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Fish communities and environmental characteristics of two lowland streams in Costa Rica

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Abstract: Fish community structure was studied in a forested stream and a stream surrounded by pasture in the Atlantic lowlands of Costa Rica during the dry season from January to May, 1985. Fishes were assigned to 6 consumer guilds (omnivore, terrestrial insectivore, terrestrial herbivore, algivore, carnivore, diatom specialist) based on the primary food in the diet. Selected physical and chemical measurements were made to identify differences in the two stream environments that may influence the type of food base.

The overall trophic structure of the fish communities did not differ greatly (similarity index = 0.40, AIDN analysis), but the largest proportion of each community belonged to only one guild. The greatest abundance of species in the forest stream were terrestrial insectivores while the greatest abundance in the pasture stream were diatom specialists. Higher maximum temperatures and greater abundances of invertebrates and periphyton were observed in the pasture stream. Substrate type differed between the two streams and may interact with light levels to influence the type of food resources.

The effects of removal of riparian vegetation on aquatic systems and fish communities have been studied extensively in temperate areas (Chapman 1965, Gunderson 1968, Moring and Lantz 1975, Karr and Schlosser 1978, Gorman and Karr 1978, Murphy *et al.* 1981). Little work has been done, however, to assess the differences between streams with intact or altered riparian zones in tropical areas.

Overall habitat diversity in the form of undercut banks, instream debris, and overhanging brush decreases as a result of removal of riparian vegetation and subsequent streambank erosion (Gunderson 1968, Meehan and Platts 1978, Chapman and Knudsen 1980). Adequate cover may limit the numbers of larger fish more than the numbers of smaller fish that a stream can support (Gunderson 1968). Secretive, nocturnal species are also strongly dependent on instream cover as resting places during the day (Power 1983). The amount and quality of cover may play an even more important role in the tropics in the distribution and abundance of fish. During the dry season, streams are low and fishes are more vulnerable to predation (Power 1983, Angermeier and Karr 1983). Even if banks are stabilized, changes in the physical and chemical nature of the water can be expected when riparian vegetation is removed.

Land use practices such as logging (Moring 1975) or conversion of forest to pasture for livestock grazing (Gunderson 1968) reduce or eliminate completely the natural riparian vegetation along streams. Removal of riparian vegetation has been found to increase stream sediment loads, maximum water temperatures, solar radiation, periphyton primary production and nutrient input and reduce habitat diversity and allochthonous input (Moring 1975, Ringler and Hall 1975, Brown and Krygier 1970, 1971, Likens *et al.* 1970, Webster *et al.* 1983). Excessive sediment loads directly cause mortality of fish eggs and larvae through suffocation (Phillips *et al.* 1975), increase turbidity and reduce benthic diversity (Newbold *et al.* 1980) by covering substrates suitable for algal attachment (Power

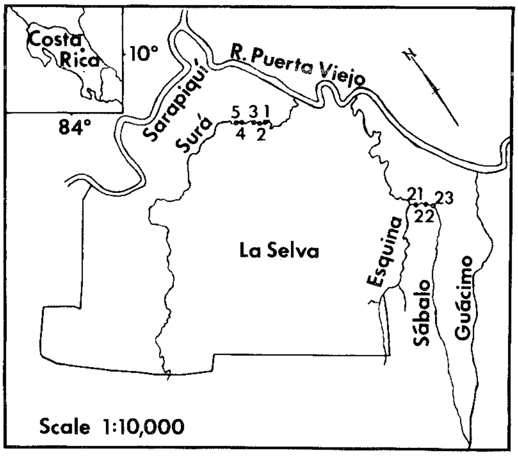

Fig. 1. Finca La Selva, Costa Rica, and sampling sites.

1983, Hynes 1970). These indirect effects disrupt the entire food web of the aquatic system (Karr and Schlosser 1978).

The main objectives of this study were to determine whether the trophic structure of the fish communities differed between a stream in undisturbed forest and one in pasture and to relate the apparent food resources to the distribution and abundances of fishes in these small, lowland streams of Costa Rica.

MATERIAL AND METHODS

Study area: The streams are located in Finca La Selva, (Fig. 1). Stout (1979) investigated biotic and abiotic factors affecting the distribution of two species of aquatic Hemiptera in the same streams. Vaux *et al.* (1984) conducted a preliminary comparison of the Sabalo to another forest stream, the Salto, during the rainy season.

La Selva is a biological reserve located in the Atlantic lowlands of Costa Rica (10°26'N, 83°59'W) about 8 km from the town of Puerto Viejo, Sarapiquí, Heredia Province. Approximately 89% of the original reserve is virgin lowland rainforest. Average rainfall is 4 m (157 inches) per year with most occurring from June to November. The mean daily temperature is 24.1°C (75.4°F).

The Quebrada El Sura within the OTS property and the Quebrada El Sabalo on private land adjacent to the east border were sampled during the dry season from January to May, 1985 (Fig. 1). The Sura is a low-gradient stream whose drainage lies mostly in La Selva borders and empties into the Puerto Viejo River. Primary and secondary forest surround the Sura for most of its length except for a short stretch in pasture which has remained ungrazed since 1982.

