

Ecology of peacock cichlids (*Cichla* spp.) in Venezuela

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ABSTRACT

Despite the fact that peacock cichlids (*Cichla* spp.) are important food and game fishes, little research has been conducted on native fluvial populations in South America. Here I review ecological information obtained for *Cichla* species based on recent research in Venezuela. *Cichla* are essentially restricted to waters of high transparency where they often are dominant diurnal piscivores. Within Venezuela, *Cichla orinocensis* is the most widely distributed species, and up to four species may coexist in certain rivers of the Río Casiquiare Basin in Amazonia. In Venezuela, *Cichla ocellaris* is restricted to the Río Cuyuní Basin, and *Cichla* cf. *monoculus* is restricted to the Casiquiare and upper Orinoco Basins. In certain rivers, up to three *Cichla* species coexist by partitioning available habitats: *Cichla intermedia* are near structure in the river channel within or near swift current, *C. orinocensis* in shallow water near the margins of lagoons and slow river reaches, and *Cichla temensis* in somewhat deeper areas of lagoons and the river channel, often near banks. *Cichla orinocensis* and *C. temensis* in blackwater rivers of the Amazon region are larger on average when compared to conspecifics in the savanna (llanos) region of the Orinoco Basin. Nonetheless, conspecifics from diverse locations conform to the same length-weight regression and have similar growth rates. *Cichla temensis* and *C. orinocensis* have been successfully introduced into Venezuelan reservoirs, where *C. temensis* tends to inhabit deeper water.

Cichla are substrate nesters with biparental care of eggs and fry lasting up to several weeks. In fluvial systems, reproduction is initiated during low-water conditions and continues into the flood period. Males of all species form nuchal humps, and both sexes have more intense coloration during the reproductive period. Characiform and perciform fishes are the major prey, and food partitioning has been documented in both reservoirs and rivers, especially during the low- and rising-water periods. *Cichla orinocensis* had a broader diet and showed less seasonal shift in diet composition than *C. temensis* and *C. intermedia* in the Río Cinaruco. In Guri Reservoir, *C. temensis* feeds more on characiforms and less on cichlids than *C. orinocensis*. Peacock cichlid populations seem to be very sensitive to fishing pressure. Given their high abundance, broad diets, and high feeding rates, peacock cichlids may have a strong influence on prey populations, especially in oligotrophic blackwater ecosystems.

INTRODUCTION

Peacock cichlids (*Cichla* spp.) are among the most widespread and conspicuous predatory fishes of lowland rivers within the large drainage basins of tropical South America. They are called pavón in Venezuela, tucunaré in most other parts of South America, and peacock bass by some English speakers. Peacock cichlid is the official common name designated by the American Fisheries Society, however this name is also used in the aquarium hobby for certain African rift lake cichlids. By most accounts, these are the largest representatives within the Cichlidae, with only

the Lake Tanganyika piscivore, *Boulengerochromis microlepis*, possibly attaining a larger maximum size than *Cichla temensis* (>12 kg).

The popularity of peacock cichlids as sportfishes derives from their ecological niche as voracious diurnal piscivores. The ferocity with which peacock

cichlids attack baitfishes and artificial lures and the power and tenacity of their resistance after being hooked is now legendary among anglers. With increasing frequency, peacock cichlid sportfishing stories are published in newspapers, magazines, books, and internet web sites worldwide. This popularity has had the unfortunate consequence of resulting in intentional introductions of *Cichla* species in tropical and subtropical freshwater systems around the world, sometimes to the detriment of native fish populations. Exotic populations of *Cichla* have been established in reservoirs of Hawaii (Devick, 1969), Panama (Zaret and Paine, 1973), Puerto Rico (Lilyestrom et al., 1994) and Brasil (Godinho et al., 1994), and canals in Florida (Shafland, 1993). Peacock cichlids also have been used in native regions to control densities of exotic tilapia in pond cultures (McGinty, 1984; Fisher and Grant, 1994)

The capacity for exotic peacock cichlids to alter, via predation, communities and entire ecosystems has been demonstrated. In the 1970s, the introduction of *Cichla ocellaris* into Lake Gatún, a man-made reservoir in Panama, resulted in massive changes in community composition, the structure of the aquatic food web, and even components of the terrestrial community (Zaret and Paine, 1979). A similar scenario of aquatic community transition followed the introduction of *Cichla orinocensis* and *C. temensis* into Las Majaguas Reservoir in Venezuela (Barbarino, 1986; Winemiller, 1989).

Paradoxically, this group of cichlids has been the focus of relatively little research. Until very recently, most of the published studies reported on exotic populations, mostly in reservoirs. Zaret (1980) presented life history information for *C. ocellaris* in Lake Gatún, Panama. Characteristics of *C. ocellaris* in Hawaiian reservoirs were summarized in technical reports (Devick 1969, 1972), and life histories of peacock cichlids in fish farms were investigated in Brasil (Fontenele, 1950; Braga, 1952, 1953). Aspects of the ecology of peacock cichlids inhabiting native rivers appear in Lowe-McConnell (1969), Goulding (1980), Goulding et al. (1988), and Cala et al. (1996). Descriptions of populations in Venezuelan reservoirs

appear in Novoa (1993), Ochoa Iturbe (1993), and Gil et al. (1993). Zaret (1977) and Winemiller (1990) discussed the adaptive function of the caudal ocellus, or eyespot (a dark spot with a well-defined light ring around it), in *Cichla*.

Over the past 12 years, my colleagues and I have studied fluvial and reservoir populations of peacock cichlids in Venezuela. Much of this research was conducted in Venezuela's Río Cinaruco (Orinoco drainage in southern llanos of Estado Apure) between 1989 and present. In addition, we examined *Cichla* in the Río Casiquiare and its tributaries (Río Negro-Amazon drainage) between 1993-1999, Río Aguaro between 1995-97 (Estado Guárico), Guri Reservoir (Río Caroní, Estado Bolívar) between 1993-4, Las Majaguas Reservoir (Río Cojedes, Estado Portuguesa) from 1984-1994, and the Modules of Apure (a system of dikes and ponds in Estado Apure) and adjacent Caño Caicara from 1982-1995. Although much additional research is needed, it is now possible to summarize and compare information to improve conservation of this ecologically and economically important cichlid.

TAXONOMIC DIVERSITY AND BIOGEOGRAPHY

According to Kullander (1986), the genus *Cichla* is distinguished by a large mouth with a forward projecting lower jaw, a large laminar infraorbital bone joined tightly to the lachrymal; a notched dorsal fin (spine length increases until the 5th and decreases posteriorly until the penultimate, the last spine longer and tightly joined with the soft-rayed portion of the dorsal fin which is as high as the spinous portion); micro-gill rakers on both sides of all arches, with spines on exposed surfaces; and scaly fins, except for the pectorals. In addition, all *Cichla* >100 mm standard length (SL) have a distinct caudal ocellus (Kullander and Nijssen, 1989). Stiassny (1982) diagnosed the genus with four shared, derived characters of skeleton and musculature, and in a later analysis (Stiassny, 1991) concluded that the neotropical pike cichlids (*Crenicichla*) were their closest relatives. Kullander's (1998) consensus tree from maximum parsimony analysis of the Cichlidae showed the neotropicals as polyphyletic and grouped *Cichla* with *Crenicichla* near the base of the main neotropical cichlid radiation. A more recent analysis based on mitochondrial DNA (Farias et al., 1999) grouped *Cichla* with *Astronotus*

