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Ecology and Status of Piscivores in Guri, an Oligotrophic Tropical Reservoir

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Abstract.—Guri Reservoir in Venezuela supports sport fisheries for two cichlid species (pavón venado or speckled pavon *Cichla temensis* and pavón mariposa *C. orinocensis*) and payara *Hydrolycus scomberoides.* The lake receives acidic, hyperoligotrophic "black waters" from the Caroní River and experiences water level fluctuations associated with seasonal precipitation and hydroelectric operations. During the early 1980s, piscivore populations expanded in the new reservoir, but the quality of sportfishing declined during the 1990s. During 1993–94, we studied the ecology of the two *Cichla* species, *H. scomberoides,* and a fourth piscivore, *Plagioscion squamosissimus* (curvinata or silver croaker) and compared our data with those from similar surveys performed 7–9 years earlier (0–2 years after attainment of the reservoir's current crest height). Seine and gill-net samples from the lake's northern region produced 50 fish species from 18 families. Seine samples were dominated by a small characid, *Hemigrammus micropterus,* whereas gill-net samples were dominated by a large detritivorous characiform, *Prochilodus rubrotaeniatus.* Gill-net catch rates were low in all three surveys. All four piscivores from our recent survey had better body condition than in a 1985–1986 study, an indication of possible growth compensation. Diet breadths of all piscivores were low, and diet overlap was low for *H. scomberoides* with the two *Cichla* species and for *P. squamosissimus* with *C. orinocensis. Hydrolycus scomberoides* and *C. temensis* consumed significantly larger prey than *P. squamosissimus,* and differences in the relative proportions of specific characid and cichlid fishes consumed by the two *Cichla* species indicate that they forage at different depths within the littoral zone. The combined effects of hyperoligotrophic waters entering the reservoir, reduced inputs of dissolved nutrients from submerged terrestrial vegetation, low retention time of the reservoir, and harvest probably influence the low abundance of the two *Cichla* species in Guri Reservoir.

Most information on reservoir limnology and fisheries comes from temperate regions, where impoundments, including those created for hydroelectric generation and flood control, have enhanced recreational fishing opportunities (Prosser 1986). In recent years, construction of large reservoirs has slowed in the United States, due, in part, to increased awareness of environmental and economic costs. However, hydroelectric facilities continue to be constructed on a grand scale in other regions, especially the neotropics (Fearnside 1989; Allan and Flecker 1993). Large hydropower impoundments can directly affect tropical fisheries through alteration of hydrology, habitat, and migration routes (Barthem et al. 1991). Some fluvial species disappear from reservoirs, whereas others persist at altered densities (Alvarez et al. 1986; Winston et al. 1991; Agostinho and Zalewski 1994). Reservoirs typically support fewer fish species than their associated rivers, often as a result of large-scale changes in the regimes of temperature, turbidity, flow, allochthonous nutrient inputs, and availability of food resources (Alvarez et al. 1986).

High productivity in new reservoirs has been attributed to retention of allochthonous and autochthonous materials during initial impoundment, release of nutrients from inundated soils, and availability of organic material from inundated

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substrates and vegetation (Prosser 1986). Following initial flooding, submerged organic matter decomposes and releases dissolved nutrients, which usually increases production at all levels, including that of predatory fishes (O'Brien 1990). Depending on local climate and the physical and chemical attributes of the reservoir, high rates of production can last for many years during a period known as the "trophic upsurge" (Kimmel and Groeger 1986). As dissolved nutrients are either depleted by the fauna (Goddard and Redmond 1986) or flushed through the spillway, this high initial fish production gradually decreases and levels off at a rate somewhere between those of natural rivers and natural lakes of the same region (Noble 1986; Randall et al. 1995). This "boom–bust" cycle of reservoir production, which may last 25–30 years, has long been recognized by reservoir managers in temperate regions (Rzoska 1966).

Tropical reservoirs differ from temperate lakes because rates of physicochemical and biological processes tend to be faster at higher mean annual temperatures. For example, the trophic upsurge may last only 6–10 years in the tropics (Lowe-McConnell 1973). Water level fluctuations associated with hydroelectric facilities affect tropical fishes, many of which spawn when water levels rise instead of responding to variation in water temperature or day length (Schwassman 1978). Increasing demands for electricity in developing countries have largely been met with hydroelectric power, yet the full effects of river impoundment on tropical river ecosystems are poorly understood.

Guri Reservoir (formed by Raul Leoni Dam), the eighth largest reservoir (4,250 km^2) and the second largest hydroelectric facility in the world, currently supplies 70% of Venezuela's electrical power (10,000 MW) (Morales and Gorzula 1986). During the 1980s, a sportfishing industry was established at Guri Reservoir, complete with hotels, boats, local guides, and tourist excursions. The primary sport fish species are two cichlid species (pavón venado or speckled pavon *Cichla temensis* and pavón mariposa *C. orinocensis*) that are locally called peacock bass or pavones. Although size (30 cm minimum) and bag (daily possession of five) limits were established by the Ministry of Environment and Renewable Natural Resources (MARN), compliance and enforcement are poor at the reservoir (L. Balbas, personal observation). In recent years, sport fishers have reported poor catches. In addition to the sport fishery, gear restrictions and catch limits are being developed for a limited-entry commercial fishery. These negotiations are being undertaken with scant information on the current population status of the two *Cichla* species and other large fishes. Despite the popularity of *Cichla* spp. as sport fish and the sport fish potential of other predatory fishes, such as payara *Hydrolycus scomberoides*, curvinata (or silver croaker) *Plagioscion squamosissimus*, and redeye piranha *Serrasalmus rhombeus*, little research has been conducted on fish ecology in Guri Reservoir. Initial assessments of the recreational and commercial fisheries potential of the reservoir documented 68 species, the most important (biomass) being *Prochilodus rubrotaeniatus*, *Plagioscion squamosissimus*, and *Hydrolycus scomberoides* (Alvarez et al. 1986; Lasso et al. 1989; Novoa et al. 1989).

