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Cyanobacteria and macroalgae from an arid environment mangrove on the east coast of the Baja California Peninsula

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Abstract

We describe the assemblage of cyanobacteria and macroalgae on *Avicennia germinans* pneumatophores, *Rhizophora mangle* aerial roots, and within the tidal channel of a mangrove located in a lagoon bordering the east coast of the Baja California Peninsula, from samples collected every 2 months from May 2005 to May 2006. A total of 68 species were found: 21 cyanobacteria, 1 Xanthophyta, 25 Chlorophyta, 1 Ochrophyta-Phaeophyceae, 19 Rhodophyta, and 1 Anthophyta. Species richness varied between habitats; pneumatophores supported 29 species of algae, aerial roots supported 20 species of algae, and the channel bottom supported 46 species. Taxa common to the three habitats were *Lyngbya* sp., *Vaucheria* sp., *Boodleopsis pusilla*, *Rhizoclonium riparium*, and *Bostrychia radicans*. Mean wet weight algal biomasses on aerial roots and in the channel were 494 g root^{-1} and 12,924 g m^{-2}, respectively. The dominant species on aerial roots and on the channel bottom were *Caulerpa sertularioides*, *Gracilariopsis lemaneiformis*, and *Spyridia filamentosa*. The channel bottom also had *Vaucheria* sp. and two cyanobacteria (*Oscillatoria* sp. and *Lyngbya* sp.). Morphotypes of two cyanobacteria (*Heteroleibleinia* sp. and *Johanesbaptistia* sp.) are recorded in this habitat for the first time.

Keywords: cyanobacteria; Gulf of California; macroalgae; mangrove; pneumatophore.

Introduction

Mangrove forests are one of the most biologically important ecosystems in coastal areas; they occur in diverse geomorphic settings, including deltas, lagoons, and estuaries in humid or dry climates, all of which vary in species diversity, energy flow, and material cycling (Chen and Twilley 1999). Mangroves on the Pacific coast of the Americas reach their northernmost distribution in the arid regions bordering the Gulf of California in the states of Sonora and Baja California Sur of Mexico. Mangroves are vital to healthy coastal environments, provide nutrients for food chains, maintain high biodiversity and productivity of the region, and sustain and improve human livelihoods (Páez-Osuna et al. 2003, Glenn et al. 2006, Aburto-Oropeza et al. 2008, López-Medellín et al. 2011). Despite their well-documented biodiversity and the services they provide, mangroves are disappearing rapidly worldwide. In the Gulf of California, they are lost at a regional rate of 2% annually from sedimentation, eutrophication, and deforestation (Aburto-Oropeza et al. 2008).

Productivity value varies with the type of primary producers (algae, mangroves, or seagrass), time of year, and the physicochemical characteristics of water (Trainor 1988). Cyanobacteria and macroalgae are primary producers within the mangroves and the first link in food chains; they are an important source in the production of oxygen and sequestration of carbon by photosynthesis (Nellemann et al. 2009). Macroalgae are food for mollusks, crustaceans, and fishes and are important as natural filters because they retain sediments and contribute detritus in mangrove ecosystems (Steinke and Naidoo 1990, Tejada-Rivas 2002). Cyanobacteria and macroalgae grow in habitats with adequate moisture, especially on mangrove tree roots and pneumatophores. Other substrata are soft mud, sand, macrophytes, sessile animals, and shell fragments (Cordeiro-Marino et al. 1992, Tejada-Rivas 2002, Roldan-Pérez and Ramírez-Restrepo 2008, Cruz-Madrid 2010). Epiphytic macroalgal mats form an important photosynthetic component of mangrove forests in the Caribbean (Rodríguez and Stoner 1990), Florida (Dawes 1974, 1996), the Philippines (Fortes 1987), and Australia (Davey and Woelkerling 1985).

Studies in Atlantic regions of Brazil, Venezuela, and Puerto Rico have focused on macroalgae associated with roots (Burkholder and Almodovar 1973, Pedrini 1980, Barrios et al. 2003), their distribution and biomass (Rodríguez and Stoner 1990), reproductive patterns (Braga et al. 1990), spatial and temporal variation, vertical distribution in pneumatophores (Yokoya et al. 1999), and taxonomy of cyanobacteria (Nogueira and Ferreira-Correia 2001). Studies on the Pacific coasts of Guatemala, El Salvador, Nicaragua, Costa Rica, Panama, and Colombia have provided a list of marine macroalgae in different ecosystems, such as mangrove forests (Fernández-García et al. 2011). There are descriptions of spatial and seasonal dynamics of populations and algal biomasses associated with *Rhizophora mangle* Linnaeus roots and *Avicennia germinans* Linnaeus pneumatophores, gradients of flooding and salinity, and zonation patterns in the mangroves (Tejada-Rivas 2002, Baos-Estupiñan and Velasco 2007, Peña-Salamanca 2008, Cruz-Madrid 2010, Fernández-García et al. 2011).

