Relationships among habitat, ecomorphology and diets of cichlids in the Bladen River, Belize

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Abstract The Neotropical Cichlidae is among the most species-rich and ecologically diverse groups of freshwater fishes. This study investigated interspecific morphological and ecological relationships within an assemblage of six cichlids in the Upper Bladen River, Belize. This portion of the river drains a nearly pristine watershed within a nature reserve, and thus should provide a natural ecological context for interpretation of ecological patterns. Species distributions within morphological, habitat and dietary space yielded patterns consistent with a hypothesis of niche partitioning. Statistical analyses of the species assemblage revealed relationships between two principal morphological gradients from multivariate analysis with several diet and habitat variables, and these patterns were consistent with prior functional morphological interpretations. Given that this local cichlid assemblage contains no congeneric species, it is apparent that morphological divergence resulting in niche segregation reflects selective establishment of species from a more species-rich regional species pool rather than in situ adaptive evolution.

Keywords Cichlidae · Central America · Neotropics · Niche relationships · Ordination · Resource partitioning · Species assemblage

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Introduction

With an estimated 600 species, the Neotropical Cichlidae is among the most species-rich and ecologically diverse groups of freshwater fishes (Farias et al. 1999; López-Fernández et al. 2005). Local cichlid assemblages that contain from one to over 20 species occur in river basins from Texas to Argentina and provide numerous opportunities to study community ecology, adaptive radiation and biogeography. The subclade Heroini includes about 30 genera and 150 species distributed in South and Central America, with a single genus in Cuba and Hispañola (Stiassny 1991; Hulsey et al. 2004). The Heroini is perhaps the most ecologically diverse clade of Neotropical cichlids, with certain species that specialize on specific resources ranging from algae and detritus to insects, crustaceans or fish (Eaton 1943; Winemiller et al. 1995; Valtierra-Vega and Schmitter-Soto 2000; Waltzek and Wainwright 2003). In addition to having diverse diets, Central American cichlids also reveal great variation in morphology, reproductive behavior and habitat use (Winemiller et

al. 1995; Hulsey et al. 2004; Soria-Barreto and Rodiles-Hernández 2008).

Evolutionary relationships within the Neotropical Cichlidae have been investigated (Stiassny 1991; Kullander 2003; Hulsey et al. 2004; López-Fernández et al. 2005), and a few studies have examined morphological relationships within an evolutionary framework (Norton and Brainerd 1993; Winemiller et al. 1995). Fishes reveal general and robust relationships between form and function involving many easily measured traits, and this makes the comparative study of morphology useful for inferring ecological patterns among fishes (Wainwright 1991; Motta et al. 1995; Norton 1995; Ruber and Adams 2001). Winemiller et al. (1995) concluded that local fluvial assemblages of Central American cichlids show greater diversification of functionally significant morphological traits than comparable assemblages of African cichlids. A possible reason for more extensive adaptive radiation among Central American cichlids may be an evolutionary history with lower competition or predation from species from other freshwater fish orders that are rich in species, such as the Characiformes and Siluriformes in South America and Africa (Winemiller 1991a, 1995).

In addition to having species with specialized morphologies, particularly with regard to feeding (Eaton 1943; Barel 1983; Hulsey and García de León 2005), species assemblages of Central American cichlids reveal evidence of dietary and habitat partitioning (Winemiller and Pianka 1990; Winemiller et al. 1995; Soria-Barreto and Rodiles-Hernández 2008). Nonetheless, cichlid species with extreme morphologies sometimes behave as ecological generalists. Liem (1980, 1991) proposed that morphological specialization permits more efficient foraging for a subset of food resources during periods of intensified competition. Others have proposed that morphological specializations are shaped by optimal foraging in response to functional tradeoffs associated with food acquisition and processing, irrespective of competition (Robinson and Wilson 1998). The present study examines associations among morphology, diet and habitat use within a natural assemblage of cichlid fishes in a Central American stream. The field study was performed during the annual dry season when stream discharge is relatively low and stable, population densities are greatest, and species interactions are most likely to influence community patterns.

Methods

Study area

The field study was conducted during December 2006 and January 2007 in the mainstem of the Upper Bladen River within the southeast portion of the Bladen Nature Reserve in the Toledo District of southern Belize (16°34′N, 88°43′W, ca. 45 m elevation). The headwaters of the Bladen River originate within the Bladen Reserve and are a part of the Monkey River Basin. This system drains the southeastern slope of the Maya Mountains and contains three branches (including the Trio and Swasey rivers), making it the fourth largest river basin in Belize (1,275 km^2). From the headwaters through the sampling area, the Bladen River lies within a nature reserve protecting the biodiversity of a landscape covered by dense and essentially undisturbed rainforest.

