ISSN 0026-2617, Microbiology, 2006, Vol. 75, No. 3, pp. 348–357. © Pleiades Publishing, Inc., 2006.
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EXPERIMENTAL ARTICLES

Bacterial Communities of Some Brown and Red Algae from Peter the Great Bay, the Sea of Japan

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Received June 28, 2005

Abstract—The structure of microbial communities of brown algae, red algae, and of the red alga *Gracilaria verrucosa*, healthy and affected with thallus rot, were comparatively investigated; 61 strains of heterotrophic bacteria were isolated and characterized. Most of them were identified to the genus level, some *Vibrio* spp., to the species level according to their phenotypic properties and the fatty acid composition of cellular lipids. The composition of the microflora of two species of brown algae was different. In *Chordaria flagelliphormis, Pseudomonas* spp. prevailed, and in *Desmarestia viridis, Bacillus* spp. The composition of the microflora of two red algae, *G. verrucosa* and *Camphylaephora hyphaeoides*, differed mainly in the ratio of prevailing groups of bacteria. The most abundant were bacteria of the CFB cluster and pseudoalteromonads. In addition, the following bacteria were found on the surface of the algae: *Sulfitobacter* spp., *Halomonas* spp., *Acinetobacter* sp., *Planococcus* sp., *Arthrobacter* sp., and *Agromyces* sp. From tissues of the affected *G. verrucosa*, only vibrios were isolated, both agarolytic and nonagarolytic. The existence of specific bacterial communities characteristic of different species of algae is suggested and the relation of *Vibrio* sp. to the pathological process in the tissues of *G. verrucosa* is supposed.

DOI: 10.1134/S0026261706030180

Key words: microbial communities, brown algae, red algae.

Brown and red algae are of industrial importance. The cell walls of brown algae contain widely used salts of alginic acid; those of red algae contain the polysaccharides agar and carrageenan. Intensive exploitation and bacterial diseases inflict great damage to the populations of commercial algae. The interrelations between algae and the associated bacteria are multifaceted and complicated. The algae are a source of dissolved organic matter, which supports growth of the associated microflora [1]. The surface of algae provides bacteria with suitable microniches where the conditions for specific microbial processes are more favorable than in the ambient water [2]. Bacteria and algae may compete for inorganic nutrients [3]. In addition, many algal taxa produce substances inhibiting bacterial growth [4]. At present, the interactions between algae and bacteria are being widely investigated. However, the ecological significance of most such natural associations remains vague. It is not known to what extent the microbial association of heterotrophic bacteria is specific for certain systematic groups of algae and how the microflora of the diseased macrophytes changes.

The composition of the bacterial associations of the macrophytes of the Russian coast of the Sea of Japan is not investigated; the available information is fragmentary [5], in spite of the obvious fact that bacteria interfere with the life of algae. The goal of the present study was to investigate the community structure of heterotrophic bacteria associated with healthy representatives of the widespread species of brown and red algae in Peter the Great Bay and the changes of the composition of microflora in the affected macrophytes.

MATERIAL AND METHODS

Heterotrophic bacteria were isolated from healthy marine algae: brown algae *Desmarestia viridis* and *Chordaria flagelliphormis* red algae *Gracilaria verrucosa* and *Camphylaephora hyphaeoides*, and *G. verrucosa* affected by rot. The samples were collected by divers in the Avangard Gulf of Peter the Great Bay in July 2004. The samples of algae were placed in sterile vials and brought to the laboratory not later than half an hour after sampling. The algae were washed thrice with sterile seawater, weighed, and a sample of 1 g was homogenized aseptically. After serial dilutions, the homogenate was inoculated on TCBS agar and a solid nutrient medium Y-K [7]. For isolation of fungi, the Sabouraud medium with streptomycin was used. The inoculated dishes with the Sabouraud medium were incubated for two weeks; those with the Y-K medium, for up to three weeks at room temperature; and those with TCBS agar, for two days at 35°C. The plates were examined daily, the number of grown colonies counted,

