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Fish communities along environmental gradients in a system of tropical streams

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Synopsis

Fish community structure was examined in 9 forested streams (1–6 m wide) in central Panama during dry seasons over a 3 year period. Study regions varied in annual rainfall, degree of canopy shading, and topographical relief. Benthic invertebrates were more abundant in riffles than in pools and more abundant in early (January) than late (March) dry season. In addition, benthos abundances were negatively correlated with canopy shading among study regions. Terrestrial invertebrate abundances were greater in January than March and were correlated with stream width. Fishes were assigned to 7 feeding guilds (algivores, aquatic insectivores, general insectivores, piscivores, scale-eaters, terrestrial herbivores, omnivores) on the basis of similarity of gut contents. Four species exhibited marked dietary shifts with increasing size. Distributions of feeding guilds (biomass) among habitats and streams were not generally correlated with availabilities of their major food resources. All feeding guilds except aquatic insectivores were most concentrated (biomass per area) into deep pools. Densities of algivores and terrestrial herbivores increased with stream size, but the density of aquatic insectivores declined. Species richness of feeding guilds increased with stream size and canopy openness. The proportion of fish biomass supported by algae and terrestrial plant material increased with stream size, while that supported by aquatic and terrestrial invertebrates declined. Small fishes (<40 mm TL) were most abundant in pools of small streams. Terrestrial predators appeared to be more important than food availability in determining distributions of fish among habitats. However, trophic diversity of fish communities may be related to the reliability of available food resources.

Introduction

A central goal of community ecology is to understand mechanisms and processes responsible for differences and similarities among communities. One approach is to compare communities occurring along environmental gradients such as physiological stress or resource availability. This approach provides valuable basic data and encourages the development of testable hypotheses. Such hypotheses will, in turn, lead to more definitive studies, including experimental manipulations.

Existing models of the structure and dynamics of stream communities are largely based on patterns observed in forested temperate streams, for example, the stream continuum hypothesis (most recently presented in Vannote et al. 1980). Briefly, this hypothesis holds that relative abundances of various food types vary predictably with stream size; relative abundances of consumer guilds are correlated with those of their major food resources. The model emphasizes the importance of trophic function and food availability to the distribution and abundance of stream organisms. Food availability and consumption patterns are regulated by fluvial geomorphic processing of organic materials in the stream. The stream continuum hypothesis, however, is less sensitive to variables such as water chemistry and the complex biotic interactions typical of streams. A conceptual model of stream communities should incorporate these other factors (Karr & Dudley 1981), especially for the assessment of human impacts on streams (Karr 1981).

Because virtually all stream models have been developed from a limited data base and geographic perspective, tests are needed in other regions. Our main objectives in this study, therefore, were to identify patterns of food and habitat availability and predator abundance, and relate those patterns to the distribution and abundance of fishes in central Panama streams. Our hope was to identify basic patterns and to generate hypotheses for future study that will elucidate the organizational processes of streams and their biotic communities.

Materials and methods

Study sites

Central Panama is a narrow isthmus extending 70 km from the relatively dry Pacific Coast to the wetter Atlantic Coast. Rainfall is seasonal with a dry season beginning in late December or early January and extending to early April. Monthly and yearly rainfall totals vary among years (Table 1), but the January through March period is always the driest. The nearest rainfall stations (Fig. 1) to our study sites are at Gamboa with an average annual rainfall of 2200 mm and Frijoles with 2680 mm.

We studied nine streams along the Pipeline Road in Parque Nacional Soberania in the Rio Chagres drainage of central Panama. This tract of lowland rainforest has remained largely undisturbed since the early 1900's. The study streams generally drain mature second-growth forest except for a few areas of immature forest as noted below.

Three groups (regions) of streams were identified on the basis of rainfall, watershed topography, and forest canopy characteristics, while streams within regions varied in size (Table 2). Region 1 contained only one stream, Quebrada Juan Grande, which drained recently disturbed forest on land with rolling topography. Region 2 contained the Rio Frijoles and 3 tributary streams: Rio Frijolito, Tower Creek, and Rio Limbo. Region 2, about 3 km from Region 1, was characterized by rolling topography and structurally mature rainforest except for a small area of immature forest upstream from sample sites on the Rio Frijoles. Region 3 contained Rio Mendosa and 2 tributaries, Rio Sirystes and Tayra Creek, as well as Rio Pilon. All 4 streams drained structurally mature forest in rugged topography. The Mendosa watershed and the Rio Pilon were about 7 and 10 km, respectively, from Region 2. Exact data are not available but rainfall at nearby sites indicate that Region 3 receives approximately 500 mm more rainfall annually than Region 1, with Region 2 intermediate between Regions 1 and 3. Most of the difference in

Table 1. Rainfall (mm) at nearby Barro Colorado Island during study periods with annual totals and variation (1979–81 data obtained courtesy of D. Windsor, Smithsonian Tropical Research Institute; 1941–1980 data courtesy of Panama Canal Meteorological Bureau).

Year	Dry season				Year total
	January	February	March	Total	
1979	5	30	8	43	2654
1980	112	48	5	165	2096
1981	399	20	61	480	4633
$\bar{x} \pm$ SD (1941–1980)	63 ± 67	32 ± 34	26 ± 27	122 ± 96	2563 ± 382

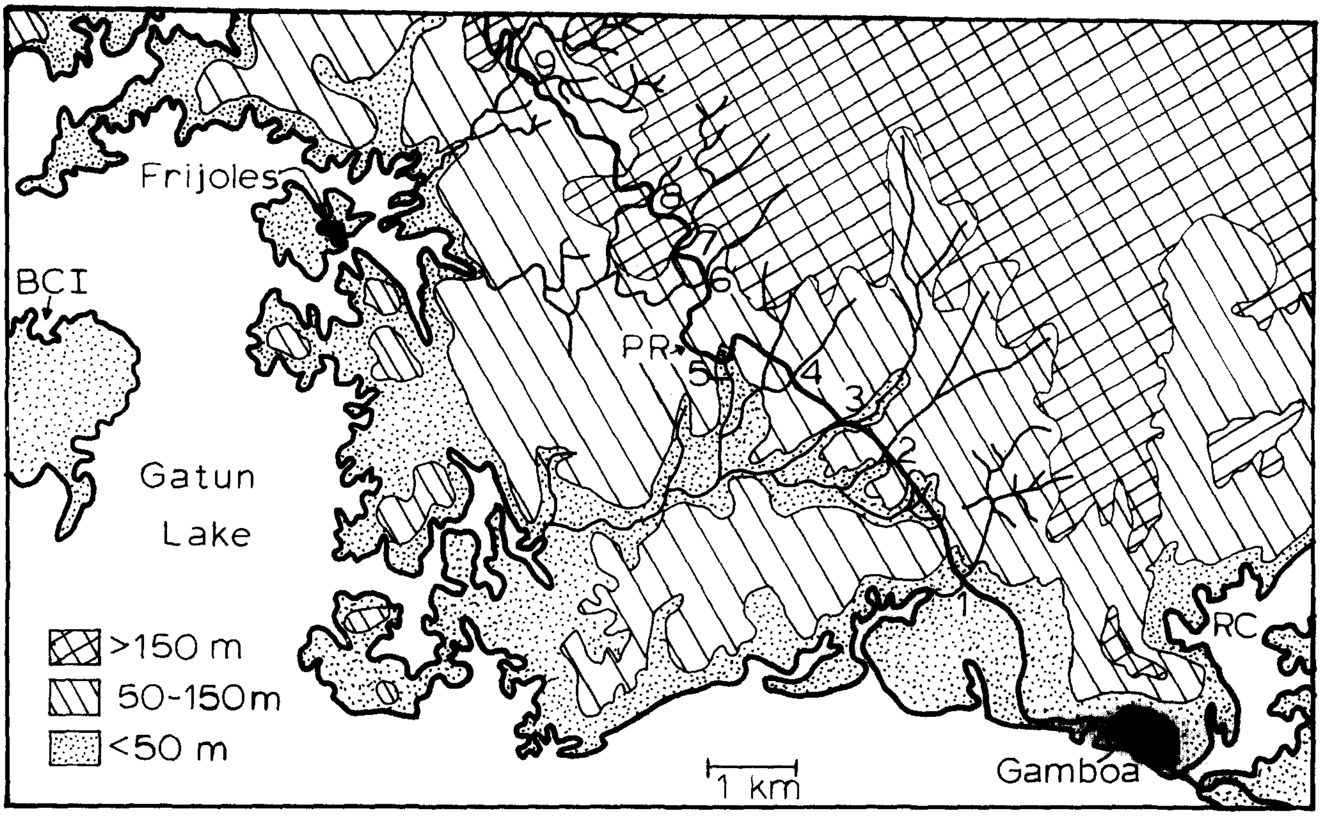

Fig. 1. Map of Pipeline Road (PR) area in central Panama showing Barro Colorado Island (BCI), Rio Charges (RC) and Gatun Lake. Study sites are located on Quebrada Juan Grande (1), Rio Frijolito (2), Rio Frijoles (3), Rio Limbo (4), Tower Creek (5), Rio Mendosa (6), Rio Sirystes (7), Tayra Creek (8), and Rio Pilon (9).

