

# Effects of seasonality and migratory prey on body condition of *Cichla* species in a tropical floodplain river

Hoeinghaus DJ, Winemiller KO, Layman CA, Arrington DA, Jepsen DB. Effects of seasonality and migratory prey on body condition of *Cichla* species in a tropical floodplain river. Ecology of Freshwater Fish 2006. © 2006 The Authors Journal compilation © 2006 Blackwell Munksgaard

**Abstract** – In this study we examine trends in body condition of three *Cichla* species native to the Cinaruco River, Venezuela. Specifically, we characterise the potential subsidy provided by migratory *Semaprochilodus kneri* to *Cichla* by comparing condition among species, hydrologic seasons and different size-classes (based on the ability to consume *S. kneri* assuming gape-limitation). All three species had lowest body condition during the rising-water season (following the reproduction period). Only *Cichla temensis* had greater body condition during the falling-water season than low-water season. During the falling-water season, *C. temensis* >300 mm SL had significantly greater condition than smaller conspecifics. Annual migration of *S. kneri* into the river during the falling-water season provides a resource subsidy to large *C. temensis*. Transfer of whitewater production into nutrient-poor rivers by migratory fishes appears to be a general phenomenon in the major Neotropical river basins and may partially account for high standing stocks of large piscivores in these unproductive ecosystems.

**D.J. Hoeinghaus<sup>1,2,\*</sup>,  
K.O. Winemiller<sup>1</sup>, C.A. Layman<sup>3</sup>,  
D.A. Arrington<sup>4</sup>, D.B. Jepsen<sup>5</sup>**

<sup>1</sup>Section of Ecology, Evolutionary Biology and Systematics, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas, USA, <sup>2</sup>Kansas State University, Division of Biology, Manhattan, KS, USA, <sup>3</sup>Marine Biology Program, Department of Biological Sciences, Florida International University, North Miami, FL, USA, <sup>4</sup>Loxahatchee River District, Jupiter, FL, USA, <sup>5</sup>Oregon Department of Fish and Wildlife, Corvallis Research Lab, Corvallis, OR, USA

Key words: gape limitation; ribazón; predation; food web subsidy; *Semaprochilodus kneri*

\*Present address: D. J. Hoeinghaus, Kansas State University, Division of Biology, 104 Ackert Hall, Manhattan, KS 66506, USA; e-mail: djhoeing@ksu.edu

Accepted for publication January 31, 2006

## Introduction

Migratory fishes are an important component of aquatic food webs worldwide. Fish migration links food webs across landscapes by transporting production among seemingly disparate systems and providing a resource subsidy to resident consumers (Polis et al. 1997, 2004). For example, marine derived nutrients are transported by anadromous fishes, such as salmon and alewife, into food webs of riverine (Garman & Macko 1998; MacAvoy et al. 2000; Chaloner et al. 2002) and terrestrial systems (Hilderbrand et al. 1999; Szepanski et al. 1999; Darimont & Reimchen 2002) through predation, gamete release, excretion or decomposition (especially in the case of salmon). In a similar manner, freshwater fishes migrating from nutrient-rich floodplains into oligotrophic rivers may

transport production among systems and represent a substantial resource subsidy for resident piscivores (Winemiller & Jepsen 1998, 2004).

In tropical river systems, massive reproductive migrations crossing hundreds of kilometres are driven by wet-dry seasonality, with reproduction of migratory fishes usually occurring during the high-water period in productive floodplains or flooded forests (Goulding 1980; Lowe-McConnell 1987). Among the most conspicuous of the Neotropical long-distance migrants are the prochilodontid fishes of the genera *Prochilodus* and *Semaprochilodus*. These large characiform fishes feed on detritus, algae and associated microorganisms (Bowen 1983; Bowen et al. 1984) and are the primary species of many commercial and subsistence fisheries in South America (Welcomme 1990). Although specifics of prochilodontid spawning migrations may vary

by region [e.g. Central Amazon Basin, Brazil – Ribeiro & Petrere (1990); Vazzoler & Amadio (1990); Upper Paraná Basin, Brazil – Agostinho et al. (1993, 2003; Orinoco Basin, Venezuela – Lilyestrom (1983); Barbarino-Duque et al. (1998)], in general, reproduction and feeding occur in productive floodplains during the high-water period, and young-of-the-year form dense schools with adults to disperse throughout the river basin as water levels fall.

In the Cinaruco River of western Venezuela, *Semaprochilodus kneri* (Pellegrin) migrate *en mass* into the system from the Orinoco floodplain during the falling-water period and provide a seasonally abundant prey resource to large piscivores. The consumption of migratory *S. kneri* may provide an important resource subsidy that allows large piscivores in this system to achieve greater condition, fecundity and population densities than based on *in situ* productivity alone (Winemiller & Jepsen 1998, 2004). In this study we analyse a database of weight and standard length (SL) data collected over 4 years to examine trends in body condition of three *Cichla* species, abundant piscivores native to the Amazon, Essequibo and Orinoco basins. Specifically, we characterise the potential subsidy provided by *S. kneri* to *Cichla* by comparing body condition among species, during different hydrologic seasons, and in relation to gape limitations of different *Cichla* size classes and the ability to consume *S. kneri*.

## Materials and methods

### Regional description

The llanos is an extensive grassland savanna in central and western Venezuela characterised by strong annual wet and dry seasonality (see Machado-Allison 1990; Winemiller et al. 1996; Sarmiento & Pinillos 2001). Whitewater rivers draining the Andes, such as the Guanare and Portuguesa Rivers, deposit nutrient-rich alluvial sediments in floodplains of the Orinoco River during flood periods when broad expanses of the lowland llanos are inundated (Hoeinghaus et al. 2004). During the rainy season, many fish species migrate into nutrient-rich lowland rivers and flooded terrain where they spawn (Machado-Allison 1990; Winemiller 1996). During the falling-water period, large schools dominated by *Prochilodus* and *Semaprochilodus*, locally called ‘ribazones’, ascend rivers of western Venezuela from the Orinoco River floodplain and Apure River delta (Barbarino-Duque et al. 1998; Layman & Winemiller 2005). School density gradually decreases as individuals remain in upstream habitat, are caught by fishermen (Rodriguez et al. in press), or are consumed by predators.