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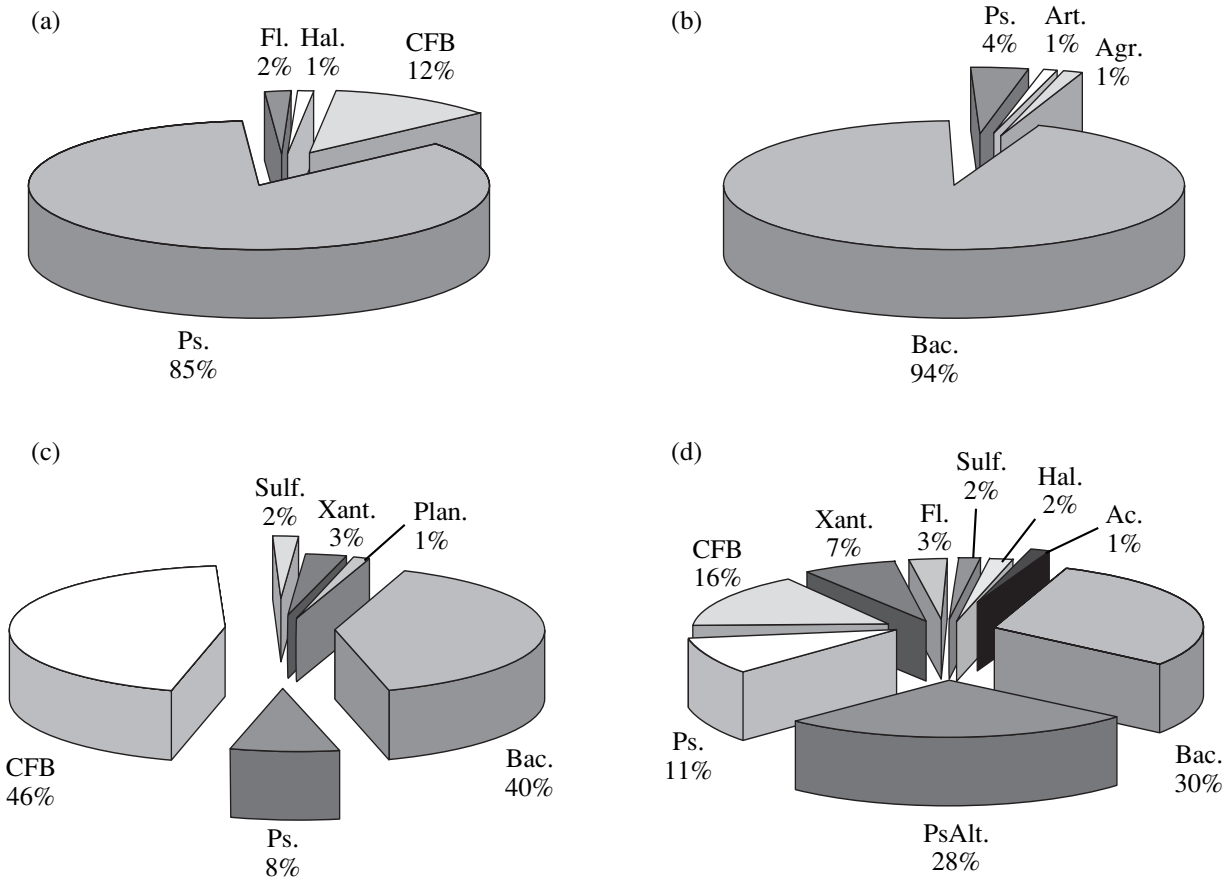

Fig. 1. Taxonomic composition of bacteria associated with various algae in Peter the Great Bay: (a) with brown alga *Chordaria flagelliphormis,* (b) with brown alga *Desmarestia viridis*, (c) with red alga *Camphylaephora hyphaeoides*, (d) with red alga *Gracilaria verrucosa.* Designations: Ps., *Pseudomonas* spp.; Bac., *Bacillus* spp.; Fl., *Flavobacterium* spp.; CFB, bacteria of the phylogenetic cluster *Cytophaga–Flavobacterium–Bacteroides*; Hal., *Halobacillus* spp.; Art., *Arthrobacter* spp.; Agr., *Agrobacillus* spp.; Xant., *Xanthomonas* spp.; Sulf., *Sulfitobacter* spp.; Ac., *Acinetobacter* spp.; PsAlt., *Pseudoalteromonas* spp.; Plan., *Planococcus* spp.

and the colonies of every morphotype were transferred to new dishes with the proper medium in order to obtain a pure culture of bacterial isolate. Morphological, cultural, and biochemical properties, chemotaxonomic analysis, and the DNA G+C content were determined as previously described [8].

