Abstract We surveyed the watersheds covering more than 80% of the surface area of Nicaragua, and review the history of deliberate introductions and unintentional invasion of tilapias, Oreochromis spp., into the freshwater of Nicaragua. The species have become widely established, with a range of negative consequences for the rich natural fish fauna of this Central American country. Tilapias compete directly with native cichlids in a number of ways, and have also supplanted native species as food fish in local markets. We suggest that introduced tilapias may have been responsible for the outbreak of blindness in native cichlids. We make recommendations on the management of these exotic species and on further introductions.
Keywords Tilapia Æ Invasive species Æ Nicaragua Æ Fisheries Æ Aquaculture Æ Cichlids

Introduction

Nicaragua is noted as an especially poor country with dependency upon foreign influence in its development. Diverse and often contradictory development models for improving nutrition, food security and incomes have been implemented in Nicaragua during recent decades, repeatedly focussing on tilapia production, Oreochromis spp. (Cichlidae), over native freshwater species,[1] and often based on erroneous claims regarding tilapia impacts on native aquatic fauna (Hughes 2002; van den Berghe et al. 2003).

Stocking of Nicaraguan natural waters with tilapia, Oreochromis mossambicus, (Peters, 1852) was initiated in 1959 with a direct release into Lake Moyua´ (Riedel 1965), in spite of warnings

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[1] ADPESCA (2003) Anuario Pesquero Acuý´cola de Nicaragua 2002. Centro de Investigaciones Pesqueras.Y Acuý´colas, Managua, Nicaragua, 92 pp; MEDEPESCA (1996) Programa para el Desarrollo de Tecnologý´a Pesquera y Acuý´cola. Managua, Nicaragua, 90 pp; Olivares I (1992) Analizan efectos de ‘‘tilapias’’ africanas. p. 6 in La Prensa, 23 August, Managua, Nicaragua.

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ORIGINAL PAPER

Tilapia (Teleostei: Cichlidae) status in Nicaraguan natural waters

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concerning the potential impacts on the native fish fauna in Nicaragua (Myers 1955), and based on a flawed claim that the lake only contained one fish species (Riedel 1965; J. McCrary unpublished data). Its introduction corresponded to the disappearance of water lily, Nymphaea sp. (Nymphaeaceae), although other explanations were initally given for the disappearance (Riedel 1965).
Intentional tilapia releases into natural waters continued in the 1960s (for instance, Lake Asososca Leo´ n; per Villa 1982) and were approved by the Nicaraguan government again in the 1980s. The Sandinista government approved a stocking program of tilapia, Oreochromis aureus, (Steindachner, 1864) and the characid pacu Colossoma sp. (Bayardo Eslaquit, personal communication) in Las Canoas reservoir, from which the tilapias colonized the Lake Nicaragua-LakeManagua-San JuanRiver system. Within a few years, three species of tilapia, O. aureus, O. mossambicus, and O. niloticus, were employed in aquaculture operations in the Lake Nicaragua watershed without mechanisms to prevent their escape into the natural water system. Instead of increasing biomass and fishery resources, this introduction actually reduced the stocks of native cichlid species (McKaye et al. 1995).
A tilapia cultivation project was installed in Lake Apoyo in the 1980s, using hand-sexed male O. aureus in floating cages. Escapes were noted during the ensuing years, but the last documented sighting of a tilapia escapee from this project occurred in 1992 (Waid et al. 1999). However, another floating cage project, this time using androgen-induced ‘‘all-male’’ O. niloticus, was installed in Lake Apoyo during the mid-1990s; both male and female feral O. niloticus were later captured from Lake Apoyo (McCrary et al. 2001).
The escape of thousands of individuals from this project coincided with disappearance of extensive beds of the macroalgae Chara sp., a preferred food source for O. niloticus, and an outbreak of blindness among native cichlids (McCrary et al. 2001).
Negative environmental consequences of tilapia introductions in natural waters, including suppression or extinction of endemic fish species, have been increasingly recognized in Nicaragua and in other tropical countries (Canonico et al. 2005). Whereas tilapia cage culture, direct introductions, and other aquaculture methods with a significant risk of release of tilapias into natural waters is generally prohibited in warm waters in the developed world[2], cage aquaculture of tilapia is expanding in Lake Nicaragua[3]. In retrospect, the species introductions in Lake Nicaragua, Lake Moyua´ and in Lake Apoyo all constitute decisions founded upon inadequate information regarding the respective ecosystems and the invasive character of tilapia. To examine the status of tilapia in natural waters in Nicaragua, we conducted a series of ecological and market surveys, which are reported below.

