ORIGINAL ARTICLE

Diversity of epiphytic bacterial communities on male and female *Porphyra haitanensis*

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Abstract

Purpose: To study the structure of the epiphytic bacterial community of the male and female *Porphyra haitanensis*, in order to explore the similarities and differences of epiphytic bacterial community structure between dioecious macroalgae.

Methods: Collection of male and female *Porphyra haitanensis* from the intertidal zone of Niushan Island, Fujian, China. Epiphytic bacteria were collected and studied, and the community composition and diversity of epiphytic bacteria were explored using high-throughput sequencing technology.

Results: There was no significant difference between male and female *Porphyra haitanensis* on α-diversity and β-diversity. Proteobacteria and Bacteroidetes were the core microbiota in male and female *Porphyra haitanensis*. Bacteria from the *Maribacter* (male 14.87%, female 1.66%) and the *Tenacibaculum* (male 1.44%, female 25.78%) were the most indicative epiphytic bacterial taxa on male and female *Porphyra haitanensis*.

Conclusions: Sex differences have some influence on the construction of epiphytic bacterial communities in *Porphyra haitanensis*, but they are not the decisive factors affecting the construction of epiphytic bacterial communities in *Porphyra haitanensis*.

Keywords: Diversity of epiphytic bacteria, Male and female *Porphyra haitanensis*, 16S rRNA high-throughput sequencing

Introduction

A rich and diverse group of microbes lives on macroalgae, which play important roles in the lives of their hosts (Hollants et al. 2013), and the interactions between macroalgae and their epiphytic bacteria are intricate. Macroalgae release many organic substances during growth (Croft et al. 2005), which are absorbed and utilized by the surrounding epiphytic bacteria. Some of these organic substances are metabolized by the bacteria and released back to the ocean in mineral or other forms, providing nutrients and essential growth factors for algal growth

(Florez et al. 2017). Meanwhile, macroalgae could also produce chemical defense agents (antibacterial compounds such as peroxides) to prevent some bacteria from adhering (Campbell et al. 2015). Nevertheless, bacteria have developed metabolic pathways to combat these chemical defenses (Oliveira et al. 2012), and they can even inhibit algal growth or disrupt algal cells. The epiphytic bacteria of macroalgae can be both mutually beneficial and antagonistic, and they can be selectively enriched through specific interactions with their host macroalgae.

There have been many studies on epiphytic bacteria in macroalgae, and it has been shown that the community structure of epiphytic bacteria in macroalgae is host-specific and varies among macroalgae. For example, Selvarajan (Selvarajan et al. 2019) studied the structure of epiphytic bacterial communities of eight common

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seaweeds growing in the intertidal zone of Cape Verde, South Africa. The results showed that the bacterial communities of brown algae were similar to those of green algae, while that of red algae formed an independent branch. The structure of epiphytic bacterial communities of the same species also varied across seasons and geographic regions. Comba González (Comba González et al. 2021) studied the epiphytic bacterial communities of *Ulva lactuca* growing in Santa Marta, La Punta de La Loma, Colombia, using the high-throughput sequencing technique and found that the changes in abundance of Rhodobacteraceae, Hyphomonadaceae, and Flavobacteriaceae might be due to the increase in seawater temperature. Roth-Schulze (Roth-Schulze et al. 2018) studied the community structure of epiphytic bacteria on *Ulva lactuca* collected from Spain and Australia. The results showed that the community structures of epiphytic bacteria on *Ulva lactuca* collected from Spain and Australia were different, and the correlation between them was slight (18% similarity), reflecting the relationship between attenuation and distance, with a decrease in similarity between microbial communities associated with an increase in geographical distance. However, most of the current studies on epiphytic bacteria of macroalgae are about monoecious macroalgae, and there are few studies on the community structure of epiphytic bacteria of dioecious macroalgae.

Porphyra haitanensis is one of the two main species of purslane cultivars in China and is abundant in the area of Pingtan, Fujian. Most of the algae are dioecious, a few are monoecious, and the male and female individuals can be distinguished by observing the morphology and color of the terminal and marginal germ cells (spermatophore and fruit spores) after the algae have matured (Pan 2006). It is an ideal object to study the structure of epiphytic bacterial communities in this particular group of dioecious macroalgae. Therefore, this study was conducted to investigate the differences in epiphytic bacterial community structure between male and female algae of Niushan Island, Pingtan, Fujian, China, by sequencing epiphytic bacteria using high-throughput sequencing technology. The results of this study provide new insights into the relationship between epiphytic bacteria and dioecious macroalgae.

Material and methods

Sampling site and sampling male and female *Porphyra haitanensis*

The sampling site was in the rocky intertidal zone of Niushan Island (25°N, 119°E) in Fujian, on January 19, 2020. Three samples from male *Porphyra haitanensis*, three from female and three samples from seawater were collected from same site.

