

Ecology, Food Habits and Spatial Interactions of Orinoco Basin Annual Killifish

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RESUMEN

Se estudiaron las asociaciones sintópicas de seis especies anuales de la ictiofauna de la Cuenca del Orinoco, en cuatro charcos temporales del Estado Portuguesa, Venezuela. Las especies difirieron en tamaño, forma corporal y distribución espacial en los charcos. Las asociaciones sintópicas son diversas combinaciones de especies de superficie: *Pterolebias hoignei* o *P. zonatus*; una especie del margen del charco: *Rachovia maculipinnis*; y especies del medio: *Terranatos dolichocheilus* o *Austrofundulus transilis* o ambas. *Rivulus stellifer* es una especie rara típica del margen del charco. Todas las especies se alimentan de insectos y pequeños crustáceos y hay considerable solapamiento en la dieta. Las dos especies de superficie están especializadas en insectos alóctonos; *R. maculipinnis* es generalista; *T. dolichocheilus* se especializa en microcrustáceos y *A. transilis* es gran depredador de microcrustáceos e insectos acuáticos. La ecología del charco temporal se complica con la invasión de especies no anuales, predominantemente caracoides, en plena temporada de lluvias. Las especies anuales desaparecen mientras los charcos están bien llenos y el alimento parece abundante. Aunque muchos individuos estaban muy cargados de parásitos, se piensa que el factor determinante de la eliminación de los peces anuales adultos es la competencia o depredación por peces no anuales.

SUMMARY

Syntopic associations among the six known Orinoco Basin annual killifish were studied in four temporary pools in Estado Portuguesa, Venezuela. The species differ in adult size, body form and spatial distribution within the pools. Syntopic associations are among various combinations of a surfacedwelling species, either *Pterolebias hoignei* or *P. zonatus*; an edge species, *Rachovia maculipinnis*; and midwater species, either *Terranatos dolichocheilus* or *Austrofundulus transilis* or both. The uncommon *Rivulus stellifer* is an extreme edge species. All species feed on insects and small crustaceans and there is considerable diet overlap. The two surface species specialize somewhat on allochthonous insects; *R. maculipinnis* is a generalist; *T. dolichocheilus* specializes on small crustaceans and *A. transilis* preys heavily on both small crustaceans and aquatic insects. Pool ecology is complicated by invasion by nonannual species, predominantly characoids, during the height of the rainy season. Annual species disappear while pools are well filled and food seems abundant. Although many individuals carried a heavy parasite load, it is thought that competition or predation by nonannual fishes is a major factor in eliminating adult annual fishes from these pools.

INTRODUCTION

Annuals (MYERS, 1952) are killifishes (cyprinodontoids) that are able to maintain permanent populations in temporary habitats by combining rapid growth and development, whereby sexual maturity is reached in as little as three to five weeks (TAPHORN and THOMERSON, 1978), with diapausing eggs (WOURMS, 1972a, b, c) which survive the dry season buried in the mud. Although techniques for raising annual fish in aquaria have been worked out, little is known concerning the biology of these fishes in their native habitats. Temporary or seasonal pools occur in a variety of habitats throughout the world; however, annual killifishes are generally limited to tropical Africa and South America (but see HARRINGTON, 1959).

The temporary pools of the tropics are perhaps the least studied of freshwater ecosystems. Although they all go through cycles of alternating wet and dry periods, physical, chemical and biological factors

vary greatly from place to place. In Venezuela we have collected annual fishes from pools ranging from puddles less than a meter wide and a few centimeters deep to extensive ponds over 1 m in depth; from clear tea-colored pools sometimes choked with aquatic vegetation, to barren muddy pools; in areas of open savannahs and semi-deserts to inner forest pools. Although most pools disappear during the dry season, occasionally pools persist through to the following rainy season. The four pools of this study include two savannah pools and two associated with forests.

Six annual killifish species occur in the Venezuelan Orinoco River Basin. All were thought to be endemic, but recently one species (*Pterolebias zonatus*) was found in a contiguous northern coastal drainage. These species occur in various syntopic combinations and up to five species can occur in the same pool (THOMERSON and TURNER, 1973). The six species are *Austrofundulus transilis* MYERS, *Terranatos dolichocheilus* (WEITZMAN and WOURMS), *Pterolebias hoignei* THOMERSON, *P. zonatus* MYERS, *Rachovia maculipinnis* (Weibezahn) and *Rivulus stellifer* THOMERSON and TURNER. Information on life histories and ecology of

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these fishes has been published as brief notes along with species descriptions or keys. Recent papers on taxonomy of these fishes are WEITZMAN and WOURMS (1967), THOMERSON and TURNER (1973), THOMERSON (1974), TAPHORN and THOMERSON (1975, 1978) and PARENTI (1981).

The species differ in adult size, body form and ecology. *R. maculipinnis* is both widespread and abundant and seems least restricted in habitat requirements. It often occurs alone and is usually present where other annual species are found. The least common species is *R. stellifer*, which lives only in very shallow areas. *T. dolichopterus* is a small midwater species. *P. zonatus* and *P. boignei* are two large surface dwelling species. *A. transilis* is also a midwater species known from a few localities. It was originally described from a single specimen (MYERS, 1932) and has been confused with *A. limnaeus* SCHULTZ and other references to this species prior to TAPHORN and THOMERSON (1978) are to *A. limnaeus*.

This paper reports trophic and spatial interactions among these annual fishes in four temporary pools in Estado Portuguesa, Venezuela. Observations on population ecology and associated nonannual species are presented. Limnological data and more detailed descriptions of study sites were given by NICO and TAPHORN 1984, in press).

METHODS AND MATERIALS

Fish were captured with hand nets and seines of 5 mm (1/4 inch) mesh during daylight hours in Portuguesa and Barinas, Venezuela, between 12 July and 30 August 1980. Most fish were preserved immediately but some were taken alive to the lab. We also examined other annual fish collections made from 1979 through 1981 deposited at the Museo de Ciencias Naturales (MCNG), Universidad Nacional Experimental de los Llanos Occidentales "Ezequiel Zamora" (UNELLEZ), Guanare, Portuguesa, Venezuela. Standard length (SL) for annual fishes was measured from tip of lower lip (TAPHORN and THOMERSON, 1978). SL was measured from tip of snout for all other species except the synbranchid eel, *Synbranchus marmoratus*, where total length (TL) was recorded.

Preserved annual fishes were weighed to nearest 0.01 g, then dissected. Gonads were weighed to nearest 0.001 g. Gonadosomatic index (GSI) is gonad weight expressed as a percent of total body weight (LARIMORE, 1957). Parasites found incidentally during dissection were recorded.

Diet determination and analyses

Only fishes preserved immediately in the field were used in diet analyses. The entire alimentary tracts of some five hundred annual fishes and an additional 37 nonannual fishes were removed and their contents examined under a stereo-dissecting microscope. A partially subjective estimate of gut fullness was made for the annual fishes. The foregut

and hindgut were scored from 0 to 3 (modified from THOMERSON and WOOLDRIDGE, 1970): 0 if empty; 1 if food items present but significantly less than half full; 2 for approximately half full; and 3 if full. Both scores were added to give a total score ranging from 0 to 6 for each individual.

Food organisms were most often identified to order. "Terrestrial insects" applied to any aerial, arboreal, or ground dwelling insect that fell into the water and became a food item. "Unidentified insects or arthropods" includes arthropods or arthropod fragments whose identity and origin, aquatic or terrestrial, were uncertain. "Debris" is a general term for both organic and inorganic material, usually soil, mud, or sand.

