Rev. Biol. Trop., 41 (3): 791-809, 1993

Fish communities and environmental characteristics of a tropical rain forest river in Costa Rica

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(Rec. 27-XI-92. Acep. 6-VII-93)

Abstract: Fish communities associated with different habitats in the Río Puerto Viejo, Costa Rica, were sampled in 1962. Forty three fish species, representing 32 genera in 17 families is a fairly rich ichthyofauna for a river of moderate size in Middle America. The macroinvertebrate fauna is also diverse, although aquatic vegetation consisted mainly of filamentous algae. A comparison of physico-chemical characteristics of the habitats and their fish communities revealed numerous examples of habitat separation of similar species. Extreme habitats (springs, swamps and an oxbow backwater) provide refuges for a few species which tolerate high CO_2 and low dissolved O_2 concentrations. A detailed analysis of food habits revealed how each species in a given habitat was able to reduce niche overlap within the fish community. Fruit and leaf-eating habits are present, but not nearly as diversified as in the Amazon. Some fish species reproduce in all months; others intermittently with peak periods; and catadromous species migrate to the sea once a year. Pronounced seasonal within-river migrations, similar to those of the Amazon are not present, perhaps because of the lack of well-defined high and low water periods of long duration in the Puerto Viejo. It is hypothesized that short-term low water temperatures during flooding may cause adhesive egg laying species to postpone spawning and thus avoid destruction of eggs that might have been laid above low water level. Egg scatterers may be stimulated to spawn by the same low temperatures, thus increasing survival of eggs and young by making them less visible and providing more potential food particles suspended in the turbid flood waters.

Key words: Fish ecology, limnology, streams, tropical rainforest, Costa Rica.

Lowe-McConnell (1977), in her critique on the ecology of fishes in tropical waters, stated that "The biology of riverine fishes is governed by the seasonality of flooding following annual or biannual rains." In high latitudes seasonality is most often controlled by the temperature regime: freezing winters, spring spates and low water flows during the summer. Most Central American rivers are short in length and do not sustain flood condition for long periods between successive downpours. The Pacific slope of Costa Rica exhibits six months of drought from November to April alternating with a rainy season with about 4000 mm precipitation. The Atlantic versant receives up to 6000 mm rainfall spread over most of the year, usually with a brief dry season during March-April or September-October. The biology of the fishes under study here is governed by severe, *unpredictable* flooding at any time of the year.

The following study is based on field work carried out between January 1962 and January 1963. Analytical work was done shortly afterwards; data and preliminary results were set aside until I was requested by the Organization of Tropical Studies (O.T.S.) to contribute a summary of fish studies to include in their upcoming book on research from La Selva Research Station (Bawa *et al.* in press). The commitment provided the stimulus to elaborate

in more detail the relationships of the Puerto Viejo fishes with their environment in the present paper.

At the outset of the field work, considerable time was spent in learning to distinguish the different species, especially cichlids, during underwater observations. Two undescribed poeciliid fishes were discovered in the Río Puerto Viejo and numerous other new species throughout Costa Rica were found in 1962. Subsequent studies dealt mainly with the systematics of the freshwater fish fauna which have lead to considerable improvement in the biosystematics of the ichthyofauna as well as a more complete understanding of each species through observations made at other localities (Bussing 1987).

MATERIAL AND METHODS

Study area: The headwaters of the Río Puerto Viejo arise on the northeastern slopes of Volcán Cacho Negro and Volcán Barba. After flowing some 20 km, the Puerto Viejo joins the Río Sarapiquí a short distance upstream from the town of Puerto Viejo. Both rivers are about equal in size at their junction which lies at about 40 m elevation surrounded by a tropical rain forest biome.

The river bed consists principally of soft clay, but in swifter portions and further upstream it is composed of vast rocky stretches. The river bank is not as steep upstream and grassy shores are occasionally present. The average width of the river in the study area is 40 m, the average depth 2 m at low water. The river in general gives the appearance of flowing at a slow to moderate speed. However, speeds up to 0.5 m/sec are recorded in flat shallow stretches and are much greater in narrow rapids.

The principal study area (Fig. 1) comprised a sector of the Río Puerto Viejo extending from the house (now part of the Biological Station) at Finca La Selva to one kilometer upstream. The environment of the river segment studied is harsh, and flooding displaces species laterally into terrestrial vegetation and can drastically modify habitats in a matter of hours.

Methods: A series of selected habitats along a one kilometer segment of the Río Puerto Viejo were observed to determine microhabitats, species composition and feeding and other behavior of the fishes and other organisms. Other sites adjacent to the main river were added later. Temperature and water level measurements were taken daily with some exceptions. A maximum-minimum thermometer was placed below the lowest water level and another in a small weather station on a semi-cleared slope above the river. A water level of 0 was chosen as the level below the very conspicuous demarcation at which terrestrial plants do not grow. These measurements and water quality data for the main river were obtained at 0.5 m below the water surface in front of the stairs leading to the house at Finca La Selva.

Dissolved oxygen, free carbon dioxide, alkalinity (methyl orange) and chloride were determined using standard methods (APHA 1955). A colorometric test for hardness was used (Golterman 1969). Hydrogen ion concentration was determined to the nearest 0.1 pH using a Helige comparator. Current velocity was measured with a Gurley No. 625 Pygmy Current Meter.

Since a Secchi disk was usually visible on the bottom at the sample site, an improvised method was employed using two long Nessler tubes and a suspension of Fuller's Earth as a standard. Readings are in mm on a scale of 0 (clear) to 680 mm (very turbid). Secchi disk readings of 1.2 m are roughly equivalent to 130 mm using this method. Precipitation at Puerto Viejo during 1962 was furnished by Dr. Holdridge.

Quantitative and qualitative plankton samples were taken once a month at the sampling site with a 15 cm fine mesh net at a depth 0.5 m below the surface of the main river.

Quantitative and qualitative invertebrate samples from all observation sites were taken using a Surber Sampler, being careful to brush all rocks from the one ft. sample area. In deeper water a 0.5 mm mesh dip net was drug over the substrate for qualitative samples. All specimens are deposited in the Natural History Museum of Los Angeles County (LACM).

Higher vegetation was exceedingly scarce at all study sites. Samples were scraped from rocks or retrieved by hand.

Fish collections and underwater observations were made to inventory fish communities and study behavior at selected sites. Collections were made primarily with 10 or 30 foot seines; rotenone was used in semi-isolated

