1976

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Published in INVESTIGATIONS OF THE ICHTHYOFAUNA OF NICARAGUAN LAKES, ed. Thomas B. Thorson
(University of Nebraska-Lincoln, 1976).

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For many decades the early Spanish conquistadors and explorers were uncertain as to whether the "Freshwater Sea" —the name given to the lake the Nicaraos called *Cocibolca* and we call Lake Nicaragua— was one or more lakes. The presence of small, volcanic *lagunas*, scattered throughout the Pacific coast, and broad, marshy pools near the coasts of Lake Managua and especially of Lake Nicaragua, and the discovery of the Río Desaguadero, or Río San Juan, added to the confusion in a time when only rough, very inaccurate maps were available.

Spanish historian Gonzalo Fernández de Oviedo y Valdés did much travelling in the area, and, after thorough consideration of previous reports, decided that it was only one lake, divided by the area ruled by the Chief Itipitapa, and that it communicated with the Caribbean Sea. His evidence for the marine communication was the presence of the "*pexe viguela*", or sawfish, in Lake Nicaragua (see Villa, 1976). Modern geography shows that two main lakes, Managua and Nicaragua, are joined by the Río Tipitapa, and that Lake Nicaragua is drained by the Río San Juan into the Caribbean Sea (Incer 1970).

A study of the fishes of Lake Xiloá, or Jiloá (Villa, 1968) and of the lakes themselves, has shown a clear faunal correspondence between Xiloá and lakes Managua and Nicaragua, and stratigraphic evidence indicates that sometime during the Pleistocene the level of the water surface was some 15 to 20 m higher than the present level of Lake Nicaragua (Hayes, 1899, cited by several subsequent authors). When the level was lowered, Xiloá became isolated from its parent basin. This basin included the present lakes Managua and Nicaragua, which were at first in broad communication in the Tipitapa area. The parent basin, because of its location and its large size, was named "El Gran Lago Nicaragüense" (the Great Nicaraguan Lake) by Villa (1968).

The ichthyofaunal similarity of the two lakes is readily explained by their common origin from the "Great Nicaraguan Lake". However, there are important differences in their ichthyofaunal composition, some of which have passed unnoticed. These differences, hitherto unaccounted for, are the topic of this paper.

Ichthyofaunal Similarities and Differences Between Lakes Managua and Nicaragua

If we accept the existence of a communication between lakes Managua and Nicaragua, we should expect the species composition of the two lakes to be identical. Villa (1968) pointed out that the shark and the sawfish inhabiting Lake Nicaragua should be present in Lake Managua, but are absent there. He suggested that they either were unable to pass through the Río Tipitapa area, or that they invaded Lake Nicaragua after the level of the lakes decreased and the communication was severed. Since the ichthyofauna of both lakes, and of Nicaragua in general, is now better known (Villa, 1971a; Astorqui, 1972) I would like to reconsider these suggestions.

A list of the fishes found in both lakes, and their distribution in Nicaragua, is presented in Table 1. Of the 45 species known, at least 25 occur in both lakes. Six others are uncertain: *Belonesox belizanus*, *Gymnotus cylindricus*, *Hemibrycon* sp., *Rhamdia* sp. (a recently discovered, perhaps new, species), *Rhoadsia eigenmanni*[1] and *Rivulus isthmensis*. Species of the genus *Poecilia*, presently under study by W. A. Bussing, are not included in the following discussion since their status remains to be clarified.

Only one species, *Rhamdia managuensis*, has been found only in Lake Managua. However, it is an apparently rare (if valid) species which has not been reported since Meek (1907) and thus it is not a good zoogeographic indicator.

A significant number (11) of species has been found only in Lake Nicaragua and not in Lake Managua. Their absence in the latter is probably not due to insufficient collecting, especially in the case of the shark (*Carcharhinus leucas*), the sawfish (*Pristis perotteti* and perhaps *P. pectinatus*), the tarpon (*Tarpon atlanticus*), the grunt (*Pomadasys boucardi*) and the róbalo (*Centropomus parallelus*). Other, less conspicuous species, are *Astyanax* sp. (of Astorqui, 1972), *Bryconamericus scleroparius*, *Cichlasoma maculicauda*, *Alfaro cultratus* and *Neoheterandria umbratilis*. These will be considered in more detail.

More than half (6) of these species are of marine origin, and only 2 are primary-division fishes (*i.e.*, unable to tolerate salt or brackish water): *Astyanax* sp. and *Bryconamericus scleroparius*.

