

EFFECTS OF SPATIAL AND TEMPORAL VARIABILITY OF SHOAL HABITAT
ON STREAM FISH ASSEMBLAGES IN CHATTAHOOCHEE
TRIBUTARIES, ALABAMA

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THESIS ABSTRACT

EFFECTS OF SPATIAL AND TEMPORAL VARIABILITY OF SHOAL HABITAT
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Abiotic factors associated with habitat quality may have profound effects on fish assemblage structure. Variability in physical habitat parameters as well as temporal fluctuation in characteristics such as water depth and flow often dictate species persistence in stream mesohabitats. Few studies have extended the study of abiotic factors to habitat patch size or spatial relationship, however. Linkages between fish assemblages and the temporal and spatial variation of shoal habitats in three streams (Little Uchee, Wacoochee, and Halawakee) of the Chattahoochee River basin in east

Alabama were investigated. Richness, composition, and density of fishes were quantified to determine their relationship with habitat type, size, physical parameters and spatial distribution. Tributaries of the Chattahoochee River in Alabama were found to have unique shoal fish assemblages. Comparison of adjacent pool/shoal fish assemblages revealed higher richness in shoals than pools and also showed low similarity between the two habitats, demonstrating the uniqueness of these habitat types. Many fishes were habitat specialists, species found in shoal samples > 75% of species occurrence included: shoal bass, *Micropterus cataractae*; bluefin stoneroller, *Campostoma pauciradii*; blackbanded darter, *Percina nigrofasciata*. These species showed variability with size, quality, and position of shoal habitats. Drought conditions were evident in 2006, causing a significant change in the size of shoal habitat patches sampled in both 2005 and 2006. Richness and density of fishes increased in 2006 across all shoals of all sizes. Fish assemblages varied annually and were best predicted by shoal volume, substrate composition, and CV of depth and flow. Spatial distribution of shoals in watersheds predicted composition and density of fishes. Results from this study suggest that shoal size may be a better predictor of species richness than spatial position. Shoals acted as islands providing structure and resources for stream fishes. Stream fish from all families were present in shoal habitats. For this reason, reaches of streams that contain shoal habitat should be the focus of managers charged with conserving stream fishes.

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INTRODUCTION

In the last 100 years, three genera, 27 species, and 13 subspecies of freshwater fishes have become extinct in North America alone (Miller et al. 1989). A number of factors have contributed to loss of fish diversity, although habitat alteration is often cited as the most significant contributor to freshwater fish decline. Physical alteration of habitat is responsible for 73% of the declines and extinctions of North American species (Miller et al. 1989; Helfman et al. 1997). The rapid loss of freshwater fish species due to habitat degradation emphasizing the importance of understanding relationships between fishes and their habitats critical for species conservation.

Stream ecologists have adopted ideas from landscape ecology and metapopulation biology to describe patterns and relationships among stream biota and their habitats. The concept of patch dynamics depicts streams as spatially continuous longitudinal and lateral mosaics of habitats and resources (Pringle et al. 1988; Townsend 1989). Pringle et al. (1988) and Townsend (1989) utilized the theory of island biogeography (MacArthur & Wilson 1967) and other landscape concepts to explain how specific patch characteristics determine stream biotic and abiotic processes over various spatial and temporal scales. The theory of island biogeography attempts to explain the correlative effect of area and proximity of patches (i.e. islands) on species richness. The theory states that the size of an island and its location are indicators of the total number of species expected to exist there

(Wilson 1992). The concept of islands has been applied to many kinds of isolated habitats such as coral reefs, natural lakes, and individual pools and riffles all have been viewed as patches (Matthews 1999; Angermeier & Schlosser 1989)

The size and physical characteristics of habitat patches play a significant role in determining the structure of fish assemblages (Schlosser 1982). Studies have shown that size of habitats (Minckley 1984; Taylor 1996), stream width (Robinson & Buchanan 1988; Smith & Miller 1986; Gelwick 1990), depth (Hocutt & Stauffer 1975; Paller 1994; Sheldon 1968; Taylor et al. 1993; Peterson and Rabeni 1996; Harvey & Stewart 1991), volume (Angermeier & Schlosser 1989; Taylor 1997), temperature (Hynes 1970; Magnuson et al. 1979; Shuter et al. 1980; Rahel & Hubert 1991; Kelly et al. 1980; Baltz et al. 1991; Hughes 1998) and habitat heterogeneity (Schlosser 1987a) determine assemblage structure.

The River Continuum Concept (RCC) Vannote et al. 1980) first described the longitudinal change in stream attributes for networks of streams from headwaters to large rivers. These changes can affect the richness, density and composition of fish assemblages (Gorman & Karr 1978; Angermeier & Karr 1983; Schlosser 1987a; Rahel & Hubert 1991; Lyons 1996). Changes in assemblages are apparent and well documented throughout the entire network of a watershed, but within parts of these networks, longitudinal relationships may be obscured by local factors.

Montgomery (1999) proposed the Process Domain Concept (PDC) as a means to explain local factors that influence ecosystem structure and function. Process domains are predictable areas of a stream where physical habitat type, structure, and dynamics are governed by geomorphic processes (Naiman et al. 2005). These processes are determined

by such natural environmental variables such as geology, climate, and vegetation.

Walters et al. (2003) identified relationships between stream geomorphology and fish assemblages and concluded that species composition was predicted by reach-level geomorphic variables of stream slope, bed texture, bed mobility, and tractive force. The spatial and temporal variability of geomorphic processes can control habitat quality, availability, and disturbance, thereby creating a mosaic of habitat patches within a stream. The mosaic of resources can govern the availability of habitat types and, ultimately, control fish assemblage structure and species interactions (Fausch 2002).

Stream networks are dendritic systems, so the movement of fishes can only occur in an up- or downstream direction, a constraint that can cause them to be highly susceptible to habitat fragmentation (Zwick 1992; Rieman & McIntyre 1995; Rahel et al. 1996; Dunham et al. 1997). In this context, fish cannot move between distant patches without first passing intervening patches; thus, the lack of suitable intervening patches can isolate populations (Fagan 2002).

Concepts presented by Schlosser (1991, 1995a, 1995b) emphasize fish movement as a means of transporting different life stages across landscape scales. The ranging movement of fish is a facultative response to resource abundance and distribution of resources along the riverscape (Behnke 1992). Mobile fish species requiring extensive ranges can become isolated (Hanski et al. 1996). Anthropogenic disturbance can cause habitat fragmentation by disconnecting reaches of stream that were once contiguous. Isolation of habitat patches reduces emigration and alters the genetic integrity of populations (MacArthur & Wilson 1967; Kindvall & Ahlen 1992; Sjogren-Gilve & Ray 1996). The connectivity of patches occurring within a stream mosaic is critical for the

proliferation of stream fish populations (Fausch 2002). The movement of stream fishes among resource patches at the landscape scale allows for recolonization after anthropogenic or natural disturbances, causing a reduction in local extinction rates as long as habitat quality remains intact. Because fishes use different habitats for a variety of life history stages (i.e. diurnal vs. nocturnal, spawning vs. nonbreeding, and juvenile vs. adult), it is important to consider the spatial and temporal variability of habitats (Matthews 1999).