The four most common, large piscivores of Guri Reservoir are *Cichla temensis*, *C. orinocensis*, *P. squamosissimus*, and *H. scomberoides*. The two *Cichla* species are nonindigenous to the Caroní River basin and were introduced into Guri when ponds were flooded during the final stage of reservoir filling during 1979 (Alvarez et al. 1986; Balbás and Pacheco 1989). Within 5 years, these cichlids colonized the entire shoreline of the lake (Alvarez et al. 1986). Both *Cichla* species are native in other rivers of the Orinoco River basin, and *P. squamosissimus* and *H. scomberoides* are native to the Caroní River Basin.

The goal of our study was to investigate angler claims of declining *Cichla* populations in Guri by surveying the fish community in the northern region of the reservoir. Our objectives were to (1) measure water quality; (2) assess the relative abundances of littoral zone fishes that form the prey base for piscivores; (3) compare gill-net catch per unit effort (CPUE) of dominant species between surveys conducted during 1985–1986, 1987, and 1993–1994; (4) evaluate population size structure and length–weight relationships of the four dominant piscivores; and (5) analyze diet composition and interspecific diet overlap of the four dominant piscivores.

Study Area

Guri Reservoir is fed by the Caroní and Paragua rivers (Figure 1), both of which drain the ancient granite outcroppings and nutrient-poor sandy soils of the Guyana Shield region. Construction of Guri Reservoir began in 1963, and a final crest height of 272 m above sea level was achieved in 1986. Currently, the reservoir has a surface area of 4,250

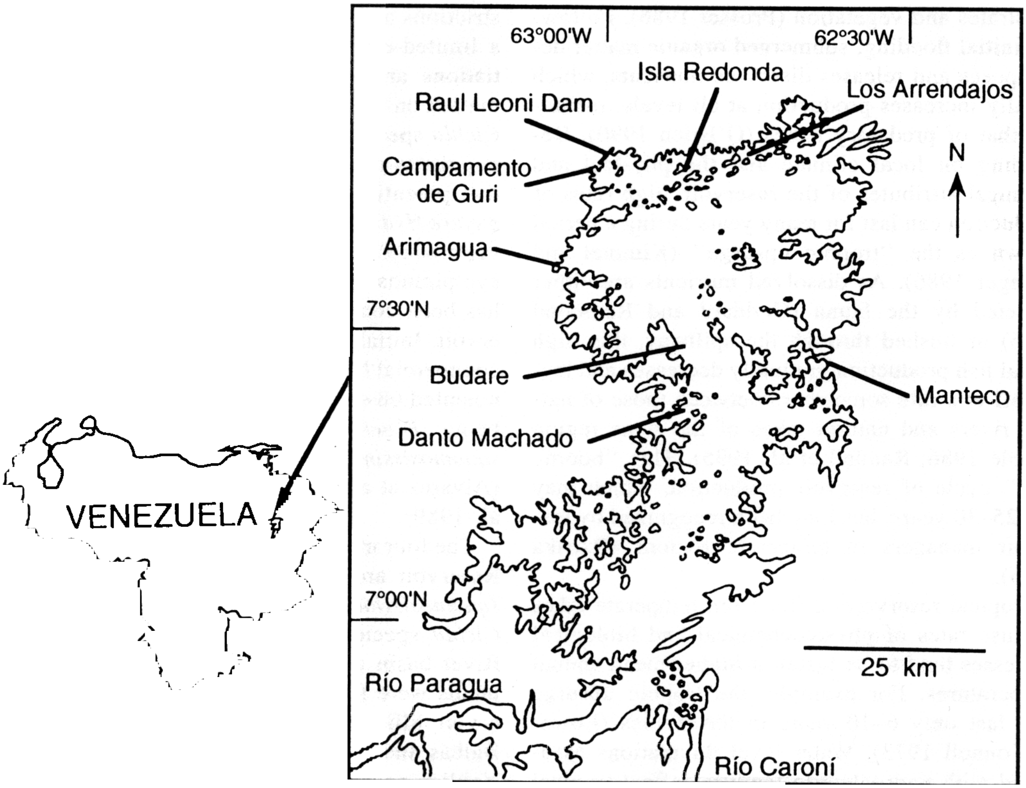

FIGURE 1.—Map of Guri Reservoir in Bolivar State, Venezuela, showing locations of sampling sites.

km² and a volume of 135,000 × 10^6 m^3 (Corporación Venezolana de Guiana–Electrificación del Caroní [CVG–EDELCA], unpublished report).

Annual rainfall at Guri is 256 cm (the majority falling between May and October) and annual mean water temperature is 26.5°C (Gonzalez et al. 1989). "Black waters" (Sioli 1975) from the tributary rivers are characterized by low pH, low nutrient content, low suspended particulates, and high concentrations of dissolved organic matter that produce a dark, tea-stained appearance. Guri has a relatively low retention time of hyperoligotrophic waters, so aquatic primary and secondary production is extremely low (Gonzalez et al. 1989; Weibezahn 1994). No true aquatic macrophytes inhabit littoral areas in the lake's northern section; however, aquatic plants were documented during the initial trophic upsurge in the reservoir (Alvarez et al. 1986; Vilarrubia and Cova 1993).