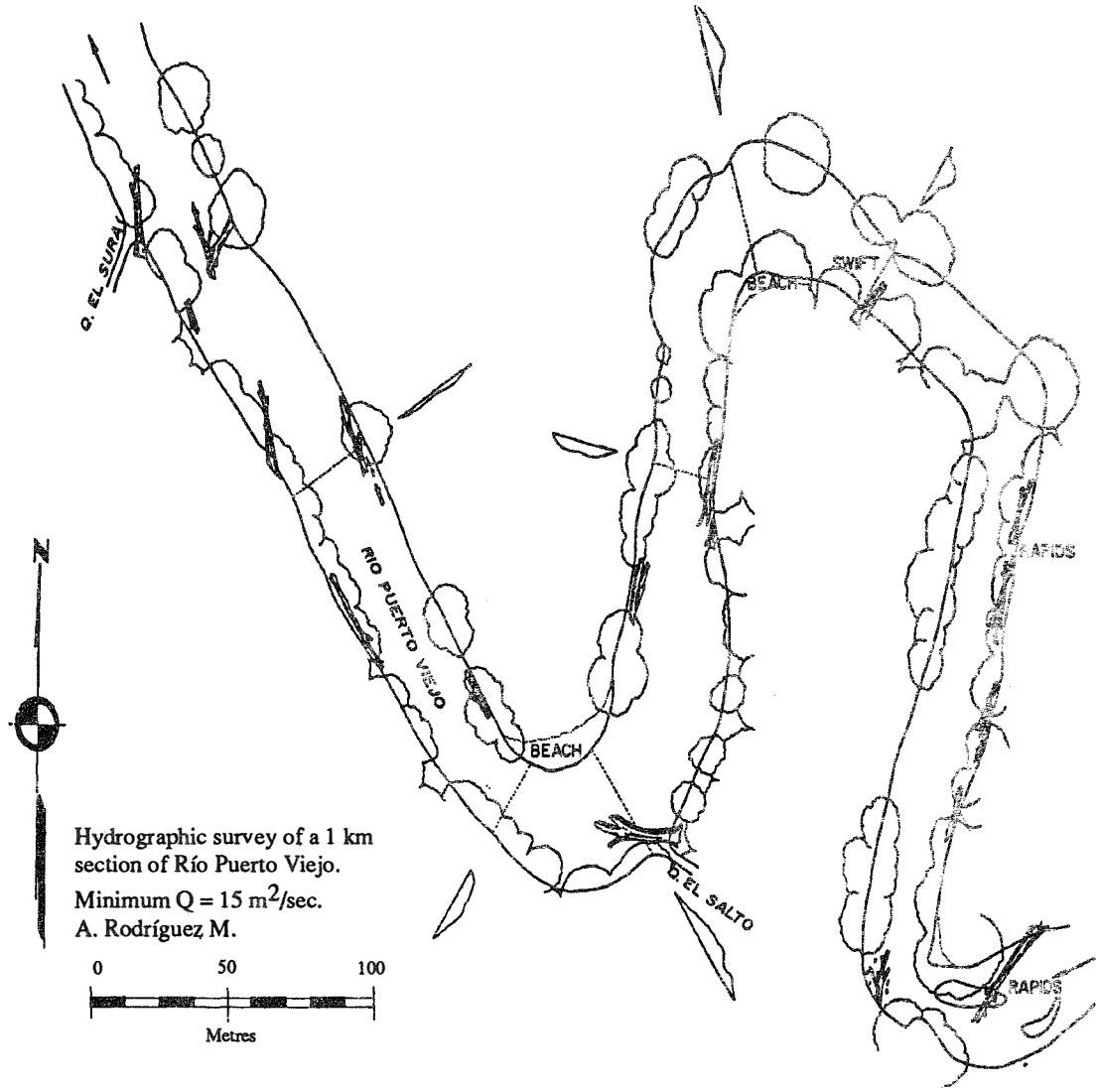

Fig. 1. A one kilometer stretch of Río Puerto Viejo to show bottom relief of principal study sites and the extent of canopy coverage on the river.

pools outside of the study areas. Valuable specimens of certain larger species were collected with spear gun, fishing gear and cast net. Observations were made by diving or lying in shallow pools with face mask and snorkel. Additional behavior notes were taken while sitting on shore.

Quantitative analysis of gut contents was made by estimating to the nearest 5% the relative percentage of each food item present in an individual fish. Gut length/standard length (GL/SL) quotients were derived in order to relate this ratio with food habits of each species. All fish specimens are deposited in the LACM.

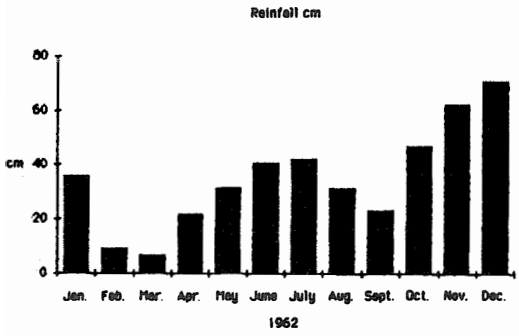

Fig. 2. Monthly rainfall in cm at Finca La Selva during 1962.

Physico-chemical features

Moderate temperature variations followed a seasonal regime, not unexpected at a lowland locality near 10° N latitude. Annual variation of air temperatures was 14° C; the mean annual temperature based on bimonthly averages was 24.8° C during 1962. The lowest temperature, 17° C, was recorded on 12 February; the maximum, 31° C was reached during the periods 1 - 5, 14 and 15 - 18 June. Daily fluctuations of 6 - 10° C were typical.

Río Puerto Viejo: Water temperatures in the Puerto Viejo fluctuated less and always remained closer to the low rather than high air temperatures. The mean annual water temperature was 23° C ranging from 19.5° C in January to 26.0° C in June (Fig. 3a). Daily extremes varied from 0.5° C on 7 November to 5° C on 26 March, although daily variations of 2 - 3° C were most common.

Mean annual rainfall between 1958 and 1986 at La Selva was 394.5 cm. The yearly total for 1962 was somewhat greater, 422.16 cm, although the dry season of February-March (15.70 cm) and "veranillo" of September (23.14 cm) were well below normal (Fig. 2). This fortuitous situation provided a marked contrast to the months of January, November and December with excessively high rainfall -up to 71.12 cm in the month of December.

Rains commencing on the night of 5 November caused the river to rise +595 cm above normal (0 cm) at La Selva by the morning of 6 November (Fig. 3b). On 10 November the river reached +850 cm at the same reference site and this highest level of the year was not considered unusual (R. Chavarría, pers. comm.). Stout (1981) recorded a level of +12 m during flooding on the Puerto Viejo. The lowest water level recorded on the Puerto Viejo was -56 cm on 29 March.

Sudden changes in water level were the rule throughout the year. High water levels occurred even in the "dry" season after a rain, but the highest levels were noted in months of heavy and continuous rain when the soil was soaked and runoff heavy. Frequent afternoon and early evening rains caused about a 1 m rise in water level, which returned to near normal in the morning.

Stretches of deeper, smooth-flowing water reached speeds up to 50 cm/s. In riffles velocities of 150 cm/s were recorded. Burcham (1984) noted water velocities of 27 - 46 cm/s at several sites on Quebrada El Surá and Quebrada Sábalo. Stout (1981) recorded a maximum velocity on El Surá of 120 cm/s and estimated greater speeds for the Sábalo during spates.

Turbidity generally increased during flooding (Fig. 3c). The extended periods of low precipitation, and thus low water levels, February-March and September showed turbidity readings consistently below 200 mm and as low as 36 mm. The highest turbidity reading of 680 mm on 1 August coincides with a heavy downpour the previous night reflected in an increase in water level from -3 to +183 cm. Ordinary turbidity was due to soil and particulate organic matter being washed into the river from surrounding lands. Pasture lands discharged enormous loads of mud into the river during downpours. In 1962 the Puerto Viejo was always much clearer several km upstream from La Selva, since poor access at that time limited the amount of cultivated lands adjacent to the river. From August to October 1962 a gray turbidity was present in the Puerto Viejo even at very low water levels. The color was due to fine gray particles washing in from upstream which may have been caolinized clay, although the heavier sediment was very similar to the volcanic ash from Volcán Irazú which began falling on San José (capital of Costa Rica) in March 1963.

Dissolved oxygen levels varied from 5.9 to 8.3 mg/l (67.9-95.1 % saturation). There was little relationship between oxygen levels and water level or turbidity readings. However, a negative relationship was clear between oxygen and carbon dioxide levels which suggests a

