

High species diversity (H') of benthic diatoms in a coastal lagoon located within a natural protected areaAlta diversidad de especies (H') de diatomeas bentónicas en una laguna costera ubicada dentro de un área natural protegidaDavid A. Siqueiros Beltrones¹, Uri Argumedo Hernández² and Oscar U. Hernández Almeida³¹ Departamento de Plancton y Ecología Marina, Instituto Politécnico Nacional- Centro Interdisciplinario de Ciencias Marinas. Av. IPN s/n, Col. Playa Palo de Santa Rita, La Paz, Baja California Sur, 23096. México² Departamento de Economía, Universidad Autónoma de B.C.S., Km 5.5. Carretera al Sur, La Paz, BCS., 23080. México³ Laboratorio de Oceanografía Biológica, Universidad Autónoma de Nayarit, Edificio CEMIC 01, Ciudad de la Cultura "Amado Nervo". Tepic, Nayarit, 63000. México
e-mail: dsiquei@gmail.com**Recibido:** 15 de mayo de 2017.**Aceptado:** 04 de noviembre de 2017.Siqueiros Beltrones D. A., U. Argumedo Hernández and O. U. Hernández Almeida. 2017. High species diversity (H') of benthic diatoms in a coastal lagoon located within a natural protected area. *Hidrobiológica* 27 (3): 293-300.**ABSTRACT**

Background. The structure of benthic diatom assemblages (diversity, equitability, dominance) may be useful in assessing their ecological status in natural protected areas. **Goals.** To describe the structure of epipellic diatom assemblages from Laguna Guerrero Negro (LGN), a protected coastal lagoon, and test the hypothesis that H' diversity values would be higher for diatom assemblages in LGN sediments than in typical benthic diatom assemblages. **Methods.** Sediment samples were collected in the lagoon on November 2013, and January, March, and July 2014. Diatoms were mounted on permanent slides and examined at 1000 \times using phase contrast microscopy. In each slide, 500 valves were counted to compute relative abundances of each taxon, and species diversity, equitability, and dominance, using Shannon (H'), Pielou (J'), and Simpson (λ) indices, respectively. Likewise, similarity between samples was measured. The calculated median value of H' from LGN was compared to previously recorded median values to test the hypothesis that significant differences exist. **Results.** A total 225 diatom taxa were counted. With few exceptions, the similarity between samples was <60%. Relative abundances depict typical benthic diatom assemblages, with an average $H' = 4.96$ bits/taxon, and corresponding values of equitability and dominance. The median value of H' ($Md = 4.9$) was significantly higher than the median value ($Md = 3.7$) found in previous studies. **Conclusions.** The structure of the epipellic diatom assemblages from LGN and their patchy distribution are similar to that of typical diatom assemblages, but with unusually high values of H' that lead us to reject the statistical null hypothesis and thus sustain our research hypothesis.

Key words: Biodiversity, diatom assemblages, Laguna Guerrero Negro, natural protected area, species richness.**RESUMEN**

Antecedentes. La estructura de asociaciones de diatomeas bentónicas (diversidad, equidad, dominancia) puede servir de referencia para evaluar su estado ecológico en áreas naturales protegidas. **Objetivos.** Describir la estructura de asociaciones de diatomeas epipéllicas de Laguna Guerrero Negro (LGN), una laguna costera protegida, contrastando la hipótesis de que la diversidad (H') sería más alta que en asociaciones típicas de diatomeas bentónicas. **Métodos.** Se recolectaron sedimentos de LGN en noviembre, 2013, enero, marzo, y julio, 2014. Las diatomeas se montaron en preparaciones permanentes y se examinaron bajo microscopía con contraste de fases a 1000 \times . Por muestra se contaron 500 valvas para estimar abundancias relativas de los taxa y calcular diversidad de especies, equidad y dominancia, utilizando los índices de Shannon (H'), Pielou (J') y Simpson (λ). Asimismo, se midió la similitud entre muestras. El valor mediano calculado de H' para LGN se comparó con la H' mediana de estudios previos contrastando la hipótesis de que existirían diferencias significativas entre estas. **Resultados.** Se contaron 225 taxa de diatomeas para LGN. Salvo excepciones, la similitud entre muestras fue <60%. Se describen asociaciones de diatomeas bentónicas con diversidad promedio de $H' = 4.96$ bits/taxón, y equidad y dominancia correspondientes. El valor mediano de H' ($Md = 4.9$) fue significativamente mayor que el valor mediano ($Md = 3.7$) de estudios previos. **Conclusiones.** La estructura de asociaciones de diatomeas epipéllicas de LGN es similar a la de asociaciones típicas de diatomeas bentónicas y su distribución en parches, pero con valores inusualmente altos de H' que rechazan la hipótesis nula estadística, y respaldan la hipótesis de investigación.

