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Dietary segregation among large catfishes of the Apure and Arauca Rivers, Venezuela

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Relative abundance, population size structure and diet composition and similarity were examined over 5 years for the nine most abundant catfish (Siluriformes) species captured in the Apure-Arauca River fishery centred around San Fernando de Apure, Venezuela, the largest freshwater fishery in the Orinoco River Basin. Based on size classes obtained by the fishery, all nine catfishes were almost entirely piscivorous. Four species that are entirely restricted to main channels of the largest rivers (*Brachyplatystoma flavicans*, *Brachyplatystoma jurunse*, *Brachyplatystoma vaillanti* and *Goslinia platynema*) fed predominantly on weakly electric knifefishes (Gymnotiformes) and had high pair-wise dietary overlap. The other five species (*Ageniosus brevifilis*, *Phractocephalus hemioliopterus*, *Pinirampus pirinampu*, *Pseudoplatystoma fasciatum* and *Pseudoplatystoma tigrinum*) occurred in a range of channel and off-channel habitats and were observed to feed on a variety of characiform, siluriform and gymnotiform prey. Diet overlap also was high among these habitat-unrestricted species, but overlap between the channel-restricted and unrestricted species was low. Within each of the two groups, species were divided into approximately equally sized subgroups based on differences in body size distributions. The two most morphologically similar species, *P. fasciatum* and *P. tigrinum*, further subdivided prey based on the vertical stratum occupied by prey species (benthic *v.* midwater). The two most morphologically dissimilar, channel-restricted species, *B. juruense* and *G. platynema*, also diverged in frequency of consumption of benthic and midwater prey.

Key words: *Ageneiosus brevifilis*; *Brachyplatystoma* spp.; *Goslinia platynema*; *Phractocephalus hemioliopterus*; *Pinirampus pirinampu*; *Pseudoplatystoma* spp.

INTRODUCTION

Catfishes (Siluriformes) support large commercial fisheries in the major river basins of South America (Castillo, 1988; Bayley & Petrere, 1989; Novoa, 1989; Petrere, 1989; Barthem & Goulding, 1997). Catfishes also are the dominant piscivores in the main channels of large rivers of South America, especially whitewater rivers with high suspended sediment loads and low transparency. The well-developed chemosensory and tactile modalities of siluriforms allow them to feed effectively at night and under conditions of low transparency.

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These capabilities presumably pre-adapt siluriforms for life in turbid waters (Barthem & Goulding, 1997; Rodriguez & Lewis, 1994, 1997). Neotropical waters with high transparency tend to be dominated by diurnal piscivores, such as characiforms (*Boulengerella* spp., *Hoplias* spp., *Hydrolycus* spp., *Serrasalmus* spp.), cichlids (*Cichla* spp., *Crenicichla* spp.), clupeids (*Pellona* spp.) and sciaenids [*Plagioscion squamosissimus* (Heckel)].

Despite their great ecological and economic importance, channel-dwelling catfishes of South America have received little study. Indeed, many of the most basic features of life history, such as fecundity, reproductive seasons, spawning and nursery habitats, growth rates, ontogentic niche shifts and longevity, are essentially unknown for most neotropical catfishes. Recently, Barthem & Goulding (1997) proposed that two species, *Brachyplatystoma flavicans* (Castelnau) and *Brachyplatystoma vaillanti* (Valenciennes), migrate hundreds of kilometres throughout the Amazon Basin over the course of their lifetimes. Non-reproductive individuals are captured by commercial fisheries throughout the basin, but individuals with ripe gonads have only been recorded from large tributary rivers in the western region of the basin. Because juveniles have only been recorded from the region of the Amazon mouth (eastern edge of the basin), these authors hypothesize that larvae and postlarvae drift thousands of kilometres from lowland rivers draining the Andes to the Amazon estuary where immature catfishes contribute heavily to the commercial fishery.

The same catfish species exploited by the commercial fisheries of the Amazon also occur in the Orinoco River Basin. Catfishes are major components of the largest inland fishery in the Orinoco Basin located in the llanos region around San Fernando de Apure, Venezuela (Fig. 1) (Castillo, 1988). The most important commercial species is the coporo *Prochilodus mariae* Eigenmann (Characiformes, Prochilodontidae). The coporo, a detritivore, is captured in great numbers during migrations from flooded lowland habitats into tributary rivers during the annual period of falling water levels (Lilyestrom, 1983; Barbarino Duque *et al*., 1998). Pimelodid catfishes and river dolphins *Inia geofrensis* de Blainville are the major piscivores inhabiting the turbid lowland rivers of the

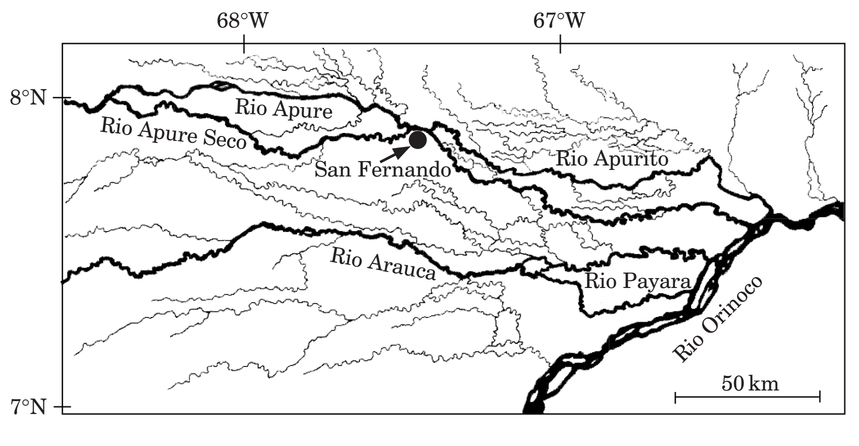

FIG. 1. Map of the study region showing the inland delta formed between the lower reaches of the Apure and Arauca Rivers, two major whitewater tributaries of the Orinoco River.

llanos. Two congeneric species, *Pseudoplatystoma fasciatum* (L.) and *Pseudoplatystoma tigrinum* (Valenciennes), are the most abundant and among the most valuable catfishes in the San Fernando fishery (Castillo, 1988).