The Sabalo is unusual because it is a short (approximately 3 km) stream that separates from the Guacimo and joins the Esquina before emptying into the Puerto Viejo River (Fig. 1). The Guacimo has an extensive watershed in the highlands south of La Selva. The Sabalo is entirely within an area deforested fifteen or more years ago for pastures that are currently grazed. Five sites totalling 156.1 m in length ranging from 24-33.6 m long were selected for sampling in the Sura and 3 sites totalling 99.8 m ranging from 24-48.5 m long were selected in the Sabalo (Fig. 1).

Physical measurements: Each site was profiled by a transect method modified from Gorman and Karr (1978). Transects were established at regular intervals (usually 4 m apart) by stretching a meter tape perpendicular to the current and measuring water depth to the nearest 0.05 m with a marked pole. Length was measured along the mid-channel. The area of a site in shade was estimated visually during a time when the greatest amount of sunlight reached a site. The hours for this estimate varied from 9:00 am to 2:00 pm depending upon the amount of canopy and orientation of the site. The area in shade was assigned to one of the following categories: 0%, 5-20%, 21-40%, 41-60%, 61-80%, > 80%. Current velocity was measured only once at each site during the study period by timing a floating object over a known distance (Lagler 1956). A gaging stick marked in 0.5 m increments was placed in the first site in each stream and water levels were periodically recorded. A maximum-minimum thermometer was placed near each gaging stick and water temperatures were periodically recorded.

Chemical measurements: Water samples were collected from each stream one to three times per month for chemical analyses with a Hach portable water testing kit. Tests performed were pH, alkalinity, hardness, NaCl and Cl. An electric pH meter was also used to measure pH and alkalinity for comparison with the color tests of the Hach kit. The meter method of alkalinity measurement involved titration of the water sample with (0.03 N) H_2SO_4 to pH 4.6. This method measured alkalinity in meq/l $CaCO_3$ which was converted to mg/l by multiplying the value by 50.04. A conductivity meter also at the station was used to measure conductivity at the time chemical analyses were being performed. Turbidity was not measured because the stream bottoms were always visible except for brief periods following heavy rainstorms.

Fish sampling: Fishes were sampled 2 to 4 times during the study period at each site. Only pools or slow raceways were sampled in both streams. Block nets of 7 m x 1.25 m, 6 mm mesh and 6 m x 1.25 m, 8 mm mesh were set at the upper and lower ends of a site to prevent their escape. A Coffelt BP-4 battery-operated backpack electroshocker was used to stun fish temporarily for capture. Three to five passes were made from the lower to upper end of the site and an equal amount of effort (shocking time) was attempted for each pass. Shocking was combined with seining in the Sabalo sites with a 6 m x 1.35 m, 4 mm mesh seine or a 2.6 m x 1.3 m, 3 mm mesh seine. Seining was not effective in the Sura because of the amount of debris in the channel. Passes were made with the seine moving downstream through the site until there was a decline by one half the number of fishes caught for two consecutive passes. Then 2 or 3 passes were made with the shocker. Fishes were identified and counted after each pass and held in a live box.

Selectivity of the gear used for capture affected sampling efficiency. Large fishes and the characid species could avoid the shocker because of its small power field in these low conductivity waters. Therefore, they were always underrepresented in the samples of the Sura. Seining was more effective in capturing the larger individuals and fast-moving species but was less effective than the shocker in the capture of cichlids, *Rhamdia, Gymnotus* and *Synbranchus* which seek crevices and roots for cover.

All fish or a random sample were measured to the nearest 1 mm standard length (Lagler 1956). Most fish were released at the site. Representatives of all species were collected and preserved, but only abundant species were collected in sufficient quantities for diet analyses.

Food habits: The contents of the stomachs or samples of the foregut of 30-50 individuals of 10 species were examined. The percent by volume of each food item was visually estimated to the nearest 1% using a dissecting or compound microscope (Angermeier and Karr 1983) and assigned to one of the following categories: aquatic insects, terrestrial insects, terrestrial plant material (including fruits, flowers, seeds or leaves), algae (filamentous algae), fish (also includes shrimp and snails) and diatoms. Sand, detritus and indistinguishable digested matter were not included because these were considered non-food items taken incidentally or were non-quantifiable. Average diet proportions were used in a cluster analysis to assign species to consumer guilds (NT-SYS; Rohlf *et al.* 1974). A resemblance matrix was generated, and a phenogram was constructed by the unweighted pair group method using arithmetic averages (UPGMA; Sneath and Sokal 1973). A cophenetic correlation coefficient was calculated to measure the agreement betwen the values of the phenogram and the original correlation matrix.

