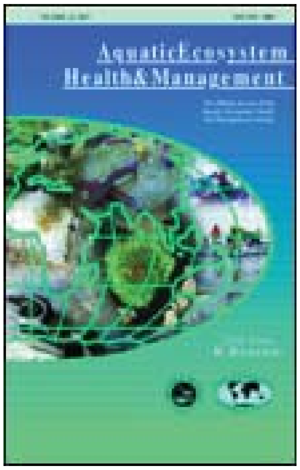

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The freshwater habitats, fishes, and fisheries of the Orinoco River basin

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The Orinoco River of Venezuela and Colombia is one of the great rivers of the world, ranking third by discharge after the Amazon and the Congo. In the Orinoco basin, riverine and floodplain habitats, including riparian forests, play key roles in the conservation of biodiversity and support commercial, sport, and subsistence fisheries. The basin's three major floodplains regulate the amplitude and duration of floods, maintain fertile agricultural terrain, provide habitat for numerous terrestrial and aquatic species, and support the fishery. The fish fauna, which includes some 1,000 species, encompasses a great deal of ecological diversity in terms of geographic distributions, habitat affinities, functional morphology, and reproductive and feeding strategies. The Orinoco fishery is still multispecific, with around 80 different species found in the fish markets at different times of year. Current estimates indicate that annual sustainable yield is 40,000 – 45,000 metric tons. Fish culture in the region is underdeveloped despite decades of research and promotion. There is no serious commercial trade for ornamental fishes. Large regions of the Orinoco basin are still in a relatively pristine state, but aquatic resources are increasingly threatened by habitat destruction, overharvesting, pollution, and hydrological perturbation. Scientific understanding of diversity hotspots, critical habitats, and conservation status of fishes in the basin is currently insufficient to satisfy management needs. Compliance to fishery regulations is low and fishing is drastically modifying the relative abundance, population structure, and distribution of fish stocks. However, many sectors of the Orinoco basin are unexploited or only lightly exploited, and fish stocks can recover quickly if given the opportunity. Stricter enforcement of current fishery regulations would reduce the likelihood of stock collapses and other, possibly irreversible, changes in the fishery.

Keywords: Aquatic resources, conservation, ecology, management, neotropical, floodplain, Venezuela

Introduction

The Orinoco River basin is a vast reservoir of natural resources. Aquatic habitats in the basin support commercial, sport, and subsistence fisheries, and harbor tremendous biodiversity, including various species of emblematic value for conservation initiatives, such as the Orinoco crocodile, the Arrau

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sideneck turtle, the Caribbean manatee, freshwater dolphins, and the giant river otter. As well, the Orinoco basin is inhabited by many indigenous cultures that derive sustenance from its resources. Although vast areas within the basin have been historically subjected only to mild anthropogenic pressures and are still in a relatively pristine state, threats from habitat destruction, overharvesting, pollution, and hydrological perturbation are rising.

This article summarizes the state of knowledge on the freshwater habitats, fishes, and fisheries of the Orinoco River basin, with particular attention to the region within Venezuela, which accounts for 71% of the total basin area. The focus is primarily on (1) the aquatic habitats of the Orinoco main stem, its tributaries, and their floodplains; (2) fish systematics, ecology, and conservation; and (3) fisheries and fish culture, including current legislation.

Overview of freshwater resources, freshwater fish fauna, and freshwater fisheries of the Orinoco basin

The Orinoco River of Venezuela and Colombia is one of the great rivers of the world, ranking third by discharge (38,000 $m^3\ s^{-1}$) after the Amazon and the Congo. The environmental and biotic components of the Orinoco River ecosystem are described in Weibezhan et al. (1990), the proceedings of a symposium on large South American rivers published in 1990 as a special issue of the journal Interciencia, Vol. 15(6), and Lewis et al. (2000).

The Orinoco River basin extends over 1.1 million km^2 and covers 84% of Venezuela's territory. The basin is bounded on its entire southern margin by the Rio Negro, a major Amazon tributary, and on the north and west by coastal drainages of the Andes (Figure 1). The southern side of the drainage is almost entirely accounted for by the Guayana Shield in the states of Bolívar and Amazonas, which consists of thoroughly weathered crystalline basement rock. To the north and west, the Orinoco is flanked for a distance of several hundred kilometers by alluvial deposits of Andean origin. Toward the periphery of the watershed, beyond these deposits, the northern and western headwaters of the Orinoco rise in the Andean montane zone at elevations above 3000 m.

The southern part of the Orinoco basin (Guayana Shield and western portion of Andean montane and alluvial zones) has high annual precipitation (1,000–4,000 mm y^{-1}), whereas the alluvial zones of the north are semiarid. The area-weighted precipitation of the entire basin (2,000 mm y^{-1}) is approximately equal to that of the Amazon basin (Lewis et al., 1995). The wettest portions of the watershed (generally to the south) consist of tropical moist forest, whereas the low-elevation portion of the northern half of the watershed is primarily savanna grassland (Figure 2). Precipitation in the Orinoco basin shows strong seasonality. River discharges throughout the watershed increase from approximately April to August and decrease thereafter to a plateau that lasts approximately two months (February, March). The annual range in water levels for the Orinoco lower main stem is approximately 12 m.

The taxonomically rich fish fauna of the Orinoco basin encompasses a great deal of ecological diversity in terms of geographic distributions, habitat affinities, functional morphology, and reproductive and feeding strategies. The morphological diversity encompassed in local fish assemblages of the high plains ("Llanos") is greater than that observed in fish assemblages in comparable habitats in North America, Central America, and Africa (Winemiller, 1991). The latest published species lists (Taphorn et al., 1997; Lasso et al., 2004a) include some 1,200 freshwater fishes, most of them from the Orinoco basin. Machado-Allison (1993) provides an overview of the natural history, ecology, and biogeography of the fishes of the Venezuelan llanos.