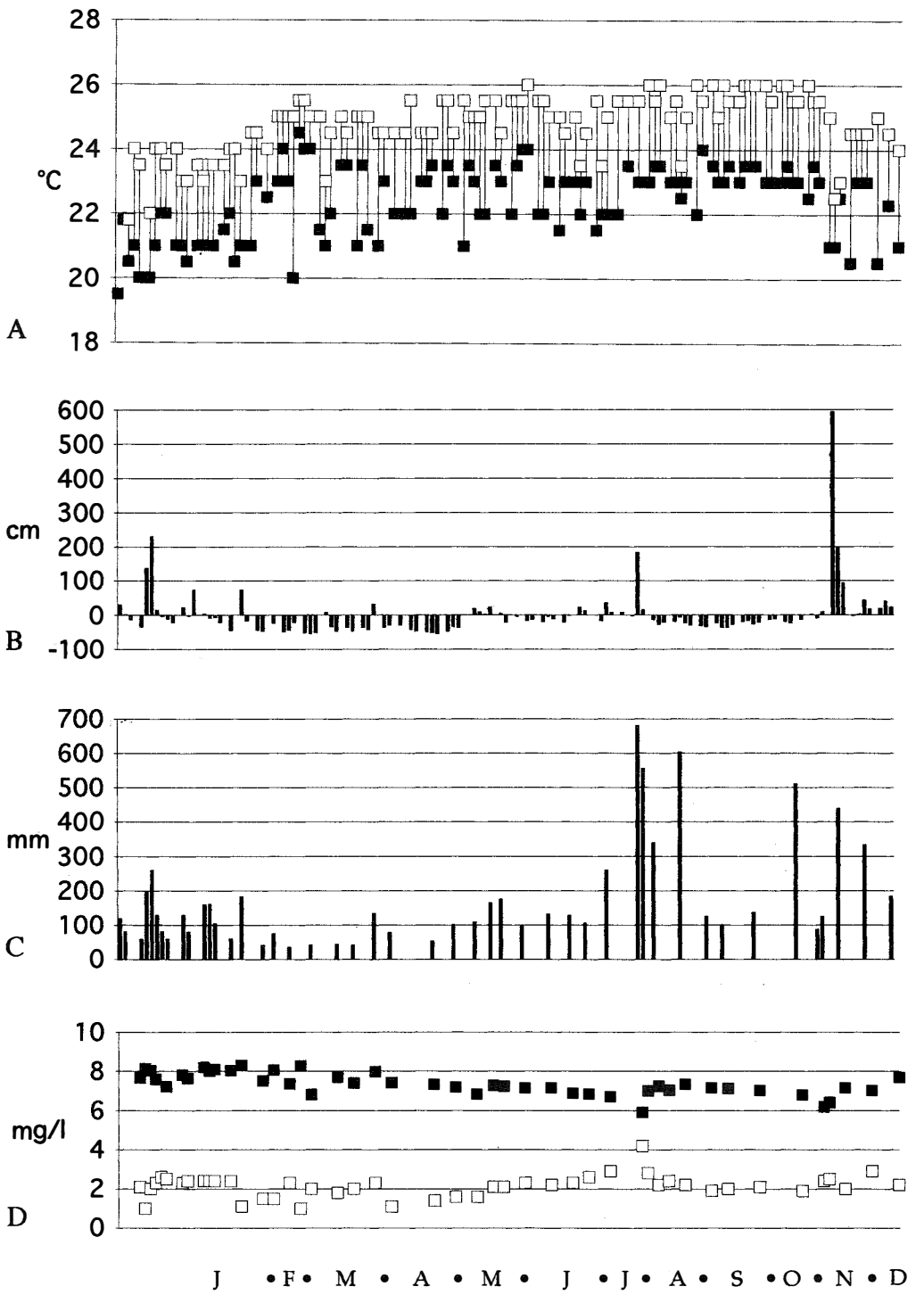

Fig. 3: a. Maximum and minimum water temperatures in °C of the Río Puerto Viejo at Finca La Selva during 1962; b. Water level fluctuations in cm of the Río Puerto Viejo during 1962. Zero level corresponds to the point where terrestrial vegetation ceases to grow; c. Relative turbidity (on a scale of 0 to 680 mm corresponding to clear to very turbid water respectively) of the Río Puerto Viejo during 1962; d. Dissolved oxygen (black squares) and free carbon dioxide (open squares) concentrations in the Río Puerto Viejo during 1962.

high Biological Oxygen Demand (B.O.D.) presumably due to considerable decomposition of suspended organic matter (Fig. 3).

Hydrogen ion concentration (pH) varied from 6.3 to 7.3 during the year. Sudden increases in acidity were typical during high waters, probably in part by the dilution by rainwater which lowered the buffer action of the already very soft river water. The slightly acid rainwater and very acid soils, and ground waters of the area (pH 6.7 and pH 4.0 - 4.5 respectively, McColl 1970) also contribute to this effect. Acid reserve pH values (sample agitated to remove CO_2) during high waters serve to reinforce this interpretation.

Free carbon dioxide levels in the Puerto Viejo were low, fluctuating between 1.0 and 4.2 mg/l, which is typical of moving water which permits gases to readily escape.

Total hardness varied between 8.0 and 48.0 mg/l in close agreement with bicarbonate values. Chloride levels ranged from 4.43 to 9.59 mg/l during the year and concentrations reflected the dilution of all solutes during high waters. Conductivity values during 17 - 28 November 1969 ranged from 15 - 52 µmhos cm^{-1}, the extremes relating to high and low rainfall, respectively, at La Selva (McColl 1970).

Other biotopes: Infrequent surveys were made of the physico-chemical composition of three tributaries of the Puerto Viejo (Quebradas El Surá, El Salto and Sábalo), a spring pool which drains to the Surá, and an oxbow backwater connected to the Puerto Viejo located about 6 km upriver from the house at La Selva. Burcham (1988) obtained considerable data for the Surà and Sábalo from January to May 1985.

The Sábalo was most similar to the Puerto Viejo, although temperatures in the shallow, highly insolated stream were higher (21° - 29°C). Both the Surá and Salto contained higher levels of dissolved substances than the main river (Fig. 4).

The waters of the oxbow backwater were sampled three times and exhibited very low O_2 levels (0.6 - 2.8 mg/l) and CO_2 (16.6 - 24.0 mg/l), bicarbonate alkalinity (80.0 - 115.8 mg/l $CaCO_3$), hardness (73.8 - 109.0 mg/l), turbidity (130 - 520 mm) and temperature (30°C) readings much higher than the main river (Fig. 5), although the backwater was freely connected with it.

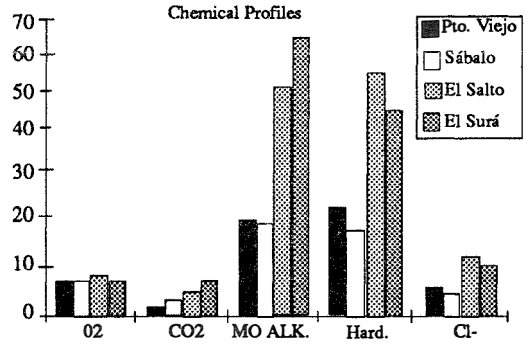

Fig. 4. Comparison of dissolved substances in the Río Puerto Viejo and three tributary streams on 6 June 1962.

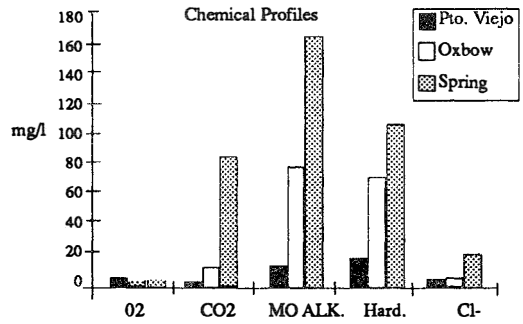

Fig. 5. Comparison of dissolved substances in the Río Puerto Viejo and an oxbow inlet of the Puerto Viejo on 14 June 1962; and on an isolated aquifert ributary to the Puerto Viejo on 4 January 1963.

The acid spring was sampled two times and was highly charged with CO_2 and low in O_2. On 25 October, after several days of little rainfall, CO_2 measured 66 mg/l and bicarbonate alkalinity 163 mg/l. During a rainy period on 4 January 1963 the CO_2 level was 90 mg/l, bicarbonate alkalinity 168 mg/l (Fig. 5), pH 6.0 and reserve pH 6.4.

