Structure of Diatom Assemblages Living on Prop Roots of the Red Mangrove (*Rhizophora mangle*) from the West Coast of Baja California Sur, México[1]

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Abstract: Samples of epiphytic diatom assemblages found on prop roots of red mangrove (*Rhizophora mangle*) from four sites were collected at two tidal levels of exposure on two different dates from the cool season (autumn, spring). The overall floristic analysis yielded 171 diatom taxa, including 16 new records for the Baja California peninsula. Diversity estimates were among the highest ever measured for benthic diatoms using Shannon's (mean H′ = 4.89) and Simpson's (0.945) indices. Many species scored high on the Biological Value Index (BVI), thus reflecting their numerical importance within the assemblages. According to diversity values and overall species composition, all sampling sites represented a similar habitat consisting of three types of substrates: prop roots, epiphytic macroalgae, and sediments. These values are considered to represent stability in the diatom assemblages living on red mangrove prop roots. Thus, the conditions determined by periodic tidal exposure are not to be considered extreme. However, principal component analysis and similarity measurements indicated that the November and April assemblages could be discriminated on the basis of taxa distribution.

Mangrove systems are often found in tropical and subtropical coastal lagoons. Mangroves occur along most of the western Mexican coast. In the Sea of Cortés (Gulf of California) they reach as far as 30° N; along the western coast of the Baja California peninsula the Bahía Magdalena-Almejas lagoon system (25° N) represents their northernmost distribution (Blasco 1984). In Baja California Sur (B.C.S.) mangrove systems have a discontinuous distribution and are composed of three species: red mangrove (*Rhizophora mangle* L.), black mangrove (*Avicennia germinans* (L.) Stearn), and white mangrove (*Laguncularia racemosa* (L.) Gaertner).

As in most shallow marine systems benthic diatoms play an important role as primary producers and as main constituents of microbial communities in mangrove systems, where they aid in stabilizing and preventing desiccation of the sediments (Navarro 1988, Siqueiros Beltrones and Sánchez Castrejón 1999, Cahoon and Safi 2002). They are also an important food source for many micro- and macroscopic invertebrates as well as for filter feeders in the form of tychoplankton (Navarro 1988). Benthic diatoms use different types of substrates including mangrove roots, such as the pneumatophores of black mangrove or the prop roots of red mangrove. Floristics on benthic diatoms carried out expressly for mangrove systems are scarce, although several floristic studies have considered these habitats (Foged 1975, 1984, Sullivan 1981, Navarro 1982, Maples 1983, Wah and Wee 1988).

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However, approximations of the assemblage structure of diatoms living on prop roots of mangroves are available. These show that few species may be occupying the surface of pneumatophores of black mangrove (Maples 1983), or that various numbers of diatom taxa, either low (Reyes-Vázquez 1975), intermediate (Sullivan 1981), or high (Navarro 1982, Navarro and Torres 1987), may be found on prop roots of red mangroves. Moreover, high values of diversity have been estimated in several studies carried out in different mangrove systems (Sullivan 1981, Navarro 1987, Siqueiros Beltrones and Sánchez Castrejón 1999).

In mangrove systems of B.C.S. as many as 289 diatom taxa have been recorded from sediments (Siqueiros Beltrones and Sánchez Castrejón 1999, Siqueiros Beltrones and Morzaria Luna 1999). The first observations on the diatom associations of red mangrove prop roots from Bahía Magdalena, B.C.S. (Siqueiros Beltrones and López Fuerte 2003) revealed a high number of taxa, several of which were abundant on macroalgae epiphytic on the prop roots. More than 25% of these species had been recorded as common constituents of the phytoplankton along with benthic diatom taxa from different substrates (Gárate Lizárraga and Siqueiros Beltrones 1998, Gárate Lizárraga et al. 2000, 2001, Martínez López and Verdugo Díaz 2000, Gárate Lizárraga and Verdugo Díaz 2001).

In this study a floristic inventory of epiphytic diatoms on mangrove prop roots from Bahía Magdalena was extended and the structure of the assemblages is further described, which, from previous results, was expected to yield high species diversity and species richness as is usually found in highly productive systems. In addition, we explore the influence of seasonal changes and of exposure to desiccation on the structure of the diatom assemblages.

Study Area

Bahía Magdalena is a shallow lagoon located on the western coast of Baja California Sur (24° 15′–25° 20′ N, 111° 30′–112° 12′ W) (Figure 1). It is part of the Bahía Magdalena–Bahía Almejas lagoon system, which is densely populated by mangroves: mainly *Rhizophora mangle* bordering the coastline and *Avicennia germinans* farther inland. This lagoon system may be divided into three zones. The northern zone consists of a series of channels with a mean depth of 3.5 m. The central part is known as Bahía Magdalena and is connected to the ocean by a wide opening. The southeastern zone, Bahía Almejas, is connected to Bahía Magdalena by a narrow mouth. The system is considered an antiestuary with irregular bathymetry. Rich upwelling waters enter the lagoon on incoming tides, and high concentrations of phytoplankton are exported to the ocean on ebbing tides (Guerrero et al. 1988). The system exhibits a mixed semi-diurnal tidal regime. Ranges of 1.16 and 1.46 m have been measured in localities inside the bay (Obeso Nieblas et al. 1999). Mean minimum and maximum salinities and temperatures were recorded in Bahía Magdalena by Alvarez-Borrego et al. (1975) as 34.08–39.2 psu and 17–28°C, and temperatures by Gárate-Lizárraga et al. (2001) as 16.7–29.8°C. In the study reported here, four sampling sites located in the Puerto San Carlos docking area (Figure 1) were chosen on the basis of their similarity; these represented a nearly homogeneous area characterized by muddy sediments where red mangrove prop roots were anchored.