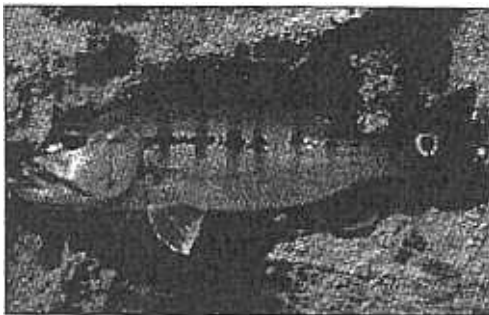
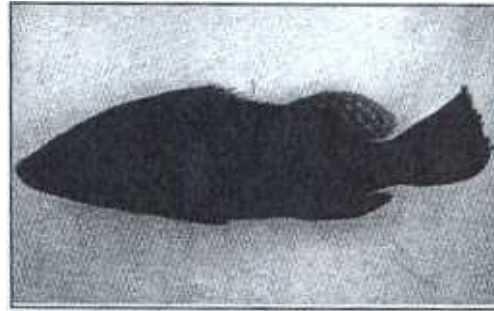
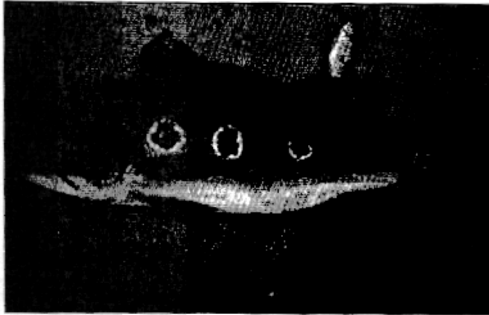
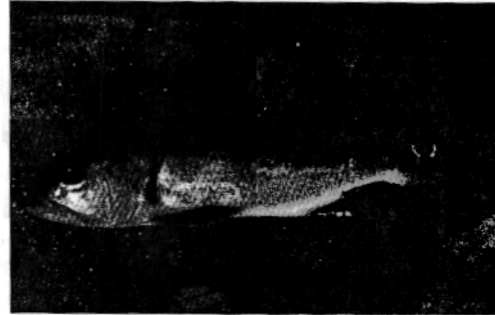
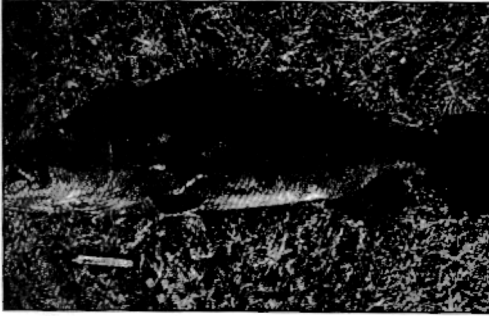


Figure 1. *Cichla* species documented in Venezuela: *C. temensis* (male in breeding condition, Río Pasimoni, Estado Amazonas) (left top), *C. orinocensis* (Río Pasimoni) (left center), *C. intermedia* (Río Cinaruco, E. Apure) (left bottom), *C. cf. monoculus* (Río Emoni, E. Amazonas) (right top) and *C. ocellaris* (preserved specimen, Río Cuyuní, E. Bolívar) (right center).

rather than the crenicichlins, and also concluded that neotropical cichlids were monophyletic as assumed previously (Stiassny, 1991).

Five *Cichla* species are currently recognized by systematists, but several additional species from the Amazon Basin apparently require description (Kullander, 1986; Kullander and Nijssen, 1989). Kullander (1986) indicated that five species were valid, but more recently suggested 11 taxa (Kullander and Nijssen, 1989). To date, the largest number of coexisting *Cichla* species have been found in the upper Río Orinoco and upper Río Negro Basins in southern Venezuela (Machado, 1971; Winemiller unpublished data). This region lies on the western fringe of the Guyana Shield and harbors some of the richest aquatic and terrestrial diversity of fauna and flora on earth (Goulding et al., 1988; Berry et al., 1995).

All five recognized species are known from Venezuela (Fig. 1): *C. ocellaris* Schneider (Cuyuní Basin), *C. orinocensis* Humboldt (Orinoco, Casiquiare-Negro), *C. temensis* Humboldt (Orinoco, Casiquiare-Negro), *C. intermedia* Machado 1971 (Orinoco, Casiquiare-Negro), and *C. cf. monoculus* Spix (Casiquiare-Negro). The geographic range of each species within Venezuela is illustrated in Figure 2, with populations established in reservoirs represented as dots. *Cichla orinocensis* and *C. temensis* are the most widespread within Venezuela, and range throughout the Río Negro Basin and into other rivers of

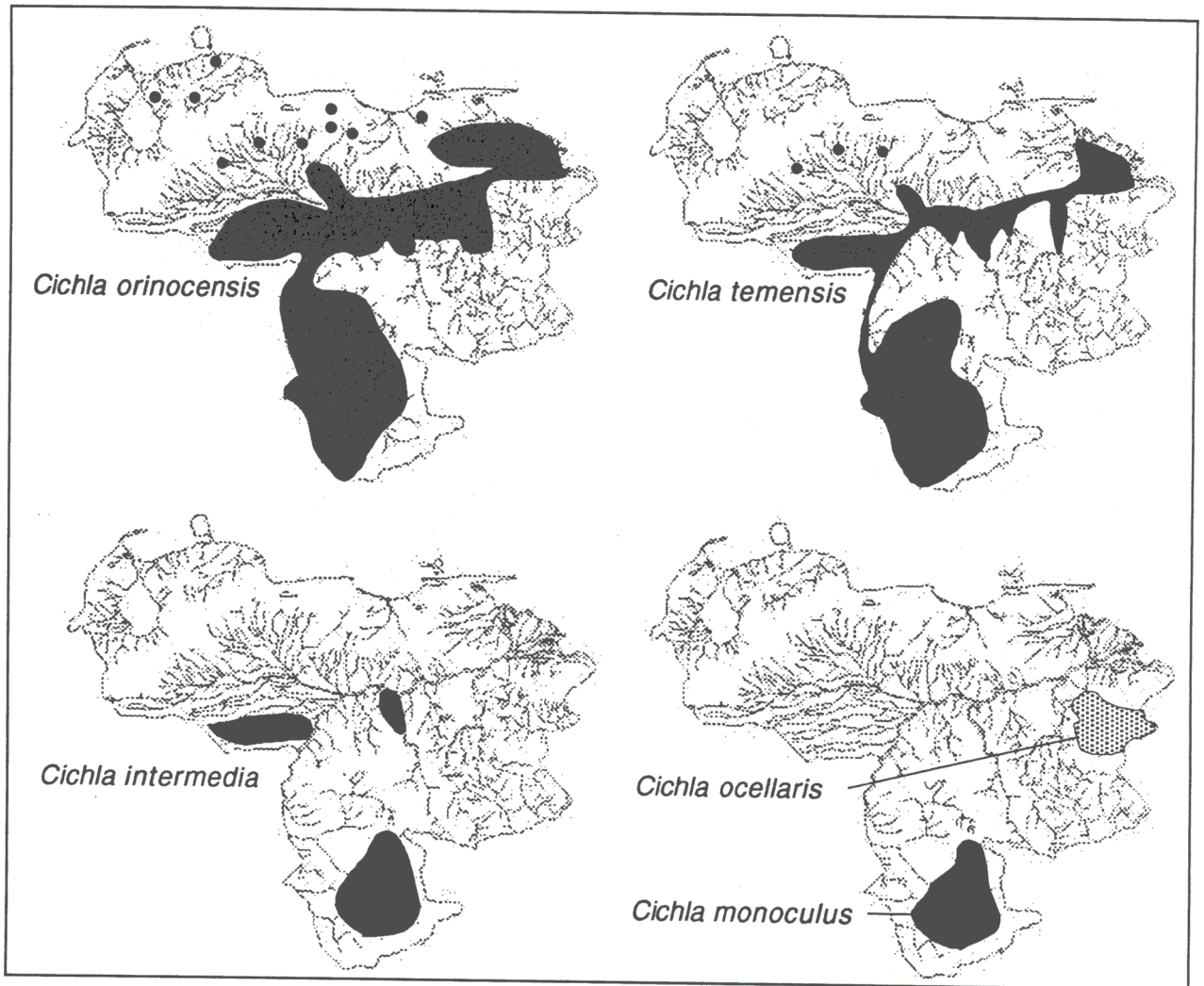


Figure 2. Map of Venezuela indicating locations of *Cichla* species based on records of the Museo de Zoología, UNELLEZ, Guanare, Estado Portuguesa and information for reservoirs (dots) reported in Rivas Larrazábal (1993).