To date, most of the ecological information gathered on catfishes of the Orinoco Basin addresses fishery yields (Castillo, 1988; Novoa, 1989). Population size structure and diets of llanos catfishes were described by Reid (1983) and Castillo (1988). Larvae and early juveniles feed on zooplankton, and juveniles gradually shift to feeding on aquatic insects then fishes (Mago-Leccia *et al.*, 1986; Castillo, 1988). Adults of most commercial species are piscivorous, although small amounts of crustaceans are consumed by some species. Based on gut samples from populations in the western llanos in Venezuela, piscivorous *P. fasciatum* and *P. tigrinum* had similar diets, and informal observations indicated a degree of habitat segregation (Reid, 1983; Loubens & Panfili, 2000).

Other than Reid's (1983) study, no assessment of niche relationships has been attempted for the ecologically and economically important catfish assemblage of lowland rivers of the Orinoco Basin. The present study investigated diets, patterns of dietary similarity and trophic niche relationships among nine common, piscivorous catfish species taken in the San Fernando fishery over a 5 year period. Although 44 species, including 25 siluriforms, are captured in this fishery, the study focussed on the nine most abundant catfishes that yielded the largest samples for dietary analysis.

MATERIALS AND METHODS

STUDY REGION

The study was conducted in the Apure and Arauca Rivers in the low llanos of Venezuela between the town of Apurito (7°56′ N; 68°30′ W) and the mouth of the Apure River (7°40′ N; 66°17′ W), and between the town of San Luis (7°19′ N; 68°56′ W) and the mouth of the Arauca River (7°23′ N; 66°35′ W). This region of *c.* 19 900 km^2 is tropical savanna and contains a network of rivers and streams that form a vast inland delta (Fig. 1) formed by deposition of nutrient-rich alluvial sediments carried from the Andes Mountains to the low plains by turbid, whitewater rivers. The region is low (46 m elevation), flat (*c.* 1% gradient) and floods extensively each year, usually between late May and October. Average annual rainfall is 1200 mm, and average temperature is 27·1° C (Meteorological Station, San Fernando de Apure). Land use is cattle ranching, with a minor presence of rice farms in the northern region of the study area. The region's numerous streams and rivers are bordered by dense gallery forests. The channels of the Apure, Apurito, Arauca and Payara Rivers meander and contain occasional braids (side channels). Main channel width of these rivers varies between *c.* 100 and 300 m with a maximum depth of *c.* 15 m during the high-water period. Discharge in the Apure River at San Fernando ranges between *c.* 200 $m^3 s^{-1}$ during the dry season (January to April) to *c.* 4000 $m^3 s^{-1}$ during the wet season (May to December).

SAMPLING AND ANALYSIS

Between January 1996 and January 2001, data were collected by surveying the catches of eight groups of commercial fishermen operating within the study region. Except for the peak wet season (July to September) when commercial fishing activity halted due to low catch rates, between 4 and 15 days per month were spent in the field with one or more groups of fishermen. The survey covered a total of 44 months. Fishing activity was conducted almost entirely in the main channels of the Apure, Arauca, Payara and

Apurito Rivers, but also in some of the larger streams of the inland delta. Fishermen used long metal canoes (11 × 1 m) powered by a 40 hp engine. Except for the period of coporo migration ('ribazon'), most fishing was conducted during daylight hours. During the migration period (mid October to late December), fishing was carried out by day and night.

Most fishes (98%) were captured using large seines. Percentages of the total number of fishes captured with nets of various mesh sizes were as follows: 4·7% (8·6 cm), 6·9% (9·2 cm), 2·4% (11·0 cm), 15% (12·0 cm), 22·6% (13·0 cm), 39·6% (14·6 cm) and 8·8% (17 cm). Seining was performed in locations that lacked submerged trunks and snags that minimized net damage and loss.

Locations with submerged woody debris were fished using baited hooks with lines that either were held (0·4% of captures) or attached to a flexible tree branch and left unattended (0·9% of captures). Fishes also were captured using harpoons (0·3% of captures) and castnets (0·4% of captures).

Each captured specimen was identified to species, measured for standard length (L_S, to the nearest cm) and weighed to the nearest 20 g with an Omega dial balance. Specimens were then dissected in the field for assessment of sex and examination of stomach contents. Only those prey located within the stomach were considered ingested and counted. Annual data were combined, and species length-frequencies were plotted based on 5 cm L_S intervals and compared.

Stomach contents were identified to the highest degree of taxonomic resolution possible given the material's state of digestion. Data were then compiled and analysed using Excel 2000 (Microsoft). Diet items were aggregated into taxonomic orders for use in calculation of dietary breadth and species pair-wise overlap. The category 'unidentified fish remains' was removed from the database prior to calculating niche indices. Diet breadth was computed using Simpson's index, $B_j = (\sum p_{ij}^2)^{-1}$, in which p_{ij} is the proportional consumption (based on per cent frequency of individual items) of item i by consumer j. Dietary similarity was computed as Pianka's symmetrical niche overlap index, $\theta_{jk} = \sum (p_{ij} \cdot p_{ik})(\sum p_{ij}^2 \cdot \sum p_{ik}^2)^{-0.5}$, in which j and k represent a pair of consumers. The matrix of pair-wise overlaps was used as input data for cluster analysis based on Euclidean distance and three alternative clustering algorithms (average, single-linkage and Ward's) using PC-ORD (1999). Results from the three methods were almost identical, and only results from the average clustering algorithm are presented.

RESULTS

At least 44 fish species (15 families) were captured during the 4 year study, 20 of which belonged to the Pimelodidae (Siluriformes). For the present study, 14 575 specimens were examined. Subjects of the present analysis are nine piscivorous catfish species, one auchenipterid (Fig. 2) and eight pimelodids (Fig. 3) that were among the most abundant fishes in the collective sample and yielded the most stomachs with contents (n = 27–435; Table I). Among these nine species, 7616 stomachs were analysed of which 82% were empty (Table I). Several catfishes were observed expelling ingested food items during failed attempts to escape from the seine.

