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RESEARCH ARTICLE

Variations in seaweed-associated and planktonic bacterial communities along the coast of Ghana

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ABSTRACT
Seaweed associated bacteria can be exploited for sustainable production and conservation of seaweeds, although limited information exists in several coastal waters in West Africa. Here, the diversity and abundance of bacteria on five seaweeds, Sargassum vulgare, Padina durvillaei, Hydropuntia dentata, Hypnea musciformis and Ulva fasciata, and surrounding seawaters across five coastal sites in the Central and Western regions of Ghana were investigated. Biochemical tests and MALDIâ€"TOF identification system were used to determine the bacteria diversity and abundance on the seaweeds and seawater. A total of 530 bacterial isolates, belonging to 28 species (and mostly Proteobacteria and Firmicutes) were identified. A higher diversity of bacteria species was found associated with the seaweeds (83%) than in seawater (17%). Bacterial composition was similar among taxonomically-related seaweeds. The brown (S. vulgare) and red (H. musciformis) seaweeds recorded the most and least diverse bacterial assemblage, respectively. Seasonally, bacterial diversity and abundance were marginally higher in the wet season. The study provides important baseline information on the spatial, temporal and taxonomic distribution of bacteria associated with commercially valuable seaweed species in the coastal areas of Ghana. The results are also important for the sustainable exploitation and conservation of these important macroalgae in Ghana and elsewhere.

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Introduction

Seaweeds, typically found between the intertidal and subtidal zones of the world's oceans, often interact symbiotically with many microorganisms such as bacteria, viruses, fungi and protozoa (Armstrong et al. 2001, Rao et al., 2006; Singh and Reddy 2014; Pérez et al. 2016; Liang et al. 2019). While some of these microorganisms are found attached to the seaweed surfaces, others occur as free-living organisms (planktonic bacteria) in the marine environment (Mahmud et al. 2007; Martin et al. 2014; Rogers et al. 2020). The most predominant seaweed–microorganisms interaction usually occurs through direct attachment to the seaweed surfaces or via secretion of mucus and biofilms, and results in several developmental and ecological benefits for the survival of both organisms (Armstrong et al. 2001; Goecke et al. 2010; Chellaram et al. 2013; Martin et al., 2014; Ramírez-Puebla et al. 2022).

Seaweed-associated bacteria influence the health and metabolism of the macroalgae (seaweeds) by providing them with vitamins, nutrients, fatty acids, antimicrobials and regulate their growth (Droop 2007; Singh and Reddy 2014; Selvarajan et al. 2019). Others fix atmospheric nitrogen (N_2) in the host plants, serve as detoxifiers, and produce antifouling compounds that repel seaweed predators (Hollants et al. 2013; Comba-González et al. 2016; Menaa et al. 2020). Conversely, seaweeds have several environmental and physiological features that influence the existence of bacteria in the marine ecosystem. Seaweeds create favourable environments for

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the colonization of bacteria by producing oxygen and secreting rich organic matter (polysaccharides) that serve as an energy source and promote bacterial growth (Armstrong et al. 2001; Goecke et al. 2010; Martin et al., 2014; Comba-González et al. 2016). Additionally, seaweeds provide anchorage, shelter and protection from predators and adverse environmental conditions to bacteria (Hollants et al. 2013; Kumar et al. 2013).

Besides the ecological benefits, epiphytic bacteria are reported to play an important economic role (Kumar et al. 2013). For example, some bacteria such as *Pseudomonas stutzeri* isolated from seaweed (*Hypnea musciformis*) are reported to possess bioactive compounds for pigment formation, which are commonly used in diverse applications such as the cosmetic industries (Kumar et al. 2013). Furthermore, bacteria have the potential of synthesizing enzymes such as agarases, amylases, phosphatases, esterases, β-galactosidases and cellulases capable of degrading a large variety of polysaccharides (Comba-González et al. 2016). These bacterial enzymes degrade the seaweeds to produce useful hydrocolloids such as alginate, agar and carrageenan often used in medicine, pharmaceutical and food industries (Alba and Kontogiorgos 2018). The epiphytic bacteria also secrete an array of antibiotic compounds which can be used in the production of antibacterial drugs for treating diverse diseases (Chellaram et al. 2013; Srilekha et al. 2017; Stincone and Brandelli 2020).

The relationship between bacteria and seaweeds is usually species-specific, partly due to the production of biological compounds in the surrounding environment (Armstrong et al. 2001). Lachnit et al. (2011) reported that specific bacteria assemblages occur on different seaweed hosts within the same marine environment. Several studies have also reported similar compositions of bacterial communities occurring on different seaweeds irrespective of their geographic locations (Staufenberger et al. 2008; Lachnit et al. 2009). Lachnit et al. (2009) further showed that the physicochemical characteristics of seaweeds influence the development and assemblage of bacteria species on the seaweeds. Selvarajan et al. (2019) also attributed the high diversity of bacteria on seaweeds to pollution of elemental substances and secretion of organic compounds. However, variations in the population of bacteria on specific seaweeds is minimal concerning the seasonal and growth cycle of the host (Chellaram et al. 2013; Comba-González et al. 2016; Phelps et al. 2021). Clearly, understanding the nature of bacteria association, diversity and abundance on seaweeds over time and space at the local level is crucial to inform the exploitation and conservation of the seaweeds.

The coast of Ghana is lavished with luxurious growth of seaweeds (John and Asare 1975; John et al., 2001; Gbedemah 2017). A recent study identified 35 seaweed species belonging to three divisions (i.e. Chlorophyta, Rhodophyta and Phaeophyta) along the central and western coastal waters of Ghana (Akrong et al. 2021) which are also documented to be of enormous economic importance (John and Asare 1975; McHugh 2003; Ganesan et al. 2006; Magdugo et al. 2020). They are used as humans and animal food sources, as well as hydrocolloid products commonly used in cosmetic, food and pharmaceutical industries and other biotechnological applications. Moreover, they possess anticoagulants, anticancer, antioxidant and anti-inflammatory properties which are used for important medicine development (McHugh 2003; Najam et al. 2010; Sumayya and Murugan 2016; Abdullah et al. 2020). Some of the predominant seaweed species identified in this study, notably *Padina durvillaei*, *H. dentata* and *H. musciformis*, have shown to be promising as new seaweed sources of highly functional hydrocolloids (Rhein-Knudsen et al. 2017a, 2017b). Hence, understanding the seaweed microbiology in Ghana may have important implications for West Africa as a new site for production of valuable seaweed hydrocolloids. Yet, research on the diversity and abundance of seaweed-associated bacteria is lacking in Ghana. Currently, there is no information regarding the diversity of epiphytic bacteria on Ghanaian seaweeds and how these bacteria communities vary across locations. The present study, thus, sought to investigate the presence and diversity of epiphytic bacteria on seaweeds of economic importance in Ghanaian coastal waters. Further, the study assessed how the diversity and abundance of the seaweed-associated bacteria varied across seasons and among the studied sites. The sites selected were the location of interest for the research because of the presence of mixed rocky and sandy shoreline suitable for seaweed growth.