MATERIALS AND METHODS

Samples were collected in Bahía Magdalena during November (autumn) 1999 and April (spring) 2000, between ca. 1000 and 1200 hours. In November two sites (1 and 2) were sampled, and in April two more sites (3 and 4) were added to the sampled area. The sampling sites were approximately 50 m apart. Samples were taken during low tide when the roots were exposed. Bark segments 30 cm² in area (2 by 15 cm) were peeled off from two areas of the red mangrove prop roots: damp segments (lower level) from the bottom, and dry segments (upper level) just below 90 cm up, limited by the high-tide mark on the roots. Exposure time of upper and lower parts of the prop roots to desiccation was ca. 12 and 6 hr, respectively. Each sample was composed of three segments (from three roots of
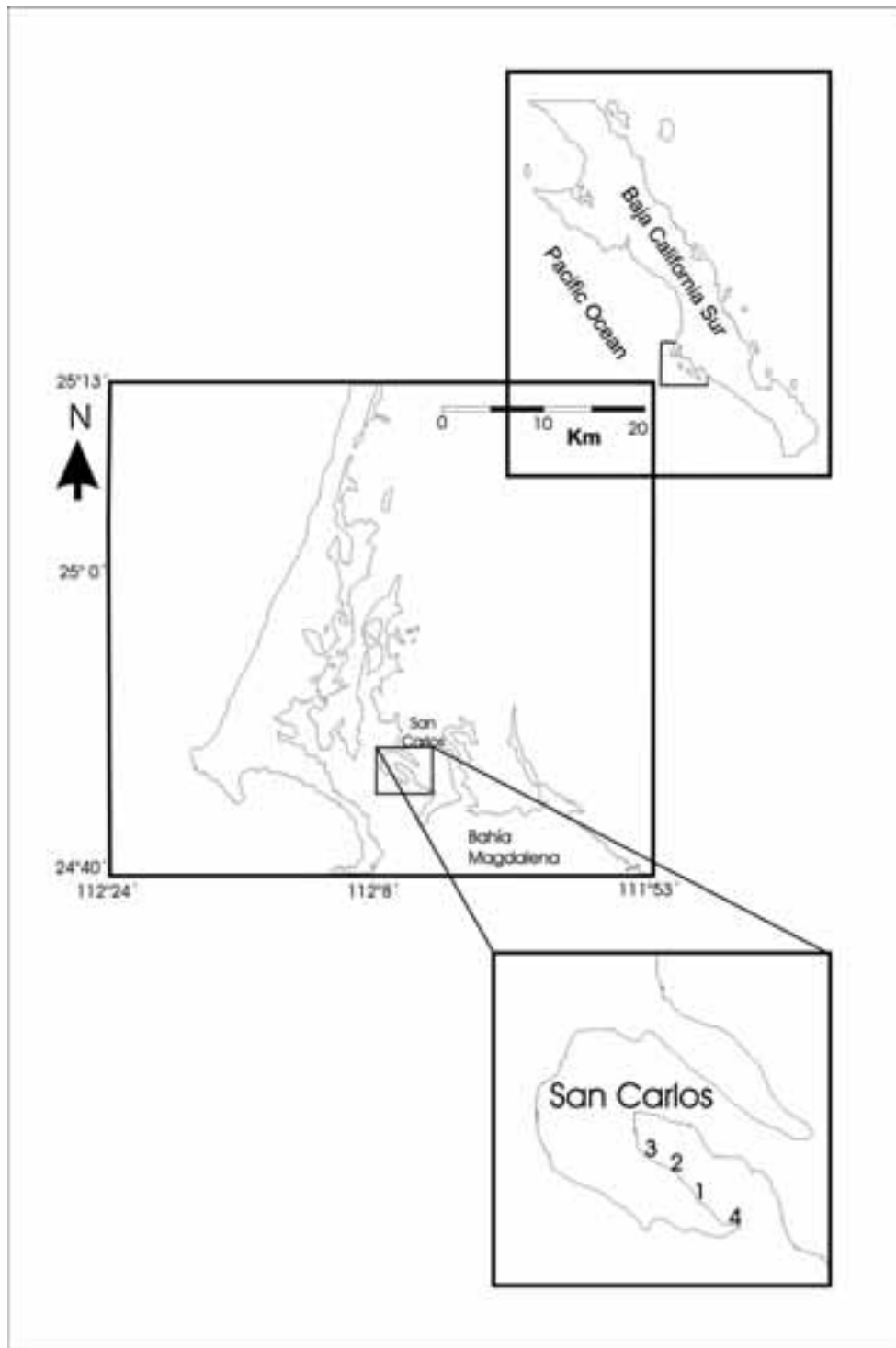
FIGURE 1. The Bahía Magdalena lagoon system and location of sampling sites.

the same tree). During November a total of 12 segments was collected (four samples), and in April a total of 24 segments (eight samples) was collected. Air temperature was recorded with a field thermometer. Because desiccation is considered the main factor determining the presence/absence of diatom taxa on exposed prop roots of *Rhizophora mangle*, and these were covered partially with sediments, salinity in the exposed bottom sediments was measured. This was done using a refractometer by squeezing out a drop of water from the sediments through filter paper.

All visible epiphytic macroalgae found (only on the lower-level segments) were removed from each bark strip under a dissecting microscope and were studied separately (Siqueiros Beltrones and López Fuerte 2003). Fresh material was observed in fresh mounts to observe the approximate proportion of empty frustules (dead) and live cells at the time of sampling. The root segments were then brushed using a toothbrush and rinsed with tap water to obtain a concentrate of sediments, organic matter, and diatoms. The organic matter inside (and outside) diatom frustules was oxidized using a 1:3:1 mixture of sample, nitric acid, and commercial ethanol (Siqueiros Beltrones 2000). The clean frustules were mounted using plastic resin mounting medium (Meltmount) (refractive index = 1.7), yielding three permanent slides from each composite sample.

The floristic analysis was carried out separately from the quantitative analysis to identify as many taxa as possible in the assemblages. Drawings were made of the observed taxa on curatorial cards, which included information on site location, habitat, frequency, and morphometric data. These were delivered, along with all 36 slides, to the Museo de Historia Natural of the Universidad Autónoma de Baja California Sur, to be deposited eventually in the diatom collection (Diatomario). As a floristic reference, color microphotographs were taken (with Kodak 800 film) of selected taxa (including new records) from the permanent slides under an Olympus CH-2 microscope using phase-contrast illumination.

Taxonomic determinations were accom-plished following the works of Schmidt et al. (1874–1959), Peragallo and Peragallo (1897–1908), Hustedt (1927–1966, 1955), Cleve-Euler (1951–1955), Hendey (1964), McIntire and Reimer (1974), Foged (1975, 1984), Reyes-Vázquez (1975), Navarro (1982), Siqueiros Beltrones and Ibarra-Obando (1985), Simonsen (1987), Moreno et al. (1996), Round and Bukhtiyarova (1996), Siqueiros Beltrones and Morzaria Luna (1999), Siqueiros Beltrones and Sánchez Castrejón (1999), Witkowski et al. (2000), and Siqueiros Beltrones (2000, 2002). The classification of Round et al. (1990) was followed.

Assemblage Structure

To determine the relative abundances of the diatom taxa, a sample size of 500 individuals (frustules) per slide was chosen based on McIntire and Overton (1971) and Siqueiros Beltrones (1990). Numerical analyses were done twice (using subsamples) based on two slides from the same sample.

To estimate species diversity in the assemblages, information theory (log_2) was used (Shannon and Weaver 1949). Values for Shannon's H′, Pielou's evenness (J′), and dominance using the redundancy index (REDI) were computed (Brower and Zar 1984). Simpson's diversity index (1-λ) was also calculated (Brower and Zar 1984), to better interpret our estimates of diversity by considering criteria that weight rare and common species differently (Siqueiros Beltrones 1990).

Under the premise that all sites represented the same type of habitat, and thus harbored diatom assemblages with similar structure, statistical analyses were carried out. A two-way analysis of variance (ANOVA) was applied to test for H_0 = no significant differences existed between the diversity values due to level of exposure and/or date of sampling (α = 0.05). This was done only for the estimated values of the diversity indices (H′, J′, and REDI), because normality (Shapiro-Wilk test) and homoscedasticity (Cochran test) tested positive (SAS Institute 2001). Other requirements were also met to comply with the use of parametric statistics. The observed values for Simpson's diversity and domi-

nance did not show a normal distribution and thus were not considered in the statistical analyses.

To measure similarity among diatom assemblages, samples were compared on the basis of presence/absence of species and their relative abundances using Horn's Index (Magurran 1988). These values were fed into an algomerative classification module of a flexible algorithm for the construction of dendrograms (de la Cruz-Agüero 1994). Because no difference existed in the resulting classification when using both sample and sub-sample values or just sample values, only the latter were represented.

A principal component (ordination) analysis (PCA) was used to determine grouping tendencies between species. A mode R matrix was selected for running the eigen-analysis of a variance-covariance matrix (de la Cruz-Agüero 1994). Only 50 species representing 85% of the total frustule count (including subsamples) were considered for the PCA computation.

Finally, to determine the dominant species based on abundance and frequency, the Biological Value Index (BVI) or species importance was estimated for 40 of the taxa with higher scores in the PCA. The BVI was computed by assigning a decreasing rank value (from 40 to 1), according to their descending abundances, to the taxa from each sample and adding up their overall rank values to give a BVI value for each taxon (Sanders 1960).

RESULTS

The floristic analysis of epiphytic diatoms living on *Rhizophora mangle* prop roots during November and April yielded a total of 171 taxa (species and their varieties) representing 49 genera. The number of dead (empty) cells was negligible. Sixteen species were new records for the NW Mexican region (Appendix), but none of these was numerically important. Other taxa, although not abundant, appear to be representative of the assemblages (i.e., large forms that occurred frequently, such as *Amphora clevei*, *Campylodiscus samoensis*, *Diploneis crabro*, *Diploneis obliqua*,

Lyrella exsula, *Lyrella irrorata*, *Oestrupia powellii* var. *vidovichii*, *Petroneis granulata*, *Surirella fastuosa* var. *suborbicularis*, *Trachyneis velata*, and *Triceratium favus* [Figures 2–12]).