RESULTS AND DISCUSSION

From four species of red and brown algae, 61 strains of heterotrophic bacteria were isolated. The major characteristics of the isolated bacteria are indicated in Table 1. Gram-negative bacteria constituted 68.9% of the total number of isolated strains. However, they predominated not in all investigated bacterial associations (Fig. 1). This seeming discrepancy can be explained by the fact that on dishes the colonies of all grown morphotypes were counted, but only one colony of each morphotype was chosen for further identification. All bacterial morphotypes were identified to the genus level and some vibrios, to the species level. The fatty acids composition of cellular lipids of some strains is presented in Table 2; it was used as an additional test for their identification to the genus level. The numbers of bacteria on healthy brown and red algae grown on Y-K-agar varied from 1.37×10^5 to 6.14×10^5 cells per 1 g of wet biomass; in the affected *G. verrucosa* it was higher by two orders of magnitude, 2.83×10^7. Higher abundance of bacteria in samples of diseased algae compared with healthy algae was reported by other authors [9].

Kharlamenko [10] investigated the epiphytic bacteria of the Vityaz Gulf (Sea of Japan) and found that the surface of algae was densely populated with microorganisms. The density indices of bacterial population of *Chordaria flagelliphormis* determined by this author by the method of direct microscopy are higher than the similar indices which we obtained for the same alga. We believe that the difference is caused by the resolution of the applied methods. Our method, in spite of its drawbacks (only the currently active cells grew on the dish), gives the possibility not only to enumerate both the entire microbial cenosis and its individual representatives, but also to isolate them.

Table 1. Principal characteristics of bacterial strains isolated from the algae of Peter the Great Bay

Taxon	Morphology	O/F test	Oxidase	Motility	Pigment	Oxidation substrate	Requirement of Na^+ ions	NO_3–reductase	Arginine decarboxylase	Agarase	G+C, mol %
Bacillus	sr	O	+, –	+	y, w	Glucose, arabinose, mannitol	–	+, –	–	–	37.5–41.4
Pseudomonas	sr	O	+, –	+	np, y, w, p	Glucose	+	+, –	–	+, –	60.2
Flavobacterium	sr	O	+	–	y	Glucose, sucrose	+	+, –	–	+, –	34.0
CFB cluster	ir	O	+, –	–	y	Glucose	+	+, –	–	+, –	34.6
Planococcus	c	O	–	+	y	–	–	–	–	–	42.3
Xantomonas	sr	O	–	+	r	Glucose	–	+	–	–	63.5
Sulfitobacter	ir	O	+	+	np	–	–	–	–	–	63.7
Halobacillus	c, rd	O	+	+	np	Glucose, mannitol	+	–	–	–	42.0
Halomonas	rd, c	O	+	+	np	Glucose	+	+	–	–	64.0
Acinetobacter	c	O	–	–	np	Glucose, maltose	+	–	–	–	39.0
Pseudoalteromonas	sr	O	+	+	y, w, o	Glucose	+	+, –	–	+	44.0–48.0
Cellulophaga	ir	O	+	–	y	–	+	+	–	+	34.6
Arthrobacter	ir	O	+	–	w	Glucose	–	–	–	–	62.3
Agromyces	ir	O	–	–	w	Glucose	–	–	+	–	71.8

Note: sr, straight rods; ir, irregular rods; c, cocci; rd, rods; np, no pigment; y, yellow; w, white; p, pink; r, red; o, orange.