Palabras clave: Área natural protegida, asociaciones de diatomeas, biodiversidad, Laguna Guerrero Negro, riqueza de especies.

INTRODUCTION

Although protected areas are strategic for the conservation of species and their habitats, there are still doubts regarding their effectiveness. Thus, the premise that such measures are effective in conserving species was recently put to the test (Gray *et al.*, 2016). These authors observed that within-sample species richness could be significantly higher inside than outside protected areas. Laguna Guerrero Negro, Baja California - Baja California Sur, Mexico (LGN) is a protected coastal lagoon for which very few ecological studies are available. Since the survey by Eberhard (1966), only recently has an interest in describing benthic biocenoses emerged, including macrobenthos (Morales-Zárate *et al.*, 2016) and microbenthos focusing on diatoms (Siqueiros Beltrones *et al.*, 2017a, b). Considering that benthic diatoms are an important food source for bivalve mollusks (Siqueiros Beltrones, 2002a), and several species of clams and oysters sustain important fisheries in LGN (Morales-Zárate *et al.*, 2016), ecological studies on these microalgae are needed in order to generate baseline data for their management.

In addition, benthic diatoms are an adequate reference for measuring biodiversity, in part because of their high species richness. In LGN, high species richness of benthic diatoms was estimated for subtidal sediments, which included 14 new species records and 24 unidentified species (Siqueiros Beltrones *et al.*, 2017a), plus the highest number of *Lyrella* species for a locality in the Mexican NW region (Siqueiros Beltrones *et al.*, 2017b). The generated species list is a baseline for further ecological and biogeographical studies that are indispensable for protecting areas in order to preserve biodiversity and support decision making. By using the available diatom floristics as a reliable reference for estimating the relative or proportional abundances of the taxa, calculation of ecological parameters can follow to better describe the assemblages, inasmuch as community studies through joint analyses of classical parameters such as species richness, diversity, dominance and equitability, can help to detect patterns in taxocoenoses that can reflect ecological status such as in assemblages from extreme environments or that reflect environmental impact (Siqueiros Beltrones, 2002b). Based on these parameters, however, few attempts have been made to detect environmental impact, (e.g., due to potentially toxic elements), by examining the structure of the diatom associations allegedly exposed to the former (Siqueiros Beltrones *et al.*, 2014). Also, a comparison of the structure of benthic diatom assemblages can be used as a reference for assessing environmental conditions in protected areas.

Typical diatom assemblages are characteristically composed of a few abundant and very common species, and many rare and uncommon species. This situation is reflected in the mathematical diversity values derived from information theory calculated with Shannon's index (H'), which has been observed to vary, mainly between modal values of 2.6 - 3.8 bits/taxon (median, 2.4-4.6) for microphytobenthic assemblages (Siqueiros Beltrones, 1998). These have been interpreted as usual or moderately high values of diversity that depict stability of the assemblages and, although higher ($H' \leq 5$) and lower ($H' < 2$) values are not uncommon, these in turn have been interpreted as indicative of a tendency towards an improbable and thus unstable state of the assemblages in nature (Siqueiros Beltrones, 2005).

However, more recent studies on the structure of benthic diatom assemblages for the Mexican NW region have yielded further reference values, e.g., extreme low (uncommon) values ($H' < 2$) were recorded for epiphytic diatom assemblages living on blades of the kelp *Eisenia ar-*

borea J.E. Areschoug (Siqueiros Beltrones *et al.*, 2016); and previously, similar values (average $H' = 2.1$) were estimated for diatom epiphytes living on blades of another kelp, *Macrocystis pyrifera* (Linnaeus) C. Agardh (Argumedo Hernández & Siqueiros Beltrones, 2008). As a comparison, other studies in the region have produced mean values of diversity of up to $H = 4.76$ in diatom assemblages from mangrove sediments (López Fuerte & Siqueiros Beltrones, 2006), and, later, from $H' = 4.58$ to $H' = 5.13$ for different substrata (Hernández Almeida & Siqueiros Beltrones, 2008, 2012). All of the above apply to undisturbed coastal environments.

In the case of LGN, the observed high number of species and subspecies taxa (S) of epipellic diatoms is considered typical of highly productive environments (Siqueiros Beltrones *et al.*, 2017a), where the values of species diversity based on proportional abundances, e.g., H' are also usually high (Siqueiros Beltrones, 2002a).

Based on the above, the aim of this study was to describe the structure of the epipellic diatom assemblages living in subtidal sediments of LGN, and contrast the hypothesis that diversity values estimated on the basis of information theory (H') would be higher than the median value of H' calculated for benthic diatom assemblages from other localities (Siqueiros Beltrones, 2005), and at least as high as the upper values recorded in the more recent studies cited above.

