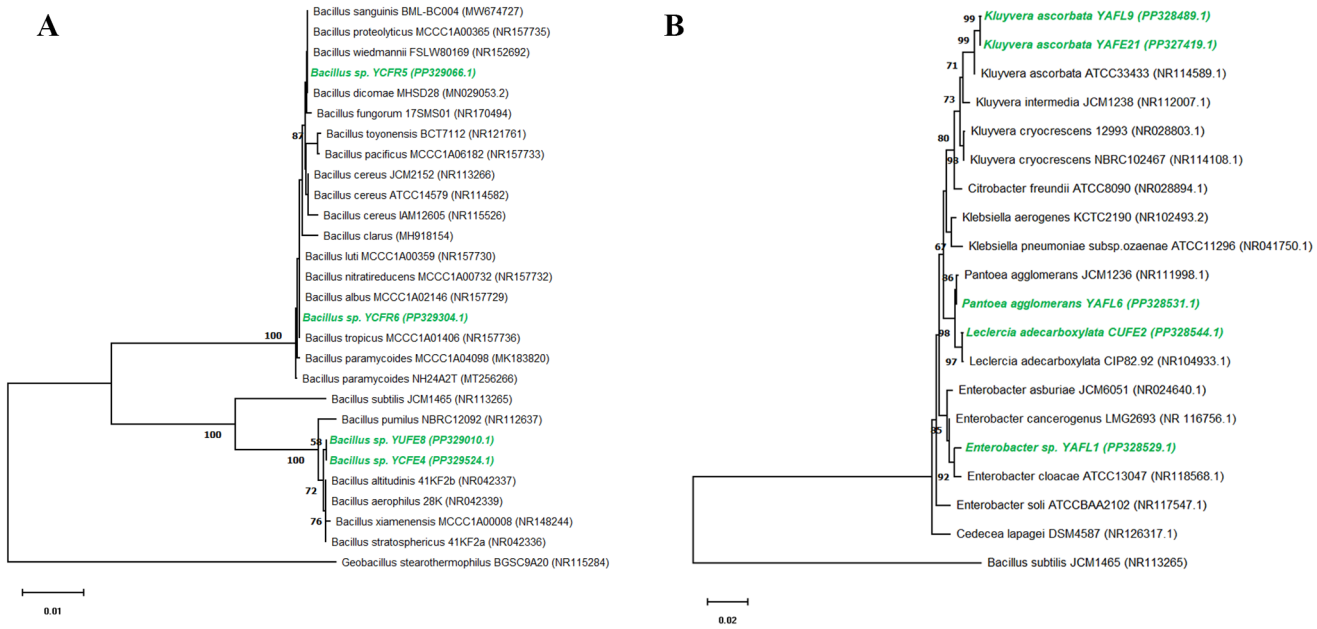

Fig. 5 Phylogenetic analysis of endophytic bacteria from marine macroalgae using 16 S rDNA. **A** Bacterial strain corresponding to the genus *Bacillus* and **B** Bacterial strains from the *Enterobacteriaceae* group. Isolated bacterial strains are in green letters, and bacterial strains obtained from GenBank-type material are in black letters. The accession number is presented in parentheses

Table 6 Anticandidal activity of endophytic bacteria from marine macroalgae by cross-culture method

Sample	Algae endophytic bacteria	C. albicans	C. tropicalis
Caulerpa sp.	*Bacillus* sp. YCFE4	++	++
Ahnfeltiopsis sp.	*K. ascorbata* YAFE21	++	+
	Enterobacter sp. YAFL1	+++	+++
	P. agglomerans YAFL6	+++	+++
	K. ascorbata YAFL9	+	++
Ulva sp.	*L. adecarboxylata* CUFE2	+++	++
	Bacillus sp. YUFE8	+++	+++
Chondracantus chamissoi	*Bacillus* sp. YCFR5	++	–
	Bacillus sp. YCFR6	++	+++

(+++) strong inhibition (≥ 90–100%), (++) moderate inhibition (≥ 50–89%), (+) weak inhibition (≥ 8.5 to 49%), (-) no inhibition

YCFE4 with a length of 269 bp corresponding to fengycin D (Mora et al. 2011) (Table 1).