Fish sampling

Fishes were collected from a range of mesohabitats including riffles, runs, deep pools, vegetated areas and connecting tributaries. Fish capture methods included cast net, seine, hook-and-line and dip net. Sampling was performed in each habitat at intervals throughout the day and evening. Because changes in fish diet and morphology depend on body size and stage of development, we summarized and analyzed data for individuals of each species that corresponded to the adult size interval. Fish specimens were euthanized in MS-222 then preserved in 10% formalin and later transferred to 75% ethanol for storage. Specimens measured for the morphological analysis were also examined for dietary analysis. *Astatheros robertsoni* was not collected during our 2006–2007 survey, but specimens were observed and a few were collected within the study reach by the second author during December 2005–January 2006. These specimens were used for comparative morphological and dietary analyses.

Habitat sampling

Several physicochemical variables were investigated at each site where fish were observed or collected. Temperature (°C), dissolved oxygen concentration (mg·L^{-1}), and conductivity (μs) were measured with

a YSI model 85 meter, and pH was determined with a handheld electronic pH meter. These variables revealed low variation and were not considered in the statistical analyses. Maximum water depth and channel width were measured with a weighted measuring tape. Flow velocity ($m \cdot s^{-1}$) was measured by timing a neutrally buoyant object drifting across a predetermined distance.

In addition to physiochemical variables, other habitat characteristics were recorded at each site where fish were collected, including presence of aquatic vegetation, types and density of instream structures (e.g., large rocks, coarse woody debris), and substrate composition. Substrate categories were bedrock, silt/clay, sand, mud rich in organic matter, leaf litter, woody debris, gravel (<3 cm diameter), cobble (4–10 cm diameter), rocks (11–25 cm diameter), and bedrock (>26 cm diameter).

Habitat data were collected at each site where fish were collected, however, these data were also collected along ten randomly selected transects along a 0.7 km stretch of the main channel where the majority of sampling took place. Transect locations were selecting using random numbers generated from a random number table. Each transect extended across the main channel perpendicular to the shoreline and was clearly marked on shore using a bright yellow piece of cloth. Temperature, pH, dissolved oxygen concentration, conductivity, channel width and bank vegetation were measured once at each transect. Water depth, flow, substrate types and densities, structural types and densities, and presence of aquatic vegetation were assessed at a point every 5.0 m along the transect using a 1.0 m×1.0 m quadrant. A measuring tape was used to determine the location of each point along the transect line.

After the collection of habitat data along each transect, snorkeling observations were made at the same designated points where habitat data were collected. All species were identifiable from external morphology. Training and testing of accuracy in species identification was provided for each observer prior to observations. Measurements with a tape measure to determine the location of each point were done 10 m downstream of the transect to prevent disturbance of fish upstream. The observer then snorkeled upstream, parallel to the shoreline through the transect line observing all fish that were within approximately one meter of either side of the line.

Snorkeling at each point was done for approximately 5 min. The observer visually identified and counted individuals of all fish species and one person on shore recorded data and time. After each point was snorkeled, 5 min was allowed to pass before snorkeling the next point in order to minimize the effect of fish disturbance. In addition, during both habitat sampling and snorkeling surveys, all movement between transects was done on shore to prevent disturbance as well.

After all habitat and snorkel data were compiled, a vegetation index, substrate index, and structural index were calculated for each transect point and collection site. Each index was calculated by dividing the total number of categories observed at the location or point by the maximum observed categories. The indices were used to calculate an overall index of habitat complexity. The following equation was used to calculate the index of habitat complexity:

$$\text{Vegetation index} + \text{Substrate index} + \text{Structural index}$$

Habitat data were recorded during snorkel surveys and for all fish collected for diet analysis. The combined sample sizes for each species were as follows: *A. spilirus*—456, *T. meeki*—158, *V. maculicauda*—154, *C. salvini*—126 and *P. splendida*—26.

Dietary data

Specimens of each species were dissected for dietary analysis using methods similar to those described by Winemiller (1990) for microscopic examination and volumetric estimation of gut contents. Food items in the anterior portion of the gut were removed and examined under a dissecting microscope and identified according to appropriate prey categories. Invertebrates were classified to the lowest feasible taxonomic level according to keys and descriptions in Pennak (1978). Diet composition of each species was quantified using both frequency of occurrence and proportional volume of each diet item. Sample sizes for dietary analysis were as follows: *Archocentrus spilurus*—65, 'Cichlasoma' salvini—62, *Thorichthys meeki*—52, *Astatheros robertsoni*—3, *Vieja maculicauda*—23, and *Petenia splendida*—12.