MATERIALS AND METHODS

Study area. Laguna Guerrero Negro (LGN) is part of a lagoon complex together with Laguna Ojo de Liebre (Fig.1) located ($27^{\circ} 35'$ and $27^{\circ} 52'$ N and $113^{\circ} 58'$ $114^{\circ} 10'$ W) on the Baja California peninsula, between B.C. and B.C.S., Mexico within the El Vizcaino Biosphere Reserve (Arellano Martínez *et al.*, 1996). Its maximum length is 13 km and maximum width is 8 km (Contreras, 1985), with a shallow bottom that varies in depth between 2-12 m (Lluch *et al.*, 1993). Eelgrass (*Zostera marina* Linnaeus) is widely distributed from six meters deep up to the high tide mark (Eberhard, 1966). Lagoon sediments are mainly grey sand and organic alluvial deposits. Normal and hypersaline salinity gradients have been recorded (Lankford, 1977), although it has been considered an isohaline lagoon with salinities between 35.5-37.5 in winter, and 34.7-35.6 in summer (Phleger & Ewing, 1962).

Sample processing. During November 2013, January, March, and July 2014, sediment samples (150 g each) were collected by scuba divers using plastic bags at twelve sites in the subtidal bottom of Laguna Guerrero Negro (1-13); site 11 was not considered because of logistic difficulties but numeration was kept in reference to other studies. (Fig. 1). Samples were then processed and mounted with Pleuraxon 48 permanent slides. These were used to prepare a floristic list of epipellic diatoms (Siqueiros Beltrones *et al.*, 2017a). The slides were then examined under a compound microscope with phase contrast at 1000 \times for a quantitative analysis. New taxa were identified (Peragallo & Peragallo, 1897). Their taxonomic status was updated according to the *Algaebase* web site (<http://algaebase.org/search/species/>) (Guiry & Guiry, 2017), and the Fourtanier & Kociolek (2017) Catalogue of Diatom Names of the California Academy of Sciences (CAS) web site <http://researcharchive.calacademy.org/research/diatoms/names/>. These, together with the previous floristic list, were used as a reference to count 500 diatom valves (n) in each slide in order to determine the relative abundance (RA) of each taxon. Said abundance was used to estimate community

parameters of the assemblages, such as species diversity, equitability, and dominance. Species diversity values were calculated based on information theory using Shannon's H' and Pielou's J' , both with \log_2 (Brower *et al.*, 1998). We thus used bits/taxon (not bits/individual) as units, as a measure of uncertainty for a randomly collected specimen in a taxocoenosis, for it to belong to a certain (specific or infra-specific) taxon (Siqueiros Beltrones, 2005). Simpson's indices of dominance and diversity (λ , $1 - \lambda$) were also used; these measure the probability that two specimens collected at random belong to the same or different species (Brower *et al.*, 1998).

To test our hypothesis, two approaches were followed: 1) a 99% bias-corrected and accelerated (BCA) bootstrap confidence interval was constructed for the median H' value of benthic diatom assemblages compiled in Siqueiros-Beltrones (1998); and 2) we compared the median values of said data vs. the median value of H' calculated for Laguna Guerrero Negro. Because of the high dispersion shown by the H' values and common occurrence of outliers, we chose to use the median and thereafter non-parametric statistical techniques. This confidence interval and the Kruskal-Wallis test for significance were done using the statistical IBM® SPSS® 23 software, and a Mann-Whitney test, using Origin Pro® 9 software. For the Mann-Whitney test, the null hypothesis was that LGN H' median values were not significantly different than those of typical microphytobenthos assemblages. Both the Kruskal-Wallis and Mann-Whitney tests were performed at an $\alpha = 0.01$. A similarity matrix between samples was also computed using presence/absence of species (Jaccard index) and another also using their relative abundances (Bray-Curtis index).

RESULTS

A total (N) of 23,325 diatom valves were counted. These included 225 taxa, out of which 52 are new additions to the LGN diatom flora (Table 1), 46 were previously recorded elsewhere for the Mexican NW region, and six were new records for Mexican littorals (Siqueiros Beltrones & Argumedo Hernández, 2017). Thus, species richness for the LGN sediments rises to 285 taxa, with 117 of these comprising 95% of the total relative abundance. Five samples could not be quantified because of the low valve abundance in the slides (Table 2). Relative abundances of the identified diatom taxa were distributed as expected with few abundant and common taxa, and many rare and uncommon species. The pennate forms *Amphora exilitata* Giffen and *Navicula bipustulata* A. Mann were the most abundant taxa (>1000 valves); 29 taxa were very common (≥ 200); 57 taxa were considered common ($200 \geq 50$); and 137 were considered rare (<50). Rare species in this study represent >60% of the taxa accounted for (Table 1); these, plus the 52 not recorded in the previous floristics, total to 189 rare taxa for the LGN over all benthic diatom taxocenoses.