Novoa (1982, 1989, 2002) reviewed the status of commercial fisheries in the Orinoco River. The largest inland fishery in Venezuela is centered at San Fernando de Apure in the western llanos. The Orinoco River and its marginal lakes, wetlands, and tributaries also support commercial fisheries, with major markets located in Puerto Ayacucho, Guasdualito, Bruzual, Caicara del Orinoco, Maripa, Ciudad Bolívar, Ciudad Guayana, and Barrancas. A great variety of species are exploited, with dominant fishes in the harvest varying according to region and time of year.

The most important sportfishes in Venezuela are the pavones, or peacock cichlids (*Cichla* spp.). Their ecology, distribution, and conservation challenges were summarized by Winemiller (2001). Other popular sport fishes include the payara (*Hydrolycus armatus*) and large pimelodid catfishes including the bagres rayados (*Pseudoplatystoma fasciatum, P. tigrinum*), valentón (*Brachyplatystoma filamentosum*), and cajaro (*Phractocephalus hemioliopterus*). These species remain common in rivers of the llanos,

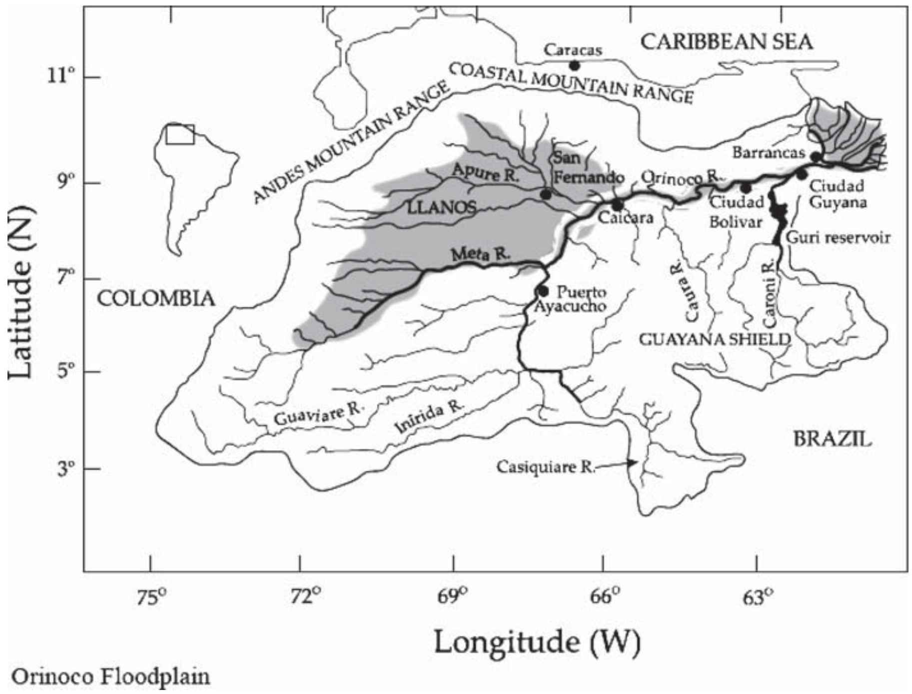

Figure 1. Map of the Orinoco River basin, showing major geographic regions, tributaries, cities, and the three major types of floodplain (internal delta, fringing floodplain, and Orinoco delta). The extent of the inundation on the internal delta was kindly provided by S.K. Hamilton (Michigan State University).

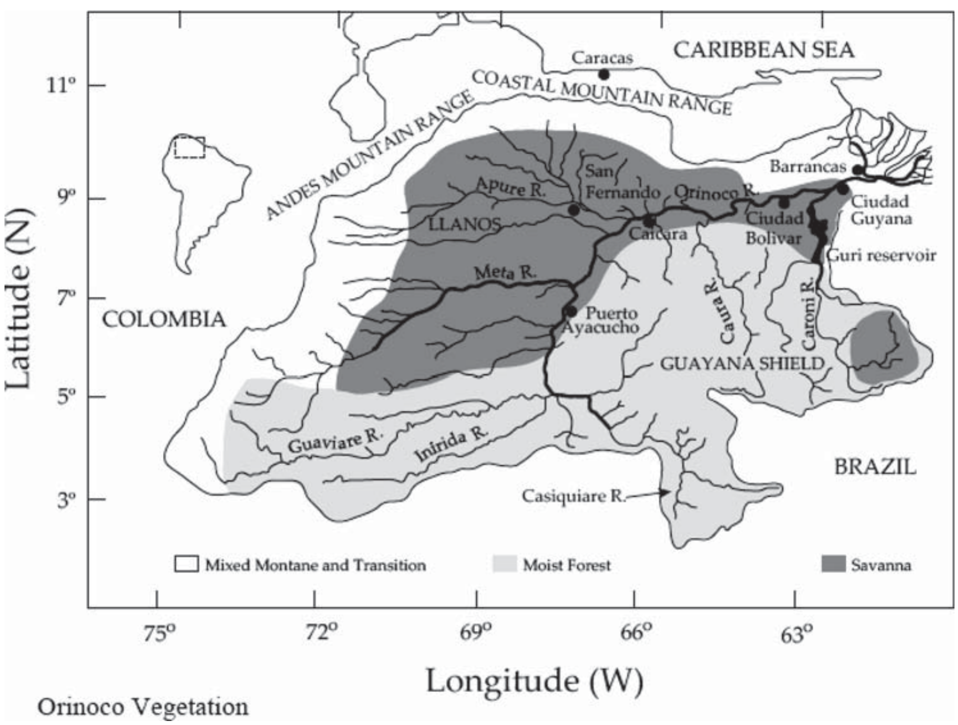

Figure 2. Map of the Orinoco River basin, showing the distribution of major vegetation types.