It is now clear that *Carcharhinus leucas* does not reproduce in Lake Nicaragua, but does so either in the sea or around the mouth of the Río San Juan (Jensen, 1976). Although *Pristis perotteti* appears to give birth to its young in Lake Nicaragua, the relative scarcity of pre-reproductive individuals there suggests that the sawfish also spends part of its life cycle in the sea (Thorson, 1976).

Not much is known about the biology of other species in the lake basin, but *Centropomus*, *Pomadasys* and *Tarpon* are probably not "permanent" residents of Lake Nicaragua. In other parts of their range they are known to migrate to and from fresh water to complete their life cycles, and this is probably true also for the Lake Nicaragua populations. This being so, it explains the absence of the above species in Lake Managua. Even if individuals had been landlocked there when the connection was severed, their populations, unable to reproduce, would have become extinct. Proof of

[1]W. L. Fink and S. H. Weitzman have recently (1974) designated this as *Carlana eigenmanni* (Smithson. Contr. Zool. 172:1–46).

TABLE 1. List of fishes known to inhabit the basin of the Great Lakes of Nicaragua, and their presence or absence in the Atlantic and Pacific versants of Nicaragua. Based on data from Astorqui (1972), Villa (1971a) and later records. Symbols: + present, − not known to be present, ? status uncertain (probably not present).

Species	Pacific	Atlantic	L. Xiloá	L. Managua	L. Nicaragua
Alfaro cultratus	−	+	−	−	+
Astyanax fasciatus	+	+	−	+	+
Astyanax sp. (*nasutus*?)	−	?	−	+	+
Belonesox belizanus	−	+	−	−	+
Bramocharax bransfordi	−	+	−	+	+
Bryconamericus scleroparius	−	+	−	−	+
Carcharhinus leucas	−	+	−	−	+
Cichlasoma centrarchus	+ (1)	+	−	+	+
Cichlasoma citrinellum	−	+	+	+	+
Cichlasoma dowi	+ (1)	+	−	+	+
Cichlasoma friedrichsthalii	+ (1)	+	−	+	+
Cichlasoma labiatum (2)	−	−	+	+	+
Cichlasoma longimanus	+ (1)	+	+	+	+
Cichlasoma maculicauda	+ (1)	+	−	−	+
Cichlasoma managuense	+ (1)	+	+	+	+
Cichlasoma nigrofasciatum	+ (1)	+	+	+	+
Cichlasoma rostratum	+	+	+	+	+
Centropomus parallelus	−	+	−	−	+
Dorosoma chavesi	−	−	+	+	+
Gobiomorus dormitor	−	+	+	+	+
Gymnotus cylindricus (3)	?	+	−	?	+
Hemibrycon sp.	−	+	−	?	+
Herotilapia multispinosa	+ (1)	+	−	+	+
Hyphessobrycon tortuguerae	−	+	−	+	+
Lepisosteus tropicus	+ (1)	+	−	+	+
Melaniris sardina	−	?	+	+	+
Neetroplus nematopus	+ (1)	+	+	+	+
Neoheterandria umbratilis	−	+	−	−	+
Poecilia sp. a	+	+	?	+	+
Poecilia sp. b	+	−	?	+	+
Poecilia sp. c	−	?	?	−	+
Poeciliopsis gracilis	+ (1)	−	+	+	+
Pomadasys boucardi	−	+	−	−	+
Pristis pectinatus (4)	−	+	−	−	+
Pristis perotteti	−	+	−	−	+
Rhamdia barbata	−	−	−	+	+
Rhamdia managuensis	−	−	−	+	−
Rhamdia sp.	−	−	−	?	+
Rhoadsia eigenmanni	−	+	−	?	+
Rivulus isthmensis (5)	−	+	−	?	+
Symbranchus marmoratus	+	+	+	+	+
Tarpon atlanticus	−	+	−	+	+

(1) Not present throughout most of the Chiapas-Nicaraguan Province, but limited to areas by "Atlantic intrusion" (Bussing, 1976).
(2) Not reported from Xiloá (Villa, 1968, 1971b) but collected since.
(3) Astorqui's (1972) *G. carapo*.
(4) Extremely rare, if present, in Lake Nicaragua.
(5) Miller (1966) states this species to be present in the Pacific versant of Nicaragua, but no records are available (see Villa, 1971a)

this could be provided by finding their fossils in Lake Managua sediments, which remains to be done. On the other hand, populations of other marine derivatives (such as *Dorosoma*, *Gobiomorus* and *Melaniris*) that were capable of reproducing after the communication was severed, not only would be present in both lakes, but also in lakes which were once part of the "Great Nicaraguan Lake", such as Lake Xiloá. Xiloá has representatives of these 3 genera (Villa, 1968).