eastern Amazonia in Brasil. Restricted to the Essequibo River Basin and coastal rivers to the east, *C. ocellaris* is not sympatric with congeners in Venezuela. Within Venezuela, *C. cf. monoculus* has only been collected in rivers of the Río Casiquiare and upper Río Orinoco basins. This species is widespread in the western, southern, and central regions of the Amazon Basin. Based on current records, *C. intermedia* has a disjunct range with populations in southern Apure and the lower Río Caura (E. Bolívar) separated from each

other by nearly 300 km, and these two separated from the population of the upper Orinoco-Casiquiare by a 700 km stretch of the Río Orinoco, a region that has not been extensively studied.

Recent surveys in the Casiquiare Basin of southern Venezuela revealed several locations where four species coexist (Winemiller, unpublished data), including the Casiquiare Channel from its confluence with the Upper Orinoco to the mouth of the Río Siapa, and two Siapa tributaries, the Emoni and Manipitare. Three species of *Cichla* (*C. orinocensis*, *C. intermedia*, *C. temensis*) are sympatric in the Río Cinaruco and Capanaparo Basins of southern Estado Apure, a region where much of my recent research has been focused. This region of the Venezuelan llanos expe-

riences markedly seasonal rainfall and contains sandy, nutrient-poor soils, savanna vegetation, and clear acidic streams. The same three *Cichla* species are also found in blackwater rivers of Venezuela's Estado Amazonas. Following Sioli (1975), blackwater rivers are stained with dissolved organic compounds and have low pH, conductivity, dissolved inorganic nutrient concentrations, and concentrations of suspended sediments. The annual distribution of rainfall is greater and less seasonal and the landscape more dominated by evergreen tropical forests as one travels southward through Venezuelan Amazonia. Both of these areas enjoy special protected status: the Cinaruco/Capanaparo as a National park and faunal reserve, and the upper Orinoco/upper Río Negro region contains national parks and reserves for indigenous peoples. Because of the remoteness of the area, the fish stocks in southern Amazonas are less exploited.

A detailed description of *C. ocellaris* appears in Kullander and Nijssen (1989). Venezuelan specimens of *C. ocellaris* are rare in museum collections, but all *Cichla* examined from the Río Cuyuní conform to this species. *Cichla ocellaris* has a moderately deep body relative to known congeners. Like all *Cichla*, coloration is variable depending on ontogenetic stage and reproductive state. Sexual dichromatism has not been documented in this species. In live adults, the background varies from grey-green to yellow or olive-green, the dorsum darker than the flanks and the belly very light. Three black vertical bars are on the flanks, the first two with a faint extension of the bar that reaches further ventrally. In adults, the dorsal portion of each bar consists of irregular dark blotches, lined by bright yellow or gold spots. Small irregular black spots are generally present on the post orbital, cheek, and opercular regions. In most individuals, black blotches and spots are sometimes present on the flanks, especially near the belly and on the caudal peduncle. Juveniles (<50 mm SL) lack vertical bars but have three large black spots on the flanks. They also lack the caudal ocellus but have a large black spot at the caudal fin base (adults of all *Cichla* species have the caudal ocellus, and small juveniles of all species lack it). Colors, especially the orange-red of the throat, pelvic fins, anal fin and lower half of the caudal fin, are more intense in breeding individuals of both sexes (Zaret, 1980). This situation holds true for the other four species studied in Venezuela (all five have the orange-red coloration in the same areas), and

males of all five species form a nuchal hump (a bulging accumulation of fatty tissue on the forehead) just prior to and during the reproductive period. In addition, the iris of both sexes of all four Orinoco-Casiquiare *Cichla* species turns blood red during the reproductive period, and this presumably is a characteristic of all members of the genus.

Kullander (1986) provides a detailed description of *C. monoculus*, and the species identified here as *C. cf monoculus* appears to agree with this description, although given its disjunct geographic distribution with Amazonian populations, further investigation is warranted. This species is present in the upper Orinoco and upper-mid reaches of the Río Casiquiare and tributaries, but no records of *C. monoculus* exist for the extreme blackwaters of the lower Casiquiare (including the Río Pasimoni and tributaries) and upper Río Negro in Venezuela and Brasil. Relative to *C. ocellaris*, *C. monoculus* is more slender in adulthood, has a discontinuous rather than continuous lateral line, wider vertical bars on the flanks that extend ventrally from the dorsum rather than beginning slightly below the dorsal fin base. To date, the only significant study of *C. monoculus* ecology was conducted in the Colombian Amazon (Cala et al., 1996).

Machado (1971) gave the taxonomic descriptions of *C. intermedia*, a species only known from Venezuelan territory, and also described general features of *C. orinocensis* (using the name *C. ocellaris*) and *C. temensis*. *Cichla intermedia*, a vividly colored fish, is sometimes referred to as the royal or blackstripe peacock cichlid, or pavón royal. Depending on environmental conditions and reproductive state, the background color of this species varies from a dull grey-green to a brilliant turquoise-green. The ventral half of the head and body is bright yellow in some individuals. There is a very distinct black lateral band, actually composed of a series of interconnected vertically-elongate blotches, along the entire length of the body. These blotches sometimes show a faint vertical bar extending dorsally to just below the base of the dorsal fin and ventrally toward the white belly. Small black flecks often appear on the post orbital region, cheeks, opercles, and especially the flanks. Juveniles

Table 1. Maximum documented length, maximum age, mean growth rate, and minimum size of maturation reported for *Cichla* species from Venezuela (from Jepsen et al., 1999; Winemiller et al., 1997; Winemiller, unpublished data).

	Maximum SL (mm)	Maximum Age ¹ (yr)	Mean Growth Rate (mm/yr)	Minimum SL Maturation (mm)
<i>C. orinocensis</i>	455 rivers 550 reservoirs	7	28.5	310 male 270 female
<i>C. temensis</i>	810 rivers 621 reservoirs	9	46.0	360 male 325 female
<i>C. intermedia</i>	429 rivers	6	19.6	320 male 270 female
<i>C. ocellaris</i>	225 rivers ²			
<i>C. cf. monoculus</i>	346 rivers ³	[5+] ⁴		[230] ⁴

¹ estimates based on annuli and assuming fishes spawn for the first time at age 1 (from Jepsen et al., 1999)
² Kullander (1986) reported maximum SL= 410 mm for *C. ocellaris* in Guyana.
³ Cala et al. (1996) reported maximum SL= 504 mm for *C. monoculus* in Peru.
⁴ estimate from the Peruvian Amazon based on a length-frequency method of age estimation (Cala et al., 1996)

have a more uniform lateral band than adults, and the faint vertical bars often are apparent.