### Study area

The Cinaruco River is a low-gradient floodplain tributary of the Orinoco River that originates and drains the south-western llanos near the Colombian border (6°32’N, 67°24’W). Rivers such as the Cinaruco, that originate in the llanos rather than the Andes Mountains, have low nutrient and suspended sediment loads because of the dystrophic nature of llanos soils (Montoya et al. 2006). Seasonal water level fluctuations exceed 5 m, with peak inundation occurring in August. During the high-water period, thousands of square kilometres of surrounding savanna and gallery forest are flooded. Width of the main channel ranges from 50 to 200 m during the lowest point in the hydrologic cycle. Over 280 fish species have been collected from the Cinaruco River, with taxa representing a wide range of ecological attributes and life history strategies (Arrington & Winemiller 2003; Hoeinghaus et al. 2003b; Arrington et al. 2005; Layman & Winemiller 2005; Layman et al. 2005c; Winemiller et al. 2006).

Three species of *Cichla*, locally called pavón, naturally occur in the Cinaruco River: *C. temensis* (Humboldt), *C. orinocensis* (Humboldt), and *C. intermedia* (Machado). *Cichla intermedia* is strongly associated with structured habitats in the main channel in or near fast currents and *C. orinocensis* is most common in shallow areas of lagoons near submerged branches or rocks (Jepsen et al. 1997). *Cichla temensis* occurs in a broad range of habitats in both lagoons and the main channel (Jepsen et al. 1997). All three species construct nests and spawn during the late low-water to early rising-water period (Winemiller et al. 1997; Jepsen et al. 1999) and cease feeding while brood guarding (Devick 1972; Zaret 1980; Jepsen et al. 1997). Pavón are voracious piscivores, capable of causing community level shifts in prey species abundances and distributions (Zaret & Paine 1973; Jepsen et al. 1997; Layman & Winemiller 2004; Layman et al. 2005a).

### Analyses

A database of weight and SL data for the three species of *Cichla* (*C. temensis*  $N = 650$ , *C. orinocensis*  $N = 675$ , *C. intermedia*  $N = 73$ ; Table 1) naturally occurring in the Cinaruco River, Venezuela was compiled from a mark-recapture study conducted between January 1999 and May 2003 (Hoeinghaus et al. 2003a). Fish were collected during all seasons from all representative habitat types (e.g. sand banks, lagoons, creeks and the main channel) in an effort to collect representative samples of the populations. All individuals were collected by hook and line, identified, weighed (g), measured (mm SL) and released at the

Table 1. Number of individuals available for analysis by species, season and size-class.

Species	<i>N</i>	Season	<i>N</i>	Size-class	<i>N</i>
<i>C. temensis</i>	650	Falling	172	<300	46
				>300	126
	Low	472	<300	116	
			>300	356	
	Rising	6	<300	2	
			>300	4	
<i>C. orinocensis</i>	675	Falling	78	<300	48
				>300	30
	Low	590	<300	202	
			>300	388	
	Rising	7	<300	6	
			>300	1	
<i>C. intermedia</i>	73	Falling	10	<300	2
				>300	8
	Low	61	<300	13	
			>300	48	
	Rising	2	<300	0	
			>300	2	

location of capture. Although individuals were collected during all seasons, sample sizes are substantially lower for all three species during the rising-water period (May to August) because *Cichla* cease feeding while brood-guarding and high water constraints limit fishing effort (Table 1). For this reason, statistical analyses primarily compare condition during periods of falling (September to December) and low water (January to April). Comparisons are further limited for *C. intermedia* because this species is less abundant than its congeners.

Individuals were separated into two size-classes based on the ability to consume *S. kneri* determined from morphological data assuming gape limitation. Maximum gape (mouth aperture in vertical dimension with jaws fully protruded) and SL was measured (to nearest mm) for a subset of *Cichla* specimens ( $N = 61$ ) to generate gape–SL relationships for each species. *Semaprochilodus kneri* SL and maximum body depth (vertical distance from the anterior insertion of the dorsal fin to the ventrum) were measured (to nearest mm) for young-of-the-year individuals and post-spawn adults (age 1+) migrating into the Cinaruco River during the falling-water period of 2003. Additional individuals were measured during the low-water period of 2004. *Semaprochilodus kneri* were collected by castnet and released following measurement. To evaluate the accuracy of gape limitation estimates based on morphological measures, stomach contents of *Cichla* were examined using the gastric lavage method (see Layman et al. 2005b) and SLs for all *S. kneri* occurring in stomachs were recorded along with the SL of the pavón in which it was found.

It is important to note that other species in the river undergo seasonal migrations similar to *S. kneri*, albeit

in much lower densities. Specifically, we have previously demonstrated that *Leporinus* spp. and *Myleus* spp. are also part of the ribazón on the Cinaruco River (Layman & Winemiller 2005). However, in more than 2400 individual *Cichla* stomachs we have examined since 1994 (*C. temensis*  $N = 1,365$ ; *C. orinocensis*  $N = 755$ ; *C. intermedia*  $N = 307$ ), we have never found a member of these two genera in the stomach contents. Likewise, other fish species we believe may undergo seasonal migrations (e.g. *Piractus brachypomum*, *Mylossoma aureus*, *Pseudoplatystoma fasciatum*) have never been identified in *Cichla* stomachs. *Semaprochilodus kneri*, however, makes up approximately 50% of *C. temensis* diet during the falling-water period (Jepsen et al. 1997; Winemiller & Jepsen 1998), strongly suggesting *C. temensis* preferentially utilises this prey species and not others that undertake seasonal migrations. As such, we base our analysis in this paper on *S. kneri* only.