Table 2. Average stream width and percentage ($\bar{x}$ ± SD) of sample points with selected habitat features in 9 Panama streams. Percentages were calculated over all available samples except in R. Limbo, an intermittent stream.

Stream	Ave. width (m)	Depth (cm)			Perceptible current	Substrate				Leaf cover	
		1–29	30–59	>60		sand	gravel	pebble	bedrock	March	January
Region 1											
Juan Grande	2.0	87 ± 2	10 ± 1	3 ± 3	21 ± 13	3 ± 0	75 ± 2	5 ± 4	0 ± 0	19	4
Region 2											
Frijoles	5.1	70	22	8	7	14	44	17	21	16	—
Frijolito	4.3	79 ± 3	15 ± 1	6 ± 2	24 ± 12	14 ± 1	45 ± 11	30 ± 5	7 ± 1	22 ± 3	6
Limbo*	2.3	77	21	2	9	9	60	12	0	—	10
Tower	1.3	89 ± 7	8 ± 3	3 ± 4	6 ± 6	16 ± 13	48 ± 18	2 ± 3	0 ± 1	50 ± 24	12
Region 3											
Mendosa	5.6	73	16	11	19	21	32	20	10	19	—
Sirystes	3.7	78 ± 5	17 ± 4	5 ± 1	21 ± 5	8 ± 2	33 ± 6	25 ± 1	20 ± 5	24 ± 8	15
Pilon	2.7	87 ± 3	13 ± 3	0 ± 0	29 ± 6	3 ± 0	63 ± 16	18 ± 8	18 ± 4	27	11
Tayra	1.6	92 ± 1	7 ± 1	0 ± 0	16 ± 10	7 ± 6	41 ± 12	25 ± 4	15 ± 5	34 ± 25	10

* Data from 1980 only.

annual rainfall among regions occurs from June through November (wet season).

Sampling schedule

All data were collected during 3 to 4 week periods in late March (1979, 1981) and early January (1980). During these dry season periods discharges are low and fishes are concentrated into limited habitat area. The 1979 dry season was especially dry at nearby Barro Colorado Island (Table 1) while 1981 dry season was wetter than average.

Most streams were sampled in at least 2 of the 3 sampling periods. The R. Frijoles and R. Mendosa were sampled in 1979, but not in 1980 or 1981 due to higher discharges during the latter 2 periods. The Q. Juan Grande and R. Pilon were sampled in 1980 and 1981, but not in 1979. The R. Limbo was sampled in 1979 and 1980, but not in 1981. The other 4 streams were sampled in all 3 years, though sampling in 1979 was less extensive than in 1980 and 1981.

Sampling methods

Habitat structure. – One to three days prior to fish sampling, structural features of each stream channel were systematically assessed along a series of transects. The method used (Fig. 2) was modified from that used by Gorman & Karr (1978). Distances between transects (T) ranged from 1.0 to 3.3 m while distances between habitat points along transects (P) ranged from 0.5 to 1.0 m. Larger intervals between transects and points were used in large streams than in small streams. At each habitat point, depth, current, bottom characteristics, and cover availability were evaluated. Depth was measured to the nearest centimeter. Surface current was gauged by the distance that the water was driven up the edge of a vertically held meter stick. When that distance exceeded 1.5 mm, current was considered perceptible. Mineral substrates were classified as silt, sand, gravel, pebble, rock, bedrock, or hard clay largely in accord with the classification given in Hynes (1970). Organic substrates included leaves and other organic litter. Cover features, including overhanging vegetation, undercut banks, branch, log, and rock structures, were noted. From 76 to 228 m of each stream channel were evaluated by this method, depending on stream size and sample period; the corresponding number of habitat points evaluated from each stream ranged from 84 to 389. Longer reaches were sampled in larger streams, and sampling in 1980 and 1981 was more extensive than in 1979. Area of a given stream reach was estimated using the number of habitat points sampled and the distances between points and transects.

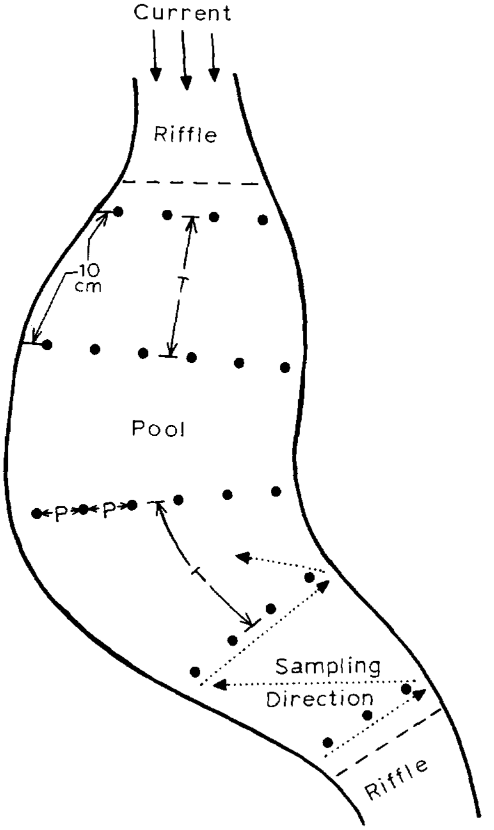

Fig. 2. Diagrammatic representation of the technique used to assess habitat structure of streams. P in the diagram varied from 0.5 to 1.0 m, while T varied from 1.0 to 3.3 m depending on stream size. At each point (darkened circles) several habitat variables were evaluated (see text). The first point of each transect was located 10 cm from the water's edge. This technique was repeated in each habitat unit (i.e. pool, riffle, raceway) of all study reaches. Dashed lines in the figure represent approximate delineations between habitat units.

Canopy closure. – Canopy closure was measured in 1980 and 1981 over streams sampled during those periods. At the center of each habitat transect the percent canopy closure was visually estimated and assigned to one of 5 categories (0–20%, 20–40%, etc.). The height at which the canopy first reached maximum closure was also estimated to the nearest 1.5 m.

Aquatic invertebrates. – Benthic invertebrates were sampled during the day from representative substrates in midstream using a Surber sampler (0.093 m^2) with 240 μm mesh. Two riffles and 2 shallow pools were generally sampled from each stream. Fifteen such samples were collected in March 1979, while 30 were collected in January 1980. Sites of invertebrate samples were nearby and similar to those used for fish sampling. All invertebrates were preserved immediately in 15% formalin. Samples were subsampled using a device similar to that of Waters (1973), then sorted to order and counted using a dissecting microscope.

Terrestrial invertebrates. – Several types of wide-mouth containers (e.g. dishpans, inflatable wading pools) were used to catch invertebrates that fell or flew onto the water surface. Containers were placed in the stream channel (though not usually in the water) and partially filled with a solution of dishwashing detergent (1–2%). Canopy characteristics above the containers were recorded. Containers were left for one to three 24 h periods, after which the contents were strained through a 240 μm mesh net, and preserved in 10% formalin. One to 4 such samples were collected from each stream; container openings ranged from 0.088 to 0.374 m^2 in area. Invertebrates were later sorted and counted under a dissecting microscope.