Discussion

Algae endophytic bacteria were isolated from four macroalgae (*Caulerpa* sp., *Ahnfeltiopsis* sp., *Ulva* sp., and *C. chamisoi*), most of them (71.7%) are from algal stipe collected in Yacila beach (Table 1). In addition, the highest number (66.7%) of endophytes belong to *Rhodophyta* phylum (*Ahnfeltiopsis* sp. and *C. chamisoi*) (Fig. 2). Several studies have reported variation of endophytic bacterial

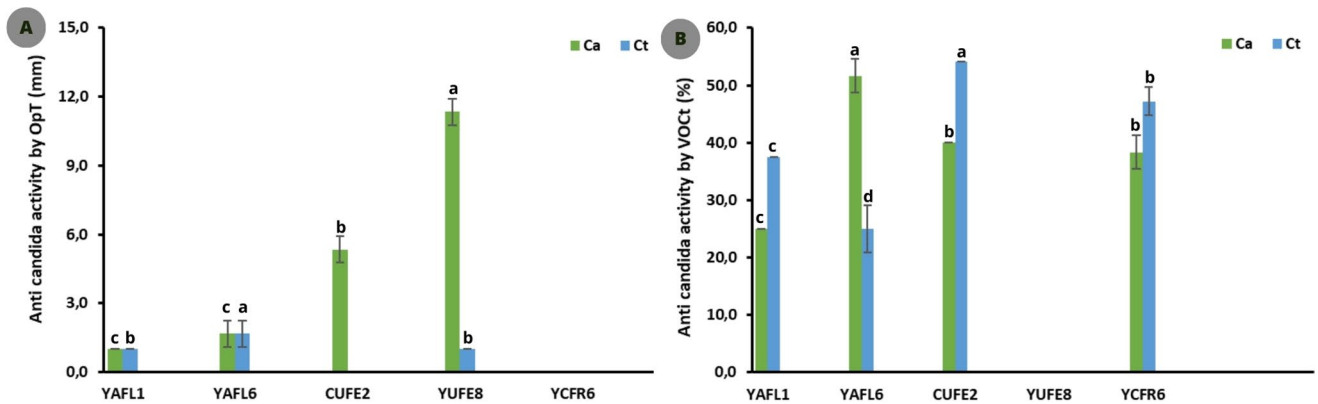

Fig. 6 Anti-candidal activity of selected algae endophytic bacteria by OpT and VOC test. **A** Activity by OpT and **B** Percentage inhibition by VOCt. Values represent the mean of three blocks ± SD. Letters indicate groups with significant differences according to Tukey's statistical test ($P < 0.05$). Ct: *Candida tropicalis* ATCC750 and Ca: *Candida albicans* ATCC90028

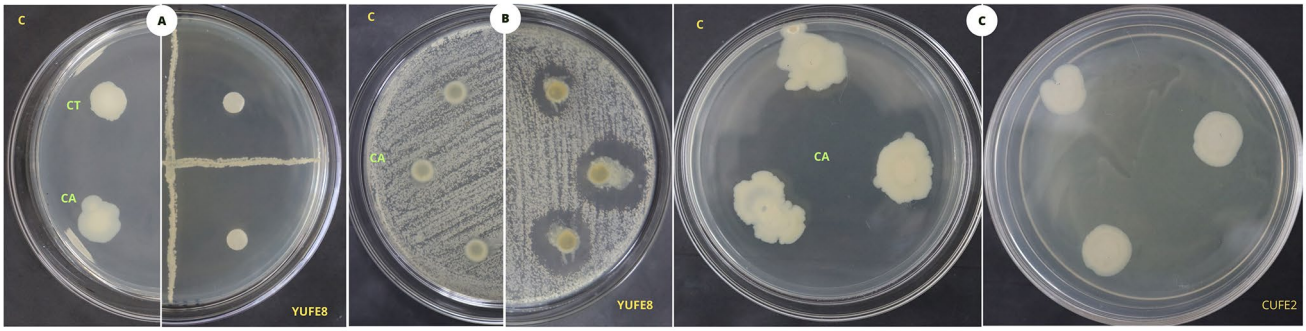

Fig. 7 Anti-candidal activity in the three methods: **A** Cross-culture method: growth control of *C. albicans* and *C. tropicalis* (left) and anti-candidal activity of *Bacillus* sp. YUFE8 (right), **B** OpT: growth control of *C. albicans* and anti-candidal activity of *Bacillus* sp. YUFE8 (right), **C** VOCt test: Control growth of *Leclercia adecarboxylata* CUFE2 (left) and *Candida albicans* growth without algae endophytic bacteria (right). Ct: *Candida tropicalis* ATCC750 and Ca: *Candida albicans* ATCC90028