*Cichla* body condition was evaluated using the relationship between weight and SL,  $W = aL^b$ , at three levels: taxonomic (among species), seasonal (among seasons within species) and size class (between size-classes within species and seasons). Weight and SL data were log-transformed to yield a linear relationship [ $\log_{10}(W) = a + b(\log_{10}L)$ ] in which  $b$  is the slope (allometric coefficient) and  $a$  is the intercept. Analysis of covariance (ANCOVA) was used to test for differences among slopes and intercepts (when slopes did not differ) of the log-transformed data for the three levels of comparison. For all tests,  $\log_{10}W$  was the dependent variable and  $\log_{10}L$  the covariate. Depending on the level of comparison, the independent variable was species, season or size-class. For significant main effects, pairwise comparisons of intercepts were performed, with the experiment-wide error rate maintained at  $\alpha = 0.05$  using Bonferroni correction. Although other indices, such as Fulton's  $K$ , are commonly used to assess fish condition, the calculation of least-squares regression parameters for a population or subgroup is a more accurate method of comparing length–weight relationships (Cone 1989).

## Results

### Taxonomic and seasonal comparisons

Significant differences in body condition were observed at the taxonomic level. Intercepts of the log-transformed weight–SL relationships were significantly different among all species (Table 2). For individuals of the same SL, *C. orinocensis* weighed slightly more than its congeners and *C. temensis* weighed the least (Fig. 1).

Table 2. ANCOVA results of body condition comparisons at the three levels of comparison: among species, among seasons within species and between size classes (<300 and >300 mm SL) within species and seasons.

Species	Factor	d.f.	F-value	P-value
All	Species × LogSL	2	0.445	0.641
	Species	2	141.185	<b>&lt;0.001</b> ; <u>O &gt; I &gt; T</u>
<i>C. temensis</i>	Season × LogSL	2	0.601	0.549
	Season	2	19.014	<b>&lt;0.001</b> ; <u>F &gt; L &gt; R</u>
	Size-class			
	Falling	1	5.442	<b>0.021</b>
Low	1	1.781	0.183	
<i>C. orinocensis</i>	Season × LogSL	2	0.187	0.830
	Season	2	5.975	<b>0.003</b> ; <u>F L &gt; R</u>
	Size-class			
	Falling	1	1.487	0.227
Low	1	0.819	0.366	
<i>C. intermedia</i>	Season × LogSL	1	0.194	0.661
	Season	1	0.123	0.727
	Size-class			
Low	1	0.674	0.415	

For significant main effects (bold values), pairwise comparisons of intercepts are provided in the adjacent column with underlined pairs not significantly different (O, *C. orinocensis*; I, *C. intermedia*; T, *C. temensis*; F, falling; L, low; R, rising). Not all possible size-class or seasonal comparisons were performed because of insufficient sample sizes for some size-classes and seasons (Table 1). For *C. intermedia*, seasonal comparisons are for the falling and low-water periods only because of limited sample size.

Significant seasonal differences in body condition were observed for *C. temensis* and *C. intermedia*. Only *C. temensis* had significantly higher condition during the falling water period (Table 2; Fig. 2b), whereas body condition of both species was significantly lower during the rising water period (Table 2; Fig. 2b,d). No difference was observed in condition of *C. intermedia* between falling and low-water periods (comparisons

were not made among the rising-water period because of limited sample size; Fig. 2f).

Size-class comparisons

Relationships between maximum gape and SL did not differ among *Cichla* species (ANCOVA,  $F = 0.835$ , d.f. = 2,  $P = 0.439$ ), so the combined relationship ( $y = 0.151x - 5.999$ ,  $R^2 = 0.924$ ) was used to estimate mouth gape for all individuals using measures of SL attained at the time of capture. Maximum body depth of *S. kneri* increased with SL according to the relationship  $y = 0.374x + 0.351$ ,  $R^2 = 0.97$ . Based on the above morphological relationships and the size of young-of-the-year *S. kneri* captured migrating into the river during the falling water period of 2003, *Cichla* were separated into two size-classes: <300 and >300 mm SL, with 300 mm representing the threshold at which *Cichla* can consume *S. kneri* assuming gape limitation.

The 300-mm threshold defined by morphological measurements conforms to dietary data from stomach contents analyses. The smallest *Cichla* from the Cinaruco River with a *S. kneri* recorded in its stomach was a *C. temensis* with 335 mm SL, captured November 1999 (number of stomachs examined = 1365). Stomach contents analyses illustrate that *C. temensis* preferentially consume young-of-the-year *S. kneri* even when their gape would allow them to consume larger individuals (Fig. 3). No *S. kneri* were identified from stomach contents of *C. orinocensis* (number of stomachs = 755) or *C. intermedia* (number of stomachs = 307), although both species attain sizes capable of consuming *S. kneri*. For