Methods

Site descriptions and sampling techniques

Nicaragua is divided into 21 freshwater drainages, plus 12 closed freshwater lake systems (Fig. 1). The Atlantic versant contains long rivers, many associated with swampy, seasonally flooded marshes near the coast, and includes the Nicaraguan Great Lakes as part of the San Juan River watershed. Apart from the Estero Real, rivers in the Pacific versant are short, with marked temporality in flow rates. Volcanoes whose craters contain standing water constitute another set of freshwater ecosystems that are ecological ''islands'' occupied by several endemic fishes (Waid et al. 1999; Stauffer and McKaye 2002).

We sampled several rivers and lakes by gill netting and seining (Table 1; Fig. 1). We sampled Lake Moyuá, a natural lake located in a depression at 420 m above mean sea level (MASL), a total of five collections on the north side of the lake, 1 November 2001 and 10 November 2002, and we interviewed fishermen and identified their catch on 20 September 2003. We sampled Lake Apanás, a hydroelectric reservoir at 660 MASL in that empties via spillways into both the Matagalpa River watershed and a tributary of Lake Managua in the

[2] Florida Department of Agriculture and Consumer Services. 2000. Rule 5L-3 Aquaculture Best Management Practices, Tallahassee, FL, 77 pp.

[3] NICANOR S.A. 2000. Documento de Impacto Ambiental Proyecto ''Cultivo de Tilapia en Jaulas Flotantes en la Isla de Ometepe'', Altagracia, Rivas, Nicaragua, 130 pp.

San Juan River watershed, near Asturias on the southeastern corner of the lake, on 15–16 January 2004. We sampled the Bocay/Coco River watershed by seining at 5 points between Ayapal on the Bocay River and Wiwilý on the Coco River 6–8 February 2001 and 20–23 April 2004. The Estero Real watershed, containing more than 15 shrimpand tilapia-producing aquaculture enterprises, was sampled at 3 points on 31 December 2001 and 1 January 2002. We sampled the Wawa-Siksikwás River watershed and the Bambana-Prinzapolka River watershed, in northeastern Nicaragua, at four points each, at elevations not exceeding 100 MASL, during 25–30 April 2002; five points in small rivers in the Pacific versant along the Chiquito River-Cosiguina watershed at 90–100 MASL on 1 June 2002; the Escondido River at El Recreo by gill netting, 6 January 2004; several tributary streams in the Escondido River watershed, in central Nicaragua at 250 to 300 melevation, during 1–4 May 2002. We snorkeled 1 km of the Buen Suceso River, on Ometepe Island, inward from the mouth on 19 December 2001.

We evaluated the abundance of submerged vegetation, Chara sp. (Characeae) and incidence of blindness among fishes in two isolated volcanic crater lakes with hard, alkaline water (Waid et al. 1999), Lake Xiloá and Lake Apoyo, monthly from January 2001 through October 2003. We inspected Lake Apoyo for tilapia breeding activity by observation of bowers, examined the eyes of several blind specimens of the native cichlid fish A. c.f. citrinellus (Günther, 1864) for determination of the cause of a sustained outbreak of

Table 1 Natural water ecosystems of Nicaragua containing tilapias (*Oreochromis* spp.)

Watershed	Tilapia species present	% Surface area of Nicaragua
Riverine systems		
Estero Real[a]	*O. niloticus*	2.80
Coco/Bocay Rivers[a]	*O. niloticus*	15.16
Lacustrine/riverine systems		
Great Lakes/San Juan River[b]	*O.* spp.	22.50
Lake Apana´s/Matagalpa River[a,g]	Hybrid?	14.01
Lake Moyua´ (Matagalpa River)[a,e]	*O. mossambicus*	0.02
Crater lakes		
Lake Asososca Leo´n[c,d]	*O. mossambicus*	0.00
Lake Apoyo[a,d,f]	*O. aureus*	0.03
	O. niloticus	

[a]This study
[b]McKaye et al. (1995)
[c]Villa (1982)
[d]Waid et al. (1999)
[e]Riedel (1965)
[f]McCrary et al. (2001)
[g]Rene´ Cassells (personal communication)

Fig. 1 Map of watersheds of Nicaragua. 1: Estero Real; 2: Chiquito River/Cosiguina; 3: Great Lakes/San Juan River; 4: Indio River; 5: Escondido River; 6: Matagalpa River; 7: Bambana/Prinzapolka Rivers; 8:Kukalaya River; 9: Wawa/Siskiskwa´ s Rivers; 10 Coco River

blindness. We filmed tilapia activity above breeding bowers on four occasions in 2002 and 2003. Tilapias captured in this study were logged according to date and location captured, preserved in 10% formaldehyde and submitted to the collection of cichlids at the University of Central America in Managua.