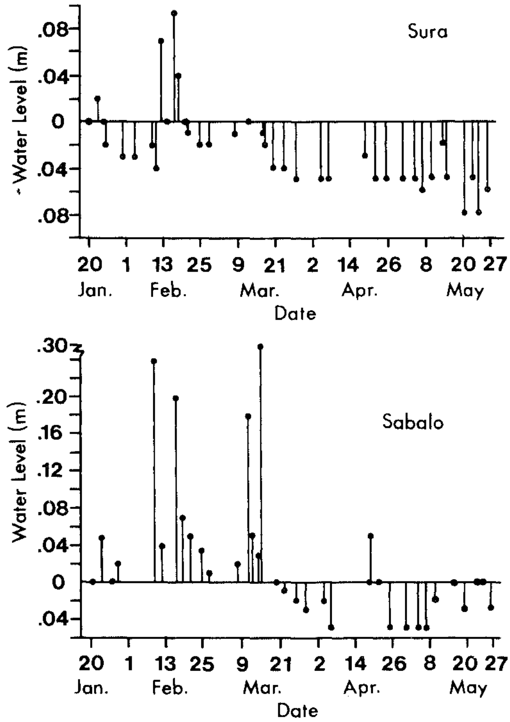

Fig. 2. Water level changes in the Sura at site 1 and the Sabalo at site 21, Costa Rica, from Jan.–May, 1985. The baseline 0 indicates water level at time of placement of gaging sticks on Jan. 21 in both streams.

Two size classes (< 80 mm, > 80 mm) were designated to distinguish possible differences in the diet of *Brycon guatemalensis.* An additional 5 species that were not abundant were assigned to guilds based on the averages of their diet categories but not included in the cluster program. The sample size for these 5 species ranged from 5 to 14 individuals.

Food availability: No attempt was made to relate food availability to fish diets. Qualitative benthic samples were taken once a month, however, from both streams to determine the orders or groups of invertebrates that were represented and an indication of abundance. Five locations in a riffle of the Sabalo were sampled by digging and scraping a small area of substrate upstream from a plankton net. The same method was used for the first sample only in the Sura but because this yielded so few invertebrates, a quantity of leaf packs were collected from instream debris and washed in the plankton net in later samples. Invertebrates were identified to order or family if possible.

Trophic structure: Total numbers of individuals were summed for species belonging to the same guild for each stream and converted to relative proportions. The Analysis of Information and Diversity program (AIDN, Overton 1974) was used to compare the overall trophic structure of the two streams. The program gives a similarity index value analogous to correlation and equivalent to the cosine of the angle measuring the distance between the two communities.

RESULTS

Physical characteristics: Water levels on January 21 were defined as an arbitrary baseline of 0 to provide a measure of range and fluctuation in water levels over the sampling period. The Sabalo was more temporally variable in flow than the Sura and subject to dramatic fluctuations in water levels during the 1985 dry season (Fig. 2). Large fluctuations in this stream were also noted by Stout (1979). Higher flows early in the dry season in the Sabalo were due to the more extensive watershed of the Guacimo, which is the source of the Sabalo. A rise in water level to over 0.27 m followed by a drop of 0.1 m could occur within a two-hour interval and was associated with rainstorms on the headwaters of the Guacimo without direct precipitation on the Sabalo. The average change in water level before and after rainstorms was 0.07 m for the Sabalo and 0.03 m for the Sura (Fig. 2). Decreasing flows as the dry season progressed were more evident in the Sura than in the Sabalo (Fig. 2) but basal flows in the Sura may be moderated by a subsurface spring (Stout 1979).

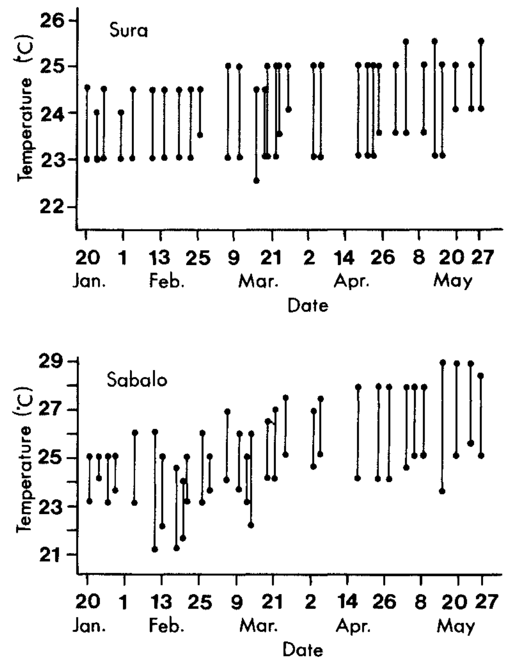

Fig. 3. Maximum and minimum water temperatures of the Sura at site 1 and the Sabalo at site 21, Costa Rica, from Jan.– May, 1985.

Extensive stretches of the Sabalo were exposed to direct sun except during early morning or late afternoon resulting in higher temperatures that fluctuated over a wider range (Fig. 3). Water temperatures were more stable and fluctuated less in the Sura (Fig. 3) due to the nearly 100% shading of the channel by the forest canopy.

