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The macrobenthic fauna of a former perennial and now episodically filled Mexican saline lake

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Abstract. Totolcingo (El Carmen), a large and now episodically filled playa lake in the easternmost portion of the Mexican Plateau, filled with water in 1993. Water persisted for just one month (May). Alkaline (pH $\approx$ 10), saline (K_{25} up to 30,000 μS/cm) waters, dominated by $NaHCO_3$ and Na_2CO_3, characterized the lake. The fauna was depauperate. The components of the fauna were *Ephydra (Hydropyrus) hians* Say (ephydrid), *Limnodrilus hoffmeisteri* Claparède (tubificid), and *Berosus* sp. (Coleoptera). The species in the lake were widely dispersed and typical inhabitants of saline lakes. Possible reasons for the depauperate fauna include (a) overall physical and chemical conditions, (b) unpredictable hydrology, and (c) the short (one month) inundation period prevented colonization.

Key words: episodic playa lakes, macroinvertebrates, Mexico, salt lakes, temporary waters

Introduction

The endorheic basin of Oriental lies within part of three Mexican states: Puebla, Tlaxcala and Veracruz. The central area of the basin is a large plateau located over 2,300 m.a.s.l. In the inner lowland are two large saline playa lakes: Laguna de Tepeyahualco or El Salado (2,312 m.a.s.l) in the north, and Laguna de Totolcingo or El Carmen (2,334 m.a.s.l) in the southern portion (Figure 1). They are very close to each other, and it is probable that they were connected in the past because both are delimited by the extent of Quaternary lacustrine saline soils. El Pinto volcano and thick deposits of volcanic clastics or sedimentary material now separate both lakes.

Tepeyahualco is now a large dry playa transformed for agricultural land use in spite of the high salt content of the soil. Due to its morphometry, Totolcingo Lake separates into separate segments while drying and local inhabitants have named some of the largest portions as different lakes (i.e., Villavicencio Lake, the westernmost portion, and Santiago Ovando Lake, the southernmost portion).

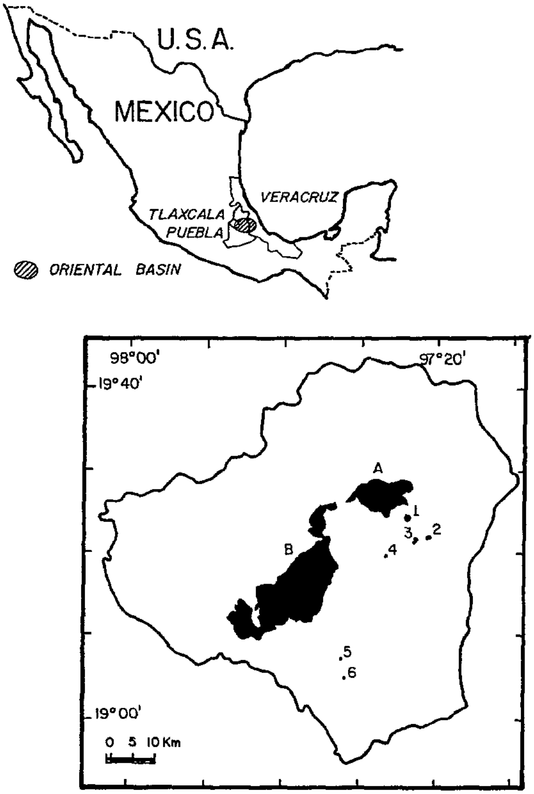

Figure 1. Location of Oriental basin, Tepeyehualco (A) and Totolcingo (B) playa lakes, and Alchichica (1), Quechulac (2), La Preciosa (3), Atexcac (4), Tecuitlapa (5) and Aljojuca (6) crater-lakes.