Fishes. – Stream reaches were divided into habitat units (e.g. pool, riffle, pool, etc.) for fish sampling. Before sampling, block nets were placed at natural barriers in the channel (Fig. 2) on the up- and downstream ends of a habitat unit. Non-stationary debris (e.g. branches, logs, etc.) and rocks that protruded into the water column were removed from the channel to facilitate seining. Four to eight habitat units were sampled from each stream studied in 1979, while 6–16 units were sampled from each stream studied in 1980 and 1981. Overall, 162 samples of habitat units were collected. An effort was made to acquire replicate samples of the predominant habitats (i.e. deep pool, raceway, riffle) in each stream. More habitat units were sampled in large streams than in small streams.

Fish sampling was performed during the day (0800–1800 h) using a 1.4 × 6.7 m bag seine with 0.48 cm mesh. The seine was drawn through each pool and emptied 3 times, then fish were counted. Riffles were sampled by thoroughly disturbing the substrates down to 10 cm by kicking while moving toward a stationary net. The stationary net was relocated at 2–3 m intervals through a given riffle, and each riffle was sampled 3 times. This 'kicking' procedure was more effective at capturing riffle fishes than the typical seining procedure used in pool sampling. Methods used here underestimate relative abundances of secretive fishes such as *Synbranchus*.

Fish were generally identified to species using keys prepared by J.D. McPhail. For *Astyanax ruberrimus* and *Bryconamericus emperador* data were pooled for analysis, but a subsequent examination of preserved collections indicated that *Astyanax* was more common than *Bryconamericus*. Most fish were measured to the nearest millimeter, total length (TL), then released. Fish to be used for stomach analyses were anesthetized in tricaine-methanesulfonate to prevent regurgitation, then preserved in 20–25% formalin. Weights of released fish were estimated from length-weight regressions generated from preserved specimens. These weight estimates are not comparable to live weights since fish specimens shrink during preservation (Parker 1963) but estimates from preserved specimens do permit comparisons of fish weights for collections that are preserved and stored similarly.

Fish food habits. – The 3 fish collections contained enough individuals of 26 species for analysis of food habits. An exception was *Synbranchus marmoratus*. Contents of foreguts and stomachs were assigned to 6 categories: algae, aquatic invertebrates, terrestrial invertebrates, terrestrial plant material, fish, and fish scales. Percent volume comprised by each food type was estimated to the nearest 5% for each gut. Averages (over individuals) of these percentages were used to assign fishes to feeding guilds. An effort was made to include individuals of various sizes and stream origins in assessing food habits. Weighted pair-group cluster analysis with arithmetic averages (Sokal & Sneath 1963) using Horn's (1966) ecological-overlap index was used to group species and size classes into feeding guilds. Average diet proportions for each size class or species were used to calculate the overlap values.

Results

Physical features

Habitat structure. – All streams were characterized by well defined pool-riffle sequences, with pool habitats comprising most of the channel area. Current through pools and raceways was usually not perceptible (Table 2) during this study, but wet season currents are substantial in all habitats. Although gravel was the most common substrate in all streams, the frequency of rocks and bedrock increased from Region 1 through Region 3 (Table 2). The proportion of the stream bottom covered with leaves decreased with increasing stream size in Regions 2 and 3. The stream in Region 1 (immature forest) consistently contained fewer leaves than streams of similar size in Regions 2 (Tower, Limbo) and 3 (Pilon, Tayra). Leaf coverage was consistently higher in March than in January.

Stream reaches were divided into habitat units (i.e. pool, raceway, riffle) on the basis of depth and current characteristics. Riffles were shallow (less than 12 cm mean depth) with turbulent flow. Pools and raceways had negligible current; maximum depth of pools was at least 50 cm, while raceways were shallower with mean depth less than 17 cm.

Canopy coverage. – The proportion of the stream channel open to direct sunlight increased with stream size (Table 3). Region 1 forest canopy was more open than that over Regions 2 and 3. Furthermore, canopy height increased from Regions 1 through 3. The difference in canopy height between Region 1 (immature forest) and Region 2 (mature forest) seemed to be largely due to differences in forest age, while the difference in canopy height between Regions 2 and 3 (both mature forest) seemed to be largely due to topographical differences. Streams in Region 3 were more completely shaded than those in Region 2 due to the higher canopy associated with the steeper banks in Region 3.

Table 3. Stream widths and percentage ($\bar{x} \pm SD$) of canopy estimates assigned to categories of canopy closure and height over 9 Panama streams. Percentages were computed from January 1980 and March 1981 data except for R. Limbo, which was only sampled in 1980.

Stream	Ave. width (m)	<40% Closed	Max. closure below 6 m
Region 1			
Juan Grande	2.0	17 ± 8	51 ± 23
Region 2			
Frijolito	4.3	10 ± 5	23 ± 14
Limbo	2.3	12	15
Tower	1.3	1 ± 2	7 ± 1
Region 3			
Sirystes	3.7	10 ± 6	0 ± 0
Pilon	2.7	3 ± 0	11 ± 7
Tayra	1.6	0 ± 0	4 ± 6

Food availability

Benthic invertebrates. – The most abundant invertebrates were Ephemeroptera, Coleoptera and Diptera larvae (Table 4). Taxonomic composition (at ordinal level) of the benthos did not differ markedly among streams. Total benthos abundances did vary significantly through space and time. Three variables accounted for 70% of the variance in benthos densities (Fig. 3) in a multiple regression analysis. This analysis estimates the effects of individual independent variables while holding others constant statistically. Invertebrates were about 3.5 times more abundant in riffles than pools, and about 3 times more abundant in Region 1 than Region 3. Benthos were also more abundant in January 1980 than March 1979.

Terrestrial invertebrates. – Invertebrates falling into collecting pans were mostly Diptera and Coleoptera adults. Two variables in a multiple regression ana-

Table 4. Percentages of total benthic invertebrate numbers comprised by 3 predominant taxa in 3 streams. Data are from Surber samples collected in January 1980.

Stream (n)	Ephemeroptera		Coleoptera		Diptera	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Queb. Juan Grande (4)	52.6	13.3	19.7	6.3	18.7	11.9
R. Frijolito (6)	35.5	7.1	22.7	6.8	27.3	8.6
R. Sirystes (4)	35.8	10.0	19.7	8.2	24.7	12.6

lysis accounted for 65% of the variance in the abundance of terrestrial invertebrates (Fig. 4). Abundances increased significantly with stream size and were about 6 times greater in January 1980 than March 1981.

Fish community

Twenty-seven fish species were captured during the study, with little variation among sampling periods in species' occurrences in each stream (Table 5). Several species known to occur in streams of the area were not captured (M. Power, personal communication). Although probably common in most streams (J. Graham, personal communication), only 3 specimens of *Synbranchus marmoratus* were collected. This species was excluded from further analysis since it was not adequately sampled with our methods.

No species were found exclusively in Region 3, but 8 species found in Region 2 were absent from Region 3 (Table 5). Species numbers increased with

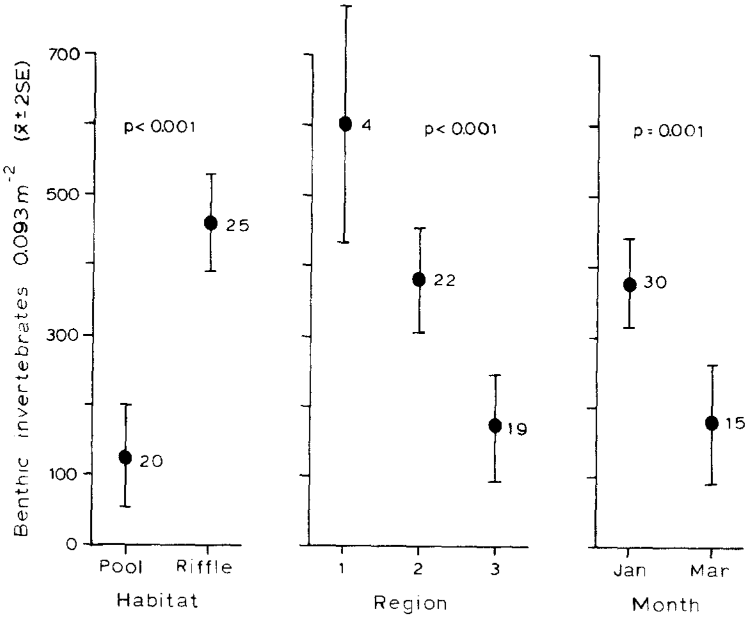

Fig. 3. Number of benthic invertebrates in Surber samples from streams along the Pipeline Road. Numbers beside means indicate the sample sizes associated with values taken by independent variables (horizontal axes). Means and standard errors are estimated from a multiple regression model.