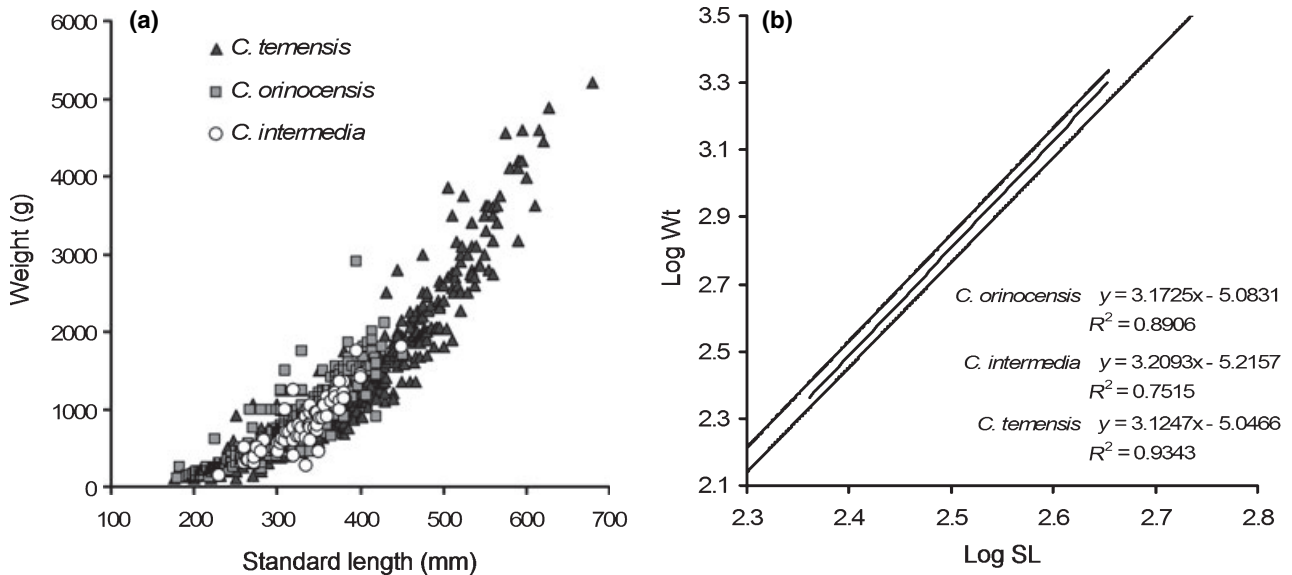


Fig. 1. Untransformed (a) and log-transformed (b) weight-standard length relationships for Cinaruco *Cichla*. Regression intercepts are significantly different, with *C. orinocensis* > *C. intermedia* > *C. temensis* (see Table 2).

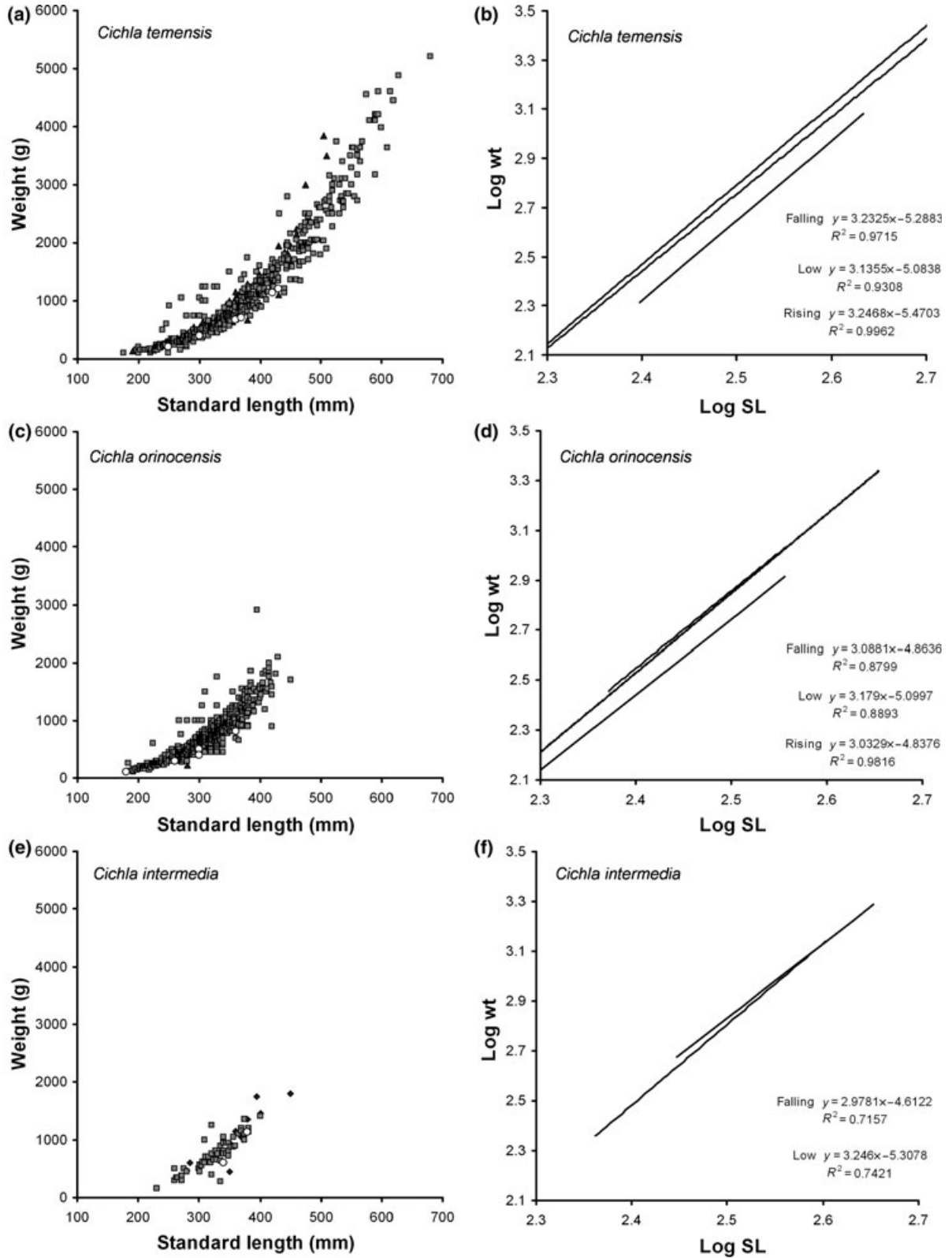


Fig. 2. Untransformed and log-transformed weight-standards length relationships among seasons for each species. Seasons: ▲ = falling, ■ = low, ○ = rising. See Table 2 for ANCOVA results.

