The Axolotl and its Native Habitat—Yesterday and Today

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The Mexican axolotl (*Ambystoma mexicanum*) has been an important laboratory animal and model system for more that a century. In spite of this long history in research, however, we know relatively little about the axolotl's natural history. And, in spite of the many axolotls that have been bred and raised in laboratory colonies, we know practically nothing about its natural habitat.

Our laboratory species of axolotl' came originally from two lakes, Xochimilco and Chalco, in the Valley of Mexico. Today, however, the Valley of Mexico is home to an estimated 18 million people. As a result of the growth of Mexico City, in this century especially, these lakes have been reduced from an area of perhaps 120 square kilometers at the beginning of the sixteenth century, to the few hundred hectares of canals and lagoons of modern Xochimilco. In fact, these canals only exist at all because they are recharged with treated sewage effluent. Figure 1 shows a sign at a site where treated effluent is pumped into Xochimilco.

Thus the natural habitat of the axolotl cannot merely be studied, it must be reconstructed, as best we can, from historical documents and from archaeological and geological studies.

The Valley of Mexico is actually a closed basin formed during the tertiary without natural drainage. In prehispanic times the lower portions of the basin were occupied by a system of five lakes. Overflow from the higher lakes, Chalco and Xochimilco in the south and Zumpango and Xaltocan in the north, flowed into Texcoco, the lowest lake in the center of the



Figure 1. Sign at a site where treated effluent is pumped into Xochimilco.

basin. Texcoco, lacking any outlet except evaporranspiration, was extremely saline (Figure 2).

Lakes Chalco and Xochimilco were situated in the southern basin at an altitude about three meters higher than Lake Texcoco and separated from it by a low range of hills known as the Sierra de Santa Catalina. In addition to precipitation and surface runoff, they were fed by deep perennial springs located near the southern boundary of Xochimilco. Although traditionally they are considered to have been two lakes, they really comprised a

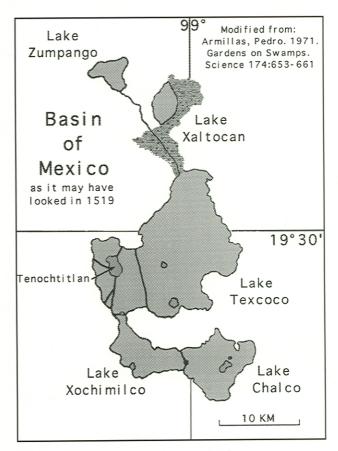


Figure 2. Basin of Mexico around 1519.

^{*}The species of neotenic salamander that we maintain in the Axolotl Colony and that is a common research animal is *Ambystoma mexicanum*, originally native to lakes Chalco and Xochimilco. Although we refer to this species as the Mexican axolotl, in reality various other lakes in central Mexico are or were home to a number of species of non-transforming Ambystomatid salamanders. See Shaffer, H.B.1989. Natural history, ecology, and evolution of the Mexican "axolotls." Axolotl Newsletter **18**:5-11.

continuous body of freshwater lagoons and swampland in a shallow saucer, the rim of which was marked by the 2240 meter contour of elevation. The actual water level would have varied with periods of drought and flood, but apparently seldom rose above the 2240 contour (Figure 3).

Ambystoma bones recovered in archaeological excavations of lakeshore sites in the Xochimilco–Chalco basin show that from at least 6000 B.C. axolotls were part of a rich freshwater lacustrine habitat. They shared this habitat with lake turtles, waterfowl (including geese, ducks, coots, and grebes), freshwater mollusks and ostracods, and fish (Chirostoma, Girodinichthys, and Cyprinids). The shorelines supported Cyperaceae, Sparganiaceae, rushes, and cattails. Sub-

have begun using a system of horticulture and irrigation known as *chinampas*. Chinampas were long, narrow fields created in swampy areas by heaping up muck and aquatic vegetation dredged up from the swamp. Willow stakes were driven into the bottoms around the edges and joined by wattles to enclose and contain the mud. Each chinampa was bordered on at least three sides by water, and was thus irrigated by seepage from the surrounding canals. The chinampas were very fertile and productive, and they yielded as many as four crops in a year (Rojas Rabiela, 1991).