In the quantitative analysis, a total of 12,422 frustules was counted in 24 sub-samples, which accounted for 147 taxa. All the samples (and their repetitions) were characterized by high species richness, with S ranging from 56 taxa in the lower-level (LL) sample Z3-LL-00 to 90 taxa in sample Z1-LL-99 (Table 1); both samples were from the lower level of the prop roots. No clear tendency was evident for whether a higher number of taxa occurred in the lower or upper level of exposure.

Diversity values showed a tendency for being higher in the assemblages collected from the lower level of the prop roots. Evenness measurements were high, with a mean J' value of 0.790. This indicates that there was also a somewhat homogeneous distribution of individuals among species with no single taxon being clearly dominant (Table 1). This is also reflected in high mean estimates of diversity using two indices (H' = 4.89 and 1-λ = 0.945) and a corresponding low mean value of dominance (REDI). The lowest diversity measured (H' = 4.35 and 1-λ = 0.925) corresponded with the lowest S but with a J' = 0.75, and the highest diversity was H' = 5.2 and 1-λ = 0.963, which corresponded to the highest S and a J' = 0.804. The highest J' (0.832) corresponded with H' = 5.19 and S = 76. The number of taxa per sample appeared to be the main component of the high diversity values estimated, although the distribution of individuals among the taxa was also fairly even.

Although tendencies may be noted in the diversity values due to level of exposure, with values of diversity being higher in the lower-level diatom assemblages, only the REDI values (of dominance) were found to be significantly different in the two-way ANOVA, albeit from date to date but not for level of exposure or due to interaction (α = 0.05). Moreover, the diversity values (H' and J') were not significantly different in any case. Because all indices are derived from information theory, they are considered comple-
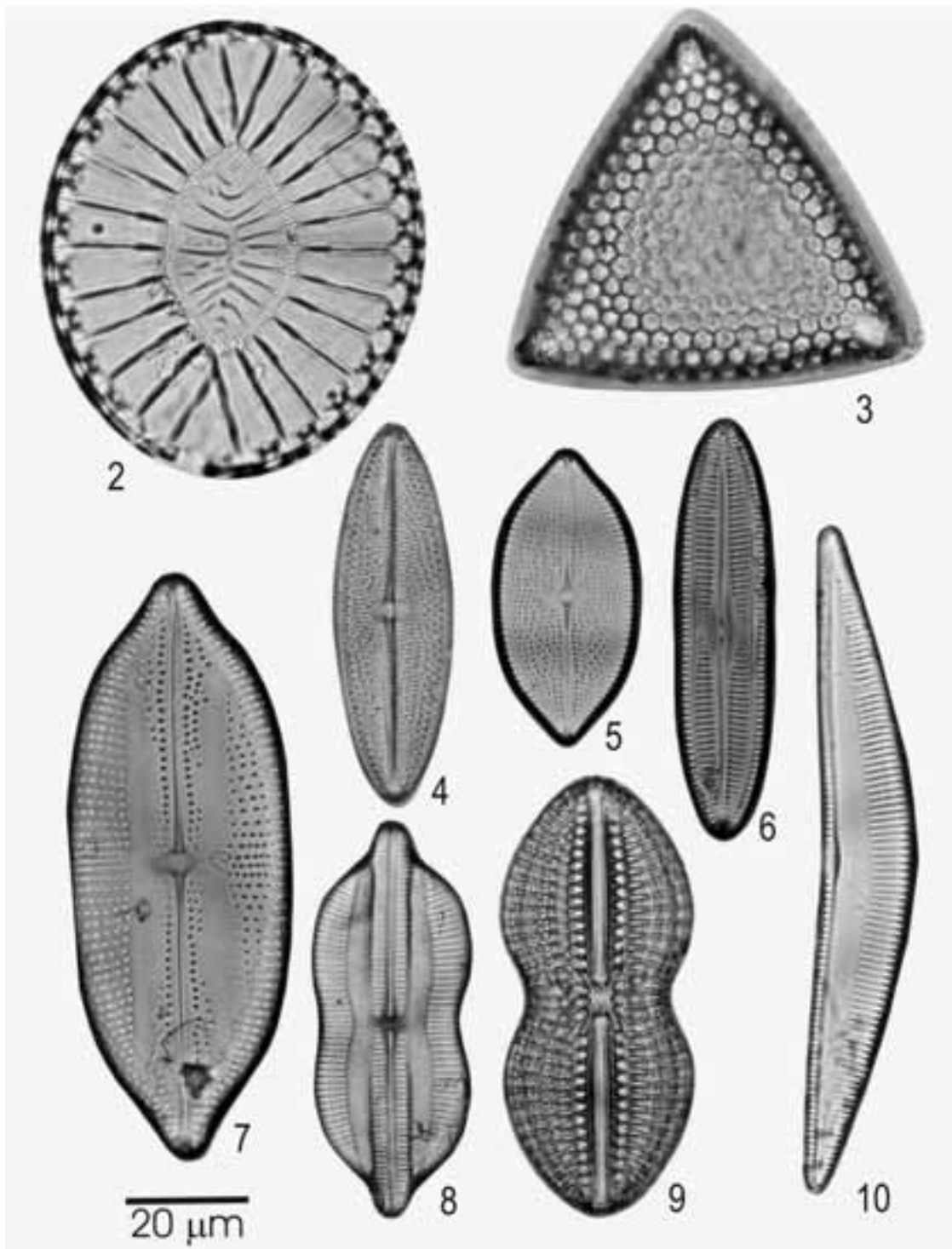
FIGURES 2–12. Common benthic diatom taxa considered representative of the mangrove prop root system. 2, *Surirella fastuosa* var. *suborbicularis* Grunow; 3, *Triceratium favus* Ehrenberg; 4, *Trachyneis velata* A. Schmidt; 5, *Petroneis granulata* (Bailey) D. G. Mann; 6, *Lyrella irrorata* (Greville) Mann; 7, *Lyrella exsula* (A. Schmidt) D. G. Mann; 8, *Diploneis crabro* Ehrenberg; 9, *Amphora clevei* Grunow; 10, *Oestrupia powellii* var. *vidovichii* (Gregory) Heiden; 11, *Diploneis obliqua* (Brun) Hustedt; 12, *Campylodiscus samoensis* Grunow.
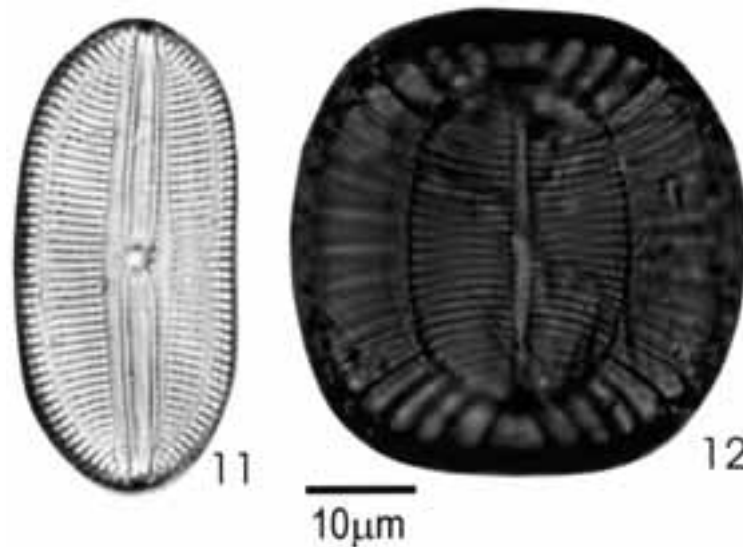
Figures 2–12. (continued)

mentary in describing the structure of the assemblages. A marked variation can be noted among the diversity values and between their repetitions, so it is likely that the REDI differences are due to chance. Thus, we cannot reject our H_0, and the measured parameters are proposed to represent similar assemblages, albeit with a high variability.

