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Ecosystem in transition

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Lake Nicaragua contains more than 40 species of fish, including 16 recognized species (Thorson 1976) of native cichlids and additional undescribed cichlids.[1] The lake is also inhabited by several large marine predators, such as the bull shark (*Charcharhinus leucas*), sawfish (*Pristis perotteti*), tarpon (*Tarpon atlanticus*), grunt (*Pomadasys* spp.), and snook (*Centropomus parallelus*; Thorson 1976). Eleven of the 16 cichlid species are confined to San Juan Province, which contains the lake (Miller 1966). The most heavily exploited fishery resources have traditionally been the native cichlids, estimated currently to constitute 58% of Lake Nicaragua's fish biomass.

Lake Nicaragua (Figure 1), the largest (8264 km²) tropical lake outside of Africa (Incer 1976), is located in a tectonic depression, which extends northwest from the mouth of the Rio San Juan to the Gulf of Fonseca in the Pacific. The depression also includes the smaller Lake Managua (also called Xolotlan). Numerous rivers flow into these two lakes, but only the Rio San Juan drains this system into the Caribbean Sea. The Rio San Juan passes through the productive Atlantic Coast–region of Nicaragua.

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Swift, aggressive management of tilapia is needed to mitigate the negative impacts of their introduction

This ecosystem of Lake Nicaragua is, therefore, intimately connected with the Caribbean Sea and adjacent coastal habitats. The most famous result of this connection is the migration of a shark, known as the freshwater shark of Lake Nicaragua, which in reality is the Caribbean bull shark, *C. leucus*.

The Caribbean Coast of Nicaragua is biologically one of the most productive and speciose systems in the world (Ryan 1992, Ryan et al. 1993). It receives a large amount of yearly rainfall, estimated at 4–6 m.

Fourteen primary rivers, draining 90% of the country's watershed (1.17×10^5 km²) flow into the Caribbean Sea and discharge an immense amount of fresh water (approximately 2.6×10^{11} m³) and suspended sediments along the 450 km of coast. Ten biologically rich estuaries, whose waters oscillate between fresh in the rainy season to moderately saline during the dry season, act as nursery areas for many marine species. These highly productive fisheries provide a livelihood for the people of the region. Populations of many of the fish species extend into Lake Nicaragua, and hence any perturbation that occurs in one system can severely impact upon the other. In order for a coastal management plan to be effective, it must encompass both the estuarine systems and Lake Nicaragua (Ryan et al. 1993).

The Lake Nicaragua ecosystem is currently undergoing major ecological changes. An extensive stocking program introduced African tilapia (genus *Oreochromis*) into the lake in the 1980s. Native cichlid populations have declined as introduced tilapia invade lake areas. The collapse of one of the world's unique freshwater ecosystems is imminent if corrective measures are not taken.

Historical perspectives

Lake Nicaragua and the Rio San Juan have long attracted the attention of the world due to their strategic location for constructing an interoceanic canal. Such a project would require deepening portions of the river and lake and cutting

[1]K. R. McKaye, personal observation.