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Most studies on the macroalgal assemblage on trunks and aerial roots of mangroves have been related to the *Bostrychietum* group, which includes 12 species among the genera *Bostrychia*, *Caloglossa*, and *Catenella* (Braga et al. 1990), with another typical group found in the sediment, the *Rhizoclonietum*, which contains more than 10 species of green algae in the genera *Rhizoclonium*, *Ulva*, and *Cladophora* (Pedrini 1980).

Mangroves along the northeastern Pacific appear to have low algal diversity, with 10 reported species, but these are the least studied on the North American continent; low diversity may be an artifact of the lack of taxonomic work in this region (Lacerda et al. 1993). Knowledge of mangrove algae in Mexico is limited and comes mainly from the Caribbean coast (Collado-Vides and González-González 1993, Collado-Vides and West 1996, González-Duran et al. 2008). Information on mangrove algae from the Pacific margin is mainly of species associated with roots (West et al. 1992, 1994), among which species of *Bostrychia*, *Caloglossa*, and *Catenella* have been recorded (Pedroche et al. 1995). There have been few studies of algae in mangroves bordering the Gulf of California. Toledo et al. (1995) found differences in general vertical zonation among cyanobacteria on *Avicennia germinans* pneumatophores in the mangrove at Bahía Balandra (~25 km to the northeast of city La Paz). Paul-Chávez and Riosmena-Rodríguez (2006) listed 13 macroalgae (5 Chlorophyta, 1 Ochrophyta-Phaeophyceae, and 7 Rhodophyta) in 10 localities with areas of mangroves in Bahía de La Paz. Recently, Riosmena-Rodríguez et al. (2011) reported 214 algae species in mangrove systems of the Baja California Peninsula (Pacific and Gulf of California coasts). This high species number is related to the number of records from algal rhodoliths, which provide habitats with high community diversity.

In our study, we describe the composition of the main cyanobacteria and macroalgae attached to *Avicennia germinans* pneumatophores, *Rhizophora mangle* aerial roots, and the bottom of the tidal channel at Estero Zacatecas, a protected inlet deep inside a large lagoon bordering the Gulf of California. Estero Zacatecas is near the northern limit of mangrove sites.

Materials and methods

Study site

Estero Zacatecas (24°10′27″ N, 110°26′06″ W) is at the landward end of a lagoon called Ensenada de La Paz in the State of Baja California Sur, Mexico (Figure 1). This is an arid, subtropical region with occasional summer rainfall from tropical cyclones and occasional winter frontal storms. The mangroves in this area grow under suboptimal conditions; the assemblages are far less extensive and contain shorter trees than in most tropical locations (Whitmore et al. 2005). Ensenada de La Paz is a lagoon that operates as an evaporation basin, especially at its landward end; it has higher salinity than the surrounding open marine waters (Espinoza-Avalos 1979). Estero Zacatecas contains ~17 ha of mangrove forest of *Rhizophora mangle*, *Laguncularia racemosa* (L.) Gaertn., and *Avicennia germinans*. The meandering tidal channel is 1.3 km long, 58 m wide at the mouth, has a maximum depth of 2.5 m (X. Zamorano, pers. comm.) and an area of 6.4 ha. There are three flood zones totaling 28.3 ha (Mendoza-Salgado 1983). The tidal regime is semidiurnal, with an average range of 1.02–1.74 m. During samplings, temperature ranged from 17.5°C to 32.2°C and salinity from 38.12 to 43.08 psu. During the study period, there was almost no rain during the year, clearly marking this mangrove as subject to high salinity where no runoff was available (López-Portillo and Ezcurra 2002, Holguin et al. 2006). The "Estero" formed where a large sand spit called El Mogote connects to the mainland of the peninsula.

