

Movement of *Cichla* species (Cichlidae) in a Venezuelan floodplain river

David J. Hoeinghaus*, Craig A. Layman*,
D. Albrey Arrington** and Kirk O. Winemiller*

In their native habitats of black- and clear-water Neotropical rivers, large predatory cichlids of the genus *Cichla* are an important food and recreational resource. Understanding patterns of movement for these species is necessary for effective management and conservation; however, no information is available on movement in natural fluvial populations. Therefore, we initiated a cooperative mark-recapture program with local sport-fishing groups to evaluate movement of *Cichla* in the Cinaruco River, Venezuela and to promote conservation awareness. Between January 1999 and May 2003, we tagged 2,224 individuals of three species of *Cichla* (*C. temensis*, *C. orinocensis*, and *C. intermedia*) with uniquely numbered floy tags. Over 52 months, 2.8% of the tagged fishes were recaptured. Most recaptures occurred within 1 km of the tagging location; however, a few large *C. temensis* moved up to 21 km, demonstrating the potential for longer distance movement in this species. The distance between tagging and recapture locations was not significantly correlated with the time interval between tagging and recapture. Distance moved was significantly related to fish size and period of the annual hydrological cycle. Implications for management and conservation of these species and future research directions are discussed.

Grandes ciclídeos do gênero *Cichla* são importantes como recurso alimentar e recreacional em seus habitats nativos de águas pretas e claras de rios neotropicais. O entendimento do padrão de movimentação dessas espécies torna-se necessário para o seu efetivo gerenciamento e conservação. Entretanto, não existe informação disponível em relação ao movimento de populações em ambientes fluviais naturais. Assim, iniciou-se um programa cooperativo de marcação e recaptura para avaliar a movimentação de *Cichla* no rio Cinaruco, Venezuela. Entre janeiro de 1999 e maio de 2003, um total de 2224 indivíduos de três espécies de *Cichla* (*C. temensis*, *C. orinocensis* e *C. intermedia*) foram marcados, utilizando-se marcadores “floy”, cada um contendo numeração própria. Durante 52 meses foram recapturados 2,8% dos peixes marcados, a maioria ocorrendo em distâncias inferiores a 1 km do ponto de marcação. Somente alguns *C. temensis* de maior tamanho, deslocaram-se a distâncias superiores a 21 km, demonstrando o potencial da espécie para movimentos a longa distância. Não houve correlação significativa entre a distância dos locais de marcação e recaptura e o intervalo de tempo existente entre os dois eventos. A distância foi significativamente relacionada com o tamanho do peixe e o período do ciclo hidrológico. Implicações para o manejo e conservação destas espécies são discutidas, além de sugerir direcionamentos para investigações futuras.

Key words: Cinaruco River, conservation, mark-recapture, pavón, tucunaré.

Introduction

Large diurnal piscivores of the genus *Cichla* (Cichlidae) are common in many clear- and black-water rivers of South America. *Cichla* (called pavón in Venezuela, tucunaré in Brazil, and peacock bass or peacock cichlid in English) are an important food and sport resource in lowland rivers of the

large tropical river basins of South America, and have also been introduced in many subtropical regions for this purpose (e.g. Florida, Hawaii, Panama, Puerto Rico, and Southern Brazil). An introduced population of *Cichla ocellaris* (Bloch & Schneider, 1801) in Panama was shown to have strong impacts on prey fish assemblages (Zaret & Paine, 1973), and *Cichla* have been introduced into aquaculture ponds to reduce

*Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, U.S.A. e-mail (DJH): djhoeinghaus@tamu.edu; (CAL): CAL1634@yahoo.com; (KOW): k-winemiller@tamu.edu

**Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487-0206, U.S.A. e-mail: albrey@bama.ua.edu

overcrowding (McGinty, 1984; Fischer & Grant, 1994). Until recently, most information regarding the ecology of *Cichla* species was from non-indigenous populations in lakes and reservoirs (but see Lowe-McConnell, 1969).