Of the remaining five species that are probably residents of Lake Nicaragua but have not been found in Lake Managua (*Alfaro cultratus*, *Astyanax* sp., *Bryconamericus scleroparius*, *Cichlasoma maculicauda* and *Neoheterandria umbratilis*), all (except perhaps the dubious *Astyanax* sp.) are also absent in Nicaragua's Pacific versant but are more or less widespread and abundant in the Atlantic versant. They probably invaded Lake Nicaragua via the Río San Juan after the communication was severed. This may also be the case with at least some of the six "uncertain" species mentioned earlier, if they prove to be absent in Lake Managua. Further collecting in this lake and its tributaries is necessary to confirm this.

THE RIO TIPITAPA AS A BARRIER

The "permanent" interruption of faunal exchange between lakes Managua and Nicaragua apparently occurred prior to Recent times, as evidenced by the incipient differentiation in some species in both lakes, and in Lake Xiloá. Bussing (1976) estimates that freshwater fishes reached the great lakes of Nicaragua between 500,000 and

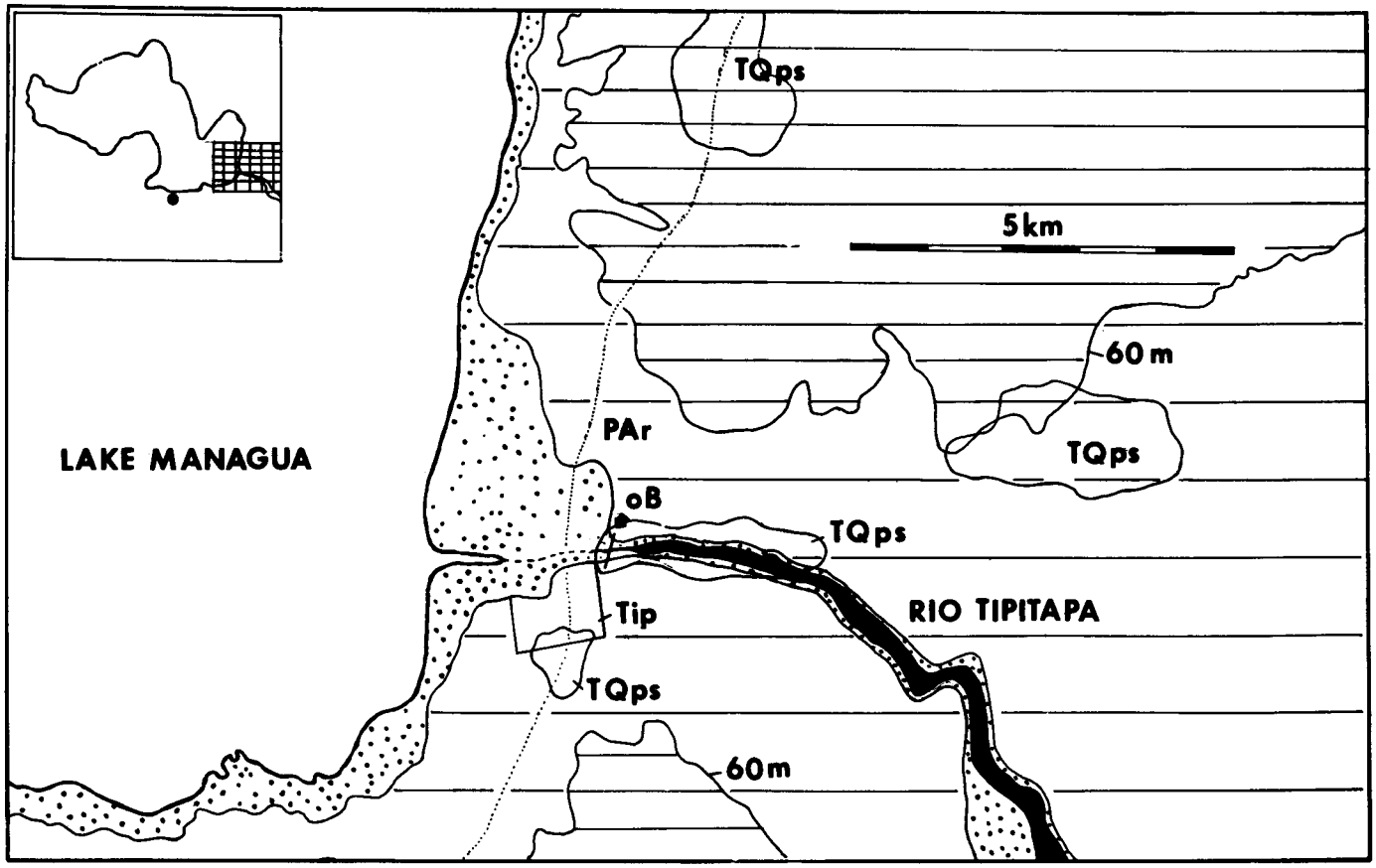

FIG. 1. Southeastern corner of Lake Managua and first 10 km of the Río Tipitapa, modified from "Mapa Geológico Hoja 2952 I" of the Catastro e Inventario de Recursos Naturales (Nicaragua). Insert: Lake Managua, showing area covered by map (cross-hatched) and the city of Managua (circle). The Río Tipitapa riverbed (stippled) is on the 40 m contour line (1 m above Lake Managua). Outcroppings of the orogenic Las Sierras Formation (TQps) are elsewhere overlaid by residual and alluvial soils, within the 40-60 m contour line. Other abbreviations: oB = Old Bridge; PAr = Pan American Road (dotted line); Tip. = Tipitapa (city).

1,000,000 years ago. Evidence strongly suggests that Lake Xiloá was part of the "Great Nicaraguan Lake" and was severed from it with the decrease of the water level (Villa 1968). This decrease, obviously, must have taken place subsequent to the invasion by freshwater fishes. As pointed out by Villa, all the species in Lake Xiloá are identical with or at least derived from those of lakes Managua and Nicaragua, and some differentiation has taken place at least in a few species. At least one, *Dorosoma chavesi*, an endemic to the lake basin, shows a certain degree of differentiation when populations from Lake Managua and Lake Nicaragua are compared (Miller, 1950; Astorqui, 1972). A sample of *Dorosoma* recently collected in Xiloá also shows some differences from the other 2 populations (Villa, unpublished data), but in all cases it is not clear if the differences warrant specific or subspecific recognition. If Lake Managua has overflowed into Lake Nicaragua occasionally, this probably has prevented a sharp separation of the populations.