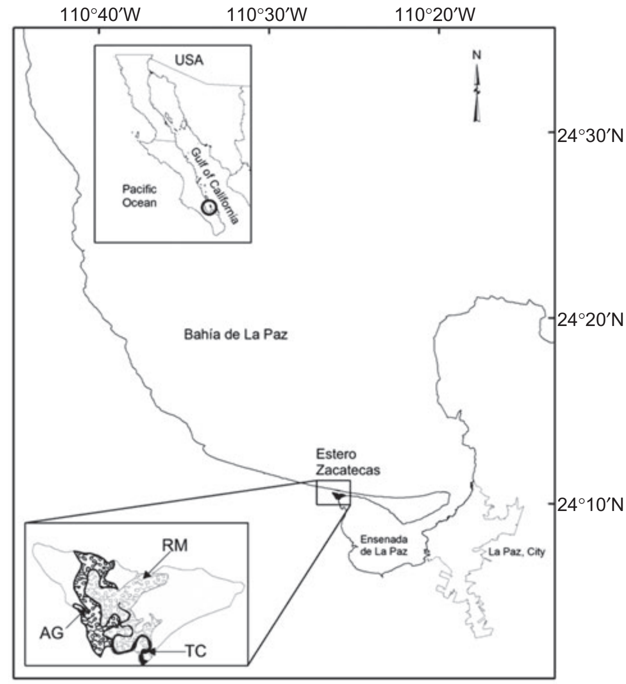

Figure 1 Map of Estero Zacatecas in the State of Baja California Sur, Mexico indicating the fringe mangrove.
AG, *Avicennia germinans*; RM, *Rhizophora mangle*; TC, tidal channel.

Sampling

In Estero Zacatecas, samples were taken from *Avicennia germinans* pneumatophores, *Rhizophora mangle* aerial roots, and the bottom of the tidal channel. Bimonthly samplings were made from May 2005 to May 2006 (n=7). Each sample was placed in a separate bottle, labeled, and fixed with 4% formaldehyde in seawater. Samples were studied under an Olympus BX51 microscope (Olympus, Tokyo, Japan). We used Komárek and Anagnostidis (1999, 2005) to identify cyanobacteria, and Dawson (1944), Setchell and Gardner (1924), Abbott and Hollenberg (1976), and Pedroche et al. (2005, 2008) to identify macroalgae. The classification system is in accord with Komárek and Anagnostidis (1999,

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2005) for cyanobacteria, and Wynne (1986) and Guiry and Guiry (2010) for macroalgae.

***Avicennia germinans* pneumatophores** To determine species composition of cyanobacteria and macroalgae, two pneumatophores were collected randomly on each of the 7 days of sampling (n=14) at the fringe of *Avicennia germinans*. Each pneumatophore was washed with fresh water to remove the sediment and organic matter. Pneumatophores were scraped with a scalpel and a dissecting needle. For species identification, semi-permanent slides of cyanobacteria and macroalgae were prepared in glycerin gel.

***Rhizophora mangle* aerial roots** To determine species composition of cyanobacteria and macroalgae and total biomass per root (wet weight), one root from three trees were collected on each sampling day (n=21). The selected trees had conspicuous algal growth. All trees were located in the central part of the channel. Each root was washed with fresh water to remove sediment and organic matter. Specimens were separated for identification and biomass measurement. Before weighing, we removed excess water by blotting with paper towels. Each species was weighed on an electronic balance (OHAUS Explorer, Pine Brook, NJ, USA) to the nearest 0.001 g.

Tidal channel bottom To determine species composition and estimate biomasses of cyanobacteria and macroalgae (wet weight), samples were collected from the bottom of the tidal channel, which was divided into three sections (entrance, middle, and end). In each section, three transverse belt transects were deployed 5 m apart. In each belt transect, four samples were taken (one on each edge and two on each side of the centerline, with about 2 m distance between them) in 10 cm×10 cm quadrats (n=4). Twelve samples were collected per section and 36 for the channel on each sampling day (n=252). Samples were treated in the same way as root samples.

Data analysis

Species richness was defined as the total number of species identified on each sampling day (Margalef 1986) for each habitat. To describe the assemblage of species on *Rhizophora mangle* aerial roots and the tidal channel bottom, we calculated frequency and biomass, and the biological value index (BVI) (Loya-Salinas and Escofet 1990). The Olmstead-Tukey test was used to determine the dominant species (Sokal and Rohlf 1979) by assigning species to one of four categories based on the means of biomass (B) and frequency (F) values (Table 1).

Table 1 Olmstead-Tukey test categories to which each cyanobacterial and macroalgal species was assigned.

Categories	Aerial root		Tidal channel	
	B	F	B	F
Dominant	>0.35	>5.26	>0.37	>2.17
Constant	<0.35	>5.26	<0.37	>2.17
Casual	>0.35	<5.26	>0.37	<2.17
Rare	<0.35	<5.26	<0.37	<2.17

B, biomass; F, frequency.

Results

A total of 68 species were recorded to be associated with the three habitats of Estero Zacatecas: cyanobacteria (21), Xanthophyta (1), Chlorophyta (25), Ochrophyta-Phaeophyceae (1), Rhodophyta (19), and Anthophyta (1) (Table 2).

Lyngbya sp. and *Vaucheria* sp. were found in the three habitats (May to September 2005 and March 2005, respectively). *Rhizoclonium riparium* (Roth) Harvey and *Bostrychia radicans* (Montagne) Montagne had higher frequencies on pneumatophores than in the other two habitats; *Caulerpa sertularioides* (S.G. Gmelin) M.A. Howe, *Cladophora* sp., *Ulva clathrata* (Roth) C. Agardh, and *Gracilariopsis lemaneiformis* (Bory de Saint-Vincent) E.Y. Dawson, Acleto *et* Foldvik most frequently occurred on the bottom of the tidal channel (Table 2).