Several recent studies have described the population structure (Taphorn & Barbarino Duque, 1993; Winemiller *et al.*, 1997), age structure and growth (Jepsen *et al.*, 1999), and patterns of resource use (Jepsen *et al.*, 1997) of *Cichla* populations naturally occurring in black-water rivers of Venezuela, especially the Cinaruco River, a lowland tributary of the Orinoco River. Three species of *Cichla* naturally occur in the Cinaruco River: *C. temensis* (Humboldt, 1833), *C. orinocensis* (Humboldt, 1833), and *C. intermedia* (Machado, 1971). All three species exhibit similar mass-length relationships, but *C. temensis* attains larger sizes (over 600 mm SL) (Winemiller *et al.*, 1997) and grows at a faster rate than its congeners (Jepsen *et al.*, 1999). *Cichla temensis* is more abundant, and occurs in the broadest range of habitats than the other species (Jepsen *et al.*, 1997). *Cichla intermedia* is strongly associated with structured habitats in the main channel in or near fast current, and *C. orinocensis* is most common in shallow areas of lagoons with structure and low-velocity shoreline areas of the main channel (Jepsen *et al.*, 1997). In seasonal tropical rivers, *Cichla* substrate-spawn during the low- and rising-water periods (Jepsen *et al.*, 1997; Winemiller *et al.*, 1997; Jepsen *et al.*, 1999) and may cease feeding while they defend their brood (Devick, 1972; Zaret, 1980; Jepsen *et al.*, 1997).

Like many other South American rivers, the Cinaruco River supports an important sport fishery focused primarily on *Cichla*. Over-exploitation and illegal netting currently threaten the sustainability of this resource (Layman & Winemiller, in press). It is necessary to understand patterns of movement of these fishes to develop effective management and conservation plans. However, to date little information has been compiled on movement in naturally occurring populations. Taphorn & Barbarino Duque (1993) demonstrated the effectiveness of mark-recapture to estimate local population abundance of *Cichla* in the Cinaruco River and an associated floodplain lake (Laguna Larga) as well as the Rio Capanaparo and an associated floodplain lake (Laguna Brava), but their study provided no information on movement because it was short term. Therefore, in 1999 we initiated a cooperative mark-recapture program with the Cinaruco River Fishing Club and Tour Apure, two sport-fishing groups that target *Cichla*, to evaluate movement of *Cichla* in the Cinaruco River and promote conservation awareness among local fishermen. Our objectives were to evaluate movement in three ways, among: 1) species, 2) size classes, and 3) hydrologic seasons. Here we present results from our study, discuss management implications, and provide hypotheses and recommendations for future research.

Study Area. The Cinaruco River is a low-gradient tributary of the Orinoco River that drains the llanos (savanna) of southern Apure State, Venezuela (6° 32' N, 67° 24' W; Fig. 1), and forms

the southern boundary of Santos Luzardos National Park. The region is characterized by nutrient-poor soils, savanna vegetation and dense riparian forest, and highly seasonal rainfall (most between May and September) resulting in predictable floods. Annual water level fluctuation of the Cinaruco typically exceeds 5 m (Fig. 2; Arrington & Winemiller 2003). Width of the main channel at the lowest point in the hydrologic cycle (Feb – Mar) ranges from 40 to 200 m. An extensive floodplain is inundated during the high water period, with peak inundation occurring in September. Many of the numerous lateral lagoons maintain connections to the main river channel throughout the hydrologic cycle. The river's black-waters (Sioli, 1975) are oligotrophic and acidic, with high levels of dissolved organic carbon in the form of humic acids. The substrate is almost uniformly sandy, with deposits of leaf litter and fine organic matter in slack-water areas. Woody debris provides habitat structure in the main channel and lagoons. Over 260 fish species have been collected from the Cinaruco River, with most species < 10 cm standard length. See Jepsen *et al.* (1997), Arrington & Winemiller (2003), Hoeinghaus *et al.* (2003), and Layman & Winemiller (in press) for additional descriptions of the region.