Food organisms were counted using a Ward counting wheel under 25X magnification. If a single gut contained several hundred small crustaceans, subsamples were taken by diluting the gut contents in alcohol to a total volume of 10 ml, shaking taking a 2.5 ml subsample, then counting the food items and multiplying by 4.

The food item (whether 50 cladocera or 1 beetle) contributing the greatest volume or bulk to the contents of each gut was recorded as dominant ("first order" of ETNIER, 1971). If gross analysis did not give a clear decision between two organisms, both were assigned dominant rank.

Percent frequency of occurrence (%O), mean number per gut (\bar{N}), and percent frequency of dominance (%D) are reported for annual fish food items. %O is defined as the number of guts sampled in which a particular food item is found expressed as a percentage of all nonempty guts examined (WINDELL and BOWEN, 1978). \bar{N} is the total number of a particular food item divided by the number of nonempty guts examined. %D is defined as the number of times a particular food item was recorded as dominant expressed as a percent of the total number of dominant rankings. Use of a single method of food analysis introduces bias (see discussions by GEORGE and HADLEY, 1979; WILLIAMS and WILLIAMS, 1980). The terms "important" and "major" in the text imply a food item had a high combined %D and %O relative to that of other food items.

STUDY AREA

The Orinoco River Basin occupies central Venezuela and parts of eastern Colombia. Much of the basin, from the Orinoco Delta in the east and stretching over 1,000 km west to the Andes Mountains, consists of flat tropical savannah lowlands called llanos. Although most of the llanos are grasslands scattered with trees and wooded areas, in Portuguesa large tracts of dry tropical forest are present. Regional climatic data (AVILES *et al.*, 1983) from the Guanare airport (9°01'N, 69°44'W, 163 m) over a 10 year period (1970-1979) are as follows: mean annual temperature 26.7°C, and mean annual precipitation 1544 mm. The rainy season, although somewhat variable, lasts some eight

months, from April through November. Monthly precipitation is usually well in excess of 150 mm and much of the llanos become inundated. During the dry season monthly rainfall is normally less than 30 mm and standing water usually becomes limited to large permanent lagoons, creeks and rivers.

RESULTS

CASE STUDIES OF SYNTOPES

Pool I

Pool I was in open country alongside a highway bordering a cattle ranch near Hwy km 287 between Guanare and Tucupido. Two annual killifish species, *P. zonatus* and *R. maculipinnis*, were syntopic.

Eleven fish collections were made from Pool I between 12 July and 30 August 1980; additional collections were made 24 April and 14 September 1981. Fifty-four annual fishes were collected from the pool, we recorded the parasites and gonadosomatic indices of most specimens and analyzed the gut contents of 52. Gut contents of 35 preserved nonannual fishes were recorded.

Visits to Pool I in 1980 yielded 12 adult *P. zonatus* (one taken live) and 21 adult *R. maculipinnis*. Nonannual fishes consisted of: *Astyanax* cf. *bimaculatus*, *A.* cf. *metae*, *ctenobrycon spilurus*, *Pyrrhulina* cf. *lugubris*, *Hoplerythrinus unitaeniatus*, *Hoplias malabaricus*, *Hoplosternum littorale*, *Synbranchus marmoratus*, *Aequidens* cf. *pulcher*, and an unidentified characin.

Total fishes collected 24 April 1981 between 0905-0930 hrs were 9 juvenile *P. zonatus* and 12 juvenile *R. maculipinnis*. No other fishes were observed. On 14 September 1981 only several small *C. spilurus* and *P.* cf. *lugubris* were taken.

Although samples are small, size distributions suggest that single generations of similar age were present in the pool at any one time. Juveniles of both species were together, restricted to the shallow grassy parts of the pool, but adult fishes were spatially segregated. Usually adult *P. zonatus* were out over deeper water while adult *R. maculipinnis* were most common along the shallow edges, even into a narrow arm of the pool, less than 10 cm deep, extending to more than 5 m inland.

P. zonatus disappeared towards the end of July 1980 and no *R. maculipinnis* were collected during the last two visits to the pool in late August 1980. Similarly, neither species was found in mid-September of 1981. During both these rainy seasons, annual fishes disappeared even though food seemed abundant and the water was near peak levels.

R. maculipinnis GSI (3.3-7.5 for females) was high throughout July and August, suggesting a prolonged spawning period, supporting aquarium observations that mature individuals spawn daily over a long period of time. Our *P. zonatus* GSI data do not document the length of the natural spawning period,

but aquarium experience (NELSON, 1980) shows prolonged spawning for this species.

Cladocerans and aquatic insects were predominant food items in juveniles of both species (Table 1). Smaller *R. maculipinnis* young ($\bar{SL} = 9$ mm) consumed some insects, mainly chironomid larvae, but larger juvenile *P. zonatus* ($\bar{SL} = 21$ mm) fed on a relatively wide range of both aquatic and terrestrial insects as well as large numbers of microcrustaceans. *P. zonatus* juveniles averaged about 238 microcrustaceans per gut (one individual had 404), but the small *R. maculipinnis* juveniles averaged only 8. Overall, size differences between the juveniles probably accounted for species differences in prey type and amount consumed. Young *P. zonatus* had a mean gut fullness of 5.6, in contrast, *R. maculipinnis* juveniles usually had guts half full (3.0) or less.

Differences in food of adults (Table 1) were less striking. However, in terms of relative importance, *P. zonatus* depended primarily on terrestrial insects, but *R. maculipinnis* relied almost equally on microcrustaceans, aquatic insects, and terrestrial insects. Gut contents and observations indicate that *P. zonatus* was primarily a surface feeder, but one male had consumed almost 300, small cladocerans (accounting for most of the crustaceans eaten by the species).

During July and August of 1980 the dense emergent vegetation supported a large number of arthropods, potential food items that might fall into the water. Adult annual fishes probably ate ants, dipterans, homopterans, and other terrestrial insects from the surface, but chironomids and snails were probable taken from substrate, and small crustaceans from the water column. *R. maculipinnis* readily takes food off the surface or bottom in aquaria.

No vertebrate remains were found even though adults of both species were large enough to eat small tadpoles or fishes (e. g., *P. lugubris*) which were relatively common in the pool. Most plant material, particularly algae, and protozoans and rotifers may have been eaten secondarily along with intended prey items. Mosquito larvae were rare in Pool I annual fish guts reflecting their rarity in the habitat. In aquaria both species readily take mosquito larvae.

The guts of annual fishes were usually more than half full even during the latter half of the rainy season, and guts of all nonannual fishes contained food. Starvation, as reported by THOMERSON (1971) in the Maracaibo Basin, was not evident.

Several adult annual fishes had slightly ragged anal and caudal fins in July and August of 1980, but none of the potentially piscivorous fishes collected from Pool I contained fish remains. All *Hoplias malabaricus* and *Hoplerythrinus unitaeniatus* specimens taken were relatively small, less than 120 mm SL, and had fed on insects (Table 2). Killifish have been found in the stomach of *H. unitaeniatus* (SAUL, 1975). The largest predator collected was the eel, *Synbran-*

chus marmoratus (505 mm TL). Unfortunately, the single specimen was found dead, with viscera eaten away. The diet of large individuals of this species includes small fish and frogs (ZARET and RAND, 1971; K. WINEMILLER, pers. comm., 1984).