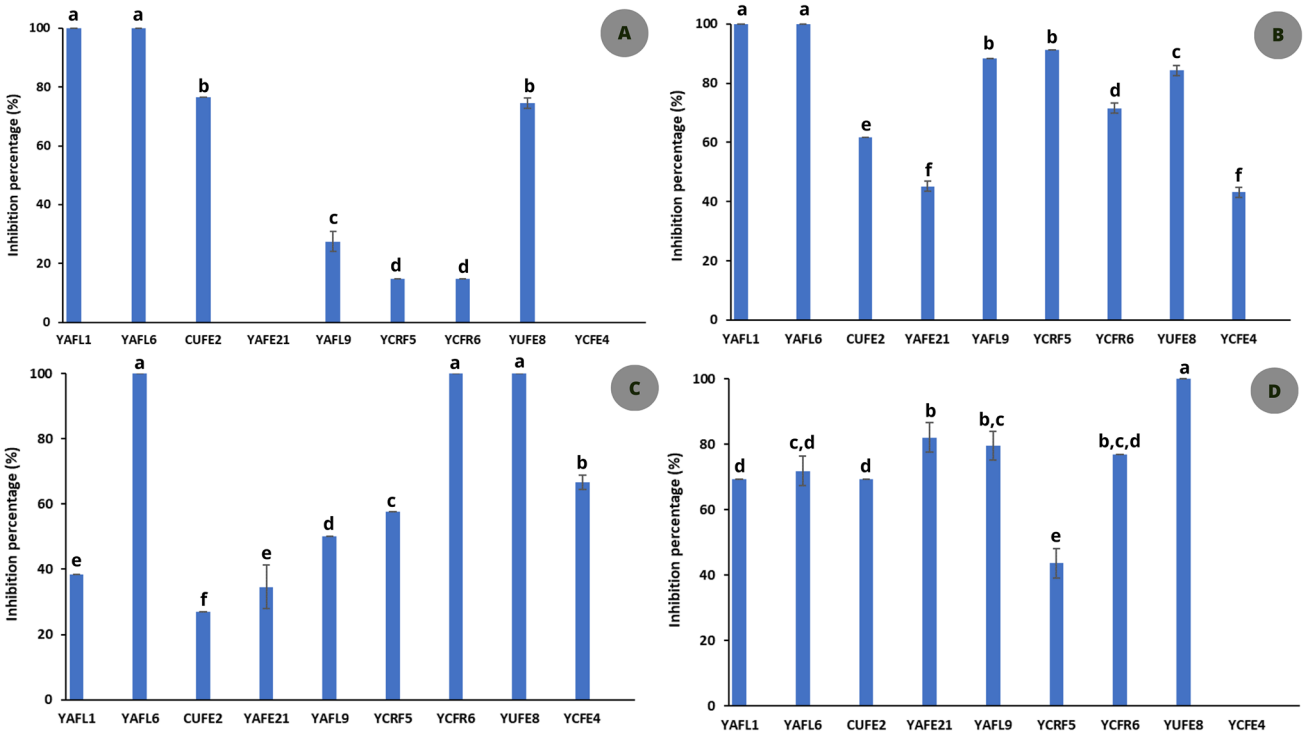

Fig. 8 Antifungal activity of algae endophytic bacteria against filamentous fungi expressed in percent inhibition: **A** Activity against *Colletotrichium gloeosporoides*, **B** Activity against *Fusarium oxysporum* CTLM12, **C** Activity against *Fusarium* sp. H and **D** Activity against *Alternaria* sp. ATCC20084. Values represent the mean of three blocks ± SD. Letters indicate groups with significant differences according to Tukey's statistical test ($P < 0.05$). YAFL1: *Enterobacter* sp., YAFL6: *Pantoea agglomerans*, CUFE2: *Leclercia adecarboxylata*, YAFE21: *Kluyvera ascorbata*, YAFL9: *Kluyvera ascorbata*, YCFR5: *Bacillus* sp., YCFR6: *Bacillus* sp, YUFE8: *Bacillus* sp. and YCFE4: *Bacillus* sp

diversity according to organ and collection place (Kizhakkekalam and Chakraborty 2020; Muñoz-Silva et al. 2019; Ulloa-Muñoz et al. 2020). This diversity could be associated with the endophyte's ability to colonize its host, as well as the genetic and nutritional status of the host-endophyte (Sarasan et al. 2020), also, geographical and seasonal variables could affect their abundance and diversity (Flewelling et al. 2013). However, there is still no clear understanding of the symbiotic relationships and possible specific associations of host-endophytes within marine environments, but it may also be related to anthropogenic factors (Hagaggi and Abdul-Raouf 2022).

