Hydrogeochemical and biological characteristics of cenotes in the Yucatan Peninsula (SE Mexico)

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Abstract

Cenotes (sinkholes) are the most peculiar aquatic ecosystem of the Yucatan Peninsula (SE Mexico). They are formed by dissolution of the carbonate rock in the karstic platform of the Yucatan Peninsula. A wide morphological variety is observed from caves filled with ground water to open cenotes. In some cenotes, particularly those close to the sea, underneath the fresh water one finds saltwater, where meromixis can take place. This occurs because in the Yucatan Peninsula there is a thin lens (10s of meters thick) that floats above denser saline water. In these cenotes, a relative enrichment of sodium related to calcium is observed while conductivity increases. In contrast, a higher increase of calcium associated to sulfate is observed in cenotes located in SE Yucatan Peninsula. A marked vertical stratification of the water is established during the warm and rainy season of the year (May–October). In cenotes with good hydraulic connection with the rest of the aquifer, the water remains clear during most of the year. However, cenotes with poor hydraulic connection with the aquifer are characterized by turbid waters and very low light transparency. In this group of cenotes, the water column contains a high concentration of chlorophyll (mostly due to chlorophyceans, cyanobacteria, diatoms and dinoflagellates); the hypolimnion and the sediment are rich in organic matter and anaerobic bacteria mediated biogeochemical processes are dominant. The upper part of the cenotes walls is well illuminated and covered by a rich microbial mat. Floating macrophytes may also occupy part of the water surface in oligotrophic cenotes. A great variety of food web paths are represented in the habitats occurring in the cenotes, in which few trophic levels are involved. A few endemic species (crustaceans and fishes) have been reported from cenotes found in the Yucatan Peninsula. Because of the high organic matter input (alochthonous) and production (autochthonous) and the low water flow, cenotes can be considered heterotrophic systems.

Introduction

Regional studies on the ecology of aquatic ecosystems have been constant during the development of limnology in many countries (Margalef, 1983). There is still a need to continue and to increase the scientific knowledge about peculiar ecosystems and unexplored limnological regions (Gopal & Wetzel, 1995; Wetzel & Gopal, 1999). Classifying the observed characteristics and typifying the water masses in relation with other already known aquatic ecosystems are major objectives of this type of studies (Hutchinson, 1957).

The Yucatan Peninsula (SE Mexico) is subject to rapid urban development, explosive in the coastal zone, particularly along the Caribbean littoral; proper management of this large ecosystem is imperative and freshwater sustainability as well as coastal water quality are subjects of major concern. The development of limnology in the Yucatan Peninsula is increasing. Up to date, at least 100 papers have been published on fresh and saline waters, but our knowledge is nonetheless sparse and fragmentary (Alcocer & Escobar, 1996; Comín et al. 1996; Herrera-Silveira et al., 1998). Part of this limnological delay (in comparison with other regions) is due to the isolation, size and difficult access to most Yucatan Peninsula inland aquatic ecosystems.

Because of its karstic nature, there are no rivers in the Yucatan Peninsula, and only 12 lakes with water volume higher than $5 \cdot 10^5$ m^3 exist, none of which occurs in the northern half (Doehring & Butler, 1974; Alcocer & Escobar, 1996). Many solution features form small ponds (sinkholes) (in Spanish *cenotes*, from the Maya word *ts'onot*), caves, and minor cavities (named locally *sartenejas*), all of them caused by the percolation of CO_2-laden water through limestone (Alcocer & Escobar, 1996; Steinich, 1996). They all are solution lakes in the terms described by Hutchinson (1957). More than 7000 solution features have been mapped just in northwest Yucatan Peninsula (Steinich, 1996).

This paper is an overview of the general limnological characteristics of cenotes in the Yucatan Peninsula. The aim is to present a classification, their characteristics and an interpretation of their functional ecology.

General characteristics of the study area

The Yucatan Peninsula is located between 19° 40′ and 21° 37′ N and 87° 30′ and 90° 26′ W, surrounded by the Gulf of Mexico and the Caribbean Sea (Fig. 1). It extends over an area of 39 340 km^2, representing 2% of the surface of the Mexican Republic. The climate has three characteristic seasons: (1) warm and dry season (March–May), (2) winter storm season with occasional short showers (November–February), and (3) rainy season from June to October.

Winds are highly seasonal, being strongest from November to February while calm condition lasts from January to October. Mean annual air temperature is 26.1 °C with a minimum of 5 °C and a maximum of 42.5 °C. Annual rainfall varies from 760 mm.yr^{-1} to 1198 mm.yr^{-1} in the north portion and from 1138 mm.yr^{-1} to 1440 mm.yr^{-1} in the southern portion. The highest precipitation occurs in September, with an average of 232 mm.

The Yucatan Peninsula is a calcareous platform which originated in the Cenozoic that averages ten meters above sea level with just one small prominent Sierra in the center of the Peninsula, where a maximum altitude of 150 m is reached (Stringfield & LeGrand, 1974). The Peninsula attained its present shape in the late Pliocene (López Ramos, 1975); however, large eolianites were deposited on the coast during the Holocene, and reefs are still developing in the north and east (Ward et al., 1985). There are Pleistocene marine deposits in the east, north and northeast coasts of the Peninsula, in Laguna de Términos (SW) and some interior paleolakes. In Campeche, the Eocenic terrain reaches the coast (López Ramos, 1975). The maximum interglacial sea level was at the time 30 m higher than today (Back, 1985). Present sea level was attained only 5500 years ago (Ward et al., 1985); in the early Holocene sea level was some 100 m lower than today (Buskirk, 1985).