Materials and method

Study sites

The study was conducted on the coasts of the Central and Western Regions of Ghana (Figure 1). The sampling sites include Mumford (N05°15.730′, W001°45.376′),

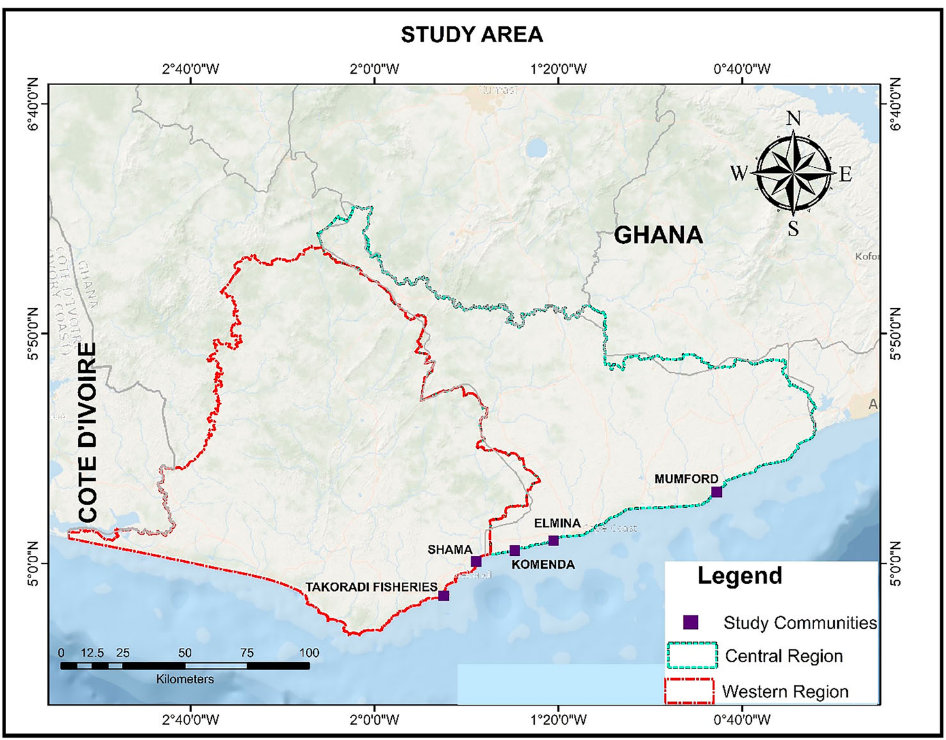

Figure 1. Map of the sampling sites in the two coastal regions of Ghana.

Elmina (N05°04.646′, W001°22.216′) and Komenda (N05°02.688′, W001°30.061′) in the Central Region, and Shama (Amenano) (N05°00.002′, W001°37.988′) and Takoradi (behind the Takoradi Fisheries Commission) (N04°52.700′, W001°45.166′) in the Western Region.

Description of the sampling sites

The study site at Mumford has a gentle sloping topography with high rocks in the intertidal zone and residential community near the sea. The common human activities at the site include swimming, human waste, fishing activities and use as landing sites for canoes. At Elmina, the coast has a gently sloped sandy shore with a short shoreline of about 40 m during low tides. Continuous gentle sloping flat rocks with few outcrops are mostly found at Komenda with anthropogenic activities such as open defecation and fishing practiced commonly at the site. The beach at Shama (Amenano) is a gentle slope and mostly filled up with sand and scattered short rocks in the intertidal zone. The site is close to the Pra River estuary. The shore at Takoradi fisheries is somewhat flattened, although it slopes gently towards the sea. Detailed descriptions of the five studied sites have been provided by Akrong et al. (2021).

Collection of seaweed and seawater for bacteriological analysis

Collection of seaweeds

Five seaweed species, belonging to the three groups of brown seaweed (*Sargassum vulgare*, *Padina durvillaei*), red seaweed (*Hypnea musciformis* and *Hydropuntia dentata*) and green seaweed (*Ulva fasciata*) were selected for the study (Figure 2). These species, which are widely distributed in Ghana, were selected for the study due to their abundance in the study sites (Akrong et al. 2021). Three species (*H. dentata*, *H. musciformis* and *U. fasciata*) were, however, present at Shama and Takoradi Fisheries during the study period. The species were collected from the upper and mid-intertidal zones of the five study sites for the determination of epiphytic bacterial diversity. The seaweeds were collected from December 2017 to June 2018 during the wet (April, May and June) and dry (January, February and December) seasons in Ghana (Lawson, 1956; Lieberman et al. 1979). Three replicates of these seaweeds were randomly collected from the growing substratum at the five sampling sites during the low tide. A pair of sterile scissors was used to cut the thallus of the seaweeds above their holdfast before placing them in well-labelled sterile zip lock bags.

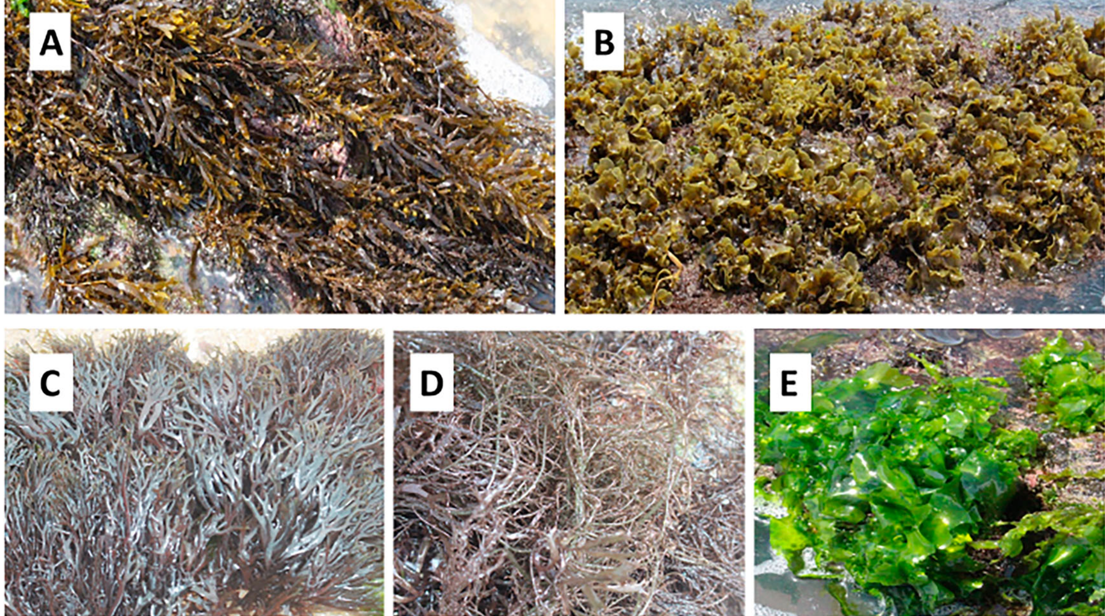

Figure 2. Morphology of seaweeds: A: *Sargassum vulgare*, B: *Padina durvillaei*, C: *Hydropuntia dentata*, D: *Hypnea musciformis* E: *Ulva fasciata*.