Material and Methods

Individuals of three sympatric species of *Cichla* (*C. temensis*, *C. orinocensis*, and *C. intermedia*) were collected by hook and line and tagged with uniquely numbered nylon floy tags (Floy-2, Floy Tag & Mfg., Inc.) between January 1999 and May 2003. Tags were inserted at the base of the posterior end of the second dorsal fin using a standard FT-2 applicator. Standard length (SL), weight (kg), species identity, and location of capture were recorded at time of original capture and tagging. Individuals were tagged, measured and released immediately following capture in most cases, although some individuals were held for a recovery period before being released. Anglers and fishing guides were included in this project to promote local conservation awareness and to increase the number of tagged fish and recaptures. Select anglers and guides were provided tags, applicators, and measuring equipment, and were instructed on how to properly implant the tag and record data by one or more of the authors. A total of eight anglers and guides were selected for inclusion in this study based on reliability and experience in facilitation of previous research projects at the Cinaruco River. Approximately 20% of the *Cichla* tagged were caught by anglers or guides.

Data from each recapture were used in multiple analyses, but the sample size for each analysis may differ due to incomplete data for some recaptures (e.g. recapture location obtained without weight or length data). Distances were measured as the shortest fluvial distance between the tagging and recapture locations during the low-water period of the annual hydrologic cycle. Relationships between the time interval to recapture and size (weight) at time of recapture with distance between tag and recapture location were

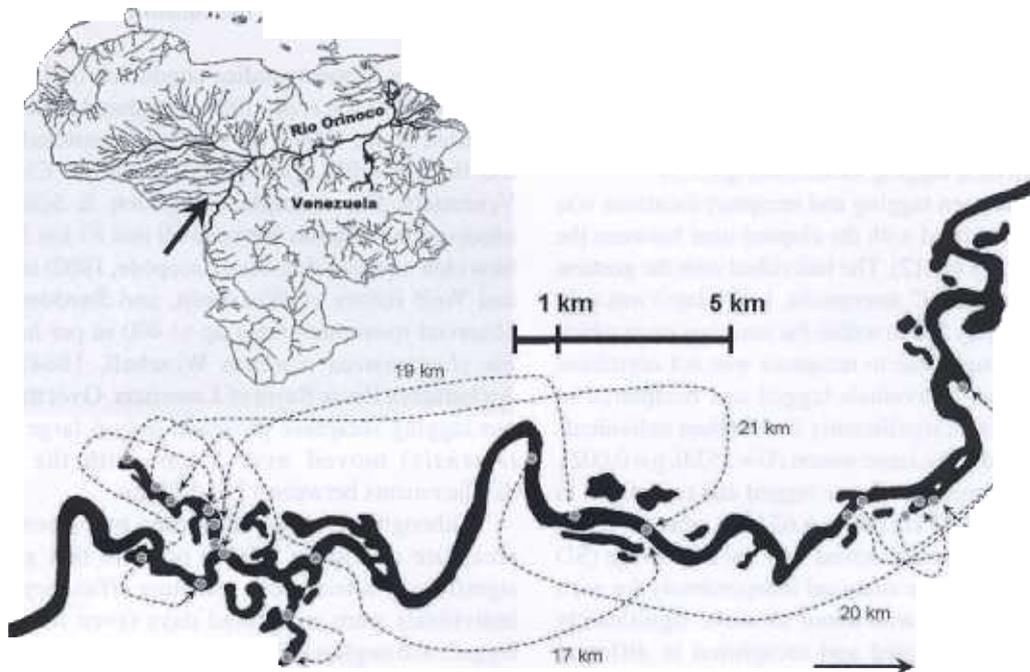


Fig. 1. Map of Venezuelan rivers with arrow depicting location of the Cinaruco River in the Orinoco River drainage. Dashed arrows illustrate movements of individuals recaptured more than 750 m from their tagging location. Flow is in the direction of the arrow at bottom right.