Studies that are limited in scale can overlook important patterns and interactions of stream fishes, which could be made more apparent with multi-scaled approaches. Recent studies have used multi-spatial and multi-temporal scaled approaches to overcome the difficulties of observing patterns and processes that may not be apparent in single scaled approaches. Schlosser (1982) noted the importance of temporal and spatial variation in habitat diversity (depth, velocity, and substrate) of streams. Lancaster (2000) and Palmer et al. (2000) used experimental designs focused on stream habitat patches ranging in type and size to provide data at multiple spatial and temporal scales, thus, they were able to draw conclusions about how patch structure in a stream landscape affects the distribution of invertebrates. A multi-scaled study by Gido et al. (1997) found spatial variation to be greater than temporal variation for the abundance of three fish species in streams, while a single species showed temporal variation. The authors also found that timing of spring run-off has the greatest temporal effect on fish communities. Matthews (1990) showed that the abundances of 3 darters were affected by both spatial and temporal variation in riffles. Variation in species diversity of stream fishes was best explained by temporal and spatial-scaled approaches (Tripe and Guy 1999). Spatial

variation in diversity was explained by longitudinal position, whereas temporal variation revealed high diversity in summer and low diversity in late fall and early spring (Tripe and Guy 1999). Gelwick (1990) described variation in stream fish assemblages of pools and riffles on both spatial and temporal scales. Assemblage structure was related to longitudinal position of pool habitats, although most of the variation in richness and abundance within riffle habitats was temporal. Species diversity, abundance and composition were determined by spatial position of habitats more so than temporal variation in 2 Texas streams (Ostrand 2002). Dunham et al. (1999) investigated patterns in bull trout (*Salvelinus confluentus*) occurrence in terms of physical, biotic, landscape characteristics, and distance to the nearest patch, and found that both patch area and isolation were related to bull trout occurrences. Smith and Kraft (2005) reported that a combination of small-scale habitat variables and stream position within a watershed influenced fish assemblages. Magoulick (2000) found high temporal variability in richness and densities of fishes in stream pools.

The above studies have shown that systematically censusing coarse-grained habitat features along entire streams and quantifying finer-grained variables within those habitats provide a more accurate depiction of patch dynamics of stream organisms across whole watersheds. Although fine spatial (e.g. 50- to 500-m reaches of stream) and temporal (e.g. hours to weeks) scaled studies are of limited use to managers, studies conducted at both fine and broad scales have become the emphasis of resource managers and conservation biologists for insight on managing populations across watersheds

Preserving metapopulations and maintaining genetic integrity of stream fishes is a primary concern for agencies and managers charged with conserving fishes. Conservation

efforts aiming to sustain threatened and endangered fish species benefit from data describing the spatial and temporal habitat requirements of stream fishes. The ability to quantify the habitat requirements of Evolutionarily Significant Units (ESU's), species, subspecies, or populations with extremely low abundance is essential for their successful management (Grossman et al. 1995). Research investigating the effects of habitat size, character, and spatial position on the distribution of stream fishes will help resource managers focus their efforts on populations that are in serious decline as a result of habitat loss or fragmentation.

In my study, I examined how temporal variation, size, quality and spatial distribution of shoals affected fish assemblages. I investigated variations in species richness, composition, density, relative abundance and size of stream fishes. My objectives were to: 1) compare how shoal and pool fish assemblages differ, 2) investigate temporal habitat variability in relation to shoals and their fish assemblages, 3) evaluate how the size and physical character of shoals affects fish assemblages, and 4) investigate how the spatial distribution of shoals within a stream affects fish assemblages.

STUDY AREA

The Chattahoochee River begins in the Appalachian Mountains of northeastern Georgia and flows 430 miles to Lake Seminole near the Georgia-Florida border. The river system flows through 3 physiographic provinces: The Appalachian Plateau, the Piedmont, and the Coastal Plain. Three streams, Halawakee Creek, Wacoochee Creek, and Little Uchee Creek were chosen for study based on physiographic and faunal similarities (Boschung & Mayden, 2004). Study streams occur in the Piedmont physiographic province. The study area encompasses a large portion of east-central Alabama and ranged in elevation from 50 to 125 m above sea level. Watershed drainage areas ranged from 85 km² for Wacoochee Creek to 255 km² for Halawakee Creek. Streams channels were characterized by alternating sand-bottom pools, gravel riffles, and bedrock-boulder shoals with moderate to swift currents.

Typically, shoals consist of exposed and submerged bedrock formations, with bedrock composing > 20 % of the habitat area. These geological formations constrict the flow of water in streams and create heterogeneous conditions and resources for fishes and other organisms. In my study, shoal habitats were bounded by stretches of pool/riffle/run habitat ranging from 50 to 5000 m, and are spatially positioned throughout the main stem of the study streams creating a close proximity among some and the isolation of others. Shoal habitats were once common throughout most of the Piedmont region, but numerous shoal habitats have been altered by reservoir construction and channelization, and the remaining still are threatened (Marcinek et al. 2003). These study streams contain some of the last remaining shoals in the Piedmont of the Chattahoochee River drainage in Alabama.

MATERIALS AND METHODS

Sampling sites were selected by locating shoals within the main stem of each of the three study streams. Canoes were used to locate all shoal habitats, and selected on the basis of accessibility. Shoals sites were chosen to provide spatial coverage of the Chattahoochee River drainage in Alabama. Streams were sampled during the summer low-water period from 23 May to 31 August 2005 and 25 May to 31 August 2006. In summer 2005, 18 shoals and 18 pools adjacent to shoals were sampled in the 3 study streams to compare habitat use by fishes. In summer 2006, 8 of the original 18 shoals were resampled, as well as 12 additional shoals (Fig. 1).

To quantify the physical structure of shoals, we used the transect method of Bain and Stevenson (1999). At each site, 5-10 transects were established such that no 2 transects were closer than 5m. The number of transects depended on the size of the habitat, such that an area 3x the width of each unit was surveyed. Each site was georeferenced with GPS. Link magnitude for each site was obtained using 7.5-min. topographical maps. Information on environmental variables were obtained at each site, including total depth, mean current velocity, and substrate were taken at 1.0-m intervals along each transect (Table 1). Temperature was recorded at the center of each shoal. Depths were recorded with a meter stick. Current velocity was measured with a Marsh McBirney Flowmate flow meter. Stream wetted width was measured with a standard tape measure. Coefficients of variation (CV) were estimated for depth, current velocity, and width to look at the heterogeneity of shoals. Habitat unit length was measured with a hip chain nearest meter. Habitat area (m^2) was calculated as the product of the length and mean width of the study site. Shoal volumes were calculated by multiplying mean width,

mean depth, and length. Substrate composition was categorized according to particle diameter using the Wentworth classification: (1) bedrock (no particles), (2) boulder (>256 mm), (3) cobble (64-256 mm), (4) pebble (16-36 mm), (5) gravel (2-15 mm), (6) sand (0.06-1 mm), and (7) silt (0-0.5 mm) (Wentworth, 1922). Simpson's diversity index was used to calculate substrate diversity for each site as a measure of habitat heterogeneity (Simpson 1949).