The body length distribution of all nine species overlapped, however, two size groups were apparent in the samples (Fig. 4). *Ageneiosus brevifilis* Valenciennes, *Brachyplatystoma juruense* (Boulenger), *B. vaillanti* and *Pinirampus pirinampu* (Spix & Agassiz) comprised the small group that ranged between 20 and 70 cm L_S. The group of larger catfishes [*B. flavicans*, *Goslinia platynema* (Boulenger), *Phractocephalus hemioliopterus* (Bloch & Schneider), *P. fasciatum* and *P. tigrinum*] ranged from 25 to 121 cm L_S, with no species having a maximum L_S <100 cm. In order of descending maximum L_S, the largest individuals examined

FIG. 2. *Ageneiosus brevifilis* ('rambao'), the most common auchenipterid catfish in the Apure-Arauca fishery. The species is sexually dimorphic, especially during the spawning period; female is above, and male with elongate dorsal spine and barbels is below.

were 121 cm for *B. flavicans* (23 kg, female, December 1999), 120 cm for *P. hemioliopterus* (39 kg, female, May 2000), 112 cm for *P. tigrinum* (18 kg, female, January 1999), 105 cm for *G. platynema* (7·97 kg, female, June 2000), 100 cm for *P. fasciatum* (13 kg, female, February 2000), 70 cm for *B. juruense* (2·7 kg, female, March 1998), 68 cm for *P. pirinampu* (4·1 kg, female, February 1999), 65 cm for *B. vaillanti* (3·6 kg, female, April 1998) and 54 cm for *A. brevifilis* (1·7 kg, female, November 1998).

The nine catfishes were piscivorous, with the only non-fish prey being crustaceans (prawns and crabs), aquatic insects consumed by a single *G. platynema*, a lizard consumed by a single *P. fasciatum* and four rats (Muridae) consumed by three *P. pirinampu* (Table II). Among fish remains that could be identified at least to order, characiforms, siluriforms and gymnotiforms were most frequently consumed. Catfish species revealed high interspecific variation in proportional utilization of prey taxa. *Pinirampus pirinampu* had the broadest diet, followed by *B. vaillanti* and *P. fasciatum* (Table I). Narrowest diets were observed for *G. platynema* and *B. juruense*, species that fed heavily on nocturnal, weakly electric knifefishes (gymnotiforms).

Cluster analysis based on dietary similarity (overlap) yielded two disparate groups (Fig. 5). One group (*B. flavicans*, *B. vaillanti*, *B. juruense* and *G. platynema*) was comprised of species restricted to the main channels of the Apure, Arauca, Apurito and Payara Rivers. The commercial fishermen never captured these species outside the main channels of those four principal rivers of the

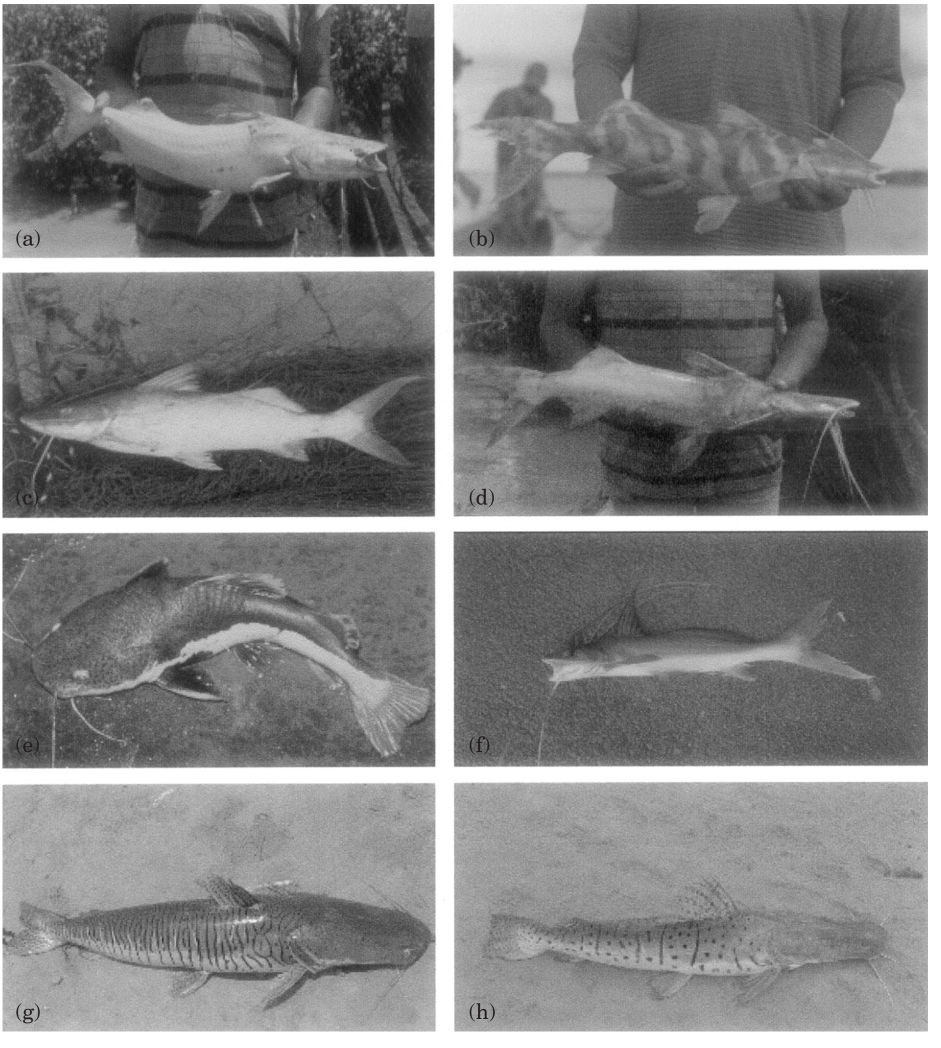

FIG. 3. The eight most common pimelodid catfishes in the Apure-Arauca commercial fishery: (a) *Brachyplatystoma flavicans* ('dorado'), (b) *Brachyplatystoma juruense* ('cunaguaro'), (c) *Brachyplatystoma vaillanti* ('atero'), (d) *Goslinia platynema* ('jipi'), (e) *Phractocephalus hemioliopterus* ('cajaro'), (f) *Pinirampus pirinampu* ('blanco pobre'), (g) *Pseudoplatystoma fasciatum* ('bagre rayado' or 'cabezón'), (h) *Pseudoplatystoma tigrinum* ('bagre rayado' or 'matafraile').