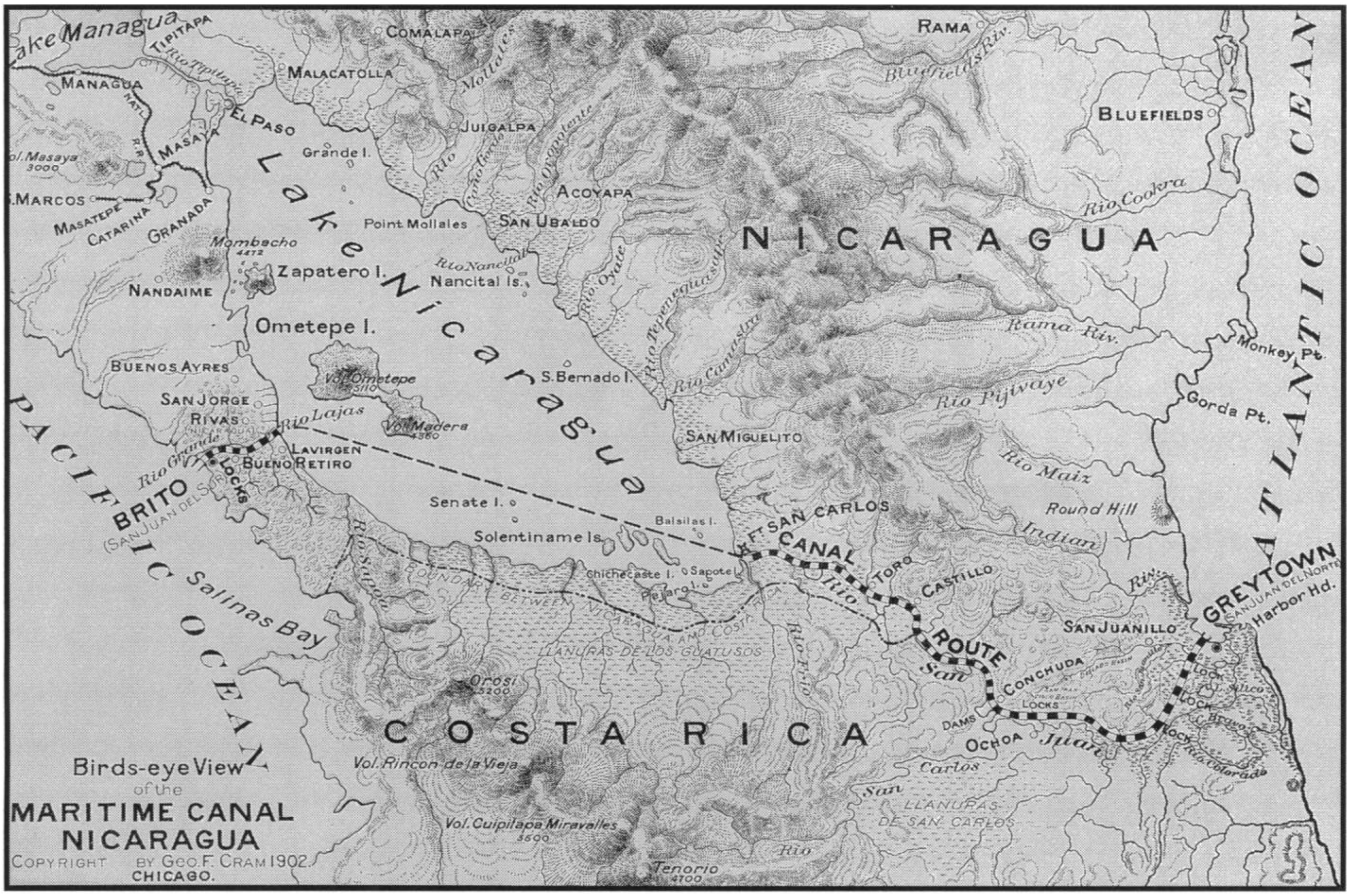

Figure 1. Map of the proposed canal route through Lake Nicaragua in 1902.

through the low-lying mountains of the Isthmus of Rivas (20 km wide at its narrowest section) to the Pacific Ocean (Figure 1). The project, however, never materialized. In 1903 Panama, with help from the United States, achieved independence from Columbia. The United States then took control of the construction of the Panama Canal and was no longer interested in a possible second canal.

During the Spanish colonial rule (1520–1821), Lake Nicaragua and the Rio San Juan served as the primary highway through which gold, cacao, indigo, and other products of Central America reached the Spanish galleons, which were constantly being pursued by British and other European buccaneers. Several times these pirates, including Sir Francis Drake, sailed up the Rio San Juan to attack Granada (located on the furthest northwestern shore of the lake), where our primary study sites are now located (Figure 1). During colonial times Granada was a world-renowned and exceedingly rich port, and thus a tempting target for pirates.