Principal habitats

The Río Puerto Viejo in the vicinity of "Finca La Selva" includes several distinctive habitats, each with specific associations of fishes and other organisms. Five basic habitats are recognized in the main river: rapids and riffles, shallow shorelines, deep shorelines, beaches and pools (Table 1). An additional five habitats are found adjacent to the river: affluent streams, side channels, oxbow backwaters, springs and swamps (Table 2). Specific sites representing these habitats were visited consistently, others less frequently. Several study sites were even abandoned during the course of this study due

TABLE 1

Summary of principal characteristics of five habitats typical of the Río Puerto Viejo

	Rapids	Shallow shores	Deep shores	Beaches	Pools
Velocity (cm/s)	25 - 150	5 - 24	>10 (bottom) >15 (surface)	<5 - 10	<5
Depth (m)	0.1 - 1.3	0.3 - 1	3 - >4	0.3 - 1	>2 - 5
Substrate	gravel, rocks	clay, branches, logs, debris	clay, boulders	sand, silt leaf litter	logs, branches, leaf litter
Stability	stable	short term	stable	stable	mostly unstable
Vegetation	Podostemonacae mosses, fil. algae	fil. algae, mosses terrest. grases	fil. algae	none	fil. algae
Invertebrates	diverse	fair diversity	not abundant	fair diversity	diverse
Fish	a few specialists	very diverse	few species	fair diversity	very diverse

TABLE 2

Summary of principal characteristics of five habitats lying adjacent to the Río Puerto Viejo

	Affluents	Side channel	Oxbow backwater	Spring	Swamp
Velocity (cm/s)	27 - >120	<5	stagnant	<5	stagnant
Depth (m)	0.5 - 1.3	0.3 - 1.5	0.5	0.2	0.2 - 1
Substrate	sand, rock,	gravel, clay leaf litter	flocculant tree roots	leaf litter, detritus	detritus
Stability	scouring during spates	stable	stable	stable	dry season drying
Vegetation	algae scarce	fil. algae in shade	phytoplankton	none	*Spathiphyllum*
Invertebrates	fair diversity	no data	few species	no data	no data
Fish	diverse	very diverse	few species	*B. holdridgei* only	*B. holdridgei*, *Rivulus* only

to movement of bottom deposits and tree trunks. Fish associations noted as typical of each habitat include resident species, not those passing through the area. Certain species in the Puerto Viejo may occupy a certain habitat preferentially, although reside in different surroundings in other regions of the country (eg. *Neetroplus nematopus* is usually found in moderate current in this and other rivers, although it is also adapted to the lentic environment of Laguna Río Cuarto and Lake Nicaragua).

Biological features

The Río Puerto Viejo carries a high load of suspended matter, especially during, and for some time after, periods of heavy rainfall. This particulate matter consists mainly of non-living materials such as silt and detritus. The proportion of silt to detritus or tripton was as high as 4 : 1 during one flood period and as low as 1 : 9 in periods of low water. The remaining or living components of the suspended matter consisted primarily of diatoms with lesser numbers

of desmids and filamentous algae. Other items included in some quantitative and qualitative plankton samples were other algae, flagellates and a variety of insect larvae (Diptera, Odonata, Ephemeroptera), Collembola, Hydracarina, Nematoda, Tardigrada, Copepoda and larval characids. Quantitative values during the year ranged from 38.9 to 217.6 organisms per liter. Regardless of whether the dominant algal component is truly plankton or drifting sessile organisms, it is a constant feature during low or high water throughout the year and could provide a ready food source for filter-feeding organisms as well as fish fry.

Aquatic vegetation is not conspicuous in the Río Puerto Viejo. Submerged higher plants include *Marathrum oxycarpum* and *Tristicha trifaria* (Podostemonaceae) found encrusting rocks in swift water and *Eichhornia* sp. (Pontederiaceae) rooted in the stream bed of Quebrada El Salto.

Terrestrial mosses, *eg. Fissidens* sp. (Fissidentaceae) and liverworts (Lejeuneaceae) are present on logs along the shore and epiphytic on leaves which fall into the river. Filamentous algae is present on all rocks and logs where adhesion is possible. These algae and associated aufwuchs in conjunction with mud and silt which periodically cover it, often form thick mats on the substrate and, although inconspicuous, may be an important producer in this ecosystem. Terrestrial plants, especially grasses and tree roots are frequently submerged during rising water and form an important refuge for aquatic animals although they are not used as food by fishes. Terrestrial vegetation, *eg.* fruits, seeds, flowers and leaves (especially of the "chilamate" tree, *Ficus glabrata*) with their associated epiphytes will be shown to be of major importance in food chains involving fishes.

Rhizopods of the genus *Difflugia* were present in bottom sediments and formed an important constituent of the diet of some fishes. The most prominent invertebrates were aquatic insects. Ephemeroptera (Baetidae and Heptageniidae) and Diptera (Tendipedidae and Tipulidae) were found in nearly all habitats. There was a high diversity of dragonfly nymphs (Anisoptera) including a fossorial form (Gomphidae) found in loose sandy substrates. A hydropschid caddis fly larva was found capable of burrowing into soft clay rocks and banks. Another minute caddis fly larva (Hydroptilidae) spun small silken cases on hard rocks which were found to be worn or dissolved away leaving conspicuous grooves. Adults of common aquatic hemipteran and coleopteran families were restricted to slack or stagnant water. Other Orders include Megaloptera, Neuoptera and Lepidoptera (Pyralididae). Decapods (Atyidae, Palaemonidae and Potamonidae) were common under rocks or in vegetation. Gastropods (Ancylidae, Physidae and Pilidae) were uncommon in the soft waters of the area. Planarians, oligochaetes, leeches and copepods were present in small numbers in samples from slow moving currents.

Other than fish, vertebrates are not conspicuous in the river. Turtles are frequently visible sunning themselves on logs. A large caiman was a frequent visitor to a stagnant oxbow backwater habitat. Snakes and frogs were seldom encountered. Otters are seen occasionally during the drier months from March to May (P. Paaby pers. comm.).

The fishes

This section provides, for each fish species occurring in the Puerto Viejo study areas, specific information concerning: microhabitat, trophic level and reproductive habits. Characteristics of young and adult stages are considered when possible. The three food categories labeled "other" may include either taxa not found in other columns or material unidentifiable to Order or other categories. Months are abbreviated by Roman numerals. Table 3 lists food habits of most Puerto Viejo fishes and Table 4 demonstrates their trophic relationships within the fish community. All lengths of fishes refer to standard length (SL).

CARCHARHINIDAE

Carcharhinus leucas "Shark, tiburón"

A shark was seen briefly at the surface close to a deep shoreline on July 31. Occasional sightings are reported by the locals each year. Carnivorous, eating mostly fish, some other vertebrates (Tuma 1976). Viviparous, breeding throughout the year principally in estuaries; parturition normally at river mouths (Jensen 1976).

MEGALOPIDAE

Tarpon atlanticus "Tarpon, sábalo real"

The tarpon is a coastal fish frequently found in Lake Nicaragua and all year in tributaries of the Río San Juan drainage. A few were seen in deep pools during the 1962 dry season; taken on hook and line or using dynamite wrapped in fish intestines (R. Chavarría pers. comm.). Piscivore, especially fond of schooling fishes. Ripe fish taken during II, III, IV from Panama Canal Zone (Hildebrand 1939).

CHARACIDAE

The majority of the fishes in the Río Puerto Viejo belong to three large familes: Characidae, Cyprinodontidae and Cichlidae. The characids or sardinas are mostly small schooling species, although *Brycon* reaches a weight of at least 2 kg. They usually have a well defined stomach, pyloric caecae and multicuspid teeth. Eggs are non-adhesive demersal type; characid larvae (7.8 individuals/l) were collected in plankton samples on 18 April. No parental care.

Astyanax fasciatus, "Tetra, sardina"

A generalist; schools, sometimes of hundreds in all habitats; browse on bottom, take midwater prey or surface insects. Consistently omnivorous, with high intake of moss, fruit and seeds. Ripe adults (smallest 44 mm) in V, VI, VII, IX, X, XI, XII. Ectoparasites common.

Bramocharax bransfordii "Tetra, sardina"

Uncommon. Solitary or schooling with *Astyanax*. Piscivorous, observed pursuing *B. parismina*, also eats characids and cichlids in addition to insects. Ingested leaves, seeds and fruit appeared undigested. A ripe male, 102 mm collected in April, but few samples taken. Ectoparasites common.

Brycon guatemalensis "Machaca"

Active schooling fish in strong to weak current. Adults gather by dozens below chilamate trees when figs ripen. Juveniles insectivorous (high occurrence of Hymenoptera); young adults omnivorous, mature adults eat fruits (mostly figs) and leaves. Four ripe males (276-350 mm) taken during XII, I, II. Terrestrial spawning near Panamanian streams was cited by Kramer (1978) for *Brycon petrosus*. Janet Burcham (pers. comm.) has noted a similar breeding behavior for *B. guatemalensis* in affluent streams of the Puerto Viejo.