Cichla orinocensis is similar in appearance to *C. ocellaris*, indeed, the species has been erroneously identified as that species in most of the literature prior to Kullander (1982) and much confusion remains even today. *Cichla orinocensis* has a discontinuous lateral line and generally has a more brilliant background coloration than *C. ocellaris* that ranges from yellow to green. Adults lack distinct vertical bars (some smaller individuals may show a very faint pattern of vertical barring above and below the spots) but instead have three large, sometimes irregular, black spots along the flanks. Similar to the caudal ocellus, each spot has a bright yellow or gold outline, which gives rise to the common name three-star or butterfly peacock (pavón tres estrellas, pavón mariposa). *Cichla orinocensis* essentially lacks any black markings on the head that are present in congeners.

Small juveniles (<50 mm SL) have two black spots on the flanks anteriorly, and a black lateral stripe on the posterior third of the body (Fig. 3). In extremely blackwaters, such as in Guri Reservoir, *C. orinocensis* sometimes has a bronze background coloration and numerous, small white spots on the body and fins.

Coloration of *C. temensis* is highly variable depending on ontogenetic stage, state of reproductive maturation, and breeding preparedness. Juveniles (<50 mm SL) have a black horizontal stripe extending from the shoulder to the base of the caudal fin (Fig. 3). Larger juveniles, subadults, and nonbreeding adults are bronze with a broad, dark lateral band that extends the length of the body and three broad vertical bars spaced apart evenly below the length of the dorsal fin. The body may be covered with white or cream spots, some diffuse, and others arranged in horizontal dashes above and below the lateral band. The head, dorsal fin, and caudal fin also have white spotting. The head has large, irregular black blotches on the postorbital and dorsal part of the opercular region. This black pigmentation seems to be larger and extends further ventrally on the head in adult females, but this requires systematic study for verification. Smaller, scattered

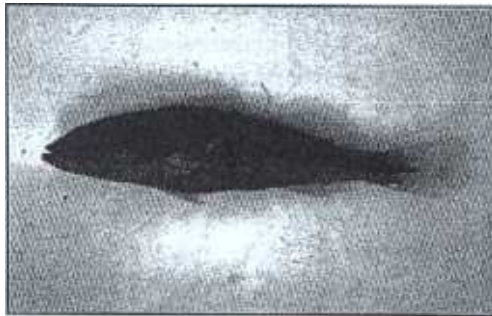
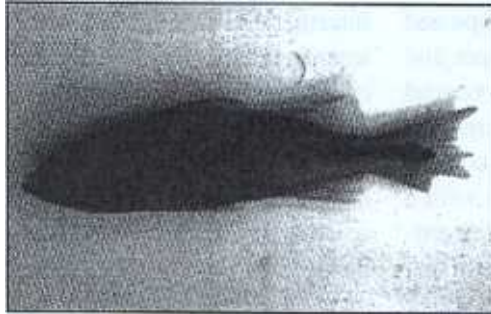


Figure 3. Preserved juvenile specimens *C. orinocensis* (top) and *C. temensis* (bottom).

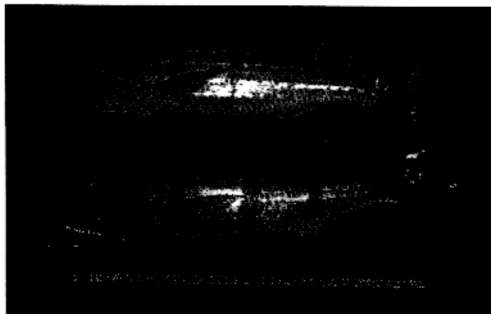


Figure 4. Female (top) and male (bottom) specimens of *C. temensis* captured from the Río Cinaruco during January 1993 with coloration in transition between nonbreeding and breeding patterns.

black spots also appear on the cheek and opercle of both sexes. Breeding adults turn green with the dorsum darker than the ventrum, and the red-orange coloration of the throat, anal fin, and lower half of the caudal fin intensifies in the manner typical of all *Cichla*. The orange coloration can extend onto the belly and ventral flanks in some individuals. Ripe and breeding adults also have three broad black bars that extend from the base of the dorsal fin to the ventral flanks, which normally are white. Fish in transition between the nonbreeding and ripe/breeding coloration pattern are encountered frequently, often with a dull olive-green background coloration, black vertical bars, and white spotting on the head, body, and fins (Fig. 4). The highly variable coloration pattern of *C. temensis* causes considerable confusion among sport anglers, many of whom erroneously conclude that multiple species are represented. Among the various local names used for this species are "pavón cinchado", "pavón trucha" and "lapa" in Venezuela, and "tucunaré pinima" in Brasil. Banded and speckled peacock are two of the most common English names used for this species.

HABITAT ASSOCIATIONS

Although peacock cichlids collectively inhabit a diversity of habitats ranging from streams to large reservoirs, each species has fairly distinct habitat affinities which are particularly apparent in regions where two or more species coexist. The universal requirement of all *Cichla* species appears to be high water transparency, warm temperatures, and access to lentic habitats for feeding and/or reproduction. The need for clear water apparently is tied to the fact that *Cichla* are strictly diurnal predators that rely on vision and rapid pursuit to capture prey. In all of my field experiences, I have never found peacock cichlids in turbid waters associated with whitewater systems (i.e., neutral pH, high conductivity, high concentrations of suspended clays and other sediments, and high nutrient concentrations). Undoubtedly, they are able to traverse stretches of turbid water within the Río Orinoco in order to disperse among the many marginal lagoons and clearwater tributaries (the latter

having few suspended particulates, high transparency, and low to neutral pH). The broader distribution of *C. orinocensis* relative to its congeners suggests that this species is more tolerant of turbidity. For example, *C. orinocensis* is well established in Caño Caicara (E. Apure), a river with characteristics that are intermediate between whitewater and blackwater systems (e.g., moderate-high transparency, staining from organic compounds, pH 6-6.5, and floating aquatic macrophytes). It is unclear if the species has a historic presence in this river, which forms the northwestern limit of its geographic range, or if it colonized from the adjacent modules, a dike/pond system constructed during the 1970s. In other regions of the llanos, *C. orinocensis* is sometimes found in excavated ponds and shallow impoundments with moderate transparency.

The five *Cichla* species in Venezuela show consistent patterns of association with waters of different physicochemical characteristics according to Sioli's (1975) classification scheme for tropical rivers. As mentioned above, *C. orinocensis* seems to be most tolerant of a wide range of conditions ranging from extreme blackwaters, to clear waters, to waters with characteristics intermediate between them and those of white waters. Even so, there is no question that *C. orinocensis* achieves greatest population densities under classic clearwater (e.g., Aguaro, Cinaruco) and blackwater (e.g., Pasimoni) conditions. *Cichla orinocensis* penetrates further into headwaters than *C. temensis*, and occurs more frequently in small tributary streams that flow directly into large rivers. Apparently, these two species are eliminated from a large region of the Guyana Shield (corresponding to most of Estado Bolívar and eastern Estado Amazonas) by the presence of cataracts. *Cichla temensis* seems to be entirely restricted to clearwater and blackwater rivers, and *C. intermedia* and *C. cf. monoculus* apparently are restricted to clearwater rivers of the upper Orinoco-Casiquiare region (plus the moderate blackwater Río Capanaparo and blackwater Río Caura as northernmost limits in the case of *C. intermedia*).