Morphological data

Traditional morphometrics were measured on three to five specimens of each cichlid species, depending on

availability. Only adult size classes were examined, and the specimen standard length (SL) ranges were as follows: *Archocentrus spilurus*—68.3–73.9 mm, '*Cichlasoma*' *salvini*—55.9–96.9 mm, *Thorichthys meeki*—54.8–90.3 mm, *Astatheros robertsoni*—88.7–103.5 mm, *Vieja maculicauda*—116.8–162.8 mm, and *Petenia splendida*—199.0–337.0 mm. Thirty-two morphological characters related to feeding, swimming behavior, and habitat (Gatz 1979) were measured as follows: 1) maximum standard length—largest standard length for specimens collected at a site; 2) maximum body depth—maximum vertical distance from dorsum to ventrum; 3) maximum body width—maximum horizontal distance from side to side; 4) caudal peduncle depth—minimum vertical distance from dorsum to ventrum of the caudal peduncle; 5) caudal peduncle width—width of the caudal peduncle in horizontal plane at midlength; 6) body depth below midline—vertical distance from midline to ventrum at position of maximum body depth, with midline defined as the imaginary line passing from the pupil of the eye through the center of the ultimate vertebrae; 7) head length—distance from tip of upper jaw to the most caudal extension of the operculum; 8) head height—vertical distance from dorsum to ventrum passing through the center of the pupil; 9) interorbital distance—maximum horizontal distance between both orbits; 10) eye position—vertical distance from the center of the pupil to ventrum; 11) eye diameter—horizontal distance from eye margin to eye margin; 12) mouth position—estimated by drawing a reference horizontal line that passes from the corner of the mouth to the middle of the insertion of caudal rays in the caudal peduncle. With the fish fixed in this position, a point was found equivalent to the anterior-most point of the orbit, and another corresponding to the tip of the upper lip. A line was traced between the two points and the angle between the two was measured with a protractor; 13) gape width—horizontal distance inside fully open mouth at widest point; 14) snout length closed—horizontal distance between an imaginary vertical line passing through the anterior edge of the orbit and an imaginary vertical line passing through the anterior tip of the upper jaw; 15) snout length open—horizontal distance between an imaginary vertical line passing through the anterior edge of the orbit and an imaginary vertical line passing through the anterior tip of the upper jaw with mouth protruded; 16) dorsal fin height—maximum distance from proximal to distal

margin of the dorsal fin (excluding filaments); 17) dorsal fin length—distance from anterior proximal margin to posterior proximal margin of the dorsal fin; 18) pectoral fin length—maximum distance from proximal to distal margin of the pectoral fin base; 19) pectoral fin height—maximum vertical distance across the fully spread pectoral fin; 20) caudal fin length—maximum distance from proximal to distal margin of the caudal fin (excluding filament); 21) caudal fin depth—maximum vertical distance across the fully spread caudal fin; 22) pelvic fin length—the distance from the base of the pelvic fin to the tip of the longest ray (excluding filaments); 23) anal fin length—distance from anterior proximal margin to posterior proximal margin of the anal fin base; 24) anal fin height—maximum distance from the proximal to distal margin of the anal fin; 25) gut length—measured from the beginning of the esophagus to the anus (fully extending without stretching); 26) ceratobranchial length—taken on dissected first ceratobranchial. The straight distance between the joint of the basibranchial with the ceratobranchial and the joint between the ceratobranchial and the epibranchial; 27) ceratobranchial gill-raker number—number of rakers between the anterior tip of the ceratobranchial and the corner of the epibranchial; 28) ceratobranchial inter-gill-raker space—the average distance between the ceratobranchial gill-rakers; 29) ceratobranchial gill-raker length—the average distance between the base of the gill-rakers and their tip; 30) lower pharyngeal jaw width—maximum distance between the horns; 31) lower pharyngeal jaw length—maximum distance from the imaginary midline between the caudal edge of the horns and the anteriormost tip of the plate; and 32) lower pharyngeal jaw depth—maximum distance between the dorsal surface of the plate and the ventral keel joining both toothplate bones. Lengths were measured to the nearest 1.0 mm with a measuring tape, and those less than 0.5 mm were recorded to the nearest 0.1 mm using calipers. Structures smaller than 0.5 were measured with an ocular micrometer attached to a dissecting microscope. All measurements were taken as the straight-line distance between points.

Statistical analysis

Values of morphological variables were averaged for all specimens of each species, log transformed, and regressed against the log of standard length. In this

manner, the morphological variables are descriptors of body and fin shape without the influence of body size. Use of these ratios to characterize aspects of shape can reflect allometric relationships during growth and ontogeny (Atchley et al. 1976); however, allometric influences should be negligible for analysis of species assemblages (interspecific comparisons) in which a consistent size class (adults) is selected to characterize species (Winemiller 1991a). Using the software package PC-Ord, principal components analysis (PCA) was used to identify patterns in morphological variation among species. PCA uses matrix algebra to model a correlation matrix as a set of orthogonal (perpendicular) axes, or principal components. Each PC axis (morphological gradient) corresponds to an eigenvector. The eigenvalue describes the variance accounted for by the corresponding axis. The first few PC axes represent the largest percentage of total variation that can be modeled by the algorithm (Ludwig and Reynolds 1988). To investigate relationships between morphology and variables related to diet and habitat, Spearman's rank correlations were performed between principal component scores of the first two gradients and the series of diet and habitat variables. Data for the correlation analyses were the species' scores from PCA of morphology data (species average, $N=5$) and species' proportional utilization values (p_{ij}) of dietary and habitat variables based on the entire sample obtained for each species.