Wilson (1980) classified the Peninsula in 14 physiographic districts. Eight of them are represented in the northern half (Fig. 1), where cenotes are more abundant: (1) the coastal zone, geologically the youngest, where most of the anchialine cenotes appear; (2) the district of Mérida, within the Ring of Cenotes (Marín, 1990); (3) the district of Chichén Itzá, with more cenotes and a coarser relief than Mérida; (4) the Puuc district, on the Sierrita de Ticul; (5) the Bolonchén district, with a less developed karst landscape; (6) the district of Cobá, with geologic faults, some of them filled with water; (7) the district of Río
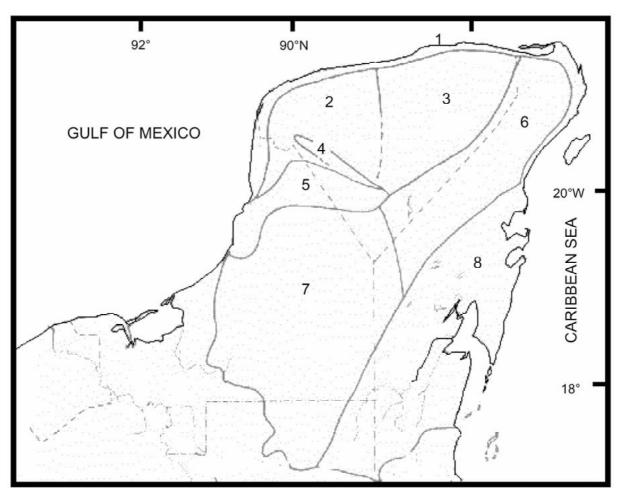
Figure 1. Map of the Yucatan Peninsula, with the physiographic districts within the study area (modified from Wilson, 1980).**1**, coastal zone. **2**, Mérida. **3**, Chichén Itzá. **4**, Puuc. **5**, Bolonchén. **6**, Cobá. **7**, Río Bec. **8**, Río Hondo.

Bec, partly outside the study area, and differing from it by a higher altitude and the presence of rivers; and (8) the Hondo river district (basin), partly outside the study area.

The Yucatan Peninsula receives on the average $172\,158 \times 10^6$ m³ of rainwater per year. Average annual rainfall increases from the northwest (500 mm) towards the southeast (2000 mm). About 85% of the precipitation is evapotranspired. The aquifer of the Yucatan Peninsula is a karstic aquifer characterized by its high permeability. Karst features such as underground channels and caverns (cenotes) are widely present throughout the Peninsula (Steinich et al., 1996). The aquifer is unconfined, except for a narrow band parallel to the coast, where it is confined (Perry et al., 1989). Ground water flows through a dual-porosity medium: flow occurs through the rock matrix and through frac-tures, joints and dissolution features. Discharge of the aquifer occurs both as diffuse flow throughout the coast and as springs (found both inshore and off-shore). Many cenotes in the North of the Peninsula are located along a semicircle, known as the Ring of Cenotes, which is centered in Chicxulub (a village in the north coast, on the east of Progreso) (Marín et al., 1990). It has been proposed that this distribution of cenotes is associated with the Chicxulub Impact Crater (Sharpton et al., 1992, 1993). The density of cenotes along the ring varies between one and a few cenotes per kilometer (Marín et al., 1990). This zone has been shown to act as an underground river or groundwater trough (Marín, 1990; Velázquez, 1995; Perry et al., 1995; Steinich & Marín, 1996; Steinich et al., 1996).

The two intersections of the ring with the coast give rise to a high density of submarine springs (Marín

et al., 1990). The water table throughout the Yucatan Peninsula is less than two meters above mean sea level (Marín, 1990; Steinich & Marín, 1996). The hydraulic gradient is very low, on the order of 7–10 mm per kilometer (Marín, 1990). As a result, the aquifer is a thin freshwater lens that floats above denser, saline water. Steinich & Marín (1996) have shown that salt water is found more than 110 km from the coast. This salt water has a dual origin: salt water intrusion and dissolution of evaporites (Perry et al., 1995; Velázquez, 1995).

Parallel to the coast, in the 'ciénagas' or wetlands, another type of cenote – locally known as 'petén' – is found where ground water dissolves the limestone as it travels along the flow lines. When it approaches the coast, CO_2 escapes, and as a result the groundwater precipitates calcium carbonate sealing the intergranular space in the rocks. This is the process that is confining the aquifer parallel to the coast (Perry et al., 1989). However, within this area, there are large cenotes that formed when sea level was lower than today. Since these cenotes range between 5 and 15 m in diameter, the precipitation of calcium carbonate can not seal these large cavities. Thus, they act as artesian springs (Marín et al., 1988). As brackish water is discharged into the ciénaga, it mixes with the waters from the swamp, creating radial patterns in salinity which in turn are colonized by different mangrove species that can tolerate different salinity concentrations. The 'petenes', when observed from the distance, show up as islands in the middle of the 'ciénaga'.

There are 16 kinds of vegetation characterizing the Peninsula, the most widely distributed are: the low caducifolium forest, medium subcaducifolium forest and medium subperennifolium forest, the two first covering the north and central regions of the Yucatan State and the other covering mostly Campeche and Quintana Roo. Redzine and litosol are among the dominant soils than cover the Peninsula (Flores & Espejel, 1994).

