Fish-assemblage variation between geologically defined regions and across a longitudinal gradient in the Monkey River Basin, Belize

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Abstract. Linkages between geology and fish assemblages have been inferred in many regions throughout the world, but no studies have yet investigated whether fish assemblages differ across geologies in Mesoamerica. The goals of our study were to: 1) compare physicochemical conditions and fish-assemblage structure across 2 geologic types in headwaters of the Monkey River Basin, Belize, and 2) describe basin-scale patterns in fish community composition and structure for the benefit of conservation efforts. We censused headwater-pool fishes by direct observation, and assessed habitat size, structure, and water chemistry to compare habitat and fish richness, diversity, evenness, and density between streams in the variably metamorphosed sedimentary geologic type typical of 80% of Belize's Maya Mountains (the Santa Rosa Group), and an anomalous extrusive geologic formation in the same area (the Bladen Volcanic Member). We also collected species-presence data from 20 sites throughout the basin for analyses of compositional patterns from the headwaters to the top of the estuary. Thirty-nine fish species in 21 families were observed. Poeciliids were numerically dominant, making up 39% of individuals captured, followed by characins (25%), and cichlids (20%). Cichlidae was the most species-rich family (7 spp.), followed by Poeciliidae (6 spp.). Habitat size and water chemistry differed strongly between geologic types, but habitat diversity did not. Major fish-assemblage differences also were not obvious between geologies, despite a marked difference in the presence of the aquatic macrophyte, *Marathrum oxycarpum* (Podostemaceae), which covered 37% of the stream bottom in high-nutrient streams draining the Santa Rosa Group, and did not occur in the low-P streams draining the Bladen Volcanic Member. Correlation analyses suggested that distance from the sea and amount of cover within pools are important to fish-assemblage structure, but that differing abiotic factors may influence assemblage structure within each geologic type. The fauna showed weak compositional zonation into 3 groups (headwaters, coastal plain, and nearshore). Nearly 20% of the fish species collected have migratory life cycles (including *Joturus pichardi*, *Agonostomus monticola*, and *Gobiomorus dormitor*) that use freshwater and marine habitats. Some of these species probably rely on a natural flow regime and longitudinal connectivity for reproduction and dispersal of young, and natural flow regime and longitudinal connectivity are important factors for maintenance of functional linkages between the uplands and the coast in the ridge-to-reef corridor where the Monkey River is located. Therefore, we suggest that the viability of migratory fish populations may be a good biological indicator of upland-to-estuary connectivity important both to fishes and coastal ecosystem function. We recommend follow-up studies to substantiate the relative strengths of relationships between community structure and abiotic factors in contrasting geologies and to examine potential bottom–up responses of stream biota to the higher nutrient levels that were observed in stream waters draining the Santa Rosa Group geologic type.

Key words: tropical streams, aquatic ecosystems, geology, longitudinal patterns, water chemistry, habitat, Mesoamerica.

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Understanding and predicting the composition and structure of biological communities in stream ecosystems is a central challenge of aquatic ecology and also is a prerequisite to the development of science-based

conservation programs. For conservation biologists working in poorly studied areas of the world, where data are scarce or absent, inferences about the factors structuring biotic assemblages must be based initially on information from elsewhere. One logical conceptual starting point is to place aquatic communities in the framework of nested-hierarchy theory, which has gained prominence in stream ecology over the past several decades. Nested-hierarchy theory suggests that stream systems are organized as a nested hierarchy of physical units, whereby larger-scale abiotic factors (i.e., surficial geology, climate, land use) constrain the structural and dynamic organization of local-scale physical-habitat elements (i.e., geomorphology, physicochemistry), which may in turn regulate biological communities (Allen and Starr 1982, Frissell et al. 1986, Poff 1997). From this theoretical perspective, one can begin to identify and understand linkages between landscape features, local abiotic conditions, and biotic assemblages.

The body of existing research on fish communities in Mesoamerica supports the idea that local-scale abiotic factors influence stream fish assemblages, and it also points to the importance of landscape position, particularly distance from the sea. Studies that attempt to relate fish-assemblage characteristics to habitat characteristics have found that substrate diversity and diversity of water depths (Gorman and Karr 1978, Angermeier and Schlosser 1989), current velocity and habitat diversity (Bussing and Lopez 1977), and habitat size (Winemiller 1983, Angermeier and Schlosser 1989) are important correlates to assemblage attributes. Several studies have demonstrated compositional zonation (Winemiller and Leslie 1992, Rodiles-Hernández et al. 1999) and declining richness, evenness, and species diversity as distance from the sea increases (Lyons and Schneider 1990). Another study has shown that fish richness and trophic function shift relative to stream size and canopy openness along a longitudinal gradient (Angermeier and Karr 1983). These studies are strongly biased geographically toward fish assemblages in streams and rivers of Panama and Costa Rica, with only one study of assemblages in streams and rivers from southern Nicaragua to southern Mexico (Lacanja River, Mexico: Rodiles-Hernández et al. 1999).

Though not yet demonstrated in Mesoamerica, surface geology is a landscape characteristic generally known to constrain and determine abiotic factors in streams and rivers. These abiotic factors include drainage-network patterns, basin hydrology, sediment supplies to local reaches, local channel morphology, ionic concentrations, and nutrient chemistry (Dillon and Kirchner 1975, Hynes 1975, Richards et al. 1996, Knighton 1998). For these reasons, geology is regularly considered in multiscale analyses of the influence of abiotic factors on stream ecosystems (e.g., Richards et al. 1996, Wiley et al. 1997, Wang et al. 2003, McRae et al. 2004, Reid et al. 2005). Several studies have implicated geology in the compositional and structural organization of stream fish populations (Hicks and Hall 2003) and communities (Wiley et al. 1997, Chen and He 2001, Yap 2002, Wang et al. 2003).

Our study, completed in the Monkey River Basin of Belize, is the first study to investigate species distributions and community structure in this small but biologically rich country. The Monkey River offers an excellent opportunity to generate and test hypotheses regarding the influence of surface geology on habitat and species assemblages because of strong geologic distinctions between its headwater branches. It is also a strategic basin in a ridge-to-reef conservation corridor called the Maya Mountain Marine Transect (MMMT), which is of key conservation significance (Heyman and Kjerfve 1999; Fig. 1A). The primary goal of our study was to compare physicochemical conditions and fish assemblages in streams across 2 major geologic types. We hypothesized that physical habitat, water chemistry, and fish community structure (richness, evenness, diversity, and density) would reflect underlying geologic differences. A secondary goal was to describe longitudinal patterns in fish-assemblage composition from the mountains to the sea to identify physical or biological attributes of conservation significance.