On the other hand, the antimicrobial activity of 46 algae endophytic bacteria showed that algae collected in this research could be better sources not only of microbial diversity but also for diverse antibacterial drugs. In this sense, selected bacteria strains (10 that inhibited gram-positive pathogen and 12 to gram-negative) were tested using two

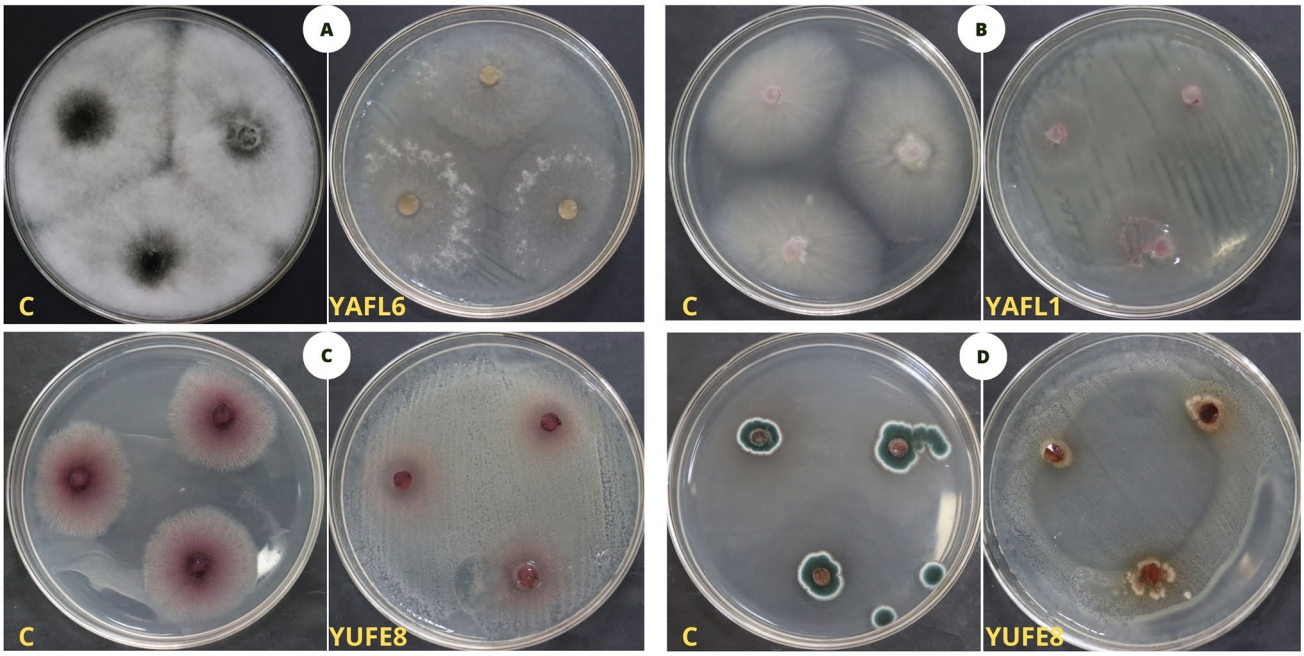

Fig. 9 Antifungal assays of algae macroalgae endophytic bacteria. **A** C: growth control of *Colletotrichium* sp. and its inhibition by *Pantoea agglomerans* YAFL6. **B** C: growth control of *Fusarium oxysporum* CTLM12 and its inhibition by *Enterobacter* sp. YAFL1. **C** C: growth control of *Fusarium* sp. H and its inhibition by *Bacillus* sp. YUFE8 and **D** C: growth control of *Alternaria* sp. ATCC20084 and its inhibition by *Bacillus* sp. YUFE8