Table 2. Composition of fatty acids of some bacterial strains associated with algae from Peter the Great Bay (% of the total)

Fatty acids	*Flavobacterium* 401	*Flavobacterium* 404	CFB 408	*Cytophaga* 416	CFB 417	*Cellulophaga* 425	CFB 426	CFB 427
13:0-*i*	–	0.3	–	0.4	0.3	–	–	–
14:0-*i*	0.5	–	1.2	0.5	–	–	–	–
14:0-br		0.6	0.7	–	–	–	–	–
14:0	2.4	2.5	0.9	0.4	0.4	1.8	2.9	1.9
15:0-*i*	17.1	29.8	16.6	31.7	36.4	16.6	18.7	14.3
15:0-*a*	3.5	–	–	3.5	5.2	2.8	1	2.2
15:1-*i*	19.5	19.5	25.7	32.3	25.8	14.8	17.4	15.2
15:0	8.1	9.7	22.5	10	11.5	18.3	13.7	15.2
15:1(*n*-8)	0.9	–	1.9	1.5	1	–	–	–
15:1(*n*-6)	2.8	0.9	4.1	1.4	1.2	2.8	2	3.2
16:0-*i*	1.4	–	1.3	0.5	–	1.1	–	–
16:0-*ai*	–	–	–	0.4	–	–	–	–
16:1-*ai*	–	–	–	0.4	–	–	–	–
16:0	1.3	3.1	1		0.5	1.4	2	1
16:1(*n*-7)	16.4	17.2	5.3	1	0.2	12.7	12	12
17:0-*i*	0.5	0.7	–	–	–	–	–	–
17:0-*a*	–	0.5	–	–	–	–	–	–
12:0-3OH	1.7	2.1	0.7	0.4		1.7	1.1	2.1
17:1(*n*-8)	0.6	0.2	–	–	–	–	–	–
15:0-*i*-2OH	–	0.2	1.3	3.8	4.3	2.5	5.8	3.8
14:0-3OH	–	–	–	–	–	1.4	1.4	2.1
15:0-*i*3OH	2.6	1.1	3.6	5	8.4	6.1	6.5	8.7
15:0-3OH	–	–	–	–	–	1.9	–	2.3
16:0-*i*3OH	2.3	0.7	3.5	1	1	6.4	3.2	7.3
16:0-3OH	0.9	2.2	0.8	–	–	1.7	–	1.9
17:0-2OH	1	3.3	1.4	1.6	1.3	–	–	–
17:0-*i*3OH	2.8	4.3	3.1	2.2	2.7	5.9	10.4	6.9
17:0-3OH	1.9	0.7	3.3	–	–	–	–	–

Table 2. (Contd.)

Fatty acids	*Pseudomonas* 402	*Pseudomonas* 406	*Pseudomonas* 420	*Pseudomonas* 405	*Pseudomonas* 411	*Hallobacillus* 403	*Bacillus* 412	*Bacillus* 428
10:0	3.4							
12:0	4.2	4.3	4.4	2.8	2.7			
13:0-*i*							0.5	
13:0-*ai*								
13:0			0.7	0.4	0.4			
14:0-*i*						8.5	5.8	4.8
14:0			2.9		2	0.8	0.7	
14:1			1.1	2	1.1			
15:0-*i*				1		16	3.8	20
15:0-*a*						48.2	57.3	53.4
15:1-*a*								
15:0			2.5	1	1.7	1.2	1.2	0.9
15:1(*n*-8)			1.3			1.8		
15:1(*n*-6)				0.8	1.5			
16:0-*i*			0.6	0.4	0.6	2.3	4.4	9.1
16:0-*ai*						7.4	8.7	2.2
16:0	18.9	24.6	12.8	17	14.2	1.4	0.6	1.1
16:1(*n*-10)						4.4	2.6	
16:1(*n*-7)	39.1	30.1	44.5	41.7	40.8			
17:0-*i*						0.5	0.5	
17:0-*a*		0.5	1	1.2	1.4	3.2	7.3	6.6
17:1-*a*						3	4.7	
17:0			2.5	2.8	3.4		1.4	
17:1(*n*-8)	7.9	4.7	8.8	5.8	8.6			
18:0				1	0.6			
18:1(*n*-9)								
18:1(*n*-7)	22.3	34.5	12.5	18.6	13.8			
18:2								
18:2								
15:0-*i*-2OH								
14:0-3OH								

Table 2. (Contd.)