region. Gymnotiforms formed the largest dietary component of each of these channel-restricted catfishes (Table II). The five remaining species in the other group were all habitat generalists that were commonly captured both in the main river channels and in larger tributary streams. These species were also common in floodplain lagoons, but the commercial fishermen rarely fished these habitats because they generally are located on private property to which they lack access. Species of this second 'unrestricted' group fed most frequently on siluriforms and characiforms (Table II) and tended to have broader diets that included other prey categories (mean diet breadth = 2·20) than the

TABLE I. Study sample abundances, numbers and percentages of empty stomachs, and diet breadths of nine common piscivorous catfishes of the Apure and Arauca Rivers

Species	Examined *n*	With contents *n*	Per cent empty	Diet breadth
Ageneiosus brevifilis	503	27	94·6	1·85
Brachyplatystoma flavicans	474	45	90·5	1·99
Brachyplatystoma juruense	224	27	87·9	1·47
Brachyplatystoma vaillanti	333	49	85·3	2·69
Goslinia platynema	1663	342	79·4	1·06
Phractocephalus hemioliopterus	179	61	65·9	2·02
Pinirampus pirinampu	312	69	77·9	3·74
Pseudoplatystoma fasciatum	1514	313	79·3	2·43
Pseudoplatystoma tigrinum	2414	435	82·0	1·65
Total mean	7616	1368	82·5	2·1

channel-restricted species (mean diet breadth = 1·22). Mean pair-wise dietary overlap between channel restricted and unrestricted species was 0·34. Mean pair-wise dietary overlap among channel-restricted species was 0·96, and among unrestricted species mean overlap was 0·81.

The two most abundant catfishes in the fishery, *P. fasciatum* and *P. tigrinum*, are also the most similar in general morphology and appearance (Fig. 3). Since large stomach content samples for these abundant species were available, it was possible to examine dietary overlap using prey categories at a finer scale of resolution (stomach contents identified to species or family in many instances). Dietary overlap between the *Pseudoplatystoma* species was 0·93, with *P. tigrinum* having a broader diet ($B = 2{\cdot}16$) than *P. fasciatum* ($B = 0{\cdot}99$). Both species fed extensively on the characiforms *Mylossoma duriventre* (Cuvier), *P. mariae* and *Schizodon* sp. (Table III). Even given high dietary overlap, *P. fasciatum* fed more frequently on benthic erythrinids, *i.e. Hoplias malabaricus* (Bloch), and catfishes, *e.g. Liposarcus multiradiatus* (Hancock), *Hoplosternum littorale* (Hancock) and *Pimelodus* sp., doradids, compared to *P. tigrinum* which fed more on midwater fishes, *e.g. M. duriventre*, *Serrasalmus rhombeus* (L.), *Triportheus* sp., *Potamorhina altamazonica* (Cope) and *Hydrolycus armatus* (Schomburgk). One *P. pirinampu* stomach contained a conspecific, and one or more individuals of each *Pseudoplatystoma* species had consumed a congeneric (these prey items could not be identified to species).

DISCUSSION

The most striking dietary pattern observed among the nine piscivorous catfishes was the clear separation into two distinct groups that corresponded to patterns of habitat use. Local fishermen consistently reported that four species (*B. flavicans*, *B. juruense*, *B. vaillanti* and *G. platynema*) were never caught in off-channel habitats such as lagoons, sloughs and streams. All of these channel-restricted species fed heavily on gymnotiform knifefishes. Based on information