Guayana Shield, and Amazonas. Two migratory characids, the saltador (*Salminus hilarii*) and the palambra (*Brycon whitei*), are also popular fish with anglers.

Fish culture centers on the cachama (*Colossoma macropomum*) (reviewed in Ginelly, 1990), which dominates commercial production, and the exotic "tilapias" (includes *Tilapia*, *Oreochromis*, and *Sarotherodon* spp.). Cultivation of cachama and its hybrid with the morocoto (*Piaractus brachypomus*) has been practiced for many years.

There is no serious commercial trade for ornamental fishes in Venezuela. Ornamental fishes have been harvested from the wild by a few companies, but these ventures have not persisted, probably because of administrative hurdles to exportation. Trade statistics are not reliable because an unknown and possibly large proportion of all exportation is made illegally via Colombia from the Amazonas region. However, overexploitation does not seem to be a major concern because operations are on a relatively small scale.

State of freshwater science in the Orinoco Basin

Habitats of the Orinoco River and its tributaries

Aquatic habitats available to fishes and other aquatic organisms vary partly by climate and geomorphology and partly by stream order. Lakes are rare, except on floodplains; there is only one large reservoir (Guri, on the Caroní). The small streams of the Guayana Shield are predominantly canopied and have relatively low gradient, with the notable exception of streams and rivers that flow from the edges of tepuys. The waters from the south are predominantly darkly colored by dissolved organic matter of terrestrial origin ("black waters"), although some are clear waters as well. Major tributaries emerge from the canopy, but are generally deep because of the abundance of rainfall and, because they are primarily darkly colored, do not efficiently transmit irradiance to the substrate. Also the substrate is often fine and mobile, which reduces habitat diversity for both fish and benthic invertebrates.

To the north, tributaries of small to intermediate size flow at high gradient from the flanks of the Andes over substrate of moderate to high coarseness beneath waters that typically are highly transparent except at times of highest flow, when turbidity intercepts light. Thus, the benthic habitat is suitable for a diversity of both fishes and aquatic invertebrates. On the alluvial plains, the gradients are low. The seasonal turbidity of these "white waters" can be high (Saunders and Lewis, 1988), but the smaller amounts of runoff per unit area and the large amount of moving alluvial material in the channels promotes the development of shallow stream channels that can produce benthic algal growth at low flow and often are connected to off-channel waters that diversify aquatic habitat.

The white waters contain large amounts of dissolved and suspended solids produced by rapid weathering in the Andes. In contrast, the black waters flow primarily through the Guayana Shield, which has been weathered so extensively that it yields only small amounts of suspended and dissolved solids. Because it receives both white-water and black-water tributaries, the Orinoco is a mixture of water types of sharply contrasting physical, chemical, and biological characteristics.

Floodplains are habitats of great consequence to the aquatic fauna and flora of the Orinoco basin. There are three major types of floodplains within the Orinoco basin (Lewis et al., 1995; Figure 2). The Orinoco delta ($\sim$21,000 km^2) consists mainly of floodplain overlying deltaic deposits and dissected by a large number of distributary channels. Aquatic grasses predominate in the freshwater portions of this floodplain, about which very little is known.

Along the main stem, extending from the delta to the Apure (approximately 600 km), a fringing floodplain ($\sim$700 km^2) encompasses both banks but is considerably wider on the north than on the south. The fringing floodplain is approximately 79% canopied. The uncanopied portion of the fringing floodplain corresponds to 2300 topographic depressions that can be called floodplain lakes. They are joined with each other and with the surrounding canopied areas at high water, but are isolated during the dry season. Within the uncanopied areas, *Paspalum repens*, an aquatic C4 grass, is the dominant vascular plant, although other vascular plants are present as well. *Paspalum* provides critical physical habitat for floodplain invertebrates and fishes (Lewis et al., 2000; Valbo-Jørgensen et al., 2000). Although water persists within the lakes during the prolonged seasonal drought (approximately 100 days), habitat space shrinks at this time to a small percentage of its annual maximum. Thus, fishes and other aquatic organisms must contend with strictly lacustrine conditions of the dry season, but also may exploit resources on the floodplain at large during the interval of full inundation. Benthic environments of the Orinoco floodplain typically are oxygenated, and thus are more habitable than similar environments of the Amazon, which may become anoxic (Lewis et al., 1995). Accumulation of organic sediment is negligible on the floodplain because of high oxidation rates; the substrates of the floodplain lakes are primarily fine and inorganic.

The third floodplain of the Orinoco consists of an large internal delta near the Apure River (~70,000 km^2) that forms as seasonal floodwaters moving toward the main stem are impeded by the high volume of water in the main stem. Thus impounded, the water fills depressions and spreads over much of the landscape, where it provides temporary aquatic habitat over many thousand square km to the north of the Orinoco main stem. These shallow ephemeral habitats are highly productive during the wet season. As rainfall and floodwaters subside drying pools often become anoxic, with struggling fishes providing an abundant food resource for birds and crocodilians.

In the main stem of the Orinoco itself, habitat for fishes and invertebrates is limited. If found in the main stem Orinoco at all, most fish species in the basin seem to use this habitat for dispersal between backwaters and tributaries. Nonetheless, a comparatively small community of specialized fishes feeds within lotic waters of the main stem (Lundberg et al., 1987; Barbarino Duque and Winemiller, 2003).