Pool I is isolated during the early rainy season, but by no later than July, nonannual fishes enter the pool by way of connections with permanent water bodies. Ten species, representing six families, were

collected. Collection efforts throughout July and August 1980 indicated that nonannuals outnumbered annual fishes. *Ctenobrycon spilurus* and *Pyrrhulina* cf. *lugubris* were the most abundant species. Nonannual fishes did not seem to decrease in numbers by the end of August 1980, even though annual fishes had disappeared. Table 2 shows the food items of nonannual and annual fishes of Pool I collected between 12 July and 30 August 1980.

TABLE 1

GUT CONTENTS OF *PTEROLEBIAS ZONATUS* AND *RACHOVIA MACULIPINNIS* FROM POOL I. %O = PERCENT FREQUENCY OF OCCURRENCE; \bar{N} = MEAN NUMBER PER GUT; AND %D = PERCENT FREQUENCY OF DOMINANCE

Food item	Juveniles: 24 April 1981						Adults: 12 July - 22 Aug. 1980					
	<i>P. zonatus</i>			<i>R. maculipinnis</i>			<i>P. zonatus</i>			<i>R. maculipinnis</i>		
Number examined	9			11			11			21		
Number empty	0			0			0			1		
SL range (mm)	17-23			8-10			35-52			29-44		
	%O	\bar{N}	%D	%O	\bar{N}	%D	%O	\bar{N}	%D	%O	\bar{N}	%D
Plant material												
Algae	—	—	—	—	—	—	27	tr	—	10	tr	—
Seeds/Vascular	—	—	—	—	—	—	—	—	—	20	nd	—
Protozoa-Testacida	11	0.1	—	—	—	—	18	nd	—	5	nd	—
Rotifera	78	2.7	—	27	0.6	—	—	—	—	5	tr	—
Nematoda	—	—	—	—	—	—	9	—	—	—	—	—
Crustacea												
Copepoda	44	0.7	—	27	0.5	—	45	0.6	—	35	0.6	—
Cladocera	100	236.4	78	100	7.5	69	82	31.0	—	65	0.7	—
Ostracoda	33	0.8	—	—	—	—	18	0.3	—	50	2.0	10
Conchostraca	—	—	—	—	—	—	18	0.4	—	45	1.0	5
Aquatic insects												
Odonata nymphs	33	0.6	22	—	—	—	9	0.1	8	10	0.1	10
Beetle larvae	11	0.1	—	—	—	—	18	0.2	—	50	0.5	14
Chironomid larvae	56	0.9	—	64	0.7	31	64	3.3	8	65	1.9	5
Mosquito larvae	—	—	—	—	—	—	9	0.1	—	—	—	—
Other	33	0.3	—	—	—	—	27	0.5	—	15	0.2	5
Terrestrial insects												
Formicidae	—	—	—	—	—	—	64	0.9	15	30	0.5	14
Other	22	0.2	—	—	—	—	100	3.1	54	55	0.6	24
Unident insects*	22	0.2	—	—	—	—	73	0.5	15	50	0.7	10
Hydracarina	—	—	—	—	—	—	9	0.1	—	5	0.1	—
Gastropoda	—	—	—	—	—	—	18	0.3	—	30	0.6	5

* Insects or insect fragments of undetermined origin; tr = less than 0.1; nd = not determined.

Pool II

Pool II was a roadside pool bordering a cattle pasture near Hwy km 29.9 between Guanare and Guanarito, Portuguesa. The pool was located in open land in an area characterized by mixed open land and forest. Three visits were made to the pool during July 1980 and one visit on 27 August 1980. We also examined annual fishes collected there on 17 June and 20 September 1979. We obtained parasites and gonadosomatic indices of most of the 190 specimens from Pool II and analyzed the gut contents of 116.

On 17 June 1979 species captured and preserved were 15 *A. transilis*, 1 *P. zonatus*, and 73 *R. maculipinnis*, and 1 characin. About 45 min (1330-1415 hrs) of effort on 20 September 1979 netted *A. transilis* (one preserved and about 20 kept live) and 30 *R. maculi-*

pinnis, 5 *Ctenobrycon spilurus*, 1 *Synbranchus marmoratus*, 1 *Hoplosternum* sp., and 5 *Poecilia* sp.

Fishes taken during visits to Pool II on 12, 19, and 27 July 1980 were 21 *A. transilis* and 16 *R. maculipinnis* (a small number, not recorded, of annual fishes were also taken live), *Astyanax* cf. *bimaculatus*, *C. spilurus*, *Curimata* sp. *Cichlasoma orinocense*, *Gymnotus carapo*, and *Poecilia* sp. On 27 August 1980 about 1 hr of collecting yielded 1 *P. zonatus* and 43 *R. maculipinnis* (32 preserved and 11 taken live). No *A. transilis* were observed. Nonannual fishes collected were: *Astyanax* cf. *bimaculatus*, *Pyrrhulina* cf. *lugubris*, and *Poecilia* sp.

Although *R. maculipinnis* were observed throughout the pool during visits in 1980, it was most common in shallow (less than 20 cm), heavily vegetated areas. On 27 August 1980 they were noticeably

crowded into the flooded grassy areas bordering the main pool. The single *P. zonatus* collected on the same date was taken in a relatively open section of the pool in water about 60 cm deep and partially shaded by trees. Most *A. transilis* collected in 1980 were from water 20 cm or more deep. *R. maculipinnis* and *A. transilis* did occur in the same areas, usually because *R. maculipinnis* entered deeper areas rather than *A. transilis* going into the shallow edges.

Comparison of numbers, size distributions, and GSI values of species from different collection period suggests several trends. At any one time each species was a single generation of similar size fish. *A. transilis*, and probably *P. zonatus* as well, emerged before *R. maculipinnis*, possibly by several weeks. *A. transilis* and *P. zonatus* (1979 data) were at or near spawning size in June but *R. maculipinnis* did not reach sexual maturity until July.

TABLE 2

FOOD ITEMS OF NONANNUAL AND ANNUAL FISHES OF POOL I COLLECTED JULY AND AUGUST 1980.
M = MAJOR FOOD ITEM (i.e., HIGH COMBINED PERCENT FREQUENCY OF DOMINANCE AND PERCENT FREQUENCY OF OCCURRENCE); x = MINOR FOOD ITEM.

Species	Number examined	Size range SL (mm)	Algae	Seeds/vascular	Small crustacea	Aquatic insects	Allochthonous arthropods	Gastropoda	Debris/detritus
<i>Astyanax</i> cf. <i>bimaculatus</i>	4	25-36	x		x	M	M		
<i>Astyanax</i> cf. <i>metae</i>	1	46				M	M		
<i>Ctenobrycon spilurus</i>	8	21-29	x?		M	M	x		x?
Characin sp.	1	41					M		
<i>Pyrrhulina</i> cf. <i>lugubris</i>	13	10-34			M	M	x		
<i>Hoplerythrinus unitaeniatus</i>	1	97				M			
<i>Hoplias malabaricus</i>	3	39-118			x	M			x
<i>Hoplosternum littorale</i>	1	91	x?		x	x		M	M
<i>Pterolebias zonatus</i>	11	35-52	x?		x	x	M	x	
<i>Rachovia maculipinnis</i>	21	29-44	x?	x?	M	M	M	x	
<i>Synbranchus marmoratus</i> *	1	505 TL							
<i>Aequidens</i> cf. <i>pulcher</i>	3	20-53	x		M	M			M?