After the end of the colonial era, the possibility of an interoceanic connection and the emergence of the United States as a commercial power generated renewed interest in Nicaragua. With the discovery of gold in California in 1848, a rapid route to the gold fields was required, and Commodore Cornelius Vanderbilt, the US shipping tycoon, realized immediately the importance of a Nicaraguan route. He organized the Accessory Transit Company (ATC) and paid the Nicaraguan government $10,000 for the right to cross the country by river and lake. The creation of this new route would cut 800 km and several days off the trip of the anxious prospectors.

The first man-made alteration to Lake Nicaragua's ecosystem occurred at this time as Vanderbilt arranged for portions of the Rio San Juan to be dredged and for large boulders, sand bars, and other obstacles to be blasted away. Docks were built on both coasts and a 20-kilometer road was constructed to his new port of San Juan del Sur on the Pacific coast. Greytown (San Juan del Norte), located at the mouth of the San Juan River, was to remain the most important port in Nicaragua until the turn of the century (Incer 1976).

With the enhanced importance of the canal route came increased political interest by the great powers of the day—Great Britain and the United States. William Walker, a filibuster invited by the Nicaraguan Liberals, arrived in Nicaragua in 1855 and shortly thereafter declared himself president of Nicaragua. Walker's goal, with the support of men and material from the slave-owning US South, was to annex Nicaragua to the United States. His presidency was initially recognized by the US ambassador in Nicaragua. This initial recognition was subsequently withdrawn from Washington, DC, due to pressure from Great Britain and the Central American governments that recognized the Nicaraguan Conservative govern-

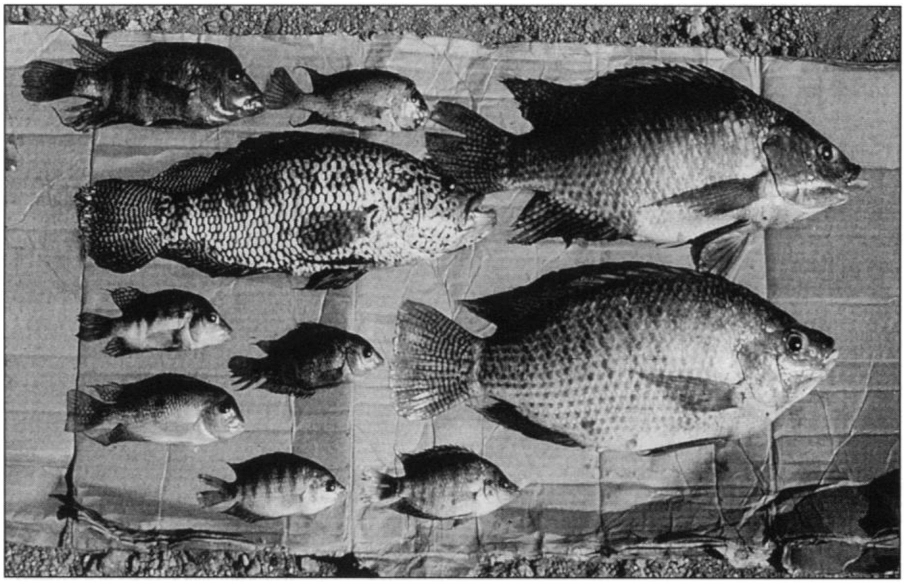

Figure 2. Common cichlids of Lake Nicaragua. The two large individuals on the right are African *Oreochromis* spp. All others are native to Lake Nicaragua.

ment. Nevertheless, it was to be the beginning of a long period of intervention of the United States in Nicaraguan affairs.

The following year, however, Walker seized the boats and other property of ATC in the name of the Nicaraguan government. His action caused a drop in ATC stock and infuriated Vanderbilt. This conflict had a profound effect upon the future history of Lake Nicaragua because thereafter Vanderbilt kept his ships idle and supported the Pacific Mail Line, which was doing business in Panama. Supplies and new recruits to man Walker's army in Nicaragua dried up, and the major route between the coasts shifted back to Panama. Walker, the only US citizen to ever be president of another country, eventually fell from power and was executed in 1860 by the army of Honduras when he tried to reconquer Central America.

At the end of the nineteenth century, competition over the location of an interoceanic canal became intense. Heavy lobbying of the bankrupt French Canal company headed by Ferdinand-Marie de Less resulted in the construction of the Panama Canal, and the Lake Nicaragua ecosystem was left untouched.