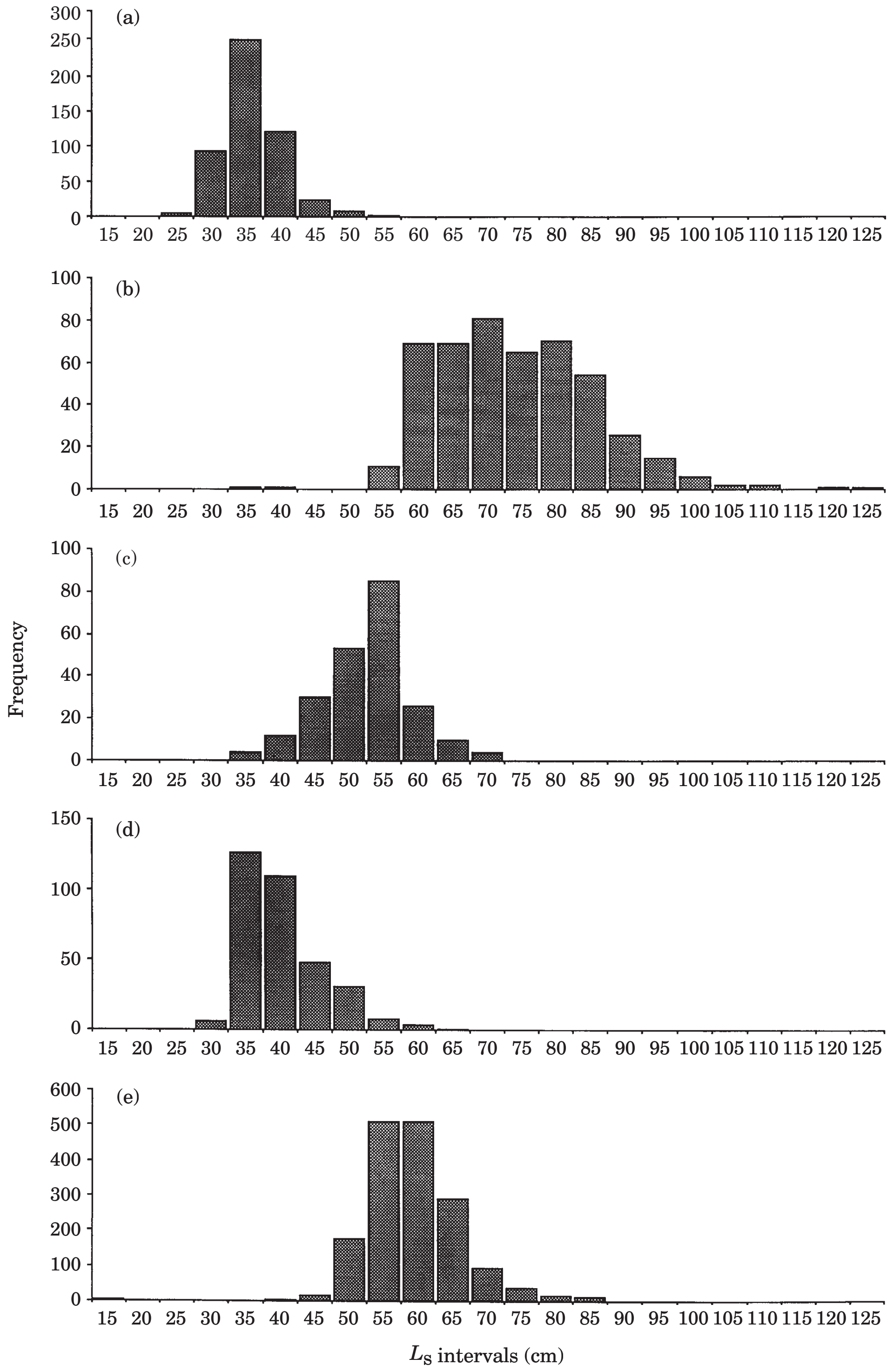

FIG. 4. Continued overleaf.

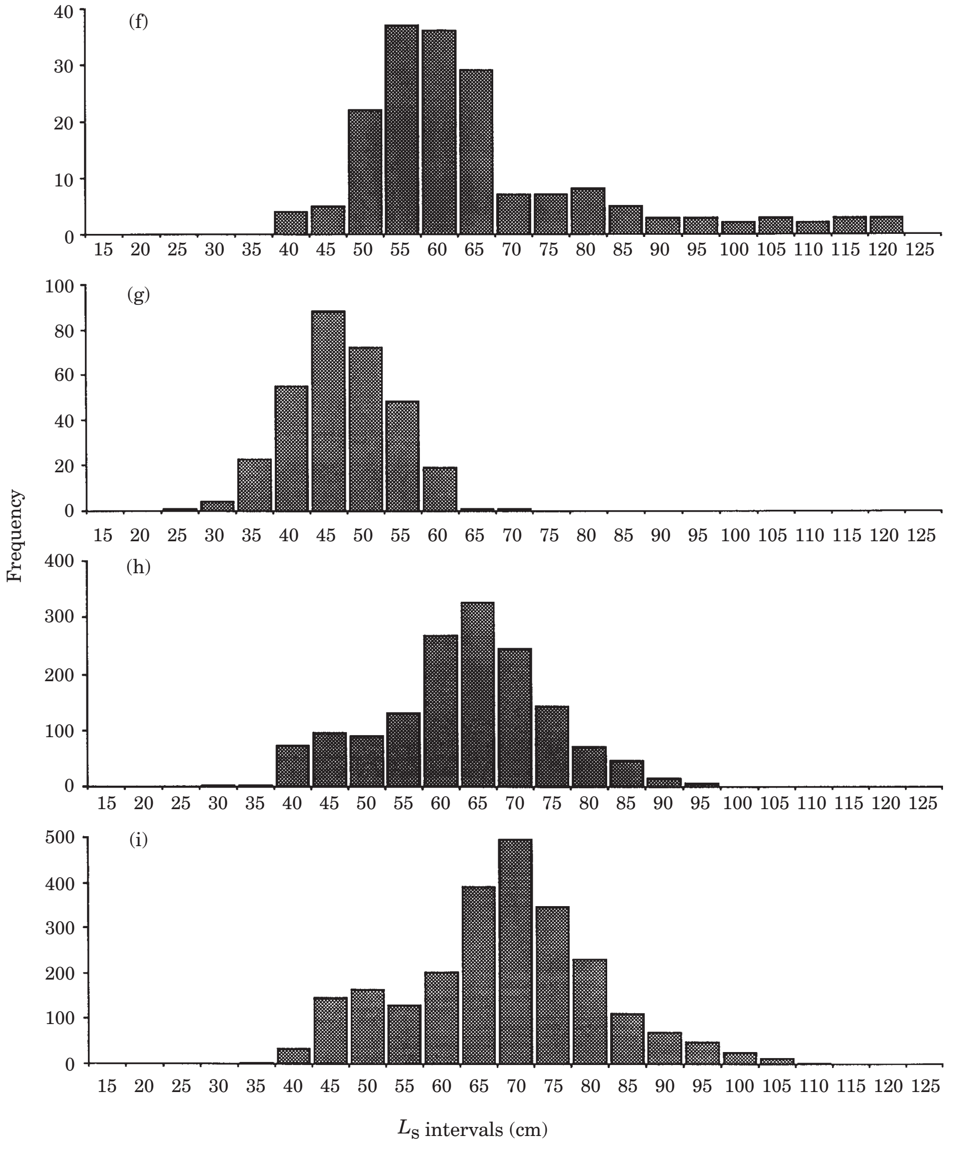

FIG. 4. Frequency distribution of standard length for samples taken from the Apure-Arauca commercial fishery over a 5 year period. (a) *Ageneiosus brevifilis*, (b) *Brachyplatystoma flavicans*, (c) *Brachyplatystoma juruense*, (d) *Brachyplatystoma vaillanti*, (e) *Goslinia platynema*, (f) *Phractocephalus hemioliopterus,* (g) *Pinirampus pirinampu,* (h) *Pseudoplatystoma fasciatum* and (i) *Pseudoplatystoma tigrinum.*

from the commercial catch, it could not be determined if these species further partition habitats within the main river channels. Conceivably, species could segregate spatially based on water current velocity and vertical position within the water column. Two species (*B. flavicans* and *G. platynema*) had larger maximum and modal sizes than the other two in this channel-restricted group,