Origin and types of cenotes

The main process in the formation of cenotes is the dissolution of the limestone by carbonic acid. In areas where there is a significant soil cover, the CO_2 concentration may increase by orders of magnitude (in the Yucatan Peninsula it takes place towards the southeast), resulting in waters that are more aggressive (i.e. with a higher capacity to dissolve the rocks). The CO_2 involved in the process may not be alochthonous, but organically generated *in situ* (Gaona-Vizcayno et al.,

1980). A second process that can contribute to the dissolution of the carbonate rocks is the mixture of fresh and salt water, which enhances the reactivity on aragonite and calcite (Stoessel et al., 1989). The third process is local and of larger importance. A high concentration of H_2S has been observed in the water of several cenotes as a consequence of the reduction of the accumulated organic matter. The H_2S may, then, dissolve the rock within these horizons (Stoessel et al., 1993). Microbial activity associated to all these processes contributes to the formation of cenotes (Martin & Brigmon, 1994).

We propose here that in younger (lotic) cenotes, the water is well interconnected with the ground water through fractures, and dissolution features, and its residence time is short. Older cenotes have a lentic condition with slow flow and turnover through sedimentation and blocking of the water source and the siphon. Although we may recognize that groundwater continues to flow through the cenote, many of the pathways are blocked, and the exchange of ground and free-overlying water in the cenote is restricted. Two processes may restrict groundwater flow to and from the cenote: roof or wall collapse and sedimentation.

This idea is proposed on the marked geochemical changes observed. Thus, it is suggested that the lentic cenotes are fed primarily by diffuse flow (low groundwater velocities, thermal stratification and other processes) and that the lotic cenotes are primarily fed by ground water flowing through fracture and dissolution cavities. Lotic cenotes have clear waters, clean, sandy or rocky bottoms, and a homogeneous, well-oxygenated water column. Lentic or near-lentic cenotes are turbid, thermally stratified; the surface water layer is alkaline, oversaturated with oxygen, while water near the bottom is acid, devoid of O_2, and with H_2S.

The cenotes have been classified according to the stages in the process described above (Hall, 1936) as: caves, jug-shaped, cylindrical, and plate-shaped cenotes. Navarro-Mendoza (1988) and Marín et al. (1990) have suggested differences between coastal and inland cenotes. The former are shallower, 3–35 m deep; their walls are rocky, often with compacted organic matter among mangrove roots. The latter with depths greater than 100 m, and walls with up to 20 m high. In both cases the diameter may go from a few meters to more than 100 m.

The 'petenes', and deep inland cenotes, whose walls penetrate below the salt/freshwater interface, have water that is stratified based on density. This sa-

line stratification produces a meromixis, that is, the partial mixing of the water column, in contrast to the holomixis, a thorough mixture of the water mass, usually the case in lotic cenotes. Between the freshwater layer in the surface, the mixolimnion, and the saline, denser, bottom layer, the monimolimnion, an abrupt transition zone occurs, the halocline. There could be also thermal stratification (i.e. thermocline). Herrera-Silveira & Comín (2000) showed that in both, lotic and lentic, types of cenotes a thermal stratification can be established during the dry and rainy seasons (March–October), while the water column remains mixed during the winter storms season (November–February). The length of the thermal stratification in lotic cenotes could vary from hours up to several days according to the sheer velocity, the water column depth, and other factors. Differences between cenotes related to the thermocline depth may be related to the transmission of convective heat between atmosphere and water.

Under chemical stratification, the monimolimnion may be stagnant and in anoxic conditions, or it may slowly flow according to groundwater input, tides and storms through tunnels and crevices. Most of the cenotes found throughout the Peninsula will usually occur in an intermediate position between these two extreme types described (Van der Kamp, 1995).

Physical and chemical characteristics of the water in the cenotes

The temperature is stable in lotic cenotes and it is controlled by the geometry of the flow system. Thermal stability reflects the constancy of water temperature below depths of 10 m (Van der Kamp, 1995). In lentic cenotes there are horizontal and vertical variations along the year. Mean water temperature in cenotes, 24–29 °C, is similar to the mean air temperature (Alcocer et al., 1998).

The pH is also homogeneous and stable in lotic cenotes, generally with acid values (<7). In lentic cenotes, there is a pH-gradient along the water column. The epilimnion is usually basic. The hypolimnion is acid, because respiration predominates, as well as the formation of H_2S under anoxic conditions. Thus, the range of pH goes from 6.7 to 8.0 in coastal cenotes, and up to 8.6 in inland cenotes (Hall, 1936).

Alkalinity fluctuates widely in cenotes, because of the variable input of meteoric water, rich in carbonates and bicarbonates (up to 696 mg l^{-1} $CaCO_3$), and of rainwater, which lowers the concentration of these ions by dilution and by neutralization with humic acids and tannins from the mangrove (Navarro-Mendoza, 1988; Alcocer et al., 1998).