Nevertheless, the idea of a canal in Nicaragua never died. Modern ships grew larger, and traffic through the Panama Canal increased and need for a second canal became apparent after World War II. In the 1970s plans were drawn up to dredge the Rio San Juan and create major lake ports at Granada in Lake Nicaragua and the capital Managua in Lake Managua. Such plans, however were shelved with the coming of the Sandinista revolution in 1979.

Both Japanese and Soviet interest in a canal route in the 1980s stimulated research on the lake ecosystem, the results of which remain unpublished in the scientific literature[2] (MEPURSS 1983). A plan for a canal, however, was eventually presented by the Japanese with an estimated cost of $25 billion (Estrada et al. 1994). The US government began to view with alarm these initiatives for developing another canal outside of US control and continued to arm and aid the contra movement in its efforts to overthrow the Sandinista government.

Many proposals are still being considered, and even today the possibility of a canal through Lake Nicaragua and the Rio San Juan is a continuing dream of many Nicaraguans (Estrada et al. 1994). Any such project, be it a sea-level canal that turns Lake Nicaragua into a marine ecosystem or one that uses atomic explosives to dig a canal that requires locks (Estrada et al. 1994), is likely to have an immense and most likely detrimental impact on the ecosystem of this region.

Introduction of tilapia

Even without the construction of a sea-level canal, the Lake Nicaragua ecosystem is undergoing major changes. An attempt to increase the fishery and to develop an export market during 1983 and 1984 resulted in an extensive stocking program of non-native tilapia in Lake Nicaragua and cage culture of tilapia in a region known as the *isletas*, near Granada, Nicaragua (Figure 1). Between 1987 and 1988, fishermen in the Granada region began reporting catches of tilapia in their nets. They correlated the catching of tilapia with a decline in the catch of native cichlids (Figure 2). Local people initially avoided fishing for the introduced tilapia because their muddy taste was disliked. As tilapia populations increase, their potential impact on the unique Lake Nicaraguan ecosystem is becoming a source of concern.

A preliminary survey in 1990 re-

Table 1. Possible characteristics of potential invaders. Adapted from Ehrlich 1989.

Successful invaders	Unsuccessful invaders
Large native range	Small native range
Abundant in original range	Rare in original range
High genetic variability	Low genetic variability
Associated with humans	Not associated with humans
Female able to colonize alone	Female alone unable to colonize
Gregarious	Solitary
Vagile	Sedentary
Broad diet	Restricted diet
Short generation time	Long generation time
Shift between r and K strategies	Unable to shift strategy
Larger than most relatives	Smaller than most relatives
Tolerates wide range of conditions	Narrow range only

[2]The Nicaraguan Center for Fish Investigation, unpublished reports.

vealed that three species of tilapia—*Oreochromis aureus*, *Oreochromis mossambicus*, and *Oreochromis niloticus*—were being caught throughout the shallow coastal regions, including the southern islands of Solentiname and Lake Nicaragua's outlet on the San Juan River, near San Carlos (Figure 1). Collections in the northern region were taken at the *isletas* near Granada, the region of the first presumed introduction, and at a site near Pt. Mayales (Point Mollales in Figure 1). The more isolated region of Ometepe Island has subsequently been invaded by tilapia. As shown in Figure 3, at Ometepe Island native cichlids averaged 4.34 kg per 100 m of experimental net, a value comparable with the 4.66 kg (standardized per 100 m) that a 1983 Soviet study (MEPURSS 1983) found throughout the lake. Along the northern shore (*isletas* and Pt. Mayales combined), however, native cichlids averaged only 0.80 kg per 100 m. Of the total biomass of cichlids captured along the northern shore, 54% consisted of tilapia, whereas the tilapia made up only 1.5% of the catch at Ometepe. No tilapia had been collected in Lake Nicaragua during the Soviet study (MEPURSS 1983).