By the mid-thirteenth century the Xochimilco-Chalco region had been incorporated into the Aztec state centered at Tenochtitlan. The Aztec capital was located on

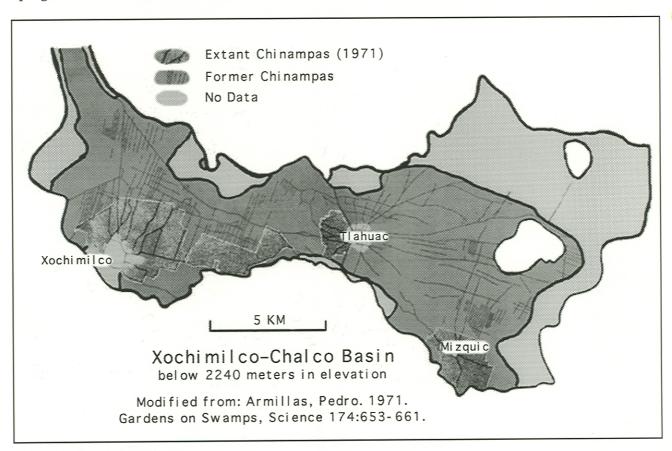


Figure 3. The southern basin.

merged and floating aquatic plants included water lentils, horsetail, *Myriophyllum*, and *Epilobium*. After 3000 B.C., willows, *Malvaceae*, *Liliaceae*, and *Umbelliferae* became more frequent (Niederberger, 1979).

People began modifying the natural habitat of the axolotl by about 1000 A.D., when the indigenous people of the region are thought to an island near the western shore of Lake Texcoco. The Aztecs constructed an elaborate system of causeways, dikes, and canals which, in conjunction with the chinampas, controlled flooding and separated fresh and saline waters. In particular, the Aztecs built a long dike that divided Texcoco into two parts and kept the saline waters of eastern Texcoco

from the western section around Tenochtitlan, which they called the Laguna de Mexico. In addition, a causeway or dike crossing from north to south through Tlahuac separated Xochimilco from Chalco (Sanders, et al., 1979).

During the Aztec period nearly the entire Xochimilco-Chalco basin was devoted to chinampas horticulture, as was the Laguna de Mexico around Tenochtitlan. Also, as a result of the Aztec waterworks, saline water was largely prevented from entering the southern lakes, even during periods of flood (Armillas, 1971).

Thus the habitat of the axolotl was significantly affected during the period of the Aztec empire in at least two ways: first, by the spread of the chinampas, which involved the construction of ditches and islands, and second, by the construction of waterworks which controlled water levels and prevented the incursion of salt water into the axolotl habitat. Its habitat may have been enlarged as well by the expansion of fresh water horticulture into the district around Tenochtitlan. The impact that these historical changes had on the species can only be speculated upon.

The chinampas system and the Aztec waterworks were at their peak when the Spanish Conquistadors arrived in 1519. What ensued was two years of warfare during which the waterworks were largely destroyed. As a result, during the sixteenth century, the southern basin experienced both flood and drought as the Spanish worked to protect the nascent Mexico City, located on the site of Aztec Tenochtitlan, from flooding. During this and subsequent periods, many of the Aztec waterworks were rebuilt, and efforts were also begun to drain the region about the city (Palerm, 1990).

Even though in time the Laguna de Mexico was drained by the construction of a canal for that purpose north from Texcoco, lakes Xochimilco and Chalco remained largely intact throughout the seventeenth, eighteenth, and nineteenth centuries. They continued to be recharged by surface runoff and by perennial springs. Moreover, throughout this period an outlet was maintained via the Canal de la Viga, which carried water and commerce from Lake Xochimilco to Mexico City, even after the original outlet to Texcoco was lost due to basin drainage. Chinampas agriculture continued to be practiced but began a long period of decline (Rojas Rabiela, 1991).