Shoal habitats were sampled with backpack shockers, seines, and dipnets. Starting at the downstream end of a shoal, 2-3 passes were made per site. The size of the area sampled was obtained after fish sampling to estimate fish density, calculated by dividing abundance in the shoal by the area of the shoal sampled. Pool habitats were sampled with a minimum of 10 seine hauls. Each seine haul covered a distance of 5 m and was made in both downstream and upstream directions. Specimens were anesthetized in MS-222, placed in 10% formalin, transferred to 50% ethanol, identified, and deposited in the Auburn University Fish Collection.

The most abundant fish species (*Campostoma pauciradii*, *Cyprinella venusta*, *Lepomis auritus*, and *Percina nigrofasciata*) were grouped into juvenile and adult size classes based on size at maturity (Boschung and Mayden, 2004), and were used as total, juvenile, and adult densities in the statistical analysis. Sizes classifications were based on the assumption of ontogenetic niche shifts and predation risk strongly affecting size of fish (Werner & Gilliam, 1984) and, thus, an important part of assemblage structure.

DATA ANALYSIS

The same areas were sampled in both years for the replicated sites, so comparisons of environmental variables, richness, and fish densities for similar months between years were made using paired *t*-test on log-transformed data.

Spearman rank correlations were used to look at compositional differences in pool shoal assemblages by stream (Lehman and D'Abrera 1998). The Jaccard similarity index (JSI) was used to compare assemblages of shoal and pool habitats and replicated shoal sites.

$$JSI = j/r$$

j represents the number of species in common between sites, and *r* represents the total number of species present in both sites (Krebs 1999). Jaccard similarity is a measure of community similarity that is based only on the presence and absences of species. Values range from 1 to 0, with 1 indicating a complete similarity between habitats, and 0 indicating complete dissimilarity (no shared species).

To improve normality, all environmental, spatial and fish variables were $\log_{10}(x+1)$ -transformed, except for temperature, which was square root-($x+1$) transformed, and the substrate composition variables, which were arcsine transformed. Linear regression analysis was used to describe the species-area relationship of each year for shoal habitats and the densities of fishes. To reduce the 16 environmental variables of shoals to fewer dimensions and remove collinearity, a principal component analysis (PCA) was performed with varimax rotation (Gordon 2005). PCs were retained for each year because of temporal variation in dependent variables. All variables with eigenvalues >1 and loading strongly ($>.80$) on measured environmental variables were retained. To

use environmental variables from all streams as predictor variables in the multiple regression analyses and to test the degree of similarity among shoals in the 3 study streams, ANOVA was used on PC environmental variables selected from the PCA. Multiple regression was used to examine relationships between selected PCs and the dependent fish variables species richness, total, juvenile, and adult densities, and density of the 4 most common species. Environmental variables selected by PCA were put into multiple regression models for each year.

Spatial variables for each site were obtained using ARCGIS (v.9), including, distance to nearest neighbor habitat and distance to the mainstem Chattahoochee River. A proximity index was adopted from Gustafson and Parker (1992), which determines the isolation of patches. This index is given by:

$$PX_i = \sum (s_k/n_k)$$

Where PX_i is the proximity index for focal patch i , and then with the specified search distance, s_k is the area of patch k within the search buffer, and n_k is the nearest neighbor distance between the focal patch and nearest patch. Low values (< 7.0) indicate patches are relatively isolated from other patches within the specified buffer distance, and high values (> 7.0) indicate patches are relatively connected to other patches Gustafson and Parker (1992). In order to include all shoals in this study into the analysis, a 5 km distance was chosen as the specified search distance. To reduce the 4 spatial variables of shoals to fewer dimensions and remove collinearity, a PCA was performed with varimax rotation. PCs were retained for the combination of years because spatial variation did not change by year. All variables with eigenvalues > 1 and loading strongly ($> .70$) on

measured spatial variables were retained. Multiple regression analysis was performed on selected spatial PCs to examine variation in fish variables. PCs were regressed by year to analyze the effects of a shoal's spatial position on fish assemblages.

RESULTS

A total of 2,164 specimens representing 41 species in 12 families were collected from pool and shoal habitats in Little Uchee, Wacoochee, and Halawakee creeks.

Dominant families in Little Uchee creek were Centrarchidae (40%), Cyprinidae (28%), and Catostomidae (8%), (Fig. 2), with the species *Cyprinella venusta* representing 34%, *Percina nigrofasciata* 30%, and *Lepomis auritus* 7% of fish relative abundance.

Dominant families in Wacoochee Creek were Cyprinidae (47%), Centrarchidae (22%), and Ictaluridae (11%), (Fig. 3), with the species *P. nigrofasciata* representing 34%, *C. venusta* 20%, and *Ameiurus brunneus* 10% of fish relative abundance. Dominant families in Halawakee Creek were Centrarchidae (34%), Cyprinidae (30%), and Catostomidae (9%), (Fig. 4), with *P. nigrofasciata* representing 20%, *L. auritus* 12%, and *L. macrochirus* 11% of fish relative abundance.

This survey showed that Little Uchee, Wacoochee, and Halawakee shoal and pool faunas contained 5 fishes endemic to the Apalachicola River System, including *C. pauciradii*, *Notropis hypsilepis*, *Moxostoma lachneri*, *A. brunneus*, and *Micropterus cataractae*. Thirty-four species were found in pool habitats, and 16 of these species were found exclusively in pools (Table 2). Eighteen species were common to both shoal and pool habitats, whereas 6 species were found exclusively in shoals, including *C.*

pauciradii, *L. zonistius*, *N. hypsilepis*, *M. cataractae*, *P. nigrofasciata*, and *Etheostoma swaini* (Table 2).

Jaccard similarity indices revealed high dissimilarity in assemblage compositions between habitat types (Tables 3,4, & 5). Scores showing low values ($< .50$) indicate a high degree of community difference between habitats. Species richness was higher in shoals than in pools, with the exception of site 12 on Little Uchee Creek, the most downstream site.

Species composition at the family level differed among streams in pool habitats. Results from Spearman rank correlation show significant differences between the pool assemblages of Little Uchee and those Wacoochee and Halawakee. Wacoochee and Halawakee pool assemblages were similar ($r_s = 1$, $p < .01$). Little Uchee pools contained primarily of Cyprinidae (83%) and Centrarchidae (13%) (Fig. 5). Wacoochee pools were composed primarily of Centrarchidae (45%) and Cyprinidae (33%) (Fig. 6). Halawakee pools were composed primarily of Centrarchidae (54%) and Cyprinidae (32%) (Fig. 7). Results from Spearman rank show non-significant differences between the assemblages of shoals at the family and species level ($r_s = 1$, $p < .01$). Little Uchee shoal compositions were composed primarily of Centrarchidae (44%) and Cyprinidae (33%) (Fig. 8), with *P. nigrofasciata* representing 37%, *C. venusta* 23%, and *L. auritus* 8% of shoal relative abundance. Wacoochee shoals were composed primarily of Cyprinidae (44%) and Centrarchidae (28%), (Fig. 9), with *P. nigrofasciata* representing 39%, *C. venusta* 22%, and *C. pauciradii* 4% of shoal relative abundance. Halawakee shoals were composed primarily of Cyprinidae (43%) and Centrarchidae (28%) (Fig. 10), with *P. nigrofasciata* representing 25%, *L. auritus* 14%, and *C. pauciradii* 9% of shoal relative abundance.