Fish market and producer assessments

We reviewed the municipal fish markets in Masaya and Granada and interviewed several riverside fishermen/vendors along the San Juan River from San Carlos to El Castillo, on 24–30 May 2002. We estimated fish biomass by subsampling and interviewed the vendors at seven sales stands in Masaya and at eight stands in Granada. This represented approximately 50–75% of the vendors in each market. We interviewed a fishermen’s cooperative in San Carlos, on the southern edge of Lake Nicaragua, on 30 May 2002, and in Miraflores and Puerto Momotombo on Lake Managua, 24–27 March 2001. We conducted interviews at the fish market and with two fishermen and two exporters in Bluefields on 24 May 2004.

Results

We found tilapias inhabiting watersheds that cover 54.5% of the surface area of Nicaragua (Table 1). We found tilapias in abundance in the Coco/Bocay, Matagalpa, Estero Real, and Buen Suceso River watersheds, and in Lake Moyua´ , and as minor species in Lake Asososca Leo´n and Lake Apoyo. They now appear in the commercial catches in the brackish Pearl Lagoon in the lower Matagalpa River watershed, at least 350 km downstream from Lake Apana´ s, where they were apparently introduced. No tilapias were encountered in the watersheds listed in Table 2, which constitute 28.5% of the surface area of Nicaragua.

We filmed tilapias in pairs over bowers in Lake Apoyo on four occasions, at depths of 2–6 m over sandy bottom. Tilapias near bowers acted aggressively toward A. c.f. citrinellus (which compete for this habitat as foraging area) in two of the four observations, as earlier reported by McCrary et al. (2001). Bowers measured 40 cm maximum depth and 1–1.2 m in diameter. Bowers were reported in every month of the monitoring period.

We monitored the status of subaquatic vegetation in Lake Apoyo, which previously consisted of extensive Chara beds, which had disappeared after release of O. niloticus (Linnaeus, 1758) in the lake in the 1990s (McCrary et al. 2001). We found on four occasions small patches of Chara (approximately 4 cm diameter) inside the nest sites of A. c.f. citrinellus and Parachromis managuensis (Günther, 1869), in 2004. Chara sprouts rapidly disappeared, however, after the nest sites were abandoned, suggesting strongly that the native cichlids deterred tilapias from consuming the Chara while on nest. Several small metacercarial cysts of trematodes were found in the soft connective tissue at the posterior of the eyeballs in the blind fishes examined from Lake Apoyo. Whereas several blind fishes were found during all 22 excursions in Lake Apoyo, only two blind fishes were seen in the 22 dives in Lake Xiloá during this period.

Fresh fish sales at the two markets surveyed included the cichlids A. c.f. citrinellus, Astatheros longimanus (Günther, 1869), P. managuensis, Parachromis dovii (Günther, 1864), and Oreochromis

Table 2 Reviewed watersheds of Nicaragua in which tilapias have not been encountered

Watersheds	% Of surface area of Nicaragua in watershed
Riverine systems	
Indio River[b]	1.69
Escondido River[a]	8.85
Kukalaya River[a]	2.97
Bambana/Prinzapolka Rivers[a]	8.57
Wawa/Siksikwás Rivers[a]	4.08
Chiquito River/Cosiguina watershed system[a]	2.24
Crater lakes	
Lake Tiscapa[c]	< 0.01
Lake Asososca Managua[a,c]	< 0.01
Lake Xiloá[a,c]	< 0.01
Lake Masaya[a,c]	0.02
Lake Apoyeque[c]	< 0.01
Lake Monte Galán[c]	< 0.01