In spite of the immense groundwater reserves of the Oriental basin that led Knoblich (1978) to suggest that groundwater extraction of 2 m^3/sec would not jeopardize the aquifer, there was later discovered (Cruickshank, 1992; Reyes, 1979) two large underground drainage areas to other basins of lower altitude [i.e., the Perote leakage to the NE (7 m^3/sec), and the Sierra de Sultepec leakage to the SW (3 m^3/sec)]. This fact led the government to restrict groundwater extraction from the porous phreatic aquifer of Oriental. Unfortunately, human activities threaten these valuable aquatic resources by diminishing groundwater reserves through over-extraction and deforestation (Alcocer et al., 1997a). Nonetheless, natural aquifer processes and long-term climatic cycles must not be neglected as possible additional factors in explaining the evolution of Totolcingo Lake as an ephemeral body of water.

It seems that Totolcingo Lake has followed the decreasing trend of the Oriental basin's groundwater resources. Totolcingo used to be a shallow perennial lake until the end of the 1970s (Knoblich, 1978; J. Alcocer, pers. obs.), with large areal and volume changes. According to its hydraulic balance (precipitation rate, evapo-transpiration, etc.), Cruickshank (1992) estimated that Totolcingo Lake must have reached a maximum depth of 1.5 m. In the 1980s, the lake became ephemeral on a regular basis (Gasca, 1981; Reyes, 1979; J. Alcocer, pers. obs.), drying up in the dry season (November–April) and filling in the rainy season (May–October). Later, at the end of the 1980s and the beginning of the 1990s, the filling pattern became episodic (irregular and associated with events of unusual heavy rains) with the lake dry almost all the time. Since 1993, Totolcingo Lake has remained dry.

Since we had the opportunity to sample the lake the last time it was inundated (a very short period – May 1993), the aim of this paper was to investigate the macrobenthic fauna inhabiting the episodically filled saline Totolcingo Lake.

Study area

Totolcingo Lake is at the boundary of Puebla and Tlaxcala states, between 19°9.6′–19°26.3′ N and 97°33′–97°47.1′ W (Figure 2). When fully inundated, its surface area reaches 857.5 km^2, with a maximum length (NE–SW) of 27 km, a maximum width (NW–SE) of 13 km, and a wind-effective length of 15.5 km. The shoreline is 114 km long with 1.1 of shoreline development. If we consider the maximum depth as 1.5 m, as mentioned by Cruickshank (1992), then the calculated relative depth is 0.05%.

The nearest climate station to Totolcingo is located on the west side of the lake close to El Carmen village. Mean annual temperature and precipitation are 13.89 °C and 426.4 mm. On a basin-wide scale, mean annual precipitation rate ranges from less than 400 mm up to 500 mm, indicating a dry steppe climate. The dry season is characterized by scarce precipitation (75–100 mm), and wide temperature fluctuation (3–21 °C). Frosts are common during this season associated with calm days (>63%) (Fuentes, 1972; García, 1988; SPP, 1984a).

Totolcingo is located over Quaternary lacustrine saline soil (SPP, 1984b). Unconsolidated material, mostly zolonchak, with high groundwater concentration, impounds the lake. Soil is over 100 cm deep with a fine texture (62% clay, 26% silt, 12% sand), and low organic matter content (0.2%). Interstitial water is highly alkaline (pH = 10.4), and saline (50 mS/cm) (SPP, 1984c, 1984d).

Saline efflorescences containing a high percentage of soda, known as ‘tequezquite’ (from the nahuatl *tequixquitl*, salt or sweat, and *tlalli*, earth), have been recovered by villagers from the edge of Totolcingo probably since