TEMPORAL ENVIRONMENTAL AND BIOTIC VARIATION

Stream drying was greater in 2006 than in 2005, with average depth of shoals significantly lower in 2006 than in 2005 ($n = 8, p \leq .001$) (Table 6). Shoal volumes were significantly lower in 2006 than in 2005 ($p \leq .01$). The difference in discharge between years was also evident from the Uchee Creek stream gauging station (Fig. 11). The gauge on Uchee Creek is the only reference gauge for stream levels in the Chattahoochee watershed of Alabama. Current velocities were significantly lower in 2006 than in 2005 ($p \leq .001$).

Species richness of shoals was significantly higher ($p \leq .001$) in 2006 than in 2005 (Table 7). Total fish density, density of juveniles, and adults was significantly higher ($p \leq .01$) in 2006 than in 2005. Densities of the families Cyprinidae and Centrarchidae were not significantly different ($p > .05$) between years. Jaccard similarity analysis of replicated shoals revealed scores ranging from moderate (.60) to low (.23). In 2006, there was an increase in the presence of all families represented in the shoal assemblages (Tables 8,9, and 10).

HABITAT QUALITY OF SHOALS

The first 4 PCs of the rotated PCA explained 70.7 and 71.4% of the environmental variation among shoals in 2005 and 2006, respectively (Tables 11 and 12). Component loadings for environmental variables on the first 4 PCs differed by years (Table 13; Figs. 12 and 13). PC1 from 2005 and 2006 were volume/size dimensions, loading positively on volume and depth in 2005, and volume and area in 2006. PC2 from 2005 and 2006 represented substrate components, loading negatively on proportion of

bedrock in 2005, and positively on proportion of bedrock in 2006. In 2005, PC3 represented habitat heterogeneity dimension loading positively on CV of current velocity. PC3 and PC4 in 2006 also represented habitat heterogeneity dimensions loading positively on CV of depth and current velocity, respectively. In 2005, PC4 reflected a substrate component, loading positively on proportion of boulder.

ANOVA of selected environmental variables showed shoal volume differing significantly ($p \geq .05$) among the 3 streams in 2006 (Table 14). Bonferroni post-hoc test showed that shoal volume was higher in Little Uchee than Wacoochee (Table 15).

ANOVA revealed no significant difference in the other 14 environmental variables among streams in 2006 (Table 16). In 2005, ANOVA of the 16 environmental variables showed significant differences in proportion of sand between Wacoochee and the other 2 streams (Table 17), but differences in proportion of sand were not significant in 2006.

Results from ANOVA suggest that the physical character of shoals in these streams was not significantly different; therefore, shoal data from all streams were pooled in regression analyses.

HABITAT SIZE / QUALITY AND FISH ASSEMBLAGES

In 2005, CV of current velocities and proportion of boulder predicted species richness (Table 18; Figs. 14 and 15). CV of current velocities showed a positive relationship, while proportion of boulder showed a negative relationship with richness. Total, juvenile, and adult fish densities were significant in 2005, indicating a negative relationship with volume (Fig. 16,17, and 18). Densities of adult *C. pauciradii* were negatively related to volume in 2005 (Fig. 19). Densities of adult *C. venusta* were

positively related to the proportion of bedrock in 2005 and significantly predicted by the regression model (Fig. 20). Densities of cyprinids were negatively related shoal volume in 2005 (Fig. 21).

In 2006, the shoal volume significantly predicted species richness (Fig. 22). In 2006, there was a significant relationship between total fish densities and volume, but was not significantly predicted by the regression model. Densities of juvenile *P. nigrofasciata* and cyprinids were negatively related to volume in 2006 (Fig. 23 and 24). For shoal habitats in 2005, the species-area relationship was not significant ($P > .05$; Fig. 25A), but was significantly positive for area ($p \leq .002$) in 2006 (Fig. 25B). In 2005, densities adult *C. pauciradii* were negatively correlated ($p < .05$) with shoal area (Table 19). Densities of *C. pauciradii* were positively related to the heterogeneity of current velocities in 2006 (Fig. 26).

SPATIAL DISTRIBUTION OF FISH ASSEMBLAGES

The amount of available shoal habitat differed by stream. Little Uchee consisted of 9.5% shoal habitat and 90.5% of pool/riffle/run habitats. In Little Uchee, shoals included both isolated and connected patches, and most were located in the middle reaches of the stream (Fig. 27). Wacoochee consisted of 12% shoal habitat and 88% of pool/riffle/run habitats. In Wacoochee, shoals expressed both isolation and connectivity, and had a high frequency in both headwater and lower reaches (Fig. 28). Halawakee consisted of 5% shoal habitat and 95% of pool/riffle/run habitats. Shoals in Halawakee were more isolated than connected (Fig. 29).

The first 2 PC's of the rotated PCA explained 74.26% of the variance in shoal position for both years (Table 20). PC1 was the connectivity dimension loading positively on proximity index and negatively on distance to nearest neighbor (Table 20). PC2 was a linear spatial dimension loading positively on distance to Chattahoochee and negatively on link magnitude (Table 20).

In 2006, species richness was inversely related to proximity index in shoals (Table 21; Fig. 30), and, density of focal species was not significantly correlated with proximity index or link magnitude. In 2005, the densities of cyprinids showed a significant negative relationship with link magnitude (Fig. 31). In 2006, link magnitude was a significant predictor of cyprinid density (Table 21; Fig. 32). In 2006, the density of centrarchids showed a significant positive relationship with link magnitude (Table 21; Fig. 33). However in 2006, the model did not significantly explain the variation in centrarchid densities.

The ranges in proximity indices varied by species (Table 22). Most species proximity indices ranged from (0.47 to 32.62). *Hybopsis sp. winchelli* had the highest average proximity average (15.12), but was found in the full range of proximities. *L. zonistius* had one of the highest proximity averages (14.12), with proximity indices ranging from (7.79 to 17.98). *Micropterus cataractae* had one of the highest proximity averages (14.05), with proximity indices ranging from (7.05 to 32.61). Both *Luxilus zonistius* and *M. cataractae* had the highest ranges of proximity indices of all species found in shoals (Table 22).

To examine longitudinal zonation of fishes by stream, shoal sites were grouped based on the link magnitude of each site (Table 23). Stream reaches were partitioned into

(link magnitude 10-20 = upper reaches, link magnitude 21-34 = middle reaches, and link magnitude 35-41 = lower reaches). In upper Little Uchee, species compositions of shoal habitats consisted primarily of the families Cyprinidae (43% of total), Centrarchidae (29%), and Catostomidae (14%), with *C. pauciradii*, *C. venusta*, *P. nigrofasciata* showing the highest relative abundance. Shoals in the middle reaches of Little Uchee consisted primarily of Cyprinidae (37%), Centrarchidae (27%), and Catostomidae (18%), with *C. venusta*, *N. texanus*, and *P. nigrofasciata* showing the highest relative abundance. Shoals in the lower reaches consisted primarily of the families Centrarchidae (43%), Cyprinidae (29%), and Catostomidae (14%). *C. venusta*, *L. auritus*, *M. cataractae*, and *Hybopsis sp.* showed the highest relative abundance in lower shoal assemblages.