Relative to the Sura, the Sabalo had more eroded banks, was less shaded, had denser periphyton growth and more distinct pools separated by riffles. The Sabalo had a cobble and gravel substrate in contrast to the clay and silt substrate of the Sura (Table 1). Both the Sura and Sabalo became turbid during high flows following heavy rains, but the Sura cleared more quickly in spite of the silty substrate. This may be due to the lower flows and intact banks.

TABLE 1

Physical measurements of sites sampled in the Sura and the Sabalo streams, Costa Rica

Sura	Length (m)	Area (m^2)	Velocity (m/sec)	Avg. Depth (m)	Shade (%)	Substrate
Site 1	24	124.8	.31	.37	> 80	silt/clay
Site 2	24.8	124	.46	.31	> 80	silt/clay
Site 3	42	262.9	.34	.36	> 80	silt/clay
Site 4	31.7	203	.31	.38	> 80	silt/clay
Site 5	33.6	235.2	.27	.34	> 80	silt/clay
Sabalo						
Site 21	24	129.6	–	.45	< 20	gravel
Site 22	27.3	163.8	.32	.39	0	gravel
Site 23	48.5	372.9	.28	.49	21-40	gravel

Chemical characteristics: Both streams have low concentrations of ions (Table 2). The difference in pH between the streams was slight. Mean alkalinity ($CaCO_3$ concentration) was 2 times higher and mean hardness was 1.8 times higher in the Sura than the Sabalo (Table 2). The differences in the mean levels are probably related to the different composition and age of the underlying igneous rock.

Fish community: Of 26 species captured during the study, all occurred in the Sabalo and 19 occurred in the Sura (Table 3). Sixteen species were caught regularly and in sufficient numbers to be included in statistical analyses. Large variability in catch data was a result of congregation of fish around cover or in schools. Efficiency of the sampling gear also varied depending upon stream conditions. *Astyanax fasciatus, Brycon guatemalensis, Bryconamericus scleroparicae* and *Melaniris hubbsi* were excluded from any analyses of the Sura because observation indicated they were common but intensive sampling with the shocker produced at most one individual for any period. *Rhamdia guatemalensis* and *R. rogersi* were pooled as one species in the calculation of mean relative abundance because they were not distinguished as two species until late into the sampling period.

Food habits and trophic structure: Diet information was obtained from examination of stomach contents of the 15 most abundant species (Table 4). Five consumer guilds were identified by cluster analysis (Fig. 4). The carnivore guild was added later based on diet data from a small number of individuals.

Two species, *Poecilia gillii* and *Phallichthys amates,* fed exclusively on diatoms. Diets of other species were usually broader except for *Neetroplus nematopus* which included filamentous algae in its diet. Omnivores consumed varying amounts of terrestrial and aquatic plant, insects, and animal material. Diets of terrestrial insectivores were composed of > 50% terrestrial insects, mostly ants. Terrestrial herbivores consumed > 20% plant material (leaves, flowers, seeds) although they were similar to omnivores in other diet categories. The guts of *Brycon* > 80 mm contained the greatest proportion of terrestrial plant material, composed largely of leaves (Table 4). *Brycon* < 80 mm were more insectivorous and their diet contained almost as large a proportion of terrestrial insects as the diet of terrestrial insectivores (Table 4). *Cichlasoma dovii* and *Rhamdia spp.,* the primary predators in both streams constituted the carnivore guild. Both species specialized on animal material (Table 4). Too few specimens were col-

TABLE 2

Chemical characteristics of the Sura at site 1 and the Sabalo at site 21, Costa Rica, from Jan. – May, 1985

Date	Time	pH		Alkalinity[a]	Hardness[a]	Nacl[b]	Cl[b]	Conductivity[c]	Level[d]
					Sura				
1/17	0 900	6.7 *	6.9 #	80.06	51.36	25	15.2	125	–
2/13	1 300	6.7	6.8	39.03	34.24	25	15.2	80	0.23
2/17	1 130	6.4	6.5	45.04	34.24	25	15.2	75	0.30
2/28	1 500	6.6	6.8	54.04	68.47	25	15.2	140	0.18
4/5	1 000	7.0	6.9	81.06	68.47	37	22.7	170	0.15
4/17	1 130	6.9	6.8	63.05	68.47	37	22.7	145	0.17
5/8	0 915	7.0	6.9	84.07	85.60	37	22.7	180	0.15
5/22	1 030	7.4	6.9	75.06	85.60	37	22.7	170	0.15
				$\bar{X}$ = 65.18	$\bar{X}$ = 62.06				
					Sabalo				
1/17	1 030	6.9 *	7.0 #	39.03	34.24	25	15.2	85	–
1/27	1 640	6.6	6.9	42.03	34.24	25	15.2	68	0.05
2/12	0 900	6.5	6.7	27.02	34.24	25	15.2	50	0.09
2/17	0 830	6.4	6.7	15.01	17.12	25	15.2	26	0.25
2/28	1 100	6.6	6.9	24.02	34.24	25	15.2	63	0.06
3/21	1 400	7.2	6.9	33.03	34.24	25	15.2	85	0.04
4/5	1 400	7.0	6.9	39.03	34.24	25	15.2	90	0.00
4/17	0 830	7.0	7.0	39.03	34.24	25	15.2	85	0.05
5/8	0 830	7.0	7.0	42.03	51.36	37	22.7	99	0.03
5/22	0 900	6.8	6.9	24.02	34.24	25	15.2	70	0.05
				$\bar{X}$ = 32.43	$\bar{X}$ = 34.24				