Fatty acids	*Bacillus* 431	*Bacillus* 432	*Bacillus* 434	*Bacillus* 435	*Bacillus* 429	*Sulfitobacter* 423	*Xanthomonas* 413	*Sulfitobacter* 415
10:0								
12:0						2.5		1.5
13:0-*i*					12.1			
13:0-*ai*					2.4			
13:0								
14:0-*i*	1	6.1	12.8	19.2	3.2			
14:0	0.9	1.1		1.6	3.6			
14:1								
15:0-*i*	1.8	33.4	6.1	20.7	28.5		27.1	
15:0-*a*	57	12.4	45.4	36.5	8.1			1.3
15:1-*a*							11.4	
15:0	1	1.1	1.2				1.4	
15:1(*n*-8)								
15:1(*n*-6)							2.6	
16:0-*i*	1.5	12.1	9.1	2.2	2.1		4	
16:0-*ai*	2.6	8.2	12.3	4.3	2.2		2.1	
16:0	2.7	3.2	0.9	1.7	4.2	8.1		
16:1(*n*-10)	3	5.1	1.4	4.7	3.1			
16:1(*n*-7)	0.8	1.2			7	0.8	15.7	
17:0-*i*		2.3			7			
17:0-*a*	20.7	4.2	4.5	2.3	10.2		3.7	
17:1-*a*	5.5	1.3	4.3		2.5		1.2	
17:0					0.6			
17:1(*n*-8)							3	
18:0	0.2				0.1	1.1		1.9
18:1(*n*-9)	0.3	1			0.2	2.9		0.4
18:1(*n*-7)						80.6		89.7
18:2						2.3		
18:2						1.8		2.1
15:0-*i*-2OH							21.6	
14:0-3OH							2.5	

In the case of the direct inoculation method on agarized media for the estimation of epiphytic bacteria on *Zostera marina*, other authors obtained results comparable with our results, 1.2×10^5 cells per 1 g of wet weight of grass [5].

The number of bacteria associated with the brown alga *C. flagelliphormis* was 3.66×10^5 CFU/g. The microbial community was represented principally by gram-negative bacteria (Fig. 1a), namely by various species of *Pseudoalteromonas* and members of the CFB phylogenetic cluster. Two strains were identified as *Flavobacterium* spp., also belonging to this cluster. Both these strains and two of the CFB cluster isolates were agarolytic. Isolation of bacteria hydrolyzing alginate, laminaran, gelatin, and some other polysaccharides from brown algae *Fucus evanescens* was reported by Ivanova et al. [6]. These authors found that the gram-negative bacteria of the genera *Pseudoalteromonas* and *Halomonas* prevailed in the microbial association decomposing *Fucus*.

Of gram-positive bacteria populating the surfaces of the investigated brown alga *C. flagelliphormis* only an insignificant number of halobacilli was found.

The numbers of bacteria on another brown alga *D. viridis* was 6.14×10^5 CFU/g. In contrast to the previous alga, its surface was colonized by gram-positive microflora. The dominant members of this bacterial association were various species of bacilli (Fig. 1b). Arthrobacters and agromycetes were present in small quantities. Among gram-negative microorganisms, we identified pseudomonads.

Thus the composition of bacterial communities of two species of brown algae, *C. flagelliphormis* and *D. viridis*, is different. In the first case, the gram-negative bacteria of the genus *Pseudomonas* prevailed and in the second case, the gram-positive *Bacillus*. These differences in the composition of the microflora lead to the conclusion of the specificity of the species composition of bacteria characteristic for each investigated alga. In the available literature, there is no information on the taxonomic composition, not only of the heterotrophic microflora, but also of any other microflora associated with the surface of brown macrophytes. Japanese authors isolated alginolytic bacteria of the genus *Alteromonas* from the surface of the brown alga *Laminaria japonica* [11]. Bacteria *Pseudomonas elyakovii*, possessing strong alginolytic properties, were isolated from laminaria cultured in Japan and affected by "perforation"; these bacteria were shown to be the pathogenic agent of this disease [12].

Kondratyeva et al. [13] studied the diversity of heterotrophic bacteria isolated from macrophytes that were stranded by a storm on the coast of the Sea of Japan and consisted of inseparable masses of thalli and branches of various algae and grasses. Among 50 isolated strains, gram-positive coryneform bacteria were predominant.