Avicennia germinans pneumatophores

Of the 29 species, there were 21 cyanobacteria: Chroococcales (10), Oscillatoriales (10), and Nostocales (1); Xanthophyta (1), Chlorophyta (6), and Rhodophyta (1). The highest species richness (23) was recorded in November 2005 (18 cyanobacteria, 4 Chlorophyta, and 1 Rhodophyta; Table 2). The largest numbers of cyanobacterial taxa are simply the most representative morphotypes. They include species within *Heteroleibleinia* and *Johanesbaptistia*, which are newly recorded in mangrove habitats bordering the Gulf of California (Table 2). Some of the morphotypes will probably be described in the future as new species, but more detailed studies are necessary. All of the reported cyanobacteria were epiphytic either directly on the pneumatophore cortex or on *Rhizoclonium riparium*, *Boodleopsis pusilla* (F.S. Collins) W.R. Taylor, A.B. Joly *et* Bernatowicz, or *Bostrychia radicans* growing on the pneumatophores.

Three different species assemblages were found on *Avicennia germinans* pneumatophores: the *Rhizoclonium riparium-Bostrychia radicans* and *Boodleopsis pusilla* assemblage in May and September 2005, the *Rhizoclonium riparium-Bostrychia radicans* assemblage in November 2005 and January and May 2006, and the *Rhizoclonium riparium-Bostrychia radicans* and *Cladophora* sp. assemblage in all periods (Table 2).

Rhizophora mangle aerial roots

Of the 20 species, there were cyanobacteria (2), Xanthophyta (1), Chlorophyta (9), Rhodophyta (7), and Anthophyta (1). Species richness was greatest in May and July 2005 (10 species; Table 2). The most representative algae and biomass

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Table 2 Spatial and temporal distributions of cyanobacteria and macroalgae by habitat in Estero Zacatecas, southwestern Gulf of California.

Species	2005				2006		
	May	Jul	Sep	Nov	Jan	Mar	May
Cyanobacteria							
Aphanocapsa sp.	1	1	1	1	1	1	1
Aphanocapsa littoralis (Hansgirg) Komárek *et* Anagnostidis	1	1	1	1	1	1	1
Calothrix spp.	1	1	1	1	1	1	1
Chamaecalyx sp.		1	1	1	1	1	1
Chroococcus sp1.	1	1	1	1	1	1	1
Chroococcus sp2.	1	1	1	1	1	1	1
Chroococcus cf. *obliteratus* Richter	1	1	1	1	1	1	1
Dermocarpella cf. *stellata* Montejano *et* León		1		1	1	1	1
Geitlerinema sp.		1	1	1	1	1	1
Heteroleibleinia sp.[a]		1					
Hydrococcus sp.	1		1	1			
Johanesbaptistia sp.[a]				1			
Leibleinia cf. *subtilis* Anagnostidis *et* Komárek		1	1	1	1		1
Leptolyngbya sp.	1	1			1		
Lyngbya sp.	1, 2, 3	1, 2, 3	1, 2, 3	1, 3	1, 3	2, 3	1, 2, 3
Microcoleus sp.				1	1	1	1
Oscillatoria sp.	2, 3	3	3	3	3	2, 3	3
Pseudanabaena sp.	1	1	1	1	1	1	1
Phormidium sp.				1			
Xenococcus sp.	1	1	1	1			
Xenococcus chaetomorphae Setchell *et* Gardner	1			1			
Xanthophyta							
Vaucheria sp.	1, 2, 3	2, 3	1, 3	2	3		3
Chlorophyta							
Acetabularia sp.					3	3	
Acetabularia caliculus J.V. Lamouroux in Quoi *et* Gaimard	3			3			
Boodleopsis pusilla (F.S. Collins) W.R. Taylor, A.B. Joly *et* Bernatowicz	1, 2, 3		1			3	
Bryopsis sp.		3					
Bryopsis hypnoides Lamouroux						3	
Bryopsis pennata Lamouroux		2	3		2	3	
Caulerpa sertularioides (S.G. Gmelin) M.A. Howe	2, 3	2, 3	2, 3	2, 3	2, 3	3	3
Chaetomorpha sp.						3	
Chaetomorpha linum (O.F. Müller) Kützing						3	3
Cladophora sp.	1, 3	1, 3	1, 3	1, 3	1, 3	1, 3	1
Cladophora albida (Nees) Kützing					3		3
Cladophora microcladioides F.S. Collins						3	
Cladophora sericea (Hudson) Kützing			3			3	
Cladophora stimpsonii Harvey					3	3	
Cladophoropsis sp.		3					
Cladophoropsis membranacea (Hofman Bang ex C. Agardh) Børgesen						3	3
Codium simulans Setchell *et* N.L. Gardner	3						2
Entocladia polysiphoniae Setchell *et* N.L. Gardner	1		1	1	1		1
Phyllodictyon robustum (Setchell *et* N.L. Gardner) Leliaert *et* Wysor						3	
Rhizoclonium riparium (Roth) Harvey	1	1	1, 3	1	1, 3	1, 2, 3	1
Ulva sp.			2, 3	1	3	3	3
Ulva clathrata (Roth) C. Agardh	2, 3	3	3	2, 3	3	2, 3	3
Ulva compressa Linnaeus						3	3
Ulva flexuosa Wulfen		2			3		
Ulvella sp.	1	1	1				1
Ochrophyta-Phaeophyceae							
Dictyota flabellata (F.S. Collins) Setchell *et* N.L. Gardner			3				
Rhodophyta							
Bostrychia radicans (Montagne) Montagne	1, 2, 3	2	1, 2	1	1		1, 2, 3
Caloglossa apomeiotica J.A. West *et* Zuccarello	2	2					
Ceramium clarionense Setchell *et* N.L. Gardner		3					