Recent studies (Jepsen et al., 1997; Winemiller et al., 1997) based on extensive sampling with hook and line and nets described the habitat associations of the three peacock cichlid species in the Río Cinaruco. Both studies discovered a high degree of habitat separation among the species (Fig. 5). *Cichla intermedia* is essentially restricted to the main chan-

Table 2. Regression equations, r-square values, and sample sizes for ln-weight x ln-length regressions for four *Cichla* species based on data pooled across sexes and populations studied by Jepsen et al. (1999).

	Regression	r ²	n
<i>C. orinocensis</i>	ln(W)= 3.16(L) - 18.5	0.97	380
<i>C. temensis</i>	ln(W)= 3.08(L) - 18.2	0.99	720
<i>C. intermedia</i>	ln(W)= 3.09(L) - 18.2	0.95	131
<i>C. cf. monoculus</i>	ln(W)= 2.83(L) - 16.0	0.75	15

nel of the river, especially areas where flowing water passes over submerged timber or rocky shoals. *Cichla intermedia* tend to swim near the bottom, and are much more hesitant than their congeners to rise high in the water column to attack bait or lures. On several occasions, I have noted isolated pairs nesting in shallow water near the edge of secondary channels. In each case, the nest was constructed over a sand substrate and located in or near slow current. The species has been observed in lagoons very infrequently, and all cases apparently involved fish searching for nesting sites (D.A. Arrington, personal communication).

Cichla orinocensis was captured near the edge of channels and lagoons, often near submerged structure where water flow is slow or absent. In the main river channel, the species seems to be less common over broad, open reaches that lack structure. *Cichla temensis* occupied the broadest range of habitats in the Río Cinaruco, and overlapped with both of its congeners. In general, *C. temensis* was about equally distributed in channels and lagoons, and larger individuals inhabit deeper waters than smaller conspecifics. *Cichla temensis* occurs in areas with or without cover (rocky shoals or woody debris) and in areas with no flow or moderate to high current velocity. When in pursuit of schooling prey, loose groups of *C. temensis* sometimes attack at the water's surface in the middle of the main channel, particularly where the channel becomes broad and shallow. *Cichla temensis*, including the largest size classes, can be captured by retrieving a surface lure over shallow areas where water flows over sand ridges into deeper troughs aligned perpendicular to the direction of flow. In the Río Cinaruco, *C. temensis* occupies deeper regions than *C. orinocensis*

and occurs more frequently in the main channel, including areas with moderate to fast water velocity. A similar pattern of interspecific habitat segregation was observed in the Río Pasimoni, a river that lacks *C. intermedia* (Winemiller et al., 1997). In the Pasimoni, *C. temensis* was captured less frequently from channel habitats when data are compared to those from the Cinaruco.

Cichla orinocensis is widely distributed in the Río Aguaro and its tributaries. In the larger downstream reaches of the Río Aguaro, the species is more abundant in lagoons, but it is found in nearly all channel and backwater habitats of small, low-velocity streams of the region. Apparently *C. temensis* was abundant in the Río Aguaro prior to the 1970s, but overfishing has reduced the population to the point that the species is captured there infrequently (D. Rodríguez and D. Taphorn, unpublished data).

In Guri Reservoir, *C. orinocensis* and *C. temensis* occupy the shallow waters of the littoral zone, especially in protected coves where small prey fishes are most abundant (Williams et al., 1998). Guri peacock cichlids are rarely captured from areas where depth exceeds 5 m, and in those instances when they are, substantial stands of submerged timber generally are present. Based on the composition of diets, Williams et al. (1998) concluded that *C. temensis* forages in deeper waters than does *C. orinocensis*. Based on gillnet catch data, *C. temensis* was estimated to be

Figure 5. Schematic diagram of a segment of the Río Cinaruco channel showing habitat affinities of *Cichla* species (I = *C. intermedia*, O = *C. orinocensis*, T = *C. temensis*). Arrows indicate regions of strongest current velocity, thin lines indicate depth contours.



more abundant in Guri, and both species have declined in abundance between the mid-1980s and present. This decline probably has been due to a gradual decline in aquatic production in this oligotrophic reservoir, rather than fishing pressure.

FEEDING ECOLOGY AND SPECIES INTERACTIONS

The vast majority of *Cichla* are piscivorous, with adult size classes only occasionally consuming shrimp and other aquatic invertebrates. The exception appears to be certain populations inhabiting reservoirs. In Las Majaguas, Barbarino found significant fractions of shrimp in the diets of both *C. orinocensis* and *C. temensis* (Table 3). Small juveniles consume aquatic microcrustacea, and fishes >50 mm consume fishes, aquatic and terrestrial insects, and shrimp, with fishes being consumed increasingly by larger size classes. In the Río Cinaruco, the system where we

have the most dietary data for *Cichla*, fishes comprised from 80-100% of the diet of peacock cichlids based on the volume of stomach contents. Resource partitioning was documented, especially during the low and rising water periods. During the dry season, Cinaruco *C. orinocensis* and *C. temensis* feed heavily on small characiform fishes, and *C. intermedia* consume a variety of fishes, including small catfishes. As water levels rose, *C. temensis* fed more on juvenile *Cichla* and siluriform fishes, *C. intermedia* fed more on insects and crustacea, and *C. orinocensis* fed on a wide variety of fish prey. *Cichla orinocensis* had a broader diet overall, and showed less seasonal shift in diet composition than *C. temensis* and *C. intermedia*. This can perhaps be explained by the fact that *C. orinocensis* forages in shallow water near the interface with terrestrial vegetation throughout the year, whereas the other two species tend to be in the channel or further from shore during the falling and low-water periods, but move into these areas during the flood period. Table 3 summarizes *Cichla* diets based on studies conducted in four systems.

In Guri Reservoir, *C. temensis* consume more

characiform fishes, and *C. orinocensis* feed more on cichlids (Gil et al., 1993; Novoa et al., 1993; Williams et al., 1998). In Guri, these two species showed no difference in the size of prey consumed (Williams et al., 1998), but in the Cinaruco *C. temensis* consumed significantly larger prey than *C. orinocensis* (Jepsen et al., 1997). When data were adjusted for predator size, there was no difference among prey sizes consumed by the three peacock cichlid species of the Cinaruco, which is to say the species are capable of consuming equal-size prey in relation to predator length. In rivers containing large *C. temensis*, most fish taxa probably are vulnerable to predation. I have received accounts from sport anglers of cases in which *C. orinocensis* fighting on the end of a fishing line have been consumed by large *C. temensis*. I have also observed large *C. temensis* attacking schools of large characiform fishes (e.g., *Chalceus macrolepidotus*, *Semaprochilodus kneri*, *Boulengerella* spp.) near the surface of the water. These attacks are quite explosive, and fishes that are not grasped on an initial attack may hover at the surface, stunned and subject to subsequent attacks. The explosiveness and power of this surface feeding behavior is a primary cause for the international sportfishing industry's interest in this species.