Methods

Habitat.—Field sampling was conducted from October 1993 through July 1994 in the northern section of the reservoir (from 07°20′N to 07°50′N and from 63°40′W to 63°05′W; Figure 1). We restricted sampling to littoral areas containing flooded timber, savanna, or sand and gravel beaches. Temperature (°C) , depth (m) , and substrate type (sand, gravel, flooded savanna, flooded forest) were recorded before sampling fishes. Dissolved oxygen (mg/L), hardness (mg/L as $CaCO_3$), pH, and alkalinity (mg/L as HCO_3^- + CO_3^{-2}) were measured by using a Hach kit.

Fish community composition.—We sampled fishes with 3-m and 6.5-m seines (6.3-mm mesh) to evaluate the prey fish assemblage. All specimens from seine hauls were preserved for taxonomic identification and calculation of species relative abundances. Species composition was compared between seasons (rainy versus dry) and among capture sites (eight locations) with a chi square contingency table (SYSTAT 1992). Sport fishers' catches, particularly *Cichla* species, were examined opportunistically, more or less at random with respect to time and location, in order to increase samples for diet and condition analyses.

To evaluate change in the piscivore assemblage, monofilament nylon gill nets (each net had three

25 × 2-m panels with one panel each 2.5-, 5.1-, and 10.3-mm-bar mesh) and multifilament nylon gill nets (two nets, 63 × 2 m with 15-mm stretch mesh and one net, 63 × 2 mm, with 11-mm stretch mesh) were fished during both day and night in the littoral zone. Gill nets were lifted after approximately 6–12 h increments to reduce the number of specimens collected with empty stomachs. The multifilament gill nets were identical to those used in the 1987 survey, and both types of gill nets were set in seven locations, which enabled comparisons between current CPUEs and those previously obtained by the EDELCA Ecology Lab during 1987 (Figure 1; EDELCA, unpublished data). During 1987, an average of 541 m of experimental gill net was set for an average of 23 h over 12 monthly outings (mean meter-hours/outing = 12,443 ± 743 SD). During 1993–1994, an average of 160 m of experimental gill net was set for an average of 18.5 h over 12 outings (mean meter-hours/outing = 2,960 ± 2,084 SD). Gill nets were set within 100 m of shore, mostly in coves with submerged timber and protection from open wind and waves. The date, starting time, sample duration, location, and habitat features were recorded for each gill-net set and seine haul. Gill-net catch (number and weight) was standardized to a common unit of effort ($\text{value} \cdot 100\ \text{m}^{-1} \cdot \text{h}^{-1}$) for each sampling period and species for the 1987 and 1993–1994 surveys.

Size distributions and weight–length relationships.—Wet weight (nearest 0.1 kg) and total length (TL, nearest millimeter) were recorded for each piscivore captured by gill net or hook and line. Preserved specimens from seine hauls were measured to the nearest 0.1 g in the laboratory. Weight–length relationship determinations included all available piscivore specimens, regardless of capture method, based on the equation $\log W = a + b(\log \text{TL})$, where W is wet weight, a is the y-intercept, TL is total length, and b is the slope of the relationship between W and TL. Given that efficiency for different size-classes varies among our sampling methods, these combined results provide a better overall assessment of populations than results from any one method.

Diets.—All netted specimens and a subsample of the angling sample were examined for stomach contents and gonad development. Stomach contents were identified to the lowest possible taxonomic level, and the volume of each prey item was estimated by water displacement in a graduated cylinder. Stomach contents were divided into 17 food categories based on higher taxonomic groupings (e.g., family). The number of stomachs examined, number of stomachs with food, total food volume, and the volumetric percentage of each food category by predator species was determined for each piscivore. Diet breadth was indexed with Levins' (1968) standardized index of niche width: $B = 1/\Sigma p_{ij}^2$, where p_{ij} is the proportion of resource i used by the consumer. MacArthur and Levins' (1967) index was used to compare diet overlap between all pairwise combinations of the four piscivores: $\phi_{jk} = \Sigma(p_{ij}p_{ik})/\Sigma p_{ij}^2$, where p_{ij} and p_{ik} are the proportions of resource i used by species j and species k, respectively, for all resources. Prey length distributions were plotted for each piscivore, and sizes of prey consumed by the four piscivores were compared with t-tests and analysis of covariance (ANCOVA), the latter method testing for an effect of predator size.

Results

Habitat

Our measurements of chemical and physical variables were consistent with the classic black water attributes previously described for Guri Reservoir (Alvarez et al. 1986; Weibezahn 1994). We obtained low values for pH (6), hardness (0–17 mg/L), and alkalinity (4–17 mg/L). Weibezahn (1994) reported pH values from 4.8 to 6.7, hardness from 1.4 to 4.4 mg/L, and alkalinity from 22 to 78 mg/L during 1991–1992 from a station in the lake's northern sector. Alvarez et al. (1986) reported pH from 4.8 to 6.9, hardness from 2.3 to 27.0 mg/L, and alkalinity from 2.0 to 20.8 mg/L during the final stage of reservoir filling. Surface water temperatures fluctuated little (27–30°C), and dissolved oxygen was moderate to high (range 3–9 mg/L) throughout our 10-month study. The most abundant substrates at sample sites were woody debris and flooded terrestrial vegetation, with few areas having sand, gravel, or rock. These latter habitats were often associated with shorelines more exposed to wave action, areas that yielded few fishes in seine and gill-net samples.