When water enters the water table, it acquires CO_2 from the soil and from the oxidation of dissolved and particulate organic matter. These processes decrease the concentration of O_2 and increase acidity, which in turn is neutralized by solution of the limestone. The total dissolved solids in rainwater are concentrated by evapotranspiration and, combined with the dissolution of minerals found in the soils, they contribute to raise the amount of total dissolved solids (TDS) in the cenote water (Van der Kamp, 1995). TDS in cenotes have a uniform concentration, typical of freshwaters (<3 g l^{-1}), except in those cenotes with marine influence. Conductivity measured in a number of cenotes (Fig. 2) ranged between 42.5 and 7390 μS cm^{-1}. Salinity of ground water in the Yucatan Peninsula lies within 0.4 and 2.9 g l^{-1} (Velázquez, 1995). In meromictic cenotes, water may go from fresh in the mixolimnion to marine in the monimolimnion. The thickness of the halocline increases in cenotes closer to the coast, because of the mixture produced by the friction between the freshwater mass going to the sea and the marine water advancing inland.

A study of 71 inland water-bodies distributed throughout the Yucatan Peninsula showed the strong influence of the process of rock dissolution on the major ionic composition of the water in the Yucatan Peninsula (Comín et al., 1996). However, the two processes of salt enrichment can be important (Fig. 3). One process, observed in localities with a higher enrichment of sodium compared to calcium, is associated with the direct influence of seawater – via groundwater – in localities close to the coast. The second process occurs in places located in the southeastern zone of the Peninsula, which includes increasing values of TDS associated with the dissolution of sulfate-rich deposits. In this case, the enrichment in calcium relative to sodium takes place as the total amount of dissolved salts increases (Herrera-Silveira et al., 1998). In some cenotes, the sulfate concentration is high (up to 2400 mg l^{-1}) due to gypsum beds, but in others it lies close to 170 mg l^{-1}; precipitation may lower it to 30 mg l^{-1}. Chloride increases from 70 mg l^{-1} in distance from the sea (Hall, 1936) to 16 200 mg l^{-1} in cenotes with marine influence.

The presence of organic matter defines the geochemical equilibrium, as shown by the recristalization observed in cenotes with low organic activity, but absent from those with high organic activity (Gaona-
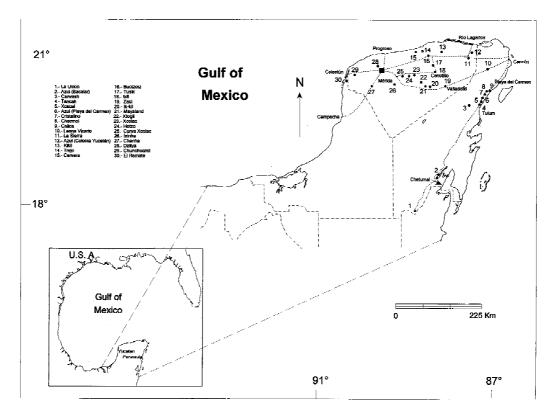
Figure 2. Localization of the Yucatan Peninsula and some of the cenotes sampled.

Vizcayno et al., 1980). Its concentration depends on the lentic or lotic character of the cenote as well as on the size of the opening, because it determines how much alochthonous matter can enter the cenote transported by rainwater. *In situ* photosynthetic production depends on exposure to light, and thus varies according to the type of cenote. Lentic cenotes easily increase their trophic state, favoring the production of large amounts of organic matter (e.g. as phytoplankton). The process brings along an increase in pH, turbidity, dissolved oxygen concentration at the surface and anoxic, acid conditions at the bottom of the cenote.

Nutrient concentration in lotic cenotes is expected to be lower than in lentic ones, because of the difference in turnover rate. On the other hand, vertical stratification concentrates nutrients in the hypolimnion, where remineralization occurs, and impoverishes the epilimnion, where primary producers consume the nutrients; in lotic cenotes, the nutrient-rich waters at the bottom are carried to the surface, where they are once again available to primary producers.

Phosphorus is scarce in cenotes, because the calcareous rocks favor its co-precipitation with calcium, abundant in the karstic environment. High concentra-

Table 1. Averages (AVG), standard error (SE), minims (MIN) and maxims (MAX) of limnological variables analyzed in 30 cenotes (Fig. 2) once during each of the seasons of the year ('nortes', dry and rainy) (from Herrera-Silveira et al., 1998)

	Avg	SE	Min	Max
Temperature (°C)	26.4	0.3	22	33.5
Suspended. Solids (mg l^{-1})	59.6	9	0.3	590.7
DO (mg l^{-1})	4.46	0.3	0.82	10.6
Conductivity (μS cm^{-1})	1645	150	42.5	7390
pH	7.5	0.08	6.31	10.36
Alkalinity (meq l^{-1})	4.33	0.2	0.8	8.51
Cl^{-} (meq l^{-1})	2.47	0.5	0.11	33.33
SO$_4$$^{-}$ (meq l^{-1})	2.12	0.8	0.06	42.2
Ca^{++} (meq l^{-1})	6.93	0.8	0.99	36.5
Mg++ (meq l^{-1})	3.97	0.5	0.29	23.05
Na^{+} (meq l^{-1})	5.96	1.2	0.20	75.52
K^{+} (meq l^{-1})	0.27	0.06	0.03	3.48
N–NO$_3$$^{-}$ (μM)	63.3	8.3	0.52	500
N–NO$_2$$^{-}$ (μM)	0.97	0.2	0.02	15
N–NH$_4$$^{+}$ (μM)	6.57	1.4	0.09	84.9
SRP (μM)	1.59	0.4	0.02	20
SRSi (μM)	227.3	19.7	1.48	550
Chlorophyll-a (mg m^{-3})	11.47	2.6	0.11	97.4

tion of nutrients is frequent near urban areas. Concentrations of soluble reactive P range from 0.02 to 20 μg l^{-1}, with a mean of 1.59 μg l^{-1} (Herrera-Silveira et al., 1998). Localities can be divided in two types based on nitrate concentration (Pacheco & Cabrera, 1997). Close to urban developments, farms, and agriculture, high nitrate concentrations have been observed. In areas with little human activity, nitrates have been observed to be more abundant affecting coastal cenotes than in inland ones. The nitrates of the latter environments come mostly from the surrounding vegetation. In contrast, nitrites and ammonia are scarce (Sánchez et al., 1998). Minimum and maximum concentrations of micronutrients observed in a number of cenotes are summarized in Table 1 (Fig. 2).