The demonstrated prowess of peacock cichlids as piscivores, when combined with their typically high abundance, suggests a potential to influence prey populations. The experiences from reservoirs and exotic peacock cichlid populations indicate a potential role for peacock cichlids as keystone predators. Keystone predators can suppress the population densities of competitively superior prey species, and as a result, foster higher levels of local species diversity (Paine, 1966). In Lake Gatún, the introduction of *C. ocellaris* was followed by radical changes in community composition and the structure of the aquatic food web (Zaret and Paine, 1972). The evidence suggests that *Cichla* predation eliminated or greatly reduced formerly dominant prey populations which in turn had a cascading effect on other aquatic species and even certain terrestrial species. For example, the elimination of small invertebrate-feeding fishes resulted in more mosquito larvae and a higher incidence of malaria around the lake. *Cichla* greatly reduced the population of pelagic atherinid fishes which was followed by a reduction in terns. This case involved *C. ocellaris* interacting as an exotic species in a

reservoir, an artificial habitat. Could peacock cichlids function as keystone predators within native fluvial communities?

Given the dominance of *Cichla* as diurnal piscivores in their native river ecosystems, it seems certain that many strong food-web effects, both direct (as keystone predators) or indirect (e.g., competitive interactions, or effects on species at nonadjacent levels in a food chain) are influenced by changes in either the numerical abundance or the size structure of *Cichla* populations. Tropical aquatic food webs are very complex, and even basic descriptive data are lacking for systems containing peacock cichlids. In recent years, my colleagues and I have been studying various aspects of the fishes and ecology of the Cinaruco.

Jepsen et al. (1997), Winemiller et al. (1997), and Winemiller and Jepsen (1999) described how *C. temensis* feed on *Semaprochilodus kneri*, an abundant characiform that migrates between the nutrient-poor Cinaruco and the nutrient-rich floodplains of the Orinoco to the east. Each year during the rainy season, the migratory fishes spawn on the rich floodplains, then adults and juveniles migrate into the Cinaruco during the falling-water period (Nov.-Jan.) and remain there until the next rains (May). *Cichla temensis* feed heavily on juvenile *S. kneri* during their mass migrations up the Cinaruco. This period of migration is also the time when *C. temensis* show the lowest frequency of empty stomachs, fastest growth, and improvement in body condition. During the months between the end of the upstream migrations and the start of the next rainy season, *Cichla* reduce their feeding activity and undergo gonadal maturation in preparation for spawning. Therefore, the peacock cichlid population is nutritionally subsidized by biomass produced on the whitewater Orinoco floodplain in the form of migratory fish.

Analysis of stable isotope data indicates that nearly half of the carbon assimilated by large *C. temensis* is derived from the whitewater system (Winemiller and Jepsen, in press). *Cichla* fitness is enhanced and its population density is increased as a result of feeding on this imported production. Since

nearly all Cinaruco fishes, including peacock cichlids, are year-round residents of the oligotrophic system, this nutritional subsidy for a large predator with a broad diet may have ramifications for the population dynamics of resident prey populations. Research that attempts to model the food web dynamics of this spatial subsidy is ongoing in my lab. Other oligotrophic rivers with peacock cichlids also support large populations of migratory prochilodontids (e.g., Rio Negro).

There are relatively few data to identify the major predators of peacock cichlids. Freshwater dolphins (*Inia geoffrensis*) are common in most rivers with peacock cichlids, but the limited dietary information available for dolphins indicates that they feed mostly on small fishes (McGuire and Winemiller, 1998). In the Río Cinaruco, dolphins sometimes capture peacock cichlids when they are released by sport anglers. Given that this has not been observed in other rivers where sportfishing is less common, the behavior appears to be learned. It seems doubtful that dolphins are able to capture and subdue large peacock cichlids.

Piranhas (serrasalmine characids) feed on peacock cichlid fins, especially when the cichlid is struggling on the end of a fishing line. Fin nips are extremely common on all species of *Cichla* in habitats where piranhas are common, i.e. virtually all fluvial habitats. Winemiller (1990) hypothesized that fin damage from piranhas has been a sufficient selective pressure to result in the evolution of the caudal ocellus (eyespot) as a deterrent. Based on field and laboratory experiments with *Astronotus ocellatus*, another predatory cichlid with a distinct caudal ocellus, Winemiller (1990; Winemiller and Kelso-Winemiller 1993) presented evidence in support of the theory that the caudal eyespot (false eye) in piscivorous cichlids is an adaptation that confuses small fin-nipping piranhas by caudal mimicry of the head. This is an alternative to Zaret's (1977) earlier hypothesis that the caudal ocellus in *C. ocellatus* functions as an intraspecific recognition signal to avert cannibalism in this piscivore. Zaret (1977) stated that cannibalism does not occur in *C. ocellatus*, however many cases have been documented among other *Cichla* species (Winemiller,

1990; Gil et al., 1993; Jepsen et al., 1997).

Whereas large adult *C. temensis* probably have relatively few natural enemies (e.g., river otters), small size classes are vulnerable to predation by a great variety of piscivorous fishes, but to date the only direct reports are for large *Cichla* feeding on smaller *Cichla*.

POPULATION STRUCTURE

The density and size structure of peacock cichlid populations varies greatly among locations and species. In addition, both the density and size structure of some populations appear to have changed over time in response to fishing pressure and/or ecosystem maturation, the latter having been observed in new reservoirs. The case for Guri Reservoir was already cited, and other Venezuelan reservoirs have shown similar patterns of community and ecosystem development following impoundment.

The initial fish community of Las Majaguas Reservoir contained a high biomass of local river species, with piranhas being the dominant piscivores (Fernandez Yopez and Antón, 1966). With time, the influx of nutrients from the flooded terrestrial ecosystem waned, and fish biomass declined. During this same period, peacock cichlids (*C. orinocensis*, *C. temensis*) and other cichlid species from other locations in the llanos were introduced into the reservoir. Control of piranhas was a major motivation for the introduction of peacock cichlids (A. Barbarino, pers. comm.). The fish community now is dominated by cichlids (Winemiller 1989), with peacock cichlids as the dominant piscivores. A similar situation appears to be underway in the Boconó Reservoir (E. Portuguesa), constructed in 1985 (pers. comm., D. Bermudez and D. Taphorn, UNELLEZ). In the case of Las Majaguas, very large peacock cichlids were captured during the mid 1980s, a period when the peacock cichlid population appeared to have reached its peak density. For example, I captured a 550 mm SL, 5 kg female *C. orinocensis* from the shore of the lake in 1984. In Las Majaguas, a reservoir constructed in a whitewater region, *C. temensis* does not achieve the same size as conspecifics in rivers or clearwater and blackwater reservoirs lying further east. This is further evidence that *C. temensis* is not as well adapted physiologically as *C. orinocensis* to variation in water chemistry. Likewise, *C. orinocensis* from native rivers never attain such large sizes, which indicates

Table 3. Comparison of dietary data for *Cichla orinocensis*, *C. temensis*, and *C. intermedia* from four locations based on results reported in ¹Gil et al., 1993; ²Williams et al., 1998; ³Jepsen et al. 1997; ⁴Winemiller et al., 1997; ⁵Winemiller, 1990; and ⁶Barbarino, 1996.

Site	Guri ¹	Guri ²	Cinaruco ³	Cinaruco ⁴	Modulo ⁵	Majaguas ⁶
Data	% wt.	% vol.	% vol.	% freq.	% vol.	% freq.
<i>C. orinocensis</i>						
crustacea	0	0.8	3.6	0	0	44.8
characiforms	35.1	31.9	43.7	81.5	32.0	2.2
perciforms	40.6	66.3	4.7	11.1	46.0	43.9
siluriforms	0	0	6.6	0	0	0
unidentified/misc.	24.3	0	41.4	7.4	22.0	24.3
<i>C. temensis</i>						
crustacea	0	0.1	0	0	0	
characiforms	66.0	70.7	57.1	53.8	0	
perciforms	19.8	21.2	17.1	15.4	22.6	
siluriforms	0	0	4.5	3.8	0	
unidentified/misc.	14.2	5.5	21.2	26.9	19.3	
<i>C. intermedia</i>						
crustacea			20.6	0		
characiforms			12.4	61.5		
perciforms			23.2	7.7		
siluriforms			5.7	15.4		
unidentified/misc.			50.3	0		

that biotic interactions in rivers, possibly in the form of competition with *C. temensis*, limit the maximum size of this species in rivers. The population size structure of peacock cichlids in Las Majaguas has declined markedly over the past 15 years, and capture rates by local fishers have declined as well (Barbarino, 1996).