Methods

Study site

The Monkey River, located on the southeastern flank of the 1120-m high Maya Mountains in southern Belize, is the 4th-largest basin in Belize (1275 km^2), and the 2nd-largest river draining the Maya Mountains. The river consists of 3 branches (Bladen, Trio, and Swasey) that join in the coastal plain, and flow 15 km to enter the Caribbean Sea as a 6th-order river (Fig. 1B). The headwaters of the Monkey River primarily drain undisturbed tropical broadleaf forest and are almost entirely protected in 3 contiguous reserves. In the coastal plains, all branches flow through a matrix of human-influenced landscape types including commercial banana cultivation, gravel mining, and subsistence agriculture. The mainstem portion of the river, below the confluence of the Bladen and Swasey Branches, is largely undeveloped.

The Monkey River Basin receives >3000 mm of precipitation annually in distinct wet and dry seasons, causing periods of flooding and drought. Most precipitation falls from July to October, when river
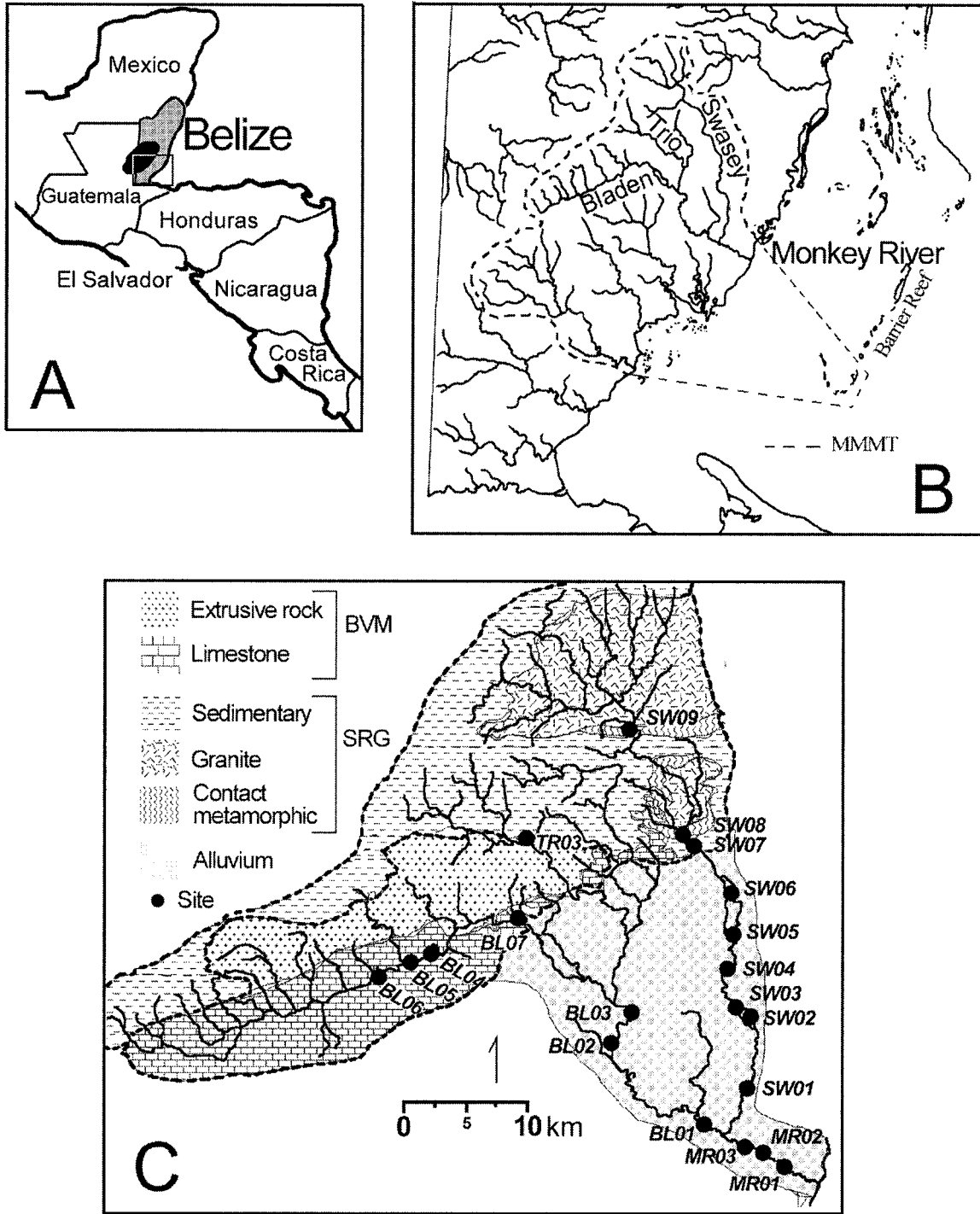
FIG. 1. A.—Central America showing the location of Belize (shaded region) and the position of the Maya Mountains (black region). B.—Major branches of the Monkey River and the Maya Mountain Marine Transect (MMMT) in Belize. C.—Geologic formations (Bateson and Hall 1977) making up the 2 geologic regions (Santa Rosa Group [SRG] and Bladen Volcanic Member [BVM]) and sampling sites in the Monkey River Basin. BL = Bladen Branch, TR = Trio Branch, SW = Swasey Branch, and MR = Monkey River.

discharges account for ~84% of the annual total (Heyman and Kjerfve 1999). In contrast, the dry season is characterized by low precipitation and stable baseflow conditions.

The headwaters of the Monkey River drain 2 distinctive geologic groupings (Fig. 1C). The 1st group, which is typical of 80% of the total area of the Maya Mountains, is a combination of local geologies

composed of variably metamorphosed sedimentary rocks, known as the Santa Rosa Group, with localized granitic intrusions and some contact metamorphism (Bateson and Hall 1977). We refer to this group simply as the Santa Rosa Group (SRG). The 2nd group consists of an anomalous geologic formation in the Maya Mountains composed of lavas and associated extrusive volcanic sediments that adjoins an area of Cretaceous karstic limestone (Bateson and Hall 1977). We refer to this group simply as the Bladen Volcanic Member (BVM). Of the 3 Monkey River headwater branches, one originates in the BVM, and the others begin in the SRG. There are multiple geologic types within the 2 groupings presented here, but we have aggregated them to reflect a clear difference between the Bladen Branch headwaters, and the mixed geologies typical of much of the rest of the Maya Mountains. We consider this reasonable because site-level substrates and water chemistry are likely to be the product of all upstream geologies combined. Within our headwater study reaches, all of the branches had typical riffle-run-pool morphology with occasional cascades. No major waterfalls existed below any of the sites studied.