Biota of the cenotes

Bacterioplankton, phytoplankton and primary production

Our knowledge of the bacterioplankton in cenotes is sparse (Edler & Dodds, 1992; Brigmon et al., 1994), however available information from cenotes and anchialine caves of Quintana Roo shows extremely low bacterioplankton densities even for oligotrophic environments (Alcocer et al., 1999). Chemoautotrophic bacteria are associated to the bottom, walls, and the halocline. Their appearance is a white-grayish mat or floating filament (Brigmon et al., 1994; Martin et al., 1995).

Cenotes of the Yucatan Peninsula can be considered as islands of aquatic life. A dense and tall vegetation made of big trees (e.g. *Ficus cotinifolia*) is frequently found in inland cenotes (Reddell, 1981), while 'petenes', near the coast, may be surrounded by mangrove, especially *Rhizophora mangle*. The small mangroves tree *Conocarpus erecta* and the emergent macrophytes *Cladium jamaicense* and *Phragmites australis* may also border 'petenes'. Other aquatic macrophytes observed in cenotes are *Typha domingensis*, *Acrostichum danaefolium*, *Nymphaea ampla*, *Sagittaria lancifolia*, *Cabomba palaeformis*, *Sesbania emerus*, *Rhabdadenia biflora*, *Thrinax radiata* and *Bravaisia tubiflora*. In shallow cenotes, the algae *Chara* is common (Esquivel, 1991; Sánchez et al., 1991; Cabrera-Cano & Sánchez-Vázquez, 1994).

The phytoplanktic flora of cenotes is largely unknown (Hernández & Pérez, 1991) compared to other aquatic ecosystems of the world. However, a relatively long list of species has been compiled during the last decade (Table 2). Almost 150 species have been
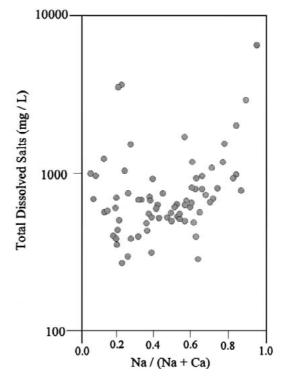

Figure 3. Total dissolved solids vs. the Na(Na + Ca) ratio (from weight data) for the localities studied in the Yucatan Peninsula.

recorded in sinkholes, where chlorophyceans, cyanophyceans and diatoms were dominant (López-Adrián & Herrera-Silveira, 1994; Díaz-Arce, 1999; Sánchez et al., 2002). The species composition is quite similar to the one found in other tropical and temperate lakes (Sánchez-Molina, 1985; Esquivel, 1991; López-Adrián et al., 1993; López-Adrián & Herrera-Silveira, 1994; Herrera-Silveira et al., 1998). Among the green algae, the genus *Monoraphidium* (*M. caribeum* and *M. tortile*) is the most common, while *Aphanocapsa* (*A. pulchra*), *Chroococcus* (*C. dispersus*) and *Microcystis* (*M. aeruginosa*) were common cyanophyceans. The genus *Microcystis*, found in eutrophic temperate lakes during summer, is also common in freshwater inland waters from Yucatan (Díaz-Arce, 1999). The most frequently found diatom species are *Achnanthes gibberula*, *Amphora ventricosa*, *Cocconeis placentula* and *Gomphonema lanceolatum*.

The highest number of cyanobacteria and chlorophycean species are found in the winter storm and rainy seasons in the lentic cenotes. Euglenophyceans are poorly represented; a few species of dinophyceans can be found in those sinkholes enriched with allocthonous organic matter.

Table 2. List of representative species recorded in cenotes of the Yucatan Peninsula