The similarity analysis using Horn's Index produced a grouping by month, with high similarity values, as it considers species relative abundances in the comparisons. It also grouped the assemblages by level of exposure (Figure 13). Several abundant species caused the definition of the three groups (Figure 13). The most abundant ones include Group A, *Diadesmis* cf. *contenta*, *Navicula platyventris*, and *Catacombas gaillonii*; Group B, *Nitzschia* sp. 1, *Achnanthidium* sp. 1, and *Achnanthes suchlandtii*; Group C, *Navicula salinarum*, *Amphora salina* var. *tenuissima*, *A. costata*, and *A. bigibba*. However, Horn's similarity index also indicates that other abundant or common species are evenly distributed among the sampling sites (those with the higher BVI values), which may be considered to have the same salinity and desiccation conditions in general, including both levels of exposure. The whole habitat may be considered some-

what hypersaline even with the relatively cooler air temperatures in November and April (Table 2).

In the PCA two main components or factors explained 56% of the total variance. These were constructed on the basis of higher abundances in the April upper-level samples, which is reflected in Axis I; the November samples gave rise to Axis II. The higher scores (i.e., the degree to which the taxa are related to the factor [component] either positive or negative) corresponded to 12 of the most abundant species (*Nitzschia frustulum*, *Gomphonemopsis pseudexigua*, *Achnanthes yaquinensis*, *Diadesmis* cf. *contenta*, *Catacombas gaillonii*, *Amphora salina* var. *tenuissima*, *Achnanthidium* sp. 1, *Nitzschia amphibia*, *Nitzschia dissipata*, *Navicula salinarum*, *Amphora bigibba*, *Nitzschia* sp. 1) (Figures 14–26), which appear quasi-isolated in the resulting diagram (Figure 27). Most of the remaining taxa had low scores and were grouped closely around the center. The PCA coincides with the fact that, although the similarity analysis yielded three groups, these were still closely related at a similarity (Horn) value of 0.705 versus a maximum computed value of 0.888 (Figure 13). This indicates that throughout the sampling sites and exposure levels species are

TABLE 1

Diversity Values Used to Describe the Structure of the Diatom Assemblages Found on Red Mangrove (*Rhizophora mangle*) Prop Roots in November 1999 (99) and April 2000 (00) in Bahía Magdalena, B.C.S.

Sample[a]	n	S	H′	J′	1-λ	REDI
November						
Z1-UL-99	504	61	4.50	0.761	0.931	0.303
Z1-UL-99-R	504	63	4.40	0.737	0.923	0.333
Z1-LL-99	553	90	5.20	0.804	0.961	0.265
Z1-LL-99-R	556	76	4.75	0.761	0.943	0.309
Z2-UL-99	519	76	4.90	0.786	0.947	0.281
Z2-UL-99-R	518	81	4.86	0.767	0.942	0.310
Z2-LL-99	509	75	4.59	0.741	0.929	0.342
Z2-LL-99-R	506	70	5.03	0.824	0.953	0.229
April						
Z1-UL-00	502	61	4.90	0.827	0.955	0.219
Z1-UL-00-R	545	66	4.89	0.811	0.954	0.238
Z1-LL-00	537	81	5.17	0.819	0.962	0.240
Z1-LL-00-R	542	78	5.15	0.823	0.963	0.232
Z2-UL-00	495	65	4.94	0.821	0.954	0.229
Z2-UL-00-R	504	58	4.46	0.762	0.931	0.296
Z2-LL-00	508	72	5.05	0.819	0.955	0.236
Z2-LL-00-R	530	76	5.19	0.832	0.956	0.218
Z3-UL-00	511	75	4.84	0.777	0.936	0.292
Z3-UL-00-R	498	82	5.15	0.811	0.956	0.256
Z3-LL-00	501	56	4.35	0.751	0.925	0.311
Z3-LL-00-R	526	68	4.62	0.761	0.937	0.306
Z4-UL-00	515	70	4.82	0.787	0.949	0.274
Z4-UL-00-R	506	66	4.47	0.741	0.926	0.333
Z4-LL-00	505	67	4.94	0.816	0.952	0.236
Z4-LL-00-R	525	72	5.16	0.841	0.962	0.207
Mean			4.89	0.790	0.945	0.271
UL Mean			4.76	0.782	0.942	0.280
LL Mean			4.93	0.799	0.948	0.260

Note: n, sample size (frustules); S, number of species; H′, Shannon's diversity index; J′, evenness; 1-λ, Simpson diversity index; REDI, redundancy.

[a] Z, site; UL, dry (upper level); LL, damp (lower level); R, repetition (subsample).

more or less evenly (or randomly for rare taxa) distributed. Although no significant differences were detected (two-way ANOVA) in the diversity values of the assemblages ($\alpha = 0.05$), thus supporting the acceptance of the H_0 (no significant differences existed between the diversity values due to level of exposure and/or date of sampling), temporal differences do exist in the distribution of taxa, including abundant species, depicted by the PCA (i.e., similar species richness and diversity but somewhat different species composition).

The BVI values computed for the 40 most abundant taxa comprising 85% of the total frustule count are shown in Table 3. These taxa are responsible for most of the similarity between the epiphytic diatom assemblages and their seasonal separation because of their abundance and frequency in the samples. Around 50% of these taxa have in fact been recorded as typical epiphytes, either on sea grasses, macroalgae, or mangroves (e.g., *A. yaquinensis*, *A. bigibba*, *C. gaillonii*, *C. scutellum*, *Diadesmis* cf. *contenta*, *G. pseudexigua*, *N. frustulum*, *O. pacifica*, and *T. tabulata* var. *affinis*, among others), and the rest have been observed to occur in sediments as epipelic or epipsammic forms.

DISCUSSION

This study gives a first insight into the structure of diatom assemblages found on mangrove prop roots from the Bahía Magdalena lagoon system during the cool season. This floristic inventory for benthic diatoms (171 taxa) is the smallest one recorded for the Baja California peninsula, where epipelic, epilithic, and epiphytic assemblages have been analyzed, both in the northern and southern parts of the peninsula (Siqueiros Beltrones 2002). Studies elsewhere on mangrove roots by Sullivan (1981), Maples (1983), and Navarro and Torres (1987) yielded an even smaller number of diatom taxa: 83, 23, and 107, respectively. Navarro (1982), on the other hand, recorded 226 taxa in 234 samples during a year cycle.