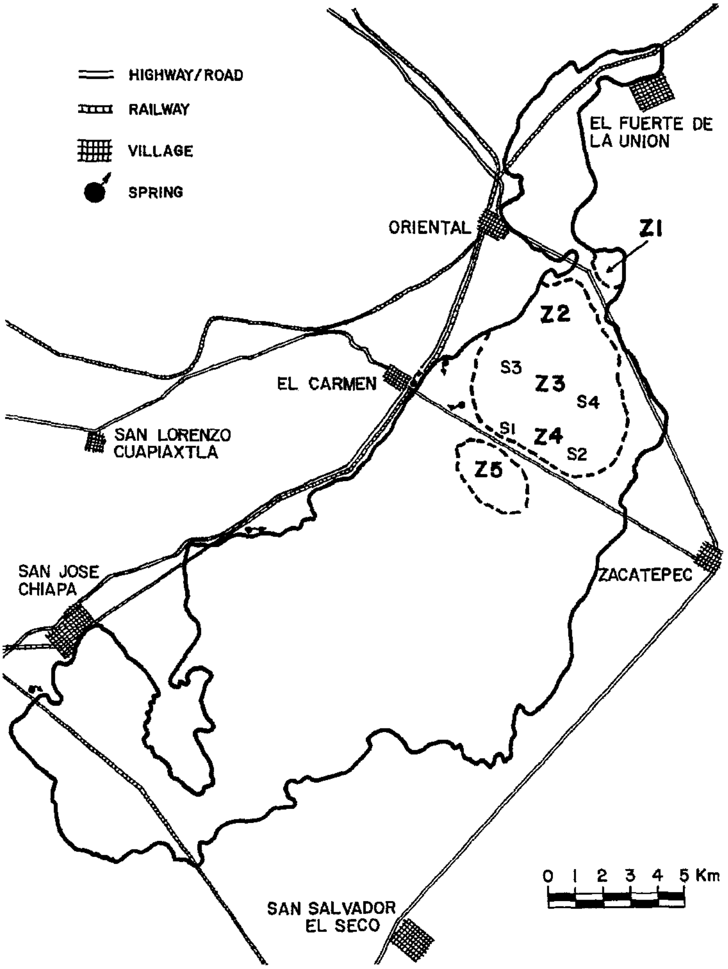

Figure 2. Position of the sampling zones (Z1–Z5) and sampling stations (S1–S4) in Totolcingo Lake (continuous line indicates coastline when fully inundated; dashed line shows approximate inundation area in May 1993).

pre-Columbian days (Ewald et al., 1994). The area is largely covered by halophytes (e.g., *Sporobolus* spp., *Suaeda* spp., etc.), and has no agriculture or forestry land use (Fuentes, 1972; SPP, 1984e). These dry playas are used for livestock pasture of donkeys, goats and sheep.

Totolcingo Lake is the easternmost record for the Mexican Plateau's endemic silverside *Chirostoma jordani* (Pisces: Atherinidae) (Barbour, 1973; Miller, 1986), presently catalogued as a threatened species (Espinoza et al., 1993). The Mexican neotenic tiger salamander, *Ambystoma tigrinum* (Amphibia: Ambistomatidae), was also found in the lake. Both organisms were once captured by local fishermen. Many salamander and fish skeletons were found along the edge of the lake among tequezquite efflorescences.

Hydrologically (SPP, 1984f), the lake is located in the Laguna de Totolcingo sub-basin (h), in the basin of the Atoyac river (A), included within the Hydrological Region RH18 (Balsas river basin). Rain water seepage rate is low ($< 5\%$) and accumulates over the highly permeable soils of Tepeyahualco and Totolcingo. Highly permeable lithology explains the poorly-developed surface hydraulic network of the Oriental basin. There are only ephemeral streams; some join with springs to feed Totolcingo Lake. The most important springs feeding the lake are El Carmen, Vicencio, Ojo de Agua or Estación Manantiales, and Lara Grajales (Gasca, 1981; Reyes, 1979).

The water-table is very close (less than one meter) to the surface in the central basin at Totolcingo Lake. Groundwater is derived mostly from snow melting from the high surrounding volcanoes such as Pico de Orizaba (5747 m.a.s.l), La Malinche (4461 m.a.s.l), and Cofre de Perote (4281 m.a.s.l) (Knoblich, 1973a, 1973b). Knoblich (1978) considered that the Totolcingo basin bottom was below groundwater mean level and thus water level of the lake fluctuated according to water-table changes. Reyes (1979) and Gasca (1981) suggested that the lake was formed through rainwater accumulation over a waterproof clay layer. Recently, Cruickshank (1992) found Totolcingo was fed by both groundwater and precipitation.