Fish Community Composition

Seining yielded 16,642 specimens representing 18 families and 50 species, most of which (90%) were from six species: *Hemigrammus micropterus* (Characidae) 80.2%, *Curimatella immaculata* (Curimatidae) 3.5%, *Bryconops caudomaculatus* (Charcidae) 2.1%, *Hemigrammus rodwayi* (Characidae) 1.6%, *Hemiodopsis gracilis* (Hemiodontidae) 1.4%, and *Mesonauta festivus* (Cichlidae) 1.2%. Species composition from seine samples did

TABLE 1.—Between-year comparisons of catch per unit effort (CPUE; value per 100 m of net per hour) for the dominant species and total gill-net catch between the 1985–1986 (Novoa et al. 1989), 1987 (Balbas, Electrificación del Caroní, unpublished data), and 1993–1994 surveys at Guri Reservoir. The CPUE for individuals was not reported for 1985–1986.

	Biomass (kg) CPUE for:			Individual CPUE for:	
Species	1985–1986	1987	1993–1994	1987	1993–1994
Prochilodus rubrotaeniatus					
Plagioscion squamosissimus					
Hydrolycus scomberoides					
Cichla temensis					
Cichla orinocensis					
Others	0.10				
Total	1.20				

[a] The 1985–1986 data were recorded for combined *Cichla* species.

not vary significantly among sites (eight sites) and seasons (rainy versus dry) ($\chi^2 = 4.71$; df = 10; $P > 0.91$). Angling produced 181 *Cichla temensis,* 19 *C. orinocensis,* and 23 fishes representing other species.

Our 1993–1994 gill-net samples yielded 103 specimens and 8 species. The 1987 EDELCA gill-net survey produced 428 specimens and 11 species, but four species each constituted 1% or less of the total weight. Based on biomass, *Prochilodus rubrotaeniatus* was the dominant fish in gill-net catches from all three surveys, and *Plagioscion squamosissimus* ranked second (Table 1). Total fish biomass CPUE was essentially the same for 1987 and 1993–1994, but the CPUE for number of individuals captured by gill nets was 71% higher during 1993–1994. The CPUE of *P. rubrotaeniatus* based on numbers was 15% higher in the last sample but biomass CPUE was 16% lower, an indication of smaller average size. Overall, CPUE for gill nets was low for the piscivores (Table 1). Cichlid numbers and biomass were very low in all three samples, and *C. orinocensis* was not captured in gill nets during 1993–1994. Numeric CPUE of *P. squamosissimus* was higher during 1993–1994, and biomass CPUEs of both *P. squamosissimus* and *Hydrolycus scomberoides* were lower in the two recent samples compared with the 1985–1986 data (Table 1).

Size Distributions and Weight–Length Relationships

Based on the total specimens obtained from all three survey methods, size frequency distributions of the two *Cichla* species were similar, except that a greater proportion of juveniles constituted our sample of *C. orinocensis* (Figure 2). The *H. scomberoides* sample was dominated by adult size-classes, whereas the sample of *P. squamosissimus* was dominated by juvenile size-classes (Figure 2). *Hydrolycus scomberoides* was the largest of the four piscivores (0.3–6.9 kg, 33.3–107 cm TL), followed by *C. temensis* (2.0–5.4 kg, 6.5–70.2 cm TL), *C. orinocensis* (0.3–6.9 kg, 3.4–56.5 cm TL), and *P. squamosissimus* (1.0–3.8 kg, 6.1–61 cm TL).

Slopes describing weight–length relationships were virtually the same for *C. temensis, C. orinocensis,* and *P. squamosissimus* (Figure 3). *Hydrolycus scomberoides* revealed a shallower slope and larger weight–length intercept than the other three piscivores because of its more elongate body form. Variance around the log–log regression model was minimal for all four species, an indication of little intraspecific variation in body condition.

Diets

Characiform fishes (Characidae and Hemiodontidae) were the most common prey of *C. temensis* (70.7%) and *P. squamosissimus* (61.7%; Table 2). *Cichla orinocensis* consumed mostly cichlids (66.3%), and *H. scomberoides* consumed primarily pimelodid catfishes (54.2%), although the small number of diet samples for *C. orinocensis* and *H. scomberoides* make these results tentative. The most common characiforms identified from *C. temensis* stomachs were *Hemigrammus micropterus, Bryconops caudomaculatus* and *Hemiodopsis gracilis.* The cichlid *Crenicichla wallacei* and the characid *H. micropterus* were the most common fishes in stomachs of *C. orinocensis.*

The diet of *C. temensis* was most similar to that of *P. squamosissimus,* followed by *C. orinocensis* and *H. scomberoides* (Table 3). *Cichla orinocensis* had low diet overlap with *P. squamosissimus* and negligible overlap with *H. scomberoides,* whereas diets of *P. squamosissimus* and *H. scomberoides* were similar (Table 3). Each piscivore population