[a] This study
[b] Fabio Buitrago (personal communication)
[c] Waid et al. (1999)

spp. (tilapia); the eleotrid Gobiomorus dormitor (Lacépède, 1800); the elopid Megalops atlanticus (Valenciennes, 1847) (tarpon); and the pimelodid catfish Rhamdia guatemalensis (Günther, 1864). Tilapias constituted 31% of the fresh fish biomass in the Masaya fish market and 42% of the Granada market (Fig. 2). Tilapias were the second-largest cichlid in the Masaya market and the largest cichlid in the Granada market (Fig. 3). Whereas the Masaya market, largely serving local consumers, was dominated by the cichlids A. c.f. citrinellus, P. managuensis and tilapias in approximately equal proportions, tilapias andM. atlanticus dominatedthe Granada market. Three tilapia vendors in Granada reported sales of cleaned and gutted tilapia to wholesalers for resale in Guatemala, Salvador and Honduras, which was not reported in Masaya. All eight vendors interviewed in Granada reported that sizes of A. c.f. citrinellus for sale have dropped in the past years, reducing the marketability of the fish.The San Carlos fishing cooperative handled only frozen tilapia and M. atlanticus, for international sale.Local fishermen on the San Juan River sold native cichlids, but not tilapias.

Discussion

Tilapias have continued their southward progress of colonization of Lake Nicaragua to the southern shore, where few tilapias were captured in the early 1990s (McKaye et al. 1995). Although many watersheds in the Atlantic versant appear to be free of tilapias, three of the largest, the Coco River, the Matagalpa River and the San Juan River, all now contain tilapias. Time will tell if

0
10
20
30
40
50
A. citrinellus
A. longimanus
P. managuensis
P. dovii
Tilapias
G. dormitor
T. atlanticus
R. guatemalensis
% of total biomass
Masaya
Granada

Fig. 2 Proportions of fresh fish biomass, Masaya and Granada fish markets

0
1000
2000
3000
4000
A. citrinellus
A. longimanus
P. managuensis
P. dovii
Tilapias
G. dormitor
T. atlanticus
R. guatemalensis
weight, g
Masaya
Granada

Fig. 3 Weights of fresh fishes, Masaya and Granada Markets

tilapias migrate from one watershed to the next along the Atlantic versant via brackish lagoons and intra-coastal canals, which interconnect many of the rivers seasonally. Another important ecosystem is the volcanic crater lake system in which there continue to exist lakes without tilapia. Helminth parasites introduced with their cichlid hosts into aquatic ecosystems have the potential to switch hosts and infect endemic species, and dramatically affect a native fish population following a species introduction (Jime´nez-Garcý´a et al. 2001). This is illustrated by extensive mortality in populations of the local sturgeon, Acipenser nudiventris (Lovetsky, 1828), following introduction of the Caspian sturgeon, Acipenser stellatus (Pallas, 1711) into the Aral Sea (Combes 1996). The helminthic parasites of fishes should be included in an overall biodiversity assessment in Nicaragua before more severe disruptions in their communities occur (Brooks and Hoberg 2000).We suggest here that the outbreak of blindness among native cichlids in Lake Apoyo (see McCrary et al. 2001) is caused by trematode infection. The trematode issue in Lake Apoyo currently is under further investigation.

We show here that Chara beds, once abundant from 3 to 18 m depth (Barlow 1976), have disappeared from Lake Apoyo. The Chara beds, preferred breeding habitat for some of the native fishes, have been essentially eliminated from the lake for more than 5 years, much longer than the expected lifetime of these fishes. Tilapia may be edging out molluscivores from the lake, thereby promoting populational instabilities and propagation of trematode infections (Stauffer et al. 1997). Chara furthermore serves as important refugia for juvenile cichlids and serves important functions in substrate stability and water quality and its loss creates a risk of endemic cichlid species extinction. The ecosystem effects caused here by the tilapias coincide with theories of introductions (Fryer 1991) and in some cases were, in fact, predicted decades earlier (see Myers 1955; Riedel 1965).

Davies (1976) mentioned the presence of the cichlids P. managuensis, P. dovii, Parachromis friedrichsthalii (Heckel, 1840), A. c.f. citrinellus and Hypsophrys nicaraguensis (Agassiz, 1859) in local fish markets, of which two species were not found in our fish market surveys. Tilapias compete for breeding and/or feeding resources directly with H. nicaraguensis, P. dovii and some forms of A. c.f. citrinellus (McKaye et al. 1995). Both P. managuensis and P. friedrichsthalii and some forms of A. c.f. citrinellus likely breed upon macroalgal mats, which are reduced or eliminated by feral tilapias (see McCrary et al. 2001), which could explain the absence of P. friedrichsthalii and the reported smaller sizes of A. c.f. citrinellus from our present market survey. Elasmobranchs Carcharhinus leucas (Valenciennes, 1841) and Pristis perotteti (Linnaeus, 1758), now practically nonexistent in Lake Nicaragua, were once the principal commercial fishery products of the lake, and both species were sold in the local markets (Davies 1976). Gar, Lepisosteus tropicus (Gill, 1864), continues to be sold dried and salted in the local markets, most notably during the dry season (December–April). We did not encounter any sales of dried Atherinella sardina (Meek, 1907) from the Great Lakes, once common in Nicaraguan markets (Villa 1982).