Species richness (S) among the samples varied between 50 and 100 taxa, with over 70% of the samples having a $S > 60$; which can be considered a high species number for benthic diatoms assemblages. Overall, 46 % of the samples showed H' values higher than 5 bits/taxon (Table 2), with an average value of 4.96 and a median of 4.9. Values ranged from 3.7 - 5.9, the former being the only calculated H' value under 4 (Table 2), vs. the calculated median value for the microphytobenthic assemblages ($Md = 3.7$) used as a reference. Although values of $H' > 5$ were frequent, in January we found the highest diversity ($H' =$

5.9) twice, which is much higher than the mean value for the whole lagoon (Table 3). Even though such frequency seemed more characteristic of the cool season (November-January) than for the warm season (March-July), the Kruskal-Wallis test did not detect significant differences between the monthly median values of H' in LGN ($\chi^2(3) = 3.842$, $p > 0.01$). Thus, differences in the calculated values of H' are considered within the range of random variations

On the other hand, the monthly median values of H' for LGN benthic diatom assemblages (Table 3) surpassed the 99 % bootstrap CI [3.52 - 3.81] constructed for the H' median value of microphytobenthic assemblages. Therefore, we see that monthly median diversity estimated for the LGN assemblages is indeed higher. These results were confirmed by the Mann-Whitney test which indicates that H' values were significantly higher for LGN ($Md = 4.9$) than for typical microphytobenthos assemblages ($Md = 3.7$), $U=10935.5$, $p < 0.01$, thus confirming our hypothesis.

The overall high values of H' correspond to the high number of species (S) in most of the samples, but there is also a correspondence with high values of equitability, and with the values of Simpson's indices (diversity and dominance), which are less sensitive to rare taxa. This indicates that the high diversity values were due to a higher number of

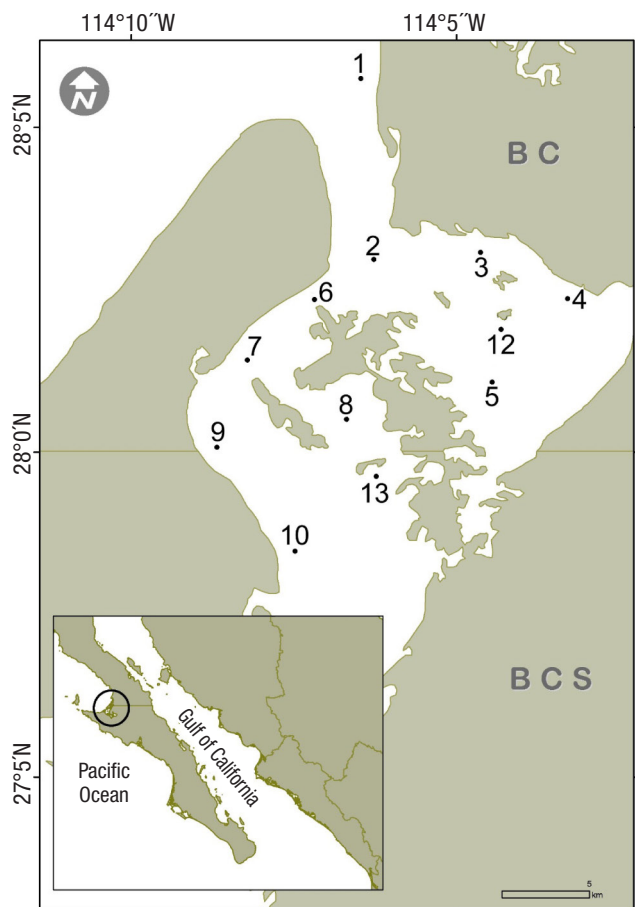


Figure 1. Location of the twelve sampling sites in Laguna Guerrero Negro, B.C.-B.C.S., Mexico. No site 11.

Table 1. New (52) subtidal epipelagic diatom taxa and their relative abundances (RA) and percentage RA (%) in Laguna Guerrero Negro, B.C.-B.C.S., Mexico (N=23,325).