Bryconamericus scleroparius "Tetra, sardina"

An active schooling fish at all levels of water column; almost exclusively a stream dweller. Consistently omnivorous, especially seeds and fruits. Ripe female (smallest, 63 mm) in VII, IX, but few collections.

Carlana eigenmanni "Tetra, sardina"

Uncommon. Small groups in stagnant side channels and oxbow backwaters. Herbivore specializing in cropping several types of filamentous algae. Indefinite stomach, but pyloric caecae present. Ripe specimens (smallest ripe female 37 mm) in all months sampled, IV, VII, IX, XII.

Hyphessobrycon tortuguerae "Tetra, sardina"

Rare, collected only once (IV). A small midwater species collected once in Quebrada Sábalo in moderate current. Eats small aquatic insects. Gut length/SL ratio 0.4. No ripe specimens.

Roeboides guatemalensis "Tetra, sardina"

Uncommon. Small groups maintain position in slow currents at mid-depth or near bottom, head down; often tilting on sides and drifting like leaves for short distances. Insectivore and dislodges and eats large numbers of characin and cichlid scales. Entirely lepidophagous in other regions. Ripe females (smallest 58 mm) in VII, IX, XII.

GYMNOTIDAE

Gymnotus sp. "Knifefish, madre de barbudo"

Rare. Benthic, under leaf litter in standing water. Nocturnal unselective insectivore ingesting considerable detritus and silt. An unripe pair collected in IV.

PIMELODIDAE

Rhamdia guatemalensis "Catfish, barbudo"

Benthic. Cryptic by day, active at night. One specimen taken in Quebrada Sábalo.

Rhamdia nicaraguensis "Catfish, barbudo"
Benthic, in recesses of overhanging banks or between roots. Nocturnal insectivore also eating shrimp, snails and fish. Unripe specimens in VI, IX, X, XII.

Rhamdia rogersi "Catfish, barbudo"
Benthic; juveniles found in riffles. Nocturnally active insectivore which also ingests seeds and other vegetable matter. A pair of ripe individuals taken in IV.

GOBIESOCIDAE

Gobiesox nudus "Clingfish, chupapiedra"
Rare. Below rocks in swift water. Eats aquatic insects. Ripe male, 55 mm, in II.

RIVULIDAE

Rivulus isthmensis "Olomina"
Rare in main river, but typical of shallow swamps and potholes where dominant. Eats aquatic insects. Gut length/SL ratio 0.4.

CYPRINODONTIDAE

Another well represented family, the viviparous tooth carps or olominas, are all small (<100 mm); anal fin of males modified into intromittent organ (gonopodium). Simple digestive tract, no distinct stomach nor pyloric caecae; teeth conical or spatulate. Viviparous, producing large broods periodically or few fry daily.

Alfaro cultratus "Olomina"
A swift fish, solitary, or mostly in groups of 5-10. In moderate current, 15 cm below water surface, of streams or in slack water, close inshore area of main river. Feeds mainly on terrestrial insects, frequently taking fallen insects at surface. Young in same habitats, but eat more aquatic and terrestrial Diptera and less Coleoptera and Hymenoptera. Gravid females (smallest 33 mm) in all months sampled (II, IV, V, VII, IX, X, XI, XII).

Brachyrhaphis holdridgei "Olomina"
Rare in main river; few individuals in oxbow backwater and swamps; principal population in spring pool where it dominates. Near-surface insectivore feeding mainly on terrestrial Coleoptera, Diptera and Hymenoptera. Gravid females (smallest 19 mm) present in both large samples made (I, X).

Brachyrhaphis parismina "Olomina"
Most conspicuous, current-loving fish along shorelines of main river; uncommon in streams. Occurs in aggregates of 20-30 members, but forms schools of 50 or more when pursued. Active near surface, darting after terrestrial insects. Young closer to shore. Like its congener, eats mainly terrestrial Coleoptera, Diptera and Hymenoptera. Gravid females (smallest 26 mm) in all months sampled (I, II, IV, V, VII, IX, X, XI, XII); numerous eggs with advanced embryos.

Neoheterandria umbratilis "Olomina"
In groups of three or four, often one male and three females constantly browsing on bottom or logs and boulders. In low to moderate current velocity in streams and main river. Detritus, aufwuchs and silt eaters, also midge larvae, filamentous algae and diatoms. Gravid females (smallest 24 mm) during I, IV, V, IX, X, XII, but not in large collections made in II, VII or XI.

Phallichthys amates "Olomina"
In groups up to 25, continually browsing on substrates near bottom. Usually in slack water of pools, side channels and backwaters of main river; also on bottom of streams. Almost exclusively a detritus, aufwuchs and silt eater; some filamentous algae. Gravid females (smallest 35 mm) in IV, V, VII, IX, X, XII. Fry born a few each day rather than large broods.

Phallichthys tico "Olomina"
Small schools on surface near grassy shoreline of oxbow backwater; otherwise strays collected in pools after flooding. Eats mainly aufwuchs, detritus and silt and in two samples, large quantities of a unicelluar alga. Few collections taken, but gravid females (smallest 15 mm) in IV, VI.

Poecilia gillii "Olomina"
In waters of low current velocity; small groups in pools, backwaters or side channels of main river. Large aggregations on exposed beaches, browsing on aufwuchs, silt and some filamentous algae and diatoms. In streams, common only in sun-lit portions providing abundant algal growth (Burcham 1984, 1988). Gravid females (smallest 35 mm) in I, IV, V, IX, X, XII; none in VII or XI. Developing eggs of two sizes.

Priapichthys annectens "Olomina"

Active in groups near surface in moderate current principally in streams. Scarce in main river. Insectivorous, specializing in Hymenoptera and Coleoptera; young eat mostly aquatic insects. Few samples taken, but gravid females in IV, IX.

ATHERINIDAE

Atherinella hubbsi "Silverside, sardina"

Active in groups or singly, usually at mid-depth, 20 cm below surface in mid-river. In moderate current velocity, offshore of main river over 0.5-1.0 m depths where it replaces most cyprinodontids. Darts after food throughout water column. Young closer inshore. Uncommon in streams. Eats very wide variety of aquatic insects, some Hymenoptera, filamentous algae and mosses. Ripe females (smallest 41 mm) in I, II, IV, V, VII, XII.

SYNGNATHIDAE

Pseudophallus mindii "Pipefish"

One specimen found in Quebrada El Surá on 9 September 1976 (Jean Stout, pers. comm,). Usually associated with aquatic vegetation or grasses in currents of moderate velocity. Eats aquatic insects.

SYNBRANCHIDAE

Synbranchus marmoratus "Swamp eel, anguila"

Uncommon. Burrows in mud or soft sand by day. Nocturnal forager of crustaceans and fish. Gut length/SL ratio 0.6.

CICHLIDAE

The cichlids, or mojarras, are the most diverse family in the region with 10 species occupying a variety of trophic niches. All are benthic. Small to moderate size, but the guapote, *Cichlasoma dovii* can reach nearly 50 cm in length and a weight of 12 lbs. A stomach, but no pyloric caecae. Jaw teeth conical, some enlarged canines; pharyngeal teeth for shredding. Pairs lay adhesive eggs (except *C. nicaraguense*) and defend fry.

Cichlasoma alfari "Mojarra"

Common in small groups along shorelines, in pools and side channels of main river and in streams. Takes large mouthfuls of bottom deposits, sifts and spits out unwanted material. Omnivorous, adults and young eat wide variety of aquatic insects, also seeds and detritus. Ripe females (smallest 91mm) in I, II, VII, VIII; not ripe in X, XII.

Cichlasoma dovii "Guapote"

Common. Individuals lurk under logs or pursue fish. Young slowly move downstream, repeatedly stopping against objects as if imitating drifting leaves. Along shorelines in shallow or deep water where cover permits; also in streams. Piscivorous at all ages; including shrimp and some larger insects in diet. Ripe females (smallest 104 mm) in II, IV, VII, IX; but not collected in all months.