Multiple sources of carbon are available to primary consumers on the Orinoco floodplain: phytoplanktonic and periphytic algae, macrophytes, litterfall, and organic matter transported by the river. Trophic flows from primary producers to top consumers on the Orinoco floodplain have been analysed by means of estimation of P:B ratios combined with trophic-level analysis through stable isotope tracers (Lewis et al., 2001). Strikingly, although macrophytes and litter jointly account for ~98% of total available carbon, production of both fish and invertebrates on the floodplain is supported primarily by algal carbon. Many fish of the Orinoco floodplain have adaptations for feeding directly on algae, a nutritious source of carbon that accounts for approximately 20% of fish production, or on herbivorous invertebrates, which account for most of the remaining 80%. Fish production is thus derived mostly from the 1st and 2nd trophic levels, rather than at and above the 2nd level as is more usual for fishes in pelagic ecosystems. Food webs of the Orinoco floodplain and its major tributaries (Jepsen and Winemiller, 2002) therefore show marked food chain compression, which is the only means of sustaining high fish production on such a small fraction of the potentially available carbon.

Current state of knowledge of Orinoco fishes

Venezuelan and Colombian ichthyologists have collaborated on a complete revision and update of the list of freshwater fishes of the Orinoco basin, including lists for each major Orinoco tributary (Lasso et al., 2004b). The most current estimate places the species richness for the Orinoco basin at 995 fish species, of which 939 are found in Venezuela and 627 in Colombia (Lasso et al., 2004a, b), but new species are being described every year. Nearly 85% of the species, including those most important to fisheries and aquaculture, fall within three major orders, the Characiformes, Siluriformes, and Perciformes (Table 1).

Within the Orinoco basin, two basic biogeographic divisions of the ichthyofauna can be recognized, each associated with a distinctive water type. The first division is found in the sediment- and nutrient-rich whitewaters concentrated in the northern portion of the drainage, such as the Apure and Meta Rivers, whose watersheds originate in the Andes Mountains. The second division is found in clear to blackwater rivers with low productivity and biomass, but relatively high fish diversity, mostly in the southern portion of the drainage, in isolated pockets of sandy or lateritic soils in the llanos, and draining the Guayana Shield. Preliminary attempts have been made to explain observed distributions (Chernoff et al., 1991; Lasso et al., 1991; Pérez and Taphorn, 1993), but biogeographical analyses for many groups are still limited by poor knowledge of alpha taxonomy. The depth of taxonomic coverage varies considerably across groups. Detailed monographs are available for some groups, e.g., the caribes or piranhas (Machado-Allison and Fink, 1996), whereas the state of knowledge for other groups is poor even at the familial level.

Venezuelan fishes occupy a broad range of ecological niches that represent the full range of consumer trophic positions in aquatic food webs. Some species feed exclusively or opportunistically on seeds/fruits, macrophytes, algae, wood,

Table 1. Distribution of Orinoco fish species among orders, family, and genera (modified from Lasso et al., 2004b). Species important to fishery or aquaculture are listed also.

Order	Families	Genera	Species	Fishery or aquaculture species
Anguilliformes	2	2	3	
Batrachoidiformes	1	1	1	
Beloniformes	2	5	8	
Characiformes	14	124	399	*Brycon* spp., *Colossoma macropomum*, *Hydrolycus armatus*, *Mylossoma* spp., *Piaractus brachypomus*, *Prochilodus mariae*, *Semaprochilodus kneri*, *S. laticeps*
Charchariniformes	1	1	1	
Clupeiformes	3	12	20	
Cyprinodontiformes	4	12	27	
Elopiformes	2	2	2	
Gymnotiformes	5	24	59	
Lophiiformes	1	1	1	
Myliobatiformes	6	9	12	
Osteoglossiformes	1	1	2	
Perciformes	15	65	126	*Cichla* spp., *Plagioscion squamosissimus*
Pleuronectiformes	3	5	11	
Pristiformes	1	1	2	
Scorpaeniformes	1	1	1	
Siluriformes	12	150	314	*Brachyplatystoma* spp., *Phractocephalus hemioliopterus*, *Pseudoplatystoma fasciatum*, *P. tigrinum*
Synbranchiformes	1	1	1	
Syngnathiformes	1	2	2	
Tetraodontiformes	1	2	3	
Total	77	421	995	

zooplankton, terrestrial arthropods, fish fins, fish mucus, or blood. This high degree of feeding specialization is assumed to allow for greater species coexistence during intervals of resource scarcity in seasonal aquatic habitats. Most fish assemblages that have been investigated at small spatial scales also reveal significant partitioning of space and time (Arrington and Winemiller, 2003; Willis et al., 2005), and marked daily fluctuations in activity patterns have been documented for individual species (Rodríguez et al., 1990). At larger spatial scales, fish assemblages are strongly patterned, with species distributions segregating to varying degrees according to longitudinal position in river gradients (Hoeinghaus et al., 2003, 2004), lateral position in floodplain rivers (Barbarino Duque and Winemiller, 2003), or water type (Rodríguez and Lewis, 1997; Jepsen and Winemiller, 2002).