* Single specimen found dead with viscera eaten away.

Field observations along with numbers of fishes collected show *R. maculipinnis* the most abundant annual species in Pool II, followed by *A. transilis*, in 1979 and 1980. *P. zonatus*, two specimens collected over two years time, apparently maintains a very small population.

Both *P. zonatus* specimens from Pool II were sexually mature. The male (42 mm SL), taken in June 1979, had a GSI of 0.9. The female (39 mm SL), from the August 1980 collection, had a GSI of 13.8; and contained several large eggs.

A. transilis and *R. maculipinnis* females reached maturity between 20 and 25 mm SL, and males became mature at 25 to 30 mm SL. Although *A. transilis* reached breeding size before *R. maculipinnis*, *R. maculipinnis* attained a similar size by July. *A. transilis* males do not grow much after reaching sexual maturity, and *R. maculipinnis* males eventually surpassed them in size.

Thirty *R. maculipinnis* and 1 *A. transilis* from September 1979 were partially or completely desexed by parasites. Nematodes and trematodes were enmeshed in gonadal tissue, often to the point of replacing it completely, and GSI values of only a few fish could be calculated.

Invertebrates, mainly insects and small crustaceans, were most of the food eaten by Pool II annual fishes. The *P. zonatus* male taken in June 1979 had a full gut containing two large aquatic insects, one a water scorpion (Nepidae). The female of August 1980 had a gut only one-third full with two small flying insects and a single chironomid larva.

Table 3 and 4 give the gut contents of *A. transilis* and *R. maculipinnis* from Pool II in 1979 and 1980, respectively. Aquatic insects are the most important food of *R. maculipinnis* collected during the various visits. Large numbers of these insects were sometimes taken; one fish had eaten no less than 170 biting midge larvae (Heleidae). Small crustaceans were usually the second major item, but terrestrial insects had been heavily exploited by fish taken 20 September 1979.

Records of piscivory by the Orinoco annual species are uncommon, however, small fish were eaten by Pool II *R. maculipinnis* in September 1979. Three large male *R. maculipinnis*, 39-42 mm SL, each contained a single guppy (*Poecilia* sp.). *Poecilia* were one of the most abundant fish in Pool II in 1980 and were often observed swimming in small schools near the surface, but none were found in the guts of annual fishes collected at that time. A few male

R. maculipinnis taken in 1980 had consumed fish scales probably those of conspecifics taken during aggressive encounters.

Small crustaceans were the mayor food item of *A. transilis*. Several individuals contained only crustaceans. Copepods were predominant in fish of June 1979, but cladocerans were the most important item in fish collected in 1980. A single female had consumed 219 copepods. In 1979 fish fed on crustaceans to near exclusion of all else, but 1980 *A. transilis* also heavily utilized aquatic insects.

No terrestrial insects were identified in the guts of annual fishes collected from Pool II in 1979; however, in 1980 all three species had fed on them to some extent. Overall differences in diets of the two most abundant annual species seemed small, but 19 of 20 *R. maculipinnis* had eaten aquatic insects, in contrast to only three of 15 *A. transilis* from June 1979.

None of the annual fishes from Pool II had empty guts, suggesting food was readily available throughout both years. Fishes from the various collections were usually more than half full. The lone exception being the average value of 2.5 for August 1980. This may indicate a lowered food supply late in the season; however, fish taken in September of the previous year showed a mean value of 4.5, approximately two-thirds full.

Pool III

Pool III was a roadside temporary pond or ditch bordering a forest near Hwy km 74.8 between Guanare and Guanarito, in Portuguesa. Three annual killifish species, *T. dolichopterus*, *P. boignei*, and *R. maculipinnis*, were syntopic. Collections were made 19 July and 27 August 1980. We also examined collections made 24 May 1980 and recorded gonadosomatic indices and analyzed gut contents of 143 annual fish specimens.

TABLE 3

GUT CONTENTS OF *AUSTROFUNDULUS TRANSILIS* AND *RACHOVIA MACULIPINNIS* FROM POOL II, 1980.
%O = PERCENT FREQUENCY OF OCCURRENCE; N = MEAN NUMBER PER GUT;
AND %D = PERCENT FREQUENCY OF DOMINANCE

Food item	12, 19, + July 1980						27 Aug. 1980		
	<i>A. transilis</i>			<i>R. maculipinnis</i>			<i>R. maculipinnis</i>		
Number examined	21			16			21		
Number empty	0			0			0		
SL range (mm)	27-37			21-40			25-43		
Food item	%O	N	%D	%O	N	%D	%O	N	%D
Plant material									
Seeds	5	tr	—	—	—	—	—	—	—
Vascular material	—	—	—	—	—	—	5	nd	—
Nematoda	10	0.1	—	—	—	—	—	—	—
Annelida	5	0.1	—	—	—	—	—	—	—
Crustacea									
Copepoda	86	10.7	4	—	—	—	14	0.1	—
Cladocera	100	27.9	42	94	12.7	17	52	1.6	5
Ostracoda	52	1.6	8	50	2.7	11	33	0.4	14
Conchostraca	24	0.6	8	—	—	—	—	—	—
Aquatic insects									
Odonata nymphs	19	0.3	4	—	—	—	14	0.1	5
Beetle larvae	29	0.5	8	31	0.7	—	38	0.4	10
Chironomid larvae	81	6.8	17	69	4.6	17	38	0.6	5
Mosquito larvae	5	tr	—	31	0.6	—	5	0.3	5
Other	38	0.8	8	75	1.7	17	38	0.8	14
Terrestrial insects									
Formicidae	—	—	—	6	0.1	—	10	0.1	14
Other	10	0.1	4	12	0.1	6	19	0.2	19
Unident insects*	29	0.3	—	31	0.4	6	14	0.2	5
Hydracarina	10	0.1	—	6	0.1	—	—	—	—
Araneae	—	—	—	6	0.1	—	—	—	—
Gastropoda	5	tr	—	6	0.1	6	5	tr	—
Fish scales	—	—	—	19	1.5	17	5	tr	—
Debris	—	—	—	—	—	—	14	nd	5

* Insects or insect fragments of undetermined origin; tr = less than 0.1; nd = not determined.

TABLE 4

GUT CONTENTS OF *AUSTROFUNDULUS TRANSILIS* AND *RACHOVIA MACULIPINNIS* FROM POOL II, 1979.
 %0 = PERCENT FREQUENCY OF OCCURRENCE; N = MEAN NUMBER PER GUT;
 AND %D = PERCENT FREQUENCY OF DOMINANCE

Food item	17 June 1979						20 Sept. 1979		
	<i>A. transilis</i>			<i>R. maculipinnis</i>			<i>R. maculipinnis</i>		
Number examined	15			20			20		
Number empty	0			0			0		
SL range (mm)	23-34			12-26			25-50		
Food item	%0	N	%D	%0	N	%D	%0	N	%D
Plant material									
Algae	—	tr	—	—	—	—	20	nd	—
Vascular material	—	—	—	—	—	—	5	nd	—
Rotifera	—	—	—	25	0.3	—	—	—	—
Nematoda	—	—	—	5	tr	—	—	—	—
Crustacea									
Copepoda	100	99.7	80	75	3.9	8	50	0.9	—
Cladocera	67	1.6	7	85	12.1	21	40	2.9	—
Ostracoda	13	0.1	—	75	2.3	8	30	0.4	—
Aquatic insects									
Odonata nymphs	—	—	—	10	0.2	8	—	—	—
Beetle larvae	7	0.1	—	45	0.7	21	45	1.1	25
Chironomid larvae	7	0.1	—	75	3.6	25	80	4.2	20
Mosquito larvae	7	0.3	7	10	0.1	—	10	0.1	—
Other	7	0.1	—	20	0.2	4	80	16.7	30
Terrestrial insects	—	—	—	—	—	—	—	—	—
Unident insects*	—	—	—	30	0.4	4	10	0.1	5
Hydracarina	7	0.1	—	15	0.3	—	10	0.1	—
Unident arthropods	—	—	—	10	0.1	—	5	tr	—
Fish**	—	—	—	—	—	—	15	0.1	15
Fish eggs	—	—	—	—	—	—	5	tr	—
Debris	7	nd	7	—	—	—	10	nd	5

* Insects or insect fragments of undetermined origin; ** *Poecilia* sp.; tr = less than 0.1; nd = not determined.