Taxón	RA	%
<i>Cocconeis molesta</i> var. <i>crucifera</i> Grunow	464	1.997
<i>Amphora graeffi</i> var. <i>minor</i> Peragallo	151	0.650
<i>Thalassiosira eccentrica</i> (Ehrenberg) Cleve	80	0.344
<i>Cocconeis scutellum</i> var. <i>parva</i> (Grunow) Cleve	66	0.284
<i>Tropidoneis pusilla</i> (Greg.) Cleve	66	0.284
<i>Gyrosigma balticum</i> (Ehrenberg) Rabenhorst	50	0.215
<i>Hantzschia marina</i> (Donkin) Grunow	48	0.207
<i>Diploneis muscaeformis</i> var. <i>constricta</i> (Grunow in Schmidt <i>et al.</i>) Cleve	46	0.198
<i>Campylo discussimulans</i> Gregory	44	0.189
<i>Cocconeis heteroidea</i> Hantzsch	42	0.181
<i>Cocconeis dirupta</i> Gregory	39	0.168
<i>Nitzschia insignis</i> Gregory	36	0.155
<i>Amphora angusta</i> Gregory	36	0.155
<i>Astartiella punctifera</i> (Hustedt) Witkowski <i>et</i> Lange-Bertalot	34	0.146
<i>Cocconeis disculus</i> (Schumann) Cleve	33	0.142
<i>Cocconeis scutellum</i> Ehrenberg	33	0.142
<i>Cymbellonitzschia</i> cf. <i>minima</i> Hustedt	33	0.142
<i>Diploneis chersonensis</i> (Grunow) Cleve	28	0.121
<i>Cocconeopsis fraudulenta</i> (A. W. F. Schmidt) Witkowski	26	0.112
<i>Grammatophora oceanica</i> Ehrenberg	25	0.108
<i>Pleurosigma formosum</i> W. Smith	25	0.108
<i>Odontella aurita</i> (Lyngbye) Agardh	24	0.103
<i>Coscinodiscus oculus-iridis</i> Ehrenberg	23	0.099
<i>Donkinia carinata</i> (Donkin) Ralfs in Pritchard	19	0.082
<i>Halamphora costata</i> (W. Smith) Levkov	17	0.073
<i>Navicula</i> cf. <i>atomus</i> (Kützing) Grunow	11	0.047
<i>Podosira stelligera</i> (J. W. Bailey) A. Mann	11	0.047
<i>Amphora tenuissima</i> Hustedt	8	0.034
<i>Pleurosigmapulchrum</i> Grunow	8	0.034
<i>Pleurosigma</i> cf. <i>affine</i> Grunow	7	0.030
<i>Campylodiscus crebrecoastatus</i> var. <i>speciosa</i> T.Eulenstein	6	0.026
<i>Achnanthes citronella</i> (A. Mann) Hustedt in Schmidt <i>et al.</i>	5	0.022
<i>Cocconeis contermina</i> A. W. F. Schmidt	5	0.022
<i>Grammatophora gibberula</i> Kützing	5	0.022
<i>Synedra crystallina</i> (Agardh) Kützing	4	0.017
<i>Fallacia diploneoides</i> (Hustedt) D. G.Mann	4	0.017
<i>Nitzschia martiana</i> (Agardh) Van Heurck	4	0.017
<i>Bacillaria paxillifera</i> (O. F. Müller) T.Marsson	3	0.013
<i>Nitzschia perminuta</i> (Grunow) Peragallo	3	0.013
<i>Achnanthes javanica</i> Grunow	2	0.009
<i>Amphora aspera</i> Petit	2	0.009
<i>Grammatophora marina</i> (Lyngbye) Kützing	2	0.009
<i>Nitzschia filiformis</i> (W. Smith) Van Heurck	2	0.009
<i>Actinopterychus vulgaris</i> Schumann	1	0.004
<i>Halamphora duseinii</i> (Brun) Levkov	1	0.004
<i>Anaulus birostratus</i> (Grunow) Grunow	1	0.004
<i>Diploneis nitescens</i> (W. Gregory) Cleve	1	0.004
<i>Gyrosigmatenuissimum</i> (W. Smith) Griffith <i>et</i> Henfrey	1	0.004
<i>Mastogloia angulata</i> Lewis	1	0.004
<i>Navicula johanrossi</i> Giffen	1	0.004
<i>Nitzschia microcephala</i> var. <i>bicapitellata</i> Cleve	1	0.004
<i>Pleurosigma acutum</i> Norman ex Ralfs	1	0.004