Shoals in upper Wacoochee consisted primarily of the families Cyprinidae (46%), Centrarchidae (27%), and Ictaluridae (13%), with *C. venusta*, *L. zonistius*, and *P. nigrofasciata* showing the highest relative abundance. Dominant families in lower Wacoochee shoals were Cyprinidae (43%), and Centrarchidae (36%), with *C. venusta*, *A. brunneus*, and *L. auritus* showing the relative highest abundance.

Halawakee shoals consisted primarily of the families Cyprinidae (34%), Catostomidae (20%), and Centrarchidae (20%) in the upper reaches, where *C. pauciradii* and *Hybopsis sp.* showed the highest relative abundance. Shoals in middle reaches of Halawakee consisted primarily of the families Cyprinidae (34%), Centrarchidae (33%), and Catostomidae (13%), with *L. auritus* and *L. macrochirus* in highest abundance. Lower Halawakee shoals consisted primarily of Cyprinidae (34%), Centrarchidae (33%), Catostomidae (13%), and Ictaluridae (13%), with *L. auritus*, *L. macrochirus*, and *M.*

punctulatus in highest abundance, but held substantial numbers of *C. pauciradii* and *Hybopsis sp. cf. winchelli*.

DISCUSSION

Shoal habitats had unique fish assemblages in comparison to pools. Size, physical characteristics, temporal variability and spatial distribution of shoals played a key role in structuring assemblages.

Species compositions in pools showed significant difference among streams. There was no significant difference in the assemblages of shoals among streams. With the exception of the presence of *M. cataractae*, which was common in shoals of Little Uchee Creek, but was not present in high numbers in the other study streams. The results from pool and shoal comparisons in Wacoochee and Halawakee support results found for pools in other studies where centrarchids have dominated pools, while cyprinids are restricted to shallower habitats (Power & Matthews 1983, Power et al. 1985). Results from shoal and pool assemblage comparison show a higher number of species using shoals more than pools in 2005. These results suggest that fishes may be utilizing shoal habitats for spawning substrate, thermal refuge or a dissolved oxygen resource. Wootton (1998) suggested that structurally complex habitats usually have higher number of species than more homogeneous habitats because structurally complex habitats provide fishes with more ways of making a living. My study supports Wootton's (1998) hypothesis, as shoals are more structurally complex and did, in fact, support more species than pools.

Data from my study indicates that temporal variation occurred in physical and hydrological habitat, species richness, and fish densities in the study streams. Shoal habitats experienced high temporal variability between 2005 and 2006. The physical characteristics of depth and volume showed significant variation between years. Based on data from our replicated shoal sites, drought conditions were evident in 2006, and thus likely influenced fish assemblages, by increasing densities and the presence all families of fishes. Changes in physical characteristics of streams caused by fluctuations in discharge have been shown to alter composition and stability of fish assemblages (Grossman et al. 1982). Natural droughts in harsh stream environments are speculated to have only transient effects on fish assemblages under natural conditions (Matthews & Marsh-Matthews 2003), and present-day fish assemblages are thought to be tolerant of environmental stressors such as droughts (Matthews 1987). Hubbs (1990) speculated that reduced flows decrease water availability and increase thermal oscillations, and that thermal effects of reduced flows may have more impact on fishes than the direct effects. . In this study there was no significant difference between temperatures in streams in 2005 and 2006 ($p \geq .05$) (Table 6).

In 2006, richness, densities, and the presence of all families of fishes increased in shoals, most likely due to decreased water levels. Results from replicated shoals sites suggest that these relationships were true for shoals of all sizes. Schlosser (1985) documented increased densities of fishes in a dry year, and attributed the increase densities to increases in juvenile fishes because of stable conditions in the stream. Magoulick (2000) documented increases in total fish densities, large central stonerollers, and small sunfish with increases in pool volume for a dry year. Gelwick (1990) showed

temporal patterns related to changes in richness and fish abundance for riffles and pools. Increases in richness and densities suggest community dynamics such as: crowding, predation, low fecundity, variations in productivity, and increased competition for resources. It is assumed that fishes choose habitats to improve fitness (Behnke 1992). The results of habitat selection may be seen at different spatial scales (Kramer et al. 1991).

The reduction in volume between years had a dramatic impact on shoal size in my study. Schlosser (1989) suggests that patch volume may be a more appropriate measure of patch size in streams. In the case of my study, shoal volume was a better predictor of species presence than area and length in 2006. A positive relationship was found between shoal size and species richness in 2006, where larger patches of habitat generally contained more species than smaller patches. This relationship was not evident in 2005 and could be contributed to increase water levels, which could have allowed fishes to disperse throughout the stream. Temporal variation seems to be a controlling factor determining variation in species richness and densities of fishes. Species-area relationships revealed in my study suggest that fish populations are responding to size of shoals. This result is critical for understanding metapopulation dynamics of stream fish and indicates the importance of temporal variability and habitat size. Numerous studies in a variety of habitat types have documented volume as a limiting factor in fish assemblages (Schlosser 1982; Taylor 1997; and Magoulick 2000). Although the species-area relationship has been documented for pool and riffle habitats (Angermeier & Schlosser 1989) no such relationship has been described for shoal habitats.

Few consistent relationships existed between the physical variables and fish variables within or between years. Consequently, fish assemblages varied considerably

between years, and the abiotic variables measured at the patch scale varied in their ability to predict variations in fish assemblages. In 2005, richness was predicted by CV of current velocities and proportion of boulder substrate. Increases in the heterogeneity of current velocities showed increases in the number of species present. Increased competition and interaction between species may force some species to occupy different niches within a habitat (Wootton 1998). Increased variability in current velocities may limit the competition and interaction of species thereby allowing more species to occur in a particular habitat. Conversely, as the proportion of boulder in a shoal increased the number of species present decreased. Walters et al. (2003) found species compositions to be limited by geomorphic variables, citing bed texture, bed mobility, and tractive forces as predictors. Shoals with abundant boulder habitat also contained larger black bass and sunfish suggested biotic variables as a factor controlling richness.

In 2005, densities of total and juvenile fishes were negatively correlated to shoal volume. Harvey (1991) found that juvenile fishes move into the shallow water to avoid predation by larger fish. In 2005, adult fish densities were predicted by shoal volume. In other words, as the volume of shoals increased the densities of adult fishes decreased. This could be attributed to the increased water levels in 2005 allowing fishes to disperse into the abundant habitat available to them. Since flows were elevated in 2005, there may be some correlation to the harsh conditions associated with high water levels. Adult fishes often retreat to deeper pools to avoid metabolic costs of maintaining position in fast current velocities (Elliot 1976). In 2006, the total density of fishes was inversely related to volume, but was not significantly predicted by the model. Densities of fishes in 2006 may have decreased due to predation risk, since there were significantly more

species using shoals. Depth of habitat has been shown to influence predation risk (Power, 1987; Schlosser, 1987a,b).