Total fishes, collected with about 20 min of seining effort on 24 May 1980, consisted of 20 *T. dolichopterus*, 94 *P. boignei*, and 4 *R. maculipinnis*. On 19 July 1980, 1.5 hr of collecting effort yielded only 30 *P. boignei* (25 preserved immediately and five kept live and preserved later). Nonannual fish species were also collected: *Aphyocharax erythrurus*,* *Astyanax* cf. *bimaculatus*, *Cheirodontops geayi*, *Ctenobrycon spilurus*, *Hemigrammus marginatus*,* *Moenkhausia dichrourea*,* *Odontostilbe pulcher*, *Tetragonopterus argenteus*, *Pyrrhulina* cf. *lugubris*,* *curimata spilurus*,* *Poecilia* cf. *reticulata*, *Cichlasoma orinocense*, and several unidentified small characins.

On 27 August 1980, 45 min of effort yielded no annual species. Nonannual species included some species taken in July (indicated by an asterisk*) and also *Charax* sp. *Poptella orbicularis*, *Salminus hilarii*, *Hoplias malabaricus*, and several unidentified small characins.

P. boignei was the most abundant fish in Pool III in May, followed by *T. dolichopterus*, and the then *R. maculipinnis*, which was rather uncommon. By July nonannual fishes were also present in the pool, *P. boignei* still had a fair population though fewer than in May. *T. dolichopterus* had also declined and *R. maculipinnis* had disappeared. All annual species were gone by August, but nonannual fishes increased.

Taking sexual dimorphism into account, size distributions of *P. boignei* (24-48 mm SL) and *T. dolichopterus* (16-28 mm SL) indicated that each was a single generation of similar age. One possible exception was a small female *P. boignei*, 24 mm SL, taken in May. The other 48 females taken at that time ranged from 35-40 mm long. Only four immature *R. maculipinnis*, 15-31 mm SL, were collected from Pool III.

On 24 May 1980 *P. boignei* was usually taken near the surface, *T. dolichopterus* from midwater areas of the pool and *R. maculipinnis* from the shallow edges (D. TAPHORN, pers. comm.). In July one of us (LGN) observed a similar distribution of *P. boignei*. The fish were usually seen hovering at or near the surface and seemed to prefer the more open central areas of the pool, more or less shaded from above by overhanging trees, in water 0.5 m or more deep. The single *T. dolichopterus* captured in July was taken with a seine from well below the surface in a deep central part of the pool. The various nonannual species which invaded the area after the May collection were found throughout the pool.

The four *R. maculipinnis* taken in May were two juveniles (15 and 16 mm SL), an immature male (GSI = 0.1, 31 mm SL) and female (GSI = 0.1, 25 mm SL).

The May *P. boignei* were all adults, 45 males and 49 females, as were the 17 males and 13 females taken in July. Although GSI values of males remained similar from May to July, females increased their reproductive capacity with time.

One juvenile (17 mm SL), six male, and 13 female *T. dolichopterus* were collected in May. Females tended to be smaller than males, SL averaged 20 (range 16-23) mm and 24 (range 22-28) mm, respectively. GSI values of males ranged from 0.2 to 0.7, mean 0.4. Females exhibited GSI values of 0.2 to 7.1, mean 2.0. Nine females were at or near breeding condition, the other four females had partially developed ovaries.

In May all three species had fed primarily on small crustaceans. The four *R. maculipinnis* ate both copepods and cladocerans; cladocerans were dominant in the female, copepods were dominant in the other three fish. Miscellaneous items included a chironomid larva, unidentified insect fragments, and debris.

Food items eaten by *T. dolichopterus* and *P. boignei* are shown in Table 5. *T. dolichopterus* fed almost exclusively on small crustaceans. Copepods were the dominant food item for all males, but cladocerans and copepods were near equal in importance for females. May *P. boignei* fed heavily on crustaceans, with terrestrial insects ranking second in importance, but July *P. boignei* contained no crustaceans and had relied almost entirely on terrestrial insects. Although the guts of July *P. boignei* were significantly less full than those collected in May, individuals of July still averaged nearly half full guts (2.9) and maintained a relatively high GSI.

Although, the only large piscivore taken, *Salminus hilarii* (175 mm SL), did not contain fish remains, the torn fins of most fishes taken in July and August indicated that predators were present and active. Predators probably included piranha since even the *S. hilarii* was missing most of its caudal fin. Few *P. boignei* taken in May had damaged fins, but all July specimens had pieces of anal fin, caudal fin, or both, missing. Some July individuals had lost nearly their entire caudal fin.

TABLE 5

GUT CONTENTS OF *TERRANATOS DOLICHOPTERUS* AND *PTEROLEBIAS HOIGNEI* FROM POOL III, 1979.
%0 = PERCENT FREQUENCY OF OCCURRENCE; \bar{N} = MEAN NUMBER PER GUT;
AND %D = PERCENT FREQUENCY OF DOMINANCE

Food item	24 May 1980						19 July 1980		
	<i>I. dolichopterus</i>			<i>P. boignei</i>			<i>P. boignei</i>		
	%0	\bar{N}	%D	%0	\bar{N}	%D	%0	\bar{N}	%D
Number examined	20			94			25		
Number empty	0			0			2		
SL range (mm)	16-28			24-48			36-63		
Plant material									
Algae	15	nd	—	—	—	—	—	—	—
Seed	—	—	—	5	0.1	—	—	—	—
Rotifera	—	—	—	1	tr	—	—	—	—
Nematoda	—	—	—	1	tr	—	—	—	—
Annelida	—	—	—	—	—	—	—	—	—
Crustacea									
Copepoda	100	51.0	65	91	40.8	1	—	—	—
Cladocera	95	61.2	30	100	739.7	81	—	—	—
Ostracoda	5	tr	—	1	tr	—	—	—	—
Aquatic insects									
Odonata nymphs	5	tr	4	6	0.1	2	—	—	—
Beetle larvae	—	—	—	4	0.1	1	4	tr	—
Chironomid larvae	10	0.1	—	—	—	—	—	—	—
Other**	—	—	—	4	0.1	—	13	0.1	8
Terrestrial insects									
Formicidae	—	—	—	10	0.1	—	83	3.1	58
Other	—	—	—	36	0.7	13	61	1.3	33
Unident insects*	5	tr	—	12	0.1	—	43	0.6	—
Hydracarina	—	—	—	2	tr	—	9	0.1	—
Araneae	—	—	—	1	tr	—	9	0.1	—
Unident arthropods	—	—	—	2	tr	—	—	—	—
Gastropoda	—	—	—	—	—	—	4	tr	—
Debris	—	—	—	1	nd	—	—	—	—

* Insects or insect fragments of undetermined origin; ** Does not include mosquito larvae; tr = less than 0.1; nd = not determined.