* pH meter   a mg/l $CaCO_3$ c umhos/cm

\# Hach method   b mg/l   d m

lected of these species to analyze diet by size class. A shift in diet from aquatic insects to fish prey as these species grow larger was suggested, however. Smaller individuals examined had a higher proportion of aquatic insects in the diet than did large individuals.

The trophic structure of the fish communities did not differ greatly (similarity index = 0.40 AIDN analysis), but the largest proportion of each community belonged to only one of two feeding guilds. The greatest abundance of species in the forest were terrestrial insectivores while

TABLE 3

Total numbers and mean relative abundance ($\bar{X}$) of fish species in the Sura and Sabalo streams, Costa Rica

	Sura		Sabalo	
Species	Total	$\bar{X}$	Total	$\bar{X}$
Alfaro cultratus	205	10	190	13
Neoheterandria umbratilis	32	3	112	8
Brachyrhaphis parismina	0	–	182	18
Priapichthys annectens	321	27	3	1
Poecilia gillii	0	–	2 266	136
Phallichthys amates	58	8	133	10
Cichlasoma alfari	216	22	241	17
C. septemfasciatum	93	6	194	15
C. dovii	20	2	83	5
C. nigrofasciatum	1	–	47	6
C. nicaraguensis	0	–	38	3
C. tuba	4	–	23	3
Neetroplus nematopus	8	2	243	13
Rhamdia spp.	7	1	18	3
*Astyanax fasciatus**	23	–	219	18
*Brycon guatemalensis**	8	–	56	4
*Bryconamericus scleroparius**	6	–	28	4
Melaniris hubbsi	1	1	360	17
Herotilapia multispinosa	1	–	9	2
Gymnotus cylindricus	3	–	3	1
Synbranchus marmoratus	19	2	1	–
*Bramocharax bransfordii**	0	–	1	–
*Carlana eigenmanni**	0	–	1	–
*Rivulus isthmensis**	–	–	1	–
Roeboides guatemalensis	1	–	4	2

* Species could not be pooled for mean frequency by stream. Caught only once: *Carlana eigenmanni, Bramocharax bransfordii. Awaous taiasica* observed in Sabalo, not caught.

the greatest abundance in the pasture stream were diatom specialists (Table 5). The terrestrial herbivore guild was excluded from analysis because *Brycon* was not caught with equal efficiency in both streams. *Astyanax fasciatus* was excluded from the proportion of each community in the omnivore guild for the same reason.

Food availability: Nineteen orders and groups of benthic invertebrates were identified from qualitative sampling in the two streams. Some orders or groups were found only in one stream, but consistently more were collected from the Sabalo than the Sura (Fig. 5). Leaf packs rather than the substrate supported more invertebrates in the Sura. No estimate of abundances within groups was made, but most orders were represented by 10 or more individuals in all samples from the Sabalo. Usually only 1 to 4 individuals were found in any order in the Sura. More quantitative sampling would be necessary to determine if total abundances of invertebrates utilized by fishes are different between the two streams and if abundances change from wet to dry season.

DISCUSSION

Physical and chemical characteristics: Geological processes are probably largely responsible for the observed physical and chemical differences between the Sura and the Sabalo. The effect of flood water from the Guacimo, which influences the overall ionic composition of the Sabalo and introduces gravel and fish must outweigh many, if not all, effects of reduced riparian vegetation in this 3 km stretch. Minshall *et al.* (1983) confirmed that local geomorphic factors were sometimes most important in explaining the variance of detritus standing crop in streams in different geographical regions.

The physical differences between the Sabalo and Sura raise interesting questions, however. The interaction of substrate type and light levels may accentuate the effects of removal of riparian canopy. Substrate type influences the distribution and abundance of invertebrates and periphyton (Hynes 1970, Power 1983, Newbold *et al.* 1980, Reice 1983). Leaf packs supported more aquatic invertebrates in the Sura than did the silt/clay substrate. Consistently more invertebrates were collected from the gravel substrate of the Sabalo than from leaf packs in the Sura. Periphyton was also visibly denser on the firm, rocky substrate. Invertebrate abundance often increases in response to opening of the riparian canopy (Newbold 1980). Substrate

TABLE 4

Average percent volumes (rounded to the nearest 1%) of food types and number of stomachs sampled (n). Fish species used in the cluster analysis from the Sura and Sabalo streams, Costa Rica, for Jan.-May, 1985