TABLE II. Per cent frequency of occurrence of dietary categories consumed by piscivorous catfishes of the Apure and Arauca Rivers

Species	Characiforms	Siluriforms	Gymnotiforms	Perciforms	Clupeiforms	Synbranchiforms	Fish remains	Crustacea	Rodentia	Amphibia	Reptilia	Insecta
Ageneiosus brevifilis	18·52	33·33	0	0	0	0	48·15	0	0	0	0	0
Brachyplatystoma flavicans	9·09	10·9	45·46	1·82	0	0	32·73	0	0	0	0	0
Brachyplatystoma juruense	0	10·34	58·63	0	0	0	27·58	3·45	0	0	0	0
Brachyplatystoma vaillanti	4·08	12·24	26·54	0	2·04	0	51·02	4·08	0	0	0	0
Goslinia platynema	0·79	0·79	72·7	0	0·26	0	25·2	0	0	0	0	0·26
Phractocephalus hemioliopterus	29·17	40·28	1·38	0	0	0	29·17	0	0	0	0	0
Pinirampus pirinampu	12·68	21·13	7·04	0	1·4	0	49·3	2·82	4·23	1·4	0	0
Pseudoplatystoma fasciatum	28·06	15·52	7·46	0	0	0	48·66	0	0	0	0·3	0
Pseudoplatystoma tigrinum	49·07	3·72	10·77	0	0	0·84	35·19	0·41	0	0	0	0

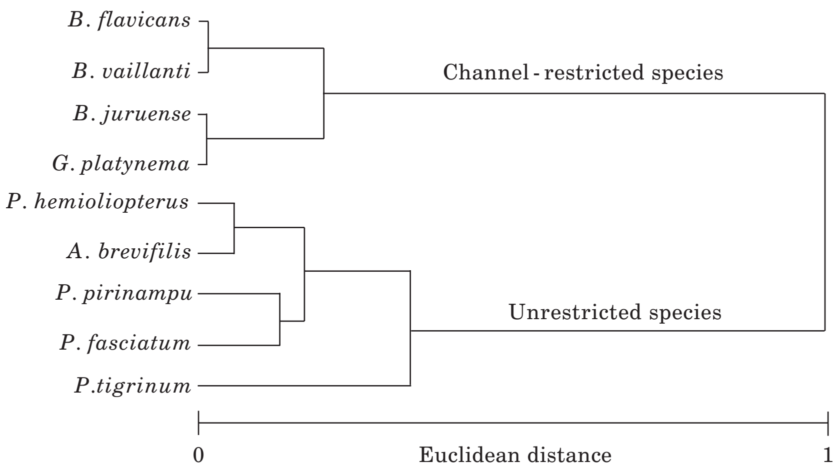

FIG. 5. Dendrogram resulting from cluster analysis (average method) based on dietary similarity of Apure-Arauca catfishes.

which suggests a potential mechanism for further subdividing food resources. In addition, the two species that consumed the greatest percentage of knifefishes (*B. juruense* and *G. platynema*, Table II) have the most dissimilar general morphology (appearance) among species in the channel-restricted group (Fig. 3). All of the channel-restricted catfishes have dorso-ventrally compressed heads and small eyes, but *B. juruense* has a deeper body and more striking pigmentation pattern than the other species, and *G. platynema* has the most elongate body. Among the channel-restricted species, *B. vaillanti* has the most generalized teleost body plan (*e.g.* relatively fusiform with shorter, deeper head, and larger eyes than the other channel-restricted pimelodids) and had the greatest dietary breadth.

Knifefishes are major faunal and food-web components of deep waters in the main channel of the Orinoco River (Lundberg *et al.*, 1987). The gymnotiform *Rhabdolichops zareti* Lundberg & Mago-Leccia inhabiting the deep, turbid, high-velocity waters of the lower Orinoco River consumes zooplankton and small aquatic insects. In the main channel of the Apure River knifefishes feed heavily on aquatic insects associated with clay nodules that constitute the substratum of deep regions with fast current (Marrero, 1987). High consumption of knifefishes by channel-dwelling catfishes could reflect prey selection, selection of deepwater habitats with little prey selection, or a combination of the two.

Stomach contents that could be identified to genus or species (Table III) provide insights into how channel-restricted catfishes with high dietary overlap at the level of prey orders may further partition food resources. Prey taxa were subdivided into two groups based on evidence from extensive field sampling from a variety of habitats in Venezuela as well as aquarium observations by the authors. Benthic fishes always rest and usually forage in close association with the substratum. Examples of benthic fishes include *H. malabaricus*, *Sternarchorhamphus* sp., and all Doradidae and Loricariidae. The second group, mid-water fishes, contains taxa that either occupy and feed in the water column or swim at variable positions in the water column but move to the substratum to

TABLE III. Numerical abundance of highly resolved dietary items consumed by piscivorous catfishes of the Apure and Arauca Rivers

	A. brevifilis	*B. flavicans*	*B. juruense*	*B. vaillanti*	*G. platynema*	*P. hemioliopterus*	*P. pirinampu*	*P. fasciatum*	*P. tigrinum*	Total prey items
Invertebrates			1	2	1		2		2	8
Pellona sp.				1	1		1		2	5
Leporinus sp.									2	2
Schizodon sp.	1					2	2	16	47	67
Characidae								1	4	5
Mylossoma duriventre	2				2	14		32	103	151
Serrasalmus rhombeus									6	6
Pygocentrus cariba	2	1			1	1	2	1		6
Triportheus sp.		1						2	8	11
Curimata cerasina				2					1	3
Potamorhina altamazonica								2	14	16
Hydrolycus armatus		1				1		1	5	8
Hoplias malabaricus							1	6		7
Prochilodus mariae		2				3	4	31	45	85
Gymnotiformes		22	13	7	190	1	4	22	32	291
Adontosternarchus sp.		1	1	5	63			2	5	77
Apteronotus sp.		1	1							2
Sternarchorhamphus sp.			2	1	1				2	6
Rhamphichthys sp.					13		1	1	6	21
Eigenmannia sp.		1			10				6	17