Our best estimates of population density and structure comes from research on the Río Cinaruco. Taphorn and Barbarino (1993) used mark and recapture method to estimate the abundance of *C. temensis* and *C. orinocensis* in a 7.3 ha lagoon connected to the Río Cinaruco (Laguna Larga) and a 3.8 ha lagoon in

the floodplain of the Río Capanaparo to the north (Laguna Brava). Because it was based on a larger total sample, they felt their best estimates were those for the two species combined: 148/ha for Laguna Larga, and 178/ha for Laguna Brava. Consistent with these estimates, angling catch per unit effort was higher in Laguna Brava (2.1 *Cichla*/person/hr) than Laguna Larga (1.65 *Cichla*/person/hr).

Cichla temensis are larger than *C. orinocensis* and *C. intermedia* in the Cinaruco (Jepsen et al., 1997; Winemiller et al., 1997). In a study of age and growth, we found that *C. temensis* grows significantly faster than its two congeners (Jepsen et al., 1999). The study by Jepsen et al. also compared maximum ages and sizes among river and reservoir populations (selected findings summarized in Table 1). Their analysis confirmed that *C. orinocensis* attains larger maximum sizes in reservoirs, but also that *C. temensis* attains its largest sizes in rivers. Based on the otolith method of age determination, the maximum age in their samples was 8 years for *C. temensis* from the Río Pasimoni (Amazonia). Using the otolith method, Winemiller et al. (1997) estimated a 750 mm SL, 9 kg *C. temensis* from the same river at 9 years. They concluded that this population was dominated by fish of 9-11 years. Their estimate of annual growth by Pasimoni *C. temensis* was based on limited data and an inappropriate model, and their estimate of 70 mm/yr should be replaced by Jepsen et al.'s value of 46 mm/yr.

Although Pasimoni peacock cichlids tend to be larger than conspecifics in the Cinaruco, their weight-length relationships are virtually identical in the case of *C. temensis* and very similar for *C. orinocensis* (Jepsen et al., 1997; Winemiller et al., 1997). The slope for the log-weight x log-length regression is used as an indicator of fish relative condition. For *C. orinocensis*, populations with the lowest slopes were from the Río Aguaro and Amazonia, and the highest was Las Majaguas Reservoir. For *C. temensis*, the slope was nearly the same for all river and reservoir populations examined. Table 2 presents weight x length regression equations for four *Cichla* species based on available data.

Repeated sampling indicates that the size structure of the peacock cichlid populations in the Río Cinaruco has not changed over the past ten years. This river receives moderate fishing pressure, mostly from sport anglers who practice catch and release. Also, based on standing densities of fishes during the low-water season, the Río Cinaruco appears to be more productive than the more extreme blackwater rivers of the Guyana Shield and Amazonia. In contrast, our

samples from the Río Pasimoni indicate a downward shift in the size distribution of the *C. temensis* population over the past six years. We first surveyed this river during 1993 just after it had been discovered by groups conducting sportfishing tourism. Although the sport anglers practiced catch and release, this new commercial enterprise stimulated greater fishing activity by local subsistence and commercial fishers, some of whom, with their increased income, were also able to buy more gasoline for the journey to this remote area. If special precautions are not taken, catch and release can result in high mortality from piranhas and river dolphins.

Nearly all Pasimoni *C. temensis* in our January 1993 sample were extremely large, with only one individual <560 mm SL. Using angling as our primary collecting method, we did not observe or capture any small immature individuals of either *Cichla* species, an unusual occurrence. Our seine samples and visual surveys also revealed no juvenile peacock cichlids. Presumably, the natural mortality among very young fish (larvae and young of the year) is very high, and recruitment of young fish into the adult populations is very low under normal conditions. This is probably due to extremely low natural productivity near the food web base within the Pasimoni's acidic, nutrient-poor waters, and also the high diversity of natural predators in the local fish assemblage. Surveys of the Pasimoni during January 1997, 1998 and 1999 resulted in captures of smaller maximum sizes and many more juveniles and small adults. Because we used the same methods, we interpret this difference as reflecting a real change in population size structure. The removal of large adults via the fishery may have resulted in increased foraging opportunities for juveniles and lower predation by larger conspecifics.

In the Río Aguaro, more than two decades of commercial and subsistence fishing has resulted in extremely low densities of *C. temensis*, and a *C. orinocensis* population comprised almost entirely of age-1 fish (Jepsen et al. 1997). Venezuelans long involved in peacock cichlid sportfishing claim that *C. temensis* formerly were abundant, with individuals 5-8 kg common in the Aguaro. The information available at this time indicate a consistent pattern that results from overexploitation of fluvial populations of peacock cichlids, in which the elimination of large adults is followed by an increase in the relative abun-

dance of small size classes and slow replacement of these large size classes. *Cichla temensis* appears to be particularly vulnerable to such changes, and this may be a function of its association with nutrient-poor ecosystems and cannibalism by large adults causing a recruitment bottleneck.

REPRODUCTION

Reproduction by peacock cichlids follows the typical pattern of substrate spawning cichlids in which both sexes defend eggs and fry. Nesting, spawning, and brood care in *C. ocellaris* was described by Braga (1952), Devick (1969), and Zaret (1980), however the identity of their species requires confirmation in light of recent taxonomic work. According to Zaret (1980), *C. ocellaris* guards its brood for a period of up to 10 weeks, at which time the juveniles are 60-70 mm SL. Zaret described how the parents move the newly hatched fry in their mouths from the oviposition nest to nest depressions that lie up to 2 m away. The parents essentially cease feeding during the period of brood care, and all attention is focused on protecting the brood from the multitude of egg and larval predators in their surroundings (ca. 250 fish species have been documented in the Río Cinaruco). Anglers catch brooding peacock cichlids, and presumably these strikes are born of aggression for brood defense rather than hunger. Jepsen et al. (1999) determined that otolith annuli are formed during the period just prior to and during nesting (end of the low-water period into the start of the annual rains), which indicates reduced nutritional status from lower food intake during the reproductive period. Zaret also discussed sexual selection in *C. ocellaris*. Since only males form large nuchal humps derived from fat deposition, this character may serve as an honest advertisement to females that indicates relative foraging success by the male during the previous growing season (and see Barlow, 1999).

The number of eggs counted in five *C. ocellaris* nests in Hawaii ranged from 4,457 to 5,744 (Devick, 1969). Zaret (1980) claimed that *C. ocellaris* nests in Panama contained up to 10,000 eggs. Cala et al. (1996) estimated mean fecundity from 10 *C. monoculus* at 7,400. Based on counts from preserved ovaries, the mean fecundity of three ripe female *C. intermedia* from the Cinaruco (270-305 mm SL) was 1,711; mean fecundity of three female *C. temensis* from the Cinaruco (330-430 mm SL) was 5,725. A single female *C.*

orinocensis from the Pasimoni contained 1,694 ripe ova. These estimates for fishes from Venezuela are based on relatively small adults. As in most batch-spawning fishes, fecundity increases with size in *Cichla*.