Species	n	Aquatic Insects	Terrestrial Insects	Terrestrial Plants	Filamentous Algae	Fish Snails Shrimp	Diatoms
Alfaro cultratus	(38)	14	81	2	0	0	3
Priapichthys annectens	(37)	15	69	11	0	5	0
Poecilia gillii	(30)	0	0	0	0	0	100
Phallichthys amates	(38)	0	0	0	0	0	100
Cichlasoma alfari	(50)	51	5	18	0	20	6
Cichlasoma septemfasciatum	(36)	40	0	18	22	14	6
Neetroplus nematopus	(37)	3	0	0	69	0	28
Astyanax fasciatus	(30)	26	20	21	26	0	7
Brycon guatemalensis < 80 mm	(21)	13	42	25	0	15	0
> 80 mm	(13)	4	29	60	0	8	0
Melaniris hubbsi	(35)	39	0	0	19	0	42
*Neoheterandria umbratilis**	(14)	26	0	0	17	0	57
*Brachyrhaphis parismina**	(11)	13	64	0	0	0	23
*Cichlasoma dovii**	(5)	50	0	0	0	50	0
*Cichlasoma nigrofasciatum**	(12)	15	7	23	33	8	14
*Rhamdia spp.**	(5)	40	0	0	0	60	0

* Species not included in NT-SYS cluster analysis.

type interaction with higher light levels may accentuate such increases in invertebrate populations. A stream such as the Sura in which leaf packs are the main sources of cover and attachment may experience reduced diversity and abundance of invertebrates if the riparian source for this substrate is removed.

Loss of terrestrial input may be more serious for streams like the Sura which have low capacities to support in-stream primary production. A cursory inventory along 300 m of the Sura showed 21 species of trees which produced fruits and flowers seasonally or throughout the year. This resource may be the main support of *Brycon guatemalensis* greater than 80 mm. Schools of 3 to 30 individuals were often seen from January – May moving up or downstream in the Sura, but only rarely were large *Brycon* seen in the Sabalo and never in large schools.

Species richness and trophic structure: Species richness has been shown to increase with stream size and the addition of energy-source levels (Lotrich 1973, Angermeier and Karr 1983, Schlosser 1982). Species richness in the periphyton feeding guilds was greater in the Sabalo than in the Sura. Different habitat affinities and stable food resources may allow species with identical or greatly overlapping diets to coexist. Two diatom specialist species were supported in the Sabalo and their location in the stream differed. *Poecilia gillii* was observed feed-

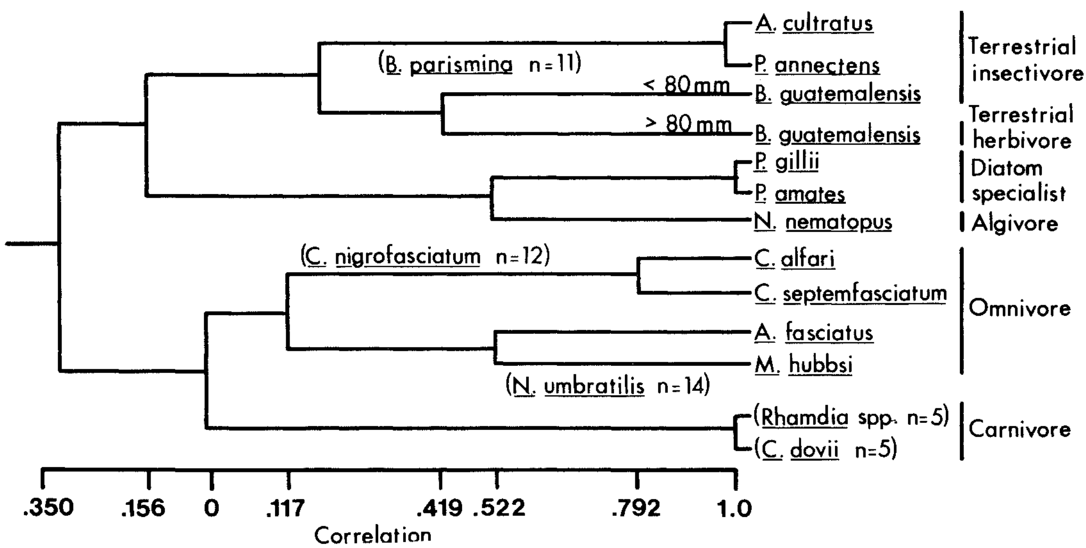

Fig. 4. Correlation phenogram of consumer guilds based on unweighted pair group method (UPGMA) using arithmetic averages for 6 diet categories. Cophenetic correlation coefficient is 0.761. Species in parentheses (spp.) were not included in NT–SYS cluster analysis.