Furthermore, in our study the total catch of fish at Ometepe was 1.8 times greater per set than in areas with the higher concentration of tilapia. *Cichlasoma citrinellum*, *Cichlasoma nicaraguense*, and *Cichlasoma longimanus* were caught significantly more frequently at Ometepe Island than on the northern shore (Mann Whitney U: P<0.01; Figure 3). Catches of the primarily sand-dwelling *C. nicaraguense, C. longimanus,* and *Cichlasoma rostratum* and *C. citrinellum/labiatum* were inversely associated with catches of the tilapia species (Figure 4).

These data confirm the reports of Nicaraguan fishermen that native cichlid yields declined with the arrival of tilapia. These African exotics possess the attributes listed by Ehrlich (1989) as potentially contributing to the rapid expansion and success of invading species (Table 1).

Many of these tilapine fishes have large native ranges and are abundant in their natural habitat. Their high degree of morphological plasticity and genetic variability is demonstrated by the presence of several species that are endemic to particular areas (Fryer and Iles 1972, Trewavas 1983); furthermore, many of the species (e.g., *O. mossambicus*) have adapted to a multitude of environments and, in fact, occupy both freshwater and estuarine areas in their native ranges (Trewavas 1983).

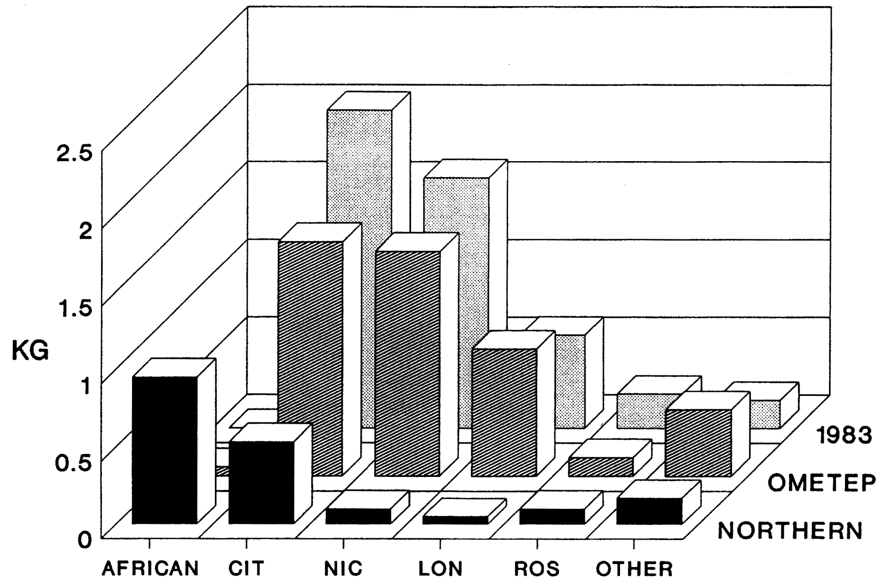

Figure 3. Average wet weight of cichlids captured by gill nets. Three sites were sampled 75, 9, and 12 times respectively for two 5-hour periods (0700–1200, 1300–1800) and one 12-hour period (1800–0600). The numbers of individuals and their standard lengths and combined weights were recorded for each species. NORTHERN = Northern Lake Nicaragua, 1991–1992; OMETEPE = Ometepe Island, central Lake Nicaragua, 1991–1992; 1983 = data from MEPURSS (1983, p. 79); AFRICAN = *Oreochromis* sp.; CIT = *Cichlasoma citrinellum*; NIC = *Cichlasoma nicaraguense*; LON = *Cichlasoma longimanus*; ROS = *Cichlasoma rostratum*; and OTHER = all other native cichlids.

Tilapine fishes are hardy and can thrive in a wide range of water qualities (Philippart and Ruwet 1982, Stauffer et al. 1984, Welcomme 1984). They have been domesticated by humans and are the primary species used in aquaculture throughout the tropics (Pullin 1991), and they are becoming increasingly important in temperate aquaculture facilities. For example, *O. niloticus* has been identified as an important species in global aquaculture (FAO 1980).