Samples of epiphytic bacteria of male and female *Porphyra haitanensis*

Sample collection of epiphytic bacteria of *Porphyra haitanensis*: take the sample of *Porphyra haitanensis*, wipe a sample evenly with 10 swabs, put swabs into sample tube after wiping, quickly put them into dry ice, take them back to the laboratory and store them in the refrigerator at -80 °C until DNA is extracted.

Environmental water sample treatment

The seawater around *Porphyra haitanensis* was collected by sterile sample bottles; 500 mL seawater was collected for each sample, and filtered through a polycarbonate membrane (Millipore, USA) with a pore size of 0.22 μm. The polycarbonate filter membrane rich in microorganisms was stored in dry ice, frozen and taken back to the laboratory, and stored in the refrigerator at − 80 °C until DNA extraction.

16S rDNA high-throughput sequencing

After extracting genomic DNA from the samples, the V3 + V4 region of 16S rDNA was amplified using the following specific primers with barcodes: 341F, CCT ACGGGNGGCWGCAG; 806R, GGACTACHVGGG TATCTAAT. The PCR amplification products were then cut, recovered, and quantified using a QuantiFluorTM fluorometer. The purified amplicons were subsequently sequenced (PE250) on the Illumina MiSeq platform according to standard protocols by Guangzhou Genedenovo Biotechnology Co., Ltd.

Data analysis

Species were clustered into a taxonomic operational unit (OTU) using Uparse software (v9.2.64_i86linux32). The resulting OTUs were taxonomically compared by Greengenes (gg_13_5) and SILVA (Version 106) databases, and the sequences were sampled using Mothur software (v.1.39.1) to calculate diversity indices Shannon, Simpson, Ace, Chao1 indices, and β-diversity was calculated and subjected to NMDS analysis. The resulting high-throughput sequencing data were clustered according to OTU classification to analyze species diversity at the phylum level, phylum level, and genus level, respectively. Differential inter-group analysis was performed using LEFse software (v1.0). The accession numbers for sequencing data presented is PRJNA 776695.