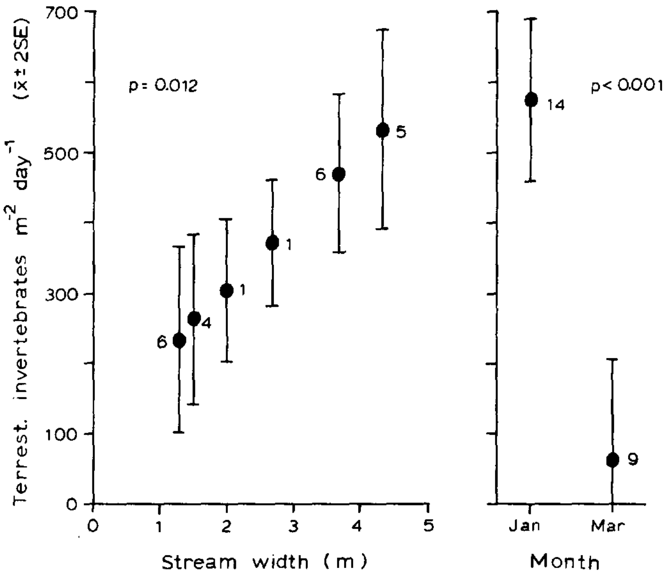

Fig. 4. Number of terrestrial invertebrates falling into collecting devices in streams along the Pipeline Road. Numbers beside means indicate sample sizes associated with values taken by independent variables. Means and standard errors are estimated from a multiple regression model.

stream size in both Regions 2 and 3. Numbers of species inhabiting the R. Frijoles and R. Mendosa were probably underestimated due to the relatively small amount of sampling done in those streams. Streams of Region 2 consistently supported more species than Region 3 streams of similar size.

Feeding guild assignment. – Average % volumes comprised by major food types (algae, aquatic invertebrates, terrestrial invertebrates, etc.) were computed over individuals of each of 30 fish species and size groupings (Table 6). Four species (*Pimelodella*, *Aequidens*, *Brycon*, *Astyanax*) exhibited substantial shifts in diet composition with increasing size. These species were divided on the basis of total length into 2 (or 3, in the case of *Brycon*) size groupings for the purposes of assigning them to feeding guilds.

Each species or size grouping was assigned to a feeding guild largely on the basis of a cluster analysis using Horn (1966) overlap measures (Fig. 5). Algivore, aquatic insectivore, and general insectivore guilds were composed of species or size groupings overlapping in food use by at least 90%. Algivores and aquatic insectivores specialized in eating attached algae and aquatic invertebrates, respectively. General insectivores consumed similar proportions of aquatic and terrestrial invertebrates. *Roeboides* was the only species that ate substantial numbers of fish scales, while *Hoplias* was the only species specializing on other fish. Five species or size groupings ate several food types (including plant and animal). These were all assigned to the omnivore guild, even though the proportions of their diets comprised by various food types were more variable than in other guilds. *Brycon* greater than 130 mm TL specialized on terrestrial plant material, and constituted the terrestrial herbivore guild. Diet differences between March and January were not sufficient to affect guild assignments of any species or size grouping. Nearly all guts contained identifiable food. In only 2 genera (*Rivulus* and *Hoplias*) were guts empty in more than 10% of individuals (Table 6).

Table 5. List of fish species used in food habits and fish distribution analyses, and total number of species per stream. Species entries indicate number of sampling periods species was captured. Numbers in parentheses indicate number of sampling periods that stream was sampled. Total species numbers were computed over the 3 sampling periods.

	Regions								
	1	2				3			
	Juan Grande (2)	Frijoles (1)	Frijolito (3)	Limbo (2)	Tower (3)	Mendosa (1)	Sirystes (3)	Pilon (2)	Tayra (3)
Characidae									
Cheirodon gorgonae	2		1	2					
Gephyrocarax atricaudata	2	1	3	2	3			2	
Astyanax ruberrimus	2	1	3	2	3	1	3	2	
Bryconamericus emperador	2	1	3	2	3	1	3	2	
Hyphessobrycon panamensis	2	1	3	2	3				
Roeboides guatemalensis	2	1	2	1				2	
Brycon petrosus		1	3			1	3	2	
Lebiasinidae									
Piabucina panamensis	2	1	3	2	3	1	1	1	3
Erythrinidae									
Hoplias microlepis	2	1	2	1	2				
Hypopomidae									
Hypopomus occidentalis	2	1	3	1	2		3	2	3
Pimelodidae									
Rhamdia wagneri	2		3	1					
Pimelodella chagresi		1	3			1	2	2	
Imparales panamensis			3		1				
Trichomycteridae									
Trichomycterus striatum	1	1	2				3	2	3
Loricariidae									
Hypostomus plecostomus		1	3	1					
Chaetostomus fischeri		1	2			1	2	2	
Ancistrus chagresi	1	1	3	1					
Rhineloricaria uracantha	2	1	3		1	1	2		
Cyprinodontidae									
Rivulus brunneus	2		3	2	3	1	3	2	3
Poeciliidae									
Poecilia sphenops	2	1	3	2	2	1	3	1	1
Neoheterandria tridentiger	2	1	3	2	3		3		
Brachyraphis episcopali	2		2	2	2	1	3	2	3
Brachyraphis cascajalensis	2	1	3	2	3	1	3		
Cichlidae									
Aequidens caeruleopunctatus	2	1	3	2	3	1	2	2	
Geophagus crassilabris		1	3		3				
Cichlasoma panamensis	2								
Total species	20	20	25	18	16	12	15	14	6

Guild distributions. – Multiple regression analyses were used to test for correlations between estimates of guild biomass densities (g m^{-2}) and 4 independent environment variables: month, habitat, region and stream width. No significant differences in feeding guild biomass were observed between January and March samples. Habitat type was the variable most often correlated with guild distribution. Six of the 7 feeding guilds were most concentrated in pools and least concentrated in riffles (Fig. 6). Similar densities of aquatic insectivores were found in riffles, raceways, and pools. Regional effects on feeding guild density were observed for *Roeboides* (scale-eater) and *Hoplias* (piscivore). *Roeboides* abundance increased from Region 3 to Region 1 ($p = 0.001$) while *Hoplias* was never captured in Region 3 (Table 5). Species richnesses of the algivore, aquatic insectivore, and general insectivore guilds were consistently higher for Region 2 than Region 3 streams of similar size (Fig. 7). Apparent declines in species richness for these guilds in the largest streams (Frijoles and Mendosa) are probably not real, but artifacts of less intensive sampling relative to other streams.

Effects of stream size were observed for both biomass density and species richness patterns of feeding guilds. Both density (Fig. 8) and species richness (Fig. 7) of algivores increased with increasing stream size. Aquatic insectivore density declined downstream (Fig. 8) even though species richness increased (Fig. 7). Terrestrial herbivores (large *Brycon*) were more abundant in larger streams (Fig. 8), and, indeed, never occurred in streams without deep pools. The number of types of omnivores present also increased with stream size (Fig. 7), while the number of general insectivore species remained relatively invariant across stream size.