The basic water chemistry of El Carmen spring (24 °C), a well near the edge of Totolcingo Lake, and from the lake itself, is given in Table 1. Chemical composition of Totolcingo water seems to differ from year to year. Besides differences in the chemical solubility of different salts in water, changes in the quality of runoff waters and of subsoil geology may account for this variability. Knoblich (1973a) suggested that the high HCO_3 and SO_4 concentrations are derived from volcanic CO_2 and H_2S, respectively. Cl is leached from volcanic rocks, and NO_3 are pollutants coming from intensive pasturing. Dominant salts in Totolcingo Lake are as follows (Orozco and Madinaveitia, 1941; Reyes, 1979): $NaHCO_3 + Na_2CO_3 > Ca(HCO_3)_2 > Na_2SO_4 > NaCl > KCl > MgCO_3 > NaNO_3$.

Methods

Five sampling zones (Figure 2) were initially established according to apparently different habitat characteristics (i.e., water color, sediment texture, transparency, etc.). Midday measurement of depth, temperature, pH, conductivity (K_{25}), dissolved oxygen, percentage of dissolved oxygen, and redox potential were carried out with a calibrated Hydrolab Datasonde3/Surveyor3 multiparameter water quality data-logger.

Table 1. Main water chemical characteristics of El Carmen well and spring, and Totolcingo Lake.

Ion	Well[a]	Spring[a,b]	Totolcingo Lake				
(mg/L)	(11/1983)	(11/1983)	(1941)[c]	(08/1960)[d]	(10/1962)[d]	(1973)[e]	(09/1977)[f]
Na	56.3	89.7	1678.5	471.0	6064.3	502.1	114.3
K	3.1	9.7	N.D.	N.D.	N.D.	N.D.	14.2
Ca	36	20	0.0	9.0	18.0	6.4	23.1
Mg	76.8	15.5	N.D.	3.0	16.0	15.5	64.7
Cl	63.9	31.9	618.7	57.0	2220.0	180.0	64.1
SO_4	145.9	41.3	910.0	22.0	1140.0	192.0	60.1
HCO_3	317.2	262.3	50.8	50.0	904.0	820.0	389.4
CO_3	6	6	1642.0	330.0	880.0	N.D.	70.7
NO_3	3.7	2.5	N.D.	0.9	0.0	0.7	0.6
T.D.S.	709	479	N.D.	488	6098.3	1700	801
E.C.	0.9	0.58	N.D.	970	13100	N.D.	N.D.
pH	8.0	8.3	N.D.	10.15	10.0	N.D.	8.8

[a] SPP (1984f). [b] SPP (1984c). [c] Calculated from Orozco and Madinaveitia (1941) data. [d] CFE unpublished data. [e] Knoblich (1973a). [f] Calculated from Reyes (1979) data.
Abbreviations: T.D.S. = total dissolved solids; E.C. = electric conductivity (μS/cm); N.D. = not determined.

At each sampling zone, triplicate bottom samples were taken with a 225 cm^2 Ekman dredge. Three (Z1, Z2 and Z5) sampling zones showed no macrobenthic fauna, while Z3 and Z4 held an abundant fauna. Because of these differences, we decided to subdivide habitats further and sample two stations within Z3 and Z4: S1 and S2 corresponding to the lake edge Z4, and S3 and S4 corresponding to the mid-portion Z3. At each sampling station (S1–S4), triplicate samples were taken. Bottom samples were screened in the field and subsequently in the laboratory through a sieve pore size of 0.42 mm. The fauna was sorted, preserved in 70% ethanol, identified, counted, wet-weighed (roughly equivalent to biomass), and transformed to gC/m^2 (10% of wet-weight) according to Margalef (1983).