evaluated by Pearson's correlation. Data for distance between tag and recapture locations and the time interval between the two events were not normally distributed, and transformation of the data did not result in normality or equal variances (evaluated using Levene's statistic). Therefore, non-parametric tests were performed with untransformed movement data. The Kruskal-Wallis test was used when factors were composed of more than two groups (i.e. species), and the Mann-Whitney U test was used when factors were composed of two groups. Tests were performed for each species independently and for all species combined. All statistical analyses were performed with SPSS (Version 11.0.1, SPSS Inc.).

Results

Between January 1999 and May 2003, 2,224 *Cichla* were tagged (*C. temensis*: $n = 1,097$; *C. orinocensis*: $n = 985$; *C. intermedia*: $n = 142$). On average *C. temensis* were larger than *C. orinocensis* and *C. intermedia* [standard length (mm): *C. temensis*: $\text{min} = 172$, $\text{max} = 700$, $\text{mean} = 351.0$, $\text{std. dev.} = 92.5$; *C. orinocensis*: $\text{min} = 180$, $\text{max} = 468$, $\text{mean} = 308.0$, $\text{std. dev.} = 49.6$; *C. intermedia*: $\text{min} = 190$, $\text{max} = 450$, $\text{mean} = 319.5$, $\text{std. dev.} = 49.1$]. During the study period we recorded 62 recaptures (61 individuals, with a single *C. intermedia* recaptured twice) for an overall recapture efficiency of 2.8% [recaptures: *C. temensis*: $n = 42$ (3.8%); *C. orinocensis*: $n = 14$ (1.4%), *C. intermedia*: $n = 5$ (3.5%)]. Time interval to recapture was highly variable, ranging between 2.5 hrs and 1,091 days (Table 1),

and was significantly different between species ($\chi^2 = 7.15$, $\text{df} = 2$, $p = 0.028$). The longest average and maximum times between tag and recapture were for *C. intermedia*, whereas *C. orinocensis* was recaptured relatively quickly compared to its congeners (Table 1).

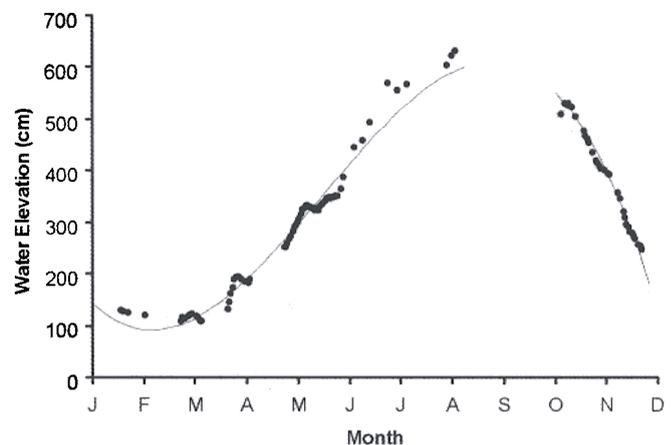


Fig. 2. Annual water level fluctuation of the Cinaruco River during 1999 (modified from Arrington & Winemiller, 2003).

Most recaptures (73%) occurred within 1 km of the tagging location, with 34% within 100 m (Fig. 2). Distance between tag and recapture locations differed significantly between species ($\chi^2 = 6.37$, $\text{df} = 2$, $p = 0.041$). *Cichla intermedia* and *C. orinocensis* tended to move relatively short distances (Table 2, Fig. 3),

whereas all but one of the individuals recaptured > 1 km from their tagging location were *C. temensis* (Fig. 3a). We observed a significant positive relationship between body size (weight) at time of recapture and distance moved ($r^2 = 0.42$, $p < 0.01$; Table 2, Fig. 3b). Four large *C. temensis* were recaptured between 17 and 21 km from their tagging locations (Figs. 1,3).