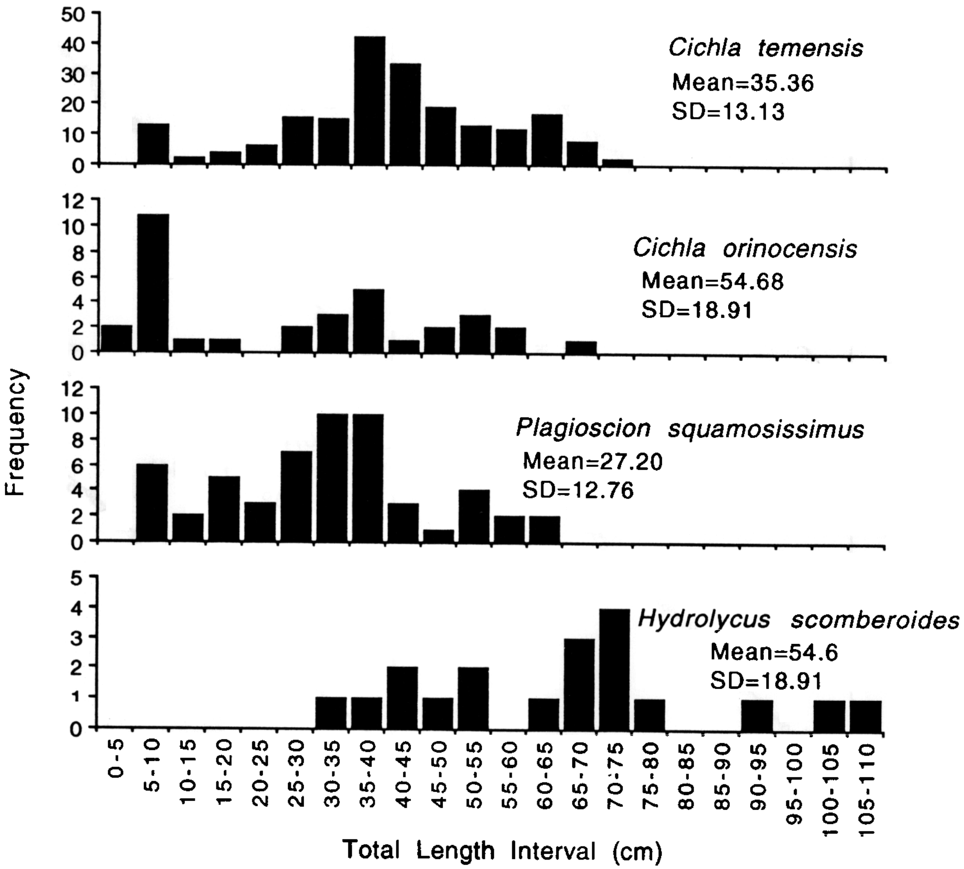

FIGURE 2.—Size distributions of the four most common Guri Reservoir piscivores, based on specimens captured by gill nets, seines, and angling.

consumed only a small portion of the available prey taxa, with standardized diet breadths ranging between 0.085 and 0.105 (Table 3).

Except for *P. squamosissimus*, most piscivores consumed fish prey between 3 and 6 cm TL (Figure 4). Many of the small *P. squamosissimus* in our sample consumed aquatic insects and penaeid shrimp shorter than 3 cm. Mean prey sizes (log-transformed prey TL) for all pairwise combinations of piscivores were significantly different (*t*-test, $P < 0.01$), with the exception of the comparison between *C. orinocensis* and *P. squamosissimus* ($P = 0.18$, due to the small sample size for *C. orinocensis*).

Predator size and prey size were strongly and positively correlated for each of four piscivores (Figure 5). *Hydrolycus scomberoides* consumed significantly larger prey than *P. squamosissimus* (ANCOVA; $P < 0.01$), but no other species pairs revealed statistically significant differences in prey size after adjustment for predator length. However, slopes of prey length–predator length for *C. temensis* and *P. squamosissimus* were significantly different, so apparent species effects could not be interpreted.

Discussion

Habitat

The extremely low nutrient content of Guri Reservoir's black waters and its low retention time are the factors that probably limit secondary production, including fishes. Gill-net CPUE estimates from three surveys during the period 1985–1994 indicate that the standing stock of fish biomass in Guri Reservoir is low relative to reservoirs worldwide. Total fish CPUEs in Guri during 1987 and 1993–1994 (0.59 and 0.60 kg·100 $m^{-1}·h^{-1}$) were within the range reported for Itaipú Reservoir, Paraná River basin, Brazil (0.3 to 0.65 kg·100 $m^{-1}·h^{-1}$), which is characterized as unproductive (Agostinho and Zalewski 1994). The highest