Many of the attributes that make these fish suitable organisms for intensive production facilities also allow them to colonize and thrive in new surroundings. They have rapid growth rates, broad diets, and the ability to withstand crowding (Hanley 1991). Most tilapine fishes are gregarious schooling species and are likely to migrate long distances (Fryer and Iles 1972, Stauffer 1984, Trewavas 1983). Introduced populations of tilapia, although primarily herbivores, feed on insects, zooplankton, phytoplankton, vascular plants, and larval/juvenile fishes (Hensley and Courtenay 1980).

Species in the genus *Oreochromis* are maternal mouthbrooders, thus a single female is able to colonize a new environment by carrying her young in her mouth (Fryer and Iles 1972). Furthermore, because they are mouthbrooders, they do not have strict habitat requirements for reproduction. Under laboratory conditions, we have observed them to spawn in gravel depressions and on clay pots, glass bottoms, and rock slabs. Introduced populations can literally occupy all available habitat with their spawning sites (Figure 5). Moreover, they are larger than all of the native cichlids (Figure 2) and are likely to displace them in territorial

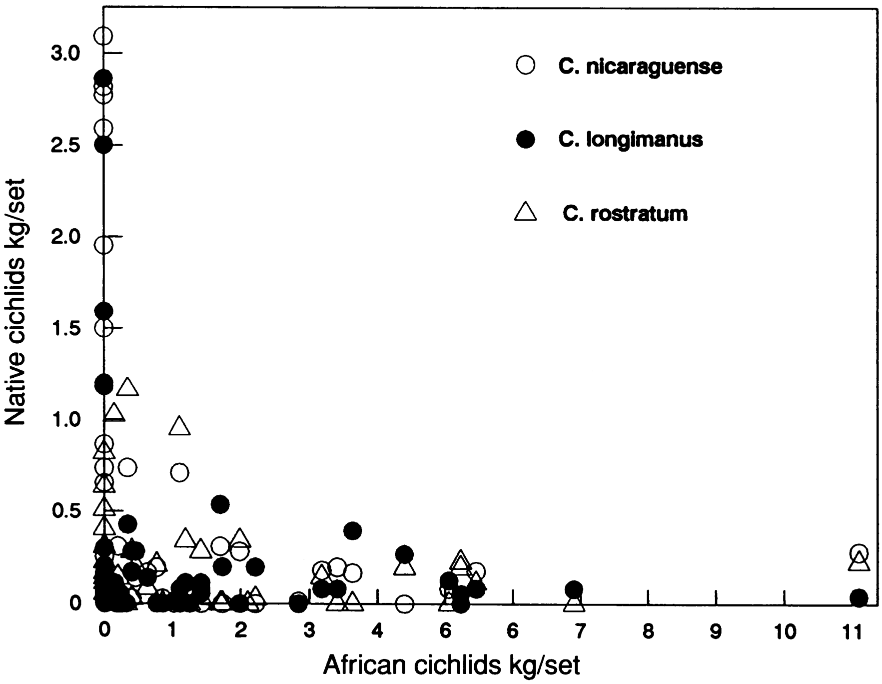

Figure 4. Weights of catches of each of the four native cichlids in relation to tilapia catches.