methodologies to evaluate antibacterial activity related to non-volatile/volatile compounds (OpT) and only volatile compounds (VOCt). Most of them exhibited better activity in VOCt than OpT, which could mean that antibacterial activities are associated with volatile compounds (Tables 3 and 4). Bacterial VOCs could regulate pathogenic infections, reduce colonization of endophytes or pathogens (Chandrasekaran et al. 2023), and activate defenses or promote the growth of their host (Poveda 2021). However, five strains (YA21, YCFE4, YAFL1, YAFL6, and CUFE2) showed antibacterial activity tested by over-plate too, which could be related to the production of non-volatile compounds associated with their activity. In addition, MIC and MBC of CUFE2 crude extract (5.662 mg/ml) were determined against *E. coli* strains. This interesting result could support deeper research, such as chemical isolation, functional genetics, and the optimization of metabolite production. Moreover, this bacterium could produce volatile and non-volatile compounds.

Microbial diversity was evaluated by molecular taxonomy identification. It was found species belong to *Bacillus* genus and enterobacteria group (Fig. 5). Concordantly, *Bacillus* strains are commonly reported as endophytes in marine macroalgae (Kizhakkekalam and Chakraborty 2020; Habbu et al. 2016; Muñoz-Silva et al. 2019), which some species have been isolated from *Rhodophyta* (Kizhakkekalam and Chakraborty 2020; Muñoz-Silva et al. 2019), *Clorophyta* (Habbu et al. 2016), and *Phaeophyta* (Deutsch et al. 2021). Furthermore, different marine *Bacillus* species have shown antimicrobial activity (Kizhakkekalam and Chakraborty 2020; Habbu et al. 2016; Muñoz-Silva et al. 2019) against *S. aureus*, *P. aeruginosa*, *B. subtilis* (Tareq et al. 2013, 2014; Shafi et al. 2017), *Salmonella typhi* (Tareq et al. 2013; Shafi et al. 2017), *B. cereus*, *E. coli* (Tareq et al. 2013), *B. cinerea* (Shafi et al. 2017); Tareq et al. 2014), *Aspergillus flavus*, *C. albicans* (Habbu et al. 2016), *F. oxysporum*, *Macrophomina Phaseolina* (Chowhan et al. 2023), *Rhizoctonia solani*, and *C. acutatum* (Tareq et al. 2014). Similarly, most species of this genus isolated from marine environments are known for their ability to produce bioactive metabolites (Gopi et al. 2012; Mondol et al. 2011) with antibacterial activities, such as alkaloids, steroids, triterpenoids, flavonoids (Habbu et al. 2016), lipoamides (Berrue et al. 2009), gageostatins A-C (Tareq et al. 2014), Ieodomycins A-D (Mondol et al. 2011), 4,4'-oxybis[3-phenilpropionic acid] (Devi et al. 2010), and macrolactins (Tareq et al. 2013), placing them as promising candidates for biotechnological applications. In addition, their ability to form endospores, thrive under extreme conditions, and antagonist ability (Galaviz-silva et al. 2018); Abdul et al. 2013); Sayem et al. 2011), make them suitable for cultivation and metabolites production at low cost. In this study, *Bacillus* strains inhibited *S. epidermidis*, *S. aureus* (YCFR6), *E. coli* O157:H7 (YCFR5, YUFE8), *E. coli* ATCC10536 (YCFE4, YUFE8 and YCFR5), *C.*

albicans (YUFE8), *Fusarium* sp. (YCFR6 and YUFE8) and *Alternaria* sp. (YUFE8) (Figs. 6, 7 and 8).