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(Table 2 continued)

Species	2005				2006		
	May	Jul	Sep	Nov	Jan	Mar	May
Ceramium equisetoides E.Y. Dawson	3				3		
Ceramium zacae Setchell *et* N.L. Gardner	3						3
Chondria dasyphylla (Woodward) C. Agardh	3				3		
Chondria repens Børgesen					3		
Gayliella flaccida (Harvey ex Kützing) T.O. Cho *et* L.J. McIvor			3				
Gracilariopsis lemaneiformis (Bory de Saint-Vincent) E.Y. Dawson, Acleto *et* Foldvik	3	3	2, 3	2, 3	3	2, 3	2, 3
Hypnea sp.	2	3				3	
Hypnea johnstonii Setchell *et* Gardner	3	3					
Hypnea valentiae (Turner) Montagne	3						
Neosiphonia simplex (Hollenberg) Y.-P. Lee			3		3		
Polysiphonia sp.							3
Polysiphonia johnstonii Setchell *et* Gardner			3				
Polysiphonia mollis J.D. Hooker *et* Harvey	3	2, 3	2, 3	3	3		
Polysiphonia pacifica Hollenberg		2	3		3		3
Polysiphonia scopulorum var. *villum* (J. Agardh) Hollenberg	3						
Spyridia filamentosa (Wulfen) Harvey	2, 3	2, 3	2, 3	2, 3	2, 3	3	2, 3
Anthophyta							
Ruppia maritima Linnaeus	3	3		2, 3	3		2, 3

[a]New genus records for mangrove habitat in the Gulf of California.
1, *Avicennia germinans* pneumatophores; 2, *Rhizophora mangle* aerial roots; 3, tidal channel.

contributors measured by BVI were *Caulerpa sertularioides*, *Gracilariopsis lemaneiformis*, and *Spyridia filamentosa* (Wulfen) Harvey; *Oscillatoria* sp. and *Lyngbya* sp. were most representative of the cyanobacteria group. The highest biomass value was 494 g root^{-1}. The greatest algal biomass occurred in May and November 2005 (196 g root^{-1} and 226 g root^{-1}, respectively; Table 3). The total biomass of the most representative species varied from 2.5 g root^{-1} (*Ruppia maritima* Linnaeus) to 237 g root^{-1} (*Caulerpa sertularioides*). The dominant species for the study period classified by the Olmstead-Tukey test were *Caulerpa sertularioides*, *Gracilariopsis lemaneiformis*, and *S. filamentosa*. The rarest species were *Boodleopsis pusilla*, *Bryopsis pennata* Lamouroux, *Caloglossa apomeiotica* J.A. West

Table 3 Total wet biomass (g root^{-1}) of dominant species on *Rhizophora mangle* aerial roots on each sampling date (n=21).

Species	2005				2006			
	May	Jul	Sep	Nov	Jan	Mar	May	TB
Cyanobacteria								
Oscillatoria sp. and *Lyngbya* sp.[a]	5.9	0.1	15.6			0.1	3.0	24.6
Xanthophyta								
Vaucheria sp.	2.3			1.8				4.1
Chlorophyta								
Bryopsis pennata		0.1			0.1			0.2
Caulerpa sertularioides	161.6	7.3	31.7	36.0	0.1			236.7
Codium simulans							1.9	1.9
Rhodophyta								
Bostrychia radicans	2.1	0.7	0.3				0.1	3
Gracilariopsis lemaneiformis			0.1	157.1		0.1	0.1	157.5
Polysiphonia mollis		1.1	0.2					1.3
Spyridia filamentosa	24.1	1.8	7.2	29	0.1		0.1	62.3
Anthophyta								
Ruppia maritima				1.9			0.7	2.5
TBS	196	11	55	226	0.3	0.2	6	494

[a]Cyanobacteria sometimes found together with filamentous algae.
TB, total biomass; TBS, total biomass sampling.