Much floristic work is yet to be done in the NW Mexican region. However, many diatom species previously have been recorded from sediments in mangrove systems farther south in the Sea of Cortés (Siqueiros Beltrones and Morzaria Luna 1999, Siqueiros Beltrones and Sánchez Castrejón 1999). Most are common epipelic forms that can easily be suspended as tychoplankton, which may eventually settle down on the prop roots where sediments also accumulate. System dynamics in Bahía Magdalena are determined by tidal ebb and flow (Acosta-Ruíz and Lara-Lara 1978) that resuspend benthic diatoms from different substrates, which are eventually transported
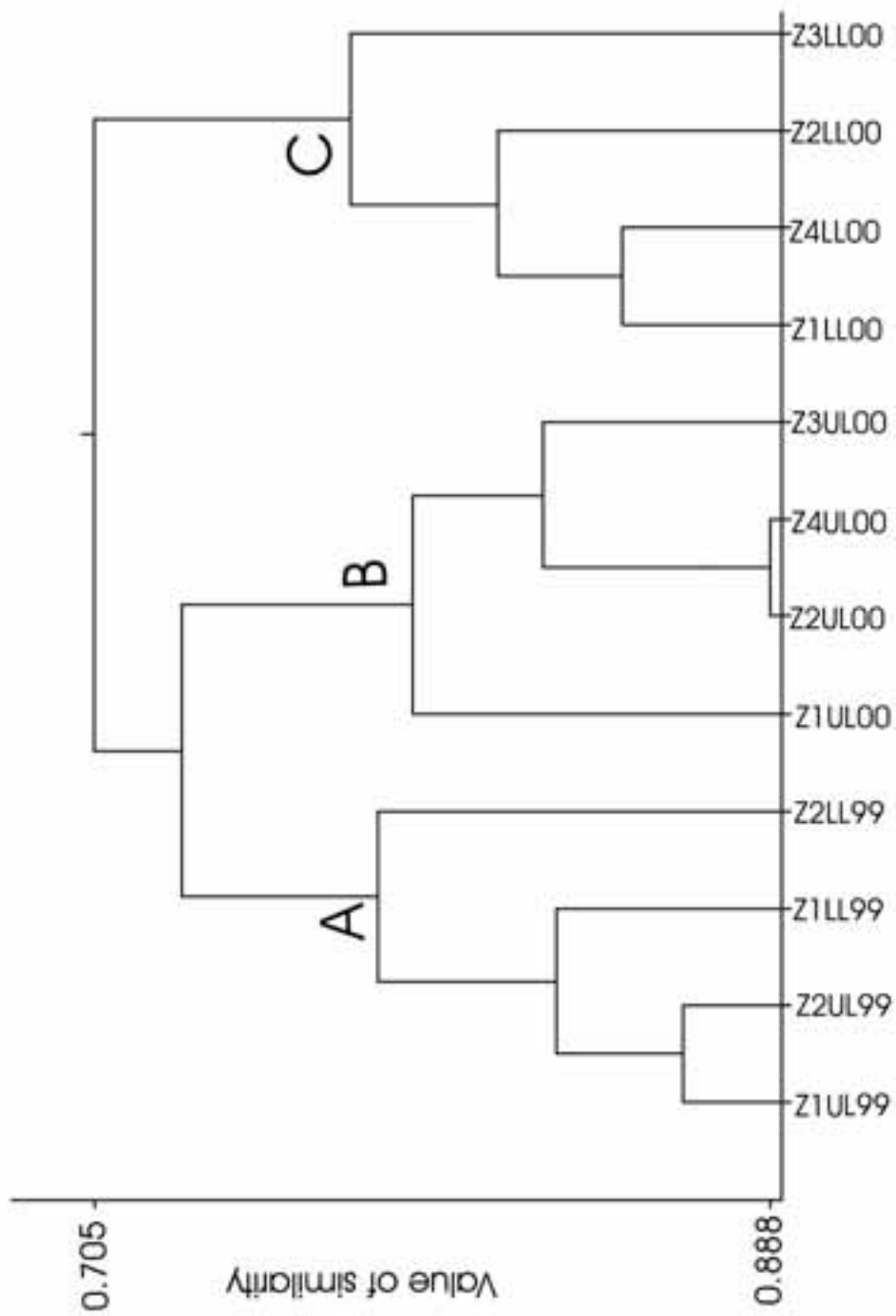
FIGURE 13. Classification analysis of epiphytic diatom assemblages from red mangrove (*Rhizophora mangle*) prop roots based on the computed values of Horn's Index for samples only. Z, site; LL, lower level of prop roots; UL, upper level of prop roots; 99, November 1999; 00, April 2000.

TABLE 2

Mean Sediment Salinity (psu) and Air Temperature
(°C) Measurements for the Sampling Dates at
Bahía Magdalena

Date	Z-1	Z-2	Z-3	Z-4	Temperature
Nov. 1999	44	43	NM	NM	22
April 2000	45	41	40	45	25

Note: Z, sampling site; NM, no measurement.

toward the Pacific Ocean. Many tychoplanktonic species of diatoms have been collected 200 km NW of Bahía Magdalena at 300-m depth (Martínez López et al. 2004). A more complete knowledge of the species composition and assemblage structure of benthic diatoms in the system will provide the basis for studies on their geographical distribution and for tracing certain oceanographic events in the area.

Many more species are expected to be found inside Bahía Magdalena when more extensive surveys get under way that consider other types of substrates. The new records of species include both epipelic and epiphytic forms found on macroalgae, and only *Achnanthes suchlandtii* (Figure 26) had a high BVI value (i.e., it was abundant and frequent in several samples). These new records along with other taxa that were not numerically important may prove more abundant in other habitats of the bay (e.g., *A. suchlandtii*, along with *Diadesmis* cf. *contenta* [also with a high BVI]). Although typical of freshwater environments, the latter taxon also occurs commonly in marine habitats (Navarro 1982). Our specimen of *D. contenta* closely resembles that of Navarro (pl. 30, figs. 1–3, as *Navicula contenta*), who stated its sublittoral distribution in warm-temperate waters. And, although no marine records for *A. suchlandtii* were found, our specimen closely resembles those in Schmidt et al. (1874–1959) and Hustedt (1927–1966), albeit Bahía Magdalena is considered an antiestuary (Guerrero et al. 1988) with low freshwater input. However, in other surveys of the region many freshwater taxa have been recorded from similar marine habitats (Siqueiros Beltrones 2002).

Differences in sediments may cause differences in the diatom assemblages (e.g., no *Mastogloia* [G. H. K. Thwaites] species were recorded in this study, but current observations by the authors are revealing a high abundance and variety of conspicuous *Mastogloia* species in sediments of Bahía Magdalena in other localities although not in this one). And, indeed *Mastogloia* and *Lyrella* species appear to be distinctive in the benthic diatom assemblages in Bahía Magdalena (López Fuerte 2004), which are distributed according to Witkowski et al.'s (2000) oases or hot spots (i.e., either absent or abundant).

The epiphytic diatom assemblages found on *R. mangle* prop roots of Bahía Magdalena are apparently similar to many other benthic diatom assemblages, having few abundant specific taxa and many rare or uncommon species. However, the species diversity (H′) values estimated here are the highest recorded in similar studies for benthic diatoms in other mangrove systems (Sullivan 1981, Navarro 1987, Siqueiros Beltrones and Sánchez Castrejón 1999). Although the high number of species per sample does influence these estimates, J′ and λ values were also higher than in other coastal environments with a high primary production (listed by Siqueiros Beltrones 1998, 2002).

Those studies were focused on diatom assemblages from well-defined substrates (sea grasses, macroalgae, and different type of sediments), whereas the specific substrate for the diatoms found on the prop roots of *R. mangle* was not well discriminated. It is evident that these diatom assemblages are part of a well-defined habitat composed of the prop roots, attached sediments, and macroalgae, all subject to high salinities and desiccation pressures. However, the high diversity of the diatom assemblages in this particular habitat suggests that salinity and desiccation conditions cannot be considered extreme, and according to Pielou (1975) a certain stability exists.