Cyanobacteria	*Staurastrum pentasterias*	**Bacillariophyta**	*Stephanodiscus niagarae*
Chroococcidiopsis indica	*Chlamydomonas paraserbinowi*	*Achnanthes gibberula*	*Fragilaria capucina*
Aphanocapsa montana	*Sphaerella lacustris*	*Cocconeis disculus*	*Synedra tenera*
Aphanocapsa pulchra	*Pandorina morum*	*Cocconeis placentula*	*Synedra ulna*
Chroococcus dispersus	*Micromonas pusilla*	*Cylindrotheca closterium*	*Terpsinoe musica*
Gloeocapsa polydermatica		*Denticula kuetzingii*	
Gloeocapsa rupestris	**Chrysophyta**	*Hantzschia amphioxys*	**Higher plants**
Gomphosphaeria aponina	*Chrysococcus minutus*	*Nitzschia closterium*	*Acrostichum danaefolium*
Merismopedia tenuissima	*Chrysococcus vulneratus*	*Nitzschia longissima*	*Cladium jamaicense*
Microcystis aeruginosa	*Dinobryon sertularia*	*Nitzschia scalaris*	*Conocarpus erecta*
Microcystis inserta	*Salpingoeca ringens*	*Cymbella amphicephala*	*Acoelorrhaphe wrightii*
Synechocystis pevalekii	*Mallomonas pulchella*	*Cymbella turgida*	*Bravaisia tubiflora*
Anabaena fertilissima		*Eunotia maior*	*Cabomba palaeformis*
Nostoc commune	**Euglenophyta**	*Eunotia monodon*	*Ficus cotinifolia*
Oscillatoria nigra	*Euglena agilis*	*Eunotia praerupta*	*Nymphaea ampla*
Trichodesmium thiebautii	*Euglena sanguinea*	*Mastogloia smithii*	*Phragmites australis*
	Phacus onyx	*Melosira granulata*	*Rhabdadenia biflora*
Cryptophyta	*Trachelomonas volvocinopsis*	*Diploneis elliptica*	*Rhizophora mangle*
Cryptomonas acuta		*Diploneis puella*	*Sagittaria lancifolia*
Cryptomonas erosa	**Pyrrophyta**	*Gomphonema acuminatum*	*Sesbania emerus*
Rhodomonas pusilla	*Gonyaulax scrippsae*	*Gomphonema angustatum*	*Thrinax radiata*
	Amphidinium crassum	*Gomphonema lanceolatum*	*Typha domingensis*
Chlorophyta	*Gymnodinium grammaticum*	*Amphiprora paludosa*	
Dictosphaerium botrytella	*Sphaerodinium polonicum*	*Anomoeneis vitrea*	
Coelastrum microporum	*Peridinium simplex*	*Frustalia vulgaris*	
Ankyra ancora	*Peridinium umbonatum*	*Gyrosigma exilis*	
Chlorella vulgaris	*Scrippsiella tochoidea*	*Navicula cryptocephala*	
Monoraphidium caribeum	*Procentrum lima*	*Navicula recens*	
Monoraphidium circinale		*Pinnularia intermedia*	
Selenastrum capricornutum	**Xanthophyta**	*Stauroneis undulata*	
Ceraterias staurastroides	*Characiopsis callosa*	*Amphora copulata*	
Scenedesmus circumfusus	*Chloropedia plana*	*Amphora ovalis*	
Scenedesmus opoliensis	*Merismogloea polychloris*	*Amphora ventricosa*	
Tetrachlorella alternans	*Chlorogibba trochisciaeformis*	*Chaetoceros gracilis*	
Cosmarium portianum	*Rhizochloris stigmatica*	*Chaetoceros muelleri*	
Cosmarium punctulatum	*Neonema quadratum*	*Rhizosolenia setigera*	
Staurastrum muticum	*Tribonema ambiguum*	*Cyclotella meghiniana*	

Using the guidelines of Carlson (1977) and based on the phytoplankton chlorophyll *a* concentration measured in 30 open cenotes, the trophic index of these cenotes can be classified into three major groups: oligotrophic (<3 mg Ch. *a* m^{-3}), mesotrophic (3–20 mg Ch. *a* m^{-3}) and eutrophic (20–150 mg Ch. *a* m^{-3}) (Fig. 4). Most of these cenotes remained in the oligo-mesotrophic range, and 15% of them were eutrophic.

Primary production studied in cenote Noc Ac in 1995 was low due to poor biomass and chlorophyll *a* concentrations (Ávila et al., 1995). The limited data existing on primary production prevent generalizations and comparisons with other tropical or temperate waters.

Invertebrates

The knowledge of protozoan, hydrozoans, gastrotrichs, tardigrads, free-living nematodes, and annelids is scarce (Suárez-Morales & Rivera-Arriaga, 1998). Reports of other invertebrates (e.g. sponge: *Spongilla*

Table 2. contd.

Rotifera	Decapoda	Strongylura notata
Brachionus spp.	*Agostocaris bozanci*	*Thorichthys meeki*
Keratella americana	*Calliasmata nohochi*	
Lecane aculeata	*Creaseria morleyi*	**Tetrapods**
Lecane furcata	*Janicea antiguensis*	*Bufo marinus*
Lecane luna	*Parahippolyte sterreri*	*Crocodylus moreleti*
Lepadella spp.	*Procaris* nov. sp.	*Ctenosaura similis*
Polyarthra vulgaris	*Somersiella sterreri*	*Chrysemys scripta*
	Typhlatya campechae	*Dermatemys mawii*
Branchiopoda	*Typhlatya mitchelli*	*Kinosternon creaseri*
Alona spp.	*Typhlatya pearsei*	*Kinosternon leucostomum*
Dunhevedia spp.	*Yagerocaris cozumel*	*Kinosternon scorpoides*
Euryalona spp.	Remipedia	*Leptodactylus labialis*
Macrothrix spp.	*Speleonectes tulumensis*	*Rhinoclemys areolata*
Moina spp.	Thermosbaenacea	*Lophogobius cyprinoides*
Moinadaphnia spp.	*Tulumella unidens*	*Ophisternon aenigmaticum*
Scapholeberis spp.		
Simocephalus spp.	**Fishes**	
Anguilla rostrata	*Archocentrus octofasciatus*	
	Astyanax aeneus	
Copepoda	*Astyanax altior*	
Arctodiaptomus dorsalis	*Belonesox belizanus*	
Leptodiaptomus novamexicanus	*'Cichlasoma' synspilum*	
Mastigodiaptomus spp.	*'Cichlasoma' urophthalmus*	
Mesocyclops spp.	*Eleotris pisonis*	
Pseudodiaptomus marshi	*Floridichthys polyommus*	
	Gambusia yucatana	
Amphipoda	*Gerres cinereus*	
Hyalella azteca	*Gobiomorus dormitor*	
Mayaweckelia cenoticola	*Lutjanus griseus*	
Quadriviso lutzi	*Megalops atlanticus*	
	Ogilbia pearsei	
Isopoda	*Ophisternon infernale*	
Bahalana mayana	*Petenia splendida*	
Creaseriella anops	*Poecilia mexicana*	
	Poecilia orri	
Mysidacea	*Poecilia velifera*	
Antromysis cenotensis	*Rhamdia guatemalensis*	

cenota by Poirrier, 1976) were published in the seventies. Most studies have dealt with macrocrustaceans and zooplankton.