The axolotl was well-known to the Aztecs and other indigenous peoples in the area, who

included it as part of their varied diet, and several early Spanish accounts describe it. For instance, Sahagún wrote in his monumental work on the indigenous people of Mexico (Sahagún, 1938):

There are some creatures in the water that are called axolotl that have feet and hands like small lizards, and they have the tail of an eel and the body as well; they have a very wide mouth and whiskers at the neck. It is very good to eat; it is the food of lords.*

Francisco Hernández also described the axolotl in his treatise on Mexican natural history. Although this work was not published until about 1648, it was based on material that he collected during his travels in central Mexico between 1570 and 1577. Other notable mentions of the axolotl include the account by Shaw in his Naturalist's Miscellany in 1798 (where it was designated *Gyrinus mexicanus*) and the description published in 1811 by Georges Cuvier, based upon preserved specimens (See Smith and Smith, 1971).

There are a few accounts which give us a glimpse of the axolotl and its habitat during the nineteenth and early twentieth century. José Velasco published a paper in 1880, "Anotaciones y observaciones al trabajo del Sr. D.A. Weismann sobre la tranformación del ajolote mexicano en Amblistoma" in La Naturaleza 5:58-84. This article has been translated into English (Dranz et al, 1971). Velasco was interested especially in neoteny and metamorphosis as he found it in the various salamander populations of the basin, but he affords us some interesting glimpses of the axolotl in its native habitat. He tells us, for instance, that at that time, lakes Chalco and Xochimilco were permanent lakes and the water was of very good quality. They were largely covered by floating vegetation and many plants also grew on the bottom. The axolotls were usually found at a depth of about one and a half meters or less, and, during the night only, near the surface. They were not to be found in the "flooded lands" or in canals, trenches, or wells.

^{&#}x27;Hay unos animalejos en el agua que se llaman *axólotl*, (que) tienen pies y manos como largartillos, y tienen la cola como anguila, y el cuerpo también; tienen muy ancha la boca y barbas en el pescuezo. Es muy bueno de comer; es comida de señores.

Velasco also reported color phases among the axolotls in the lakes. He described "yellow-spotted" individuals in Lake Chalco that lived in "salty water." He also mentions two types in Lake Xochimilco, one darker than the other. According to Velasco the water in the southern lakes was "not completely uniform throughout, in some localities being lightly salty and in others fresh. Each type [of axolotl] is limited precisely to a certain type of water: the darkest ones live in that which contains the least salt and the yellow-spotted ones in that which is more salty."

This description can be supplemented by that of H. Gadow, writing in 1903. At this time lakes Chalco and Xochimilco were still fed by deep springs, "thirty or forty [9 to 12 meters] and more feet in depth." About half the surface was filled with chinampas. The depth of the lake averaged around "five to ten feet [1.5 to 3 meters], shallower to the northwest," where it was swampy. Water near the springs was clear, but muddier and darker the farther from the springs one moved. It was full of decomposing vegetable matter, fish, insect larvae, Daphniae, worms, and axolotls. The Canal de la Viga continued to be an important artery for the transport of the produce of the chinampas to Mexico City.

Gadow reported that the axolotls bred at the beginning of February, fastening the eggs to the water plants. By June "they were all grown into big, fat creatures ready for the market." Later in the summer, according to Gadow, "they take to the rushes, in the autumn they become scarce." These axolotls were dark in color "never piebald or marbled with yellow."

Velasco claimed that at least some axolotls from Xochimilco and Chalco transformed into a terrestrial form. Gadow, however, asserted that axolotls in these lakes remained entirely aquatic.

Urban growth eventually took its toll on lakes Xochimilco and Chalco, although the impact was apparently not large until the twentieth century.

In 1846 well drilling began in the basin after it was discovered that potable groundwater was available under artesian pressure. By the early twentieth century, drainage works were underway in the southern basin. As Mexico City continued to grow, so did the need for water, and Xochimilco's springs were tapped by an aqueduct during the 1920s. The springs dried up entirely during the 1930s. In 1953 well drilling accelerated in the southern basin,

when many wells in the central basin were closed because of severe subsidence as sediments compacted after ground water removal. As a result of all these changes, today Lake Chalco is gone and only a small remnant of Lake Xochimilco remains (National Research Council, 1995).

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