My colleagues and I have only made informal observations of nesting and brood care by peacock cichlids in Venezuela. In the Río Pasimoni (January 1993), we found six nests of *C. orinocensis* with fertilized eggs. All of these nests were constructed on rock substrates in shallow water (ca. 30 cm) near the shore of lagoons. During a period of unusually low water levels (January 1998), we captured many *C. temensis* in advanced stages of spawning preparedness from a single lagoon that was connected to the main channel of the Pasimoni. The fish appeared to be at highest densities over broad shallow reaches 3-15 m from the shoreline. I concluded that the fish were either nesting or preparing for nesting. During January 1998, we caught seven male *C. temensis* with nuchal humps and bright coloration and 9 adults lacking humps (presumed females) from a cut-off pool (ca. 450 m²) in the Río Siapa, a Casiquiare tributary. When we released one of these captured fish into the river channel, it quickly returned to the lagoon through a shallow (15 cm), narrow (ca. 3 m) channel in the sandbank.

In the Río Cinaruco, sport anglers target a broad shallow section of one particular lagoon during the late dry season, because *C. temensis* are known to form nesting aggregations there each year. Zaret (1980) described how male *C. ocellaris* behave aggressively toward each other during the period of nest site selection and courtship. Therefore, it appears likely that *C. temensis* form nesting aggregations as a function of limited suitable nesting habitat rather than social instincts. I have observed nesting *C. orinocensis* as isolated pairs in several rivers and reservoirs, and D. Rodríguez (unpublished data) reported *C. orinocensis* nesting aggregations in lagoons of the Aguaro.

Most studies report that spawning *Cichla* can be found during any time of the year, but that spawning peaks generally occur just prior to and during the early

part of the rainy season (Fontenele, 1950; Lowe-McConnell, 1969; Zaret, 1980; Jepsen et al., 1999). In general, it seems that spawning is more synchronized in more seasonal habitats. For example, *Cichla* of the Río Cinaruco, an intensely seasonal floodplain river, show gradual gonadal maturation over the course of the falling-water season (December-May) and evidence of nesting and spawning during the final weeks of the dry season (Jepsen et al., 1999). Lowe-McConnell (1969) reported identical spawning dynamics for *C. ocellaris* of the Rupununi savanna region of Guyana.

Presumably, nesting and mate choice are achieved more easily under conditions of low water and high fish density. Likewise, larval feeding and brood defense may be achieved more effectively within the inundated floodplain. The same pattern of reproductive seasonality is observed in large piscivorous cichlids (*Serranochromis* spp.) of the seasonal Zambezi River floodplain (Winemiller, 1991). In less seasonal habitats, such as reservoirs, *Cichla* spawning probably is much less synchronized. The low rate of detection of annuli (annual growth checks) on the otoliths of *Cichla* from Guri Reservoir (Jepsen et al., 1999) supports this contention. Zaret (1980) reported spawning activity during all months of the year in Lake Gatún, however two periods of peak activity were noted. In the Peruvian Amazon, where rainfall is not as seasonal as the llanos, ripe *C. monoculus* were found during 9 of 12 months surveyed, and spawning began during the annual period of increasing rainfall and peaked about one month prior to the period of peak rainfall (Cala et al., 1996).

CONSERVATION

Despite the fact that they are often the most abundant and conspicuous piscivores in South American aquatic systems, peacock cichlids seem to be very sensitive to overharvest. In the Río Pasimoni of Venezuela's remote Amazonian region, the population size structure of *C. temensis* underwent a significant change just 5-6 years following the initiation of organized sportfishing. Numerous independent accounts reveal

that the Río Aguaro (central llanos) used to support a fishery for trophy *C. temensis*, which together with *C. orinocensis* was abundant 20-30 years ago. Now *C. temensis* are relatively uncommon in this river, and the *C. orinocensis* population is dominated by age-1 fish. From the late 1980s to the early 1990s, Guri Reservoir could boast one of the premiere peacock cichlid fisheries in the world. Although large peacock cichlids still can be found in this giant blackwater reservoir, much of the sportfishing activity has been shifted to the upper portion of the impoundment where the discharge from the Río Cuyuní and Río Paragua is first received and aquatic primary production is higher.

In short, it appears that peacock cichlid populations are vulnerable to impacts from a variety of causes ranging from watershed changes to overharvest. When compared to the accumulated knowledge that provides the basis for management of sportfish stocks in North America or Europe, it seems there is very much that remains to be learned about the ecology of peacock cichlids. We have more information for non-native populations of peacock cichlids than native stocks in South American waters. For species such as *C. monoculus* and those in Brasil yet to be described, we have little or no ecological information.

Within pristine native habitats, peacock cichlids appear to live a decade or more, so that, once removed, old large individuals are not replaced for several years. The very successful largemouth bass fisheries of North America might provide a management model, and size-based catch limits (including slot limits that allow possession of fish smaller or larger than a prescribed size interval) might facilitate sustained harvest of the largest size classes. Obviously, enforcement is critical to the success of catch limits. However, enforcement has been lacking in many regions of South America where commercial and subsistence netting of peacock cichlids is conducted illegally (a detailed discussion of Venezuelan regulations and management recommendations appears in Taphorn and Barbarino, 1993).

Some features of peacock cichlid ecology and the aquatic ecosystems they inhabit make over harvesting a resource problem that transcends just fishery concerns. The popularity of peacock cichlids as sportfishes obviously stems from their ecological niche as voracious, diurnal piscivores. Because of the foreign exchange generated by the international sportfishery,

it remains in the best interest of South American countries to manage these fisheries on a sustainable yield basis.

In addition to having economic relevance, peacock cichlids may influence the community dynamics of oligotrophic aquatic ecosystems with low *in situ* production. As already noted, the introduction of exotic peacock cichlids into Lake Gatún, Panama resulted in large-scale changes in the aquatic food web. Similar scenarios of community transition following the introduction of *Cichla* into Venezuelan reservoirs were noted as well. Experiences based on the introduction of peacock cichlids into impoundments suggests that these predators can significantly influence the structure and function of aquatic ecosystems. Because tropical rivers that contain peacock cichlids have not been studied as well as reservoirs, the issue deserves further attention. Peacock cichlids have all the characteristics of keystone predators and theoretically could function as promoters of biological diversity in tropical rivers via negative impacts on competitive dominants, thus facilitating coexistence among diverse prey taxa.

CONCLUSIONS

Over the past 10 years, research on peacock cichlids in Venezuela has greatly increased our knowledge of the ecology of this important group of cichlids within their native geographic distribution. Prior to these efforts, most ecological information was derived from research conducted in aquaculture facilities and on non-native populations introduced into reservoirs. We still have much to learn. Systematic relationships, taxonomy, and biogeography of the genus *Cichla* remains poorly known, with several apparently undescribed taxa in Brasil (*pers. comm.*, S. Kullander). Basic ecological information, including habitats, trophic ecology and species interactions, is lacking for most native *Cichla* populations. Because of their appeal as sportfish and novelty fish for the aquarium trade, *Cichla* are being transported to locations the world over with increasing frequency. In tropical regions, these piscivores have great potential to impact native faunas, a lesson learned from the scenario in Lake Gatún, Panama. Yet in their native South American rivers, peacock cichlids may play an important role in regulating high community diversity. Given the great ecological and economic importance of these cichlids, considerably greater investment in research is clearly warranted.

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