Results

Sequencing summary by 16S rRNA high-throughput sequencing

A total of 1,146,486 tags were obtained. After quality control, a total of 1,119,154 effective tags were retrieved
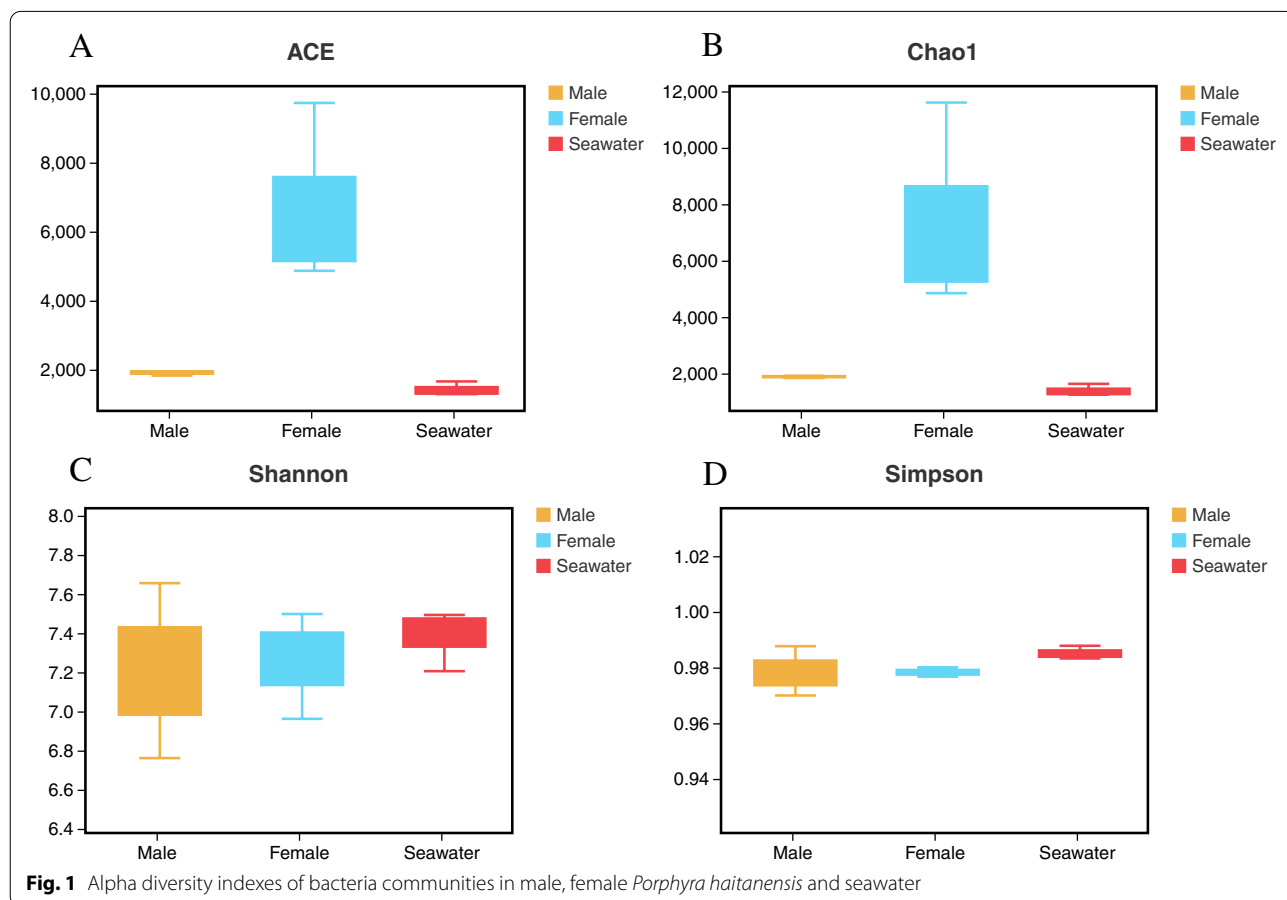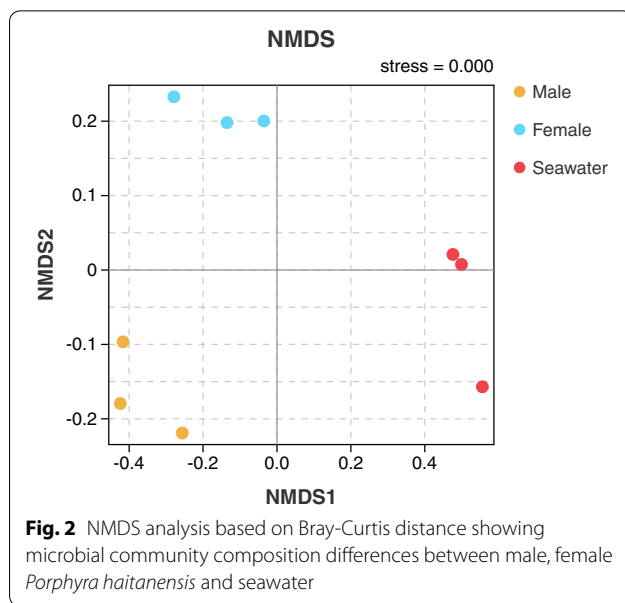
(Table S1), and these samples were assigned to a total of 3310 OTUs. The rarefaction analyses indicated that the diversity of all samples was well represented by the number of sequences analyzed (Figure S1). The bacterial sequences in the female and male microbial communities were clustered into 1335 and 1666 OTUs at a 97% sequence similarity, respectively. The bacterial sequences in the microbial community in the surrounding seawater were clustered into 1453 OTUs with 97% sequence similarity (Figure S2).
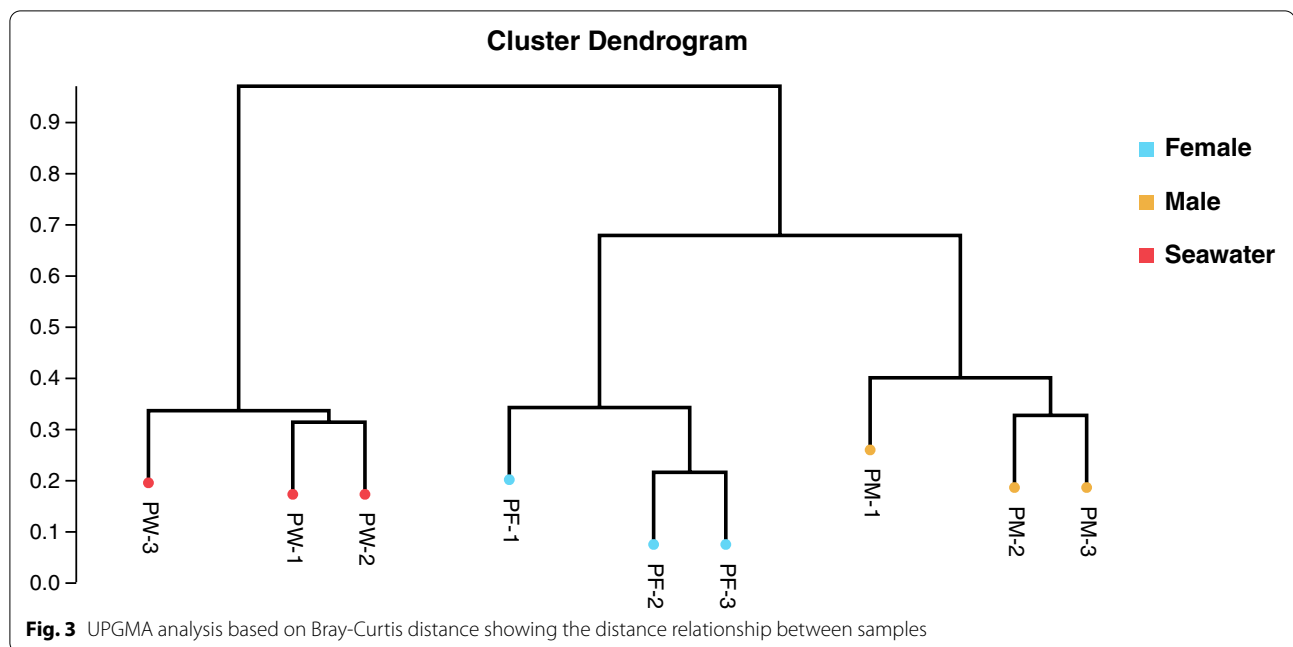
Sexual differences in α-diversity and β-diversity

The results of α-diversity and β-diversity showed that there was no significant gender difference ($p > 0.05$) in the diversity of *Porphyra haitanensis* (Figs. 1 and 2), but the epiphytic bacterial communities were clustered separately according to gender (Fig. 3).