Densities of *C. pauciradii*, a species endemic to the Chattahoochee drainage, was inversely related to volume in 2005. *C. pauciradii* may be selecting shallower habitat to avoid predation by larger fishes found in larger shoals (Schlosser 1987b). Another explanation for decreased densities may be that *Camptostoma* species are grazers that feed on periphyton (Fowler and Taber, 1985). Light is commonly thought to be a limiting factor in the distribution and abundance of stream periphyton (Allan 1995). So, deeper shoals may not support dense growth of periphyton, and, therefore, may not be preferred by *C. pauciradii*. *C. pauciradii* were positively related to the heterogeneity of current velocities in 2006. Current influences the distribution of periphyton, provides a continual renewal of gases and nutrients for proliferation, and can control the biomass of periphyton colonies (Allan 1995). This may be one reason why *C. pauciradii* occupied shoal habitats with a high degree of current velocity variation.

Density of *C. venusta* showed a significant positive relationship to proportion of bedrock in shoals in 2005. Like most *Cyprinella*, *C. venusta* are crevice spawners (Boschung & Mayden 2004), so an increase in the availability of preferred spawning habitat may account for increase densities of shiners. Density of *P. nigrofasciata* decreased with an increase in the volume of shoals. Predator avoidance may explain why *P. nigrofasciata* prefer habitats with lower volumes. The density of cyprinids was negatively related to shoal volume in both 2005 and 2006. Cyprinids may also be avoiding predation risk by occupying shallower shoals. Schlosser (1987b) showed that bass in an experimental stream caused cyprinids to seek refuge in shallow structurally

complex habitats to avoid predation. Schlosser (1987b) also noted the implications for crowding suggesting increases in intra- and inter-specific competition for resources. This could be critically important for specialist species that live exclusively in habitats that are preferred by all species during times of extended disturbance. In my study, crowding in shoals could have an impact on shoal specialist populations, who may not be able to survive such biotic constraints.

Results from the spatial analysis further support the concept of longitudinal zonation, which is one of the most commonly cited concepts of fish assemblages (Sheldon 1968; Horowitz 1978; Evans & Noble 1979; Schlosser 1982; Minckley 1984; Oberdorff et al. 1993). Both abiotic and biotic variables have been shown to change with stream order (Vannote et al. 1980). Some commonly observed changes with increase in stream order have been documented as environmental heterogeneity (Matthews & Styron 1981; Williams et al. 1996), habitat structure (Gorman & Karr 1978; Schlosser 1982), and biotic interactions (Matthews et al. 1987; Capone and Kushlan 1991). Headwater and downstream reaches contrast in the variability in environmental conditions and fish assemblage structure. Headwater reaches are generally depauperate and comprised of species tolerant of harsh conditions (Rahel & Hubert 1991). Environmental conditions in the lower reaches of streams are comparatively stable and less variable, allowing more species to exist. It is speculated that in lower reaches biotic interactions, such as predation and competition, may be more important in structuring fish assemblages (Matthews & Styron 1981; Schlosser 1987b; Lohr & Fausch 1997). Longitudinal patterns described by researchers are evident in the shoal habitats of my study. Centrarchids were added to assemblages in the lower reaches of both Little Uchee and

Halawakee. *M. cataractae* and *M. punctulatus* were present in the assemblages of shoals in the lower reaches of Little Uchee. *M. cataractae* was present in very low numbers in the lower reaches of Halawakee Creek. Typically, *M. punctulatus* dominated the assemblages of Halawakee Creek shoals. Wacoochee is a smaller stream, so there was no zonation in species compositions; here, cyprinids dominated the shoals throughout the entire length of the stream.

Proximity indices were negatively correlated to species richness in 2006, suggesting that as proximity of neighbors increased the number of species present decreases. These results are contrary to the theory of island biogeography (MacArthur and Wilson 1967) which suggests that as the proximity of an island increases so too does the number of species occupying the island. Interestingly, some of the larger shoals in 2006 had low proximities indices and high richness. This suggests that the effects of shoal size may override the effects of proximity in stream systems. Smaller shoals may have a certain carrying capacity of species regardless of proximity, and may experience more instability in assemblage structure than larger shoals. Larger shoals could also have well-established assemblages with biotic variables expressing more control over assemblage structure.

Proximity index ranges differed by species. Most species were found in the full range of proximities. Only *L. zonistius* and *M. cataractae* were present in shoals with higher ranges of proximity indices. The differences in proximity indices for these fishes suggested that some species might have a requirement for habitat connectivity, while others do not. *M. cataractae* is one of the largest species in these stream systems and has the highest range and one of the highest averages of proximities indices of all species,

suggesting that this species may require a high frequency of large shoal habitat in a reach of stream. Because of their large sizes, migration may be beneficial to *M. cataractae*. Roff (1988) suggested that migration is correlated to increased size at maturity, and stated that small individuals do not migrate as far as larger individuals. By moving from shoal to shoal throughout the corridor of a reach of stream, *M. cataractae* may be able to improve gene flow and increase survival.

CONCLUSIONS

Shoals are unique and rare habitat units in stream ecosystems. These structurally complex habitats provide fishes with several key resources. Shoal and pool assemblages are different from one another, as are assemblages in a particular habitat type between years of contrasting stream flow. In my study shoal volume, substrate, flow, and depth indicated variability in fish assemblages. Size of shoal habitats indicated the number of species expected to be present. The variability in the densities of certain species suggests that these species may be selecting shoals based on their physical characteristics and resources. The spatial and temporal variability in shoals causes fluctuations in the availability and quality of shoals. Although proximities of shoals did not influence assemblage structure, longitudinal arrangement and watershed position did play a role in predicting the occurrence of fishes. The interaction of spatial position and temporal pattern cause changes in the structure of fish assemblages emphasizing the importance of patch connectivity to some species. Conservation of fish communities requires an understanding of populations and habitat characteristics. Understanding temporal and spatial variability in fish assemblages is imperative if fisheries managers want to establish

long-term monitoring or detect the effects of anthropogenic disturbances. There are few resource agencies with multi-scaled data sets for managing stream fishes and their habitats. Data collected at landscape scales give managers a broad template for viewing the dynamics of fish communities in stream systems.

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APPENDIX. COLLECTION LOCALITIES FOR ALL SITES SMAPLED FROM RECENT SURVEY OF LITTLE UCHEE, WACOOCHEE, AND HALAWAKEE CREEKS. COLECTION RECORDS INCLUDE DATE, LOCALITY, GPS OF COLLECTION SITE.