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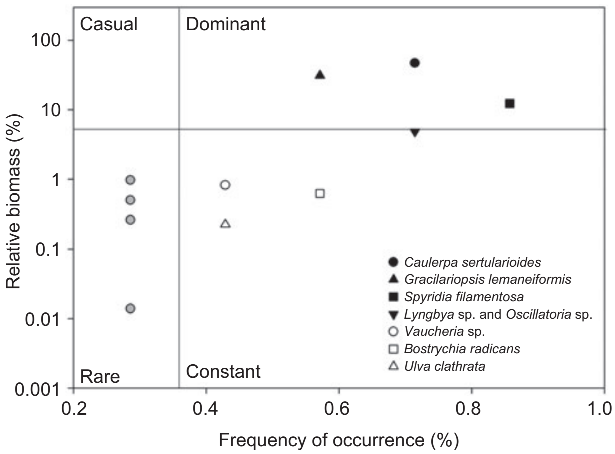

Figure 2 Dominant algal species on *Rhizophora mangle* aerial roots (Olmstead-Tukey classification – see Table 1).

et Zuccarello, *Codium simulans* Setchell *et* N.L. Gardner, *Ulva* sp., *U. flexuosa* (Wulfen), *Rhizoclonium riparium*, *Hypnea* sp., *Polysiphonia mollis* J.D. Hooker *et* Harvey, and the seagrass *Ruppia maritima* (Figure 2).

Tidal channel bottom

Of the 46 species, there were cyanobacteria (2), Xanthophyta (1), Chlorophyta (23), Ochrophyta-Phaeophyceae (1), Rhodophyta (18), and Anthophyta (1). Species richness was greatest in March 2006 (22 species; Table 2).

The most representative algae according to the BVI were *Caulerpa sertularioides* (41%), *Gracilariopsis lemaneiformis* (33%), *S. filamentosa* (7%), cyanobacteria group (*Oscillatoria* sp. and *Lyngbya* sp.; 10%), and *Vaucheria* sp. (5%). The total biomass for the study period was 12,924 g m^{-2}. The largest algal biomass (7137 g m^{-2}) occurred in November 2005 (Table 4). The total biomass of the most representative species varied from 4 g m^{-2} (*U. compressa* Linnaeus) to 5306 g m^{-2} (*Caulerpa sertularioides*). Olmstead-Tukey test classification for the study period indicated that the dominant species in terms of relative biomass and frequency of occurrence were *Caulerpa sertularioides*, *Gracilariopsis lemaneiformis*, cyanobacteria group (*Oscillatoria* sp. and *Lyngbya* sp.), *Spyridia filamentosa*, and *Vaucheria* sp. About 48% of uncommon and rare species comprised small, filamentous algae, such as *Bryopsis* sp., *Bryopsis hypnoides* Lamouroux, *Bryopsis pennata*, *Chaetomorpha* sp., *Chaetomorpha linum* (O.F. Müller) Kützing, *Cladophora albida* (Nees) Kützing, *Cladophora microcladioides* F.S. Collins, *Cladophora sericea* (Hudson) Kützing, *Cladophora stimpsonii* Harvey, *Cladophoropsis* sp., *Cladophoropsis membranacea* (Hofman Bang ex C. Agardh) Børgesen, *Phyllodictyon robustum* (Setchell *et* N.L. Gardner) Leliaert *et* Wysor, *Ceramium clarionense* Setchell *et* N.L. Gardner, *Ceramium equisetoides* E.Y. Dawson, *Ceramium zacae* Setchell *et* N.L. Gardner, and *Gayliella flaccida* (Harvey ex Kützing) T.O. Cho *et* L.J. McIvor (Figure 3).

Some algal species collected from the bottom of the tidal channel were growing on the sediment, but most were attached to harder substrata, such as leaf fragments, twigs,

Table 4 Total wet biomass (g m^{-2}) of dominant species from the bottom of the tidal channel on each sampling date (n=36).