Rotifers are one of the most diversified group, with 102 species in only 12 sampled localities of the Peninsula (Sarma & Elías-Gutiérrez, 1999). Eutrophic systems are characterized by the dominance of brachionids, such as *Brachionus* and *Keratella*. In oligotrophic cenotes, the number of species is higher, including species of the groups *Lecane*, *Lepadella* and bdelloids.

Up to 30 species of branchiopods have been recorded (Elías-Gutiérrez et al., 1999) in the Yucatan Peninsula; the species are smaller in size, a fact attributed to a more intense predation.

Ostracods were initially studied by Furtos (1936), who described seven species, three of them within the cave connected to the cenotes: *Cypridopsis inaudita*, *C. mexicana* and *C. yucatanensis*. *Danielopolina mexicana* was recently described by Kornicker & Iliffe (1989); it is the most primitive species in the genus (Danielopol, 1990).

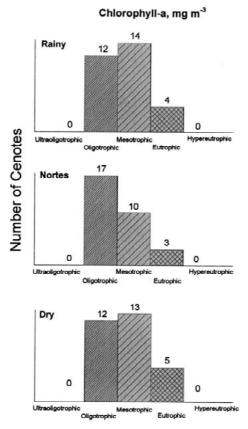## Chlorophyll-a, mg m^{-3}

Figure 4. Trophic classification of 30 cenotes based on the phyto-plankton chlorophyll *a* concentration.

Thirty-five copepod species have been recorded in the Yucatan Peninsula (Suárez-Morales & Reid, 1998). The biogeography of *Arctodiaptomus* and *Mastigodiaptomus* suggests an affinity of the calanoids of the Yucatan Peninsula with those from the insular Caribbean (Suárez-Morales et al., 1996). Endemism is characteristic to the region, not one copepod species is distributed all over the Peninsula (Reid, 1990; Suárez-Morales et al., 1996; Suárez-Morales & Reid, 1998). Most cyclopoids are benthic, two *Mesocyclops* species from cenotes in the Yucatan Peninsula are adapted to planktic life (Fiers et al., 1996). Marine forms occur in coastal cenotes.

Most amphipods occurring in cenotes derive from marine ancestors. Some of them are cosmopolitan species, such as *Hyalella azteca* and *Quadriviso lutzi*; others have restricted distributions, indicating a strong isolation among cenotes (Fiers et al., 1996). The same is true for cirolanid isopods, such as *Bahalana mayana* and *Creaseriella anops* (Wilkens, 1982), and mysids, among them *Antromysis cenotensis* (Iliffe, 1992).

In the case of decapods, diverse species, among which *Creaseria morleyi*, *Typhlatya mitchelli*, *T. pearsei* and *T. campechae*, seem to derive from Caribbean marine ancestors (Hobbs & Hobbs, 1976; Reddell, 1977; Wilkens, 1982). *Somersiella sterreri* is considered a Tethyan relict (Iliffe et al., 1983), as is the thermosbaenacean *Tulumella unidens* (Cals & Monod, 1988).

Other macrocrustaceans from the Peninsula include *Agostocaris bozanci*, *Yagerocaris cozumel*, *Janicea antiguensis*, *Calliasmata nohochi* (Escobar-Briones et al., 1997) and an undescribed *Procaris* (Iliffe, 1992). The remipedian *Speleonectes tulumensis*, one of the most primitive crustaceans, is endemic to some localities in the region (Yager, 1987); a new remipedian is to be described this year in caves near Mérida (Álvarez, pers. com).

Hubbs (1936) was the first to explore systematically the ichthyofauna of the Yucatan Peninsula; he described most of the endemic species. Fish diversity increases southwards and in more coastal cenotes (Wilkens, 1982; Schmitter-Soto, 1998a). The most isolated sites are located in the geologically oldest areas, that remained dry during the Quaternary transgressions, which have been colonized only by two species: *Rhamdia guatemalensis* and *Gambusia yucatana*. *R. guatemalensis*, a fish with nocturnal habits, could have reached this cenote through underground tunnels (Wilkens, 1982), while *G. yucatana*, a small livebearer, tolerant to environmental extreme conditions, could have arrived as hurricane-transported gravid females.

In coastal cenotes cichlids are dominant. Other frequent and abundant species are *Astyanax aeneus* and *R. guatemalensis*, together with poeciliids. In systems close to the sea associated with sea inlets diverse marine invaders occur, mostly as juveniles of gerreids, lutjanids, gobiids, eleotrids, belonids and even the tarpon, *Megalops atlanticus*, and the eel, *Anguilla rostrata* (Navarro-Mendoza, 1988; Schmitter-Soto, 1998a). In between these coastal cenotes and those in more ancient zones, the fish fauna is dominated by *Astyanax altior*, 'Cichlasoma' urophthalmus*, *Poecilia mexicana* and *P. velifera* (Wilkens, 1982), as well as the ubiquitous *Rhamdia* and *Gambusia*.