Site #	Date	Stream ID	Long	Lat	Locality	County
1	8/4/05 & 8/1/06	LU	-85.2786	32.5494	2 mi. NW of Meadows Mill, CR 144	Lee
2	5/22/06	LU	-85.2543	32.5283	Meadows Mill	Lee
3	6/5/05	LU	-85.2446	32.5000	2 river miles down from CR 175	Lee
4	5/23/06	LU	-85.2089	32.5383	5 river miles down from CR 175	Lee
5	7/10/05 & 5/23/06	LU	-85.2123	32.5386	5.5 river miles down from CR 175	Lee
6	6/30/05	LU	-85.2032	32.5374	3.5 river miles N of CR 240	Lee
7	6/30/05	LU	-85.1938	32.5287	2 river miles N of CR 240	Lee
8	7/29/05 & 7/23/06	LU	-85.1800	32.5069	Moffitts Mill at CR 240	Lee
9	6/5/30	LU	-85.1794	32.5061	300m down from CR 240	Lee
10	8/11/05 & 7/23/06	LU	-85.1783	32.5017	1.5 river mi down from CR 240	Lee
11	7/7/06	WA	-85.1646	32.6181	1.98 river mile N of CR 279	Lee
12	7/7/06	WA	-85.1639	32.6182	1.9 river mile N of CR 279	Lee
13	7/7/06	WA	-85.1623	32.6200	1.56 river mile N of CR 279	Lee
14	7/7/06	WA	-85.1618	32.6196	1.55 river mile N of CR 279	Lee
15	7/7/06	WA	-85.1598	32.6183	1.5 river mile N of CR 279	Lee
16	7/7/06	WA	-85.1590	32.6182	1.2 river mile N of CR 279	Lee
17	7/7/06	WA	-85.1560	32.6180	1 river mile N of CR 279	Lee
18	8/4/5 & 8/2/06	WA	-85.1506	32.6162	3 miles N of Bleeker, CR 279	Lee
19	6/9/05 & 8/2/06	WA	-85.1152	32.6281	1.5 river miles down from CR 379	Lee
20	6/9/05	WA	-85.1097	32.6278	2.5 river miles down from CR 379	Lee
21	6/9/05	WA	-85.1078	32.6289	3 river miles down from CR 379	Lee
22	6/18/05	HA	-85.2947	32.7156	2.3 mi NW of Bean Mill, CR 177	Lee
23	7/27/06	HA	-85.2720	32.7067	1.26 river mile N of Hwy 29	Lee
24	7/27/06	HA	-85.2718	32.7063	1.25 river mile N of Hwy 29	Lee
25	7/27/06	HA	-85.2715	32.7056	1.2 river mile N of Hwy 29	Lee
26	7/27/06	HA	-85.2709	32.7050	1 river mile N of Hwy 29	Lee
27	6/18/05 & 7/27/06	HA	-85.2669	32.6967	Bean Mil, Hwy 29	Lee
28	6/17/05	HA	-85.2427	32.6916	2.5 river miles down from CR 390	Lee
29	6/17/05	HA	-85.2361	32.6869	4 river miles down from CR 390	Lee
30	6/17/05	HA	-85.2297	32.6922	4.5 river miles down from CR 390	Lee
31	6/13/06	HA	-85.2064	32.6883	500m N of CR 259	Lee
32	7/25/05 & 7/18/06	HA	-85.2044	32.6864	Mouth of Halawakee Cr., CR 259	Lee

Table 1. Names and descriptions of physical variables used in principal component analyses and regression analyses

Environmental Variable	Description
Temp	Mean water temperature (°C) within shoal
Depth	Mean shoal depth (cm)
CV Depth	Coefficient of variation of depth
Thalweg	Thalweg depth of shoal (m)
Velocity	Mean current velocity (m/s)
CV Velocity	Coefficient of variation of velocity
Width	Mean shoal width (m)
Length	Shoal length (m)
Area	Shoal area (m ²)
Volume	Shoal volume (m ³)
Bedrock	Proportion bedrock in shoal
Boulder	Proportion boulder in shoal
Cobble	Proportion cobble in shoal
Gravel	Proportion of gravel in shoal
Sand	Proportion sand in shoal
SubDiv	Simpson's diversity index for substrate

Table 2. Species list and type of habitat in which each species was collected. (P = pool, S = shoal)

Species	Habitat type	% occurrence in shoal	% occurrence in pool
<i>Lepisosteus oculatus</i>	P	0	100
<i>Amia calva</i>	P	0	100
<i>Anguilla rostrata</i>	P	0	100
<i>Dorosoma cepedianum</i>	P	0	100
<i>Campostoma pauciradii</i>	S	100	0
<i>Cyprinella venusta</i>	P,S	70	29
<i>Ericymba buccata</i>	P,S	77	22
<i>Hybopsis sp. winchelli</i>	P,S	86	13
<i>Lythurus atrapiculus</i>	P,S	33	66
<i>Luxilus zonistius</i>	S	100	0
<i>Nocomis leptocephalus</i>	P	66	33
<i>Notropis ammophilus</i>	P	0	100
<i>Notropis baileyi</i>	P,S	54	45
<i>Notropis hypsilepis</i>	S	100	0
<i>Notropis longirostris</i>	P	0	100
<i>Notropis texanus</i>	P,S	57	42
<i>Cyprinus carpio</i>	P	0	100
<i>Opsopoeodus emiliae</i>	P	0	100
<i>Semotilus thoreauianus</i>	P,S	85	14
<i>Hypentelium etowanum</i>	P,S	83	16
<i>Minytrema melanops</i>	P,S	66	33
<i>Moxostoma lachneri</i>	P,S	77	22
<i>Ameiurus brunneus</i>	P,S	94	5
<i>Noturus leptacanthus</i>	P,S	65	34
<i>Gambusia affinis</i>	P	0	100
<i>Fundulus olivaceus</i>	P	0	100
<i>Labidesthes sicculus</i>	P	0	100
<i>Lepomis auritus</i>	P,S	75	25
<i>Lepomis cyanellus</i>	P,S	80	20
<i>Lepomis gulosus</i>	P,S	33	66
<i>Lepomis macrochirus</i>	P,S	66	33
<i>Lepomis megalotis</i>	P,S	66	33
<i>Lepomis microlophus</i>	P	0	100
<i>Lepomis miniatus</i>	P	0	100
<i>Micropterus cataractae</i>	S	100	0
<i>Micropterus punctulatus</i>	P,S	83	16
<i>Micropterus salmoides</i>	P,S	75	25
<i>Pomoxis nigromaculatus</i>	P,S	33	67
<i>Perca flavescens</i>	P	0	100
<i>Percina nigrofasciata</i>	S	100	0
<i>Etheostoma swaini</i>	S	100	0

Table 3. Jaccard similarity values and richness for Little Uchee Creek pools and shoals sampled in 2005 (P = pool, S= shoal).