Results and discussion

The area of Totolcingo Lake was greatly reduced and partitioned (dotted lines in Figure 2) at the single sampling date (mean depth $\approx$ 0.1 m), with a small portion slightly north of Oriental-Zacatepec highway, and another one slightly south of El Carmen-Zacatepec highway separated from the main body of the lake. Z5 and Z1 were situated in these two small fragments of the lake respectively. Z2, Z3 and Z4 were located in the medial part of the lake

Table 2. Comparative physical and chemical parameters of Totolcingo Lake sampling zones.

Parameter	Z1	Z2	Z3	Z4	Z5
Depth (m)	0.1	0.1	0.1	< 0.1	0.1
Temp. (°C)	19.9	31.0	22.9	31.4	21.0
pH	9.96	10.14	10.04	10.0	9.37
K_{25} (μS/cm)	3416	30397	29070	10616	1949
D.O. (mg/L)	4.91	4.85	9.6	1.75	> 20
D.O. (% Sat.)	72.6	96.5	164	32.5	Over range[a]
Transp. (m)	0	To the bottom	To the bottom	To the bottom	To the bottom
Color	Dark brown	Light yellow	Light yellow	Light yellow	Greenish

[a] It was not possible to calculate the percentage D.O. because of the D.O. concentration surpassed the sensor detection range (0–20 mg/L).

between the two highways. Both highways and railways divide Totolcingo Lake into several (≈ 5) portions (Figure 2).

Sampling zones were shallow (≈ 0.1 m), warm (> 19 °C) and alkaline (pH > 9), but nonetheless differed in salinity, dissolved oxygen concentration, transparency, and color (Table 2). Northern and southern zones (Z1 and Z5) were freshwater; the central portion (Z2–Z4) was saline. There was a trend of increasing salinity from the lake edge (Z2) toward the 'deeper' central zone (Z4) where salts accumulate as water evaporates. Fresher parts (Z1 and Z5) were colder and less alkaline (lower pH) than saline sites (Z2–Z4).

Dissolved oxygen concentration fluctuated widely between sampling zones. Although undersaturated, Z1 did not have too low a dissolved oxygen concentration. Z2 and Z3 were almost saturated or oversaturated because of their high temperature and salinity. Z4 displayed the lowest dissolved oxygen concentration; this was probably associated with the large density of organisms (high respiration rates) and decomposing organic matter (ephydrid exuviae). Oversaturation was measured at Z5 and was presumably associated with high primary production rates of filamentous algae. But at Z1, where transparency was null, water was totally clear although colored. The deep sepia or dark brown color at Z1 was presumably derived from the presence of colloidal silica or humic substances, and at Z5 the greenish color to algae. The yellowish color of Z2–Z4 was similar to other soda alkali lakes (i.e., Texcoco).