Lake Managua is presently 9 m above Lake Nicaragua, which is in turn 31 m above sea level (Incer, 1976). The lakes communicate by the Río Tipitapa, which bridges the 25 km gap between them. All maps consulted, even detailed topographical sheets, depict the Río Tipitapa as running continuously from one lake to the other. This representation is erroneous; a more accurate one is presented in Fig. 1. There is conflicting evidence as to the condition of the Tipitapa area in the past. Oviedo (1851–55), writing of the Sixteenth Century, claimed that the water was only chest-high, and Squier (1852) noted waterfalls forming during the rainy season. They were probably referring to different parts of the river. I last toured the area on 3 different occasions in 1974: at the end of the summer, the beginning of the rainy season, and the height of the rainy season. Talks with many eldermen in the city of Tipitapa and along the river disclosed that none of them recalled a continuous flow of water during their lifetime.

The southeastern end of Lake Managua becomes progressively more shallow, eventually forming a marshy area near the city of Tipitapa. The first 1000 m of the Río Tipitapa are the most crucial ones in the dispersal of Lake Nicaragua's fishes. There are numerous thermal springs (Fig. 2) bubbling boiling sulphureous water at isolated spots for some 500 m. Some of the major springs have been channelled to a series of touristic pools, but many still pour into the marsh and the river itself. The Pan American Road crosses at a point between Lake Managua and the Río Tipitapa proper. There is an extensive marsh on both sides of the road, but water flows mostly by seepage through the underlying sandstone. For about 400 m the "river" disapperars, re-appearing in several spots at the base of a sandstone ledge about 2-4 m high (Figs. 3 and 4). The marsh here becomes deeper and, toward the east, more or less discrete streams are formed and join near the "Old Bridge" (Fig. 5), forming the Río Tipitapa proper. Still, water flows

FIG. 2. One of the many sulphureous thermal springs that pour into the Río Tipitapa.