Results

Body shapes of the cichlid species that occur in the upper Bladen River show a high degree of interspecific variation, ranging from both large and small species with elongate bodies, large mouths and relatively highly protrusible jaws to large and small species with deep bodies, broad fins and compact jaw structure (Fig. 1). *Cichlasoma salvini* and *P. splendida* grouped closely in morphospace as defined by PC 1 and 2 and were strongly distinguished from other species by large inter-gillraker distance and snout length (Fig. 1; Table 1). *Archocentrus spilurus* also was morphologically distinct from other species, with a low PC 2 loading that corresponded to a long gut, short ceratobranchials and lower pharyngeal jaw compared to the other species. *Vieja maculicauda* was distinguished from the other species by having low loadings on the first axis corresponding to a relatively tall head, deep body, and short snout with compact jaws. The morphospace occupied by *Astatheros robertsoni* was associated with long pectoral fin length, short snout, long ceratobranchials and long lower pharyngeal jaw. *Thorichthys meeki* was intermediate in morphospace (closest to the assemblage centroid) and most similar to *A. robertsoni*.

Despite weak relationships, correlations between diet variation and morphological attributes revealed logical associations within the species assemblage (Table 2). The first principle component axis has high

Fig. 1 PCA ordination of Bladen River cichlid species based on morphological characters. The variables with highest loadings, positive or negative, are shown; Table 1 provides vector loadings for all 32 morphological variables
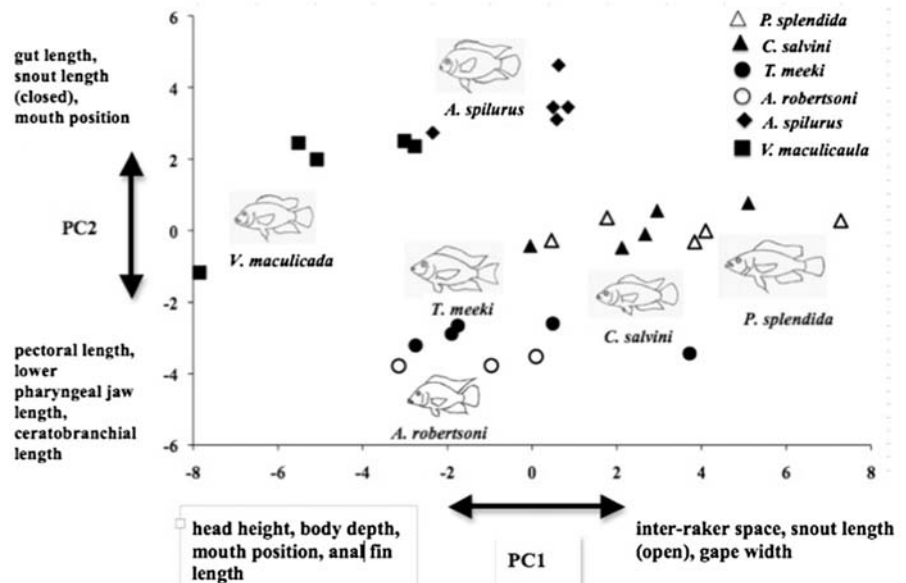
Table 1 Results from principal components analysis of six Bladen River cichlid species and 31 morphological attributes

	PCA axis	
	1	2
Eigenvalue	11.20	6.15
Percent of variance	34.12	18.65
Mean standard length	−0.009	0.016
Head length	0.141	−0.257
Head height	−0.270	−0.051
Gape width	0.182	−0.281
Interorbital distance	−0.171	−0.178
Eye position	−0.217	−0.176
Eye diameter	−0.018	−0.198
Snout length closed	0.061	0.271
Snout length open	0.199	−0.196
Body depth	−0.261	0.012
Body width	−0.199	−0.090
Peduncle depth	−0.229	0.014
Peduncle length	0.022	−0.256
Body depth below midline	−0.178	−0.039
Mouth position	−0.228	0.167
Gut length	−0.092	0.351
Dorsal length	−0.220	0.063
Dorsal height	−0.223	−0.044
Anal length	−0.236	0.042
Anal height	−0.174	0.013
Caudal depth	−0.115	0.114
Caudal length	−0.241	0.059
Pectoral length	−0.015	−0.334
Pectoral height	−0.126	−0.163
Pelvic length	−0.130	−0.207
Ceratobranchial length	0.022	−0.288
Gill raker number	0.145	0.041
Inter-raker space	0.235	−0.011
Gill raker length	−0.074	−0.055
Lower pharyngeal jaw width	−0.235	−0.034
Lower pharyngeal jaw length	−0.100	−0.302
Lower pharyngeal jaw diameter	−0.205	−0.162

negative correlations with snails and oligochaetes (benthic items), and high positive correlations with decapod crustaceans and fish. This axis presents a gradient from microphagous benthivorous fishes (*A. robertsoni*, *T. meeki*) to omnivorous midwater forms in the middle of the gradient (*A. spilurus*, *V. maculicauda*) to relatively elongate, large-mouthed macrophagous feeders (*C. salvini*, *P. splendida*).