A stratified-random sample of 20 study sites was selected from streams of $\geq$4th-order. Four sites were selected from each geologic type (4 BVM sites from Bladen Branch [BL04–BL07], 3 SRG sites from Swasey Branch [SW07–SW09], and 1 SRG site from Trio Branch [TR03]) (Fig. 1C). Remaining sites were selected from the coastal plains portion of the Bladen Branch (3 sites: BL01–BL03), Swasey Branch (6 sites: SW01–SW06), and Monkey River mainstem (3 sites: MR01–MR03). The Swasey coastal plain was represented by more sites to better assess effects of banana agriculture in that area (results not presented here). Because of the remoteness of upper river reaches, only those reaches within 2 full days of hiking were entered into the pool of potential study sites. To select specific study sites, a map of the river was divided into 1-km segments.

Segments were selected randomly, and our upstream-most transect was placed in the nearest riffle to the top of each selected segment. All sites were visited twice during baseflow conditions between February and May 2000. On the 1st visit, a team of 4 people assessed habitat and fish assemblages and, on the 2nd visit, samples for water chemistry were collected.

Sampling methods

Habitat conditions.—Methods for physical habitat sampling were adapted from approaches outlined by Simonson et al. (1993) and Gorman and Karr (1978). Thirteen transects separated by a distance equal to 3× the mean stream width were sampled at each site. At each transect, wetted width, water depth, fish cover type and extent, and habitat type (e.g., riffle, run, pool, or backpool) were determined. Depth and dominant substrate type (Table 1) were recorded at 5 equidistant points across each transect. Fish cover types (Table 1) were rated from 0 to 4 according to the % of a 10-m-wide zone centered on each transect line occupied by each cover type (0 = cover type absent, 1 = 0–10% covered, 2 = 10–40%, 3 = 40–75%, 4 = >75%; after Lazorchak et al. 1998). At each site, the % of the bottom of the entire reach covered by aquatic plants or algae was estimated visually. Water-quality and plant-cover-age data were collected at the site level, but our analysis of pool fish-assemblage attributes was based on habitat data collected in pools only.

Discharge was measured at one transect for each site in representative run habitat. We used a Marsh McBirney® flow meter to measure water velocity at 60% of depth for each of 20 uniformly spaced segments of the transect. Discharge was the sum of the water velocities multiplied by the area of each segment.

Water quality.—A YSI/Grant® automated portable water-quality meter and sonde were used to measure dissolved O_2, temperature, conductivity, and turbidity

TABLE 1. Depth, substrate, and fish cover categories used in diversity calculations with the Shannon index. Within each fish-cover category, values between 0 and 4 were assigned based on the % of a 10-m wide zone around the transect occupied by the cover type (0 = cover absent, 1 = 1–10% covered, 2 = 10–40%, 3 = 40–75%, 4 = >75%). These weighted values were summed for all cover types at each transect before being used in calculations.

Habitat variable		Category							
		1	2	3	4	5	6	7	8
Depth	Range (cm)	0–25	25–50	50–75	>75				
	Description	Very shallow	Shallow	Moderate	Deep				
Substrate	Diameter (mm)	0.06–2	2–16	16–64	64–250	250-4000			
	Description	Sand	Fine gravel	Coarse gravel	Cobble	Boulder	Bedrock		
Cover	Description	Filamentous algae	Macrophytes	Large woody debris	Small woody debris	Overhanging vegetation	Boulders	Undercut banks	Artificial structures

at the top of each study reach at the beginning of the first day of sampling. On a separate day, three 250-mL water samples were collected at each site and immediately placed in a dark cooler on ice until they could be frozen solid (within 24 h). Samples were transported frozen to the analytical chemistry laboratory at the University of Georgia Institute of Ecology, thawed, and processed. In the lab, pH was measured on thawed unfiltered samples. Unfiltered samples were then digested (persulfate digestion) and total P and total N were analyzed using automated colorimetry. Soluble reactive P (SRP), NH_4^+, and NO_3^- in filtered samples were analyzed using automated colorimetry (APHA 1998).

Community composition.—A combination of methods was used to collect fishes for our analysis of longitudinal patterns in assemblage composition. Our goal was to capture or observe as many species as possible in all habitats present within the limitations of available time and shocker battery life. All wadeable habitats at a site were sampled using a battery powered Smith--Root backpack electrofisher. Electrofishing samples were collected by making one pass through each habitat type (riffle, run, pool, and backpool). In riffles, fishes were shocked in the area above a 2×5 m seine (5-mm mesh) that blocked the channel. In runs and shallow pools, samples were collected by shocking and dip-netting fishes near cover (e.g., boulders, woody debris, undercut banks), from open areas free of cover, and from within the water column. At coastal plain stations, shocking in the daytime yielded a narrow subset of the assemblage. Therefore, sampling was done during the moonless portion of the night to capture more taxa. Riffles were still sampled during the day. Deep pools in the coastal plain were fished by angling and trotlines to add species for our presence/absence analysis. In addition, snorkeling transects were completed (see description below) in clear headwater pools to add species to the presence list. We cannot claim that all species at a site were captured because we were unable to exhaustively sample any site. We are confident that we captured most of the common species at each site, but it is likely that we missed some uncommon species. For these reasons, we conservatively interpret our presence data as representing common species within the assemblage.

All fishes were identified to species in the field, using the dichotomous key of Greenfield and Thomerson (1997), and released once positively identified. Individuals with uncertain identifications were preserved in 10% formalin for later confirmation, as were voucher specimens. Voucher collections were deposited at the Georgia Museum of Natural History (Athens, Georgia, USA) and at St. John's College (Belize City, Belize).

Headwater community structure.—Headwater pool habitats routinely had water clarity >4 m, allowing efficient census of fishes by direct observation. Our method involved 10-min snorkel counts along transects perpendicular to the direction of flow. Ten minutes was long enough to swim an entire transect, yet short enough to prevent recounts of individual fish. Transects were spaced 15 m apart perpendicular to the channel length in all available pool habitat at a given site to ensure that no 2 observers counted fishes within the same area. This spacing was determined based on a maximum underwater visibility of 7.5 m observed in pilot studies. The same 4 observers were trained and tested for identification accuracy prior to fieldwork and made all observations. To avoid recounts and chasing fishes ahead of the observers, all transects in a pool were assessed simultaneously, if possible, and movement between transects was done out of the water along the banks.

During timed transects, each observer visually identified and counted individuals of all species on both sides of the transect line. Data were recorded on an underwater writing cuff. All species were readily identifiable to species from external morphology with the exception of catfishes in the genus *Rhamdia*, of which 2 species may have been present. Thus, this taxon was identified only to genus. The small-bodied but highly abundant tetra (*Astyanax aeneus*) could not be counted accurately because of their schooling behavior, but were present and assumed to be numerically dominant at all sites. It also is likely that cryptic species (e.g., *Gobiomorus dormitor*, *Ophisternon aenigmaticum*, *Awaous banana*) were underrepresented in our visual samples.

For each site, the maximum horizontal underwater visibility was estimated underwater by determining the limit of visibility using a Number 10 tin can painted with a Secchi black-and-white pattern (sensu Helfman 1983). Two times this value was multiplied by transect length to estimate the area sampled by each visual transect using the equation $A = 2vL$, where A is the area of transect surveyed, v is visibility, and L is transect length.