The distance between tagging and recapture locations was not significantly correlated with the elapsed time between the two events ($r^2 = 0.21$, $p = 0.12$). The individual with the greatest time interval to recapture (*C. intermedia*, 1,091 days) was only displaced approximately 500 m within the same lagoon in which it was tagged. Although time to recapture was not correlated with distance moved, individuals tagged and recaptured in different seasons moved significantly farther than individuals tagged and recaptured in the same season ($U = 253.0$, $p = 0.002$). The average displacement for fishes tagged and recaptured in different seasons was 4.25 km (SD = 6.63 km); whereas fishes recaptured in the same season moved 1.07 km on average (SD = 3.22 km). However, when analyzed independently for each species, only *C. temensis* was found to move significantly longer distances when tagged and recaptured in different seasons (*C. temensis*: $U = 115.5$, $p = 0.02$; *C. orinocensis*: $U = 7.0$, $p = 0.38$; *C. intermedia*: no recaptures in different seasons). For individuals recaptured in a different habitat type (lagoon, river channel) from the tagging location, 62% had moved from the river channel into lagoons. Seventy-five percent of the individuals that moved into lagoons were tagged during the falling water-period and recaptured during the low-water period.

Table 1. Mean, minimum, and maximum number of days between tagging and recapture events for three species of *Cichla* in the Cinaruco River, Venezuela. *individual was recaptured after 2.5 hrs

Species	N	Interval to recapture (days)			
		Mean	Std Dev	Min	Max
<i>C. temensis</i>	39	216.97	232.90	2	771
<i>C. orinocensis</i>	13	68.69	128.24	0*	400
<i>C. intermedia</i>	7	274.71	439.53	7	1091

Table 2. Mean distance (km) between tag and recapture locations by species and size class at the time of recapture.

Species	N	Weight (kg)	Mean	Std. Dev.
<i>C. temensis</i>	11	< 1	0.827	1.149
	15	1 - 2	1.120	1.179
	7	2 - 3	6.885	9.536
	7	> 3	6.385	8.214
<i>C. orinocensis</i>	6		0.300	0.219
	6	2	0.700	0.903
<i>C. intermedia</i>	4	< 1	0.200	0.200
	2	1 - 2	0.300	0.282
Combined	21	< 1	0.557	0.874
	23	1 - 2	0.939	1.072
	7	2 - 3	6.886	9.536
	7	> 3	6.386	8.214

Discussion

Relative to most studies conducted on large river fishes (e.g. Hendrickson *et al.*, 1987; Langhurst & Schoenike, 1990; Snedden *et al.*, 1999), we observed restricted movement by the three *Cichla* species native to the Cinaruco River, Venezuela. For example, Langhurst & Schoenike (1990) observed movements between 69 and 87 km for smallmouth bass (*Micropterus dolomieu* Lacepede, 1802) in the Embarrass and Wolf Rivers of Wisconsin, and Snedden *et al.* (1999) observed movement rates up to 400 m per hour for spotted gar (*Lepisosteus oculatus* Winchell, 1864) in the lower Atchafalaya River Basin of Louisiana. Over the 52 months of our tagging-recapture program, only 6 large *Cichla* (all *C. temensis*) moved over 5 km, with the four longest displacements between 17 and 21 km.

Although we observed limited movement, we had low recapture efficiency. We do not feel that gear avoidance significantly affected our recapture efficiency because some individuals were recaptured days (even hours) after being tagged, and anglers utilized a variety of tackle and baits during the tagging program. Low recapture efficiency was probably a combination of several factors including: 1) characteristics of the *Cichla* populations and our study system, 2) mortality from illegal netting practices in some lagoons, 3) predation, and 4) failure to report recaptures.