The second principle component axis reflects a strong positive correlation with detritus, and a strong negative correlation with snails (Table 3). This axis presents a gradient between benthivorous invertebrate feeders (*A. robertsoni*, *T. meeki*) to macrophagous elongate fishes (*C. salvini*, *P. splendida*) to omnivorous fishes (*A. spilurus*, *V. maculicauda*). Specifically, the substrate sifters (*A. robertsoni* and *T. meeki*) had diets comprised of invertebrates and microfauna that were associated with narrow lower pharyngeal jaws, deep heads, and broad pectoral fins. *Archocentrus spilurus* consumed mostly benthic algae, and this was associated with a long gut and short snout with low protrusibility. *Petenia splendida* had a diet comprised mostly of fish, which was associated with large inter-gillraker space, long snout and wide gape.

Correlations between morphological gradients and habitat variables also yielded logical associations. The first axis revealed positive correlations with structural density ($r_S=0.90$, $p=0.037$) and algae ($r_S=0.90$, $p=0.037$), and negative correlations with sand ($r_S=-0.90$, $p=0.037$) and channel width ($r_S=-0.90$, $p=0.037$) (Table 3). This axis presents a gradient between macrophagus elongate species that feed predominately upon fish and invertebrates found among large structure (*P. splendida* and *C. salvini*, respectively), an algae feeder (*A. spilurus*) and, a substrate sifter that feeds upon benthivorous invertebartes within sandy or flocculent substrate (*T. meeki*).

The second principle component axis yielded a significant positive correlation with cobble ($r_S=1.00$, $p<0.0001$). This correlation is strongly associated

Table 2 Spearman rank correlation coefficients (r_S) between principal component scores and diet data. No statistically significant correlations ($P<0.05$, $N=6$) were found

	PC 1		PC 2	
	r_S	P	r_S	P
Algae	−0.31	0.805	0.65	0.158
Detritus	−0.12	0.827	0.78	0.066
Oligochaetes	−0.66	0.156	−0.49	0.329
Decapoda	0.54	0.268	0.27	0.604
Fish	0.68	0.140	0.13	0.798
Snails	−0.70	0.125	−0.64	0.173

Table 3 Spearman rank correlation coefficients (r_S) between principal component scores and habitat data. Significant correlations ($P<0.05$, $N=5$) are in bold

	PC 1		PC 2	
	r_S	P	r_S	P
Width	**−0.90**	**0.037**	−0.10	0.873
Depth	0.50	0.391	−0.50	0.391
Flow	0.60	0.285	0.40	0.505
Algae	**0.90**	**0.037**	0.10	0.873
Bedrock	0.80	0.104	−0.30	0.624
Rock	−0.30	0.624	0.30	0.624
Gravel	0.50	0.391	0.50	0.391
Cobble	0	1.000	**1.00**	**<0.0001**
Sand	**−0.90**	**0.037**	−0.10	0.873
Silt	−0.70	0.188	−0.30	0.624
Leaf litter	−0.70	0.188	0.20	0.747
Boulder	0.10	0.873	−0.10	0.873
Rock structure	−0.30	−0.624	0.30	0.624
Snags	−0.10	0.873	−0.40	0.505
Structural density	**0.90**	**0.037**	−0.40	0.505
Habitat complexity	0.30	0.624	0.70	0.188

with *A. spilurus*, an algae-picker. This species was most often observed maneuvering within stretches of cobble substrate with swift current.

Discussion

Our study investigated relationships among morphology, diet and habitat use within an assemblage of cichlids in the upper Bladen River, Belize, an assemblage that was expected to demonstrate a relatively high degree of niche divergence and resource partitioning compared with similar studies of temperate stream fish assemblages (e.g., Douglas and Matthews 1992), but perhaps revealing less ecological specialization when compared to more species-rich cichlid assemblages, such as those in the lowlands of the Río Usumacinta Basin in Mexico (Soria-Barreto and Rodiles-Hernández 2008) or Río San Juan Basin in Costa Rica (Winemiller et al. 1995). Principal components analysis of morphometric data indicated a wide separation of species based on traits that should influence foraging performance and microhabitat use (Fig. 1). The first axis separated a piscivore (*P.*