The remaining endophytic bacterial strains isolated from macroalgae in this study were enterobacteria species. YAFL9 and YAFE21 are *Kluyvera ascorbate* strains, an environmental bacterium that can develop resistance to aquatic environments, giving it an adaptive advantage and allowing it to outcompete other microorganisms (Alves Resende et al. 2020). It is employed to transfer resistance genes to bacterial species for medicinal or animal (wild fish) purposes (Sellera et al. 2018). Furthermore, *K. ascorbate* showed antimicrobial activity against plant phytopathogens (Timofeeva et al. 2022), *Pseudomonas* sp., *Bacillus* sp., and *S. aureus* (Amraoui et al. 2017). Similarly, *K. ascorbata* strains evaluated in this research showed antibacterial activity against *E. faecalis*, *S. epidermidis*, and *L. monocytogenes* (Table 4), also moderate antifungal activity was exhibited against *F. oxysporum* and *Alternaria* sp. (Fig. 8). Another endophytic species found was *Leclercia adecarboxylata* CUFE2; this species was previously described as *Escherichia adecarboxylata*, a non-lethal Enterobacteriaceae that regularly colonizes soil, water (Sellera et al. 2018; Timofeeva et al. 2022), and marine environments (Broderick et al. 2019). Some strains of this species were reported as maize endophyte (Snak et al. 2021), as well as they showed plant growth-promoting traits and silver nanoparticle production (AgNP) which inhibited *S. aureus*, *B. cereus*, *E. coli*, *Vibrio cholera*, *P. aeruginosa*, *K. pneumoniae*, *C. albicans* (Abdelmoneim et al. 2022), and *A. flavus* (Tong et al. 2018). In this work, *L. adecarboxylata* CUFE2 showed bacteriostatic and bactericidal activity against *E. coli* O157:H7 and *E. coli* ATCC10536 (Table 5, MIC, and MBC), furthermore, it displayed broad-spectrum antifungal activity over 50% of growth inhibition against *Candida tropicalis*, *C. gloeosporoides*, *Fusarium oxysporum* CTLM12, and *Alternaria* sp. ATCC20084 (Fig. 8). Previous studies reported that *K. ascorbate* and *L. adecarboxilata* strains displayed antimicrobial traits but the chemical compounds associated with their activities have not been described yet, giving an interesting topic for continuing future research.

Pantoea agglomerans YAFL6 was another species isolated in this research. This species was not reported for marine environments but is distributed in agricultural environments as an epiphyte and endophyte bacteria of several plants (Amraoui et al. 2017; Snak et al. 2021). It was also isolated from humans and animals (Gutiérrez-Barranquero et al. 2019) and is widely used in biological control against bacterial and fungal plant and human pathogens (Edoamodu and Nwodo 2022; Rangarajan et al. 2015; Gong et al. 2019), such as *Penicillium citrinum* (Thissera et al. 2020), *Vibrio alginolyticus*, *V. haeveyi*, *S. iniae*, *S. agalactiae* (Amenyogbe et al. 2021), *E. coli*, *S. aureus* (Said 2020; Wright et al. 2001), *S. pyogenes*, *K. pneumoniae*, *S. typhi*, *P. aeruginosa*, *P. mirabilis* (Aldujaili et al. 2017), *Acinetobacter hemolyticus*, *Serratia marcescens* (Said 2020), *Erwinia amylovora*. Its activities are possibly associated with the synthesis of pulicatin H and F, aeruginaldehyde, (Thissera et al. 2020), pantocin A and B (Wright et al. 2001), and microcin (Vanneste et al. 2002) reported for this species. Furthermore, these compounds could be utilized to prevent and treat infectious diseases because they have a wide range of therapeutic properties (Gong et al. 2019; Zhou et al. 2021a, b). Concordantly, *P. agglomerans* YAFL6 isolated from macroalgae *Ahnfeltiopsis* sp. also showed a wide range of antimicrobial activity against some bacteria and fungi, such as *S. aureus*, *S. enterica* (Tables 4 and 5), *C. albicans*, *C. gloeosporoides*, *F. oxysporum*, and *Fusarium* sp. (Figures 7 and 8). Another species found in the present work was *Enterobacter* sp. YAFL1. Species of this genus have been reported as sugarcane (Dao-Jun et al. 2020), mulberry (Zhou et al. 2021a, b) and other terrestrial plant endophytes (Asis and Adachi 2004; Patil et al. 2022). Moreover, some *Enterobacter* species displayed plant growth-promoting traits (Singh et al. 2021) and have been isolated from marine sediments (Edoamodu and Nwodo 2022). *Enterobacter* sp. isolated from fish showed a probiotic role with a broad antibacterial spectrum (Gopi et al. 2012). Furthermore, some marine *Enterobacter* species exhibited antifungal activity against *Fusarium moniliforme*, *F. cubense*, *Botrytis cinerea*, *Ceratocystis paradoxa*, *Sporisorium scitamineum* (Dao-Jun et al. 2020; Gnanasekaran et al. 2023), and *Aspergillus flavus* (Gong et al. 2019). This species may produce antifungal peptides (Dao-Jun et al. 2020), moreover, VOCs yielded by *Enterobacter asburiae* Vt-7 displayed antifungal activity and down-regulated the aflatoxin gene expression of *A. flavus* preventing its production (Gong et al. 2019). Similar, *Enterobacter sp.* YAFL1 isolated from *Ahnfeltiopsis* sp. showed a wide range of antifungal activity against *C. gloeosporoides*, and *F. oxysporum* (Fig. 8), also it exhibited antibacterial activity against *E. coli* ATCC10536 and *S. enterica* (Table 5).