In summary, distributions of guild biomass among habitats and streams were complex. Algivores reached greatest densities in large pools of Region 2, but their presence was sporadic and variable. Aquatic insectivores became less abundant in larger streams, but were found regularly in all habitats. More species of aquatic insectivores occurred in Region 2 than Region 3. Scale-eaters (*Roeboides*) achieved highest densities in deep pools

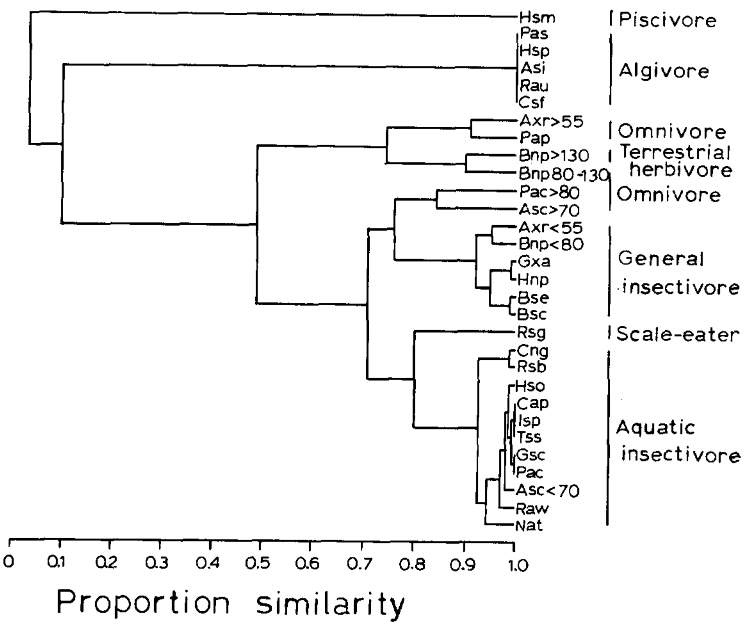

Fig. 5. Dendrogram used to assign fish species and size groupings to feeding guilds. Clusters are based on Horn (1966) overlap values of diet compositions as listed in Table 6.

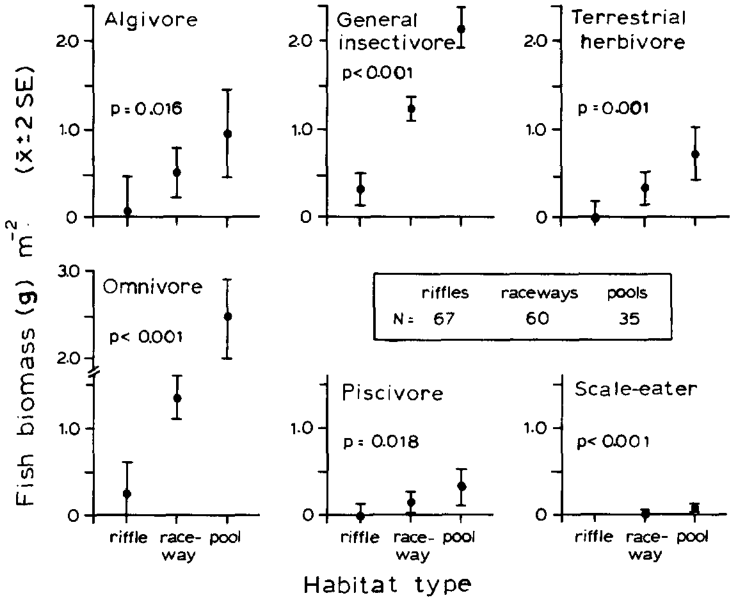

Fig. 6. Distribution of fish feeding guilds among habitat types in streams along the Pipeline Road. Means and standard errors are estimated from multiple regression models.

Table 6. Percent volumes ($\bar{x} \pm$ SE) of various food types found in guts of fish species from Pipeline Road streams for March 1979 and January 1980. Acronyms beside species names are used as reference in Figure 5. Four genera (*Pimelodella*, *Aequidens*, *Astyanax* and *Brycon*) are listed in separate size classes.

Guild/genus (code)	% Algae	% Aquatic invertebr.	% Terrest. invertebr.	% Terrest. plant mat.	% Fish	% Fish scales	No. of guts with food
Algivores							
Ancistrus (Asi)	100 ± 0						5
Hypostomus (Hsp)	100 ± 0						3
Chaetostomus (Csf)	100 ± 0						3
Rhineloricaria (Rau)	100 ± 0						5
Poecilia (Pas)	100 ± 0						5
Aquatic insectivores							
Hypoponus (Hso)	3 ± 2	97 ± 2		1 ± 0.3			37
Trichomycterus (Tss)		90 ± 7		0.3 ± 3			18
Pimelodella (Pac)							
<80 mm		99 ± 1	1 ± 1				9
Rhamdia (Raw)		94 ± 5	1 ± 1	3 ± 3		2 ± 2	13
Imparales (Isp)		100 ± 0					12
Aequidens (Asc)							
<70 mm	0.5 ± 0.4	95 ± 2	2 ± 1	0.2 ± 0.2	2 ± 2		30
Geophagus (Gsc)		98 ± 1	1 ± 1	1 ± 1			12
Cichlasoma (Cap)		90 ± 10					10
Rivulus (Rsb)		87 ± 7	15 ± 6	1 ± 0.4	2 ± 2		26
Neoheterandria (Nat)	9 ± 5	88 ± 6	3 ± 3				30
Cheirodon (Cng)	0.8 ± 0.8	87 ± 13	13 ± 13				6
General insectivores							
Brachyraphis cascajalensis (Bsc)	2 ± 2	47 ± 7	51 ± 6	0.2 ± 0.2			24
B. episcopali (Bse)		49 ± 6	49 ± 6	1 ± 1			39
Hyphessobrycon (Hnp)	1 ± 1	32 ± 6	61 ± 7	6 ± 3			35
Gephyrocarax (Gxa)		25 ± 6	73 ± 6	3 ± 1			38
Brycon (Bnp)							
<80 mm		54 ± 8	31 ± 7	15 ± 6			26
Astyanax (Axr)							
<55 mm	7 ± 4	45 ± 7	39 ± 6	9 ± 3			33
Omnivores							
Aequidens (Asc)							
≥70 mm	1 ± 1	45 ± 16	6 ± 4	22 ± 11	25 ± 16		7
Pimelodella (Pac)							
≥80 mm		46 ± 18	16 ± 15	38 ± 15			4
Piabucina (Pap)	19 ± 5	14 ± 5	39 ± 7	20 ± 5	6 ± 3	0.2 ± 0.2	41
Brycon (Bnp)							
80–130 mm		10 ± 5	18 ± 6	72 ± 7			28
Astyanax (Axr)							
≥55 mm	10 ± 4	6 ± 3	39 ± 6	47 ± 6		0.3 ± 0.2	38
Terrestrial herbivores							
Brycon (Bnp)							
>130 mm		0.4 ± 0.4	6 ± 3	89 ± 4	4 ± 3		14
Piscivores							
Hoplias (Hsm)					100 ± 0		6
Scale-eaters							
Roeboides (Rsg)		58 ± 9	3 ± 3	4 ± 4		27 ± 9	17

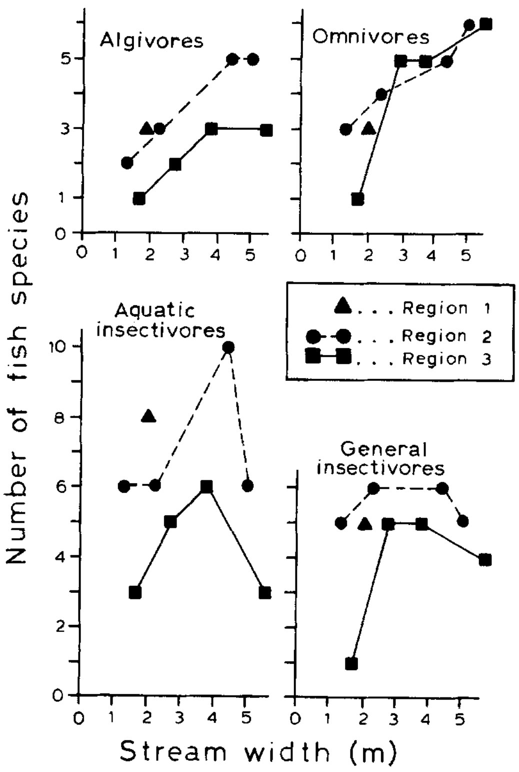

Fig. 7. Species richness patterns of fish feeding guilds illustrating effects of region and stream size. Species numbers were computed over all samples. Guild assignments are given in Table 6.