Species	2005				2006			
	May	Jul	Sep	Nov	Jan	Mar	May	TB
Cyanobacteria								
Oscillatoria sp. and *Lyngbya* sp.[a]	288	22	117	313	310	77	212	1339
Xanthophyta								
Vaucheria sp.	188	197	5		302		<1	691
Chlorophyta								
Caulerpa sertularioides	25	802	324	3880	65	47	163	5306
Cladophora sp.				67				67
Codium simulans	20							20
Ulva clathrata	2	10		2	1	10	1	26
Ulva compressa						4		4
Ulva flexuosa					67			67
Rhizoclonium riparium						76		76
Rhodophyta								
Gracilariopsis lemaneiformis	50	183	536	2647	106	735	67	4324
Hypnea johnstonii		64						64
Polysiphonia mollis	7	6	<1	6	<1			19
Spyridia filamentosa	261	248	1	222	148	<1	13	893
Anthophyta								
Ruppia maritima	<1	5		<1	9		14	28
TBS	841	1536	983	7137	1008	949	470	12,924

[a]Cyanobacteria sometimes found together with filamentous algae.
TB, total biomass; TBS, total biomass sampling.

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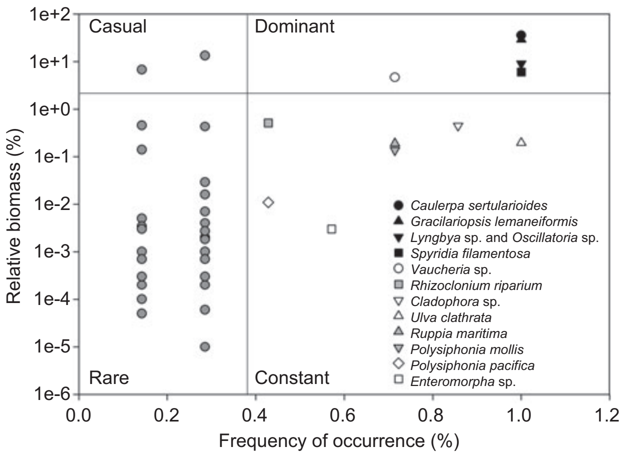

Figure 3 Dominant algal species in the tidal channel (Olmstead-Tukey classification – see Table 1).

bark, or macroalgae. They were cyanobacterial (*Oscillatoria* sp. and *Lyngbya* sp.), or macroalgal (*Caulerpa sertularioides*, *Cladophora albida*, *U. flexuosa*, *Rhizoclonium riparium*, *Vaucheria* sp., and *Gracilariopsis lemaneiformis*). Other species were epizoic on dead animals, such as gastropods (*Ceramium equisetoides*, *Polysiphonia mollis*), bivalves (*Bryopsis* sp., *Cladophora* sp., *Cladophora microcladioides*, *Ulva* sp., *Chondria repens* Børgesen, and *Hypnea* sp.), and sponges (*S. filamentosa*), and others were epilithic (*Codium simulans*, *Cladophora stimpsonii*, and *S. filamentosa*). Cyanobacterial species, *Vaucheria* sp., *Rhizoclonium riparium*, and *S. filamentosa* were epiphytic, epilithic, and epizoic.

Discussion

The arid conditions surrounding the Estero Zacatecas mangrove were not a limitation for the establishment of the 68 species in the different cyanobacterial and macroalgal groups. The algal groups growing on pneumatophores, aerial roots, and in the tidal channel at Estero Zacatecas included cyanobacteria, Xanthophyta, Chlorophyta, Ochrophyta-Phaeophyceae, and Rhodophyta. An anthophyte, *Ruppia maritima*, was also included in the results because it one of the swamp's most important primary producers (Hartog and Kuo 2006, López-Calderón et al. 2010). *Ruppia maritima* was present in all samples from the tidal channel. There is no marsh at Estero Zacatecas, but this seagrass could have drifted here on currents from marshes elsewhere in the Ensenada de La Paz (C. Pérez-Estrada, pers. observation). Wigeongrass serves as a substratum and habitat for cyanobacteria, macroalgae, and animals.

We found an outstanding richness of cyanobacteria (21 morphotypes) and macroalgae (46 species) at Estero Zacatecas, which was about as rich as that reported by Riosmena-Rodríguez et al. (2011) for the same three habitats of mangrove assemblages along the Baja California peninsula. Estero Zacatecas was more diverse than other mangroves along Bahía de La Paz (Paul-Chávez and Riosmena-Rodríguez 2006) and other localities, such as Bahía de La Ascensión in the Mexican Caribbean (17 species; Inclán-Rivadeneyra 1989), Isla Guayacan, Puerto Rico (28 species; Almodovar and Pagan 1971), Isla La Parguera, Puerto Rico (22 species; Burkholder and Almodovar 1973), South Africa (18 species; Phillips et al. 1996), and Australia (15 species; Beanland and Woelkerling 1983). The composition of algal groups we studied differed from the flora of tropical Pacific mangroves, in which red algae are the main taxonomic group and where the studies focused on the *Bostrychietum* complex on the roots of *Rhizophora mangle* (West et al. 1992, 1994, Tejada-Rivas 2002, Baos-Estupiñan and Velasco 2007, Peña-Salamanca 2008 and Cruz-Madrid 2010). Cyanobacteria, one green alga (*C. sertularioides*) and two red algae (*G. lemaneiformis*, *S. filamentosa*) are the dominant photosynthetic group in the Estero Zacatecas mangrove. Richness varied among the habitats. *Avicennia germinans* pneumatophores contained 43% of the species, most of them cyanobacteria. *Rhizophora mangle* roots contained 29% of the species, mainly filamentous species of Chlorophyta and Rhodophyta. The tidal channel contained 68% of the species, chiefly growing on the soft mud and sand substratum but also on many other substrata, including remnants of dead gastropods, bivalves, and sponges, small rocks, and fragments of leaves, twigs, and bark. A high degree of filamentous species epiphytism on macroalgae occurred mostly in the tidal channel, a result of the larger number of substrata where epiphytes could establish themselves. The tidal channel also contained some foliose algae, usually Chlorophyta species that formed thick carpets in the mud (Dawson 1966, Cordeiro-Marino et al. 1992). In tropical Pacific mangroves, where >50% of the species grow on roots and pneumatophores, 20% grow on the soft mud and sandy substrata, and 30% grow on macrophytes, sessile animals, tree bark, and shell fragments (Cordeiro-Marino et al. 1992, Tejada-Rivas 2002, Roldan-Pérez and Ramírez-Restrepo 2008, Cruz-Madrid 2010).