Statistical analyses

Longitudinal patterns in assemblage composition at the basin scale were investigated using cluster analysis, correlation analysis, and qualitative examination of species presence/absence data. Cluster analysis was used to examine patterns in compositional similarity between different sites for presence/absence data with the Unweighted Pair-Group Method Using Arithmetic Means (UPGMA) and Jaccard's coefficient as a

measure of similarity (PC-ORD, version 4.10, MjM Software Design, Gleneden Beach, Oregon). After verifying approximate normality of data, Pearson product–moment correlation was used to evaluate the relationship between distance from sea and species richness. In addition, fish species lists compiled for headwater areas, coastal plains area, and the Monkey River mainstem were qualitatively examined.

For the headwater pool fish data, fish–habitat relationships were analyzed for all sites regardless of geology by examining the strengths of correlations between fish species richness, diversity, and evenness and measures of longitudinal position (distance from sea), habitat size (wetted width and depth), habitat heterogeneity (Shannon diversity of depths, substrates, and cover types, and proportional abundance of different substrates), and fish cover (fish cover index). Pearson product–moment correlation was used as our test statistic because these data met the assumption of normality. Water chemistry, habitat measures, and fish community metrics were compared between sites in the 2 geologic groups with Student's t-tests or Wilcoxon rank-sum tests. If the data were approximately normally distributed and had roughly equal variances, Student's t-tests were used; otherwise, Wilcoxon rank-sum tests were used.

Physical habitat data from points along transects in pool habitats were combined and used to calculate mean wetted width, mean water depth, and mean fish cover ratings. Width estimates for pool habitats from underwater visual samples were used to calculate mean wetted width. The Shannon index of diversity ($H' = -\sum_{i=1}^{n} p_i \ln(p_i)$, where n = the number of categories and p_i = the proportion of category i in the total sample) was used to calculate diversity values for depth categories, substrate size-class frequencies, and frequency occurrences of different fish cover types (Table 1).

For pool fish data, species counts from underwater visual transects were used to calculate species richness, species diversity, and evenness. Richness was estimated at each site using the Jackknife estimator (model M_h) developed by Burnham and Overton (1979; see also Nichols et al. 1998) using the interactive online version of the CAPTURE program (White et al. 1978; www.mbr-pwrc.usgs.gov/software.html). This procedure reduces bias in estimates of richness by accounting for unequal detection probabilities among species using occurrence information for each taxon across transects. Assumptions to run this test are that: 1) populations are closed, 2) species detection probabilities are constant across transects, 3) observations at transects are independent events, and 4) sampling effort is equal for each transect (Burnham and Overton

1979). These assumptions were reasonably met for our sampling approach and data. Species diversity, evenness, and fish density were calculated for each transect and averaged across all transects at a site to yield a mean value. Comparisons of diversity, evenness, and density (excluding *A. aeneus*) potentially would have been biased by unmeasured differences in electrofisher sampling efficiency among sites; therefore, these analyses were restricted to visual data collected in pools, where the sampling protocol was the most standard. The Shannon index of diversity was used as the measure of species diversity, and evenness was calculated by dividing species diversity by the natural logarithm of the total number of species in the sample (ln$S$; Magurran 1988). All of the above analyses except cluster analysis and jackknife richness were done with JMP Software (version 3.2, SAS Institute, Cary, North Carolina).

Results

A total of 5714 fishes were captured by electrofishing, angling, and trotlines. An additional 6113 fishes were counted during underwater visual assessment. Assemblage samples contained 39 species in 21 families (Table 2). Poeciliids were numerically dominant across electrofishing samples and made up 39% of individuals captured. They were followed in abundance by characins (25%), and cichlids (20%). Cichlidae was the most species-rich family (7 spp.), and Poeciliidae was the 2nd-most species-rich family (6 spp.).

Longitudinal patterns

The correlation between number of species observed and distance from sea was strongly negative (Fig. 2). The importance of longitudinal position was further reinforced by the site-by-species dendrogram of compositional similarities among sites. The dendrogram showed 3 site groupings with most headwater sites in one group, all coastal plains sites of both major branches in another group, and Monkey River mainstem sites in a *nearshore* group (Fig. 3). Station TR03, a high-elevation station on the Trio Branch, grouped alone. Careful examination of the site-by-species matrix revealed that the TR03 assemblage was compositionally most similar to other headwaters sites (with *Agonostomus monticola* and *Heterandria bimaculata* present) but had a lower species count (14 spp. vs mean = 17.29 spp. for other headwaters sites) because several common species were absent.

Several qualitative observations can be made by hierarchically arranging species captured in each of these longitudinal zones (Table 2). Seventeen species occurred in all zones and made up the species core for

TABLE 2. Species present at study sites grouped as headwaters, coastal plains, and nearshore faunal groups. Sites are listed in order of distance from sea (furthest [left] to nearest [right]) and are labeled as in Fig. 1. Bold font indicates species names of the core faunal group (see text for explanation). x indicates species presence at a site, blank indicates absence. – = nonmigratory or status unknown.

Species	Headwater								Coastal plains									Nearshore			Family	Migratory status
	BL06	SW09	BL05	BL04	TR03	BL07	SW08	SW07	SW06	SW05	BL03	SW04	BL02	SW03	SW02	SW01	BL01	MR03	MR02	MR01		
Joturus pichardi	x	x																			Mugilidae	Catadromous[a]
Heterandria bimaculata	x	x	x	x	x	x	x	x							x						Poeciliidae	–
Agonostomus monticola	x	x	x	x	x	x	x	x	x	x											Mugilidae	Amphidromous[b]
Rhamdia laticauda	x	x	x	x		x	x	x	x	x	x	x	x	x							Pimelodidae	–
Astyanax aeneus	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	Characidae	–
Brycon guatemalensis	x	x	x	x	x	x	x								x	x	x	x	x	x	Characidae	–
Belonesox belizanus	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	Poeciliidae	–
Gambusia luma	x	x	x	x		x	x	x	x	x	x	x	x	x	x			x	x	x	Poeciliidae	–
Poecilia mexicana	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	Poeciliidae	–
Xiphophorus helleri	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			Poeciliidae	–
Atherinella sp.	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	Atherinopsidae	–
Ophisternon aenigmaticum		x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	Synbranchidae	–
Pomadasys crocro			x			x	x				x	x	x	x	x	x		x			Haemulidae	Catadromous[c]
Amphilophus robertsoni	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		Cichlidae	–
Archocentrus spilurus	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x	x	x	Cichlidae	–
Cichlasoma salvini		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	Cichlidae	–
Vieja maculicauda	x	x	x			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	Cichlidae	–
Gobiomorus dormitor	x					x			x	x	x	x			x	x	x	x	x	x	Eleotridae	Catadromous[d]
Awaous banana	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x		x	Gobiidae	Amphidromous[e]
Hyphessobrycon compressus									x	x	x	x	x	x	x	x		x	x		Characidae	–
Petenia splendida									x		x		x						x		Cichlidae	–
Thorichthys meeki				x				x	x	x	x	x	x		x						Cichlidae	–
Rhamdia guatemalensis									x	x	x	x	x	x	x	x	x	x			Pimelodidae	–
Xiphophorus maculatus													x								Poeciliidae	–
Achirus declivus																x					Achiridae	–
Microphis brachyurus																x					Syngnathidae	Amphidromous[c]
Eucinostomus melanopterus									x						x		x	x	x	x	Gerreidae	–
Megalops atlanticus																				x	Megalopidae	–
Anchoviella belizensis																				x	Engraulidae	–
Ariopsis assimilis																		x	x	x	Ariidae	–
Strongylura timucu																		x	x	x	Belonidae	–
Centropomus ensiferus															x			x	x		Centropomidae	–
Centropomus parallelus																			x		Centropomidae	Juvenile
Lutjanus griseus																		x	x	x	Lutjanidae	–
Lutjanus jocu																		x	x		Lutjanidae	–
Eugerres plumieri																		x		x	Gerreidae	–
Cichlasoma urophthalmus																		x	x		Cichlidae	–
Eleotris amblyopsis																		x	x		Eleotridae	–
Cytharichthys spilopterus																				x	Paralychthyidae	–