Collection of seawater

Seawater samples were collected from the same location where the seaweed samples had been taken. Composite water samples were collected, immediately after the collection of the seaweed, into sterile and well-labelled polypropylene 500 ml bottles during low tides. All seawater and seaweed samples from the various study sites were transported on ice to the laboratory for analyses.

Isolation of heterotrophic bacteria on seaweed and seawater

Seaweed samples were separately washed with autoclaved/sterile seawater. A measured weight of 20 g of the thalli was separately placed in sterile Whirl-Pak bags containing 200 ml of sterilized seawater. The bag containing the washed seaweed and seawater was shaken for about 1 min and the washed water was poured out. This process was repeated three times for all the seaweed species collected. The washing was done to eliminate attached invertebrates, settled sand particles and all loosely attached bacteria, leaving only those that were strongly bound on the surface of the seaweeds (Karthick & Mohanraju, 2018). One gram (1 g) each of the washed fresh seaweed tissues (*S. vulgare*, *P. durvillaei*, *H. dentata*, *H. musciformis* and *Ulva fasciata*) were separately placed aseptically in sterile 50 ml Falcon tubes and 20 ml of sterile seawater was added to each sample to ensure that the seaweed is fully immersed in the seawater. The tubes containing the individual seaweeds were then placed in the shaker (SHEL lab SI6-2 Shaking Incubator) set at 250 rpm and run for 30 min at room temperature to ensure bacteria cells detachment from the surfaces of the seaweeds. A 10-fold serial dilution of the resulting solution in the Falcon tube was made using sterilized seawater in test tubes. Using the spread plate technique (APHA/AWWA/WEF 2017), the serially diluted (10^{-2}) sample in the test tube was vortexed for 1 min and an aliquot of 0.1 ml was spread on to Zobell marine agar (2216, Biomark Laboratories) using a sterilized metal rod and was followed by incubation at 37°C for 48–72 h (Fisher Scientific Isotemp 600 Standard Incubator) until the growth of bacterial colonies was fully formed. Similar culture techniques were used for the isolation of bacteria in the seawater sampled from the various sites.

Characterization of bacteria on seaweeds and seawater

Bacterial colonies isolated from seaweeds and the surrounding seawater were used for further characterization and identification. Morphologically distinct and dominant colonies were randomly selected for this analysis. The selected bacterial colonies were purified by repeated subculturing on marine agar (APHA/AWWA/WEF 2017). Pure colonies were characterized

cytologically (Gram staining and motility) and biochemically (catalase, oxidase, urease, indole and citrate) as described in the Medical Laboratory Manual for Tropical Countries (Cheesbrough 1984) and Bergey's Manual of Determinative Bacteriology.

Further identification was carried out to the species level using the Matrix Assisted Laser Desorption Ionization–Time of Flight (MALDI–TOF) Mass spectrophotometer (MS) system (Bruker Daltonic, GmbH, Leipzig, Germany). The application of MALDI–TOF MS in the identification of bacteria from environmental substrates is well documented, and particularly for clinically relevant bacteria (Siegrist et al. 2007; Giebel et al. 2008; Eddabra et al. 2012; Emami et al. 2016; Popović et al. 2017). This technique has several advantages including its reliability and rapidity in obtaining results, requiring limited training, cost-effectiveness and ability to identify diverse microorganisms. While MALDI–TOF's application may be limited by inadequate environmental bacteria isolates in its database or the requirement for relatively large numbers of pure bacteria colonies (Popović et al. 2017), previous investigators have posited that it produces comparable level of efficiency as the 16S rRNA gene sequence analysis (Silva-Jiménez et al. 2018; Ashfaq et al. 2022). The MALDI–TOF MS system comprises two software programs (i.e. FlexControl and Biotyper real-time classification (RTC) for protein spectra acquisition and automated spectral analysis, respectively) and Microflex LT/SH MS instrument.

The isolate identification process involves sample preparation, mass spectra acquisition and raw spectra pre-processing and normalization, as well as peak detection and peak matching which are described below.

Sample preparation

Pure colonies of freshly cultured bacterial isolates on the Petri dish were transferred and smeared on the MALDI target plate position with a sterile disposable loop. The sample spot on the plate was then overlaid with 1 µl Bruker HCCA (α-Cyano-4-hydroxycinnamic acid) and allowed to dry at room temperature. The target plate was slotted in the plate disc.

Mass spectra acquisition and raw spectra pre-processing and normalization

The isolates were identified using the Microflex LT/SH MS instrument. The setting properties of the instrument includes IS1, 20.08 kV; IS2, 16.77 kV; lens, 7.03 kV and detector gain, 1634 V. FlexAnalysis software (Bruker Daltonics GmbH, Bremen, Germany) was applied in the visual inspection of the mass spectra in a linear positive ion mode. Bacterial test standard comprising of a mixture of proteins was used for the external mass calibration. The MALDI Biotyper software was used to determine raw spectra for unknown bacteria and list of most significant peaks (m/z values) of the spectrum after smoothing, normalization, baseline subtraction and peak picking processes.

Peak detection and peak matching, dendogram construction and database for identification

All peaks acquisition and analysis were done automatically using the following installed software: Microflex/Biotyper MALDI, MBT Compass, MBT Explorer, MBT Filamentous Fungi Library, MBT Mycobacteria IVD Suite, MSP Septsityper Module and MBT Subtyping Module. Outputs of the spectra from the MALDI Biotyper were in a log (score) and vary from 0–3.0. A score > 2.3 indicates 'highly probable species identification', a score > 2 and < 2.299 indicates 'secure genus identification, probable species identification', a score > 1.7 and < 1.999 indicates 'probable genus identification', and a score < 1.7 indicates 'unreliable identification' (Normand et al. 2017).

Data analysis

The Shannon diversity (H′), Margalef species richness (d) and evenness (J) of bacteria species on seaweeds and seawater were calculated using the Paleontological Statistics (PAST) Version 3.2.