Algal epiphytes on pneumatophores grow under stressful conditions because Estero Zacatecas has an arid climate. Still, we found a dense, mixed algal layer of spongy appearance composed of *Rhizoclonium*, *Bostrychia*, and *Cladophora* (the *Rhizoclonietum* complex). It is likely that the gregarious habit of *Rhizoclonium* thalli, together with their thick mucilaginous cell walls and the ability of *Bostrychia* to synthesize polyols, facilitate water retention and protect them from desiccation (Phillips et al. 1996, Tejada-Rivas 2007). These mats of algae retain moisture during low tides and compensate for the extreme conditions. The arid conditions at Estero Zacatecas are probably not as favorable for the occurrence of the *Bostrychietum* complex as more humid conditions in tropical mangrove areas of the Mexican Pacific and other parts of the world (Post 1963, West et al. 1992, 1994, King and Puttock 1994, Pedroche et al. 1995).

We also found differences in seasonal diversity of algal species, with only 14 present throughout the year: *Aphanocapsa* sp., *Aphanocapsa littoralis* (Hansgirg) Komárek *et* Anagnostidis, *Chroococcus* sp. 1., *Chroococcus* sp. 2., *Chroococcus* cf. *obliteratus* Richter, *Pseudanabaena*

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sp., *Lyngbya* sp., *Oscillatoria* sp., *Caulerpa sertularioides*, *Cladophora* sp., *Rhizoclonium riparium*, *Ulva clathrata*, *Gracilariopsis lemaneiformis*, and *Spyridia filamentosa*. Analysis based on the Olmstead-Tukey test classification indicated that most algal species on *Rhizophora mangle* aerial roots and in the tidal channel were rare. According to Littler and Littler (1980), these are considered opportunistic taxa. The annual production of biomass on roots was 494 g $root^{-1}$ and 12,924 g m^{-2} in the tidal channel. Seasonal biomass was highest in November 2005, probably as a result of a hurricane in late September 2005. Wave action and tidal surges from hurricanes cause resuspension of sediments, which releases nutrients into the water column, potentially supporting growth of mat algae that rapidly become available for consumption by herbivores (Russ and McCook 1999).

We gave special attention to the marine cyanobacteria, which are little known in Mexico. This group had high species richness (21), compared to Florida mangroves (3; Dawes 1996), Puerto Rico (4; Rodríguez and Stoner 1990), South Africa (9; Phillips et al. 1996), Saudi Arabia (15; Saifullah 1994), and the Philippines (16; Fortes 1987). Among the 21 morphotypes we identified as the most common and frequent on *Avicennia germinans* pneumatophores, there were many new records for the Gulf of California region. Many of the cyanobacteria had morphological characteristics and dimensions not previously reported for marine species; therefore, some of them will likely represent ecomorphs or morphospecies new to science. All of the cyanobacteria species were epiphytic, either directly on the *Avicennia germinans* cortex or on *Rhizoclonium riparium*, *Boodleopsis pusilla*, and *Bostrychia radicans*, and some were even present on other cyanobacteria that were also mangrove epiphytes. Cyanobacteria species are tolerant of extreme and variable environmental conditions, as demonstrated by the richness and range of seasons in which they are present on pneumatophores (Phillips et al. 1996). The importance of this group is also tied to their role as atmospheric nitrogen fixers (*Aphanocapsa* spp. and *Calothrix* spp.), which is an important ecological function, especially in arid zones (Ramachandran and Venugopalan 1987, Ramachandra Rao 1992) and on low-oxygen mangrove substrata.

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