At the watershed scale, fish distribution patterns are strongly associated with landscape characteristics and water quality features. Water type is a particularly strong predictor of ichthyofaunal assemblages. Suites of species are affiliated with blackwater (low pH, low conductivity, intermediate transparency), clearwater (variable pH and conductivity, high transparency), or whitewater (high pH, high conductivity, low transparency) lakes, rivers and streams. In some cases, geographic barriers limit fish dispersal, but in many other cases water quality features appear to limit dispersal and gene flow (Turner et al., 2004). Taxonomic structure of fish assemblages of the Casiquiare region (river connecting the headwaters of the Orinoco and Negro/Amazon basins) is significantly associated with a longitudinal clearwater-blackwater gradient (Winemiller et al., unpublished). Species primarily restricted to black waters of the Amazonian forests in southern Venezuela (e.g., the cardinal tetra, *Paracheirodon axelrodi* and the Orinoco angelfish, *Pterophyllum altum*) are sometimes encountered as isolated populations in small blackwater tributaries of the Orinoco located hundreds of kilometers to the north in the vicinity of Puerto Ayacucho.

Fish assemblages of Orinoco floodplain lakes are structured by causal relationships connecting piscivory to transparency and transparency to lake morphometry (Rodríguez and Lewis, 1997). During the dry season, fish with sensory adaptations to low light are dominant in turbid lakes, whereas fish relying on vision predominate in clear lakes. Piscivores modify assemblage structure by culling the most vulnerable prey species. Vulnerability in turn is strongly related to transparency and to the sensory and foraging capabilities of individual species. Transparency at low water is predictably related to the depth and size of lakes: resuspension of sediment leading to turbidity occurs at specific thresholds of depth and fetch. In addition to its role as a determinant of transparency, lake morphometry affects vulnerability through the relationship between lake relative depth and availability of structural cover. Furthermore, prey species may be able to use lake morphometry as an indicator of predation intensity, and predators may select lakes that are most compatible with their mode of predation. Although assortment of fish among lakes seems largely unpatterned at the onset of the dry season, assemblages are molded by predatory interactions that are intensified by the shrinking volume of lakes during the dry season (Rodríguez and Lewis, 1994). Assemblage structure is thus strongly deterministic in the dry season because lake morphometry channelizes the outcome of interactions between predators and prey in the same way from year to year.

Most fishes move between aquatic habitats on a seasonal basis, and this behavioral pattern is particularly prevalent in floodplain regions where annual flood pulses create and destroy shallow aquatic habitats (Arrington et al., 2005). Local fish assemblages in floodplain creeks are influenced by local-scale movements in response to variation in water quality and availability of habitats for feeding, sheltering, and reproduction (Winemiller, 1996a; Winemiller and Jepsen, 1998; Hoeinghaus et al., 2003). Fish assemblages in floodplain lakes show marked interannual stability despite strong seasonal fluctuations in abundance that are driven by movements between the lakes and adjacent floodplain (Rodríguez and Lewis, 1990, 1994). Some of the most important fishery species perform seasonal, long-distance migrations of several hundred kilometers (Saldaña and Venables, 1983). Most notable are the annual migrations of the coporo between rivers draining the Andean piedmont and lowland rivers of the western llanos (Lilyestrom, 1983). During the early wet season, ripe coporos migrate from these rivers to the lowlands where they spawn in midriver and then remain to feed in rain-swollen rivers and seasonal wetlands. During the falling-water period (November-January), huge schools of coporos and several other migratory species such as the mije (*Leporinus friderici*), morocoto, and bagres rayados, participate in "ribazones" (annual migrations at the end of the flood season) where they move upstream then gradually disperse within major tributary rivers (Barbarino Duque et al., 1998).

Current status of freshwater fisheries and fish culture

The Orinoco fishery is still multispecific, with around 80 different species found in the fish markets at different times of year, but the bulk of the harvest consists of prochilodontids and pimelodid catfishes. Novoa (1989) reported that commercial fisheries of the Orinoco basin expanded during the 1980s accompanied by shifts from large pimelodid catfishes to greater proportional reliance on migratory prochilodontids. Novoa previously calculated an estimated annual yield of 40,000–45,000 metric tons for the Orinoco River and noted that yields appear to be correlated with intensity of annual floods. The multispecies fishery yields were estimated at about 12,000 metric tons in the mid 1980s. Between 1984 and 2000, INAPESCA, the Venezuelan national fishery agency, reported annual harvests of 16,000–60,000 tons, representing between 3–12% of the country's total fishery production (Novoa, 2002). A comprehensive foodweb analysis yielded an estimate of 79,000 metric tons for total fish production on the Orinoco floodplain (Lewis et al., 2001). This value supports Novoa's estimate of annual yield, which represents just over half of total fish production, as an upper limit for harvests in the Orinoco fishery.

The western llanos of Venezuela is an important nursery area for major commercial species such as the coporo, bagres rayados, mije, and morocoto. Coporos and bagres rayados dominate fisheries in San Fernando and other areas in the western llanos (Apure-Arauca basin). The main stem Orinoco River yields large catches of catfishes (*Brachyplatystoma* spp.), morocoto, palometas (*Mylossoma* spp.), payara, palambra (*Brycon* spp.), and prochilodontids. The fishery of the Caura River is dominated by the morocoto and bagres rayados, but at least 27 species comprised an estimated 250 metric tons of fishe harvested annually (Vispo et al., 2003). Slightly less than half of the annual harvest was taken by subsistence fishers.

The fishery has drastically modified the relative abundance, population structure, and distribution of fish stocks in the Orinoco basin. Overharvesting of large fishes began with the arrival of nylon seines over 30 years ago and has been compounded recently by habitat destruction and the doubling of Venezuela's population in the last 25 years. Patterns of human consumption have responded to selective reduction or depletion of fish stocks. Caribes, doradid catfishes, and payara, once considered "trash" fish and discarded from catches, are now common in markets because previously preferred species have disappeared or become rare and expensive.