These indices were also calculated using the following equation:

a) Shannon–Wiener Index $H = -\Sigma (Pi)(\ln Pi)$, where $Pi = S/N$
b) Margalef species richness $(d) = (S-1)/\ln N$
c) Evenness $(J) = H/\ln S$

Where S = Number of individuals of one species, N = Total number of all individuals in the sample, In = Natural log and H = Shannon–Wiener (Aslam 2009).

Pattern dendrograms were generated with the Bray–Curtis similarity index to visualize the similarity in the bacterial communities among the seaweeds and the sampling sites using the programme PAST (Hammer et al. 2001). The abundance and dominance of bacteria among the sites, seaweeds as well as between the seasons were compared using the analysis of variance and the t-test, respectively, at 5% significance level. In addition, the correspondence analysis (CA) was used to examine the association between the abundance of the bacteria species and the seaweeds/seawater.

Results

Diversity and distribution of bacteria associated with seaweeds

A total of 530 bacterial isolates were recorded on the five dominant seaweeds studied. The isolates belonged to 28 bacterial species and two species that could not be classified by the MALDI–TOF identification (Table I). Among the 28 bacterial isolates identified, 23 (i.e. 83%) were observed on the seaweeds whereas 12 (17%) were found in the surrounding seawater. The results revealed four major bacterial phyla, namely Proteobacteria (54%; chiefly Gammaproteobacteria (93%) and Betaproteobacteria (7%)), Firmicutes (31%), Actinobacteria (11%) and Bacteriodetes (4%) (Supplementary Materials 1). Species of the phylum Proteobacteria were dominant in all three seaweed groups (red, brown and green); Firmicutes were dominant among the green, whereas Actinobacteria were mostly in the red and brown seaweeds. At the lower taxonomic level, 12 families were identified in all samples across the studied sites (Supplementary Materials 1). However, most bacterial species in the samples were identified as members of the Pseudomonadaceae and Bacillaceae families. At the genus level, *Pseudomonas* (18%) and *Bacillus* (14%) were observed to be dominant in all samples. About 60% of the isolated bacteria were Gram negative (S2). Shared and unique isolated bacteria species from the five seaweeds are shown in Figure 3. Bacteria species that were unique to the seawater were *Citrobacter* sp., *Enterococcus* sp., *Flavobacterium* sp., *Klebsiella* sp. and *P. oleovorans*.

Bacterial diversity differed among the studied sites, with the highest richness observed at Mumford (134 isolates) and Komenda (123 isolates) (Table II). Similarly, Mumford recorded the greatest Margalef and Shannon–Wiener diversity indices of 3.88 and 2.61, respectively. In contrast, lower diversity indices (Margalef and Shannon–H′) were recorded at Takoradi Fisheries (1.58 and 1.92) and Shama (Amenano) (1.89 and 1.89) across all samples (Table II).

Statistical results confirmed the higher diversity of the bacterial isolates on the seaweeds than in the seawater ($P < 0.05$), evidenced by the greater values of Margalef and Shannon indices for the former (3.94 and 2.55, respectively) compared with the latter (2.45 and 2.11, respectively).

Among the three seaweed groups, the brown seaweed, *Sargassum vulgare*, recorded the highest

Table I. Bacterial isolates identified in seaweeds and seawater across the studied sites.

Bacterial isolate	Phylum	Number of isolates		Score values
		Seaweeds	Seawater	
Acinetobacter haemolyticus	Proteobacteria	2	0	1.96–2.21
Acinetobacter radioresistens	Proteobacteria	1	0	1.83–2.27
Alcaligenes sp.	Proteobacteria	4	3	1.79–1.85
Bacillus infantis	Firmicutes	5	0	2.16–2.40
Bacillus licheniformis	Firmicutes	8	0	2.15–2.26
Bacillus megaterium	Firmicutes	4	0	1.83–1.93
Bacillus sp.	Firmicutes	58	9	1.68–1.92
Corynebacterium casei	Actinobacteria	9	0	1.88–2.01
Corynebacterium coyleae	Actinobacteria	2	0	1.95–2.12
Citrobacter sp.	Proteobacteria	0	2	1.81–1.90
Escherichia coli	Proteobacteria	2	0	1.71–1.89
Enterococcus sp.	Firmicutes	0	10	1.75–1.92
Flavobacterium sp.	Bacteriodetes	0	6	1.34–1.87
Klebsiella sp.	Proteobacteria	0	10	1.72–1.95
Micrococcus luteus	Actinobacteria	46	4	2.11–2.26
Pseudomonas composti	Proteobacteria	16	6	1.89–2.17
Pseudomonas mendocina	Proteobacteria	18		1.95–2.51
Pseudomonas stutzeri	Proteobacteria	12	5	1.88–2.03
Pseudomonas oleovorans	Proteobacteria	0	2	1.92–2.25
Pseudomonas sp.	Proteobacteria	37	31	1.71–1.96
Psychrobacter sp.	Proteobacteria	27	0	1.69–1.85
Shewanella algae	Proteobacteria	5	0	1.96–2.27
Shewanella putrefaciens	Proteobacteria	90	0	2.16–2.43
Staphylococcus hominis	Firmicutes	11	2	2.03–2.26
Staphylococcus cohnii	Firmicutes	6	0	2.00–2.33
Staphyloccocus warneri	Firmicutes	7	0	2.00–2.15
Solibacillus silvestris	Firmicutes	2	0	2.10–2.27
Vibrio alginolyticus	Proteobacteria	65	0	2.04–2.33
Unknown species 1 (A1)	-	1	0	1.10–1.12
Unknown species 2 (A2)	-	2	0	1.08–1.21

A score > 2.3 indicates 'highly probable species identification', a score > 2 and < 2.299 indicates 'secure genus identification, probable species identification', a score > 1.7 and < 1.999 indicates 'probable genus identification', and a score < 1.7 indicates 'unreliable identification' (Normand et al., 2017).