Community structure of the epiphytic bacterial community

A total of 3310 OTUs were identified in 9 samples (Figure S2), which were distributed in 34 phyla and 84 classes and 410 genera.

Fig. 2 NMDS analysis based on Bray-Curtis distance showing microbial community composition differences between male, female *Porphyra haitanensis* and seawater

Fig. 1 Alpha diversity indexes of bacteria communities in male, female *Porphyra haitanensis* and seawater

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Fig. 3 UPGMA analysis based on Bray-Curtis distance showing the distance relationship between samples

In this study, 34 phyla were identified (Fig. 4A). Proteobacteria was the most abundant phylum in most samples. Other dominant taxa included Bacteroides, Actinomycetes, and Cyanobacteria. The abundance of Proteobacteria was higher in seawater (61.59%) than in male *Porphyra haitanensis* (41.25%) and female *Porphyra haitanensis* (32.43%).

At the class level, a total of 84 classes were identified. The bacterial taxa with high relative abundance at the class level (Fig. 4B) were Bacteroidia, Alphaproteobacteria, and Gammaproteobacteria. The average relative abundance of Bacteroidia were male *Porphyra haitanensis* (41.61%), female *Porphyra haitanensis* (49.82%), and seawater (8.48%); the average relative abundance of Alphaproteobacteria were male *Porphyra haitanensis* (26.30%), female *Porphyra haitanensis* (25.96%), and seawater (25.07%); the average relative abundance of Gammaproteobacteria were male *Porphyra haitanensis* (14.42%), female *Porphyra haitanensis* (5.87%), and seawater (34.64%).

At the genus level, a total of 410 genera were identified. The bacterial taxa with high relative abundance at the genus level (Fig. 4C) were *Tenacibaculum*, *Maribacter*, and *Granulosicoccus*. The average relative abundance of *Tenacibaculum* were male *Porphyra haitanensis* (1.44%), female *Porphyra haitanensis* (25.78%) and seawater (0.06%); the average relative abundance of *Maribacter* were male *Porphyra haitanensis* (14.87%), female *Porphyra haitanensis* (1.66%), and seawater (0.22%); the average relative abundance of *Granulosicoccus* were

male *Porphyra haitanensis* (12.20%), female *Porphyra haitanensis* (3.04%), and seawater (0.15%).

Core microbiota in male and female *Porphyra haitanensis*

A total of 752 OTUs were common in male and female *Porphyra haitanensis*, being mapped to 17 phyla and 31 classes and 147 genera. Proteobacteria and Bacteroidetes were the core microbiota in male and female *Porphyra haitanensis*. Proteobacteria was represented by *Granulosicoccus*, *Hellea*, *Litorimonas*, *Marinicella*, and *Sphingorhabdus*, which were present in all male and female *Porphyra haitanensis* samples. The phylum Bacteroidetes was represented by *Maribacter*, *Lewinella*, *Euzebyella*, *Tunicatimonas*, and *Wenyingzhuangia*, which were present in all male and female *Porphyra haitanensis* samples.

Indicative species of the epiphytic bacterial communities on male and female *Porphyra haitanensis*

There were 33 and 31 indicative epiphytic bacteria taxa for the male and female *Porphyra haitanensis*, respectively (Fig. 5) and among them, bacteria from the *Maribacter* (male 14.87%, female 1.66%) and the *Tenacibaculum* (male 1.44%, female 25.78%) were the most indicative for male and female *Porphyra haitanensis*, respectively, according the negative linear discriminant analysis (LDA) score (Figure S3).