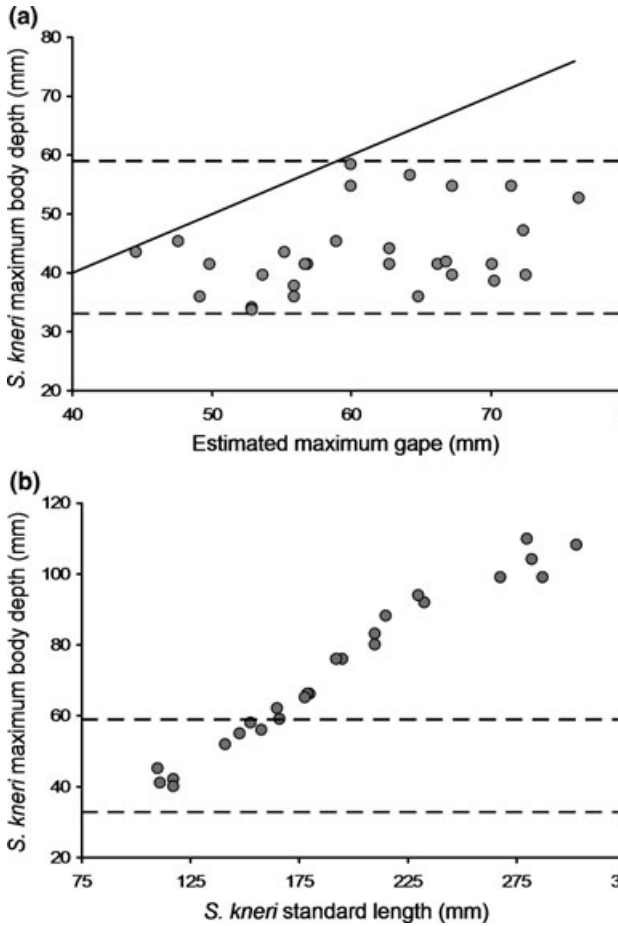


Fig. 3. Relationship between (a) *Semaprochilodus kneri* body depth and *Cichla temensis* maximum gape based on stomach contents analysis and (b) standard length and maximum body depth for *S. kneri* across the range of size classes that occur in the Cinaruco River throughout the hydrologic cycle. The solid line denotes mouth gape–body depth ratio = 1 and dashed lines bound the size of *S. kneri* found in stomach contents.

example, this dataset contains 419 *C. orinocensis* and 58 *C. intermedia* that were >300 mm SL, more than half of the individuals measured for each species (Table 1).

A single significant difference was observed in body condition among size-classes for all intra-seasonal species comparisons. Large *C. temensis* (>300 mm SL) had significantly higher condition than smaller individuals during the falling-water period, as evidenced by a significantly higher regression slope (Table 2; Fig. 4).

## Discussion

We observed significant species, seasonal and size-based differences in body condition of naturally occurring *Cichla* species of the Cinaruco River, Venezuela. Relationships between weight and SL

likely differed among species because of differences in allocation of energy for growth. Based on growth rate estimates, *C. temensis* are longer and heavier than its congeners for individuals of the same age (Jepsen et al. 1999). *Cichla temensis* therefore have lower condition values because they increase body length at a faster rate than the other species, i.e. more biomass is allocated to increasing length rather than girth (Jepsen et al. 1999). General trends in *Cichla* body condition among seasons, on the other hand, are because of seasonal variation in prey densities, as well as seasonal reproduction by all three species.

Tropical fishes reveal diverse morphological and physiological adaptations to wet–dry seasonality, most notably reproductive seasons that coincide with rising water levels that allow juveniles to feed in resource-rich floodplains (Goulding 1980; Lowe-McConnell 1987). During floodwater recession, fishes are forced from the shallow refuges of the floodplain and prey densities increase in shrinking aquatic habitats. Large-bodied predators in tropical floodplain systems generally exhibit increased foraging activity during the falling and low-water periods as prey are forced into deeper creeks, lagoons and the main river channel (Jepsen et al. 1997; Arrington et al. 2002; Hoeinghaus et al. 2003b; Arrington et al. 2006).

Reproductive behaviour of *Cichla* species (nesting and brood-guarding) and low densities of optimally sized prey (e.g. depleted populations of *S. kneri*) combine to create a physiological winter during the end of the dry season and initial stages of the rising-water period (when remaining prey become widely dispersed), as evidenced by annual otolith bands (Lowe-McConnell 1964; Jepsen et al. 1999). We observed significantly lower condition of both *C. temensis* and *C. orinocensis* during the rising-water period, but do not have sufficient data to fully investigate seasonal trends in condition for *C. intermedia*. Jepsen et al. (1999) observed otolith bands for all three *Cichla* species of the Cinaruco River, revealing that growth of all three species is lowest following the reproductive and brood-guarding period.

*Cichla temensis* was the only species with significantly greater body condition during the falling-water period than the low-water and rising-water periods. Comparison of *C. temensis* body condition among seasons, while excluding individuals >300 mm SL during the falling water period, yields the same trend observed for *C. orinocensis* and suggested for *C. intermedia*: condition did not differ significantly among the falling and low-water periods, but was significantly lower during the rising-water period. *Cichla temensis* large enough to consume *S. kneri* had significantly higher condition than smaller individuals during the falling-water period. Although all three *Cichla* species in the Cinaruco exhibit seasonal variations in diet