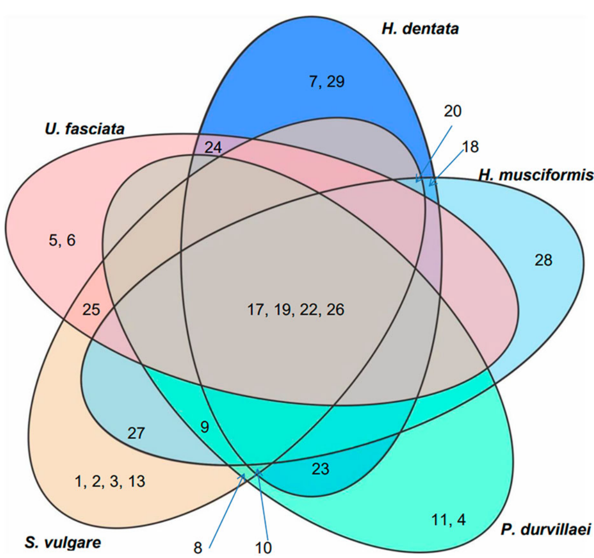

Figure 3. Venn diagram of shared and unique isolated bacteria on five seaweeds: 1: unidentified species (A1), 2: unidentified species (A2), 3: A. *haemolyticus,* 4: *A. radioresistens*, 5: Alcaligenes sp., 6: *B. infantis*, 7: *B. licheniformis*, 8: *B. megaterium*, 9: *Bacillus* sp., 10: *C. casei*, 11: *C. coyleae*, 13: *E. coli*, 17: *M. luteus*, 18: *P. composti*, 19: *P. stutzeri*, 20: *P. mendocina*, 22: *Pseudomonas sp.*, 23: *Psychrobacter* sp., 24: *S. algae*, 25: *S. hominis*, 26: *S. putrefaciens*, 27: *S. cohnii*, 28: *S. warneri*, 29: *Solibacillus silvestris*, 30: *V. alginolyticus.*

Shannon diversity (2.46) and Margalef richness (3.28), whereas the red seaweed, *Hypnea musciformis*, recorded the least Shannon diversity and Margalef richness of 1.98 and 1.74, respectively, across the studied sites (Table III).

Generally, *Bacillus* sp., *Micrococcus luteus*, *Shewanella putrefaciens* and *Vibrio alginolyticus* emerged as the most abundant bacterial species on the seaweeds whereas *Enterococcus* sp., *Klebsiella* sp. and *Pseudomonas* sp. were dominant in the seawater (Figure 4).

Association and distribution of planktonic and seaweed bacterial species

The corresponding analysis (CA) of the bacterial species in seawater and seaweed revealed a close association of some bacterial species on the different seaweeds and in the surrounding seawater. Also, the majority (72%) of bacterial species present on the seaweeds was distinct from those identified in the seawater. However, bacteria species such as *Alcaligene* sp., *Bacillus* sp., *M. luteus*, *Pseudomonas composti*, *Pseudomonas stutzeri*, *Pseudomonas* sp. and *Staphylococcus hominis* were common to both the seaweeds and seawater. Predominant bacteria species such as *Bacillus* sp., *M. luteus*, *P. stutzeri*, *Shewanella putrefaciens* and *Vibrio alginolyticus* were found growing in association with most of the seaweeds. Among the different seaweeds, bacterial species including *Bacillus magaterium*, *Corynebacterium casei*, *M. luteus* and *V. alginolyticus* were found to be dominant on the brown seaweeds *P. durvillaei* and *S. vulgare.* Bacteria species such as *Bacillus infantis* and *Alcaligens* sp. were mostly associated with the green seaweed *U. fasciata* (Figure 5).

The cluster analysis, based on the Bray–Curtis similarities, showed a high similarity between seaweeds of the same group (Figure 6). For example, the brown seaweeds (*S. vulgare* and *P. durvillaei*) formed a separate cluster from the red seaweeds (*H. dentata* and *H. musciformis*) at similarity indices of about 63% and 57%, respectively (Figure 6a: Seaweed and seawater). However, seaweed-associated bacteria identified on the brown seaweeds exhibited a closer association (48%) with the green seaweed, *U. fasciata*. Evidently, the bacterial community on the seaweeds was different from that of the seawater. With respect to sampling sites, three major clusters

Table II. Variations in the diversity of seaweed-associated and planktonic bacteria among the study sites.

Diversity indices	Elmina	Komenda	Mumford	Shama (Amenano)	Takoradi Fisheries
Number of isolates	121	123	134	69	83
Number of genera	8	11	13	7	6
Number of species	12	15	20	9	8
Margalef index (d)	2.29	2.91	3.88	1.89	1.58
Shannon diversity (H′)	2.13	2.18	2.61	1.89	1.92
Evenness (J′)	0.86	0.81	0.87	0.86	0.92

Table III. Diversity indices for isolated bacteria on seaweeds and seawater across the studied sites.

Diversity Indices	*H. dentata*	*H. musciformis*	*P. durvillaei*	*S. vulgare*	*U. fasciata*	Seawater
Number of isolates	103	100	55	71	111	90
Number of genera	8	5	8	11	7	9
Number of species	13	9	11	15	10	12
Margalef index (d′)	2.59	1.74	2.50	3.28	1.91	2.45
Shannon diversity (H′)	2.06	1.98	2.15	2.46	1.89	2.11
Evenness (J′)	0.80	0.90	0.90	0.91	0.82	0.85

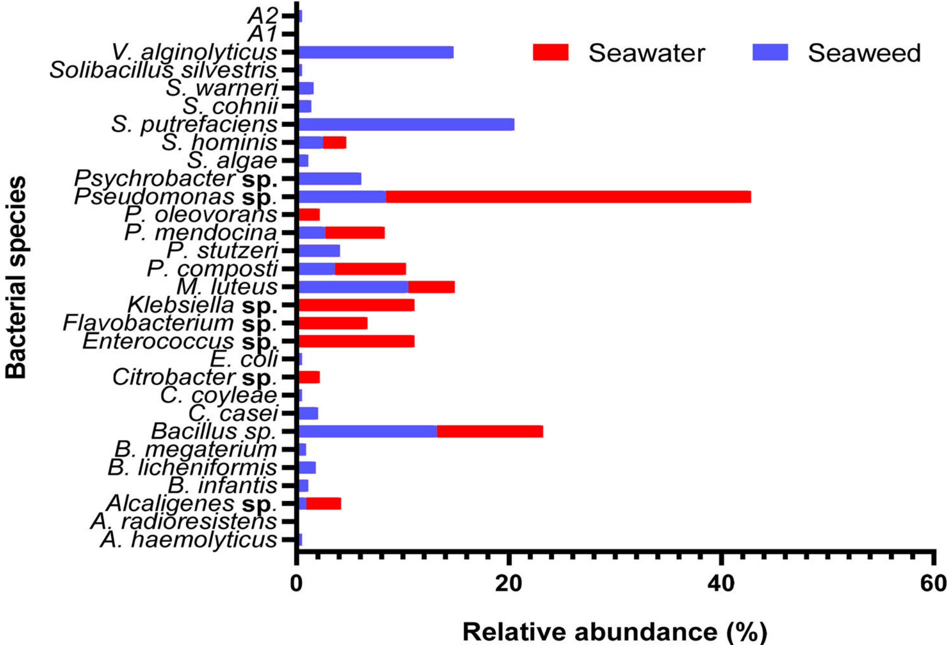

Figure 4. Relative abundance of bacteria isolates in seawater and seaweeds.