Discussion

Our results indicated that the influence of male and female *Porphyra haitanensis* on epiphytic bacterial community was statistically not significant, which is
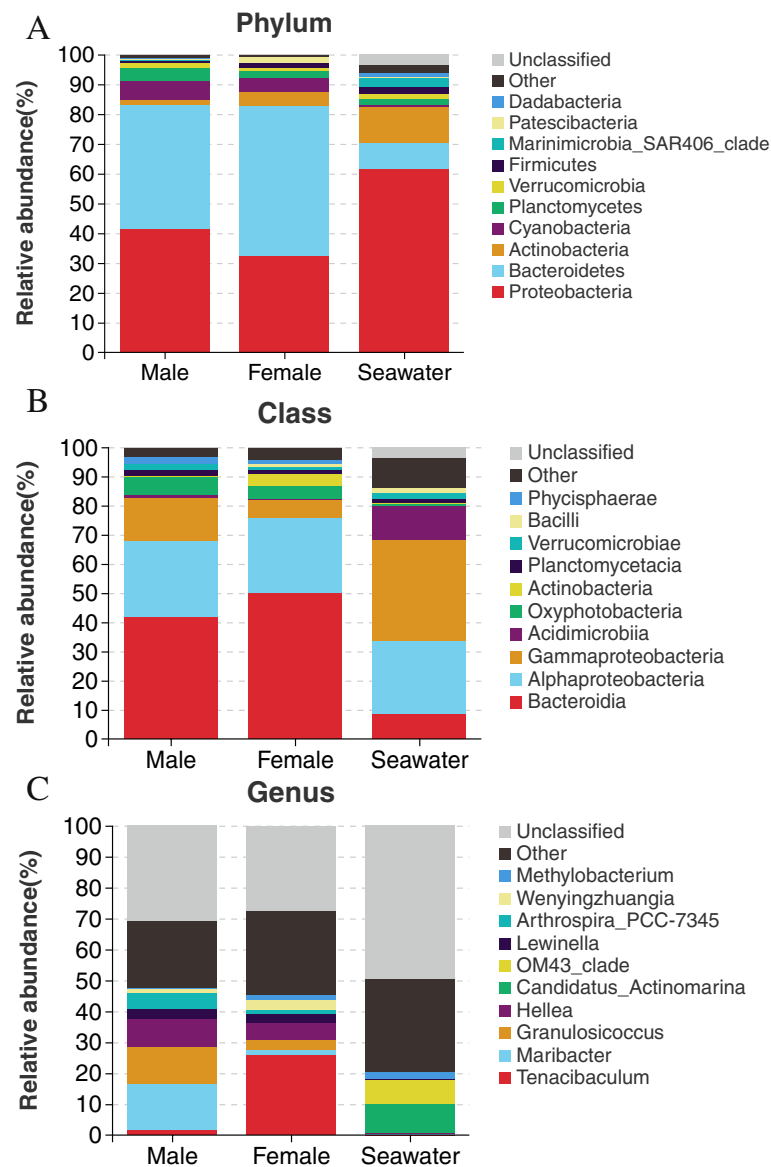
Fig. 4 **A** Phylum-level taxonomic composition of the bacterial community. **B** Class-level taxonomic composition of the bacterial community. **C** Genus-level taxonomic composition of the bacterial community

consistent with previous studies on male and female epiphytic bacteria in higher plants. Liu (Liu et al. 2021) found that there was no significant difference between female and male phyllosphere bacterial communities; however, there was significant difference in the relative abundance of phyllosphere bacterial and fungal at genus level between female and male *Populus cathayana* by using 16S rRNA/ITS1 gene-based MiSeq sequencing. Our results are similar to those above and support the view that sex has little effect on epiphytic bacterial diversity. It is speculated that sex differentiation of *Porphyra*

haitanensis has minor impact on the epiphytic bacterial communities. There were bacteria with significant differences in relative abundance at the genus level between male and female algae, and both male and female algae had their unique flora.