[a] Cruz (1987)
[b] Considered amphidromous by Loftus and Gilbert (1992) from a review of indirect evidence, but designation uncertain
[c] Greenfield and Thomerson (1997)
[d] Considered catadromous by Gilmore (1992) from a review of indirect evidence, but designation uncertain
[e] Gilmore and Yerger (1992)

the assemblages measured. In each longitudinal zone, several specialists were added to this core group, probably driving the longitudinal distinctions indicated by the cluster analysis. In the headwaters, the core group was joined by several species that seem to thrive in high-elevation habitats. These species include the migratory mullets *Joturus pichardi* and *A. monticola* that feed in the fast-flowing waters of riffles and cascades; and the two-spot live bearer, *H. bimaculata*. The coastal plain fauna consisted of the core group plus several species with affinities for slow, warmer waters, such as the Guatemalan chulin (*Rhamdia*
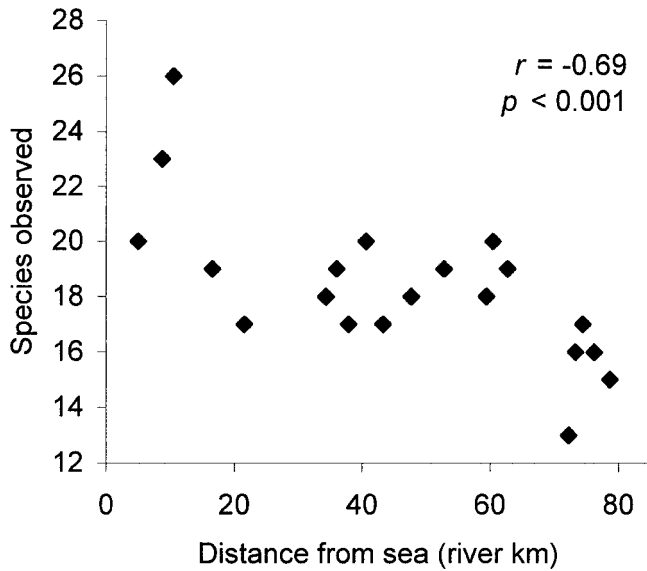
FIG. 2.   Scatterplot showing the number species collected at a sampling site vs the distance of the site from the sea.

guatemalensis), the southern platyfish (*Xiphophorus maculatus*), and several fishes from marine-affiliated families (*Microphis brachyurus*, *Eucinostomus melanopterus*). Nearshore sites in the mainstem consisted of the core group plus a number of salt-tolerant species, even though our lowest site was still above the dry-season saltwater wedge.

Headwater assemblage structure

Headwater sites were located between ~59 and ~79 river km from the sea and ranged in length from 507 to 1170 m. Headwater-pool habitats ranged in width from 13.1 to 31.3 m (Table 3). Twenty-one species of fishes were observed in headwater pools in 51 underwater transects at 8 sites (mean = 6.4 transects/site). With *A. aeneus* excluded from the sample because of the infeasibility of counting this abundant species, *Archocentrus spilurus*, the blue-eye cichlid, was the numerically dominant species in visual samples (mean = 39% of individuals counted; Table 3) followed by *Poecilia mexicana* (28%). From jackknifed richness estimates, the mean richness across headwater sites averaged 12.5 (SE = 2.2; Table 3).

Patterns across geologies.—Correlation strengths were examined for all pairwise combinations of community metrics and habitat variables to identify relationships between species richness, diversity, evenness, and abiotic variables (longitudinal position, habitat size, and habitat heterogeneity) regardless of geology. Only 2 correlations with $p < 0.05$ resulted. In a result that mirrors the pattern for electroshock data at all sites, jackknifed species richness decreased with distance from sea ($r = -0.77$, $p = 0.03$), and fish density was negatively related to the amount of fish cover in pools ($r = -0.70$, $p = 0.05$).

Patterns between geologies.—Comparisons of habitat and water-quality variables between the 2 geologic
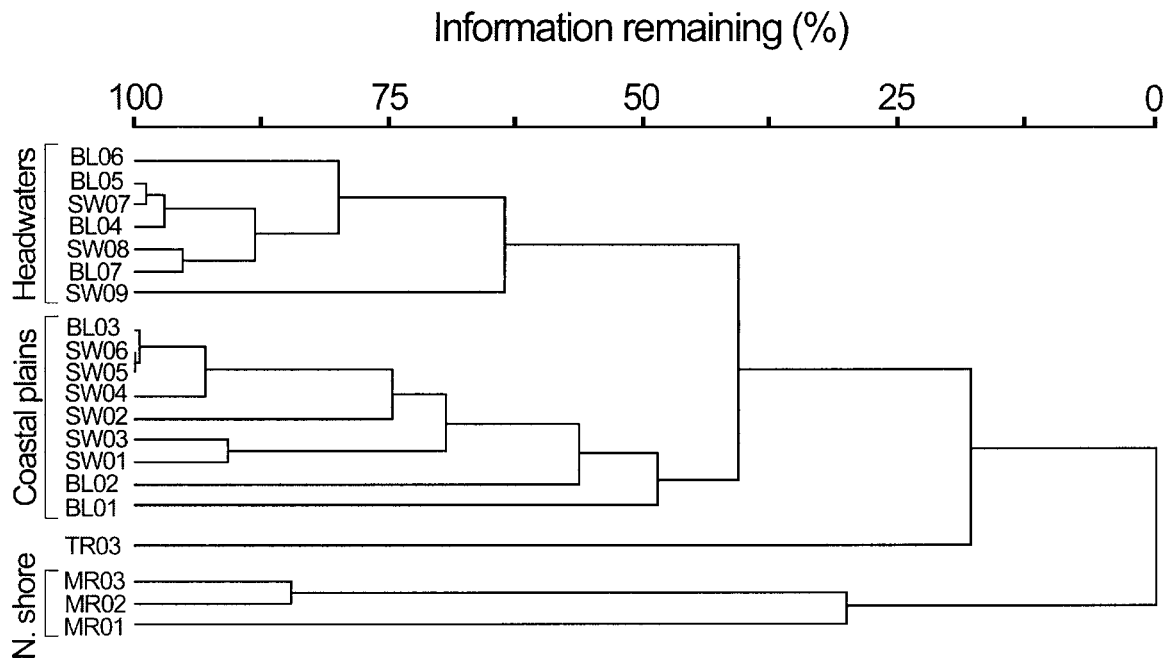