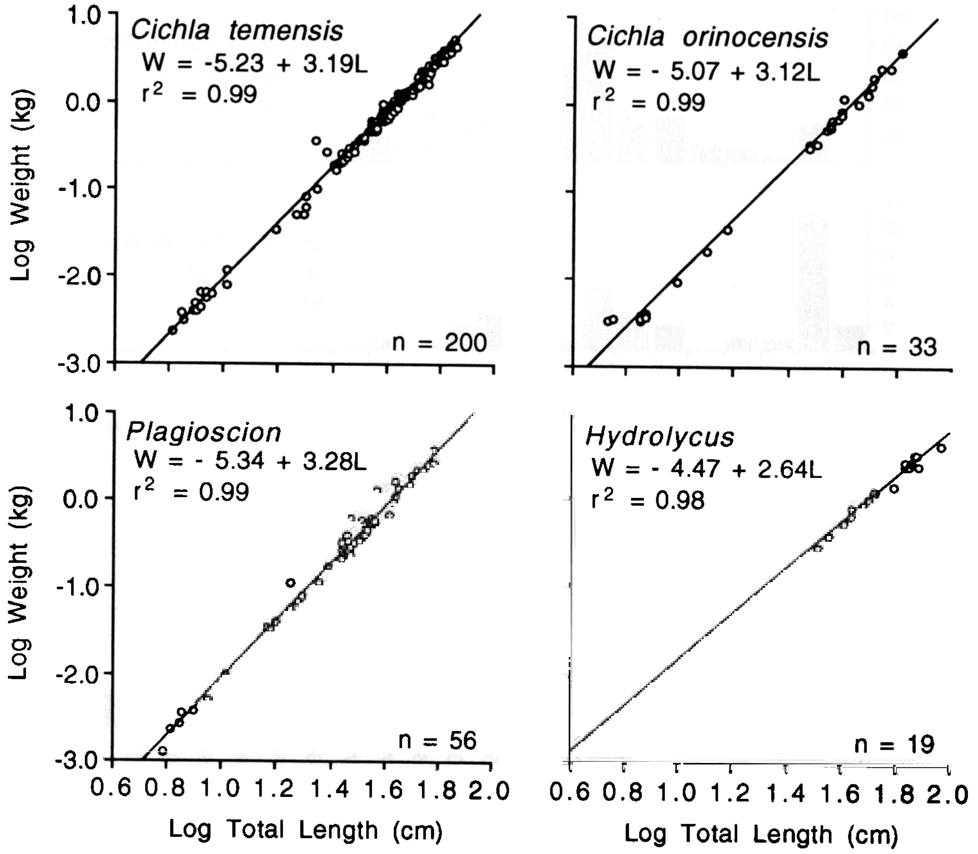

FIGURE 3.—Weight (W) to length (L) relationships for *C. temensis*, *C. orinocensis*, *P. squamosissimus*, and *H. scomberoides*. Data points with equal values on both axes appear as a single dot.

TABLE 2.—Data on fish stomachs and volumetric percentages of major food categories consumed by four Guri Reservoir piscivores.

Variable or food category	*Cichla temensis*	*Cichla orinocensis*	*Plagioscion squamosissimus*	*Hydrolycus scomberoides*
Total volume (mL)		48.3	48.8	32.5
Number of stomachs		17	54	16
Number of stomachs with food	58	10	36	6
Food category (%)				
Plants	0.2	0	2.0	0
Crustacea	0.1	0.8	5.1	0
Insects	0	0	3.8	0
Unidentified fish	2.3	0	7.4	1.5
Characidae	60.0	17.4	56.8	10.2
Hemiodontidae	10.7	14.5	4.9	0
Pimelodidae	0	0	19.3	54.2
Sciaenidae	0	0	0.6	34.2
Cichlidae	21.2	66.3	0	0
Synbranchidae	5.5	0	0	0
Tadpoles	0	1.0	0	0

CPUE value for Guri Reservoir is from a 1985–1986 survey (Novoa et al. 1989), which was conducted in newly flooded savanna coves near Manteco (Figure 1). Fish biomass appears to have declined just 2 years after impoundment in Guri Reservoir, compared with 6 years after impoundment in Itaipú Reservoir.

Fish Community Composition

The domination of the littoral zone in Guri Reservoir by a few small fish species is not unusual compared with Itaipú Reservoir, where 90% of the fishes comprised only nine species, mostly characiforms (Agostinho and Zalewski 1994). The numerically dominant species in our seine samples, *H. micropterus*, feeds on zooplankton, seeds, and aquatic and terrestrial invertebrates in shallow nearshore waters. Species of *Hemigrammus* from Venezuela's savanna region have an opportunistic life history strategy that enables rapid colonization of disturbed habitats (Winemiller 1989), and Guri

TABLE 3.—Standardized diet breadths and pairwise diet overlaps for the four most common piscivores at Guri Reservoir.

		Diet overlap for:			
Species	Diet breadth	*Cichla temensis*	*Cichla orinocensis*	*Plagioscion squamosissimus*	*Hydrolycus scromboides*
C. temensis	0.086		0.57	0.88	0.14
C. orinocensis	0.064		1	0.24	0.03
P. squamosissimus	0.105			1	0.41
H. scomberoides	0.085				

Reservoir's annual water level fluctuations create a changing environment to which *H. micropterus* is well suited. No prior data exist for relative abundances of species in seine samples, but our overall species list contains 46 of the 68 species collected by EDELCA during 1985–1987 and reported by Lasso et al. (1989). In addition, our survey produced eight species not reported by Lasso et al. (1989). Among these was the dominant species, *H. micropterus,* and *H. rodwayi,* the fourth most abundant species from our seine samples. The differences in community samples between the two survey periods may reflect temporal change in the fish community, differences in the locations surveyed (the earlier survey included the lake's southern region), or a combination of both. It is unlikely that the absence of the abundant *H. micropterus* and *H. rodwayi* from the earlier survey was due to sampling error.

Prochilodus rubrotaeniatus dominated the biomass in all gill-net surveys of Guri Reservoir (Novoa et al. 1989), and there are several reasons why this large migratory characiform continues to thrive in the lake. *Prochilodus rubrotaeniatus* is a detritivore, and as such, probably is less resource-limited than other species that are more directly dependent on primary production. Detritivores, especially prochilodontids, also constitute a major fraction of the fish biomass of the Río Negro, Río Orinoco, and Itaipú Reservoir (Goulding et al. 1988; Novoa 1989; Agostinho and Zalewski 1994). *Prochilodus rubrotaeniatus* apparently migrate up the major tributaries of Guri Reservoir for spawning, and their larval and juvenile stages inhabit floodplains in the lake's southern region. We captured only two juveniles within the lake's northern region. Spawning migrations to upstream river floodplains and juvenile use of floodplain habitats have been described for *Prochilodus scrofa* in the Itaipú Reservoir of southern Brazil (Agostinho et al. 1993).