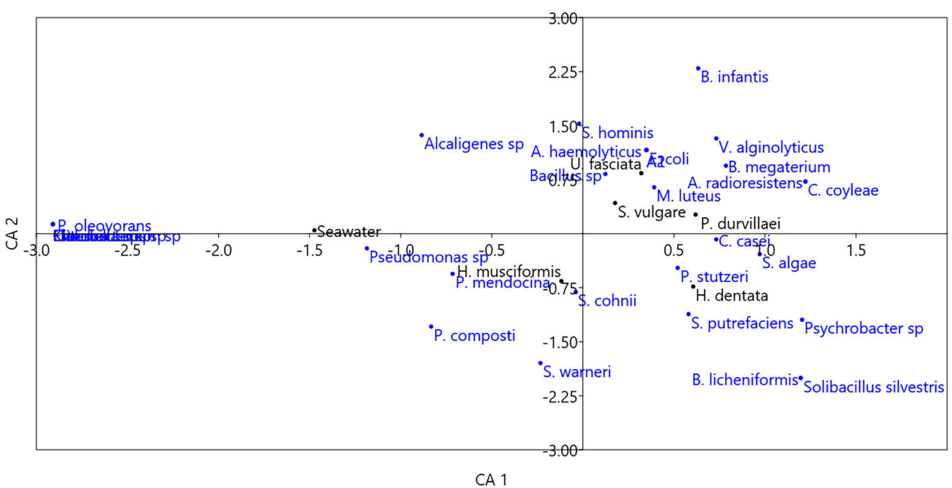

Figure 5. Association of bacteria diversity on seaweeds and seawater across the studied sites.

were observable; Elmina and Komenda in the Central Region showed the highest similarity index (53%), Shama (Amenano) and Takoradi Fisheries (50%) in the Western Region, whilst Mumford formed a different cluster from the rest (Figure 6b: Site).

Seasonal variations of bacterial species

When all the samples were combined, a slightly higher but statistically insignificant Shannon diversity index (2.65) of bacteria species was observed in the wet season than in the dry season (2.55) (Table IV). With respect to the individual seaweed species and the seawater, the diversity of bacterial species did not differ between the dry and wet seasons except for *U. fasciata*, where a significantly higher Shannon index was found in the dry season relative to the wet season. Similar patterns were found for the Margalef richness and the evenness values.

With the exception of Mumford and Takoradi Fisheries, no significant differences were observed in the diversity of the bacterial species between the wet and dry seasons (Table V). Mumford recorded higher Shannon diversity (2.53) and Margalef (3.33) indices in the dry season. However, at Takoradi Fisheries, the wet season had higher diversity than in the dry season.

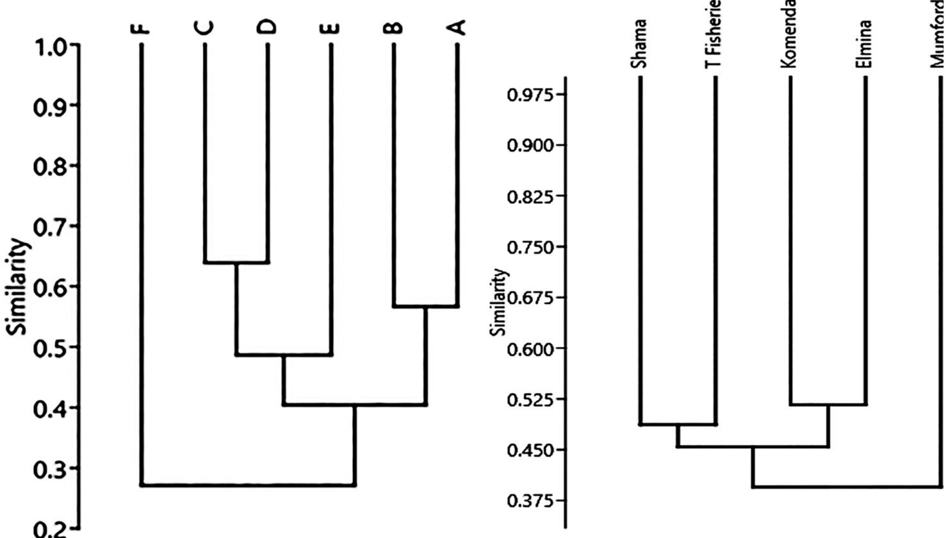

Figure 6. Cluster analysis of bacterial diversity in the seaweeds and seawater (5a: A–F represents: *H. dentata*, *H. musciformis*, *P. durvillaei*, *S. vulgare*, *U. fasciata* and Seawater, respectively), and across the five sites (5b) using the Bray–Curtis similarity index.

Table IV. Seasonal diversity and species richness of bacteria in samples across studied sites.

Seaweed/Seawater	Number (n)	Seasons	Shannon diversity (H′)	*P*-value	Margalef index (d)	Evenness (J′)
Bacteria on all samples	286	Dry	2.55	0.002	4.24	0.79
	244	Wet	2.65		3.82	0.86
Hydropuntia dentata	57	Dry	1.61	0.065	1.48	0.83
	46	Wet	1.88		1.83	0.9
Hypnea musciformis	51	Dry	1.63	0.122	1.53	0.84
	49	Wet	1.87		1.8	0.9
Padina durvillaei	33	Dry	1.86	0.337	2.00	0.89
	22	Wet	1.65		1.94	0.85
Sargassum vulgare	40	Dry	1.98	0.553	2.17	0.9
	31	Wet	2.05		2.33	0.93
Ulva fasciata	60	Dry	1.98	**0.012**	1.95	0.9
	51	Wet	1.58		1.78	0.76
Seawater	45	Dry	1.59	0.082	1.84	0.76
	45	Wet	1.89		1.58	0.97

Table V. Seasonal composition of diversity and species richness of bacteria in samples across studied sites.