Spatial shifts in the fishery have occurred at several scales. Near fishing centers, the largest species of commercial fishes are now scarce or absent, and fishers are required to make longer journeys and stay out more days to fill their boats. At larger scales, the commercial fishery for prochilodontids has shifted and is now concentrated in the lower portions of the Orinoco tributaries. Highland rivers with dams or dykes and irrigation canals that block migration have lost significant portions of their prochilodontid populations (Barbarino Duque et al., 1998). Agricultural development has led to extensive deforestation and concomitant sedimentation of the upper sections of rivers draining the Andes mountain range. The dry season is more severe and extended, permitting fishers to completely fish out these smaller rivers. These conditions, along with peak demand for fish for Holy Week during the dry season, have caused severe overexploitation. The practice of blocking rivers downstream with large seines to harvest the blocked migrators with cast nets has contributed to declines in population sizes and earlier maturation in the prochilodontids.

The effects of overharvesting generally are most notable in the upper sections of the Orinoco basin. On the delta, catch per unit effort has actually increased in the last 25 years, but the composition of the catch has changed over the same period (Novoa, 2002). The largest predatory species are now caught at much smaller sizes or have disappeared completely from the commercial harvest, but stocks of smaller detritivores and herbivores are still healthy in the delta.

Most sport fishing in Venezuela centers on the pavones. Five *Cichla* species occur in the country, but only three (*C. intermedia*, *C. orinocensis*, and *C. temensis*) appear to be widespread. Pavón populations appear to be highly sensitive to overharvest, and this is probably a function of their occupation of unproductive ecosystems, their reproductive strategy involving nesting and parental care, and their trophic position as top predators. Overharvest has been a serious problem in all areas with good access to anglers and net fishers. In recent years, pavón populations in remote areas in Amazonas (Casiquiare region) and the Guayana Shield (Caura and Caroní rivers) have begun to be exploited more heavily. Impressive pavón fisheries in the Aguaro River and Las Majaguas Reservoir were destroyed after only about a decade of illegal fishing activity.

The saltador, a predatory characid, is a sport fish that was once common in rivers of the Andean piedmont but has now been nearly eliminated by overfishing, deforestation and siltation, and dam construction (Winemiller et al., 1996). The saltador has a migratory life history similar to the coporo in this region. Blockage of migration routes by dams is particularly damaging to these species. The palambra, another migratory characid, has been reduced in numbers due to dams and other human impacts in this heavily populated region of Venezuela (Lilyestrom and Taphorn, 1983).

Cachama hatcheries have been in existence in Venezuela since the 1970's (Ginelly, 1990). Most stations use earthen ponds to cultivate the cachama, but cage culture has also produced positive experimental results. Artificial feeds incorporating industrial byproducts and locally produced ingredients are the key to successful commercialization.

Several species of cultivated tilapia have escaped into the wild. Use of these exotics poses a serious potential threat to native species and the integrity of the ecosystems on which they depend. Expecting extraordinary profits and high production, many farmers abandoned the cachama in favor of tilapia. Unfortunately, there was little appreciation for the pitfalls associated with tilapia culture: reproduction of commercial numbers of these mouth-brooders is expensive, labor intensive, and time consuming. Although tilapias were first introduced into Venezuela in 1959, the currently cultivated variety, red tilapia, is a relative newcomer.

Survey of freshwater management in the Orinoco basin

Water quality and fisheries laws in Venezuela

A regional development agency, the Corporación Venezolana de Guayana (CVG), is a major player in environmental management in the lower Orinoco basin. The agency is responsible for planning, promoting, and implementing projects in agriculture, forestry, mining, tourism, urban development, and water resources. Historically, there has been a lack of concerted efforts by CVG and other governmental institutions to manage water quality and discharges with conservation as an explicit aim. In 1995, new regulations were created that tightened the standards for treatment of effluents (BOD; solids) prior to release into natural waters. However, these regulations contain a "grandfather" clause which provides exemptions from environmental rehabilitation and the aluminum industry, among others, has legally discharged effluents into natural lakes. Without remedial treatment, the pollutants accumulated in the lakes may be sporadically washed into the river by extreme floods.

The Ministry of Agriculture (MAC) is responsible for management of the fisheries in Venezuela, including stock assessment, issuing of permits, and regulation of fishing gear and effort. Unfortunately, harvest regulations are often violated by all sectors of society throughout the country. Law enforcement entities make occasional citations and arrests of illegal netters, often confiscating nets and boat motors, but these are too few and infrequent to create an environment of widespread deterrence.

Although more than 70% of all fishery harvests in Venezuela are captured by rural fishers using traditional gear, the relatively low value of these fisheries has led to official neglect. Both the MAC and the Ministry of the Environment (MARNR) have assumed roles in regulating the harvesting of fishes, sometimes with conflicting objectives and ineffective results. Between 1999 and 2001, legislators established regulations that permitted harvests during reproduction and migration phases and were thus highly detrimental to the fishery. This undesirable situation might be corrected under the newly enacted fishery law (Novoa, 2002).

Linkages with biodiversity conservation and ecosystem management

Riverine and floodplain habitats, including riparian forests, play a key role in conservation of biodiversity in the Orinoco basin. For example, the floodplain regulates the amplitude and duration of floods, maintains fertile agricultural terrain, provides refuge and feeding or breeding grounds for numerous terrestrial and aquatic species, and supports the fishery. Strategies for preserving aquatic habitats and biota in the basin will be more likely to succeed if they account for and adapt to local needs and constraints. In the llanos, the development of ecotourism ventures on private lands managed for ranching of cattle and capybaras (large cavimorph rodents) has proven economically viable. Similar management schemes, encouraging conservation by the landowners, could be promoted to maintain key aquatic habitats in a natural state even as economically profitable activities develop around these areas.