Many fish populations in cenotes have peculiar morphological features, and they have been described as subspecies. The status of some of these taxa has been questioned, but some have been included among the vulnerable, given their reduced, isolated habitats (Williams et al., 1989). Some subspecies include *R*.

guatemalensis decolor, *R. g. depressa*, *R. g. sacrificii*, *R. g. stygaea*, '*C.*' *urophthalmus conchitae* (extinct by disappearance of its only known locality, a cenote within the city of Mérida), '*C.*' *u. ericymba*, '*C.*' *u. mayorum* and '*C.*' *u. zebra* (Hubbs, 1936, 1938). The anchialine cenotes of Tulum (northeast Yucatan Peninsula) share four endemic species with localities in northwestern Yucatan: *A. altior*, *P. velifera* (Schmitter-Soto, 1998a, b), *Ophisternon infernale* and *Ogilbia pearsei* (Navarro-Mendoza & Valdés-Casillas, 1990).

In addition to fishes, vertebrates observed in the waters of cenotes include crocodiles, iguanas, turtles and anurans (Navarro-Mendoza, 1988; Pozo et al., 1991). Many birds and bat species live temporarily in the walls and trees of the cenotes.

Energy flow

The organic matter (OM) in cenotes has both autochthonous and alochthonous origins. The former enters the cenotes through solar radiation and is incorporated into organic matter via aquatic primary producers (mostly phytoplankton, rooted and floating macrophytes) and vegetation in the shores of the cenotes.

The latter enters the cenotes during the rainy season by soil lixiviation, the weathering of logs, leaves and transport of animal carcasses, and anthropogenic sewage. This OM is not incorporated immediately into the trophic web by the cenote fauna. Its main components, chitin and cellulose, are slowly degraded by fungi and bacteria. Eventually this OM dissolves and is utilized by bacteria found on the walls of the cenote, in the halocline and throughout the water column. Larger particulate matter is fragmented by the biological activity and enters the detritus pathway. The larger input of external organic (and inorganic) matter and the higher sedimentation rate in the cenotes autochthonous OM is photoautotrophic and chemoautotrophic in origin. Sulfate-reducer bacteria in the bottom of the cenote supports chemoautotrophy in the water-sediment interface.

Most lotic cenotes have a continuous water flow (1–3 cm s^{-1}) and their photosynthetic production is low, due to the limited availability of nitrogen and phosphorus; it is based on the phytobenthos and the epiphyton in the border of the cenote. Their waters are transparent. In contrast lentic cenotes contain nutrient and phytoplankton rich waters which give brilliant colors to the waters when they are observed from the shores.

In lentic cenotes, cyanobacteria dwell in the photic layer. Some insect larvae, filtering bivalves and occasionally some fishes eat these bacteria, which give a greenish tint to the cenote waters. This production is not fully utilized. Cyanobacteria are replaced near the bottom or at the halocline (chemocline) by purple bacteria, which may form a turbid layer, often mistaken as a false bottom. At the true bottom, a marine, transparent, anoxic layer is found, where non-described associations of bacteria and fungi occur, forming large mats. Stable isotope data confirm the origins of the two organic carbon sources in cenotes (Pohlman, 1995).

Suspended particulate OM remaining in the cenotes is transported by the slow flow into the tunnels, where the concentrations of organic carbon nitrogen decrease because of its use by bacteria. Some crustaceans and fish, which specialize in particulate OM (ostracods, mysids and carideans), bacterial film (carideans), and corpses and detritus (amphipods, isopods, thermosbaenaceans, carideans, benthic fishes) are the final recipients of these pathways. This fauna supports predators (carideans, remipedians, and fishes). There is a clear-cut niche separation in the cenote (e.g. between walls and bottom), which continues into the submerged tunnels. Potential prey and flow velocity are the two main factors in faunal distribution in cenotes (Culver, 1985).

Food webs in cenotes are relatively simple; few trophic levels and an efficient energy transfer characterize them. Bacteria, fungi, algae, and protozoa are the first levels, and non-specialized micro and macroinvertebrates consume them. Most species are polyphagous, and some are top consumers; as a response to oligotrophy, all of them are starvation-resistant and efficient in food processing (Culver, 1985). These food webs are fragile and easily altered in higher trophic levels.

Epiphyte algae and macrophytes support the herbivorous food web in lotic cenotes, where crustaceans and insect larvae are primary consumers. Isotopic records confirm that this web is complemented by particulate matter from outside the cenote, enriched by bacteria and assimilated by copepods, which in turn are predated by *Astyanax* and other fishes. *Astyanax* is a prey of top predators, notably the eel and *Rhamdia*, which in other habitats tends to be an omnivore rather than a predator (Navarro-Mendoza, 1988).

The accumulation of OM in the sediment, as well as the anoxic or near-anoxic conditions at the bottom, leads to the generation of H_2S or HS^- (Stoessel et al., 1993). This is transformed to S^0 and subsequently

to sulfide by bacteria (*Beggiatoa*, *Thiobacillus*, *Thiothrix*) (Jorgensen, 1983). In cenotes of Quintana Roo there are mollusks associated to bacterial patches, probably consuming them.

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