In summary, the diatom assemblages found on prop roots of *R. mangle* are characterized by a high species diversity that is similar in both levels of exposure (desiccation) and sampling dates representing the cool season.
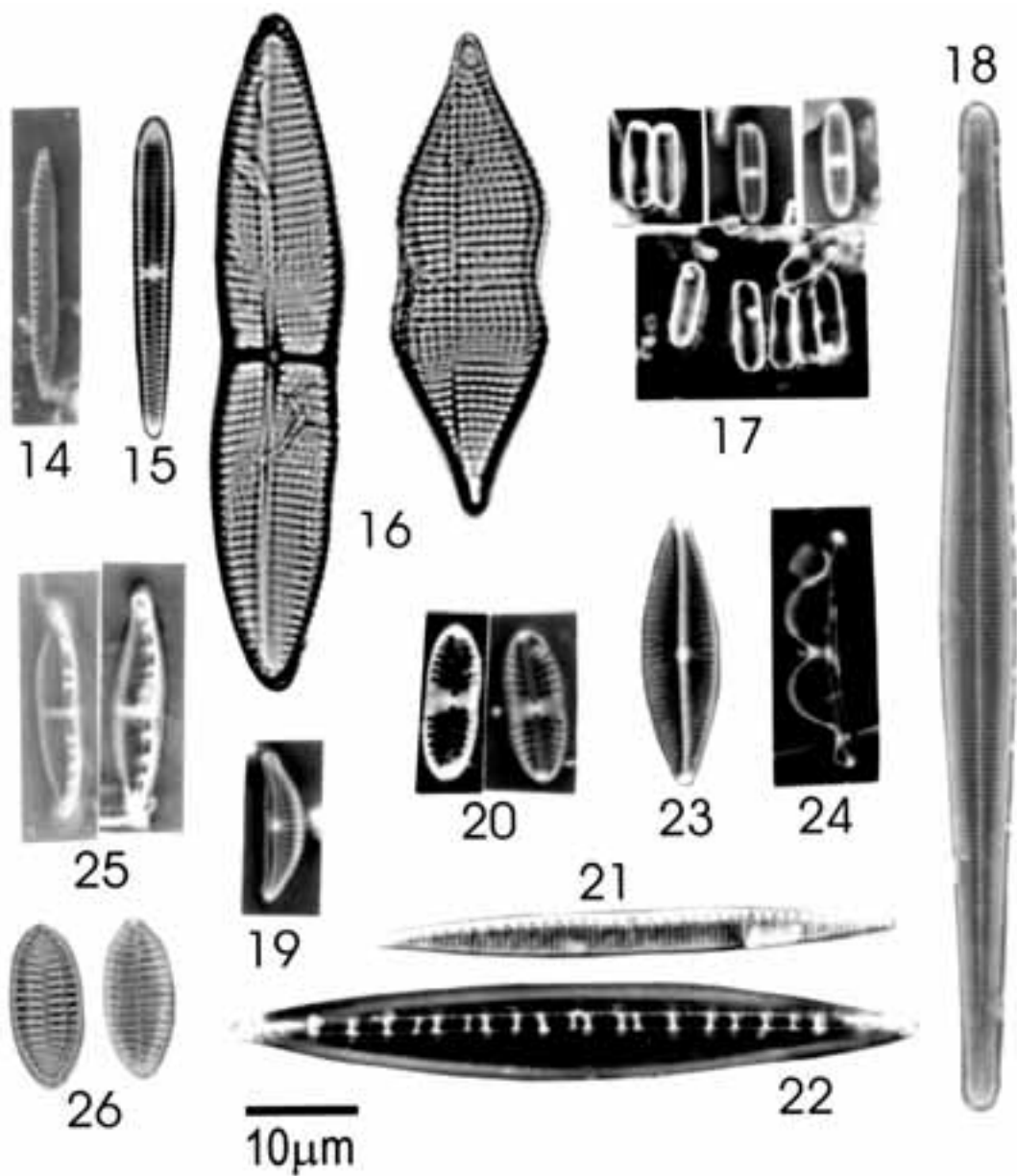
FIGURES 14–26. Taxa (abundant) showing the highest scores with the first two factors computed in the PCA: 14, *Nitzschia frustulum* var. *frustulum* (Kützing) Grunow; 15, *Gomphonemopsis pseudexigua* (Simonsen) Medlin; 16, *Achnanthes yaquinensis* McIntire & Reimer; 17, *Diadesmis* cf. *contenta* Grunow; 18, *Catacombas gaillonii* (Bory) Williams & Round; 19, *Amphora salina* var. *tenuissima* Hustedt; 20, *Achnanthidium* sp. 1; 21, *Nitzschia amphibia* Grunow; 22, *Nitzschia dissipata* (Kützing) Grunow; 23, *Amphora bigibba* Grunow; 24, *Navicula salinarum* Grunow; 25, *Nitzschia* sp. 1; 26, *Achnanthes suchlandtii* Hustedt.
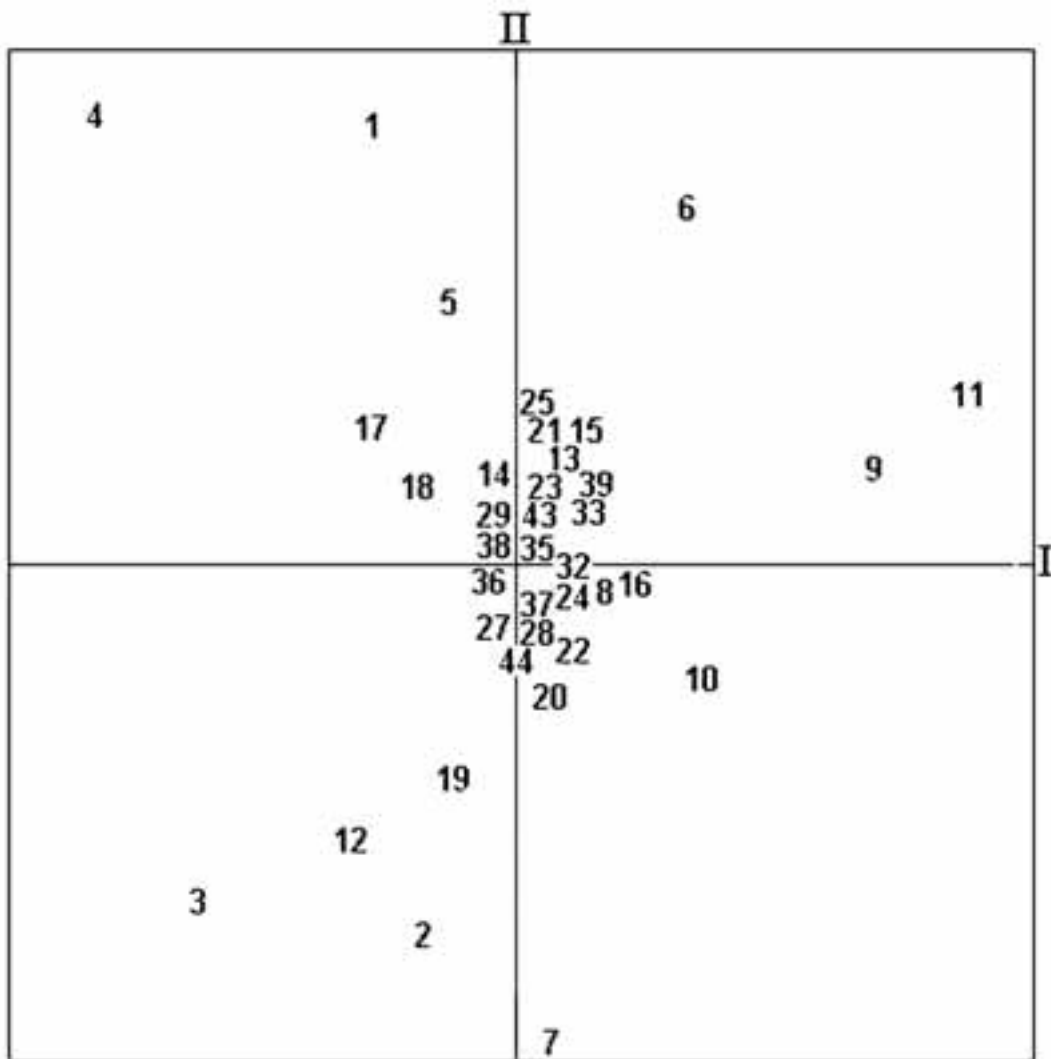
FIGURE 27. Distribution of PCA scores for 50 species of epiphytic diatoms from red mangrove (*Rhizophora mangle*) prop roots. Numbers not shown were concentrated in the center of the diagram. 1, *Nitzschia frustulum*; 2, *Gomphonemopsis pseudexigua*; 3, *Achnanthes yaquinensis*; 4, *Diadesmis* cf. *contenta*; 5, *Catacombas gaillonii*; 6, *Amphora salina* var. *tenuissima*; 7, *Achnanthidium* sp. 1; 8, *Nitzschia amphibia*; 9, *Nitzschia dissipata*; 10, *Navicula salinarum*; 11, *Amphora bigibba*; 12, *Nitzschia* sp. 1; 13, *Nitzschia frustulum* var. *perminuta*; 14, *Opephora pacifica*; 15, *Navicula platyventris*; 16, *Amphora costata*; 17, *Navicula pennata*; 18, *Nitzschia denticula*; 19, *Achnanthes suchlandtii*; 20, *Nitzschia brittoni*; 21, *Navicula parva*; 22, *Achnanthes brevipes* var. *intermedia*; 23, *Amphora acutiuscula*; 24, *Seminavis* sp. 1; 25, *Psammodyction constrictum*; 26, *Nitzschia grossestriata*; 27, *Planothidium hauckianum*; 28, *Achnanthes kuwaitensis* cf. *parvula*; 29, *Cocconeis scutellum*; 30, *Achnanthes brevipes* var. *parvula*; 31, *Paralia sulcata* var. *radiata*; 32, *Tabularia tabulata* var. *affinis*; 33, *Nitzschia angularis*; 34, *Paralia sulcata*; 35, *Amphora coffeaeformis* var. *salina*; 36, *Catenula adhaerens*; 37, *Cyclotella striata*; 38, *Navicula agnita*; 39, *Hyalosynedra laevigata*; 40, *Thalassionema nitzschioides*; 41, *Trachyneis velata*; 42, *Tryblionella acuminata*; 43, *Nitzschia lanceolata* var. *minor*; 44, *Achnanthidium minutissima*; 45, *Cocconeis scutellum* var. *parva*; 46, *Cocconeis placentula*; 47, *Cyclotella litoralis*; 48, *Cocconeis diminuta*; 49, *Cocconeis dirupta*; 50, *Lyrella clavata* var. *subconstricta*.