FIG. 3.   Cluster dendrogram showing similarities between fish species compositions at 20 sampling stations in the Monkey River Basin. Sample sites are labeled as in Fig. 1. N. shore = nearshore.

Table 3. Selected physical and biological variables for headwater sampling stations; BVM = Bladen Volcanic Member geologic combination, SRG = Santa Rosa Group combination.

Station	Geological region	Distance from the sea (km)	Station length (m)	Stream discharge (m^3/s)	Mean pool width (m)	Mean pool depth (cm)	*Archocentrus spilurus* (% of individuals counted)	Species censused	Jackknife richness
BL04	BVM	73.3	644	1.5	13.1	50.1	41	9	11
BL05	BVM	74.5	702	1.5	31.3	60.4	16	10	10
BL06	BVM	78.6	585	3.2	17.5	104.5	49	9	10
BL07	BVM	62.7	1170	1.0	20.3	65.8	30	14	16
Mean	BVM	72.3	775	1.8	20.6	70.2	34	10.5	12
SW07	SRG	59.4	780	8.8	18.1	114.1	29	9	12
SW08	SRG	60.4	780	5.9	29.1	103.4	20	14	17
SW09	SRG	76.2	624	2.9	13.0	122.1	3	8	11
TR03	SRG	72.2	507	2.8	20.6	85.8	65	11	13
Mean	SRG	67.05	673	5.1	20.2	106.4	29	10.5	13

combinations (BVM and SRG) revealed a pronounced pattern (Fig. 4A–H). Eight of the variables measured showed significant differences ($p < 0.05$) between geologic combinations based on Student's t-tests (pool depth [Fig. 4A], underwater visibility [Fig. 4B], pH [data not shown]) and Wilcoxon rank-sum results (SRP [Fig. 4C], NO_3^- [Fig. 4D], N:P ratio [Fig. 4E], conductivity [Fig. 4F], % aquatic vegetation cover [Fig. 4G]). Significant differences were not evident between depth diversity ($Z = 1.3$, $p = 0.19$; data not shown), substrate diversity ($t = 1.4$, $p = 0.21$; data not shown), or cover diversity ($t = 1.4$, $p = 0.20$; data not shown). Discharge was higher in SRG sites, though this difference was not significant ($Z = 1.59$, $p = 0.11$; Fig. 4H). Sites in the BVM were characterized by neutral pH, high conductivity, elevated N values, and low P values (mean SRP = 0.002 mg/L; Fig. 4C). Sites in the SRG exhibited the opposite pattern, with significantly more alkaline pH, lower conductivity, lower N, and higher P values (mean SRP = 0.024 mg/L; Fig. 4C). N:P ratios (calculated as the molar ratio of NH_4-N + NO_3-N to SRP-P; Fig. 4E) indicated that BVM sites were likely to be P limited (mean N:P = 243.37), and SRG sites were likely to be N limited (mean N:P = 5.77; Redfield 1958). SRG streams also had a large proportion of their substrates covered in dense stands (mean = 37.5% of area covered) of the macrophyte *Marathrum oxycarpum* (Podostemaceae, Burger 1983; Fig. 4G). BVM sites were without macrophytes.

Comparisons of community metrics between geologies with Student's t-tests did not show significant differences for jackknifed richness, species diversity, or evenness. Only pool fish density showed a statistically significant difference between geologies, with sites in the SRG having more fish per unit area (0.52 fish/m^2 ± 0.01 SE) than those in the BVM (0.47 fish/m^2 ± 0.01 SE; Fig. 4I).

Our examination of nonparametric correlation strengths between the habitat data and community metrics within each geologic combination revealed statistically significant relationships in both the BVM and SRG sites (Table 4). In the SRG geologic combination, richness was positively related to both fish cover diversity (H'cover) and % sand substrate, and evenness was positively related to depth diversity (H'depth) and negatively related to average pool depth. In the BVM geologic combination, species richness was positively related to % cobble substrate, and negatively related to distance from sea; fish density was negatively related to cover diversity; evenness and species diversity were both negatively related to depth diversity and positively related to % gravel substrate.