Site	Number (n)	Season	Shannon diversity (H′)	*P*-value	Margalef index (d)	Evenness (J′)
All sites	265	Dry	2.50	0.045	4.08	0.79
	265	Wet	2.70		3.98	0.86
Elmina	68	Dry	1.8	0.613	1.9	0.82
	53	Wet	1.74		1.51	0.89
Komenda	68	Dry	1.91	0.294	2.37	0.8
	55	Wet	2.07		2.25	0.9
Mumford	67	Dry	2.53	**0.005**	3.33	0.94
	67	Wet	2.16		2.62	0.87
Shama (Amenano)	34	Dry	1.43	0.372	1.13	0.89
	35	Wet	1.57		1.4	0.88
Takoradi Fisheries	46	Dry	1.5	**0.012**	1.09	0.93
	37	Wet	1.83		1.78	0.94

The abundance of the isolated bacteria on the different seaweeds and seawater varied between the dry and wet seasons (Figure 7). Whereas some bacteria species, such as *Bacillus* sp., *M. luteus*, *P. composti* and *P. stutzeri*, were dominant in the wet season, *Pseudomonas* sp., *Psychrobacter* sp. and *S. putrefaciens* were more prevalent in the dry season. There were other species that exclusively dominated in the wet season, including *Klebsiella* sp., *B. licheniformis* and *Flavobacteria.* Others such

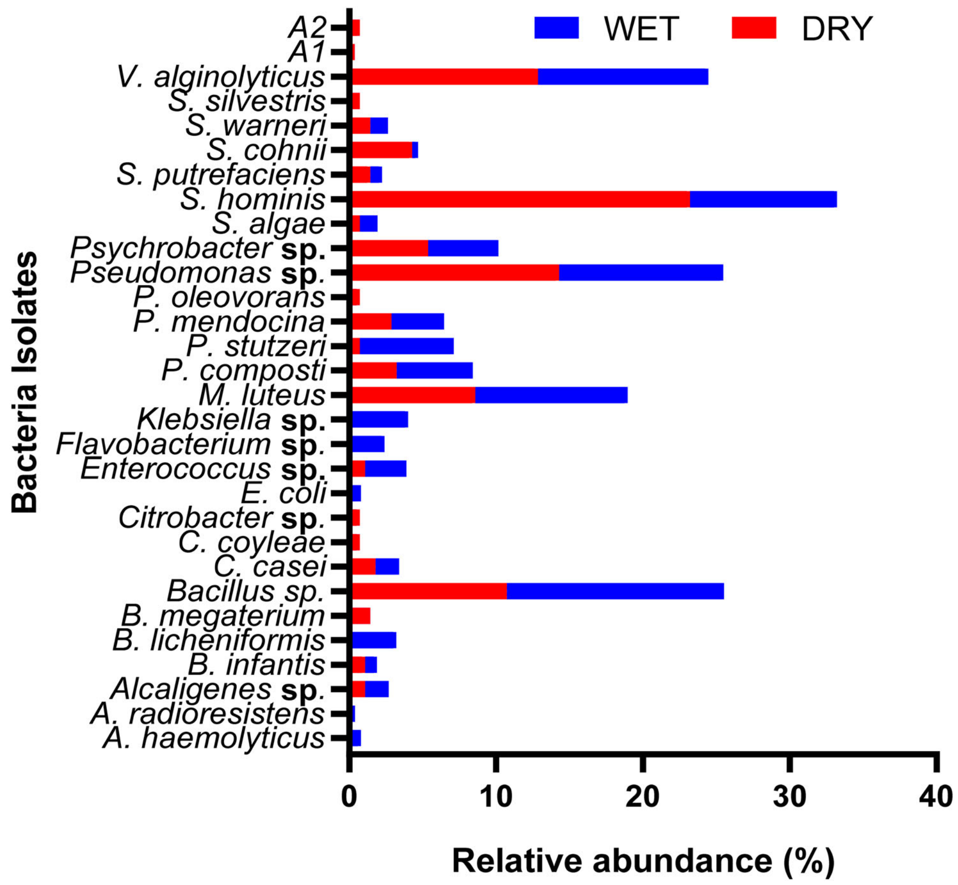

Figure 7. Relative abundance of bacterial species on seaweeds and seawater during wet and dry seasons across the study sites.

B. megaterium, *Citrobacter* sp. and *C. coyleae* were more dominant in the dry season (Figure 7).

Discussion

Diversity of bacteria in the coastal waters of Ghana

The study revealed diverse assemblages of bacteria species associated with the dominant seaweed and surrounding seawater across the five sampled sites in the central and western coasts of Ghana. The dominant seaweeds were of the divisions Rhodophyta (*Hydropuntia dentata* and *Hypnea musciformis*), Chlorophyta (*Ulva fasciata*) and Phaeophyta (*Padina durvillaei* and *Sargassum vulgare*). According to Singh and Reddy (2014) seaweed-associated bacteria are fast colonizers of seaweed surfaces, which are occasionally adaptive and possess the ability to rapidly utilize exudates from the seaweeds. Dominant bacteria phyla associated with seaweed and seawater at our study sites included Firmicutes and Proteobacteria with others belonging to Actinobacteria and Bacteroidetes phylum. These taxonomic compositions corroborate the findings of Singh and Reddy (2014) who reported the high dominance of Firmicutes and Proteobacteria on seaweed species globally. The Actinobacteria, Bacteroidetes, Firmicutes and Proteobacteria, have similarly been identified as the major phyla of epiphytic bacteria on seaweeds in China and South Africa (Selvarajan et al. 2019; Zhang et al. 2019). The presence of these bacteria on the seaweeds and in the seawater could partly be attributed to increased runoffs and anthropogenic activities such as defecation and degutting of fishes as observed at the sites. These factors could promote bacteria diversity as observed in this current study (Nimnoi and Pongsilp 2020), albeit, further studies on the interaction of the environmental factors on seaweed diversity is needed. Additionally, identification of bacteria isolates from environmental sources such as seaweeds using Matrix Assisted Lesser desorption ionization time of flight mass spectrometry (MALDI–TOF MS), though novel, is limited (Giebel et al. 2008; Eddabra et al. 2012; Kizhakkekalam and Chakraborty 2019). This identification system lacks a comprehensive database of bacteria isolates from environmental origin in the system and this could influence the quantum of bacteria identified in the study (Popović et al., 2017).

The dominance of these phyla Firmicutes and Proteobacteria on the seaweeds and seawater was expected since they have been reported to be well equipped to survive the effect of varied stress parameters and may also have the capacity of a high-efficient energy generation system (Singh and Reddy 2014). Species in the phyla Bacteroidetes and Actinobacteria are reported to possess alginolytic and carrageenanolytic activities, which facilitate their harbouring on seaweed surfaces compared with other bacteria strains (Lachnit et al. 2011; Singh and Reddy 2014). At the genus level, species belonging to *Pseudomonas* (24%) and *Bacillus* (16%) were dominant in all the samples. *Bacillus* sp. provides protection for seaweeds from harmful heavy metal contamination, in addition to supplying them with nitrogen-based growth supplements through fixation of atmospheric nitrogen. These bacteria also secrete antibacterial compounds as secondary metabolites that serve as antifouling compounds (Egan et al. 2013). Thus, the presence of these bacteria on the seaweeds could partly explain their luxurious growth at the sites (Akrong et al. 2021).