TABLE III. Continued overleaf

	A. brevifilis	*B. flavicans*	*B. juruense*	*B. vaillanti*	*G. platynema*	*P. hemioliopterus*	*P. pirinampu*	*P. fasciatum*	*P. tigrinum*	Total prey items
Sternopygus sp.									1	1
Ageneiosus sp.		3						3	4	10
Entomocorus sp.					1					1
Hoplosternum littorale						1		7		8
Doradidae	1		1			2		3		6
Loricariidae	2		1	1		2	4	2	2	12
Liposarcus multiradiatus	4		1			21	5	19	4	50
Cetopsidae		1			1					2
Pimelodidae							4	5		9
Hypophthalmus edentatus									1	1
Pimelodus sp.	2			5	1	3	1	8	3	21
Pimelodina flavipinnis		1								1
Pinirampus pirinampu							1	1		2
Pseudoplatystoma sp.								4	1	5
Sorubim sp.								2	3	5
Synbranchus marmoratus									4	4
Plagioscion squamosissimus		1								1
Fish remains	13	18	8	25	96	21	35	163	170	536
Other vertebrates							4	1		5
Total prey items	27	54	29	49	381	72	71	335	483	1474

feed (*i.e.* epibenthic feeders). Midwater prey are represented by *M. duriventre*, *Pygocentrus cariba* Valenciennes, *P. altamazonica*, *Adontosternarchus* sp., *Eigenmannia* sp. and *Sorubim* sp. Benthic fishes comprised 86% of the identifiable prey consumed by *B. juruense*, but only 2% of prey consumed by *G. platynema*. *Brachyplatystoma flavicans* is the species most similar in general morphology to *G. platynema* and the former also consumed a low percentage of benthic prey (20%). The more generalized *B. vaillanti* consumed similar percentages of benthic (47%) and midwater (53%) prey in the main channel.

Catfishes that are unrestricted to channel habitats probably have even greater opportunities to segregate by micro- and meso-habitats (tributary streams and lagoons of various dimensions, geomorphologies and limnological conditions). Again, catch data cannot distinguish among various habitats, and most captures were made in main river channels and tributary streams rather than lagoons, which typically were inaccessible on private lands. Nonetheless, *A. brevifilis* is an active swimmer in the water column (pers. obs.), *P. pirinampu* is an active swimmer on the bottom, and *P. hemioliopterus* and the two *Pseudoplatysoma* species are relatively slow-moving, bottom-dwellers that probably attack mostly by probing and ambush.

Body size differences notwithstanding, the habitat-unrestricted group also showed differences in the percentages of specific taxa consumed. Three of these unrestricted catfishes consumed more benthic prey than pelagic prey: *A. brevifilis* (64% benthic prey), *P. hemioliopterus* (58% benthic) and *P. pirinampu* (65% benthic prey). The two 'bagre rayado' species, *P. fasciatum* and *P. tigrinum*, only consumed 38 and 8% benthic prey, respectively. In the Mamoré River, Bolivia, *P. fasciatum* consumed 36% catfishes *v.* <17% for *P. tigrinum* (Loubens & Panfili, 2000). *Pseudoplatystoma fasciatum* and *P. tigrinum* of the Mamoré River consumed mostly detritivorous and herbivorous characiforms. Similarly, the principal prey of the bagres rayados in the Orinoco llanos region were large characiforms that occupy low trophic positions in the food web. *Mylossoma duriventre* is a herbivore that feeds on leaves, seeds and flowers, *P. mariae* is a detritivore and *Schizodon* sp. is a herbivore that feeds on aquatic macrophytes. The principal food chains directing primary production to top piscivores in both of these systems are therefore short (three trophic levels and two links).

The bagre rayado species are very similar morphologically (Fig. 3) but were observed to exhibit different escape tactics during capture in seines. *Pseudoplatystoma fasciatum* frequently were observed to hover near the weighted line of the seine, probing for gaps as the net was drawn to shore. Sometimes, *P. fasciatum* were observed escaping through gaps between the weighted line and the substratum. In contrast, *P. tigrinum* typically thrashed about and 'charged' into the sides of the seine as it was drawn to shore. These behavioural observations and the greater consumption of midwater prey by *P. tigrinum* suggest that the two congeneric species use different foraging behaviours with different efficiencies in different microhabitats. Slow movement accompanied by probing with the barbels (tactile and chemosensory organs) would be advantageous in pursuit of prey that take refuge in or near structures such as large woody debris. Actively swimming midwater prey probably require these catfishes to use swift, deliberate ambush attacks. Reid (1983) examined diets of the bagre rayados in the Apure river and tributary streams in the area around Bruzual, Venezuela (200 km west of San Fernando de Apure) and obtained findings similar to those presented here. Both species fed heavily on a variety of fishes (fishes comprised 99% of the diet) with high dietary overlap. An analysis of Reid's (1983) high taxonomic resolution dietary data revealed that both species consumed *c.* 30% benthic taxa, a finding that contrasts with those presented here. The present study examined 748 bagre rayado stomachs containing food and Reid (1983) examined 240 stomachs with food. Reid (1983) concluded that *P. fasciatum* feeds more frequently in sheltered sites and *P. tigrinum* feeds more often over open substrata. He also hypothesized that *P. fasciatum* feeds more diurnally, and stated that large catfishes of the Apure basin follow migrations of *P. mariae* and other migratory fishes (Lilyestrom, 1983; Barbarino Duque *et al.*, 1998), a belief universally held by local fishermen.