Discussion

Comparison of geologies

To our knowledge, our study represents the first detailed account of fish communities in rivers of Belize that considers longitudinal patterns and community structure. As such, it is a valuable foundation of baseline information with the potential to inform aquatic conservation efforts and to generate hypotheses for future research. We investigated hypotheses about the influences of geology on local habitat and biota by comparing physicochemistry and community metrics across BVM and SRG geologies. Our hypothesis that physical habitat and chemistry would clearly reflect differences in underlying parent geology was well supported for headwater pools, although some important factors (notably diversities of substrate, depth, and habitat) did not differ significantly between geologies. Our hypothesis that fish community structure (richness, evenness, diversity, and density) also would reflect geology was not well supported for reasons discussed below.
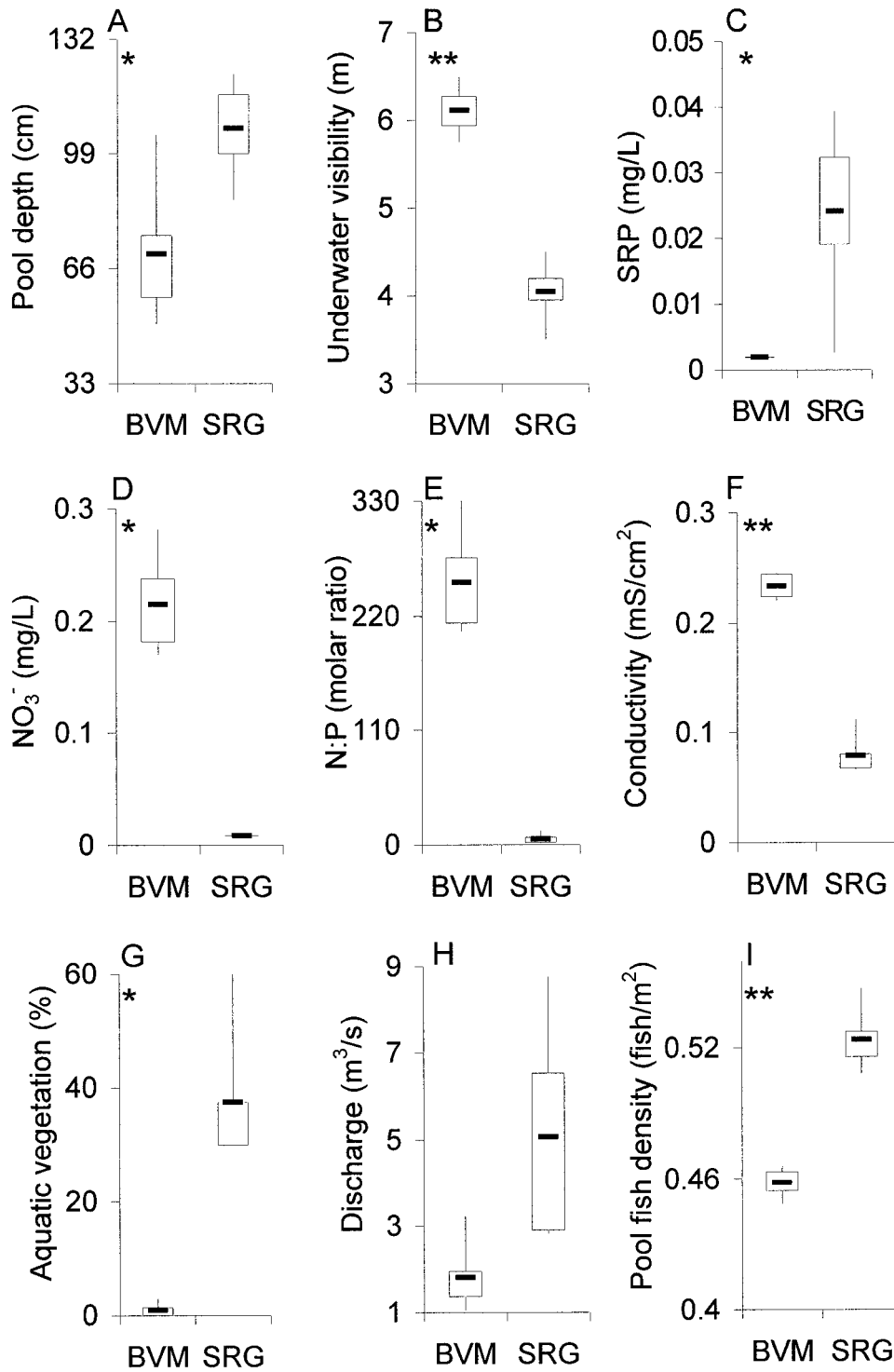
FIG. 4. Box-and-whisker plots of physical or chemical variables that differed significantly between sites in Bladen Volcanic Member (BVM) and sites in Santa Rosa Group (SRG) geologies. The top and bottom of a box indicate 25% and 75% quartiles, respectively, the dark bar inside the box is the mean, and the vertical lines show the range of values. A.—Pool depth. B.—Underwater visibility. C.—Soluble reactive phosphorus (SRP). D.— NO_3^-. E.—N:P ratio. F.—Conductivity. G.—% aquatic vegetation cover. H.—Discharge. I.—Pool fish density. Asterisks represent significance levels from t-tests or Wilcoxon rank-sum tests (* = $p < 0.05$, ** = $p < 0.01$).

Table 4. Correlation results by geologic combination, community metric, and habitat variable. BVM = Bladen Volcanic Member geologic combination, and SRG = Santa Rosa Group geologic combination (see text for details). $n = 4$ for each correlation. H' = Shannon diversity.

| | | Community metrics | | | | | | | |
| | | Richness | | Diversity | | Evenness | | Density | |
Geology	Correlate	r	p	r	p	r	p	r	p
SRG	H'cover	1.00	0.000	–	–	–	–	–	–
	% sand	1.00	0.000	–	–	–	–	–	–
	H'depth	–	–	–	–	1.00	0.000	–	–
	Pool depth	–	–	–	–	−1.00	0.000	–	–
BVM	Distance from the sea	−0.95	0.05	–	–	–	–	–	–
	% cobble	0.95	0.05	–	–	–	–	–	–
	H'cover	–	–	–	–	–	–	−1.00	0.000
	H'depth	–	–	−1.00	0.000	−1.00	0.000	–	–
	% gravel	–	–	1.00	0.000	1.00	0.000	–	–

The geology of the Monkey River headwaters related strongly to aspects of the size and physicochemistry of local pool habitats. However, strong linkages between geology and assemblage structure were not clear in our data. Only one measured biotic variable, fish density, differed statistically across geologies despite the many abiotic differences. Thus, our data suggest that fish assemblages did not differ strongly across geologies based on the metrics we assessed. It is debatable whether a fish density difference of 0.05 fish/m^2 is biologically significant. This number represents a 10% difference in density, but translates to only ~6 more fishes counted in the average 120-m^2 SRG transect. Our cluster-analysis results and qualitative examination of species presence suggest that the composition of fish communities in each geology type is also very similar. However, despite structural and compositional similarities, our nonparametric correlation analysis (Table 4) suggests that different abiotic factors may be important in structuring the fauna in the different geologic groups. In addition, significant correlations between headwater species richness and distance from sea and between fish density and fish cover suggest that certain abiotic factors are important regardless of geology. Understanding the physical bases for variation in fish assemblages is an important area of future research on the Monkey River, and one that requires a more robust headwater data set. Thus, specific questions to be addressed in future research include: which abiotic factors most strongly influence headwater community structure, and how do patterns differ between geologies?

It is not particularly surprising that the composition and structure of assemblages across geologies did not differ. Compositional similarity is not surprising because many of the species found in the Monkey River headwaters are habitat generalists. Many of the species that occur in headwater pools also occur in the coastal plains and nearshore reaches. Other studies of Mesoamerican fish assemblages have shown that habitat structure and diversity are important determinants of community structure (Gorman and Karr 1978, Angermeier and Schlosser 1989). In our study, all habitat diversity measures and substrate composition measures were similar across geologies. If fish assemblages in the Monkey River are determined by these factors (as they are in Panama; Gorman and Karr 1978, Angermeier and Schlosser 1989), then it follows logically that they would not differ across geologies with similar habitat diversity and substrates.