Cichlasoma loisellei "Guapote amarillo"

Inhabits oxbow backwater in dense stands of grasses along shore; collected once in side channel when isolated at low water level. One adult taken, piscivorous; young mostly insectivorous, eat large variety of aquatic insects, some fish, terrestrial insects and leaves. Most specimens collected immature.

Cichlasoma nicaraguense "Moga"

Fairly common. Adults usually in pairs, young in groups browsing on substrates. In water of all depths along shorelines of main river and in streams. Adults consistently eat detritus or seeds if available. Young consume more aquatic insects and may or may not eat detritus. Ripe fish (smallest 42 mm) taken in I, II, III, IX, XII; adults not collected in all months.

Cichlasoma nigrofasciatum "Congo cichlid, mojarra"

Not common in this region. Typically in pools searching in series of short darting movements for specific food items on logs; also turning over leaves searching for food. Also seen under rocks in deep water in moderate to swift current velocity. Few in streams. Insectivore specializing in midge larvae and to lesser extent mayfly and damsefly nymphs; also ingests seeds, leaves and detritus. Ripe fish (smallest ripe female 35 mm) in IX, XII, but seldom collected.

Cichlasoma rostratum "Mojarra"

Seldom seen. Young observed searching for food over algae-covered logs along shore in moderate current. Adults in deeper water in

pairs. Insectivorous, but large quatitities of sand and detritus ingested; adults and young specialize in midge larvae, also mayfly nymphs, some seeds. A ripe male (185 mm) in II.

Cichlasoma septemfasciatum "Mojarra"

Adults and young common in all habitats, mainly in shallow water. Actively nipping at algae; frequently courting and defending nests and fry. Consistently eats equal parts vegetable matter (filamentous algae, moss, leaves, seeds), mayflies, midges and detritus. Ripe specimens (smallest ripe male 40 mm) in nearly all months sampled: I, IV, VII, IX, X, XII.

Cichlasoma tuba "Vieja"

Common, browsing in small groups along shore, at foot of rapids, close inshore on sand beaches with fry. Often seen with "chilamate" leaf protruding from mouth. Young between rocks in riffles. Adults herbivorous, eating (and digesting) "chilamate" leaves with epiphytic liverworts, mosses and fruits; also an occasional shrimp. Young insectivorous, eating aquatic insect larvae and nymphs. Groups of large males with nuchal humps seen frequently with numerous females in January. Batches of large eggs (200-400) guarded by both parents and placed in cavities in logs, under rocks or in holes in vertical banks. Newly hatched young attach to nest by nuchal adhesive organ. Ripe examples (smallest a 175 mm female) taken in I, II, VII, but few samples made.

Herotilapia multispinosa "Mojarra"

Seldom seen. Occurs in oxbow backwater and pairs seen occasionally in slack water along shorelines and in small pools. Detritus feeder; seen clipping filamentous algae with vigorous side-twisting movements; also leaves and some midge larvae. Seen browsing on logs and rocks. Only immatures collected.

Neetroplus nematopus "Moga"

Usually observed along shores of moderate depth and moderate current velocity; also in quiet pools, swift current and in streams. Constantly browsing on logs and rocks; only fish that feeds upside down on underside of logs and branches. Omnivore specializing in midge larvae, mayfly nymphs, filamentous algae and considerable detritus and silt. Pair seen in hole in vertical clay bank in breeding pattern; pairs fiercely defend fry against much larger fish. Ripe females (smallest 49 mm) in I, III, IV, VII, IX, XII.

MUGILIDAE

Agonostomus monticola "Mountain mullet, tepemechín"

A schooling fish, very active at all depths; most common in swift water along shores of moderate depth in main river. One adult had eaten shrimp; juveniles largely insectivorous on wide variety of aquatic insects, also Hymenoptera and Diptera; algae and moss appears undigested in gut. Small sample revealed no mature fish.

Joturus pichardi "Bobo"

Most common below and in riffles and rapids; also said to frequent large pools. Very active in swift water in schools scraping rocks with fleshy lips. Herbivore, eating filamentous algae, mosses and considerable detritus; also shrimps and some insects. Breeding cycle unconfirmed; adults said to leave Puerto Viejo at end of year and adults reappear with young in January or February; supposed to spawn in coastal waters or estuaries (R. Chararría pers. comm.). No ripe fish taken.

HAEMULIDAE

Pomadasys crocro "Grunt, roncador"

Uncommon. Large (40-50 mm) individuals seen moving slowly or lurking along log-strewn shorelines. Carnivorous; one specimen had eaten shrimp.

CENTROPOMIDAE

Centropomus undecimalis "Snook, robalo"

No specimens collected. Large snook (>1 m) observed in groups of two to four several times. Seen along shore maintaining position with respect to fallen logs; near surface. Known to be piscivorous.

ELEOTRIDAE

Gobiomorus dormitor "Sleeper, guavina"

Uncommon. Benthic, sedentary form taken in swift water over rocky bottom; also in pools and along shorelines in slow to moderate current. Carnivorous; one specimen ate only fish, two others ate shrimp. A ripe female (320 mm) taken in June.

GOBIIDAE

Awaous banana "Goby, guavina"

Benthic, found over sand substrates in slow to moderate current. In pools or sand beaches. Seen filtering sand through gill openings. Buries itself when startled. Omnivorous, mainly algae, midge larvae, *Difflugia*, detritus and sand. A ripe male (100 mm) in XII.

Sicydium altum "Goby, chupapiedra"

Benthic, found over rocky bottom in riffles; pelvic fins modified into sucking disc. Seen browsing on rock surfaces scraping algae and aufwuchs with close-set flattened teeth. Herbivorous; gut length/SL ratio 2.2.

To date, 43 fish species are confirmed for the study area representing 32 genera in 17 families. Another species, the "jurel" (jack) is reported for the region, but it is uncertain which species, or even genus of carangid is involved. Possibilities include: *Caranx latus* which was reported from Zent about 15 km from the sea and *Oligoplites* sp., which I have seen at El Castillo on the Río San Juan. On the basis of verbal account (Norman Scott, pers. comm.), an eleotrid, *Eleotris* sp., apparently occurs in the Puerto Viejo. Fishermen have reported "anguilas" from the Puerto Viejo and it is quite possible that the common eel, *Anguilla rostrata*, is found there. However, their reports usually refer to the swamp eel, *Synbranchus marmoratus*, a confirmed Puerto Viejo resident.

Other potential visitors to the area include freshwater species found in Lake Nicaragua and waters close to the Río San Juan, the gar, *Atractosteus tropicus* and several cichlids of the genus *Cichlasoma: centrarchus, citrinellum, longimanus* and *managuense*. Marine forms also found in Lake Nicaragua and effluents include: *Centropomus parallelus, Pomadasys boucardi, Diapterus plumieri* and *Pristis perotteti*.

DISCUSSION

Zoogeography: The Puerto Viejo fish fauna is situated in the San Juan Fish Province which extends on the Atlantic versant from the Río Prinzapolka in northern Nicaragua to the Golfo de los Mosquitos in western Panama. The San Juan ichthyofauna is principally composed of descendants of an ancient assemblage of fishes which penetrated Middle America during the Late Cretaceous or Paleocene from South America (Bussing 1976, 1985). At least 138 species are found in the freshwaters of the San Juan Province. Most of these occur in the San Juan watershed whose diversity of habitats ncludes the Great Lakes of Nicaragua and the Río San Juan whose tributaries drain the entire northern sector of Costa Rica. The Great Lakes proper contain about 54 species while many other species occur in running water or near the river delta. The 43 species known from the study area should be considered a diverse fish community for the Province, although in similar regions of the Amazon for example, many more species, often of the same genera, would be expected (Bussing in press).