splendida) and invertebrate feeder (*C. salvini*), two cichlids with relatively slender bodies, widely spaced gillrakers and long snouts, from the other four cichlids. Piscivory often is associated with gape size and low numbers of widely spaced gillrakers, whereas large jaw protrusion should be associated with enhanced suction feeding. Suction feeding is one of two principal feeding modes observed in cichlids (Barel 1983). Suction involves opening the mouth with premaxillary protrusion and flaring of the opercula to produce an increase in buccal volume. Negative pressure generated inside the expanded orobranchial chamber causes an influx of water that drags prey into the mouth (Norton and Brainerd 1993; Norton 1995). *Petenia splendida* reveals an extreme level of jaw protrusion. Higham et al. (2007) found that 96 percent of *P. splendida*'s diet consisted of evasive prey, and he linked this diet to a large gape and high ram speed during prey capture. Ram speed is enhanced by jaw protrusion during the final approach to the prey item.

Another mode of feeding employed by cichlids is biting. Fishes with morphological features that enhance biting force should have lower suction efficiency due to reductions in protrusibility and orobranchial volume (Barel 1983, 1993; de Visser and Barel 1996). *Vieja maculicauda*, *C. spilurus* and other species with small compact jaws, massive jaw muscles, and numerous oral jaw teeth should be effective biters. *Vieja maculicauda* and *C. spilurus* fed on a mixture of algae and macrophyte material, and these items probably are obtained by using the biting mode of foraging. The second author has observed aquarium-housed specimens of *V. maculicauda* and other *Vieja* species ingesting pieces of leaves that are torn away with quick powerful bites.

The second PCA axis was strongly influenced by morphological traits that should influence substrate sifting (winnowing), including ceratobranchial length and lower pharyngeal jaw length. These two characteristics of the pharyngeal apparatus separated the substrate sifters, *A. robertsoni* and *T. meeki*, from the other four cichlid species, with *A. robertsoni* having the more extreme attributes. The pharyngeal jaws are of particular interest in cichlid ecology, because adaptive changes in this apparatus are believed to have led to the extensive trophic diversification observed among cichlids in Africa (Liem 1973, 1980), South America (López-Fernández et al. 2005), and Middle America (Hulsey 2006). In many bony fishes,

the pharyngeal apparatus assumes great importance for processing food prior to entry into the gastrointestinal tract. Food items often are sorted by winnowing within the orobranchial chamber, then sheared and fragmented by the action of the pharyngeal jaws. Modifications of the pharyngeal jaws partially determine the efficiency of processing alternative types of food items (Liem 1973; Wainwright 1989; Drucker and Jensen 1991; Grubich 2003). *Astatheros robertsoni* and *T. meeki* have comparatively long ceratobranchials and pharyngeal jaws, and these species had diets dominated by benthic aquatic macroinvertebrates that included small snails. In cichlids, fusion of the pharyngeal jaw and hypertrophy of the associated muscular sling is associated with enhanced ability to crush shelled molluscs and other hard prey (Hulsey 2006).

The correlation between morphological gradients and environmental variables revealed several relationships with functional interpretations. Morphologically, *P. splendida* was distinguished from other species by its relatively long snout, highly protrusible jaws, and a large inter-gillraker space. When correlated with habitat variables, these morphological traits were linked with large structural density. Association of the largest cichlid in the Bladen River with large structure, including submerged trees and boulders, is logical because most of the rocks in the streambed are not large enough to provide effective cover from aquatic predators, such as caimans or otters. Correlations also revealed an association between *C. salvini* and structural density. Having an elongated body and wide gape, *C. salvini* feeds on invertebrates attached to the underside of large rocks, including ephemeropterans and megalopterans.

In the PCA, *A. spilurus* was distinguished by a long gut length and short snout. These morphological features were associated with algae and cobble. *Archocentrus spilurus* was often observed biting algae from the surface of rocks in the middle of long shallow runs where the current velocity was relatively high. The correlation also revealed logical associations between morphological attributes and habitat features for *T. meeki*. Possessing morphological traits that are linked with substrate sifting (ceratobranchial length and lower pharyngeal jaw length), correlations associated these traits with soft, sandy substrates.