From 1983 to 1988, Castillo (1988) examined the abundance, population structure and diets of catfishes captured by commercial fishermen in the region around San Fernando de Apure, Venezuela and obtained similar results. Castillo (1988) did not report how survey effort was distributed over the 5 year period, but his capture per effort data indicated that no surveys were made during August; June and July were sampled during a single year and September was sampled during two years. Most survey effort was concentrated during the low-water months from November to February (each month surveyed during all 5 years). A notable difference in the findings of the two studies is the greater consumption of *P. mariae* by catfishes in Castillo's (1988) study. Castillo (1988) reported *P. mariae* as the dominant prey for *B. vaillanti* (73% of total prey items), *P. fasciatum* (54%), *P. tigrinum* (51%), *P. pirinampu* (41%) and *P. hemioliopterus* (36%). Two factors could account for the greater consumption of coporos in Castillo's (1988) study. First, sampling bias could have resulted from sample sizes that were generally smaller than those of the present study. Secondly, and probably more importantly, Castillo's (1988) surveys were biased toward the peak low-water season when coporos undergo massive upstream migrations in the major rivers of the western llanos (Barbarino Duque *et al.*, 1998). Whereas coporos clearly are the major food resource for many large river catfishes during this period, their importance in terms of annual food intake may be exaggerated unless other seasons are surveyed with comparable intensity. The present study also was biased toward surveys during the low-water period, because that is when catch per effort and fishing activity are greatest. Despite the fact that local fishing activity wanes during the high-water season, attempts were made in the present study to obtain surveys throughout the year, and, indeed, data were obtained for every month. As in the present study, Castillo (1988) found that gymnotiform knifefishes were the major prey of three of the four channel-restricted catfishes (*B. juruense*, 88%; *B. rousseauxii* (=*flavicans*), 64%; *G. platynema*, 89%). Furthermore, his rank order for the percentage of gymnotiforms consumed by the four channel-restricted catfishes exactly matches that of the present study. Castillo (1988) likewise found a greater percentage of benthic fishes consumed by *P. fasciatum* (18%) relative to *P. tigrinum* (2%).

Barthem & Goulding (1997) reported the only dietary data for large river catfishes of the Amazon River. In several aspects, their Amazon findings differ from those from the Apure River studies in Venezuela. Barthem & Goulding (1997) examined diets of two of the four channel-restricted species studied in the Apure-Arauca system, and found relatively few gymnotiforms in stomachs. In the Amazon, *B. flavicans* consumed mostly characiforms of the families Hemiodontidae (41·7%) and Curimatidae (9·6%), and *B. vaillanti* consumed mostly *Semaprochilodus* spp. (Characiformes, 53·8%) and *Doras* spp. (Siluriformes, 19·2%). Dietary data apparently were collected throughout the Amazon Basin and, although not specified, it may be inferred that most specimens of these two species came from the important estuarine fishery in Belem. Therefore, the paucity of gymnotiforms in their diet analysis may reflect low abundance or absence of this group in the Amazon estuary or differences in water depth and fishing methods. In the Amazon, curimatids (Characiformes) were the most important prey of both *Pseudoplatystoma* species (Barthem & Goulding, 1997), whereas in the Apure-Arauca system *M. duriventre* was the major prey of both species (Castillo, 1988; present study). The Amazon and Apure-Arauca studies both found high dietary overlap between the two *Pseudoplatystoma* species (0·90) and between *B. flavicans* and *B. vaillanti* (0·68). Likewise, overlap between *Pseudoplatystoma* and *Brachyplatystoma* species was low (0·09–0·32). The percentage of empty stomachs (92%) was greater in Barthem & Goulding's (1997) Amazon study than the present study (82·5%) and Castillo's (1988) study (82%).

In the Rio Branco and upper Rio Negro of the northern Amazon Basin, *P. hemioliopterus* have been captured with fruits and seeds in their stomachs (Goulding, 1980). This contrasts sharply with data from the Apure-Arauca system wherein *P. hemioliopterus* consumed no plant material (Tables III; Castillo, 1988). The only terrestrial food resources encountered in any of the nine catfishes examined from the Apure-Arauca system were four rats (Muridae) consumed by three *P. pirinampu* and an anoline lizard (Iguanidae) consumed by a *P. fasciatum*. Aquatic invertebrates (prawns and crabs) were infrequently consumed by the size classes examined. Because the present survey obtained few fishes from off-channel habitats, the possibility exists that greater consumption of aquatic invertebrates and terrestrial resources might still occur in seasonally flooded habitats.

The Apure-Arauca fishery centred around San Fernando is the largest in the Orinoco Basin, with harvests estimated from $2{\cdot}19 \times 10^6$ to $3{\cdot}77 \times 10^6$ kg year^{-1} during the period 1981–1987 (Castillo, 1988). The most abundant catfishes in this fishery, the two 'bagre rayado' species (*P. fasciatum* and *P. tigrinum*) and the 'bagre jipi' (*G. platynema*), are also among the most prized by commercial fishermen because of their popularity with consumers. The high abundance of these species in the commercial catch probably derives from an interaction among three factors: high natural abundance, occupation of habitats that can be effectively seined with large nets and targeting of effort in habitats that yield these high-value species. Two additional species that command high prices in regional markets (*B. flavicans* and *B. vaillanti*) were caught less frequently, probably because they are less abundant and restricted to river channel habitats with swift currents that are difficult to fish with nets. Accurate estimation of the natural abundances of fishes in these rivers requires standardized sampling methods in both in-channel and off-channel habitats, but swift currents and obstructions (large woody debris) hinder large-scale use of conventional nets.

In summary, large catfishes captured in the Apure-Arauca fishery are almost entirely piscivorous at sizes >25 cm L_S. Despite the fact that all of these species consume a wide range of prey taxa, strong patterns of dietary segregation were observed. Even though all four of the channel-restricted species fed heavily on gymnotiform knifefishes, food resources may be further partitioned based on location in the water column, possibly body size and behaviour. Percentages of specific prey taxa consumed by catfish species unrestricted to main river channels suggested similar means of niche segregation for this group as well. To reveal niche relationships and patterns of biological diversification among piscivorous catfishes of neotropical rivers, further research is needed that examines patterns of food resource and habitat use at finer scales of taxonomic, spatial and temporal resolution. Greater understanding of ecological attributes and relationships, including life history, diet and habitat requirements, will be critical for future management of these top predators and valuable fishery resources.

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