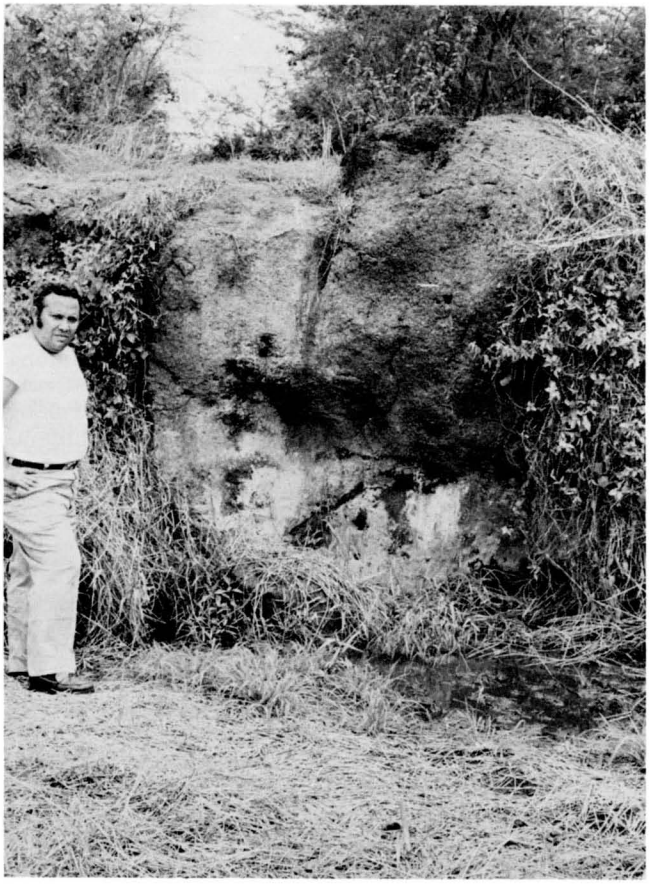

FIG. 3. One of the more precipitous parts of the sandstone ledge that at one time formed a strong waterfall, but is now dry most of the time.

very slowly, sulfur springs pour into it, and water hyacinths (*Eichornia* sp.) form a thick mat concealing the water almost uninterruptedly for 3-4 kms. During severe rainy seasons, however, Lake Managua's water level has increased, overflowing the Pan American Road and the dropoff itself, forming what Squier (1852) described as "waterfalls." To prevent this, a modest ditch has recently been dug between Lake Managua and the "Old Bridge". This has somewhat obscured the past situation and may even allow some fishes to go through, downstream. However, at least during 1974, the water was at all times observed to filter from the sides of the ditch (and from nearby sewers) forming a small stream (Fig. 6) which widens as it moves east. The fully-formed river is shown in Fig. 7.

It appears the the topography of the Tipitapa area, and especially of its critical first 1000 m, including the sandstone dropoff, the lack of running water, and the thermal springs, together act as a barrier which prevents the dispersal of fishes from Lake Managua to Lake Nicaragua. The "waterfalls", however small, seem to be an insurmountable barrier for fishes not adapted to them, preventing the movement in the opposite direction. Thus, Lake Nicaragua has more fish species than Lake Managua, even if the truly marine species (*e.g.*, shark, sawfish, etc.) are discounted. Apparently no one has critically compared large samples of fishes from lakes Managua and Nicaragua, but some differences, although not important ones, will likely be found.

ACKNOWLEDGMENTS

This paper is primarily based on the analysis of the distributional data provided by Astorqui (1972), supported by collections I made in Nicaragua between 1966–74, part of which have been deposited in the museums of the Universities of Costa Rica, Nicaragua, Kansas and Cornell. Considerable input has resulted from discussions with William A. Bussing, Jaime Incer, Robert R. Miller and Thomas B. Thorson, although they cannot be held responsible for my conclusions. A. M. Fletcher, R. R. Miller and T. B. Thorson also reviewed the typescript critically. It is my privilege to acknowledge their skillful assistance.

SUMMARY

The available evidence indicates that Lakes Managua and Nicaragua were broadly connected in the past, when most of the fish species invaded the "Great Nicaraguan Lake". Due to the lowering of the water level (caused perhaps by tectonic movements and/or erosion produced by the Río San Juan), Lake Managua became separated from Lake Nicaragua in the Tipitapa area. Water movement from Lake Managua is achieved mostly by seepage through a porous dropoff which prevents the exchange of fishes between the lakes. At about the same time, if not earler, Lake Xiloá also became separated. After the more or less permanent separation of the great lakes, other fish species, from the Atlantic versant, invaded Lake Nicaragua, probably via the Río San Juan, but they have been unable to move into Lake Managua because of the barrier in the Tipitapa River. Occasionally, Lake Managua overflows into Lake Nicaragua, allowing movement of fishes in that direction, but migration in the opposite direction has been effectively restricted.