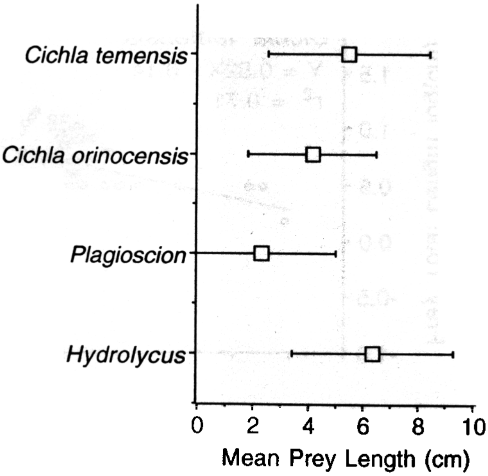

FIGURE 4.—Mean prey lengths (whiskers = ±SE) for four common Guri Reservoir piscivores: *C. temensis, C. orinocensis, P. squamosissimus,* and *H. scomberoides.*

Gill-net CPUE data suggest that abundance of the two *Cichla* species in the littoral zone of Guri has decreased only slightly from 1987 to 1994, whereas *P. squamosissimus* has increased slightly. Novoa et al. (1989) reported declines in the percentages of *Cichla* species in gill-net samples over three consecutive years (from 6.6% to 4.9% to 4.5% between 1985–1987), whereas *P. squamosissimus* averaged 10.8% of their gill-net catch over this period. According to our 1993–1994 seine samples, *P. squamosissimus* appeared to have good recruitment at least to 40 cm TL. Because it has pelagic eggs and larvae, *P. squamosissimus* is less impacted by seasonal water level fluctuations than *Cichla* spp., which construct and guard nests in shallow littoral regions (Zaret 1980).

Size Distributions and Weight–Length Relationships

Fishes from our survey showed a greater increase in mass with increasing body length than those in an earlier study (Novoa et al. 1989), which implies better condition as a result of greater per capita prey availability. Condition slopes (based on log-transformed weight–length data) were higher for all four piscivores in our study than in a previous study in Guri Reservoir (Novoa et al. 1989): 2.77 versus 3.14 for *Cichla* spp. combined; 2.52 versus 2.64 for *P. squamosissimus*; and 2.52 versus 3.27 for *H. scomberoides.* This pattern suggests that a recent decline in densities of *Cichla* spp. from fishing or predation mortality might have resulted in growth compensation through greater

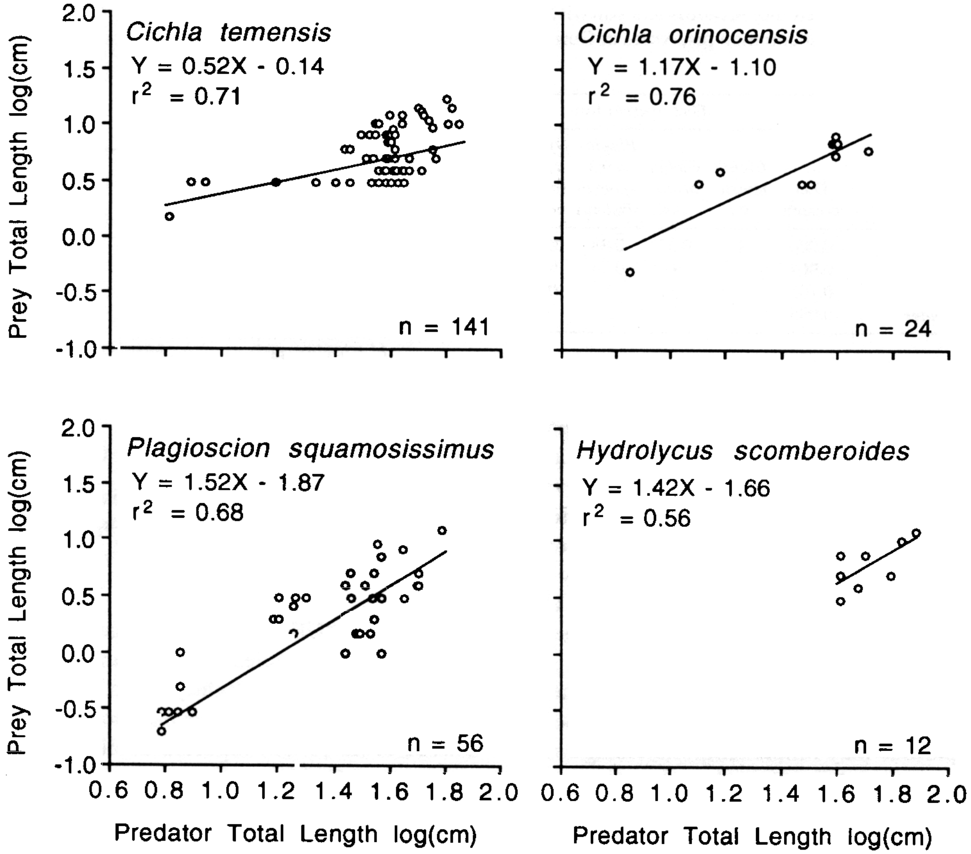

FIGURE 5.—Relationships of prey length (Y) to predator length (X) for four common Guri Reservoir piscivores. Data points with equal values on both axes appear as a single dot.

resource availability in this hyperoligotrophic ecosystem.