TABLE 3

Biological Value Index (BVI) Estimates for the 40 Species That Comprised ≈85% of the Total Frustule Count in the 24 Subsamples

Species		BVI
Achnanthes brevipes var. *intermedia*	E[a]	156
Achnanthes brevipes var. *parvula*	E	112
Achnanthes cf. *kuwaitensis parvula*	E	137
Achnanthes suchlandtii		148
Achnanthes yaquinensis	E	508
Achnanthidium minutissima	E	66
Achnanthidium sp. 1	E	255
Amphora acutiuscula		107
Amphora bigibba	E	228
Amphora coffeaeformis var. *salina*		85
Amphora costata		261
Amphora salina var. *tenuissima*	E	370
Catacombas gaillonii	E	416
Catenula adhaerens		96
Cocconeis scutellum	E	132
Cyclotella striata		105
Diadesmis cf. *contenta*	E	296
Gomphonemopsis pseudexigua	E	591
Navicula agnita		92
Navicula parva		170
Navicula pennata		161
Navicula platyventris		228
Navicula salinarum		327
Nitzschia amphibia	E	397
Nitzschia angularis		126
Nitzschia brittonii		155
Nitzschia denticula		193
Nitzschia dissipata	E	261
Nitzschia frustulum var. *frustulum*	E	553
Nitzschia frustulum var. *perminuta*	E	355
Nitzschia grossestriata		137
Nitzschia sp. 1		243
Opephora pacifica	E	285
Paralia sulcata	E	62
Paralia sulcata var. *radiata*	E	94
Planothidium hauckianum		152
Psammodyction constrictum		112
Seminavis sp. 1	E	150
Tabularia tabulata var. *affinis*	E	122
Trachyneis velata	E	62

[a] E, commonly recorded as epiphyte.

However, the taxa composing the assemblages may differ according to level of exposure and date. Thus, based on the structure of the diatom assemblages (species diversity and its components), it is concluded that all the sampling sites represent a similar habitat, and in spite of the similar salinity and temperature the November and April assemblages could be discriminated in the analysis due to the differential distribution of taxa.

The distribution of epiphytic macroalgae on the prop roots of *R. mangle* depends on the different physiological response to desiccation stress and photosynthetic recovery capacity of the specific taxon (Peña et al. 1999). This may well be expected to occur in diatoms distributed in different levels of exposure. Thus, the observed variations may represent this type of physiological adaptation, but during warmer months other strategies may be detected.

In the warm period air temperatures easily surpass 35°C, and water temperatures range from 20°C in April to 28°C in September (Gárate-Lizárraga and Siqueiros Beltrones 1998). Cool and warm seasons are clearly defined in this area and are associated with a high and low species diversity in phytoplankton assemblages, respectively (Gárate Lizárraga et al. 2000, 2001). This same effect may characterize the epiphytic diatom assemblages on red mangrove prop roots. Epiphytic diatom assemblages during the warm period are thus hypothesized to be quite different from the surveyed assemblages of the cool season, exhibiting strategies more suitable to more extreme conditions. Also, because different diatom species are found on different species of macroalgae (McIntire and Moore 1977, Main and McIntire 1974, Tanaka 1986, Tanaka and Asakawa 1986, Siqueiros Beltrones 2002, Siqueiros Beltrones and López Fuerte 2003) the structure of the diatom assemblages in the epiphytic macroalgae occurring on the prop roots is also expected to vary, mainly rhodophytes and chlorophytes on which dense growths of diatoms have been observed (Siqueiros Beltrones and López Fuerte 2003). These may contribute to the diatom diversity in any given habitat. In our study site the red alga *Spyridia filamentosa* (Wulfen) Harvey is common throughout the year (Sánchez Rodríguez et al. 1989). However, many of the diatom taxa in this study were better represented on macroalgae separated from the root segments: *Ulva* sp. (chlorophyte), and the red alga *Polysiphonia* sp. and a species of the Gelidiales that

were densely covered by diatoms (Siqueiros Beltrones and López Fuerte 2003).

Bahía Magdalena represents the northern limit of mangrove systems (Blasco 1984) and many species of macroalgae (Dawson 1960, Riosmena Rodríguez and Siqueiros Beltrones 1996). The effects of the transitional nature of the study area have been observed on the phytoplankton assemblages inside the bay, where temperate and tropical species co-occur. Complex oceanographic conditions in this area may explain the high diversity of diatoms in mangrove prop root assemblages. Their biogeographical affinities reflect the influence of temperate and warm waters (Gárate Lizárraga and Siqueiros Beltrones 1998, Gárate Lizárraga et al. 2001) most likely related to the California and Costa Rica Currents. However, to determine the similarity between this and other mangrove systems in the NW Mexican region, it is necessary to compare both floristics and assemblage structure of the benthic diatoms occurring in the different substrates.

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Appendix

List of (171) Epiphytic Diatom Taxa from Red Mangrove (*Rhizophora mangle*) Prop Roots in Bahía Magdalena, B.C.S., México