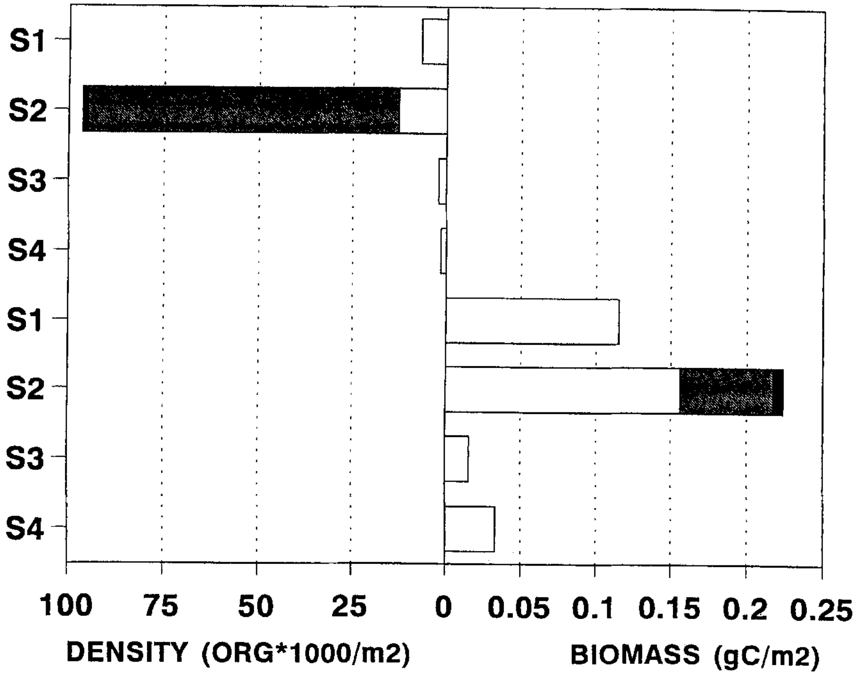

Figure 3. Abundance (thousands of organisms/m^2) and biomass (gC/m^2) of macrobenthic fauna in sampling stations (S1–S4) of Totolcingo Lake. (*Ephydra hians* = solid white lines, *Limnodrilus hoffmeisteri* = cross-hatched, *Berosus* sp. = solid black).

The benthic substrate at all sites was homogeneous, consisting of clay and lacking aquatic macrophytes The wind-mixed shallow waters lacked vertical thermal stratification.

Three widely distributed species formed the benthic macroinvertebrates community of Totolcingo Lake: the alkali fly *Ephydra Hidropyrus hians* Say (Diptera: Ephydridae), the blood worm *Limnodrilus hoffmeisteri* Claparède (Oligochaeta: Tubificidae), and the water beetle *Berosus* sp. (Coleoptera: Hydrophilidae). All have been reported from many other saline lakes (e.g., Colburn, 1988; Galat et al., 1981; Hammer et al., 1990; Timms, 1983, 1993; Timms et al., 1986; Tudorancea and Harrison, 1988; Williams and Kokkinn, 1988; Williams et al., 1990).

L. hoffmeisteri density (ind/m^2) was greatest, but the standing stock biomass of *E. hians* was higher (gC/m^2) due to the larger size of the flies. The beetle had the lowest density and biomass (Figure 3). Only the alkali fly was widespread, found in all twelve samples taken [four sampling stations (S1–S4), three replicates each], while the bloodworm and the beetle were captured in just one (S2).

Ephydrids are commonly found worldwide inhabiting salt lakes. They can withstand high salinity and temperature and low dissolved oxygen concentrations (Stephens, 1990). *Ephydra hians* has been reported by Herbst (1988) living in salinities ranging between 20–30 g/L (Abert Lake, Oregon) and 80–90 g/L (Mono Lake, California). Stephens (1990) reported *E. hians* in the Great Salt Lake, Utah, when salinity reached between 20–26 g/L. However, Hammer et al. (1990) found *E. hians* at 118 g/L in Little Manitou, Canada. *Ephydra hians* lives in perennial, temporary or episodic, and mostly soda lakes (Na_2CO_3, $NaHCO_3$, NaCl), within a wide salinity range. *Ephydra hians* grows abundantly in a small alkaline soda pond (Tecuitlapa Norte) within Tecuitlapa Lake's crater (unpublished information). A few larvae of what appeared to be *E. packardi* have been found in Alchichica crater-lake (Alcocer, 1995; Alcocer et al., 1993). Since *E. hians* is abundant in other Oriental basin water-bodies (i.e., Totolcingo and Tecuitlapa), it is possible the specimens from Alchichica were *E. hians* as well (Alcocer et al., 1997b).

Limnodrilus hoffmeisteri is a cosmopolitan species. Eutrophic lakes favour massive oligochaete development, with food provided by the bacteria growing on sediments (Prat, 1993); *L. hoffmeisteri* prefers nutrient-rich lakes (Lang, 1984; Milbrink, 1980). It is probable that Totolcingo's worms feed on decomposing organic matter colonized by bacteria such as algal mats and exuviae. *Limnodrilus hoffmeisteri* is the dominant organism of the littoral macrobenthos of the six crater-lakes of the Oriental basin, making up over 90% of the total abundance (Alcocer et al., 1993, 1997b; Alcocer, 1995). Although it is unusual to find numerous oligochaetes in the littoral area of saline lakes, the species also occurs in other saline and freshwater crater-lakes of the basin (Alcocer, 1995).