In the results of this high-throughput sequencing, Proteobacteria and Bacteroidetes constitute the most abundant bacterial phylum of *Porphyra haitanensis*, which is consistent with previous studies on other algae (Serebryakova et al. 2018; Mancuso et al. 2016). In previous studies, Alphaproteobacteria exhibited functions such as
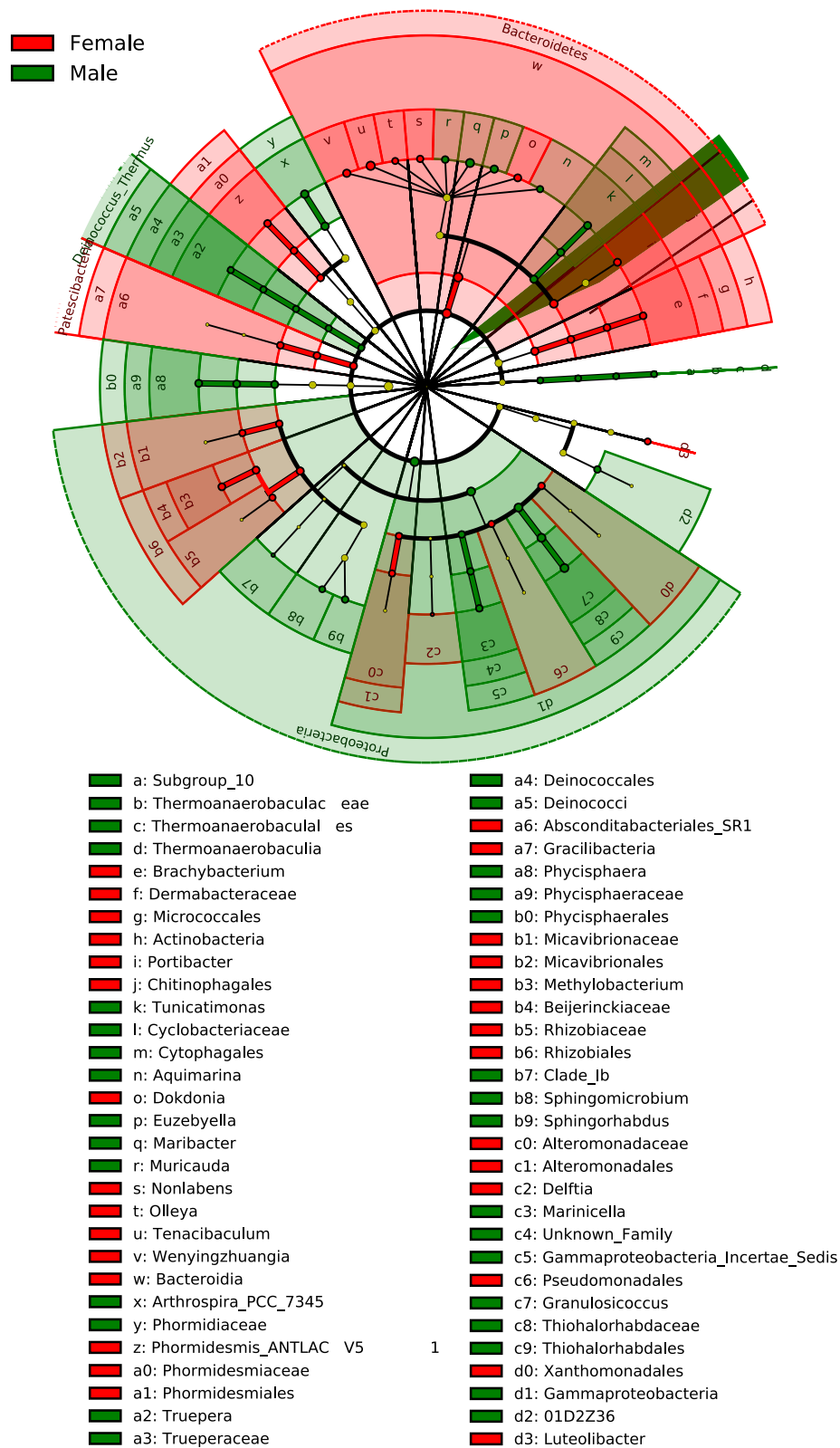
Fig. 5 Indicative species of the epiphytic bacterial communities on male and female *Porphyra haitanensis*. LDA score indicating significant differences in bacterial taxa (LDA score > 3.0)

a: Subgroup_10
b: Thermoanaerobaculac eae
c: Thermoanaerobaculal es
d: Thermoanaerobaculia
e: Brachybacterium
f: Dermabacteraceae
g: Micrococcales
h: Actinobacteria
i: Portibacter
j: Chitinophagales
k: Tunicatimonas
l: Cyclobacteriaceae
m: Cytophagales
n: Aquimarina
o: Dokdonia
p: Euzebyella
q: Maribacter
r: Muricauda
s: Nonlabens
t: Olleya
u: Tenacibaculum
v: Wenyingzhuangia
w: Bacteroidia
x: Arthrospira_PCC_7345
y: Phormidiaceae
z: Phormidesmis_ANTLAC_V5_1
a0: Phormidesmiaceae
a1: Phormidesmiales
a2: Truepera
a3: Trueperaceae

a4: Deinococcales
a5: Deinococci
a6: Absconditabacteriales_SR1
a7: Gracilibacteria
a8: Phycisphaera
a9: Phycisphaeraceae
b0: Phycisphaerales
b1: Micavibrionaceae
b2: Micavibrionales
b3: Methylobacterium
b4: Beijerinckiaceae
b5: Rhizobiaceae
b6: Rhizobiales
b7: Clade_Ib
b8: Sphingomicrobium
b9: Sphingorhabdus
c0: Alteromonadaceae
c1: Alteromonadales
c2: Delftia
c3: Marinicella
c4: Unknown_Family
c5: Gammaproteobacteria_Incertae_Sedis
c6: Pseudomonadales
c7: Granulosicoccus
c8: Thiohalorhabdaceae
c9: Thiohalorhabdales
d0: Xanthomonadales
d1: Gammaproteobacteria
d2: 01D2Z36
d3: Luteolibacter

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nitrogen fixation and degradation of phenolics (Cernava et al. 2017). Most of the macroalgae-related functions reported by these bacteria are related to the growth and development of macroalgae.