Among non-ribosomal peptide synthetases (NRPS) known, three genes coding antimicrobial compounds were evaluated with specific primers (Table 6) finding the presence of iturin and fengycin genes. NRPS consists of a hydrophilic amino acids chain linked to a hydrophobic fatty acid tail, moreover, these compounds are antimicrobial lipopeptides highly effective for controlling agricultural pathogens (Patil et al. 2022). Iturin has been associated with antifungal activity but has limited antibacterial activity (Zhao et al. 2021). However, *K. ascorbata* YAFE21, which showed the presence of iturin C gene, strongly inhibited *S. epidermidis* and *L. monocytogenes*, whereas antifungal activity against *Alternaria* sp. was only moderate. Then, it was possible that

YAFE21 could produce another metabolite with antibacterial activity. Moreover, it was the first report of the presence of iturin gene in *K. ascorbata*. Fengycin is a potent antifungal lipopeptide (Piewngam et al. 2018) with broad-spectrum antibacterial activity (Medeot et al. 2023). *Bacillus* sp. YCFE4 showed fengycin gene presence concordant with other species of *Bacillus* genus (Tambekar and Bhutada 2010; Piewngam et al. 2018). However, YCFE4 only inhibited *E. coli* ATCC10536 and did not show antifungal activity. These results could be associated with the cultural conditions required to induce fengycin gene expression and bioactive compound production. In this sense, fengycin production from *Bacillus megaterium* MTCC8280 was conditioned to aeration and agitation during culture (Rangarajan et al. 2015). In addition, the non-presence of these NRPS genes in seven algae endophytic bacterial strains does not mean their absence in these bacteria genomes because they might not have been detected with the primers used. Therefore, in the future, it is required to increase the primer sets or apply other genomic or transcriptomic techniques that allow to deepen the knowledge of the NRPS genes, which are so diverse and varied (Baunach et al. 2021), especially in those strains with the highest antimicrobial activity.

Conclusion

It was isolated 46 endophytic bacteria from macroalgae *Caulerpa* sp., *Ahnfeltiopsis* sp., *Ulva* sp., and *Chondracantus chamissoi*, mostly from the Yacila beach and phylum *Rhodophyta*. According to antibacterial tests (cross-culture, Opt, VOCt, and MIC/MBC assays), the bacterial strains *Leclercia adecarboxylata* CUFE2, *Pantoea agglomerans* YAFL6, *Enterobacter* sp. YAFL1, *Kluyvera ascorbata* YAFE21, *K. ascorbata* YAFL9, and four *Bacillus* sp. (YCFR5, YCFR6, YUFE8 and YCFE4) showed higher activity. YAFE21 and YCFR6 showed better antibacterial activity against *Staphylococcus epidermidis* and *Listeria monocytogenes*, while CUFE2 against *Escherichia coli* O157:H7 and *Escherichia coli* ATCC10536. In addition, *Bacillus* sp. YUFE8, *P. agglomerans* YAFL6, *L. adecarboxylata* CUFE2, *Enterobacter* sp. YAFL1, and *Bacillus* sp. YCFR6 showed broad-spectrum antifungal activity, YUFE8, YAFL1, and YAFL6 showed higher activity against *Candida albicans*, *C. tropicalis*, *Colletotrichium gloeosporoides*, *Fusarium oxysporum*, *Fusarium* sp., and *Alternaria* sp. Furthermore, *K. ascorbata* YAFE21 and *Bacillus* sp. YCFE4 exhibited iturin C and fengycin D genes, respectively. Finally, these results highlight algae endophytic bacteria *K. ascorbata* YAFE21, *Bacillus* sp. YCFR6, *L. adecarboxylata* CUFE2, *Bacillus* sp. YUFE8, *Enterobacter* sp. YAFL1, and *P. agglomerans* YAFL6 as important and promising sources of antimicrobial agents. Also, they are candidates for deeper studies focused on optimizing culture conditions to better metabolite production and description of chemical structures and studies of genes associated with antimicrobial activities, which support their pharmacology, food, agriculture, industry, and environment application.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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