Hydrophilid beetles such as *Berosus* are characteristic of athalassohaline waters. This genus, although widely reported from mesohaline lakes, is numerically unimportant (Williams et al., 1990). Herbivorous in the adult stage (McCafferty, 1981; Williams and Felmate, 1992), *Berosus*, as well as *E. hians*, consumes algal mats. *Berosus* has been reported from the Oriental basin (Alcocer et al., 1993, 1997b), inhabiting the littoral zone of Alchichica, La Preciosa and Tecuitlapa crater-lakes (Alcocer, 1995).

The abundance and biomass of Totolcingo benthic macroinvertebrates varied widely between sampling stations (Table 3, Figure 3). This fact is undoubtedly related to the patchy distribution of benthic organisms (Herbst, 1988), and food availability. There were significant differences ($P < 0.05$) among sampling station abundances and biomasses (ANOVA, ln+1 transformed data). Sampling stations S1 and S2 (Z4) held the highest densities and biomasses, while S3 and S4 (Z3) had the low values. Dense patches of algal mats developing in Totolcingo Lake's edge and/or at some distance from

Table 3. Macroinvertebrate fauna of Totolcingo Lake [first row abundance (org/m^2), second row, in brackets, biomass (gC/m^2)].

Station	Species	AVG	STD	MAX	MIN
	E. hians	6789	4239	10183	2037
		(0.1154)	(0.0470)	(0.1426)	(0.0611)
S	*L. hoffmeisteri*	0	0	0	0
		(0)	(0)	(0)	(0)
1	*Berosus* sp.	0	0	0	0
		(0)	(0)	(0)	(0)
	Total	6789	3461	10183	2037
		(0.1154)	(0.0384)	(0.1426)	(0.0611)
	E. hians	12899	5879	16293	6110
		(0.1561)	(0.0655)	(0.2037)	(0.0815)
S	*L. hoffmeisteri*	82145	142280	246436	0
		(0.0611)	(0.1058)	(0.1833)	(0)
2	*Berosus* sp.	1358	1921	4074	0
		(0.0068)	(0.0096)	(0.0204)	(0)
	Total	96402	113291	256620	16293
		(0.2237)	(0.0436)	(0.2842)	(0.1833)
	E. hians	2045	1135	3289	1067
		(0.0156)	(0.0093)	(0.0262)	(0.0089)
S	*L. hoffmeisteri*	0	0	0	0
		(0)	(0)	(0)	(0)
3	*Berosus* sp.	0	0	0	0
		(0)	(0)	(0)	(0)
	Total	2045	927	3289	1067
		(0.0156)	(0.0076)	(0.0262)	(0.0089)
	E. hians	1452	530	2044	1022
		(0.0335)	(0.0403)	(0.0800)	(0.0084)
S	*L. hoffmeisteri*	0	0	0	0
		(0)	(0)	(0)	(0)
4	*Berosus* sp.	0	0	0	0
		(0)	(0)	(0)	(0)
	Total	1452	433	2044	1022
		(0.0335)	(0.0329)	(0.0800)	(0.0084)

shore could explain this. Algal mats, ephydrid exuviae and associated bacteria provide the food that nourishes *E. hians*, *L. hoffmeisteri* and *Berosus*; adult flies also deposit their eggs over the algae (MacCafferty, 1986).