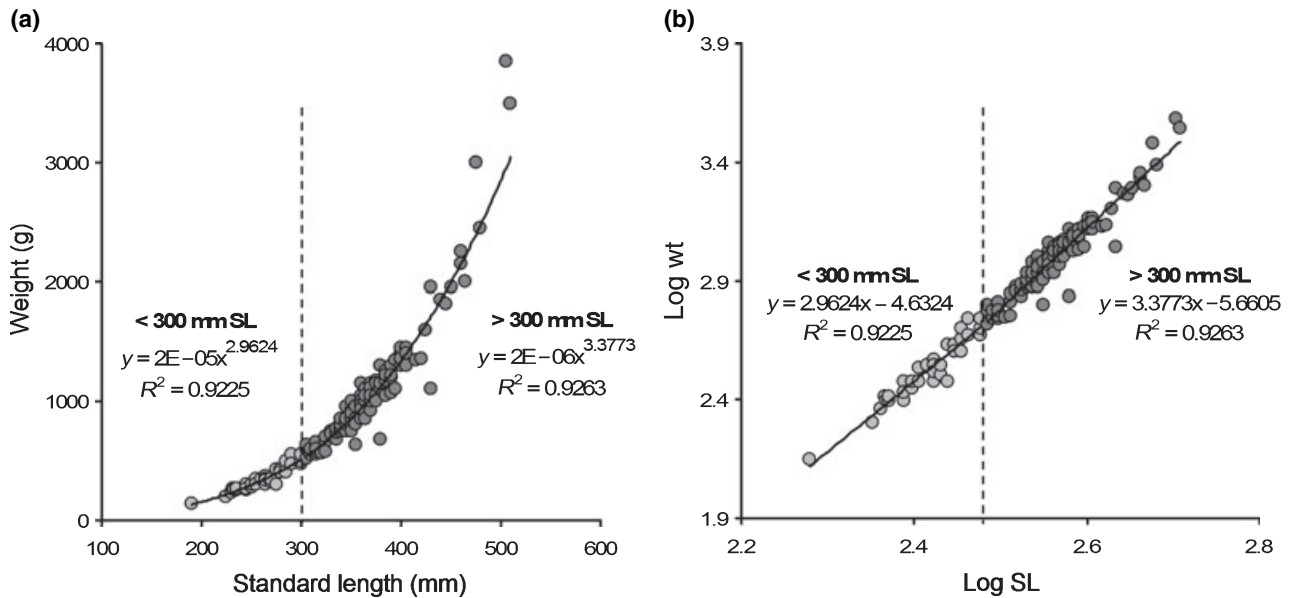


Fig. 4. Untransformed (a) and log-transformed (b) weight–standard length relationships among size classes (<300 and >300 mm SL) for *Cichla temensis* during the falling water period. Slopes are significantly different ( $P = 0.021$ ; Table 2).

(Jepsen et al. 1997), large *C. temensis* appear to gain a growth advantage over its congeners and smaller conspecifics by exploiting the annual arrival of large schools of *S. kneri*.

Results from dietary and stable isotope analyses support the conclusion that greater body condition of large *C. temensis* during the falling-water period is because of the consumption of young-of-the-year *S. kneri* migrating into the system. During the falling water period, young-of-the-year *S. kneri* comprises approximately 50% of the prey volume in stomach contents of large (>40 cm SL) *C. temensis* (Jepsen et al. 1997; Winemiller & Jepsen 1998). Stable carbon isotope results directly tie the observed growth advantage of large *C. temensis* during the falling water period to assimilation of carbon ultimately derived from the Orinoco floodplain, i.e. through consumption of *S. kneri* (Winemiller & Jepsen 2004). While other species may move into the Cinaruco from the Orinoco floodplain, diet data suggests that *S. kneri* are by far the most important prey species (Layman et al. 2005c).

Lipid concentration of dorsal muscle tissue in *C. temensis* is greatest during the falling-water period (Arrington et al. 2006). Energy stored in the form of lipids can be readily used for reproduction in the subsequent low water period. The previous studies mentioned above, combined with the body condition results presented here, indicate that young-of-the-year *S. kneri* provide large *C. temensis* with a substantial resource subsidy prior to the spawning season. This additional nutrition should permit them to attain higher fecundities and population densities

than would be possible based on *in situ* production alone.

Movement patterns and behavioural observations also suggest that young *S. kneri* are especially important for large *C. temensis*, whereas habitat associations or behaviours of *C. orinocensis* and *C. intermedia* may prevent or limit consumption of *S. kneri*. Hoeninghaus et al. (2003a) observed short-distance movement (~500 m) of *C. orinocensis*, *C. intermedia* and small *C. temensis* in the Cinaruco River throughout the hydrologic cycle, however large *C. temensis* moved into the main river channel and exhibited longer downstream movements (up to 21 km) associated with the falling-water period. Observations of aggregations of large *C. temensis* attacking migrating schools of young-of-the-year *S. kneri* within lower reaches of the Cinaruco River during the early falling water period (October to December) suggest that some *C. temensis* move downstream prior to the upstream migration of *S. kneri* in order to maximise their opportunity to consume this seasonally abundant food resource. In contrast, *C. orinocensis* is widely and evenly distributed within flooded gallery forest during the falling-water period and *C. intermedia* is strongly associated with structured habitats with high current velocity. *Semaprochilodus kneri* are most abundant in relatively open low-velocity areas of the main river channel and connected lagoons, especially sandy beaches where they graze algae and detritus. Thus, large *C. orinocensis* and *C. intermedia* may not consume *S. kneri* simply because they do not occur in the same habitats.



By consuming migratory *S. kneri*, *C. temensis*, which only occur in clear or blackwater rivers, assimilate carbon originating from the vast and productive floodplains of the whitewater Orinoco River (Winemiller & Jepsen 2004). Consumption of *S. kneri* also increases ecological efficiency as large piscivores, such as *Cichla*, are able to exploit prey of nearly optimal size (Winemiller & Taylor 1987) that also occupy low positions in the food web (Winemiller & Jepsen 1998; Layman et al. 2005b). The importation of production from whitewater floodplains, together with the increased ecological efficiency associated with short food chains, could account for the impressive secondary productivity of relatively nutrient-poor tropical rivers such as the Cinaruco.

The transport of primary production from nutrient-rich whitewater rivers into oligotrophic clearwater and blackwater ecosystems by migratory fishes appears to be a general phenomenon within the major Neotropical river basins. In the Amazon Basin for example, migratory species of the genera *Mylossoma*, *Colossoma*, *Anodus*, *Triporthus*, *Semaprochilodus*, *Prochilodus* and *Brycon* (which all feed at relatively low positions in the food web) occur in multiple river types as adults, but only reproduce in whitewater systems during the high-water period (Carvalho de Lima & Araujo-Lima 2004). Whitewater floodplains function as source habitats, and upstream migrations that distribute these species within the basin also serve to transport whitewater production into oligotrophic systems. Disruption of seasonal migrations by river impoundment or overfishing, already widespread in the Orinoco Basin (Winemiller et al. 1996; Barbarino-Duque et al. 1998), is likely to have profound effects on ecosystem processes of the Cinaruco and other oligotrophic tropical rivers.