Conservation of aquatic habitats in Venezuela is fostered by the existence of a network of protected areas (ABRAE, or areas under special administration regime), which collectively cover two thirds of the country's territory. Most of these areas, though, afford only nominal protection because they are not actively managed or monitored. The categories of protected areas most relevant to conservation, National Parks, Natural Monuments, Faunal Refuges, Faunal Reserves, and Biosphere Reserves (26% of Venezuelan territory), are concentrated in the southern part of the Orinoco basin and the Orinoco delta. With some exceptions, surveillance and control of fishing in protected areas is minimal or altogether lacking, even within the National Parks. Protected areas therefore probably contribute to the maintenance of aquatic biodiversity mostly by preventing large-scale degradation of the watersheds from forestry, urban development, and mining.

Although most of the Orinoco basin is relatively unaltered physically, the conservation status of fishes and the state of local fisheries is correlated with human presence. The most deteriorated regions in the Orinoco basin are the once extensively forested Andean piedmont regions and high plains regions in the states that border the Andes mountains in the north, Apure, Barinas, Portuguesa, Cojedes, and Guárico, and the eastern plains of Anzoátegui, Monagas, and Delta Amacuro. Agriculture and cattle ranching are extensive in these regions and deforestation has reached over 80% of original existing forests (Winemiller et al., 1996). In the still sparsely settled southern Apure state and the rivers draining the Guayana Shield, the vegetation has suffered less and rivers are in better shape. However, gold mining in many rivers of Bolívar and Amazonas has contaminated the water and the aquatic food chain with mercury.

Conservation of biodiversity has been hindered by an almost exclusive focus by fisheries managers on harvest, with little attention to preservation of a diversified fishery, genetic integrity, and balanced trophic structure (including large predators). Although maximum sustainable yield perhaps has not been attained in the Orinoco fishery, various indicators point to overexploitation for almost all of the large predatory catfishes. Though still classified as a low technology fishery, the use of nylon seines pulled by small boats or canoes with outboard motors and cast nets has greatly increased fishing efficacy and contributed to the decline of stocks of large catfishes. Declining mesh sizes in the commercial seines indicate that the larger individuals are no longer present in commercially attractive quantities. There is evidence that commercial netting is also causing reductions in the average size and age at maturity. In the Orinoco delta, threats to biodiversity include trawling of channels and use of unselective fishing gear, which result in habitat destruction and high by-catches and discarding of non-commercial species.

Management success stories

Regrettably, Venezuela provides few examples of specific management practices that have protected or enhanced stocks of freshwater fishes or their natural habitats. We are only able to cite a couple of exceptions: the pavón sport fisheries of the Cinaruco River, forming the border of Santos Luzardo National Park, and Guri Reservoir, where access is controlled by EDELCA, a government-run mining and power company. In both cases, local sportfishing interests were sufficiently motivated to request increased enforcement of fishing laws. Protection of pavón stocks was the primary concern. Sometimes aided by donations of boats, motors, and fuel from sportfishing groups, the Guardia Nacional was able to periodically patrol these areas, which provided a degree of deterrence. Following recent political and social conflicts in Venezuela, these patrols have all but stopped, and illegal net fishing has increased in both areas. The law was recently changed to allow commercial fishing of pavón for the first time in Venezuela, and this is certain to have negative impact on populations.

The creation of dams, while devastating to migratory fishes, has created new habitat for lentic-adapted sport fishes, especially the pavones. New pavón fisheries have been established in reservoirs within piedmont regions of the Andean and Coastal mountain ranges. These reservoirs bring a valuable new fishery resource to people in areas having the highest human population densities. Unfortunately, these fisheries are no better regulated than those of the rivers, and, following the initial production burst after reservoir formation, pavón populations have been depleted by illegal fishing over intervals as short as a decade (e.g., Las Majaguas Reservoir in Cojedes state).

Conclusions

Science and management: Summary overview and priority gaps and needs

Scientific understanding of diversity hotspots and critical habitats in the Orinoco basin, including their distribution and the ecological processes that maintain them, is currently insufficient to satisfy management needs. Various knowledge gaps hamper the management of freshwater resources in the Orinoco basin. For example, basic data on population status, demographic parameters, and genetic structure are unavailable for most fish species. Only 13 fishes are listed (all risk categories combined) in the second edition of the Venezuelan Red List of threatened animals (Rodríguez and Rojas-Suarez, 1999), up from five in the 1995 edition. A minority of the 13 species is from the Orinoco basin and the rest are from densely populated areas near the coast. The sparse representation of Orinoco fishes in the Red List probably reflects current lack of knowledge on population status rather than true absence of risk. Various potentially effective and relatively inexpensive tools for evaluating and managing freshwater resources, such as biotic metrics of habitat quality (indicator species; indices of biotic integrity) and rapid assessment protocols, still await development and implementation in Venezuela. The feasibility of rapid biological appraisals to map diversity and assess management needs is illustrated by the Aquatic Rapid Assessment Program (AquaRAP) conducted recently (2000) in the Caura River basin.

Management priorities for fishes in the Orinoco basin are associated with four major threats: deforestation, dams, overfishing, and pollution (summarized in Winemiller et al., 1996). The introduction of exotic species, such as tilapias, can be added to this list of threats most of which now exist throughout the country. Deforestation has perhaps the most widespread and far-reaching impacts on aquatic life within the Orinoco basin. Deforestation in the Andean piedmont results in erosion and siltation of streams and rivers, greater solar radiation and stream desiccation, and alteration of instream habitats and food webs. Deforestation has the same effects in the llanos and Amazonian/Guayana Shield regions; however, siltation is usually not as extensive in these regions.