Alkali fly abundance ($\approx$16,000 org/m^2) is lower than that reported by Herbst and Bradley (1993) from Mono Lake soft bottom (50,000 org/m^2). Totolcingo sediment is also soft and muddy but is dominated by clay and silt. Rock and plant substrates are preferred for aggregation and persistence of ephydrid immature stages, as in Mono Lake where abundances reach 1,000,000 org/m^2 (Herbst and Bradley, 1993). Biomass ranged from 0.0156 to 0.1561 gC/m^2, lower than that recorded in Abert Lake (0.7–1.5 gC/m^2) and Mono Lake (0.4–3.6 gC/m^2) by Herbst (1988) and Herbst and Bradley (1993).

Totolcingo Lake was thus entirely populated by widespread forms, supporting Williams and Kokkinn's (1988) findings on the fauna of episodically filled salt lakes. As in Lake Gnotuk, Australia (Timms, 1981), and Lake Ureg, Mongolia (Egorov, 1993), with four and two species each, respectively, three species populated Totolcingo Lake. This is a low value when compared to values in the perennial Atexcac (21) and Alchichica (44) saline crater-lakes (Alcocer, 1995; Alcocer et al., 1997b).

Additionally, it is important to consider the short period Totolcingo Lake remained inundated (i.e., one month – May 1993). A shortened inundation phase should reduce or prevent the possibilities for the lake to be colonized, thus reducing species richness. In spite of this, we sampled *E. hians* as larvae, pupae and adults, and sexually mature *L. hoffmeisteri*, suggesting either that there had been time enough to complete reproductive cycles, or the presence of a close dispersion centre that allowed rapid colonization.

There are two important *loci* within the local endorheic drainage basin that could act as potential dispersion centres for Totolcingo colonization. The closest *loci* are the springs flowing along the west coasts of the lake, three at the base of a small hill near El Carmen, and one in Estación Manantiales. Other springs (i.e., Vicencio, Ojo de Agua, and Lara Grajales) are already dry. Two of the three springs of El Carmen are freshwater and are now channelized all the way down to El Carmen town as a source of drinking water. The third spring, named 'azufroso' (sulphur ladden), is the only one which now scarcely flows first into a pool and from there to the lake. Estación Manantiales spring has been dammed and drains only when full during the rainy season.

Although there are fishes inhabiting the springs [the poeciliids *Heterandria bimaculata,* and *Xiphophorus variatus evelinae*, and a new (?) cyprinid species (H. Espinoza, pers. comm.)], none of these is of the same species (*Chirostoma jordani*) found by Alvarez (1950) in Totolcingo Lake. Ambystomatid salamanders (*Ambystoma tigrinum*) and the alkali fly (*Ephydra hians*) are also absent in the springs. On the other hand, the oligochaete (*Limnodrilus hoffmeisteri*) and the beetle (*Berosus*) were abundant in both places.

The six crater-lakes (Alchichica, Atexcac, La Preciosa and Quechulac in Los Llanos de San Juan, and Aljojuca and Tecuitlapa in Los Llanos de San Andrés) are the second potential dispersion centres from which organisms could be carried by the wind, waterfowl, or other means. These crater-lakes are inhabited by closely allied species of fish (*Poblana alchichica, P. squamata, P. Letholepis*, Alvarez 1950) and salamander (*Ambystoma taylorii, A. tigrinum*-like, Brandon et al. 1981).

Oligochaetes disperse easily throughout drainage systems, but passive and accidental overland transport presumably is most effective during the cocoon stage. Some other oligochaetes are known to encyst. Hydrophilid beetles also form hard cocoons. The resistant mucus cyst stage and cocoons may be easily transported from place to place. Adult beetles and alkali flies colonize other places by flying (Pennak, 1978).

Totolcingo, which is now an episodically-filled salt lake, has been populated by three widely dispersed species. Possible reasons for its depauperate fauna include (a) overall physical and chemical conditions (i.e., high salinity, temperature, and pH, low dissolved oxygen concentrations, habitat homogeneity lacking aquatic macrophytes and the absence of substrate and water column stratification), (b) unpredictable filling patterns, and (c) short (one month) inundation periods inhibiting colonization.

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