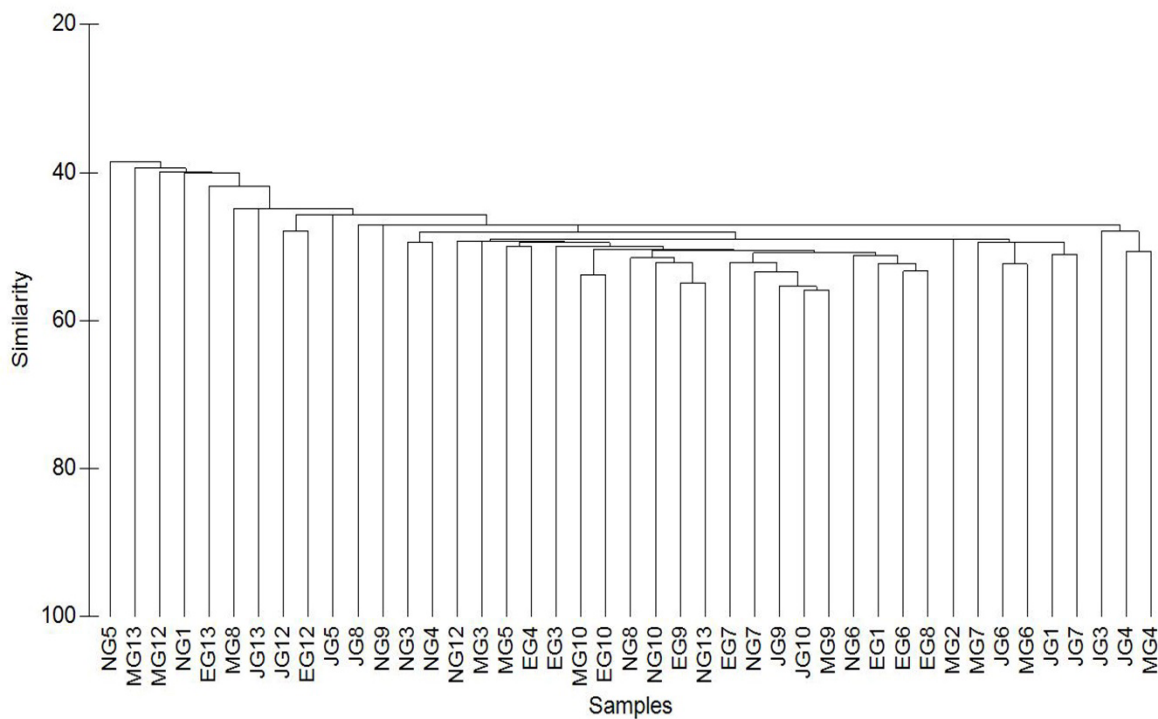


Figure 2. Jaccard similarity values in benthic diatom species composition between all samples collected at Laguna Guerrero Negro, B.C. -B.C.S., Mexico. The low values suggest the typical patchy distribution of the taxa in benthic diatom assemblages.