Although coryneform bacteria were present in our samples of *D. viridis*, bacilli were dominant, as noted above. The coryneform bacteria are known to possess a complicated complex of enzymes decomposing high molecular weight polymers [14]. Microorganisms with such properties dominate in the stranded macrophytes. This fact indicated their active participation in the transformation of a wide range of polymeric substrates present in remains of vegetation [15]. It is obvious that the physiological and biochemical properties of substrata, in the present case, of algae containing complex polysaccharides, predetermine the composition of the microflora adhering to these substrata.

The microflora associated with the surface of red alga *C. hyphaeoides* comprises an equal proportion of both gram-positive and gram-negative heterotrophic bacteria (Fig. 1c). Their numbers were 1.37×10^5 CFU/g. The number of yellow- and white-pigmented colonies on the dishes inoculated with homogenized alga was identical. Of gram-positive, the dominant were bacteria with low DNA G+C content, *Bacillus* spp., of gram-negative, *Cytophaga* sp. Kurilenko et al. [5] observed that the bacteria of the phylogenetic cluster *Flavobacterium–Cytophaga–Bacteroides* dominated on the surface of sea grass *Zostera marina* in Peter the Great Bay. The prevalence of gram-positive bacteria with a high G+C content on the surface of another red alga *Delicea pulchra* was reported [16]. Presence of agarolytic *Pseudomonas* in the microbial community of *C. hyphaeoides* should be noted. The ability to utilize algal polysaccharides is known in many representatives of the genus *Alteromonas* isolated from algae [17]; most species of this genus are now reclassified within the genus *Pseudoalteromonas*. The isolation of bacteria with carrageenase and agarase activity from the homogenate of red algae *Chondrus* sp., *Polysiphonia* sp., and *Tichocarpus* was reported by Russian authors [18].

The presence of sulfite bacteria in the microflora of the investigated red algae is remarkable. These gram-negative aerobic heterotrophs belong to the α subclass of proteobacteria. They play an important role in the cycle of organic sulfur and were originally isolated from seawater. Later, they and the related bacteria of the group *Roseobacter–Sulfitobacter–Silicibacter* were found in the composition of the population of the toxic microalga *Alexandrium* in Japan [19]; they were also isolated from a starfish and from sea grass [20]. Obviously, these bacteria are rather widely distributed in the marine environment and are, in particular, the representatives of microbial associations of various algae.

The microflora of another investigated red alga *Gracilaria verrucosa* consisted of both gram-negative and gram-positive bacteria. The former dominated in the ratio 7 : 3 (Fig. 1d); the numbers of bacteria were 1.71×10^5 CFU/g. Pseudoalteromonads prevailed, which were not found in any of the investigated bacterial associations. Many of them rapidly hydrolyzed agar. The bacteria of the CFB cluster constituted a con-

siderable part of the microbial association; some of them also possessed agarolytic properties.

The composition of the microflora of the two investigated red algae, *C. hyphaeoides* and *G. verrucosa*, was different, but mainly in the numerical ratio of the dominant bacterial groups. We believe that the prevalence of agarolytic isolates of *Pseudoalteromonas* spp. on the surface of an agar-containing alga is an important fact. This fact may indicate the presence of specific interrelations between macro- and microorganisms and thus the formation of a specific bacterial community associated with the macrophyte.

The interrelations between marine algae and their microflora are little known. Recently, the red alga *Delisea pulchra* attracted great attention. The halogenated furanons produced by the microorganism inhibit the colonization of its surface by bacteria [16]. This results in the formation of a specific microbial association whose members are capable of minimizing the effect of furanons [21]. The formation of a specific bacterial association on the surface of sea grass *Zostera* was reported [5]. The latter controls the adsorption of microorganisms by secretion of various classes of extracellular products.

Decomposition of the complex polysaccharides comprising the cell walls of marine algae is performed by a complex of enzymes synthesized by a consortium of epiphytic bacteria. Not all the members of such an association possess an equally high metabolic activity [6]. While the members of CFB cluster and *Pseudoalteromonas* spp. can hydrolyze a wide range of complex polysaccharides, other representatives of the associated microflora, e.g., *Halomonas* spp., *Sulfitobacter* spp., and *Bacillus* spp., may supply additional growth factors to the consortium.