While our statistical approach demonstrates many expected ecological associations, the failure to identify more significant correlations among morphological traits, diet and habitat should not be entirely surprising. Ecomorphological patterns can be influenced by a variety of factors related to morphology, behavior, physiology and ecology (Motta and Kotrschal 1992). Morphological traits may have multiple functions with regard to feeding, locomotion, reproduction and defense from predators. For example, cichlids use their pectoral fins not only for locomotion, but also to fan developing eggs and larvae in their nests. Also, morphology, just like physiology and behavior, can be modified to some degree by local environmental conditions during ontogeny. Another factor that could have influenced our ecomorphological findings is the potential influence from ecological interactions with non-cichlid fishes found in the upper Bladen (e.g., *Astyanax bimaculatus*, *Brycon guatemalensis*, *Rhamdia guatemalensis*, *Poecilia mexicana*, *Xiphophorus helleri*, *Gobiomorus dormitor*, *Awaous banana*). As Liem (1991) observed, feeding specializations in fishes seem to be expressed only during certain periods of the year when food is limited. Patterns of ecological specialization tend to be more difficult to identify among river fishes, because flooding cycles generally alter the availability of resources and ratios of consumer demand and supply (Winemiller 1989, 1990, 1991b). In the present study, only the low-water season was considered, but this generally has been found to be the period when food is least available for tropical fishes. Interspecific interactions are more effectively estimated by examining patterns of resource use over extended periods, preferably encompassing a full annual cycle.

Conclusions

The present study provided evidence of a comparatively high degree of habitat and food resource partitioning among cichlid fishes inhabiting the Upper Bladen River. Niche overlap tended to be low among species pairs, and patterns of morphological variation were consistent with a hypothesis of adaptive divergence in several key functional morphological traits among regional herione cichlids. Given that the Upper Bladen cichlid assemblage contains no congeneric species, these patterns of morphological divergence reflect selective establishment of species from a more species-rich regional species pool rather than *in situ* character displacement. The Bladen cichlid assem-

blage contains one algivore with a long coiled gut (*A. spilurus*), one large piscivore with an elongated body and highly protrusbile jaws (*P. splendida*), two substrate sifters that possess long ceratobranchials and pharyngeal jaws that feed extensively on benthic invertebrates (*A. robertsoni* and *T. meeki*), one mid-water/epibenthic macroinvertebrate feeder (*C. salvini*), and one large trophic generalist with compact jaws (*V. maculicauda*). Thus, within this cichlid assemblage, species possess morphological adaptations that facilitate partitioning of food resources and habitats during the annual low-water period. Whereas numerous studies of African cichlids have shown that adaptive radiations related to feeding ecology have led to coexistence of many closely related species (e.g., Fryer and Iles 1972; Greenwood 1978; Seehausen 2006), there have been few studies addressing adaptive radiation within the Neotropical cichlid clade (López-Fernández et al. 2005). Recent phylogenetic studies of heroine cichlids provide a taxonomic framework to better understand the morphological and ecological relationships of these fish (see Concheiro Pérez et al. 2007; Rican et al. 2008); however, we did not find that species most closely related were also the most ecologically and morphologically similar. This assemblage contains no congeneric species, and morphological divergence resulting in niche segregation reflects selective establishment of species from a more species-rich regional species pool rather than in situ adaptive evolution. Results from our study contribute to a growing body of ecological data from Neotropical cichlid assemblages that, when analyzed in conjunction with new phylogenetic findings and data from ecological studies of other cichlid species, will elucidate the evolutionary ecology of this diverse family.

References

Atchley WR, Gaskins GT, Anderson D (1976) Statistical properties of ratios. I. Emperical results. Syst Zool 25:137–148

Barel CDN (1983) Towards a constructional morphology of cichlid fishes (Teleostei, Perciformes). Neth J Zool 33:357–424

Barel CDN (1993) Concepts of an architectonic approach to transformation morphology. Acta Biotheor 41:345–381

Concheiro Pérez GA, Rican O, Orti G, Bermingham E, Doadrio I, Zardoya R (2007) Phylogeny and biogeography of 91 species of heroine cichlids (Teleostei: Cichlidae) based on sequences of the cytochrome b gene. Mol Phylogenet Evol 43:91–110

de Visser J, Barel CDN (1996) Architectonic contraints on the hyoid's optimal starting position for suction feeding of fish. J Morphol 228:1–18

Douglas ME, Matthews WJ (1992) Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. Oikos 65:213–224

Drucker EG, Jensen JS (1991) Functional analysis of specialized prey processing behavior: winnowing by surfperches (Teleostei: Embiotocidae). J Morphol 210:267–287

Eaton TH (1943) An adaptive series of protractile jaws in cichlid fishes. J Morphol 72:183–190

Farias IP, Ortí G, Sampaio I, Schneider H, Meyer A (1999) Mitochondrial DNA phylogeny of the family Cichlidae: monophyly and fast molecular evolution of the Neotropical assemblage. J Mol Evol 48:703–711

Fryer G, Iles TD (1972) The cichlid fishes of the Great Lakes of Africa. Oliver and Boyd, Edinburgh

Gatz AJ Jr (1979) The ecological morphology of freshwater stream fishes. Tulane Stud Zool Bot 21:91–124

Greenwood PH (1978) A review of the pharyngeal apophysis and its siginificance in the classification of African cichlid fishes. Bull Br Mus Nat Hist (Zool) 33:297–323