Pool IV

Pool IV was actually a mosaic of shallow small pools and puddles in a forest and on a narrow dirt road within the forest. Its location was approximately 2.1 km north of the Guanarito bridge (Río Guanare). Three annual killifish species, *R. maculipinnis*, *R. stellifer*, and *P. boignei*, occurred in the flooded forest. Fishes were collected on 27 August 1980. We examined the gut contents of 64 of 101 preserved annual fishes from Pool IV. Unfortunately, *R. maculipinnis* collected in 1979 were not available for analysis.

On September 1979, 15 *R. stellifer* and 10 *R. maculipinnis* were collected. On 27 August 1980, approximately 2 hr of collecting yielded 10 *R. stellifer*, 75 *R. maculipinnis*, and 1 *P. boignei*. Nonannual fishes collected were: *Curimata* sp. and *Poecilia* sp.

Most *R. stellifer* collected in August 1980 were restricted to three isolated puddles on the dirt road, but several were also taken from adjacent forest pools. Even though few *R. maculipinnis* occurred in puddles with *R. stellifer*, it was the most abundant fish species overall. In one forest pool, choked with filamentous algae, *R. maculipinnis* were so numerous that three or more were easily captured with each pass of the hand net. The single *P. boignei* was probably taken with *R. maculipinnis* in a forest pool.

The *P. boignei* specimen was a female (42 mm SL). 1980 *R. stellifer*, collected in September, were larger than August 1979 *R. stellifer*. In 1980 *R. maculipinnis* was the smallest annual species present, although several males were larger than the smaller *R. stellifer* females.

In aquaria *R. stellifer* are known to be very aggressive, and males often attack and kill one another (THOMERSON and TURNER, 1973). THOMERSON and TURNER (1973) noted that in nature individuals seem to space themselves rather evenly along the edges of pools and suggested that the species may defend territories. We found scales or fin rays in the gut of one male collected in 1980 and in four male *R. stellifer* from 1979. Analysis of scales indicated they were of conspecifics. Examination of 1980 specimens revealed five of 10 fish had ragged fins, usually the caudal but degree of damage was slight. All 15 *R. stellifer* taken in 1979 had some form of fin damage, ranging from slightly ragged caudal or anal fin in eight specimens to a male and female with at least two-thirds of their caudal fin missing. In both 1980 and 1979 specimens, all sizes of individuals had been attacked, and nearly as many males as females showed signs of fin damage. The higher aggression of 1979 males may be due to crowding and low food resources.

All annual fishes were mature and were considered to be in breeding condition. The *P. boignei* specimen was visibly gravid and contained several large mature eggs. Although *R. stellifer* males from 1979 and 1980 had similar GSI values, 1980 females showed a much higher GSI, a mean of 6.3, than those

collected in 1979 (mean of 3.7). All *R. maculipinnis* males exhibited secondary sexual characteristics, and had GSI values similar to *R. stellifer*. 1980 female *R. maculipinnis*, as indicated by the GSI, degree of abdominal distention, and number of mature oocytes, were probably near peak reproductive condition even though the relatively small sizes suggested both sexes had only recently reached sexual maturity.

The major food items of the single *P. boignei* was terrestrial insects, although seeds and a chironomid larva were also eaten. Small crustaceans, aquatic insects and terrestrial insects were near equal in importance in the diet of 1980 *R. maculipinnis* (Table 6). Ostracods were the major food of 1980 *R. stellifer* (Table 6) with allochthonous insects second in importance. The stomachs of some *R. stellifer* specimens also contained seeds, suggesting a rather generalized, sometimes omnivorous diet. Overall, the types of food eaten by the two species of 17 August 1980 were similar. Mean gut fullness of 1980 *R. stellifer* and *R. maculipinnis* were 2.9 and 3.3, respectively.

The primary item ingested by 1979 *R. stellifer* was debris (Table 6) usually consisting of mud, sand, or setae, and fish scales. Seven of the 15 specimens had empty guts and only three fish had guts as much as half full. The low diversity and types of items eaten in combination with a mean gut fullness of 1.0 indicates the habitat was food-limited at the time.

DISCUSSION

Use of Resources by Annual Fish Communities

Space, food, and time are three general dimensions along which organisms typically partition resources (PLANKA, 1973; SCHOENER, 1974). Table 7 summarizes characteristics of Orinoco River Basin annual fishes, some relating to these dimensions. Field observations suggest that space was the parameter most often divided by adults of different species and perhaps explains how syntopic annual fishes coexist. In every case except Pool IV (where habitat diversity was limited) the syntopic associations involved a surface-dwelling species (*P. zonatus* or *P. boignei*), an edge species (*R. maculipinnis*), and in Pools II and III a midwater species (*A. transilis* or *T. dolichopterus*).

Observed differences in spatial utilization and behavior agree with basic morphological differences in body form and, in general, agreed with published information (THOMERSON and TURNER, 1973; THOMERSON, 1974; TAPHORN and THOMERSON, 1975, 1978). These differences also suggest different food habits (KEAST and WEBB, 1966; ENDELSON, 1975), but differences in diet were not always obvious. Although certain species occasionally fed on small fish or frogs (i.e., *R. maculipinnis* in Pool II, *P. zonatus* and *A. transilis* of other localities), we did not find the marked trophic differentiation, suggested by

TURNER (1967) for neotropical annual syntopes, into piscivorous versus invertebrate diet for associated species. As would be expected, surface species specialized somewhat on terrestrial insects, mid-water species on small crustaceans, and edge species had generalized food habits. However, diets often widely overlapped even though differences in either proportional importance or overall diversity of food items were usually present. For example, small crustaceans were the most important food item of

syntopic *T. dolichopterus* and *P. boignei* (Pool III) in May, even though the two species differed in use of space and differed significantly in size. However, *T. dolichopterus* (Table 5) fed primarily on copepods and its diet was almost exclusively small crustaceans, but cladocerans were the most common microcrustacean taken by *P. boignei*, in addition to large amounts of terrestrial insects. These diet differences suggest, but do not prove, partitioning of food resources, possibly as a result of competition.