Diets

On average, *H. scomberoides* consumed the largest prey, and *P. squamosissimus* consumed the smallest prey. This result may reflect resource partitioning or it may be an artifact of sampling techniques that selected for larger *H. scomberoides.* The two *Cichla* species did not differ in the mean size of prey consumed, even when adjusted for predator length. The diets of the two cichlids were similar based on prey type as well, so there was potential for resource competition. Even so, *C. temensis* consumed mostly characids, followed by cichlids, whereas *C. orinocensis* consumed mostly cichlids, followed by characids. Gil et al. (1993) and Novoa (1993) reported similar findings from Guri Reservoir for *C. temensis* and *C. orinocensis.* Most *C. orinocensis* probably forage in shallow, structured habitats near shore where *Crenicichla wallacei,* other cichlids, and the abundant characid *H. micropterus* are common. In contrast, *C. temensis* (especially larger individuals) apparently forage in deeper and less structured habitats where they capture midwater characiforms, such as *Bryconops caudomaculatus* and *Hemiodopsis gracilis.*

The diets of *C. temensis* and *P. squamosissimus* were similar based on prey type, but *C. temensis* consumed larger prey. (However, relatively few large *P. squamosissimus* were captured from shallow littoral habitats.) Competition between *Cichla* species and *H. scomberoides* was unlikely as these two species consumed similar-sized prey but had very low diet similarity. *Hydrolycus scomberoides* showed the same trends with *C. orinocensis. Cichla orinocensis* and *P. squamosissimus* consumed different sizes and types of prey. *Plagioscion squamosissimus* and *H. scomberoides* consumed significantly different-sized prey, yet did show some overlap based on prey type. Whereas *P. squamosissimus* ate mostly characids and pimelodids, *H.*

scomberoides ate mostly pimelodids and, to a lesser extent, sciaenids (i.e., *P. squamosissimus*). *Hydrolycus scomberoides* therefore has the potential to influence abundance of *P. squamosissimus.*

Diet breadths for all four piscivores were low: *P. squamosissimus* had the broadest diet, *C. orinocensis* had the narrowest diet (but sample sizes were small), and *C. temensis* and *H. scomberoides* had intermediate diet breadths. *Cichla temensis* fed heavily on the three most abundant fishes in the littoral zone of the reservoir, an indication of an opportunistic feeding strategy. Similarly, *C. orinocensis* consumed the two most abundant littoral zone fishes, but not in accordance with their rank abundance. *Plagioscion squamosissimus* consumed mostly small characids and pimelodid catfishes, the latter being bottom-dwellers most abundant in deeper waters farther offshore. Despite the fact that its superior mouth, large pectoral fins, and keeled chest are designed for midwater and surface feeding, *H. scomberoides* in Guri Reservoir fed heavily on benthic catfishes and *P. squamosissimus.*

Management Implications

Sport fish catch rates often are inversely correlated with reservoir age (Ploskey 1986). Because of the low nutrient content of the region's soils and Guri Reservoir's low retention time, the initial pulse of nutrients associated with reservoir filling was probably weak and short lived. Alvarez et al. (1986) estimated yearly fish production for Guri at just 10 kg/ha, based on the morphoedaphic index (conductivity/lake depth) and biological assumptions borrowed from work on Lake Kariba in Africa (Marshall et al. 1982). For comparison, they cited the yearly estimate of 23.5 kg/ha for Brokopondo Reservoir in Suriname (Kapetsky 1978), another unproductive reservoir of the Guyana Shield. They also cautioned against the use of estimates of production based on the trophic upsurge phase of reservoir development. The gill-net data of Novoa et al. (1989) for the period 1985–1986 (Table 1) were collected from some locations different than ours, so the difference between their total hourly CPUE (1.2 kg/110 m) and our values for 1987 and 1993–1994 (0.59 and 0.60 kg/100 m) probably reflects the combined influence of a decline in the lake's trophic upsurge and within-lake spatial heterogeneity of productivity (nets were fished day and night in both studies).

Our gill-net CPUE data indicate that the lake's already low overall fish abundance has not changed appreciably between 1987 and 1994 but that average fish size has decreased. The two principal sport fishes, *Cichla* spp., appear to have declined slightly in numbers and biomass in association with the waning of the lake's trophic upsurge phase. To sustain the sport fishery for *Cichla* spp. in Guri, current harvest limits should be enforced. Given the exceedingly low primary and secondary productivity of the reservoir, a policy of catch-and-release sportfishing would better protect fragile stocks of *Cichla* spp. Yet, regulation of sportfishing is only one aspect of fisheries management in Guri Reservoir, as commercial fishing is being considered. The initial proposal for commercial fishing in Guri Reservoir was based upon model projections that used yearly fish production estimates (80–220 kg/ha) extrapolated from a block-net sample from a single cove (flooded savanna) in the middle region of the reservoir during the trophic upsurge phase (Novoa et al. 1989). The model simulations indicated that even moderate sportfishing negatively impacted populations of *Cichla* spp. and that commercial fishing reduced the impact of sportfishing on *Cichla* spp. because many large predators that feed on small *Cichla* spp. would be removed by the large-mesh gill nets used to harvest large *Prochilodus rubrotaeniatus.* Given the model's gross assumptions regarding the influence of food web structure on population dynamics, we urge caution in the interpretation of these simulations. Also, the reservoir's heterogeneity, especially gradients of primary productivity, should be considered carefully when evaluating alternatives for fisheries management on a whole-lake basis (Silver et al. 1986). To improve future model projections, additional surveys that compare sites along the reservoir's south–north (i.e., inflow–dam) productivity gradient should be conducted.

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