The Cinaruco River and the aquatic habitats of its floodplain constitute a large heterogeneous ecosystem that supports large *Cichla* populations (Taphorn & Barbarino Duque, 1993). Recapture rate and population abundance are inversely correlated, which provides the basis for mark-recapture methods of population estimation (Krebs, 1999). Although recent reductions in maximum sizes of *Cichla* captured by anglers indicate negative impacts of harvest, the three species remain abundant and attract anglers to the region. Moreover, some habitats are relatively inaccessible to anglers and could have harbored tagged fishes. During the flood period, fishes may enter lagoons that are isolated during the low-water period. Most of these isolated lagoons are inaccessible to anglers who fish only during the falling- and low-water periods (November - April).

Commercial netters harvest large-bodied fishes from some lagoons of the Cinaruco River. *Cichla* are particularly valued by this fishery which is unregulated and illegal within the national park. Netters use small boats to deploy long beach seines (~ 300 m) in a large semi-circle; the seine is then pulled to shore, effectively removing large-bodied fishes (Layman & Winemiller, in press). In one instance, netters showed us a collection of over 100 tags (all without accompanying data), and have potentially removed many more tagged individuals.

In addition to humans, natural predators of *Cichla* are common in this species-rich ecosystem. River dolphins (*Inia geoffrensis* de Blainville, 1817) are common in the Cinaruco system (McGuire & Winemiller, 1998) and sometimes consume *Cichla* from anglers' lines or following catch and release by anglers. A few tags have also been recovered in stomachs

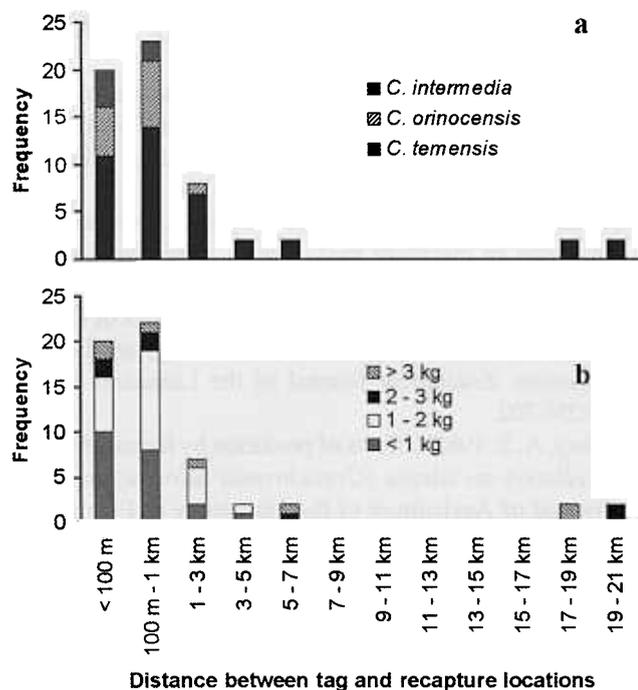


Fig. 3. Frequency histograms of distance between tag and recapture locations by (a) species and (b) size class (weight) at time of recapture. Note: distance range is not standardized for the first two categories to illustrate localized movement.

of piranhas (*Serrasalmus* spp.), abundant predators that feed primarily on chunks of flesh and fins.

The use of anglers and local fishing guides in our tagging program increased the number of tagged fish and recaptures. However, one drawback of this participation was that some anglers reported recaptures but failed to record data, or data were recorded incompletely. Anglers and guides may also selectively fish habitats with higher densities of *Cichla*, which may account for the longer period observed between tagging and recapture for *C. intermedia*. This species has relatively low abundance in lagoons (Jepsen *et al.*, 1997), which is the habitat where most fishing pressure is concentrated. Cooperative tagging programs facilitate scientist – angler dialog, promote conservation awareness, and can provide valuable ecological data (e.g. movement and growth), yet these programs generally do not provide detailed information about movement patterns and population dynamics (Gillanders *et al.*, 2001).