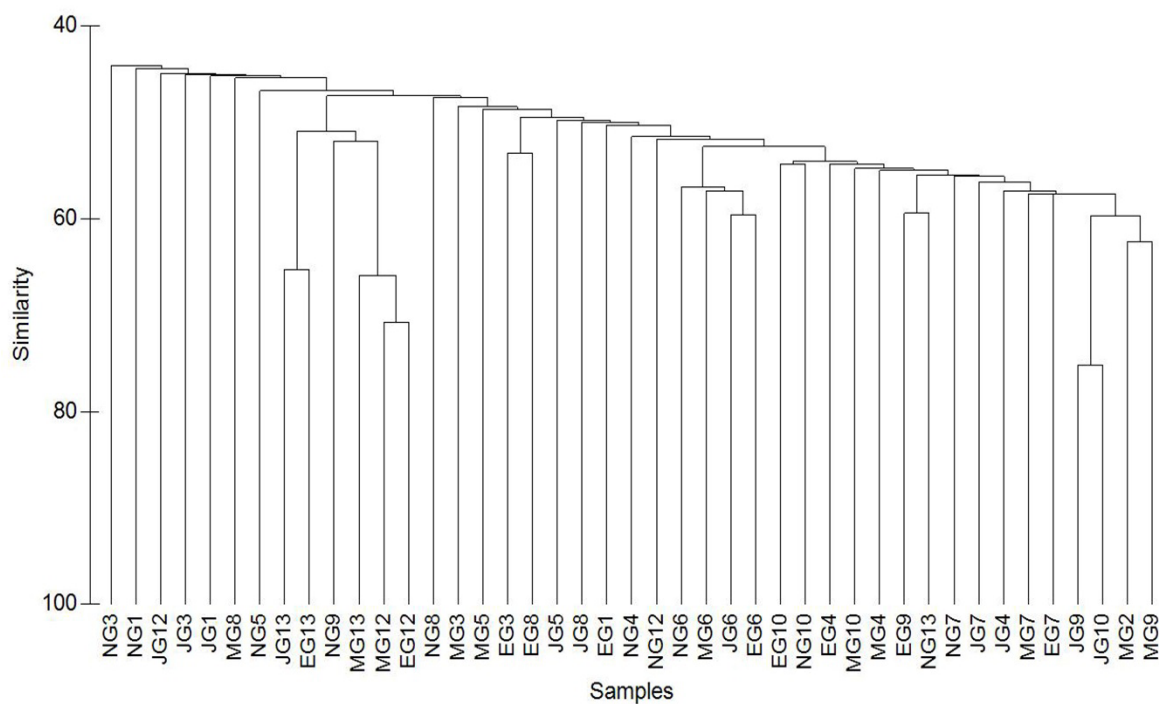


Figure 3. Bray-Curtis similarity values in benthic diatom species composition between all samples collected at Laguna Guerrero Negro, B.C. - B.C.S., Mexico. The patchy distribution of benthic diatom taxa suggested in general by low values (although higher than with Jaccard) combines with high values that are caused by the shared presence of taxa with high relative abundances in several sites, e.g. 6, 12, 13.

Table 2. Estimated community parameter values for benthic diatom assemblages from Laguna Guerrero Negro (G), BC-BCS, Mexico. N = November; E = January; M = March; J = July; S = species richness; n = sample size; J' = equitability (bits/taxon); H' = Shannon's diversity (bits/taxon); λ = Simpson's dominance (probability); $1-\lambda$ = Simpson's diversity. ND = not determined. No site 11.

Sample	S	n	J'	H'	λ	$1-\lambda$
NOVEMBER (2103)						
NG1	83	539	0.86	5.5	0.04	0.96
NG2	ND	ND	ND	ND	ND	ND
NG3	78	560	0.84	5.3	0.04	0.96
NG4	52	577	0.83	4.8	0.06	0.94
NG5	64	521	0.84	5.1	0.04	0.96
NG6	85	509	0.89	5.7	0.02	0.98
NG7	69	515	0.83	5.1	0.05	0.95
NG8	76	558	0.86	5.4	0.04	0.96
NG9	53	490	0.78	4.5	0.08	0.92
NG10	71	550	0.79	4.8	0.07	0.93
NG12	50	528	0.76	4.3	0.09	0.91
NG13	63	498	0.82	4.9	0.05	0.95
JANUARY (2014)						
EG1	100	551	0.89	5.9	0.02	0.98
EG2	ND	ND	ND	ND	ND	ND
EG3	73	515	0.85	5.3	0.04	0.96
EG4	87	526	0.88	5.7	0.03	0.97
EG5	ND	ND	ND	ND	ND	ND
EG6	95	594	0.89	5.9	0.02	0.98
EG7	74	569	0.76	4.7	0.08	0.92
EG8	89	617	0.86	5.6	0.03	0.97
EG9	61	515	0.83	4.9	0.05	0.95
EG10	84	560	0.84	5.4	0.03	0.97
EG12	52	534	0.74	4.2	0.11	0.89
EG13	59	522	0.76	4.5	0.10	0.90
MARCH (2014)						
MG1	ND	ND	ND	ND	ND	ND
MG2	75	617	0.83	5.1	0.05	0.95
MG3	61	507	0.79	4.7	0.06	0.94
MG4	55	575	0.81	4.7	0.06	0.94
MG5	87	563	0.81	5.2	0.05	0.95
MG6	74	491	0.86	5.3	0.04	0.96
MG7	62	514	0.79	4.7	0.06	0.94
MG8	95	576	0.87	5.7	0.03	0.97
MG9	54	576	0.80	4.6	0.07	0.93
MG10	76	597	0.80	4.9	0.06	0.94
MG12	39	438	0.69	3.7	0.13	0.87
MG13	43	539	0.77	4.2	0.09	0.91
JULY (2014)						
JG1	62	526	0.84	5.0	0.05	0.95
JG2	ND	ND	ND	ND	ND	ND
JG3	56	535	0.81	4.7	0.06	0.94
JG4	46	534	0.81	4.5	0.07	0.93
JG5	70	587	0.81	4.9	0.05	0.95
JG6	83	486	0.88	5.6	0.03	0.97
JG7	71	571	0.86	5.3	0.04	0.96
JG8	83	525	0.88	5.6	0.03	0.97
JG9	63	512	0.73	4.4	0.12	0.88
JG10	52	522	0.75	4.3	0.11	0.89
JG12	56	564	0.76	4.4	0.07	0.93
JG13	69	526	0.73	4.5	0.11	0.89

more common taxa rather than to rare species. All this is in accordance with the proposed hypothesis.