Tilapias have clearly succeeded in the Nicaraguan Great Lakes ecosystem, and their presence has corresponded to a reduction in the number of species and in the market share of native species. The perceptions of vendors coincide with the earlier demonstration that native cichlid biomass correlates negatively with presence of tilapias in Lake Nicaragua (McKaye et al. 1995), although the link between tilapia introduction and the size reduction in mojarras is not proven. The dangers that tilapia may present in natural waters in Nicaragua are especially difficult to evaluate because native species inventories are not adequate in virtually any watershed. Without more detailed information on the niches of feral tilapias and native fishes in Nicaragua, the potential impact of tilapia introductions cannot be estimated conservatively, as recommended by Stauffer (1984).

Principle II of the Principles of Conservation of Wild Living Resources (Mangel et al. 1996) states: ''The goal of conservation should be to secure present and future options by maintaining biological diversity at genetic, species, population, and ecosystem levels; as a general rule neither the resource nor other components of the ecosystem

should be perturbed beyond natural boundaries of variation''. In Nicaragua and in many other developing countries, tilapia aquaculture is not consistent with this principle, given that tilapia are known to colonize tropical lacustrine and estuarine ecosystems with great ease, to cause marked changes in vegetation structure where they colonize, to accompany important changes in ecosystem structure and to depress local fish populations (Canonico et al. 2005). The presence of the A. c.f. citrinellus species flock with dozens of endemic species in waters potentially or already colonized by tilapia (McKaye et al. 2002) underscores the importance of adherence to this principle. The principle of avoidance of introductions as an extension of the precautionary approach is not new to biologists and aquaculturists. Prevention of practices that may lead to introductions is the most effective measure in almost any scenario of human activity (McNeely 2001) and has been specifically recommended for the aquaculture industry (FAO 1995a, b; ICES 1995; Bartley and Minchin 1996). Yet in poor, governmentally weak countries such as Nicaragua, avoidance of externalities is not well-developed, leaving the country open to risk-taking activities without accountability when environmental damage occurs (Jenkins 2001). Aquaculture activities are actively advocated by firstworld academics, businesses, and foreign government donors in Nicaragua (Engle et al. 2002), although biological invasions are generally an overlooked consequence of international trade (Low 2001) in spite of documented and potential impacts on biodiversity of releases of exotic species into natural freshwaters in the tropics (e.g., Hargreaves and Alston 1991).

Among the dangers of tilapia introductions is the difficulty of eliminating them, once they are established. Most management techniques to control undesired fish populations are not effective for control of tilapia (Stauffer et al. 1988), although a management program to increase the abundance of potential predators of large tilapias such as alligators, Crocodrilus acutus (Cuvier, 1807), gars and elasmobranchs, all vastly reduced in Lake Nicaragua from just a few decades earlier, has been recommended (McKaye et al. 1995).

There is potential for reducing the tilapia populations in Lake Apoyo by targeted netting given its lack of vegetation, limited tilapia habitats, and relatively small size. The sizes of tilapias encountered in the Masaya and Granada markets far exceed the sizes sought by the aquaculture industry, suggesting resource under-exploitation in Lake Nicaragua and its tributaries. Increased fishing pressure on tilapia would likely eliminate the larger fishes, which might aid in maintaining niche availability for native species without harming the marketability of the caught tilapia.

We agree with Riedel (1965), who stated many years ago regarding tilapia introductions in Nicaragua: ''A successful eradication programme, if so desired, appears extremely difficult, if applicable at all, when the financial requirements for such an action are taken into account.''

We recommend an immediate moratorium on activities that carry risks of tilapia introductions as per international guidelines, via the following steps: (1) totally closed systems should always be used when cultivating tilapia, and only in watersheds where tilapia have already penetrated; (2) tilapia aquaculture should be banned from watersheds and lakes in which tilapia have not become established; (3) augmentation of fishing pressure on tilapias in Lake Nicaragua to reduce the average fish size and thereby free niche space for other fishes; (4) limitation of use of tilapia in Nicaragua to those varieties proven to be already introduced into its natural waters, thereby limiting the genetic diversity of its feral stocks.

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