We were somewhat surprised that fish density, an indicator of fish abundances, did not respond more strongly to greater coverage by *M. oxycarpum* in P-enriched conditions in the SRG. N:P ratios from the 2 geologies suggest strong P limitation in BVM streams where *M. oxycarpum* is absent, and N limitation (i.e., excess P) in SRG waters where dense stands of *M. oxycarpum* are present (Redfield 1958). We propose that increased ambient P in SRG streams may lead to a bottom–up trophic cascade (Peterson et al. 1993, Harvey et al. 1998) in which P fuels productivity of *M. oxycarpum*. It is surprising that this productivity did not transfer to markedly higher abundances of fishes in SRG because enhanced invertebrate production (i.e., food for fishes) has been observed in other systems with *Podostemum* species present (Freeman and Wallace 1984, Grubaugh and Wallace 1995, Hutchens et al. 2004). Such a trophic cascade is not very obvious in our density data, but studies with fish biomass or production as response variables would provide more definitive tests.

It is important to note that the source of elevated P is yet unknown. Increased P in SRG may be linked to the underlying parent material (Dillon and Kirchner 1975),

or may be caused by geothermally modified waters. Studies from Costa Rica have indicated that geothermally modified groundwater can cause elevated P levels in streams near volcanic mountain ranges and that these inputs are patchy but biologically important (Pringle and Triska 1991). Pringle and Triska (2000) pointed out that the occurrence of geothermal waters in Central America can be qualitatively assessed by examining maps for stream names that indicate geothermal modification (e.g., Agrio = sour, Salitral = salty, Caliente = hot). Salada Creek in the Swasey area is the only creek name in the study area that suggests the potential presence of salty geothermally modified water, and active hot springs are present 60 km to the south of the most remote reaches studied here.

Longitudinal patterns in species composition

Three faunal groups were distinguished in the Monkey River assemblage from species presence data: a headwaters group, a coastal plains group, and a separate marine-influenced nearshore group. Distinctions between these groups are largely driven by the presence of a few distinct species added to a fairly ubiquitous group of species that was found at most sites. For instance, the migratory mugilids *J. pichardi* and *A. monticola* dropped out of our catch in the coastal plains as we left the headwaters, whereas other species were added (*R. guatemalensis*, *X. maculatus*). Our collection of the large herbivore *J. pichardi* (maximum standard length = 540 mm at SW09) from high-flow riffle and cascade habitats is the first published record of this species in Belize, although it is reported from countries to the south (Cruz 1987) and north in Mexico (J. Schmitter-Soto, El Colegio de la Frontera Sur, personal communication). Given the migratory tendencies of some species in our headwaters group, these groupings may be valid for dry-season conditions only when adults are in their feeding habitats and not engaged in coastal migrations.

Our species list shows a fauna rich in cichlids and poeciliids, a finding consistent with Miller's (1966) characterization of the northern Mesoamerican (Usumacinta) faunal province as rich in these 2 families. The shortfin molly (*P. mexicana*) and the sleek mosquitofish (*Gambusia luma*) drove the high relative abundances of poeciliids in our electroshock and visual samples, and the small omnivorous blue-eye cichlid, (*A. spilurus*) was particularly dominant in headwater pool assemblages. On average, 32% of the individuals observed were *A. spilurus* (excluding the abundant characid *A. aeneus*), and this cichlid made up 65% of the individuals at one site.

Our work relates to previous studies in several ways. As in previous studies, longitudinal position was an important factor for Monkey River fish-assemblage composition and structure. Two previous studies of basin-scale longitudinal patterns in Central American systems also reported biotic zonation relative to longitudinal position (Winemiller and Leslie 1992, Rodiles-Hernández et al. 1999). Winemiller and Leslie (1992) reported high species turnover across 4 habitats spanning a freshwater–marine ecotone on the Caribbean slope of Costa Rica that correlated to habitat size and salinity gradients. Had we continued to sample to the ocean, it is likely that elements from the headwaters–coastal plain zone would have been replaced by a wholly marine assemblage, similar (but without the lagoon groups) to the assemblage described from the Atlantic coast of Costa Rica (Winemiller and Leslie 1992). Rodiles-Hernández et al. (1999) reported waterfall-induced longitudinal zonation in an inland tropical rainforest river in southern Mexico, with continual addition of species downstream and little species deletion. In the Monkey River, we observed weak zonation in the absence of strong barriers to dispersal. Our species counts at the basin and headwaters levels agree with the counts made by Lyons and Schneider (1990), who documented decreasing species richness with increasing distance from sea in a small Pacific coastal drainage in Costa Rica.

Conservation implications

The information we gathered provides baseline information on fish species and their distributional patterns and provides a starting point from which to develop conservation targets that reflect ecological attributes of central importance to healthy riverine and coastal ecosystems. The Monkey River is the largest basin in the MMMT ridge-to-reef conservation corridor, which encompasses 6 basins, an important estuarine area (Port Honduras), and the southern tip of the Mesoamerican Barrier Reef (Fig. 1). Conservation in this area is largely centered on protecting functional linkages between the uplands and the coast, particularly the tight coupling between basin hydrology and nutrient regime and coastal primary and secondary production (Heyman and Kjerfve 1999). Nearly 20% of the freshwater fishes surveyed in our study also rely on the hydrologic connection between freshwater habitats and the coast to fulfill their migratory life histories. These fishes often rely on longitudinal connectivity and a natural flow regime for their population viability and, thus, may also be good biological indicators of these factors within basins. For example, *J. pichardi* lives its adult life in the headwaters, migrates downstream in floods to the coast where it spawns near the river mouth, and then

returns upstream (Cruz 1987). Timing of high and low flows are assumed to be important cues for this fish's reproduction (Cruz 1987), and disruption of these factors would presumably have a negative effect on *J. pichardi* populations. Longitudinal connectivity that allows passage of migratory fishes is another factor of importance to such species (Ward and Stanford 1989); physical alteration of connectivity can significantly affect up- and downstream migrants (McDowall 1995, Pringle 1997). We suggest that conservationists should focus on migratory fishes as potential indicators of the hydrologic linkages that are so important to conservation of the MMMT.

Geology is an important factor shaping abiotic conditions in the Monkey River headwaters. Our data suggest that fish assemblages in different geologies may be structured according to different habitat factors (Table 4). Identifying the specific habitat factors in each geology that relate to assemblage structure will be a prerequisite to the development of future habitat conservation approaches for freshwater fish habitat. Furthermore, our data clearly suggest that water-quality standards should account for the geologic origins of water sources.

From the standpoint of nested-hierarchy theory, we conclude that geology does constrain physicochemistry, but that this constraint does not translate to major differences in fish community structure. We strongly recommend that future research continue to focus on understanding how abiotic factors influence headwater fish assemblages and the role of underlying geologic variation. At a more general level, we call for increased attention to description of fish communities of Mesoamerica, particularly the western (Chiapas–Nicaraguan) and northern (Usumacinta) faunal regions.

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