Dams have multiple impacts on rivers and aquatic life, including alteration of natural hydrologic regimes and nutrient cycles, reduction of sediment transport, and blockage of fish migrations. Alteration of river hydrological regimes in Venezuela has serious consequences for fishes, most of which are adapted for seasonal spawning in response to seasonal flood pulses (Winemiller, 1989). Dams tend to reduce flows in downstream reaches during normal high-flow periods, and often increase flow during the annual dry period that normally has low flows. Seasonal, or periodic, spawning fishes depend on annual floods for spawning cues and creation of seasonal wetlands in floodplains that function as nursery areas. Dams also trap sediments and nutrients, especially in whitewater ecosystems. These rivers normally show high primary and secondary productivity in low-velocity habitats within channels and floodplains. Lentic habitats of whitewater rivers generally support dense growth of emergent and floating aquatic macrophytes, that in turn support high densities of aquatic invertebrates and fishes, especially juveniles.

As discussed above, overfishing is a serious problem throughout Venezuela. Most of the major commercial and sportfish stocks already have been fully or overexploited throughout their ranges. Only populations in remote regions of the Guayana Shield and Amazonas have escaped heavy exploitation by commercial and subsistence fishers. Large piscivorous catfishes and pavones tend to be the first species to show signs of overharvesting (i.e., reduced average size and stock abundance). The coporo and other species that mature in 1-2 years and produce large numbers of eggs seem to withstand harvesting better, but even these populations have been reduced in areas where gillnets stretched across the river channel can catch virtually every migrating individual. Fish populations in the western llanos seem to be relatively resilient to fishing pressure, probably because these populations normally experience explosive growth and catastrophic decline in concert with habitat changes and ecological dynamics derived from the annual flood pulse (Winemiller 1996a, b). Fish populations in unproductive blackwater rivers appear to be more sensitive to exploitation (e.g., pavón discussed above).

Pollution in Venezuela derives from several sources, most of which have severe negative impacts on fish stocks. In the Guayana Shield, large mining operations for bauxite, iron, and gold cause siltation and introduce toxic chemicals and elements into rivers. In regions exploited by gold miners, mercury contamination poses a particularly acute threat to fishes and other aquatic organisms (Nico and Taphorn, 1994). Organic waste from sewage and agriculture results in severe aquatic hypoxia in several rivers and streams in Venezuela. Sugar cane processing plants in the western llanos release large amounts of liquid organic waste into streams that provide critical dry-season habitat for a great diversity of fishes (Winemiller et al., 1996). Normally, adult fishes from these dry-season refugia move into seasonally flooded marshes to spawn during the rainy season. Thus, induction of severe hypoxia during the dry season has the potential to completely extirpate entire populations from watersheds.

Future trends and potential for habitats, fishes, and fisheries

More than half of the population in southern Venezuela lives in poverty, and this region is therefore a high development priority for the country. The decline of opportunities in the large northern cities has led to massive migrations to the Guayana region of people seeking new economic opportunities. Three zones potentially threatened by rapid development in the future merit special notice. First, aquatic environments in the scarcely populated delta will likely be degraded by the development of infrastructures (dredging, channeling of wetlands, road construction, drainage networks, and peat mining), and burning and clearcutting of forests to create agricultural land and rangeland. Second, the Orinoco oil belt, which spans the states of Guárico, Anzoátegui, Monagas, and Delta Amacuro, contains huge reserves of extra-heavy oil and bitumen. The belt may be soon subject to large scale exploitation, especially given the increasing worldwide demand for oil. Extractive activities pose the risk of oil spills, salinization of soils, and hydrological alterations. Finally, plans for building a hydroelectric dam in the south-eastern Caura River, a pristine region of high biodiversity, or to divert the Caura's waters to the Caroní River, have been under study for a long time. Additionally, dredging is planned to improve navigation along both the Orinoco, which accepts ocean-going vessels, and the Apure rivers. In addition to encouraging development in unaltered sectors, such plans may degrade aquatic and floodplain habitats, release pollutants stored in the sediments, modify erosion and siltation patterns, affect groundwater flow, and promote saltwater intrusion in the delta. Use of low-draft vessels may reduce the need for dredging.

In spite of recent successful efforts to modernize fishery legislation, the lack of institutional will to enforce the law bodes for a bleak future of Venezuela's inland fisheries. Near major fishing centers such as San Fernando de Apure, Cabruta, and Barrancas, attempts to implement the fishery law have been ineffective. As a result, fishers operate out of season, use nets with illegal mesh sizes, and capture fish below the legal size limits. The gradual but continual decline in harvests seen in the last decades will likely worsen under these conditions. There is, however, some reason for hope because many sectors of the Orinoco basin are only lightly exploited or unexploited. Furthermore, fishes adapted to the annual pulse of the wet and dry seasons typical of the entire Orinoco drainage can recover lost habitat and recover from low population sizes quickly if given the opportunity. Timely enforcement of fishery regulations can help prevent stock collapses and other, possibly irreversible, changes in the fishery.

Fish culture in Venezuela is still underdeveloped despite decades of research and promotion, partly because of the absence of strong research centers with steady funding. Commercial ventures in cultivation of cachama and red tilapia are hindered by the unavailability of high quality fingerlings and absence of extension programs to provide advice and guidance on fish culture. Extensive cultivation of these species by small scale producers could effectively promote fish culture while lessening risk to the environment.

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