In this study, there were sex variations in the relative abundance of some taxa in the bacterial community, with different indicator bacteria for male and female *Porphyra haitanensis*. *Maribacter* was the most indicative for male *Porphyra haitanensis*. Research shows that (Mark et al. 2020) the engineered *Maribacter* sp. and *Roseovarius* sp. consortium modulate *Ulva mutabilis* growth rate and photosynthate content of constituents relevant for bioethanol production. And, in a study by Alsufyani (Alsufyani et al. 2020), Thallusin released by *Maribacter* sp. can induced rhizome and cell wall formation. It is hypothesized that *Maribacter* can help male *Porphyra haitanensis* to adapt to environmental changes. The relative abundance of *Arthrospira_PCC_7345* in male *Porphyra haitanensis* was also significantly higher than its relative abundance in female *Porphyra haitanensis* in a study by Lochab (Lochab et al. 2014), where *Arthrospira_PCC_ 7345* has the ability to perform nitrate uptake and assimilation. Another indicator species in the male *Porphyra haitanensis* was *Euzebyella* who has been claimed to contain a large number of carbohydrate-active enzymes with carbohydrate utilization capacity (Liu et al. 2019). The most significant difference in female *Porphyra haitanensis* was *Tenacibaculum* which is a bacterium with algaecidal ability (Li et al. 2013). *Nonlabens*, *Luteolibacter*, and *Olleya* were also indicator species for female *Porphyra haitanensis*, and their relative abundance in female *Porphyra haitanensis* was significantly higher than that in male *Porphyra haitanensis*. *Nonlabens* has been reported to degrade green algae (Ulaganathan et al. 2017). *Luteolibacter* has also been reported to degrade fucoidan (Ohshiro et al. 2012). Studies have shown that *Olleya* can degrade agar (Sánchez Hinojosa et al. 2018). In this study, the indicator species in the male *Porphyra haitanensis* are mostly bacteria that help *Porphyra haitanensis* to grow and adapt to the environment, while the indicator species in the female *Porphyra haitanensis* are mostly bacteria that have the ability to kill algae.

Conclusion

In conclusion, this study explored the influence of sex in the construction of epiphytic bacterial communities in *Porphyra haitanensis*. No significant differences were found in the abundance and diversity indices of the epiphytic bacterial communities on the male and female *Porphyra haitanensis*. However, the results of bacterial community composition showed that some bacteria were differentially enriched on the male and female *Porphyra haitanensis*. These bacteria have specific ecological functions, but more experiments are needed to verify whether these functions are consistent with the physiological responses of the male and female *Porphyra haitanensis*. The present study contributes to our understanding of the mechanisms underlying the construction of bacterial communities attached to dioecious macroalgae.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13213-022-01675-7.

Additional file 1: Table S1. Summary of sequenced data and the OTUs number of all samples. **Figure S1.** Rarefaction curves for the number of observed species against the total number of sequence 30 reads at a dissimilarity of 3%. **Figure S2.** The shared and unique bacteria OTUs between male, female *Porphyra haitanensis*. and seawater. **Figure S3.** LDA score of the epiphytic bacterial communities on male and female *Porphyra haitanensis* (LDA score >3.0).

Authors' contributions
Yang Zhibo did the field sampling and physiochemical data analysis, and wrote the draft manuscript. Wang Jing and Xue Song did the field sampling. Chen Jun, Shang Shuai, Tang Xuexi, and Xiao Hui supervised the project and finalized the manuscript. All authors read and approved the final manuscript.

Availability of data and materials
The dataset(s) supporting the conclusions of this article is(are) available in the NCBI Sequence Read Archive database under Bioproject PRJNA776695.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
All authors of the manuscript have read and agreed to its content and are accountable for all aspects of the accuracy and integrity of the manuscript in accordance with ICMJE criteria. That the article is original, has not already been published in a journal, and is not currently under consideration by another journal. That you agree to the terms of the BioMed Central Copyright and License Agreement.

Competing interests
The authors declare that they have no competing interests.

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References

Alsufyani T, Califano G, Deicke M, Grueneberg J, Weiss A, Engelen AH, Kwantes M, Mohr JF, Ulrich JF, Wichard T (2020) Macroalgal-bacterial interactions: identification and role of thallusin in morphogenesis of the seaweed Ulva (Chlorophyta). J Exp Bot 71(11):3340–3349. https://doi.org/10.1093/jxb/eraa066

Campbell AH, Marzinelli EM, Gelber J, Steinberg PD (2015) Spatial variability of microbial assemblages associated with a dominant habitat forming seaweed. Front Microbiol 6:230. https://doi.org/10.3389/fmicb.2015.00230

Cernava T, Erlacher A, Aschenbrenner IA, Krug L, Lassek C, Riedel K, Grube M, Berg G (2017) Deciphering functional diversification within the lichen microbiota by meta-omics. Microbiome. 5(1):82. https://doi.org/10.1186/s40168-017-0303-5

Comba González NB, Niño Corredor AN, López Kleine L, Montoya CD (2021) Temporal changes of the epiphytic bacteria community from the marine macroalga ulva lactuca (Santa Marta, Colombian-Caribbean). Curr Microbiol 78(2):534–543. https://doi.org/10.1007/s00284-020-02302-x

Croft MT, Lawrence AD, Raux-Deery E, Warren MJ, Smith AG (2005) Algae acquire vitamin B12 through a symbiotic relationship with bacteria. Nature. 438(7064):90–93. https://doi.org/10.1038/nature04056