Water quality effects: Seasonality and periodic extremes in water level provide stimuli which can permit fishes to adapt their reproductive cycles to the most favorable period. Even differences of a few degrees Celsius influence time of incubation of egg-laying species. Also short-term reduction of temperature during high water conditions could prevent spawning of adhesive egg layers such as cichlids from choosing sites which may be above water level a few hours or days later. On the other hand, the turbid water during flooding can be beneficial to egg scatterers such as characids; eggs and larvae are less visible and more suspended organic food material is available in the water column.

No truly "black water" acidic conditions occur in the study area as in the Río Negro (Goulding 1988). Aquarists have known for years that acid waters produced by leaching of soils and vegetation are necessary to induce spawning in a number of small fishes endemic to acid, mineral deficient waters. In the Puerto Viejo and adjacent habitats acid waters are due principally to the high CO_2 content of springs and stagnant waters. Fishes from these habitats breed freely in neutral or alkaline waters and are thus not restricted to extreme chemical conditions. The fact that very few species are found in such habitats in the Puerto Viejo region suggests that the combination of low pH, dissolved oxygen and high carbon dioxide content may be perjudicial to most species (Fig. 5). Thus, these habitats may serve as a refuge for those forms able to thrive in such conditions. Aside from

these extreme habitats, the water chemistry of the main river and affluents probably present no restrictions on the ichthyofauna.

Habitats: The Río Puerto Viejo can be considered a typical river of median size and moderate current velocity in the tropical rain forest biome of Central America. Because of the historical factors mentioned, the fish species diversity is neither as rich, for example as that of the Usumacinta drainage of Mexico and Guatemala, nor as depauperate as the Atlantic-slope drainages of Honduras, Nicaragua and Panama (Miller 1966, 1976). The considerable species diversity is due to the wide variety of riverine as well as the adjacent aquatic habitats. The fish biomass in the Puerto Viejo is considerably less however, than that found at lower elevations in the same drainage in smaller, sluggish streams of less gradient and with abundant cover such as floating grasses or aquatic plants.

Habitat separation between fish species in the region is considerable. Often distinct species of similar food habits occupy different habitats (cf. species accounts) and thus competition is reduced. Perhaps the region least exploited is mid-river where the current is swiftest. Occasional fish such as *Brycon* and *Agonostomus* are seen in midwater and larger cichlids amongst rocks on the bottom.

Most species are active during the day, others such as *Gymnotus* and *Synbranchus* and the species of *Rhamdia* are mostly nocturnal. Periodic fluctuations in water level throughout the year oblige most species to temporarily shift their habitats into flooded terrestrial shorelines. Although silting and severe alteration of habitats occur at this time, perhaps more beneficial results accrue in the form of additional food sources and space at the same time that considerable cover is provided by terrestrial vegetation. This brief, periodic flooding may occur nightly on the Puerto Viejo, sometimes rising 5 m at the sampling site, returning to normal the following morning. After several days of heavy rainfall over a vast area, the river can rise over 9 m as happened on 10 November 1962. Several days passed before the river reached a normal level after such a deluge. This severe, yet unpredictable phenomenon is totally different and probably less beneficial than the annual rainy season flooding of vast regions for months at a time as occurs in the Amazon basin (Goulding 1980).

Food habits: As seen in Tables 3 and 4, trophic specialization is considerable. The relationship between dietary habits and length of digestive tract of fishes is borne out in Table 4. Carnivores nearly always have a GL/SL ratio of less than 1, whereas herbivores and most omnivores and detritus feeders have a >1 ratio. A similar relationship exists between dentition and food habits. In general, browsers have numerous comb-like teeth; carnivores have enlarged, pointed teeth; and omnivores have conical teeth often in conjunction with rasping pharyngeal teeth.

If one were able to identify insects and algae found in stomach contents to the species level, considerably more specialization would be apparent. As mentioned earlier, even terrestrial insects which fall into the river are selected for by size, palatability or perhaps other features, before being eaten by fishes. On the other hand, many fish species in the Puerto Viejo are opportunists and eat what is available. *Atherinella hubbsi* is insectivorous in the Puerto Viejo, whereas the similar *A. chagresi* eats zooplankton in Lago Gatun, Panama (Zaret & Paine 1973). *Roeboides* is mainly insectivorous, eating few fish scales in the Puerto Viejo, whereas the same species is principally lepidophagous at other localities in Costa Rica and the rest of Central America as are its congeners in South America (Roberts 1972). Adult *Brycon* are principally herbivorous in the study area (Table 3), but predominantly piscivorous in Lago Arenal where it preys on schools of *Atherinella hubbsi* (J. Cabrera pers. comm.). Additionally, almost all fish species will devour fish fry if given the opportunity. Areas of the river where there is considerable tree overhang clearly provide more terrestrial insects and fruits than sections flowing through deforested regions and this is clearly reflected in the dietary differences of local fish communities.

Fishes of similar food habits often occupy different microhabitats which may reduce niche overlap. For example: three surface-dwelling insectivorous cyprinodontids inhabit entirely different habitats: *Brachyrhaphis parismina* in the main river, *B. holdridgei* in spring waters and *Priapichthys* in streams. Most of the cichlids which search for insects, also ingest considerable detritus and silt. Three insectivores such as *Cichlasoma alfari*, *C. nigrofasicatum* and *C. rostratum* may appear to share roughly

TABLE 3

Average percent volumes of food types and number of digestive tracts examined (n). Gut length/standard length (GL/SL) quotients included.

			Plants			Aquatic animals					Terrestrial animals					
SPECIES	n	GL/SL	algae	leaves	other	Ephe.	Odon.	Dipt.	other	fish	Coleo.	Hyme.	Dipt.	other	detrit.	silt
Astyanax	145	0.6	5	7	39	3	1	4	11	1	4	9	3	5	6	2
Bramocharax	18	0.4		1	10	5	<1	3	13	51	<1	5	4	4	2	1
Brycon (juv)	124	1		4	14	15	<1	5	11	<1	12	24	8	4	<1	<1
Brycon (adults)	5	2		40	60											
Bryconamericus	56	0.6	<1	8	45	1	<1	3	9	<1	9	11	4	6	1	<1
Carlana	25	1.2	82		<1	2		1	<1					<1	7	6
Roeboides	28	0.3		<1		35	7	15	20	20		<1	<1	2	<1	<1
Gymnotus	2	0.3				3		3	50						30	14
Rh. nicaraguensis	13	0.9	<1		3	3	3	28	37	10	<1		3	5	6	<1
Rh. rogersi	2	0.6			17				28			50		5		
Gobiesox	1	0.3				65		35								
Alfaro	94	0.9			<1	5	<1	4	19	1	10	34	12	6	7	1
Br. holdridgei	19	0.6			8	11	<1	3	9		13	18	10	28		
Br. parismina	99	0.6	<1		1	2	1	4	14	<1	13	33	23	6	<1	<1
Neoheterandria	89	2.6	6	<1	<1	2	<1	10	2			<1	<1		46	33
Ph. amates	79	4	6	<1	<1	<1		1	<1			<1			56	36
Ph. tico	23	2.2	<1		17	<1		2	<1						60	20
Poecilia	75	3.4	5	<1	<1	1		1	<1						55	37
Priapichthys	33	0.6				13		7	21		12	28	3	14	2	
Atherinella	71	0.5	6	<1	7	17	1	24	28		2	4	6	2	2	<1
Ci. alfari	64	1.3	<1	3	13	10	2	18	24	1	2	4	<1		15	6
Ci. dovii	70	0.8		1	1	9	3	<1	26	46	3	5	2	2		<1
Ci. loisellei (juv)	23	0.7		2	4	7	5	8	49	12	3	6	<1	4		
Ci. nicaraguense	82	2.6	4	3	14	13	2	19	14	<1	<1	1	<1	<1	20	9
Ci. nigrofasciatum	22	1.1	1	5	10	15	10	25	6	5	4	<1	<1		15	2
Ci. rostratum	33	0.9	1		4	13	<1	34	8		<1	2	1		14	20
Ci. septemfasciatum	86	1.8	10	8	15	11	2	10	11	1	<1	1		<1	26	5
Ci. tuba	33	1.9		35	58			1	4		<1				1	<1
Herotilapia	17	3.5	6	3				1	1						48	41
Neetroplus	34	2.6	21		1	14		24		2			<1		21	16
Agonostomus (juv)	23	0.6	7		4	25	10	23	26	<1		3		<1		<1
Joturus	18	5.2	51	3	19	<1		4	<1						17	6
Pomadasys	1	0.6								100						
Gobiomorus	3	0.6		2					65	33						
Awaous	7	0.8	14	2	<1	2		33	23	3		<1			9	13

the same food niche as seen in Table 4, however it was noted that often different species of insects were taken by these different cichlids, indicating a different microhabitat or manner of feeding.