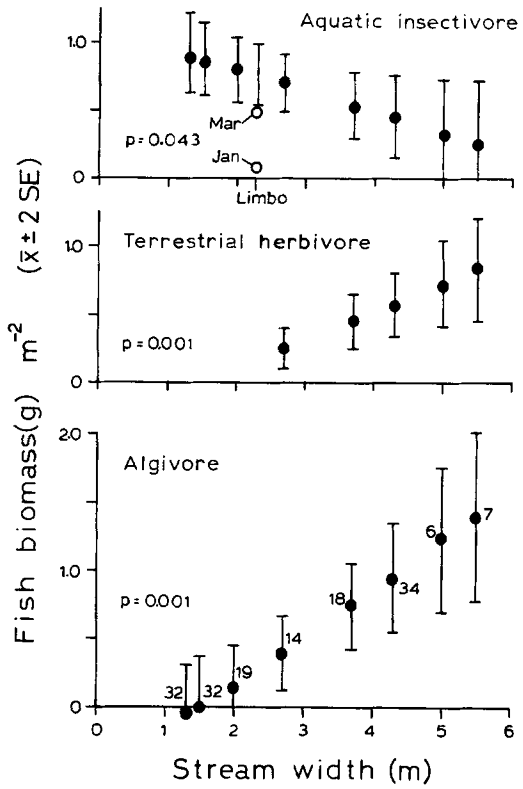

Fig. 8. Effects of stream size on biomass densities of fish feeding guilds. Numbers beside means in the bottom graph indicate the number of habitat units sampled in each stream. Means and standard errors are estimated from multiple regression models. Open circles in the top graph indicate biomass values observed in R. Limbo in March 1979 and January 1980.

of Region 1. Piscivores (*Hoplias*) were most common in pools of Region 1 and 2. General insectivores were abundant in most pools, particularly Region 2. Terrestrial herbivores (large *Brycon*) occurred sporadically, but only in deep pools. Omnivores were also widespread and abundant especially in pools.

Fish distributions. – Fish distributions were also affected by severe seasonality in discharge. All stream discharges were low during March 1979, but only R. Limbo (Region 2) was reduced to widely separated pools. Fish density was comparable to that expected on the basis of stream size, with most fish biomass being small general insectivores. In January 1980, R. Limbo's discharge was substantial, but fish density was low compared to other streams. This effect was observed for aquatic insectivores (Fig. 8) as well as general insectivores and omnivores.

Relative importance of food types. – The importance of 5 major food resources (algae, aquatic invertebrates, fish, terrestrial invertebrates, terrestrial plants) was assessed by attributing fish biomass to a given food resource in proportion to the volume occupied by that food resource (from Table 6) in fishes' guts. For example, we assumed that 2%, 97%, and 1% of the biomass of *Hypopomus* was supported by algae, aquatic invertebrates, and terrestrial plant material respectively, while 100% of the biomass of *Imparales* was supported by aquatic invertebrates. Allocation of fish biomass to various food resources was performed for each stream each

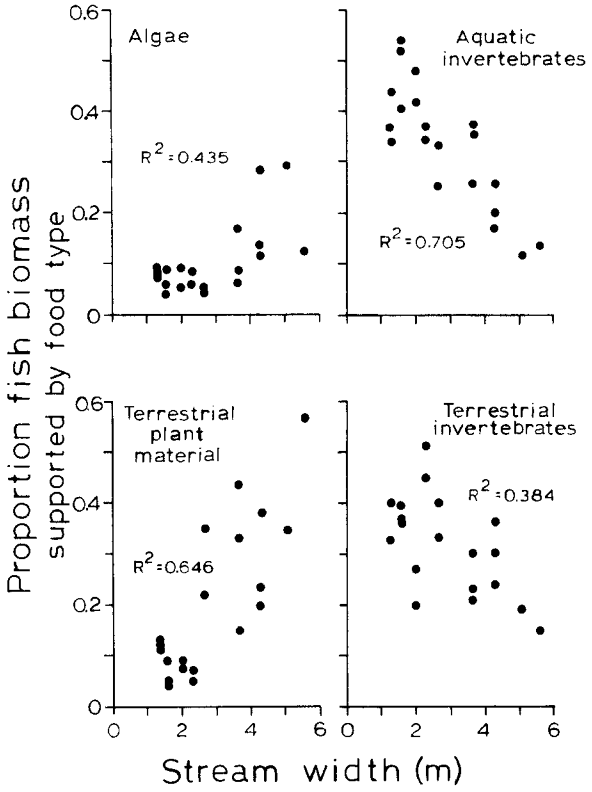

Fig. 9. Effect of stream size on the relative importance of 4 major food resources in supporting fish biomass. Each point represents data pooled from all habitats sampled from a stream during a sample period. All 4 regressions are significant at p <0.004.

time it was sampled. These data were then converted to proportions to yield relative importance values of each food resource in supporting the fish community.

Relative importance values of each food resource were regressed on 3 independent environmental variables: month, region and stream width. No food resource differed in the proportion of the fish biomass it supported between January and March samples. A regional effect was significant only for the relative importance of fish (including scales) as food. Proportion of fish biomass supported by other fish increased from Region 3 through Region 1 ($p < 0.001$; $R^2 = 0.628$). Stream width was the best predictor of the importance of food resources to the fish community (Fig. 9). Both terrestrial and aquatic invertebrates declined in relative importance as stream size increased, while algae and terrestrial plant material became proportionally more important food resources downstream.

Food resources can be more broadly classified as autochthonous (i.e. algae, aquatic invertebrates, fish) or allochthonous (i.e. terrestrial invertebrates, terrestrial plant material). Regression analyses indicated that the relative importance of allochthonous foods increased slightly but significantly ($p = 0.016$) with stream size. A regional effect was also significant ($p = 0.040$) for the relative importance of aquatic versus terrestrial foods. Seven fish species found in Region 2, but not in Region 3, specialized on aquatic foods. This effect suggests that for a given stream size, the effectiveness of canopy shading is correlated with the proportion of the fish biomass supported by terrestrial foods.

Size distribution of fish. – Most individual fishes in our study streams were less than 90 mm TL. We analyzed the distributions of particularly small (<40 mm TL) and large (>100 mm TL) fish using multiple regression techniques to ascertain differences in distribution by size groups. Data from the R. Frijoles and R. Mendosa were not available for this analysis. Abundances (number m^{-2}) of small fish were correlated with habitat type, stream width and month (Fig. 10). Small fish were most common in deep pools and least common in riffles, a pattern observed for most feeding guilds. Small fish became less abundant in larger streams despite the fact that deep pools were more common there. Furthermore, most small fishes were general insectivores, which did not become less abundant with respect to biomass as stream size increased (see Guild distributions). Thus, small fishes were most common in deep pools of small streams. Small fishes were less abundant in the R. Limbo than expected for a stream its size (Fig. 10), again illustrating the impact of severe seasonality in discharge. Small fishes were also more abundant in March than January (Fig. 10) probably a result of reduced habitat availability at the end of the dry season. A similar pattern of seasonality was observed for numbers of fish >100 mm TL ($p = 0.005$).

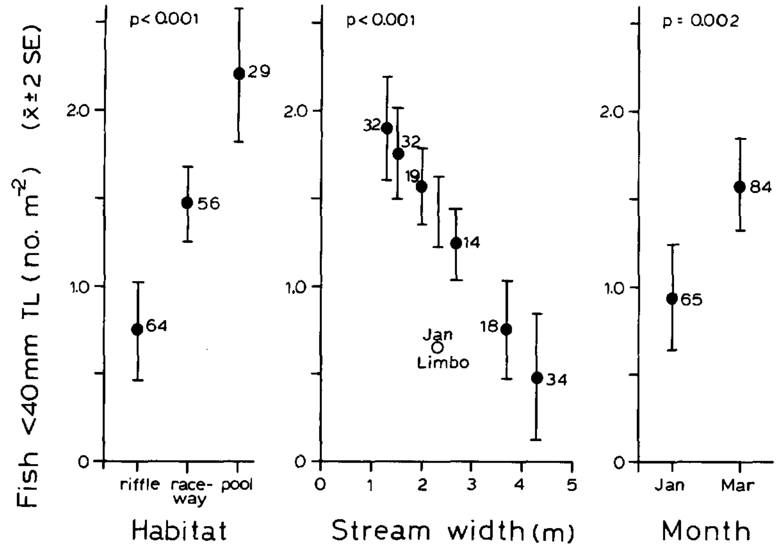

Fig. 10. Densities of small fish (< 40 mm TL) as a function of habitat type, stream size, and month. Numbers beside means indicate sample sizes associated with values taken by independent variables (horizontal axes). Means and standard errors are estimated from a multiple regression model.