Florez JZ, Camus C, Hengst MB, Buschmann AH (2017) A functional perspective analysis of macroalgae and epiphytic bacterial community interaction. Front Microbiol 8:2561. https://doi.org/10.3389/fmicb.2017.02561

Hinojosa V, Asenjo J, Leiva S (2018) Agarolytic culturable bacteria associated with three antarctic subtidal macroalgae. World J Microbiol Biotechnol 34(6):73. https://doi.org/10.1007/s11274-018-2456-1

Hollants J, LeliaertF DC, O, WillemsA. (2013) What we canlearn from sushi: a reviewon seaweed-bacterial associations. FEMS Microbiol Ecol 83:1–16. https://doi.org/10.1111/j.1574-6941.2012.01446

Li Y, Wei J, Yang C, Lai Q, Chen Z, Li D, Zhang H, Tian Y, Zheng W, Zheng T (2013) Tenacibaculum xiamenense sp. nov., an algicidal bacterium isolated from coastal seawater. Int J Syst Evol Microbiol 63(Pt 9):3481–3486. https://doi.org/10.1099/ijs.0.050765-0

Liu J, Xue CX, Sun H, Zheng Y, Meng Z, Zhang XH (2019) Carbohydrate catabolic capability of a Flavobacteriia bacterium isolated from hadal water. Syst Appl Microbiol 42(3):263–274. https://doi.org/10.1016/j.syapm.2019.01.002

Liu L, Lu L, Li H, Meng Z, Dong T, Peng C, Xu X (2021) Divergence of phyllosphere microbial communities between females and males of the dioecious populus cathayana. Mol Plant Microbe Interact 34(4):351–361. https://doi.org/10.1094/MPMI-07-20-0178-R

Lochab S, Kumar PA, Raghuram N (2014) Molecular characterization of nitrate uptake and assimilatory pathway in Arthrospira platensis reveals nitrate induction and differential regulation. Arch Microbiol 196(6):385–394. https://doi.org/10.1007/s00203-014-0973-3

Mancuso FP, D'Hondt S, Willems A, Airoldi L, De Clerck O (2016) Diversity and temporal dynamics of the epiphytic bacterial communities associated with the canopy-forming seaweed Cystoseira compressa (Esper) Gerloff and Nizamuddin. Front Microbiol 7:476. https://doi.org/10.3389/fmicb.2016.00476

Mark P, Gianmaria C, Nico D, Thomas W, Alexander G (2020) Engineering bacteria-seaweed symbioses for modulating the photosynthate content of Ulva (Chlorophyta): Significant for the feedstock of bioethanol production. Algal Res 49:101945, ISSN 2211-9264. https://doi.org/10.1016/j.algal.2020.101945

Ohshiro T, Harada N, Kobayashi Y, Miki Y, Kawamoto H (2012) Microbial fucoidan degradation by Luteolibacter algae H18 with deacetylation. Biosci Biotechnol Biochem 76(3):620–623. https://doi.org/10.1271/bbb.110911.Sánchez

Oliveira LS, Gregoracci GB, Silva GGZ, Salgado LT, Filho GA, Alves-Ferreira M et al (2012) Transcriptomic analysis of the red seaweed Laurencia dendroidea (Florideophyceae, Rhodophyta) and its microbiome. BMC Genomics 13:487. https://doi.org/10.1186/1471-2164-13-487

Pan (2006. Master Dissertation. Ocean University of China) Comparison of growth, development and biochemical characteristics of Porphyra haitanensis var. Huabei and Porphyra haitanensis from different gender sources. https://doi.org/10.7666/d.y988923

Roth-Schulze AJ, Pintado J, Zozaya-Valdés E, Cremades J, Ruiz P, Kjelleberg S, Thomas T (2018) Functional biogeography and host specificity of bacterial communities associated with the Marine Green Alga Ulva spp. Mol Ecol 27(8):1952–1965. https://doi.org/10.1111/mec.14529

Selvarajan R, Sibanda T, Venkatachalam S, Ogola HJO, Christopher Obieze C, Msagati TA (2019) Distribution, interaction and functional profiles of epiphytic bacterial communities from the rocky intertidal seaweeds, South Africa. Sci Rep 9(1):19835. https://doi.org/10.1038/s41598-019-56269-2

Serebryakova A, Aires T, Viard F, Serrão EA, Engelen AH (2018) Summer shifts of bacterial communities associated with the invasive brown seaweed Sargassum muticum are location and tissue dependent. PLoS One 13(12):e0206734. https://doi.org/10.1371/journal.pone.0206734

Ulaganathan T, Boniecki MT, Foran E, Buravenkov V, Mizrachi N, Banin E, Helbert W, Cygler M (2017) New ulvan-degrading polysaccharide lyase family: structure and catalytic mechanism suggests convergent evolution of active site architecture. ACS Chem Biol 12(5):1269–1280. https://doi.org/10.1021/acschembio.7b00126

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