FIG. 4. Depression at the eastern side of the Tipitapa "falls", where the seeping water collects to form the Río Tipitapa proper. After severe rainy seasons water overflows the dropoff forming modest waterfalls.

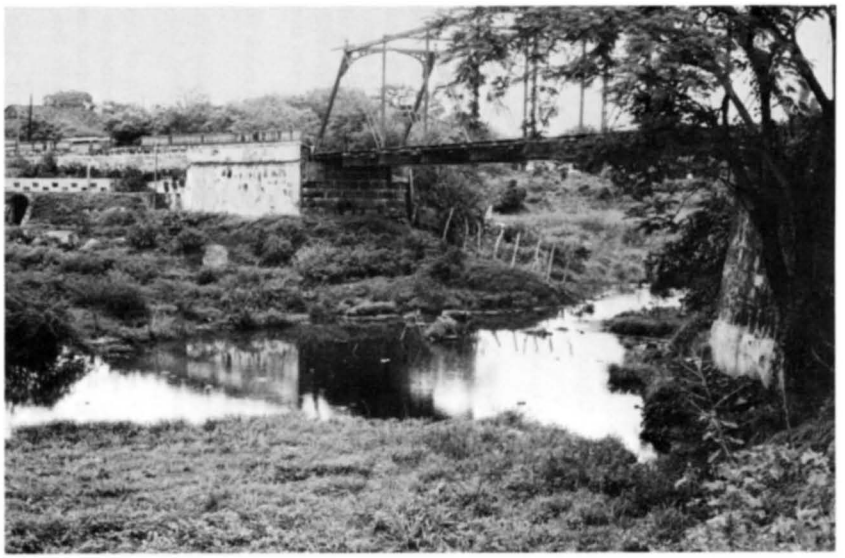

FIG. 5. Eastern side of the "Old Bridge" where enough water collects to form the Río Tipitapa proper. At this point, the water may reach 40-60°C due to scattered thermal springs.

FIG. 6. Shallow ditch dug to prevent the occasional overflows. Usually the water is a few cm deep, seeping through the sides of the ditch and collecting from nearby sewers.

FIG. 7. The Río Tipitapa proper, about 10 km southeast of the "Old Bridge."

Resumen

El estudio le la distribución de los peces de Nicaragua, junto con evidencia estratigráfica y geológica, parece indicar que los lagos de Managua y Nicaragua estuvieron ampliamente conectados en el pasado reciente, cuando la mayoría de las especies actuales (o sus ancestros) invadieron la cuenca del llamado "Gran Lago Nicaragüense." Debido al descenso del nivel del agua, se produjeron dos cuerpos principales de agua, separados en el área de Tipitapa. Debido a los accidentes topográficos locales, Tipitapa ha servido como una barrera contra la migración de peces de un lago a otro, aunque esta barrera — debido a fuertes y prolongadas lluvias— ocasionalmente permite el paso de peces del Lago de Managua al de Nicaragua, pero no en dirección opuesta. Debido a que una parte de su ciclo vital ocurre en el mar, peces como los tiburones (*Carcharhinus*), las sierras (*Pristis*), sábalos reales (*Tarpon*), los roncadores (*Pomadasys*) y los róbalos (*Centropomus*), han quedado excluídos del Lago de Managua. Posiblemente las poblaciones originales de estas especies, si existieron, se extinguieron en el Lago de Managua al perder su communicación con el mar Caribe. Especies periféricas (de origen marino) que pudieron reproducirse sin necesidad de la conexión con el mar (*Dorosoma, Gobiomorus, Melaniris*) no sólo se encuentran en los Grandes Lagos, sino también en la Laguna Xiloá, que antiguamente formaba parte de la cuenca. Otras especies, que posiblemente invadieron el Lago de Nicaragua después de su separación del de Managua, no han podido atravesar la barrera de Tipitapa y todo parece indicar que no se encuentran en el Lago de Managua. Estas son: *Astyanax* sp., *Bryconamericus scleroparius, Cichlasoma maculicauda, Neoheterandria umbratilis*, y tal vez varias especies de los géneros *Belonesox, Gymnotus, Hemibrycon, Rhamdia, Rhoadsia* y *Rivulus*.

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