Grubich J (2003) Morphological convergence of pharngeal jaw structure in durophagus perciform fish. Biol J Linn Soc 80:147–165

Higham TE, Hulsey CD, Rican O, Carroll AM (2007) Feeding with speed: prey capture evolution in cichlids. The European Journal of Evolutionary Biology 20:70–78

Hulsey CD (2006) Function of a key morphological innovation: fusion of the cichlid pharygeal jaw. Proc Royal Soc 273:669–675

Hulsey CD, García De León FJ (2005) Cichlid jaw mechanics: linking morphology to feeding specialization. Funct Ecol 19(3):487–494

Hulsey CD, García de León FJ, Sanchez-Johnson Y, Hendrickson DA, Near TJ (2004) Temporal diversification of Mesoamerican cichlid fishes across a major biogeographic boundary. Mol Phylogenet Evol 31:754–764

Kullander SO (2003) Cichlidae (Cichlids). In: Reis RE, Kullander SO, Ferraris CJ Jr (eds) Checklist of the freshwater fishes of South and Central America. EDIPUCRS, Porto Alegre, pp 605–654

Liem KF (1973) Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. Syst Zool 22:425–442

Liem KF (1980) Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. Am Zool 20:295–314

Liem KF (1991) Functional morphology. In: Keenleyside MHA (ed) Cichlid fishes: behavior, ecology and evolution. Chapman and Hall, New York, pp 129–150

López-Fernández H, Honeycutt RL, Winemiller KO (2005) Molecular phylogeny and evidence for an adaptive radiation

of geophagine cichlids from South America (Perciformes: Labroidei). Mol Phylogenet Evol 34:227–244

Ludwig JA, Reynolds JF (1988) Statistical ecology. Wiley, New York

Motta PJ, Kotrschal KM (1992) Correlative, experimental, and comparative evolutionary approaches in ecomorphology. Neth J Zool 42:400–415

Motta PJ, Norton SF, Luczkovich JJ (1995) Perspectives on the ecomorphology of bony fishes. Environ Biol Fish 44:11–20

Norton SF (1995) A functional approach to ecomorphological patterns of feeding in cottid fishes. Environ Biol Fish 44:61–78

Norton SF, Brainerd EL (1993) Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. J Environ Biol 176:11–29

Pennak RW (1978) Fresh-water invertebrates of the United States. Wiley, New York

Rican O, Zardoya R, Doadrio I (2008) Phylogenetic relationships of Middle American cichlids (Cichlidae, Heroini) based on combined evidence from nuclear genes, mtDNA, and morphology. Mol Phylogenet Evol 49:941–957

Robinson BW, Wilson DS (1998) Optimal foraging, specialization, and a solution to Liem's paradox. Am Nat 151:223–235

Ruber L, Adams DC (2001) Evolutionary convergence of body shape and trophic morphology in cichlids from Lake Tanganyika. J Evol Biol 14:325–332

Seehausen O (2006) African cichlid fish: a model system in adaptive radiation research. Proc Biol Sci 273(1597):1987–1998

Soria-Barreto M, Rodiles-Hernández R (2008) Spatial distribution of cichlids in Tzendales River, Biosphere Reserve Montes Azules, Chiapas. Mexico Environ Biol Fishes 83:459–469

Stiassny MLJ (1991) Phylogenetic relationships of the family Cichlidae: an overview. In: Keenleyside MHA (ed) Cichlid fishes: behavior, ecology, and evolution. Chapman and Hall, London, pp 1–18

Valtierra-Vega MT, Schmitter-Soto JJ (2000) Hábitos alimentarios de las mojarras (Perciformes: Cichlidae) de la laguna Caobas, Quintana Roo. México Rev Biol Trop 48:503–508

Wainwright PC (1989) Prey processing in haemulid fishes: patterns of variation in pharyngeal jaw muscle activity. J Exp Biol 141:359–375

Wainwright PC (1991) Ecomorphology: experimental functional anatomy for ecological problems. Amer Zool 31(4):680–693

Waltzek TB, Wainwright PC (2003) Functional morphology of extreme jaw protrusion in Neotropical cichlids. J Morphol 257:96–106

Winemiller KO (1989) Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. Environ Biol Fish 26:177–199

Winemiller KO (1990) Spatial and temporal variation in tropical fish trophic networks. Ecol Monogr 60:331–367

Winemiller KO (1991a) Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. Ecol Monogr 61:343–365

Winemiller KO (1991b) Comparative ecology of Serranochromis species (Teleostei: Cichlidae) in the Upper Zambezi River. J Fish Biol 39:617–639

Winemiller KO, Pianka ER (1990) Organization in natural assemblages of desert lizards and tropical fishes. Ecol Monogr 60:27–55

Winemiller KO, Kelso-Winemiller LC, Brenkert AL (1995) Ecomorphological diversification and convergence in fluvial cichlid fishes. Environ Biol Fish 44:325–261