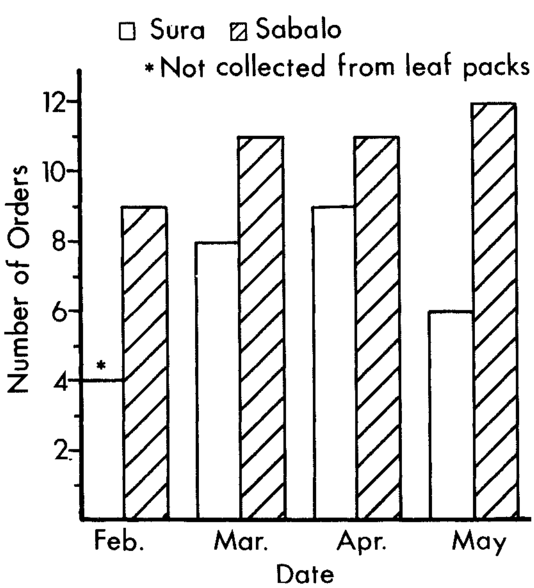

Fig. 5. Total number of orders of benthic invertebrates sampled from leaf packs in the Sura and riffles in the Sabalo streams, Costa Rica.

ing in faster water at mid-channel. *Phallichthys amates* occurred in the still water along the stream edge. In contrast, two terrestrial insec-

TABLE 5

Proportion of fish community in each consumer guild from the Sura and Sabalo streams. Proportions are based on total counts of individuals.

Consumer Guild	Sura	Sabalo
Terrestrial insectivore	48	9
Algivore	0.9	6
Diatom specialist	7	60
Carnivore	3	1
Omnivore	42	24

similarity index = 0.40

tivores were dominant in the Sura. Their behavioral separation resembled that of the diatom specialists. *Alfaro cultratus* maintained position near the surface in faster water at mid-channel. *Priapichthys annectens* remained near the bottom in still water along the stream edge and dashed up to capture objects throughout the water column. Large proportions of the fish community of the Sura in the terrestrial insectivore and omnivore guilds suggests that species that selectively feed near the surface as do *Priapichthys annectens* and *Alfaro cultratus* or have a generalized, omnivorous diet are better able to exploit the limited food resources of the Sura. Species with more specialized diets such as diatoms and algae can dominate in the Sabalo where these food resources appear to be more abundant.

Terrestrial vegetation, fruits and seeds were the major source of energy for two forest streams of Corcovado National Park, Costa Rica (Winemiller 1983). He found that the major portions of the diets of *Astyanax fasciatus* and *Hyphessobrycon savagei,* were made up of fruits and seeds. The diet of *Astyanax fasciatus* in the present study was more evenly divided betwen aquatic insects, terrestrial insects, terrestrial plant material and algae (Table 4). Although most diet data were obtained for this species from Sabalo samples, a larger sample size from the Sura may show *A. fasciatus* relying more on fruits and seeds in that stream.

Autochthonous primary productivity was extremely low in both streams studied by Winemiller (1983), but diatoms and blue-green algae were utilized by more species in the larger of the two streams. More species in relatively greater abundance were supported by the terrestrial insects and terrestrial plant material in the smaller of the two streams than were supported by the same food sources in the larger stream (Winemiller 1983). These observations suggest that the type and relative abundance of food resources in two streams equally poor in nutrient levels reflects the influence of stream size on the amount of effective shading by riparian canopy (Winemiller 1983). Data from the present study tend to agree with this.

Seasonal comparisons: A preliminary survey of the feeding ecology of fishes in La Selva streams by Vaux *et al.* (1984) during the wet season (September) revealed some similarities and differences in the diets of certain species compared to the present dry season study. The comparisons with their samples can only be qualitative due to the small sample sizes and different methods of analyses. Most of the wet season samples were from the Sabalo.

Similarities between seasons: Vaux *et al.* (1984) determined that *Astyanax* was omnivorous and included terrestrial aquatic insects, seeds and diatoms in its diet. This agrees with the food habits for this species from the dry season samples (Table 4). A shift in diet from mainly aquatic and terrestrial insects to terrestrial plant material was noted for *Brycon* greater than 80 mm by Vaux *et al.* (1984) and in the present study (Table 4). Bussing (1962) unpubl. data) recorded the same shift in samples taken from the Río Puerto Viejo. Angermeier and Karr (1983) observed a similar shift in *Brycon petrosus* in Panama.

The shift in diet with size noted for *Brycon guatemalensis* may mean that habitat alterations due to human activity can have differential effects on *Brycon* populations in Costa Rica. Young (small) *Brycon* may do very well in streams receiving more sunlight which leads to higher periphyton and benthic invertebrate production. Older age classes (larger fish) require substantial input of fruits and leaves from the forest. The largest *Brycon* (>250 mm) were most abundant in the main river, the Puerto Viejo, where riparian input of fruit and leaves from large fig trees constituted the main food source (pers. obs.). Large fig trees are common along the Puerto Viejo, but rare, if present at all, along the Sura. A medium size class of *Brycon* (100 - 210mm) was seen most abundantly in the Sura cruising up- and downstream and responding immediately to objects falling into the stream. This age class may depend on smaller, forested streams where larger fish are absent due to their size of food preference. Thus, oldest and youngest age classes may suffer less from localized destruction of riparian vegetation, while the intermediate age class may be forced into more intense competition in larger river systems as streams become deforested.