In the course of taking samples of *G. verrucosa*, both healthy algae and numerous affected algae were found. Their thalli were fragile and discolored, from pink to white in color. Direct microscopic examination of the homogenate of affected thalli revealed numerous rod-shaped bacteria, identical in their morphology. The numbers of bacteria in the affected alga determined by colony count on agar reached 2.83×10^7 CFU/g. The quantity of agarolytic and nonagarolytic bacteria was approximately equal (1.30×10^7 and 1.53×10^7, respectively).

The colonies grown after inoculation of the homogenate of the affected algae on Y-K medium and on TCBS agar were morphologically identical. There was no growth on Sabouraud medium for fungi. On TCBS agar, the bacteria grew as yellow round colonies with even margin; on Y-K medium, they grew as round beige slightly convex colonies. Under some of them, the agar was eroded, i.e., the cultures were agarolytic. Pure cultures of 12 strains of bacteria from the affected *G. verrucosa* were gram-negative, oxidase-positive rods with fermentative metabolism (Table 3). They were assigned to the genus *Vibrio* on the basis of analysis of morphological and biochemical features of isolates.

Table 3. Biochemical characteristic of bacterial isolates from the affected *G. verrucosa*

Characteristic	Agarolytic strains	Strains not hydrolyzing agar
O/F test (glucose)	+/+	+/+
Oxidase	+	+
Motility	+	+
Indole	+	+
Arginine decarboxylase	–	–
Lysine dihydrolase	+	+
Ornithine dihydrolase	–	–
Acid from:		
lactose	–	–
sucrose	+	+
arabinose	–	–
mannose	+	+
mannitol	–	+
inositol	–	–
Urease	–	–
NO_3–reductase	+	+
Amylase	+	+
Gelatinase	+	+
Agarase	+	–
DNase	+	+
Growth at NaCl, %		
0	–	–
3	+	+
6	+	+
8	+	+
10	+	+
Growth at temperature, °C		
5	–	–
10	+	+
15	+	+
37	+	+
43	–	–
Simmons citrate	+	+
Methyl red	+	+
Voges-Proskauer	–	–

By the combination of properties, the isolates lacking agarase were tentatively assigned to *V. alginolyticus*. Identification of agarolytic strains of vibrios to the species level is difficult as they differ from *V. alginolyt-*

icus in the presence of this enzyme, in the absence of acid formation from mannitol, and do not conform to the description of other known *Vibrio* species [14]. All the isolated vibrios were sensitive to vibriostatic agent 0-129, polymyxin, and nalidixic acid, and were resistant to oxacillin, benzylpenicillin, and streptomycin.

There is published information on the isolation of *Vibrio* spp. causing diseases of algae. Tsukidate [22] reported vibrios causing white rot of *Porphyra* spp. in Japan. Agarolytic strains of *Vibrio* spp. caused rot of thalli of *Gracilaria* spp. cultivated in the Philippines [9]. In these publications, the isolated vibrio cultures were also not identified to the species level.

The fact that vibrios were isolated from the affected thalli of *G. verrucosa* practically as a monoculture may indicate that these bacteria are involved in the pathological process in algal tissues. One has to be very careful making this conclusion since Koch's postulates should be followed in the determination of an etiologic agent of any infection. We did not arrange experimental infestation of *G. verrucosa* with the bacterial isolates. Therefore our conclusions are tentative and preliminary. The vibrios isolated from affected thalli may be an opportunistic infection and affect the algae suffering from some physiological stress. The absence of vibrios in the composition of the microflora populating the surfaces of healthy algae and their domination in diseased *Gracillaria* indicated the existence of a bacterial community characteristic of the normal physiological state of a macrophyte and the change of the community with the changes in the state of the alga. The identification of bacteria associated with healthy and diseased macrophytes is a major method in the complex investigation of the biology and ecology of algae.

ACKNOWLEDGMENTS

This study was supported by a grant of the Russian Academy of Sciences "Response of the Marine Biota to Changes of Natural Environment and Climate."

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