Measurements with both similarity indices ranged between 45% and 60% that comprised most of the samples (Figs. 2-3). No patterns were apparent within dendrograms, confirming a lack of statistical differences between monthly H' values. The only exception is the group of four samples from site 6 with Bray-Curtis. However, when compared with Jaccard values, it is evident that the same (few) abundant species were present at this site during all dates, while also sharing high values of equitability, which confirms that a significant number of common taxa were similarly distributed at these sites. Spatially, however, sites differed in overall species composition at around 50%. All these observations from the similarity analysis corresponds to the typical patchy distribution of taxa usually observed in benthic diatom assemblages.

DISCUSSION

Almost as many taxa (225) were included in this quantitative analysis of the epipelagic diatom assemblages of LGN as those recorded (232) in the supporting floristic study (Siqueiros Beltrones *et al.*, 2017a). Of the 52 additions to the LGN diatom flora, 46 taxa were previously recorded elsewhere for the Mexican NW region, while six taxa turned out to be new records for the Mexican littorals: *Achnanthes citronella* (A. Mann) Hustedt; *Amphora graeffi* var. *minor* Peragallo; *Navicula* (*Cocconeopsis*?) *aspera* Hustedt; *Diploneis muscaeformis* var. *constricta* (Grunow in Schmidt *et al.*) Cleve, *Pleurosigma affine* Grunow; *Pleurosigma pulchrum* Grunow (Siqueiros Beltrones & Argumedo Hernández, 2017). This, along with the low similarity values demonstrates the typical patchy distribution of benthic diatoms that causes floristics in discrete surveys to be underestimated.

On the other hand, the high number of diatom species (S) per sample and their proportions (J') are reflected in the estimated mean values of diversity (H') in sediments of LGN, some of which are among the highest ever recorded in the Mexican NW region (*Jan H' = 5.2 bits/taxon*), and much higher than the aforementioned median values that allegedly reflect stability (Siqueiros Beltrones, 2005), and higher than those within the confidence interval constructed in this paper. Although this could suggest that the LGN assemblages may not be stable (Siqueiros Beltrones, 2005), recent studies in undisturbed coastal localities report similar mean values of diversity ($H' = 4.76 \text{ bits/taxon}$) in mangrove sediments from Bahía Magdalena (López Fuerte & Siqueiros Beltrones, 2006). Besides, these authors recorded the most taxa hitherto for a single locality in NW Mexico ($S = 325$) in a previous floristic phase, while in the quantitative phase, the number of taxa per sample ranged

Table 3. Statistical parameters for the calculated values of H' of benthic diatom assemblages from Laguna Guerrero Negro (LGN), Mexico. N = number of samples.

	N total	Mean	Median	Mode	Minimum	Maximum
Nov.	11	5.03	5.1	4.8	4.3	5.7
Jan.	10	5.21	5.35	5.9	4.2	5.9
Mar.	11	4.8	4.7	4.7	3.7	5.7
Jun.	11	4.83	4.7	4.4	4.3	5.6
LGN	43	4.96	4.9	4.7	3.7	5.9

from 64 to 119 in 11 of their 12 samples ($S = 251$). They attributed the high estimated values of species diversity (H') to the better represented taxa, rather than to overall species richness, although they did record a larger proportion (68.5%) of rare species (172), with 83 taxa accounting for 95% of the relative abundances. Also, Hernández Almeida and Siqueiros Beltrones (2008; 2012) estimated high mean values of $H' = 4.58$ and $H' = 5.13$ for epilithic and epiphytic assemblages, respectively. In the former case, 55 epiphytic taxa on macroalgae comprised 95% ($N=211$) of the RA. In contrast, in seagrass epiphytes, 25 taxa ($S = 115$) comprised 95% of the RA, with corresponding H' values of 3.42-4.15 Siqueiros Beltrones *et al.* (1985). Compared with the 117 taxa in this study, it seems evident why the values of H' in LGN were significantly higher. The above values, coupled with the distribution of relative abundances, species richness, the patchy distribution suggested by the new taxa, and the similarity values are typical of benthic diatom taxocoenoses from undisturbed environments. The high species diversity of benthic diatom assemblages observed for LGN is what we would expect to find in a protected area. However, Gray *et al.* (2106) observed that within-sample species richness could be significantly higher inside than outside protected areas, but they did not find consistency in their observations when using rarefaction-based species richness. In our study, the high number of benthic diatom taxa and their proportions suggest that analyzing the structure of benthic diatom taxocoenoses may prove useful as an alternative for direct rarefaction techniques that permits reliable comparison between different taxocoenoses. Moreover, community parameter values could be used for assessing environmental impact or as a reference for characterizing undisturbed conditions in marine environments (Siqueiros Beltrones *et al.*, 2014). Thus, on the basis of the present structure of the benthic diatom assemblages from LGN, no environmental impact, either natural or anthropogenic, is suspected at this lagoon, and we expect these characteristics to be similar for benthic diatom assemblages in other undisturbed subtropical coastal lagoons.

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