### Acknowledgements

Edgar Pelaéz, Jim Marzoula, Carol Marzoula and Glenn Webb provided logistical support through the Cinaruco River Fishing Club and Tour Apure. Don Taphorn at UNELLEZ provided logistical support and helped obtain sampling permits. Fish collections were made with fishing permits 0439 and 0192 issued by the Servicio Autonomo de los Recursos Pesqueros y Acuicolas of Venezuela. We acknowledge reviewer suggestions, which improved the manuscript. This study was funded in part by a Texas Water Resources Institute Mill's Scholarship and Research Scholarships from the Society of Wetland Scientists and TAMU Office of Graduate Studies (DJH), a US Environmental Protection Agency STAR Graduate Fellowship and Texas A & M Regents Fellowship (CAL), Tom Slick and William 'Bill' Baab Conservation Fellowships (CAL and DAA), The L.T. Jordan Institute (DAA), The International Sportfish Fund (KOW, CAL and DAA), and National Science Foundation grants DEB-0411978 (KOW and CAL) and DEB-0089834 (KOW). Facilities were made available to DJH at the

Research Nucleus in Limnology, Ichthyology and Aquaculture (Nupélia) at the State University of Maringá (UEM), Brazil, during manuscript preparation.

### References

- Agostinho, A.A., Vazzoler, A.E.A.d.M., Gomes, L.C. & Okada, E.K. 1993. Estratificación espacial y comportamiento de *Prochilodus scrofa* en distintas fases del ciclo de vida, en las planicie de inundación del alto río Paraná y embalse de Itaipu, Paraná, Brasil. *Revista de Hydrobiologia Tropical* 26: 79–90.
- Agostinho, A.A., Gomes, L.C., Suzuki, H.I. & Júlio, H.F. Jr 2003. Migratory fishes of the upper Paraná River basin, Brazil. In: Carolsfeld, J., Harvey, J., Ross, C. & Baer, A., eds. *Migratory fishes of South America: biology, fisheries and conservation status*. Victoria, Canada: International Development Research Centre and The World Bank, pp. 19–98.
- Arrington, D.A. & Winemiller, K.O. 2003. Diel changeover in sandbank fish assemblages in a neotropical floodplain river. *Journal of Fish Biology* 63: 1–18.
- Arrington, D.A., Winemiller, K.O., Loftus, W.F. & Akin, S. 2002. How often do fishes “run on empty”? *Ecology* 83: 2145–2151.
- Arrington, D.A., Winemiller, K.O. & Layman, C.A. 2005. Community assembly at the patch scale in a species rich tropical river. *Oecologia* 144: 157–167.
- Arrington, D.A., Davidson, B.K., Winemiller, K.O. & Layman, C.A. 2006. Influence of life history and seasonal hydrology on lipid storage in three Neotropical fish species. *Journal of Fish Biology* 68: 1347–1361.
- Barbarino-Duque, A., Taphorn, D.C. & Winemiller, K.O. 1998. Ecology of the coporo, *Prochilodus mariae* (Characiformes, Prochilodontidae), and status of annual migrations in western Venezuela. *Environmental Biology of Fishes* 53: 33–46.
- Bowen, S.H. 1983. Detritivory in neotropical fish communities. *Environmental Biology of Fishes* 9: 137–144.
- Bowen, S.H., Bonetto, A.A. & Ahlgren, M.O. 1984. Microorganisms and detritus in the diet of a typical neotropical riverine detritivore, *Prochilodus platensis* (Pisces: Prochilodontidae). *Limnology and Oceanography* 29: 1120–1122.
- Carvalho de Lima, Á. & Araujo-Lima, C.A.R.M. 2004. The distributions of larval and juvenile fishes in Amazonian rivers of different nutrient status. *Freshwater Biology* 49: 787–800.
- Chaloner, D.T., Martin, K.M., Wipfli, M.S., Ostrom, P.H. & Lamberti, G.A. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1257–1265.
- Cone, R.S. 1989. The need to reconsider the use of condition indices in fishery science. *Transactions of the American Fisheries Society* 118: 510–514.
- Darimont, C.T. & Reimchen, T.E. 2002. Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. *Canadian Journal of Zoology* 80: 1638–1642.
- Devick, W.S. 1972. Life history study of the tucunare, *Cichla ocellaris*. Federal Aid in Sportfish Restoration Project F-9-1, Job Completion Report. Honolulu: Hawaii Department of Land and Natural Resources.