Species	Species
Achnanthes brevipes var. *angustata* (Greville) Cleve*	*Caloneis permagna* (Bailey) Cleve
Achnanthes brevipes var. *intermedia* (Kützing) Cleve	*Campylodiscus samoensis* Grunow*
Achnanthes brevipes var. *parvula* (Kützing) Cleve	*Campylodiscus thuretii* Brébisson
Achnanthes groenlandica var. *phinneyi* McIntire & Reimer	*Catacombas gaillonii* (Bory) Williams & Round
Achnanthes cf. *kuwaitensis* var. *parvula* McIntire & Reimer	*Catenula adhaerens* Mereschkowsky
Achnanthes manifera Brun	*Cocconeis diminuta* Pantocsek
Achnanthes parvula Kützing	*Cocconeis dirupta* Gregory
Achnanthes suchlandtii Hustedt*	*Cocconeis dirupta* var. ?
Achnanthes yaquinensis McIntire & Reimer	*Cocconeis dirupta* var. *flexella* (Janisch & Rabenhorst) Grunow
Achnanthidium minutissima Kützing	*Cocconeis diruptoides* Hustedt
Achnanthidium sp. 1	*Cocconeis distans* (Gregory) A. Schmidt
Actinoptychus adriaticus Grunow	*Cocconeis peltoides* Hustedt
Actinoptychus aster Brun	*Cocconeis placentula* Ehrenberg
Actinoptychus splendens (Shadbolt) Ralfs	*Cocconeis pseudomarginata* Gregory
Amphora acutiuscula Kützing	*Cocconeis scutellum* var. *scutellum* Ehrenberg
Amphora bigibba Grunow	*Cocconeis scutellum* var. *parva* Grunow
Amphora cingulata Cleve*	*Coscinodiscus radiatus* Ehrenberg
Amphora clevei Grunow	*Cyclotella kutzingiana* Chauvin*
Amphora coffeaeformis (Agardh) Kützing	*Cyclotella litoralis* Lange & Syvertsen
Amphora coffeaeformis var. *salina* (W. Smith) Cleve	*Cyclotella striata* (Kützing) Grunow
Amphora costata W. Smith	*Cyclotella* sp. 1
Amphora elegantula Hustedt*	*Cymatoneis circumvallata* Cleve*
Amphora exigua Gregory	*Cymbella subturgida* Gregory
Amphora obtusa var. *oceanica* Castracane	*Cymbella ventricosa* Kützing
Amphora obtusa var. *rectangulata* Peragallo*	*Delphineis surirella* (Ehrenberg) Andrews
Amphora ocellata Donkin	*Diadesmis* cf. *contenta* Grunow
Amphora proteus Cleve	*Dimeregramma maculatum* (Cleve) Frenguelli
Amphora proteus var. *contigua* Cleve	*Dimeregramma minor* var. *minor* (Gregory) Ralfs
Amphora proteus var. *kariana* Grunow	*Diploneis chersonensis* (Grunow) Cleve
Amphora robusta var. *hemicostata* Peragallo*	*Diploneis crabro* Ehrenberg
Amphora salina var. *tenuissima* Hustedt	*Diploneis gravelleana* Hagelstein
Amphora sp. 1	*Diploneis gruendleri* (A. Schmidt) Cleve
Astartiella punctifera (Hustedt) Witkowski, Lange-Bertalot & Metzeltin	*Diploneis litoralis* (Donkin) Cleve
Auliscus caelatus Bailey	*Diploneis obliqua* (Brun) Hustedt
Auliscus punctatus Bailey	*Diploneis smithii* (Brébisson) Cleve
Bacillaria paxillifer (Müller) Hendey	*Diploneis splendida* Gregory
Biddulphia alternans (Bailey) van Heurck	*Diploneis suborbicularis* (Gregory) Cleve
Caloneis elongata (Grunow) Boyer	*Diploneis vacillans* (A. Schmidt) Cleve
Caloneis latiuscula f. *minor* (Kützing) Cleve*	*Eunotograma laeve* Grunow
Caloneis liber (W. Smith) Cleve	*Fallacia forcipata* (Greville) Stickle & D. G. Mann
Caloneis linearis (Grunow) Boyer	*Fallacia litoricola* (Hustedt) D. G. Mann
	Fallacia nummularia (Greville) D. G. Mann

Appendix (continued)

Species	Species
Fallacia pygmaea (Kützing) Stickle & D. G. Mann	*Nitzschia subvitrea* Hustedt
Fallacia vittata (Cleve) D. G. Mann	*Nitzschia vitrea* Norman
Gomphonemopsis pseudexigua (Simonsen) Medlin	*Nitzschia* sp. 1
Grammatophora marina Ehrenberg	*Odontinium marinum* Grunow
Gyrosigma balticum (Ehrenberg) Rabenhorst	*Opephora marina* (Gregory) Petit
Hantzschia virgata (Roper) Grunow	*Opephora pacifica* (Grunow) Petit
Huttoniella reichardtii Grunow*	*Opephora schwartzii* Petit
Hyalosynedra laevigata (Grunow) Williams & Round	*Oestrupia powellii* var. *vidovichii* (Grunow) Heiden
Lyrella approximatoides Hustedt	*Paralia sulcata* var. *sulcata* (Ehrenberg) Cleve
Lyrella clavata var. *subconstricta* (Gregory) D. G. Mann	*Paralia sulcata* var. *radiata* Grunow
*Lyrella exsul*a (A. Schmidt) D. G. Mann	*Petroneis granulata* (Bailey) D. G. Mann
Lyrella irrorata (Greville) D. G. Mann	*Plagiogramma pulchellum* var. *pygmaea* Greville
Navicula agnita Hustedt	*Plagiotropis vitrea* (W. Smith) Kuntze
Navicula auriculata Hustedt	*Planothidium delicatulum* var. *subcapitata* (Östrup) Round & Bukhtiyarova
Navicula cancellata Donkin	*Planothidium hauckianum* (Grunow) Round & Bukhtiyarova
Navicula diversistriata Hustedt	*Planothidium lanceolatum* (Brébisson) Round & Bukhtiyarova
Navicula grimmei Krasske*	
Navicula longa Gregory	*Pleurosigma formosum* W. Smith
Navicula parva (Meneghini) A. Cleve	*Pleurosigma salinarum* Grunow
Navicula parvillardi Hustedt	*Podosira montagnei* Kützing
Navicula pennata Schmidt	*Psammodyction bombiforme* (Grunow) D. G. Mann*
Navicula platyventris Meister	*Psammodyction constrictum* (Kützing) D. G. Mann
Navicula salinarum Grunow	*Psammodyction panduriforme* (Gregory) D. G. Mann
Neodelphineis pelagica Takano	*Rhaphoneis nitida* (Gregory) Grunow
Nitzschia amphibia Grunow	*Seminavis* sp. 1
Nitzschia angularis W. Smith	*Seminavis* sp. 2
Nitzschia brittoni Hustedt	*Staurophora amphioxys* (Gregory) D. G. Mann
Nitzschia denticula Grunow	*Staurosirella pinnata* (Ehrenberg) Williams & Round
Nitzschia dissipata (Kützing) Grunow	*Surirella fastuosa* var. *fastuosa* Ehrenberg
Nitzschia fasciculata Grunow	*Surirella fastuosa* var. *suborbicularis* Grunow*
Nitzschia frustulum var. *frustulum* (Kützing) Grunow	*Tabularia tabulata* var. *affinis* (Kützing) A. Cleve
Nitzschia frustulum var. *perminuta* Grunow	*Tabularia tabulata* var. *parva* (Hustedt) Lange-Bertalot
Nitzschia gandersheimiensis Krasske*	*Terpsinoë americana* (Bailey) Ralfs
Nitzschia gracilis Hantzsch	*Thalassionema nitzschioides* (Grunow) Hustedt
Nitzschia granulata (Grunow) D. G. Mann	*Thalassiosira* sp. 1
Nitzschia grossestriata Hustedt	*Trachyneis aspera* Ehrenberg
Nitzschia hybridaeformis Hustedt	*Trachyneis clepsydra* (Donkin) Cleve
Nitzschia lanceolata var. *minor* Grunow	*Trachyneis velata* A. Schmidt
Nitzschia longa Grunow	*Triceratium favus* Ehrenberg
Nitzschia longissima var. *parva* (Brébisson) Ralfs	*Tryblionella acuminata* Wm. Smith
Nitzschia obtusa var. *obtusa* W. Smith	*Tryblionella apiculata* Gregory
Nitzschia obtusa var. *parva* Hustedt	*Tryblionella compressa* (Bailey) Poulin
Nitzschia obtusa var. *scalpelliformis* Grunow	*Tryblionella navicularis* (Brébisson ex Kützing) Ralfs
Nitzschia ovalis Arnott*	
Nitzschia sigma (Kützing) W. Smith	
Nitzschia socialis Gregory	

* New records for the Baja California peninsula.