The substantial differences observed in the diversity of bacteria communities between the seaweeds and seawater is consistent with studies of Grueneberg et al. (2016), who also found considerable differences between the bacteria community present on macroalgae and their immediate surrounding water using the Polymerase Chain Reaction–Denaturing Gradient Gel Electrophoresis (PCR–DGGE) techniques. Similarly, using Bray–Curtis similarity analysis, Burke et al. (2011) reported a distinctly different library of bacteria communities between the seaweed *Ulva australis* and the seawater. This difference could be attributed to the protective and conducive environment provided by seaweeds including the availability of organic matter such as agar and carrageenan in the cell walls of red seaweed for bacteria growth and microbial process (Paerl and Pinckney 1996; Beleneva and Zhukova 2006; Michel et al. 2006). It has also been established that type of seaweed species, seasonal changes and specific interactions of the bacteria with abiotic factors could also influence the diversity and distribution of the seaweed-associated and planktonic bacteria (Hengst et al. 2010; Selvarajan et al. 2019; Juhmani et al. 2020).

The attachment and growth of bacteria on surfaces of seaweeds greatly depend on the type of metabolites and composition of seaweeds (Lam and Harder 2007; Lachnit et al. 2011). This may account for the higher compositional similarity of bacteria observed on seaweeds from the same divisions. For instance, the brown algae, *P. durvillaei* and *S. vulgare*, exhibited high similarity (64%) in their bacteria assemblage while those of the red seaweeds, *H. musciformis* and *H. dentata*, were 57% similar. Besides their taxonomic relatedness, entanglement of the red seaweed, *H. musciformis*, with *H. dentata* possibly contributed to the high similarity index of bacteria diversity displayed between the two seaweeds.

Shewanella was identified as the predominant bacteria genus in the study irrespective of the seaweed division, location and growth period. This largely indicates a high association of this bacteria with seaweeds of different divisions from all geographic locations (Stabili et al. 2017). Notwithstanding their beneficial effects, seaweed-associated bacteria can also be detrimental to their hosts (Goecke et al. 2010). The dominant bacteria, *Shewanella putrefaciens*, that was commonly found on all the seaweeds have been previously implicated in causing diseases such as nosocomial pneumonia and bacteraemia in humans (Ullah et al. 2018; Zhang et al. 2018). The bacteria species are described as saprophytic while others are reported to be opportunistic pathogens or pathogenic (Vignier et al. 2013). The high association of the brown seaweeds (*S. vulgare* and *P. durvillaei*) with *Vibrio alginolyticus* corroborates the findings of several studies that *Vibrio* species are associated with brown seaweeds (Wang et al. 2008; Barberi et al. 2020) and could act as opportunistic pathogens to cause disease. Research has indeed shown that despite their ability to produce antimicrobial compounds, *Vibrio* sp. have also been reported to be potentially pathogenic (Selvarajan et al. 2019). This suggests that the occurrence of pathogenic bacteria on seaweeds could pose a health risk to cultivators and consumers (Albakosh et al. 2016). This calls for careful handling during cultivation of seaweeds and thorough washing if they are to be used as a food source. The extensive alkaline treatment and alcoholic (isopropanol) precipitation during hydrocolloid extraction from seaweeds (Rhein-Knudsen and Meyer 2021) are also important to reduce the risk of bacterial contamination. Careful rinsing is also crucial to avoid bacterial proliferation during transport or storage of the seaweeds for food processing.

Variation in the diversity of seaweed-associated and planktonic bacteria across sites

Variations in the diversity of seaweed-associated and planktonic bacteria observed at the different sampled sites suggest strong influences of various environmental factors and anthropogenic activities (Zhang et al. 2019; Juhmani et al. 2020). For instance,

the proximity of the community to the shore and anthropogenic activities such as open defecation (Akrong et al. 2021), sales of premix fuel, fishing, degutting and descaling of fish by fishmongers could account for the high bacteria diversity recorded at Mumford. In contrast, the lower bacteria diversity indices observed at Shama (Amenano) and Takoradi Fisheries could be due to the reduced availability of the brown seaweed (*S. vulgare* and *P. durvillaei*) and thus their respective bacteria isolates at the sampled point during the study period. These differences may also explain the clustering (similarity) of Shama (Amenano) and Takoradi Fisheries (both in the Western Region) relative to Komenda and Elmina in the Central Region in the cluster analysis.

Seasonal changes in seaweed-associated and planktonic bacterial community

The general lack of difference in bacterial diversity between the wet and dry seasons largely corroborates the postulation of Chellaram et al. (2013), that there is a minimal seasonal difference in bacteria species on seaweeds. This finding suggests that the type of seaweed and their location could largely influence the distribution and diversity of bacteria found on the seaweeds between the two seasons. Notwithstanding, the slightly higher diversity of bacteria observed in the wet season at the Takoradi Fisheries could be attributed to increased runoffs into the intertidal marine environment as reported by Nogales et al. (2011). Additionally, the marginal changes in anthropogenic activities observed between the seasons at the sites, especially Shama, Komenda and Elmina might have trumped the seasonal effects on the diversity of bacteria on seaweeds.

Conclusion

The study demonstrates the diverse bacterial communities associated with seaweeds of economic importance across the coastal waters of Ghana. Proteobacteria and Firmicutes were the major and common phyla found associated with the seaweeds across the studied sites. The identified bacteria in the current study included species such as *Bacillus* sp. and *Vibrio* sp. reported to have both beneficial (promote growth and development of host plant) and detrimental (causing disease to host plant) effects on seaweeds. Marginal seasonal differences in bacterial diversity were observed among the various seaweed species with the higher diversity generally recorded during the wet season. The findings of the current study provide important baseline information on the spatial, temporal and taxonomic distribution of epiphytic bacteria associated with economically valuable seaweed species in the coastal areas of Ghana. The presence of various opportunistic pathogens on the seaweeds could suggests health risk concerns for immunocompromised individuals, requiring careful handling by farmworkers involved in the cultivation of seaweeds, and thorough washing or rinsing prior to their use for food purposes, e.g. the extraction of potential food components (e.g. hydrocolloids). Information gathered from this study is vital for sustainable exploitation and conservation of these important macroalgae in this country and beyond. Moreover, results from the current study suggest further studies are necessary on the association of these bacteria with seaweeds in relation to varying environmental conditions in space and time and also to identify bacteria species with different identification systems (e.g. 16S rRNA).

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Disclosure statement

No potential conflict of interest was reported by the author(s).

Contribution

Conceptualization and design A.M.O, A.M., A.J.A., Sample collection and analysis A.M.O., A.G.N.D., d.K.A.A., A.A., Writing of original draft preparation A.M.O. Data analysis A.M.O., A.A.K, A.J.A. Supervision A.A.K, H.J.N, A.G.N.D., d.K.A.A, A.J.A. Revision of manuscript A.M.O., A.A.K, A.G.N.D., d.K.A.A., A.A., H.J.N., A.J.A., A.M., M.A.S. Funding acquisition M.A.S., A.G.N.D. All authors read and approved the final manuscript.

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