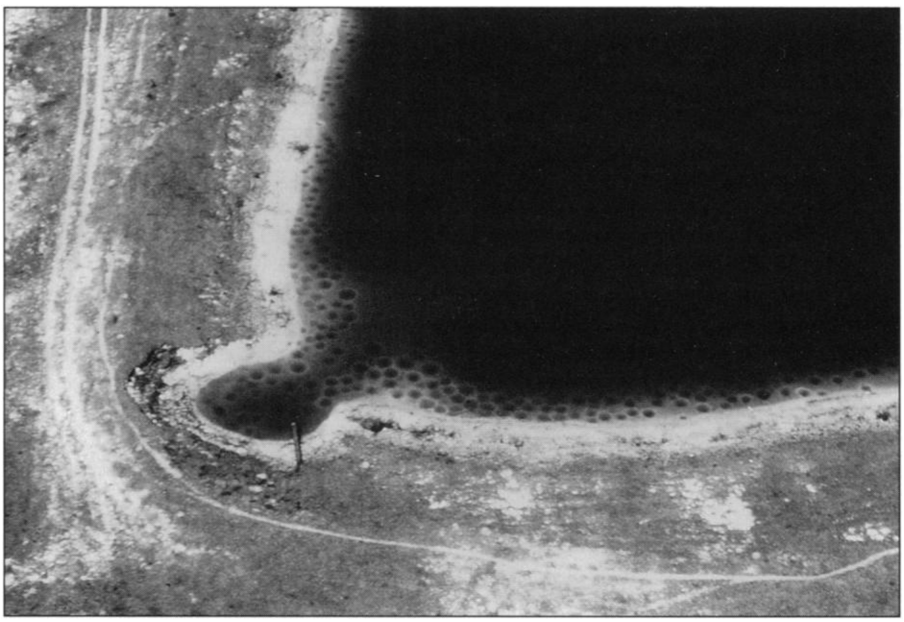

Figure 5. Aerial view of spawning sites of *Oreochromis aureus* in a lake in southern Florida. The spawning sites are depressions in the sand.

conflicts or severely interfere in the defense of their young (McKaye 1977, 1984, McKaye and McKaye 1977). Finally, they have a short generation time, reaching reproductive maturity in six months and having multiple broods each year (Stauffer 1984); or conversely they can delay reproduction and breed at larger sizes (Trewavas 1983).

We, therefore, predict that suitable habitat and food resources would be available to tilapia on the coral reefs found off the Nicaraguan coastline. In support of this contention, we note that *Oreochromis zilli* has established a population in the Salton Sea (Hensley and Courtenay 1980) and that *O. mossambicus* has invaded a Pacific atoll (Lobel 1980).

There is a great potential for an ecological disaster in Lake Nicaragua, such as those experienced in other tropical and semitropical freshwater ecosystems (Barel et al. 1985, Baskin 1992, Courtenay and Stauffer 1984, Zaret and Paine 1973). If these species move down the Rio San Juan and invade saltwater habitats along the Atlantic coast, the productive marine fisheries and valuable estuarine nursery grounds (Ryan 1992) could also be affected.

The presence of tilapia could directly affect not only Lake Nicaragua's fish community but also the general aquatic environment (Welcomme 1984). In Lake Victoria, for example, where the Nile perch, *Lates* sp., has devastated the native cichlid fauna, the entire ecosystem has undergone dramatic changes (Barel et al. 1991, Baskin 1992). Trophic cascade theory (Carpenter et al. 1985) predicts that the alteration of Lake Nicaragua's ecosystem is likely to have effects on the planktonic community and primary productivity of the lake. Besides the destruction of the native fish populations and loss of genetic diversity, the environmental degradation of Lake Nicaragua may have consequences not yet anticipated.

We still have cause for hope that the tragedy of Lake Victoria (Kaufman 1992) will not be repeated in the great lakes of Latin America. Twenty years elapsed from the time the Nile perch was introduced into Lake Victoria until it began eliminating the native cichlid population. Swift and aggressive management of tilapia in Latin America could mitigate the negative impacts of their introduction.

Immediate actions hypothesized to protect the native fauna include: the establishment of a fishery that focuses upon capturing tilapia in the coastal regions; the development of management plans to protect the large predatory marine species that inhabit Lake Nicaragua, because these fishes can easily prey upon adult tilapia that venture into open portions of the lake; and the monitoring of the Rio San Juan and the establishment of a tilapia fishery to prevent or slow the movement of the tilapia toward the Atlantic coast. Few fish species have been successfully eradicated once they have become established (Courtenay and Stauffer 1984, Stauffer et al. 1988). Therefore, it is key that markets and other economic incentives be provided to convince local fishermen to prey upon these exotics and thus keep their populations at a level that allows coexistence with the native species.

The value and importance of a unique ecosystem as diverse as that of Lake Nicaragua is well recognized (Norton 1986, Wilson 1988). The lesson of Lake Victoria (Baskin 1992, Kaufman 1992) is simple: Act now before it is too late.

Acknowledgments

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