TABLE 6

GUT CONTENTS OF *RIVULUS STELLIFER* AND *RACHOVIA MACULIPINNIS* FROM POOL IV.
%O = PERCENT FREQUENCY OF OCCURRENCE; \bar{N} = MEAN NUMBER PER GUT;
AND %D = PERCENT FREQUENCY OF DOMINANCE

Food item	9 Sept. 1979			<i>R. stellifer</i>			17 Aug. 1980		
	<i>R. stellifer</i>			<i>R. stellifer</i>			<i>R. maculipinnis</i>		
	%O	\bar{N}	%D	%O	\bar{N}	%D	%O	\bar{N}	%D
Number examined	15			10			38		
Number empty	7			0			2		
SL range (mm)	33-46			40-62			25-46		
Plant material									
Vascular material	12	nd	12	—	—	—	—	—	—
Algae	—	—	—	—	—	—	3	nd	—
Seeds	—	—	—	50	1.2	9	—	—	—
Nematoda	—	—	—	10	0.2	—	—	—	—
Annelida	12	0.1	—	—	—	—	3	tr	2
Crustacea									
Copepoda	—	—	—	50	1.3	—	17	6.6	5
Cladocera	—	—	—	20	0.8	—	36	33.5	5
Ostracoda	25	0.2	—	80	17.7	45	42	5.2	12
Aquatic insects									
Beetle larvae	—	—	—	10	0.1	—	8	0.1	2
Chironomid larvae	—	—	—	60	2.7	9	36	1.2	7
Mosquito larvae	—	—	—	—	—	—	3	0.1	—
Other**	—	—	—	80	1.4	9	36	1.4	7
Terrestrial insects									
Formicidae	25	0.2	—	30	0.5	—	33	0.5	5
Other	—	—	—	20	0.5	9	47	0.9	10
Unident insects*	—	—	—	60	1.8	9	67	2.8	30
Araneae	—	—	—	10	0.1	—	—	—	—
Gastropoda	—	—	—	40	0.4	—	8	—	2
Fish scales	50	nd	25	10	nd	—	6	nd	—
Debris	75	nd	62	50	nd	9	25	nd	10

* Insects or insect fragments of undetermined origin; tr = less than 0.1; nd = not determined.

If food resources are not limiting, then wide overlaps in diet can be expected. ZARET and RAND (1971), studying small fishes in a tropical stream in Panama, found high food overlaps during the wet season when food was abundant, but fish species began to specialize during low water when food resources were scarce. As suggested by ZARET and RAND, in order for the different species to survive during periods of intense food competition it becomes necessary for each to fall back on their individual feeding specializations. If distribution of diet fullness values indicates the amount of food available to annual fishes, then Pool III was not food limited in May. However, food may have been limiting in July because gut fullness of July *P. boignei* was significantly less (i.e., emptier) than that of May specimens. If so, the July switching of *P. boignei* to a

diet of almost exclusively terrestrial insects with complete absence of crustaceans (Table 5) follows the predictions of ZARET and RAND. The presence of numerous characins in Pool III at the time may have further increased competition for food.

On the other hand, a diet shift may simply indicate a species responding opportunistically to the most readily available prey at any given time (WIENS, 1977). KNÖPPEL (1970) analyzed gut contents of fishes from small Amazonian rainforest streams and suggested all were generalists. However, GOULDING (1980) pointed out that KNÖPPEL had not observed fishes taken over a long period of time. GOULDING conducted an extensive ecological study of medium and large fishes in the southern Amazon. He showed that even though a fish has anatomical specializa-

tions to more efficiently use a particular type of food, it is not necessarily "trophically straitjacketed". We think a main reason dietary differences were not always evident between syntopic annual species is that the habitat diversity of a temporary pool is relatively limited (TURNER, 1967). An annual fish pool is usually relatively small and shallow. Thus, for example, an annual fish, specialized for surface feeding, might easily make the short dive necessary to feed on benthic organism in a shallow pond, whereas a similarly specialized nonannual species might not be able to reach the bottom in a deeper permanent habitat. Many annual pools are small enough that they might be smaller than the potential home range of even the small annual species.

What determines the species composition of a temporary pool is unclear. In general, it would seem that the type and diversity of the pool habitat strongly influence which annual species are present as well as their relative abundance. Thus, a temporary pool habitat composed primarily of shallow grassy areas would likely contain mostly *R. maculipinnis* while one with more open and deeper areas would favor *P. zonatus*. When species have the same needs then competition may be important. In theory, the degree or intensity of competition should be correlated with species similarity (JAEGER, 1974) and we found that those annual fishes occurring together were usually species showing the most difference in body form. Of course, as previously mentioned, such things as behavior, diet, and spatial utilization are related to body form. The most similar and closely related Orinoco Basin annual species are *P. hoignei* and *P. zonatus* (THOMERSON, 1974). The two have never been found together although they often occur in close proximity (THOMERSON, 1974; our observations) which THOMERSON felt argues for competitive exclusion. Both are surface-dwelling species with allochthonous insects a main part of their diet. Although they are very similar, it may be just that *P. zonatus* and *P. hoignei* have different habitat requirements. *P. zonatus* is usually restricted to rather open savannah pools (e.g., Pools I and II) and *P. hoignei* to forest pools (e.g., Pools III and IV) (THOMERSON, 1974; TAPHORN and THOMERSON, 1975; personal observations). TAPHORN and THOMERSON (1975) found that *P. hoignei* would not spawn in a brightly lit aquarium, but *P. zonatus* readily spawned regardless of light intensity. Pooling of collections from various localities suggests the species may also have different sex ratios (Table 7). Although more data are needed, annual species associations probably indicate different habitat needs. *T. dolichopterus* is commonly associated with *P. hoignei* (TAPHORN and THOMERSON, 1975), and rarely occurs with *P. zonatus*. In contrast *A. transilis* is not known to be syntopic with *P. hoignei*, but in pools where it is found, *P. zonatus* is also usually taken.

T. dolichopterus and *A. transilis* were not found together during collecting visits to various sites throughout Portuguesa and Barinas, but the two do

occasionally occur syntopically (TAPHORN and THOMERSON, 1975). Both are midwater species that were found to feed primarily on small crustaceans (Tables 3, 4, and 5). Because *A. transilis* is larger and able to feed on a wider range of food items, it is thus ecologically segregated from *T. dolichopterus*.

Our categorization of *R. stellifer* and *R. maculipinnis* as generalized feeders and edge species is interesting because the former is the rarest and most restricted, and the latter is the most widespread and abundant, Orinoco Basin annual species. Whether *R. maculipinnis* somehow restricts the geographical distribution of *R. stellifer* is not known. In all pools where *R. stellifer* occurs, *R. maculipinnis* is also found.

Concentration of *R. maculipinnis* along the shallow edges of temporary pools is well documented (THOMERSON and TURNER, 1973; TAPHORN and THOMERSON, 1975; L. HOIGNE, pers. comm., 1966) and we have observed it many times. On the other hand, *A. transilis*, *T. dolichopterus*, *P. hoignei*, and *P. zonatus* are commonly associated with deeper areas. This, together with size differences between coexisting *R. maculipinnis* and one or more of the other four species (e.g., juvenile *P. zonatus* and *R. maculipinnis* of Pool I), suggests that they deposit their eggs in different area of the pool. Eggs of *P. zonatus*, *P. hoignei*, *A. transilis* and *T. dolichopterus* are probably laid in the deeper central sections of the pool the areas that flood first, and would thus be the first eggs to hatch and begin fry growth. *P. maculipinnis* eggs laid in very shallow sections of the pool the last areas to be inundated during the early wet season, would thus begin to hatch later than the other four species. Those four species probably have the longer growing and reproductive season, but *R. maculipinnis* is less likely to lose individuals to false rains which produce ephemeral pools which do not last long enough for the life cycle to be completed.

However, in the very shallow pools of Pool IV habitat, *R. stellifer* were much larger than *R. maculipinnis*. *R. stellifer* may have had a much faster growth rate there, although this was not the case in aquarium reared individuals (THOMERSON, pers. obs.).

The fact that *R. maculipinnis* is found throughout the llanos in most types of temporary pools appears to be related to a life history strategy which is highly opportunistic both in terms of feeding and habitat requirements. These characteristics, combined with the species apparent preference for shallow areas, and perhaps a seeking out of new areas, probably increases the likelihood of successful dispersal.

Why Do Annual Fishes Disappear?