Despite the inherent limitations of a long-term, large-scale tagging study in a dynamic and heterogeneous river-floodplain ecosystem, we were able to obtain direct estimates of movement for a subset of the tagged fishes. Distance and direction of movement appear to be correlated with seasonal water-level changes. Movement into lagoons during the low-water period could have been associated with reproductive activity. *Cichla* species are substrate nesters and bi-parental brood guards, and many *Cichla* captured during reproductive periods (low-

and rising-water) may have been brood guarding (Devick, 1972). During the falling-water period, *Semaprochilodus kneri* (Pellegrin, 1909), a migratory prochilodontid that spawns in the productive floodplain of the whitewater Orinoco River, migrates *en mass* into the Cinaruco River. Large individuals of *C. temensis* feed heavily on *S. kneri* during the falling-water period, but *C. orinocensis* and *C. intermedia* generally do not attain sizes sufficient for feeding on these large prey (Jepsen *et al.*, 1997; Winemiller *et al.*, 1997). We have observed aggregations of large *C. temensis* feeding on migrating schools of young-of-the-year *Semaprochilodus* within lower reaches of the Cinaruco River during the early falling water-period (October-December). Individuals exhibiting the longest movements (17-21 km) in our study were large *C. temensis* that were either tagged or recaptured in the main river channel during the falling-water period.

Taken in context with previous work on the Cinaruco River, findings from our study illustrate the need for management to conserve the *Cichla* fishery. Because most *Cichla* apparently undertake only limited movements, continued illegal netting could have severe impacts. Some large *C. temensis* make longer movements, but our limited information indicates that long-distance dispersal probably would be a relatively ineffective mechanism for restocking local habitats once depleted. Most *Cichla* remained within a kilometer of their original capture location, even after an interval of months or, in some cases, years.

Our study has prompted several specific questions for future research. Do spawning and non-spawning *Cichla* use main channel and lagoon habitats in a predictable manner? Do large *C. temensis* undergo long distance downstream movements at the start of the falling-water period to exploit the influx of migratory *Semaprochilodus*, and if so, do they return to their original location later in the dry season? To what extent does movement occur during the high-water period when habitat connectivity is greatest? More research, employing alternative tracking methods, is needed to address these questions. Radio telemetry has been successfully used to evaluate patterns of movement and habitat use of large cichlids in the floodplain region of the Zambezi River in Africa (Thorstad *et al.*, 2001), and should be an effective technique to examine movement patterns of *Cichla* and other large Neotropical fishes.

Acknowledgements

We thank Edgar Pelaéz, Jim Marzoula, Carol Marzoula, and Glenn Webb of the Cinaruco River Fishing Club and Tour Apure for logistical support and involvement throughout the project. We also thank the anglers and guides that participated in this study. Don Taphorn at the Experimental University of the Western Llanos (UNELLEZ) provided logistical support. Fernando M. Pelicice and Milza C. F. Abelha translated the abstract to Portuguese. Eric Dibble, Luiz Gomes and Miguel Petre Jr. provided thoughtful comment on the manuscript. Fish collections were made under permits #0439 and #0192

issued by the Servicio Autonomo de los Recursos Pesqueros y Acuicolas of Venezuela. Various aspects of this project were supported by a U.S. Environmental Protection Agency Science to Achieve Results Graduate Fellowship (CAL), William "Bill" Baab Conservation Fellowships (CAL and DAA), Texas A & M Regents (CAL) and Tom Slick Fellowships (CAL and DAA), The L.T. Jordan Institute (DAA), The International Sportfish Fund (KOW, CAL and DAA), a Society of Wetland Scientists Student Research Scholarship (DJH), and National Science Foundation grant # DEB-0089834 and an associated REU grant (KOW).