Cichlasoma nigrofasciatum consumed algae, aquatic insects and diatoms in both seasons (Vaux *et al.* 1984; Table 4). *Cichlasoma dovii* was the major piscivorous species in their samples (Vaux *et al.* 1984). Smaller individuals also contained aquatic insects in the gut. This agrees with dry season data which suggests a diet shift as individuals grow. Stomach contents of *Cichlasoma septemfasciatum* collected after a wet season flooding event in the Sabalo, indicated the species was omnivorous then as well as during the dry season (Vaux *et al.* 1984). Apparently, food resources are of sufficient quantity in either season that these three species do not need to utilize alternative food types. Both *Poecilia gillii* and *Neetroplus nematopus* maintained their specialized diets of diatoms or diatoms and filamentous algae before and after the September spate. Evidently these two species are specialists that do not change their diet with season (Table 4). More quantitative sampling of periphyton abundance might reveal whether this resource is limiting in the wet season when scouring floods are frequent. The diet of *Melariris hubbsi* did not differ greatly between the two seasons' collections in choice of food items (Vaux *et al.* 1984; Table 4). This species' manner of feeding high in the water column in swift water probably allows it first access to preferred food items even during periods when those items are less abundant.

Differences between seasons: Although *C. septemfasciatum* was omnivorous in post-flood samples taken in September (Vaux *et al.* 1984), diatoms and filamentous algae were the major food types in stomachs prior to the flood. This species may be a facultative omnivore that concentrates on the most abundant food type present.

Alfaro cultratus exhibited the most distinctive difference in diet from dry to wet season. Vaux *et al.* (1984) reported that diatoms were the major food item for this species before the September flood, but switched to insects almost exclusively, especially ants, after the flood. This species ate mainly ants in the dry season also (Table 4). Ants may be a preferred food that is more available in the dry season. If ants are less active during the rainy season, they may only become abundant or available to fish when major rainstorms transport them into the stream.

Very low aquatic insect densities were observed for the Sabalo and the Salto, a forest stream, in September (Vaux *et al.* 1984). This may account for the slightly different diets between the two seasons.

Major energy sources: Lotrich (1973) found that terrestrial invertebrates were the main energy source utilized by fish in first order streams, and aquatic invertebrates and primary productivity became important sources in second order streams. One possible interpretation of the patterns observed in the present study is the resemblance of the Sura to a heterotrophic headwater temperate stream in its structural and functional characteristics and the resemblance of the Sabalo to a second order or possibly third order stream (Vannote *et al.* 1980). Whether the comparisons should be made with stream orders rather than using variables such as watershed area and discharge to predict changes in community structure is questioned by some authors (Hughes and Omernik 1983).

CONCLUSIONS

1. The trophic structure of the fish communities was different in the two streams studied. A greater proportion of the fish community was supported by autochthonous food resources in the pasture stream while a greater proportion was supported by allochthonous resources in the forest stream.
2. Seven more species occurred in the pasture stream than in the forest stream. Some species common to both streams such as *Alfaro cultratus, Neoheterandria umbratilis, Phallichthys amates, Cichlasoma septemfasciatum* and *Neetroplus nematopus* were relatively more abundant in the pasture stream suggesting more diverse or abundant food resources.
3. Sites in the pasture stream were less shaded than those of the forest stream. The gravel/cobble substrate of the pasture stream supported visible mats of periphyton while the silt/clay substrate of the forest stream did not. These two physical features, light and substrate, may have an interactive effect on autochthonous primary productivity. Periphyton production may be limited in streams with silt/clay substrate even under increased light levels.
4. Large schools of *Brycon guatemalensis* greater than 80 mm but less than 250 mm (a terrestrial herbivore) were present in the forest stream and generally absent from the pasture stream. This suggests that this age class would be reduced in abundance or eliminated locally if fruiting trees are removed from the banks of small streams.
5. Studies of streams with similar substrate types and watershed characteristics would eliminate some variation which cannot be attributed to the effects of land use practices. For example, comparison of two streams with silt/clay substrate, one in forest and one in pasture, may illustrate whether increased light can enhance primary productivity sufficiently to support a fish community dominated by periphyton feeders.

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RESUMEN

Se estudió las comunidades de peces en una quebrada de bosque y otra de pastizal en la vertiente caribeña de Costa Rica, durante la época seca (enero hasta mayo, 1985). Se distinguió 6 gremios de peces (omnívoro, insectívoro terrestre, herbívoro terrestre, algívoro, carnívoro, y especialista de diatómeas), según el tipo principal de alimento.

La estructura trófica total de cada comunidad no se diferenció mucho (índice de semejanza = 0.40, análisis AIDN), pero la proporción mayor de cada comunidad perteneció a solo uno: en la quebrada del bosque al gremio insectívoro terrestre y en la de pastizal al gremio de consumidores de diatómeas.

La temperatura máxima y abundancia de invertebrados acuáticos y perifiton fueron mayores en la quebrada del pastizal. El tipo de sustrato del fondo difirió entre las dos quebradas y podría interactuar con los niveles de luz influyendo sobre el tipo de recursos alimentarios.

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