- Garman, G.C. & Macko, S.A. 1998. Contribution of marine-derived organic matter to an Atlantic coast, freshwater, tidal stream by anadromous clupeid fishes. *Journal of the North American Benthological Society* 17: 277–285.
- Goulding, M. 1980. *The fishes and the forest*. Berkeley, CA: University of California Press.
- Hilderbrand, G.V., Hanley, T.A., Robbins, C.T. & Schwartz, C.C. 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* 121: 546–550.
- Hoeinghaus, D.J., Layman, C.A., Arrington, D.A. & Winemiller, K.O. 2003a. Movement of *Cichla* species (Cichlidae) in a Venezuelan floodplain river. *Neotropical Ichthyology* 1: 121–126.
- Hoeinghaus, D.J., Layman, C.A., Arrington, D.A. & Winemiller, K.O. 2003b. Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks. *Environmental Biology of Fishes* 67: 379–387.
- Hoeinghaus, D.J., Winemiller, K.O. & Taphorn, D.C. 2004. Compositional change in fish assemblages along the Andean piedmont – Llanos floodplain gradient of the río Portuguesa, Venezuela. *Neotropical Ichthyology* 2: 85–92.
- Jepsen, D.B., Winemiller, K.O. & Taphorn, D.C. 1997. Temporal patterns of resource partitioning among *Cichla* species in a Venezuelan blackwater river. *Journal of Fish Biology* 51: 1085–1108.
- Jepsen, D.B., Winemiller, K.O., Taphorn, D.C. & Rodríguez-Olarte, D. 1999. Age structure and growth of peacock cichlids from rivers and reservoirs of Venezuela. *Journal of Fish Biology* 55: 433–450.
- Layman, C.A. & Winemiller, K.O. 2004. Size-based prey response to piscivore exclusion in a Neotropical river. *Ecology* 85: 1311–1320.
- Layman, C.A. & Winemiller, K.O. 2005. Patterns of habitat segregation among large fishes in a Venezuelan floodplain river. *Neotropical Ichthyology* 3: 103–109.
- Layman, C.A., Langerhans, R.B. & Winemiller, K.O. 2005a. Body size, not other morphological traits, characterizes cascading effects in fish assemblage composition following commercial netting. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 2802–2810.
- Layman, C.A., Winemiller, K.O., Arrington, D.A. & Jepsen, D.B. 2005b. Body size and trophic position in a diverse tropical food web. *Ecology* 86: 2530–2535.
- Layman, C.A., Winemiller, K.O. & Arrington, D.A. 2005c. Describing the structure and function of a Neotropical river food web using stable isotopes, stomach contents, and functional experiments. In: de Ruiter, P.C., Wolters, V. & Moore, J.C., eds. *Dynamic food webs: multispecies assemblages, ecosystem development, and environmental change*. Amsterdam: Elsevier, pp. 395–406.
- Lilyestrom, C.G. 1983. Aspectos de la biología del coporo (*Prochilodus mariae*). *Revista UNELLEZ de Ciencia y Tecnología* 1: 5–11.
- Lowe-McConnell, R.H. 1964. *The fishes of the Rupununi savanna district of British Guiana*, Pt. 1. Groupings of fish species and effects of the seasonal cycles on the fish. *Zoological Journal of the Linnaean Society* 45: 103–144.
- Lowe-McConnell, R.H. 1987. *Ecological studies in tropical fish communities*. Cambridge, UK: Cambridge University Press.
- MacAvoy, S.E., Macko, S.A., McIninch, S.P. & Garman, G.C. 2000. Marine nutrient contributions to freshwater apex predators. *Oecologia* 122: 568–573.
- Machado-Allison, A. 1990. Ecology of fishes of the floodplain areas of the Venezuelan Llanos. *Interciencia* 15: 411–423.
- Montoya, J.V., Roelke, D.L., Winemiller, K.O., Cotner, J.B. & Snider, J.A. 2006. Effects of hydrological seasonality and lateral connectivity on environmental variables and algal biomass of a tropical floodplain river. *Journal of the North American Benthological Society* 25: 157–170.
- Polis, G.A., Anderson, W.B. & Holt, R.D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28: 289–316.
- Polis, G.A., Power, M.E. & Huxel, G.R., editors. 2004. *Food webs at the landscape level*. Chicago: University of Chicago Press.
- Ribeiro, M.C.L.d.B. & Petrere, M. Jr 1990. Fisheries ecology and management of the jaraquí (*Semaprochilodus taeniurus*, *S. insignis*) in Central Amazonia. *Regulated Rivers Research and Management* 5: 195–215.
- Rodríguez, M.A., Winemiller, K.O., Lewis, W.M. & Taphorn, D.C. in press. The freshwater habitats, fishes, and fisheries of the Orinoco River Basin. In: Minns, C.K. & Munawar, M., eds. *Freshwater fishes, their biodiversity, fisheries and habitats: health and prospects*. *Ecovision World Monograph Series*.
- Sarmiento, G. & Pinillos, M. 2001. Patterns and processes in a seasonally flooded tropical plain: the Apure Llanos, Venezuela. *Journal of Biogeography* 28: 985–996.
- Szepanski, M.M., Ben-David, M. & Van Ballenberghe, V. 1999. Assessment of anadromous salmon resources in the diet of the Alexander Archipelago wolf using stable isotope analysis. *Oecologia* 120: 327–335.
- Vazzoler, A.E.A.d.M. & Amadio, S.A. 1990. Aspectos biológicos de peixes Amazônicos. XIII. Estrutura e comportamento de cardumes multiespecíficos de *Semaprochilodus* (Characiformes, Prochilodontidae) no baixo rio Negro, Amazonas, Brasil. *Revista Brasileira Biologia* 50: 537–546.
- Welcomme, R.L. 1990. Status of fisheries in South American rivers. *Interciencia* 15: 337–345.
- Winemiller, K.O. 1996. Dynamic diversity in fish assemblages of tropical rivers. In: Cody, M.L. & Smallwood, J.A., eds. *Long-term studies of vertebrate communities*. Orlando: Academic Press, pp. 99–132.
- Winemiller, K.O. & Jepsen, D.B. 1998. Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology* 53: 267–296.
- Winemiller, K.O. & Jepsen, D.B. 2004. Migratory neotropical fish subsidize food webs of oligotrophic blackwater rivers. In: Polis, G.A., Power, M.E. & Huxel, G.R., eds. *Food webs at the landscape level*. Chicago: University of Chicago Press, pp. 115–132.
- Winemiller, K.O. & Taylor, D.H. 1987. Predatory behavior and competition between smallmouth and largemouth bass. *American Midland Naturalist* 117: 148–166.
- Winemiller, K.O., Marrero, C. & Taphorn, D.C. 1996. Perturbaciones causadas por el hombre a las poblaciones de peces de los llanos y del piedemonte Andino de Venezuela. *Biollania* 12: 13–48.

**Hoeinghaus et al.**

- Winemiller, K.O., Taphorn, D.C. & Barbarino-Duque, A. 1997. Ecology of *Cichla* (Cichlidae) in two blackwater rivers of southern Venezuela. *Copeia* 1997: 690–696.
- Winemiller, K.O., Montoya, J.V., Layman, C.A., Roelke, D.L. & Cotner, J.B. 2006. Experimental demonstration of seasonal fish effects on benthic ecology of a Neotropical floodplain river. *Journal of the North American Benthological Society* 25: 250–262.
- Zaret, T.M. 1980. Life-history and growth relationships of *Cichla ocellaris*, a predatory South American cichlid. *Biotropica* 12: 144–157.
- Zaret, T.M. & Paine, R.T. 1973. Species introduction in a tropical lake. *Science* 182: 449–455.