Size distributions of single collections suggest that recruitment is confined to an initial burst of hatching near the start of the rainy season. Thus, peak annual fish populations occur early in the season. Series of fish collections made over the course of one or more rainy seasons from Pools I, II, and III show that annual fish populations may disap-

pear during the latter half of the rainy season when pools were at or near peak levels. Because this disappearance seems correlated with the seasonal influx of nonannual fishes, predation or competition from nonannuals may be a factor. The disappearance of annual fishes can be tied to dispersal or increased mortality rates. Mortality could result from low dissolved oxygen, high water temperatures, dessication, senescence, parasitism, predations, or starvation. These causes of fish death in temporary pools should intensify with onset of the dry season as pools shrink and stranded fish become more and more

concentrated. Evaporation of surface water ultimately kills all fishes that do not die otherwise. During the rainy season these factors are usually not important because pools are large and water levels high. However, exceptions do occur. Rainfall pattern in the llanos can vary dramatically between nearby localities even during the wet season (TAPHORN and THOMERSON, 1975). Certain pools, such as the extremely shallow habitats of *R. stellifer* (THOMERSON and TURNER, 1973; e.g., Pool IV), could dry up during the middle of the rainy season with just a slight drop in water level.

TABLE 7

CHARACTERISTICS OF ORINOCO RIVER BASIN ANNUAL FISHES BASED ON 1979-1981 COLLECTIONS FROM VARIOUS LOCALITIES IN THE VENEZUELAN STATES OF PORTUGUESA AND BARINAS

Species	Relative sizes	Principal habitat and microhabitat	Major food items	Sex ratio males : females
<i>Austrofundulus transilis</i>	medium	midwater; savannah pools?	small crustaceans, aquatic insects	(44:42) 1:1
<i>Terranatos dolichopterus</i>	small	midwater; forest pools?	small crustaceans	(7:14) 1:2
<i>Pterolebias boignei</i>	large	surface; forest pools	allochthonous insects, small crustaceans	(64:62) 1:1
<i>Pterolebias zonatus</i>	large	surface; savannah pools	allochthonous insects; juveniles eat small crustaceans and aquatic insects	(22:39) 1:1.8
<i>Rachovia maculipinnis</i>	medium	edge; most habitats	small crustaceans, aquatic insects, and allochthonous insects; juveniles eat small crustaceans	(100:104) 1:1
<i>Rivulus stellifer</i>	large	edge; very shallow forest pools	ostracods, probably generalist	(14:14) 1:1

With invasion of temporary pools by nonannual fishes during the height of the rainy season, the fish community changes from one composed only of annual fishes to one increasingly dominated by characoids. In a similar situation in Florida marsh areas, KUSHLAN (1976) concluded that movement of piscivores into the areas during high water periods and subsequent predation were responsible for observed changes in community structure. We believe, but cannot demonstrate, that predation by nonannual fishes caused declines in numbers of annual fishes in Pools, I, II, and III. Apparent absence of large piscivores probably is a reflection of collecting methods used. Methods for annual fishes

are not very efficient in sampling larger fishes. Perhaps the clearest evidence for predation by nonannual fishes was from Pool III: In May the pool was isolated and *P. boignei* were in good condition. By July nonannual fishes were present and *P. boignei* had badly damaged fins. Annual fishes had disappeared, but nonannual fishes were more abundant, by August.

Although predation on annual fishes by nonannuals is probably common, the only documentation in the llanos is a report of the digested remains of a cyprinodont found in the stomach of the piranha, *Pygocentrus notatus* (NICO and TAPHORN, in prep.).

Because annual fishes are in breeding condition continuously after reaching maturity, their coloration and attention-getting spawning behavior make them highly visible to predators. *Notobranchius guentheri*, an African annual fish, inhabits pools which receive few, in any, nonannual species, however, HAAS (1969) found that fish placed in a pool where wading birds were later introduced were easy prey to the birds. He also discovered that males were selectively taken over the less visible females, causing a significant change over time in sex ratio. Wading birds probably prey on a large number of adult Orinoco Basin annual fishes and probably feed most effectively in open shallow areas. The shallow areas inhabited by *R. maculipinnis* and *R. stellifer* probably provide protection from piscivores, and avoidance of large nonannual fish may explain why *R. maculipinnis* were still found in Pools I and II after other annual species had disappeared in 1980. However, they may be more vulnerable to predation by wading birds.

Gut fullness distribution of Pool IV fishes, the types of items eaten (Table 6), and the absence of piscivores suggest that this population was food limited. Although no specimens were emaciated, it seems likely that they could have starved before the rainy season ended. In pools which receive large numbers of nonannual species food shortages may also occur.

At one site in the Maracaibo Basin in Venezuela, THOMERSON (1969) found many emaciated *Austrofundulus limnaeus* including dead and dying specimens. It was obvious that the habitat was food-limited because some of these fish quickly recovered when placed in aquaria and fed.

The Maracaibo Basin has a different, although closely related, annual fish fauna from that of the Orinoco Basin. In contrast to the Orinoco, the region is more arid and its temporary pools often remain isolated from permanent water. When nonannual fishes do gain access they are usually small and few in number. Rarely do large piscivores invade the habitat. Thus, such pools are probably food-limited rather than predato-limited and their fishes usually die by starvation or dessication.

Orinoco annual fishes are able to maintain permanent populations in pools invaded by predaceous nonannual fishes. HAAS (1969) even suggested that predation might actually benefit *N. guentheri* populations by effectively reducing competition for limited resources. However, the distribution of annual fishes in the Orinoco is often spotty even though seemingly suitable temporary pool habitat is widespread. It may be that competition and predation by nonannual fishes excludes annual species from these areas.

Because annual fish biotopes are rather poor in ecological diversity, syntopic associations of annual species are "worthy of intensive investigation" (TURNER, 1967). The Orinoco Basin situation is more complex than we had expected it to be. Perhaps

study of the apparently less complicated Maracaibo Basin annual fish communities would give clearer understanding of how annual fishes coexist.

In conclusion:

Spatial distribution, diet, body form and size of Orinoco Basin annual fish are correlated. Syntopic associations are usually combinations of the most different species.

There is, even so, considerable diet overlap because species have some flexibility in feeding habits. Thus, differences in spatial distribution within the pool are probably the most important factors in allowing coexistence of syntopes.

P. boignei and *P. zonatus* are surface-dwelling species which specialize somewhat on terrestrial insects. Although very similar, they have somewhat different ecological requirements. *P. zonatus* is more common in rather open savannah pools and *P. boignei* is restricted to forest pools. They are not known to occur syntopically.

T. dolichopterus and *A. transilis* are midwater species. The former specializes on small crustaceans, and the latter preys heavily on both small crustaceans and aquatic insects. They were not found together during this study, but do occasionally occur syntopically.

R. maculipinnis is an edge species. Its high relative abundance is the result of a life history strategy which includes opportunistic food habits and broad habitat tolerance.

R. stellifer is an extreme edge species. It is uncommon and lives in very shallow forest pools where food is scarce. However, large nonannual fish do not enter these areas.

Parasite load tends to increase with age and often causes reduced fecundity and probably occasional death.

Nonannual species, primarily characoids, invade temporary pools during the height of the rainy season. During this period annual fish often disappear.

Because food usually seems abundant, pool water levels are still high, and annual fish are sometimes taken with badly damaged fins, it is thought they disappear because of competition or predation or both by nonannual fishes.

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