Discussion

Distributions of animals among available habitats are generally mediated by 3 factors: food availability, predation intensity and tolerance of physicochemical conditions (Connell 1975). Commonly, these factors impose conflicting selection pressures on an individual's habitat use and, as a result, adaptations evolve to reconcile opposing selective forces. In fishes and other vertebrates, which are characterized by complex sensory capabilities and behavioral responses, habitat selection is an important adaptive component of a species' ecology (Partridge 1978, Morse 1980). Habitat selection by fishes may vary with age, sex, reproductive state, geographic area, and environmental conditions (Karr et al. 1982), and represents an integration of numerous ecological factors. The fluvial processes responsible for forming pools and riffles, however, are similar in all streams, and provide a basis for comparing patterns of habitat use among streams.

The impacts of physicochemical stresses on fish communities of tropical streams are most apparent in waters with exceptionally low pH (Roberts 1973, Janzen 1974, Lowe-McConnell 1975) or strongly seasonal discharge (Lowe-McConnell 1975, Goulding 1980). To our knowledge, pH, temperature, dissolved oxygen, or other physicochemical features of streams along the Pipeline Road are not particularly stressful to the fishes living there. Thus, we interpret observed differences in fish distribution among habitats and streams only in light of distributions of food resources and predators since these two factors are probably the primary determinants of habitat selection by these fishes.

Food availability patterns

Benthic invertebrates. – A major food resource used by stream fishes is benthic invertebrates. Benthic invertebrate abundances in this study varied among habitats, streams and seasons (Fig. 3). Other workers have reported invertebrates to be more abundant in riffles than in pools for both temperate (Rabeni & Minshall 1977, Slobodchikoff & Parrott 1977) and tropical (Fittkau 1964, Petr 1970, Bishop 1973) streams. Temperate populations of invertebrates undergo marked seasonal fluctuations in abundance, perhaps in response to pulses in availability of the organic material on which they feed (Hynes 1970). Lowest invertebrate numbers usually occur during late summer when discharges are also likely to be lowest, a pattern analogous to that reported here for tropical streams. A study by Power (1983) on the R. Frijoles indicates that algal productivity is low in the dry season despite an increase in light availability. This result is consistent with the seasonal patterns we observed for benthic invertebrates, many of which rely on algae for food.

The differences in benthic invertebrate abundances we observed among regions along the Pipeline Road may be explained on the basis of presumed productivity differences among regions. Increasing abundances through Regions 1, 2 and 3 are consistent with patterns expected if light limits primary productivity, which, in turn, limits secondary productivity. Reduced invertebrate abundances in tropical streams due to scouring discharge have been recently reported by Stout (1982) but since dry season rainfall differs little among Regions 1, 2 and 3 (Panama Canal Co. climatological data), differences in benthos abundances among regions are probably not due to differences in scouring frequency.

Terrestrial invertebrates. – The importance of terrestrial invertebrates as a food resource for stream fishes is particularly apparent in tropical systems (Inger & Chin 1962, Lowe-McConnell 1975). Yet, to our knowledge, no data on temporal and spatial variability of this resource are available for comparison. Anecdotal reports (Zaret & Rand 1971, Lowe-McConnell 1975) support the pattern observed here (Fig. 4) of lower abundances during the dry season. Our results are also consistent with data from Barro Colorado Island where canopy insects >5 mm were more numerous in January than March for 4 of the 5 years from 1972–1976 (Rubinoff 1974, Windsor 1975, 1976, 1977). Terrestrial invertebrates may usually be more available to stream fish in wet seasons due to higher general productivity and greater stream area relative to dry seasons. Furthermore, rain and runoff are probably effective means of transferring invertebrates from their normal substrates to streams.

Spatial variation in terrestrial invertebrate abundances is probably more complex than seasonal variation. One might expect terrestrial invertebrates to be most abundant where foliage is most dense. Our data indicate, however, that wide streams (effectively more open canopies) have greater numbers of terrestrial invertebrates than narrow ones (Fig. 4). The causal mechanisms for this pattern are unknown, but may be related to changes in foliage density profiles or air turbulence along the canopy openness gradient.

Other food resources. – Data on the temporal and spatial dynamics of other major food resources used by stream fish are rarely seen in the literature, yet certain patterns are expected. For example, the availability of attached algae to fish and invertebrates should increase as the canopy opens due to higher light availability, provided that stable substrates are available. However, reductions in algal availability during the dry season were reported by Power (1983) as a result of siltation and a decline in the amount of submerged substrate. Other potential food resources such as terrestrial fruits, flowers, and green leaves are probably also available seasonally due to pulses in production. Seasonal fluctuations in the availability of these foods are pronounced in South American forests (Gottsberger 1978, Goulding 1980) and are accentuated by seasonal changes in fishes' accessibility to them. Fishes relying on fruits and seeds for food have evolved seasonal migratory behaviors to effectively exploit this resource when the forest is inundated (Gottsberger 1978, Goulding 1980).

Food use by fishes

Dietary shifts with maturity. – Fish diets represent an integration of food preferences with food availability and accessibility. Changes in diet with fish size were apparent in: *Aequidens*, *Astyanax*, *Pimelodella*, and *Brycon* (Table 6). In all 4 species diets of small individuals were predominantly composed of insects, while larger individuals increased their intake of other food types. In *Brycon* the largest individuals specialized on terrestrial plant material. It is unknown whether these dietary shifts resulted from changes in food preferences or changes in the abilities of fish to acquire preferred foods. For example, larger fishes may be more adept, because of their greater speed, at acquiring food items striking the surface than smaller fishes. Certainly, larger fish are morphologically capable of using a wider range of food sizes. Changes in diet with fish size have been reported for numerous North American species that grow relatively large (Pflieger 1975, Keast 1977a, 1977b, Smith 1979). In a study of Amazonian fishes Knoppel (1970) concluded that dietary differences among conspecifics of different sizes were not substantial, although 4 of the 7 species he examined increased the proportion of terrestrial insects eaten as they matured, and 5 of the 7 species decreased the proportion of aquatic invertebrates eaten as they matured. The degree of change in food habits with fish size may be related to the relative importance of intra- and interspecific competition for food (Keast 1977b).

Fish distributions

Food and predator abundances in this study varied along gradients of habitat type, stream size and region. We examined these distributions with respect to fish distributions in an attempt to estimate the relative importance of food availability and predation to the organization of fish communities.

Habitat gradients. – Aquatic invertebrates were more abundant in riffles than pools (Fig. 3), yet aquatic insectivore fishes were not particularly concentrated into riffles. However, some benthic genera (e.g. *Imparales*, *Trichomycterus*) were found almost exclusively in riffles. Terrestrial foods are presumably equally abundant in all habitats, yet fishes relying on those foods were most concentrated into pools. The relative paucity of fish in riffles might be explained on the basis of the energetic expense incurred by a fish trying to maintain its position in fast turbulent water. However, this argument does not account for the differences in fish densities observed between raceways and pools (Fig. 6), where currents were negligible. A simpler explanation for the concentration of fishes into deep habitats is that deep water affords refuge from numerous avian and mammalian predators that inhabit the area (4 species of kingfishers, several species of herons and numerous mammals). Power (1983) presents evidence for the importance of predation pressure as a determinant of loricariid distribution in the R. Frijoles. Additional support comes from the low densities of fishes observed in the highly seasonal R. Limbo where predation by birds and mammals is probably particularly intense during dry periods.