Literature Cited

- Arrington, D. A. & K. O. Winemiller. 2003. Diel changeover in sandbank fish assemblages in a Neotropical floodplain river. *Journal of Fish Biology*, 63:1-18.
- Devick, W. S. 1972. Life history study of the tucunare, *Cichla ocellaris*. Federal Aid in Sportfish Restoration Project F-9-1, Job Completion Report, Hawaii Department of Land and Natural Resources, Honolulu.
- Fischer, G. W. & W. E. Grant. 1994. Use of a native predator to control overcrowding in warm-water polyculture ponds: simulation of a tucunare (*Cichla monoculus*) tilapia (*Oreochromis niloticus*) system. *Ecological Modeling*, 72:205-227.
- Gillanders, B. M., D. J. Ferrell & N. L. Andrew. 2001. Estimates of movement and life-history parameters of yellowtail kingfish (*Seriola lalandi*): how useful are data from a cooperative tagging programme? *Marine and Freshwater Research*, 52:179-192.
- Hendrickson, D. A., K. R. Bestgen, D. M. Kubly & D. L. Probst. 1987. Movements and growth of fishes in the Gila River drainage, Arizona and New Mexico. *Southwestern Naturalist*, 32:351-356.
- Hoeinghaus, D. J., C. A. Layman, D. A. Arrington & K. O. Winemiller. 2003. Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks. *Environmental Biology of Fishes*, 67:379-387.
- Jepsen, D. B., K. O. Winemiller & D. C. Taphorn. 1997. Temporal patterns of resource partitioning among *Cichla* species in a Venezuelan blackwater river. *Journal of Fish Biology*, 51:1085-1108.
- Jepsen, D. B., K. O. Winemiller, D. C. Taphorn & D. Rodriguez Olarte. 1999. Age structure and growth of peacock cichlids from rivers and reservoirs of Venezuela. *Journal of Fish Biology*, 55:433-450.
- Krebs, C. J. 1999. *Ecological Methodology*. Menlo Park, Addison-Welsey, 620p.
- Langhurst, R. W. & D. L. Schoenike. 1990. Seasonal migration of smallmouth bass in the Embarrass and Wolf Rivers, Wisconsin. *North American Journal of Fisheries Management*, 10:224-227.
- Layman, C. A. & K. O. Winemiller. (in press). Size-based prey response to piscivore exclusion in a Neotropical river. *Ecology*.
- Lowe-McConnell, R. H. 1969. The cichlid fishes of Guyana, South America, with notes on their ecology and breeding behavior. *Zoological Journal of the Linnaean Society*, 48:255-302.
- McGinty, A. S. 1984. Effects of predation by tucunare (*Cichla ocellaris*) on tilapia (*Oreochromis nilotica*) in ponds. *Journal of Agriculture of the University of Puerto Rico*, 68:101-105.
- Sioli, H. 1975. Tropical rivers as an expression of their terrestrial environment. Pp. 275-288. In: Golly, F. B. & E. Medina (Eds.). *Tropical Ecological Systems*. New York, Springer-Verlag.
- Snedden, G. A., W. E. Kelso & D. A. Rutherford. 1999. Diel and seasonal patterns of spotted gar movement and habitat use in the lower Atchafalaya River Basin, Louisiana. *Transactions of the American Fisheries Society*, 128:144-154.
- Taphorn, D. C. & A. Barbarino Duque. 1993. Evaluacion de la situacion actual de los pavones, *Cichla* spp., en el Parque Nacional Capanaparo-Cinaruco, Estado Apure, Venezuela. *Natura*, 96:10-25.
- Thorstad, E. B., C. J. Hay, T. F. Næsje & F. Økland. 2001. Movements and habitat utilization of three cichlid species in the Zambezi River, Namibia. *Ecology of Freshwater Fish*, 10:238-246.
- Winemiller, K. O., D. C. Taphorn & A. Barbarino-Duque. 1997. Ecology of *Cichla* (Cichlidae) in two blackwater rivers of southern Venezuela. *Copeia*, 1997:690-696.
- Zaret, T. M. 1980. Life-history and growth relationships of *Cichla ocellaris*, a predatory South American cichlid. *Biotropica*, 12:144-157.
- Zaret, T. M. & R. T. Paine. 1973. Species introduction in a tropical lake. *Science*, 182:449-455.

Received September 7, 2003
Accepted November 28, 2003