Terrestrial insects are selected for by size and species by the various species of insectivorous fishes. *Astyanax* for example, were seen to seize, but immediately reject certain ants which were engulfed without hesitation by *B. parismina*.

Four cyprinodontids and one cichlid, *Herotilapia*, eat predominately particulate matter which has settled on logs, rocks, fallen leaves and other substrates. From half to three-quarters of this material is detritus and the remainder sand or silt. It is known that these latter inorganic sediments also may harbor significant quantities of bacteria which may be of some nutritional value to these constantly-browsing species. The four cyprinodontids occupy rather different habitats: *Phallichthys ti-*

TABLE 4

Trophic relationships of the Puerto Viejo fish community. Gut length/standard length quotients are included in parentheses

HERBIVORES (70-100% vegetable matter)

Algae eaters (51-82% algae)

Carlana (1.2)
Joturus (5.2)
Sicydium (2.7)

Macrophyte eaters (93-100% plants)

Brycon (2.0)
Ci. tuba (1.9)

CARNIVORES (85-100% animal matter)

Predators - piscivores (46-100% fish)

Carcharhinus
Tarpon
Bramocharax (0.4)
Ci. dovii (0.8)
Pomadasys (0.6)
Centropomus

Predators - generalized (100% fish, invert.)

Synbranchus (0.6)
Agonostomus (0.6)
Gobiomorus (0.6)
Ci. loisellei (0.7)

Insectivores - terrestrial insects (55-75%)

Rh. rogersi (0.6)
Alfaro (0.9)
Br. holdridgei (0.6)
Br. parismina (0.6)
Priapichthys (0.6)

Insectivores - aquatic insects (55-100%)

Hyphessobrycon (0.4)
Gymnotus (0.3)
Rh. nicaraguensis (0.9)
Gobiesox (0.3)
Rivulus (0.4)
Atherinella (0.5)

Pseudophallus
Ci. alfari (1.3)
Ci. nigrofasiatum (1.1)
Ci. rostratum (0.9)
Awaous (0.8)

OMNIVORES

Equal plant : animal matter

Astyanax (0.6)
Bryconamericus (0.6)

Equal plant : animal : detritus

Ci. nicaraguense (2.6)
Ci. septemfasciatum (1.8)
Neetroplus (2.6)

DETRITUS/SEDIMENT FEEDERS (79-92% particulate matter)

Neoheterandria (2.6)
Ph. amates (4.0)
Ph. tico (2.2)

Poecilia (3.4)
Herotilapia (3.5)

LEPIDOPHAGE

Roeboides (0.3)

co in the oxbow backwater, *P. amates* in slack water in the main river, *Poecilia* on shallow insolated beaches in the Puerto Viejo and Sábalo and *Neoheterandria* along shallow shores of the Puerto Viejo in moderate current.

Reproduction: Data on reproductive seasons is incomplete for all but the commonest species, but it is evident that at any given time of the year a large number of species are reproducing in the Puerto Viejo. Ripe individuals of *Astyanax* were taken from May to December, but not during the driest period of January through April. Some ripe *Brycon* and *Carlana* were collected throughout the year during both wet and dry seasons, but it is not clear if reproduction is intermittent or continuous. Sufficient data is unavailable for other characids.

Cyprinodontids reproduce during most of the year; individuals of most species produce large broods at well-separated intervals. Gravid specimens of *Alfaro* and *Brachyrhaphis parismina* were found during the entire year; gravid *Phallichthys amates* in slack water of the main river; *Poecilia* on shallow insolated beaches and *Neoheterandria* along shallow shores in moderate current.

Two species of cichlids, *Cichlasoma dovii* and *C. tuba* breed during most months of the year, although they appear to avoid the rainiest months from October to December. Ripe specimens of *C. septemfasciatum* and *Neetroplus* were collected throughout the year, although not in every month. Spawning activity in *C. alfari* occurs during two peaks, January-March and July-August, periods of lower than average rainfall. Insufficient data is available for other cichlid species. Silversides of the genus *Atherinella* were in breeding condition throughout the year, although not in all months.

The unpredictable and short-term nature of flooding on the Puerto Viejo is quite different from the steady rising and falling of rivers in the Amazon basin (Goulding 1980). This may account for the lack of seasonal spawning migrations so typical of Amazonian rivers. Additional discussion of Puerto Viejo fishes can be found in Bussing (in press).

ACKNOWLEDGEMENTS

This study would not have been possible without the generous offer of their home at "La Selva" and continuous advice of Leslie R. Holdridge and Lydia Holdridge. Precipitation at Finca La Selva during 1962 was furnished by L. Holdridge. At their direction, their foreman, Rafael Chavarría S., collaborated by transporting me to and from the finca and on numerous fishing trips upriver; a keen observer, Rafael also furnished a great deal of information on the natural history of local fishes.

Jay M. Savage, then of the University of Southern California, suggested that I apply for an Inter-American Cultural Convention (IACC) Scholarship to study Costa Rican fishes. The scholarship provided jointly by the Costa Rican Government and the U.S. State Department enabled me to spend the year in the field. Laboratory space was provided by the University of Costa Rica.

Robert J. Lavenberg of the Natural History Musem of Los Angeles County (LACM) provided free access to their fish collections and library; Fred Truxal (LACM) kindly identified the aquatic insects. Three anonymous reviewers greatly improved a draft of this manuscript.

I am grateful to the following for assisting in the collection of data and specimens, Lydia, Leslie and Elliot Holdridge, J. Robert Hunter, Salvador Jiménez C., my wife Myrna I. López S., Alexis Obando, John R. Paxton, Carlos Roldán and members of my 1962 ichthyology class at the University of Costa Rica.

RESUMEN

Este estudio se realizó en 1962 para determinar las relaciones entre una comunidad bastante diversa de peces en sus ambientes bióticos y abióticos. Los cuarenta y tres especies de peces pertenecientes a 32 géneros en 17 familias representan una ictiofauna bastante rica para un río de tamaño moderado en Mesoamérica. La fauna de macroinvertebrados también es diversa, mientras la vegetación acuática la constituyen principalmente algas filamentosas. Una comparación físico-química de los biótopos y sus respectivas comunidades de peces, demostró varios ejemplos de separación de hábitats

entre especies parecidas. Los biótopos extremos (manantiales, pantanos y una entrada estancada), sirven de refugios para las pocas especies que toleran altas concentraciones de CO_2 y bajas concentraciones de O_2. Un análisis detallado de las hábitos alimenticios demostró cómo cada especie logra reducir el traslape del nicho. El comportamiento alimenticio de algunos peces que comen frutos y hojas es mucho más restringido aquí que en el Amazonas, donde tanto la diversidad de peces como de alimento es mayor. Los ciclos reproductivos varían desde reproducción continua, intermitente (a veces con picos), hasta especies catádromas que migran al mar una vez al año. Las migraciones dentro del río, tan conspicuas en la cuenca del Amazonas, no se notan en el río Puerto Viejo debido a la falta de estaciones de larga duración que determinen niveles del agua altos y bajos bien definidos. Se propone que las bajas temperaturas durante las inundaciones, son las responsables para la postergación de la puesta de huevos adhesivos de ciertos peces, lo que evita su destrucción al quedar expuestos al aire cuando bajan las aguas. En cambio los peces ovíparos con huevos demersales o pelágicos posiblemente se estimulan a reproducirse con la baja temperatura, lo que aumentaría la supervivencia de huevos y larvas al ser menos visibles y tener más alimento suspendido en las aguas turbias.

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