A trade-off exists for small fishes that enter pools to avoid terrestrial predators in that piscine predators (generally relatively large fishes) are more common in deep habitats. Small fishes could concentrate into pools of smaller streams where piscine predators are not very common. Our results are consistent with this hypothesis, but the majority of small fishes in our study streams were poeciliids and juvenile characoids, mostly general insectivores. Since their numbers declined significantly downstream (Fig. 9) but general insectivore biomass did not, small fishes seemed to be replaced by larger characoids downstream. Further study is necessary to distinguish whether small general insectivores concentrate into upstream pools to avoid larger competitors or piscine predators.

The concentration of small fish into pool habitats in Panama streams is in contrast with the pattern observed by Schlosser (1982) in a similar size stream in Illinois. In Illinois, young-of-the-year cyprinids and centrarchids, which feed largely on aquatic invertebrates, were most abundant in riffle habitats. Similarly, Power (1983) reported that juvenile loricariid catfishes (algae grazers) were more abundant in riffles, where algal densities were greatest.

Gradients among streams. – Aquatic invertebrates were more abundant in less shaded streams (Fig. 3) while terrestrial invertebrates were more abundant in larger streams (Fig. 4). Neither aquatic insectivore nor general insectivore densities were closely correlated with abundances of their food resources among streams. In contrast, algivore densities increased downstream, a pattern that might also be expected for abundance of attached algae since light availability increases downstream. *Hoplias* (piscivore) was never found in Region 3 and *Roeboides* (scale-eater) was found in only 1 stream of Region 3. Since fishes in general were least abundant in Region 3, the distributions of these 2 fish-exploiters seem to correspond to the distribution of their food resources. Unfortunately, we have no data on variation in abundances of fish-eating birds among different streams and regions. We assume, therefore, that they exert similar fishing pressures on all streams.

We conclude that fish biomass distributions among habitats within a stream appear to be more closely related to dangers of predation by birds and mammals than to the distribution of food resources. Distributions of small fish, however, are more closely correlated with food abundance. Distributions of fish biomass along gradients of stream size and canopy openness are complex, the correlations with food abundances varying among feeding guilds.

Relative importance of feeding guilds. – Streams along the Pipeline Road were dominated (both biomass and numbers) by fishes with relatively generalized diets (general insectivores and omnivores). Fishes with more specialized diets (algivores, terrestrial herbivores, piscivores) generally comprised minor components of the fish community, but often became relatively more abundant in larger streams (Fig. 8). In addition, species richness of feeding guilds increased with stream size and canopy openness (Fig. 7). At the community level, biomass of fish dependent on autochthonous food resources (i.e. algae, benthos, fish) decreased as stream size increased but increased as canopy openness increased for a given stream size.

These patterns suggest that increases in trophic diversity may be generally correlated with increases in food resource 'reliability', where reliability is some measure of productivity and predictability. This hypothesis, supported by a theoretical model of species packing developed by MacArthur (1970), can be used to explain differences in stream trophic diversity between such widely separated regions as Panama and the midwest United States. Midwestern U.S. streams typically support 1 or 2 algivorous species (Pflieger 1975, Smith 1979) compared with 5 algivores in the R. Frijoles. In addition, no fish species in the Midwest specialize on terrestrial plant material as do adult *Brycon* in Panama. The relative importance of terrestrial invertebrates as a food resource is typically less in the Midwest than in Panama (Lotrich 1973, Pflieger 1975, Smith 1979, Angermeier 1982). Parallel explanations of trophic diversity have been proposed to account for differences in feeding guild structure between temperate and tropical communities of forest birds (Karr 1975) and bats (Fleming 1973). Temperate system patterns similar to those observed here for Panama include downstream additions of species and guilds (Kuehne 1962, Sheldon 1968, Lotrich 1973, Gorman & Karr 1978, Horwitz 1978). (In contrast to our observations, Lotrich 1973, reported a decline in the importance of allochthonous foods to the fish community as stream size increased in Kentucky.)

Our work in small streams in Panama, as well as studies by others in large tropical rivers (Lowe-McConnell 1975, Goulding 1980), indicates that tropical fishes are dependent on foods derived directly from the riparian forest. This pattern suggests that large scale alterations in forest composition and structure may have serious impacts on the integrity of tropical stream communities. Deforestation, pollution and other human disturbances are likely to impose major effects on shading, discharge variability, siltation, nutrient loads and availability of various foods. Precise predictions of how these environmental changes will affect fish community structure are not possible, in part, because little is known of the natural history of most tropical species, but analogous modifications in Midwest streams have resulted in lower species and trophic diversities and higher rates of disease and hybridization (Greenfield et al. 1973, Karr 1981). Indirect effects of deforestation on Midwest streams include elevated and more variable water temperatures, lower discharge during drought periods, and shifts in habitats toward shallower pools and finer substrates. These conditions select for species that are more tolerant of physicochemical stress, generalized in food habits, and lack strict spawning requirements. Species that depend directly on allochthonous foods such as fruits may be lost since such resources probably become more scarce. Increases in siltation would likely inhibit autochthonous productivity, perhaps resulting in fewer fish and invertebrates that require algae for food. Loss of deep pools through siltation or channelization could shift the size structure of the fish community toward small individuals. Clearly, more information on the requirements and interactions of stream organisms is necessary if the integrity of tropical streams is to be maintained in the face of expanding human populations and technology.

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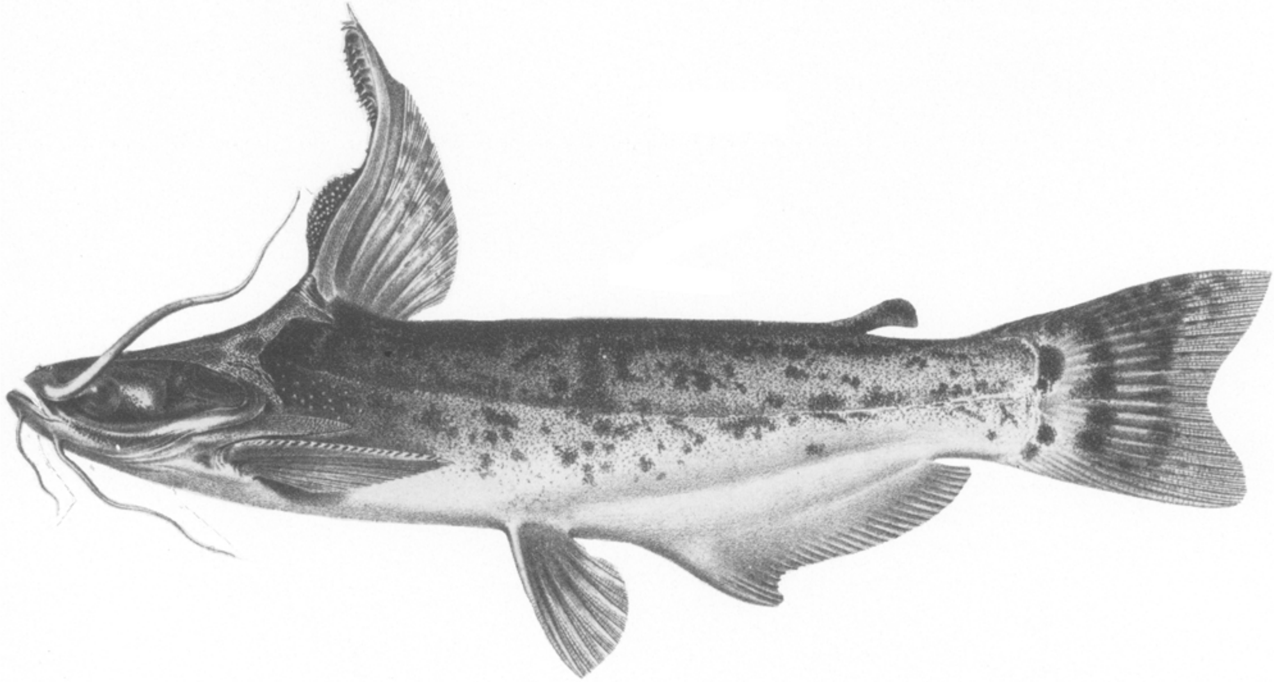

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