Species	Site #	1S	1P	3S	3P	5S	5P	6S	6P
<i>L. oculatus</i>									
<i>A. calva</i>									
<i>A. rostrata</i>									
<i>D. cepedianum</i>									
<i>C. pauciradii</i>		9		14		1		3	
<i>C. venusta</i>		5	1	24	7		45	15	26
<i>C. carpio</i>									
<i>E. buccata</i>		1	2						
<i>H. sp. winchelli</i>								1	
<i>L. zonistius</i>									
<i>L. atrapiculus</i>									6
<i>N. leptocephalus</i>									
<i>N. baileyi</i>									
<i>N. hypsilepis</i>									
<i>N. longirostris</i>									
<i>N. texanus</i>				3	6	5	6	3	1
<i>O. emiliae</i>									
<i>S. thoreauianus</i>									
<i>H. etowanum</i>				3				3	1
<i>M. melanops</i>									
<i>M. lachneri</i>		1		1					1
<i>A. brunneus</i>		1		3			1	2	
<i>N. leptacanthus</i>									
<i>L. sicculus</i>									
<i>F. olivaceus</i>									
<i>G. affinis</i>									
<i>L. auritus</i>		2	2	3		2		3	
<i>L. cyanellus</i>		3							
<i>L. gulosus</i>									
<i>L. macrochirus</i>		6	5	1		1			1
<i>L. megalotis</i>							1		
<i>L. microlophus</i>									
<i>M. cataractae</i>						1		1	
<i>M. punctulatus</i>					1				
<i>M. salmoides</i>									
<i>P. nigromaculatus</i>									
<i>P. nigrofasciata</i>		20		9		6		4	
Richness		9	4	9	3	6	4	9	6
Jaccard Index			0.40		0.20		0.22		0.23

Table 3. (continued)

Species	Site #	7S	7P	8S	8P	9S	9P	10S	10P
<i>L. oculatus</i>									1
<i>A. calva</i>									1
<i>A. rostrata</i>									
<i>D. cepedianum</i>									
<i>C. pauciradii</i>						1			
<i>C. venusta</i>		8	25	6	6	18	2	2	32
<i>C. carpio</i>									
<i>E. buccata</i>									
<i>H. sp. winchelli</i>						6			
<i>L. zonistius</i>									
<i>L. atrapiculus</i>			1						
<i>N. leptcephalus</i>									
<i>N. baileyi</i>									
<i>N. hypsilepis</i>									
<i>N. longirosris</i>									
<i>N. texanus</i>			2		3	3	2		3
<i>O. emiliae</i>									
<i>S. thoreauianus</i>							1		
<i>H. etowanum</i>				6		1			1
<i>M. melanops</i>									
<i>M. lachneri</i>		1				1			
<i>A. brunneus</i>		2				1			
<i>N. leptacanthus</i>									
<i>L. sicculus</i>									
<i>F. olivaceus</i>									
<i>G. affinis</i>							5		
<i>L. auritus</i>		2	3	5		2	2	3	1
<i>L. cyanellus</i>							7		
<i>L. gulosus</i>							1		
<i>L. macrochirus</i>									1
<i>L. megalotis</i>				1					1
<i>L. microlophus</i>									
<i>M. cataractae</i>		1		2		1		2	
<i>M. punctulatus</i>									2
<i>M. salmoides</i>						1			
<i>P. nigromaculatus</i>									1
<i>P. nigrofasciata</i>		5		11		4		3	
Richness		6	4	6	2	11	7	4	10
Jaccard Index			0.25		0.14		0.20		0.16

Table 4. Jaccard similarity values and richness for Wacoochee Creek pools and shoals sampled in 2005 (P = pool, S= shoal).

Species	Site #	18S	18P	19S	19P	20S	20P	21S	21P
<i>L. oculatus</i>									1
<i>A. calva</i>									
<i>A. rostrata</i>									
<i>D. cepedianum</i>									
<i>C. pauciradii</i>				1	1	3		4	
<i>C. venusta</i>		25		1		15	3	1	2
<i>C. carpio</i>									
<i>E. buccata</i>				1		3			1
<i>H. sp. winchelli</i>			1	3	4	3			3
<i>L. zonistius</i>									
<i>L. atrapiculus</i>		8							
<i>N. leptocephalus</i>									
<i>N. baileyi</i>									
<i>N. hypsilepis</i>								3	
<i>N. longirosris</i>									
<i>N. texanus</i>				2	2		1	4	
<i>O. emiliae</i>						2			
<i>S. thoreauianus</i>									
<i>H. etowanum</i>									
<i>M. melanops</i>									
<i>M. lachneri</i>		1	1	3		3	2		
<i>A. brunneus</i>		1		5	1	5		5	
<i>N. leptacanthus</i>									
<i>L. sicculus</i>		1	1		1				2
<i>F. olivaceus</i>									2
<i>G. affinis</i>									
<i>L. auritus</i>		1	3	4	1	10	2	2	1
<i>L. cyanellus</i>		2	2	2		1			
<i>L. gulosus</i>									
<i>L. macrochirus</i>		1		1	4		3		
<i>L. megalotis</i>						1			
<i>L. microlophus</i>									
<i>M. cataractae</i>									
<i>M. punctulatus</i>						1			
<i>M. salmoides</i>				1	1				
<i>P. nigromaculatus</i>									
<i>P. nigrofasciata</i>		13			1			12	
Richness		9	5	11	9	11	5	7	6
Jaccard Index			0.40		0.53		0.23		0.18

Table 5. Jaccard similarity values and richness for Halawakee Creek pools and shoals sampled in 2005

Species	Site #	22S	22P	27S	27P	28S	28P	29S	29P	30S	30P	32S	32P
<i>L. oculatus</i>				1									
<i>A. calva</i>													
<i>A. rostrata</i>													
<i>D. cepedianum</i>				1									
<i>C. pauciradii</i>	11					4		5		2		1	
<i>C. venusta</i>	5				5	2	2		10		6	1	4
<i>C. carpio</i>				2									
<i>E. buccata</i>													
<i>H. sp. winchelli</i>								3		1			
<i>L. zonistius</i>						1							
<i>L. atrapiculus</i>													
<i>N. leptcephalus</i>								1		1			
<i>N. baileyi</i>				1		4		1		4	1		
<i>N. hysilepis</i>	1												
<i>N. longirosris</i>													
<i>N. texanus</i>			2								1		
<i>O. emiliae</i>													
<i>S. thoreauianus</i>													
<i>H. etowanum</i>					1			1		3		1	
<i>M. melanops</i>									1				
<i>M. lachneri</i>	1			5	1				1	3		1	
<i>A. brunneus</i>						1						1	
<i>N. leptacanthus</i>						2		1		4			
<i>L. sicculus</i>													1
<i>F. olivaceus</i>					2			2					2
<i>G. affinis</i>													
<i>L. auritus</i>	2			15	1	8	1			4	1	2	
<i>L. cyanellus</i>													
<i>L. gulosus</i>					1								
<i>L. macrochirus</i>			4	5	6	5	1			2	4	1	
<i>L. megalotis</i>			6			1		1					
<i>L. microlophus</i>				1									
<i>M. cataractae</i>													
<i>M. punctulatus</i>	3			2			1						
<i>M. salmoides</i>													
<i>P. nigromaculatus</i>				1	1								
<i>P. nigrofasciata</i>				2		6		8	2	2		1	
Richness	6	3	11	8	10	4	9	4	10	5	8	3	
Jaccard Index		0.00		0.26		0.27		0.08		0.25		0.10	

Table 6. Paired *t*-test (n = 8) results for temporal variability in environmental variables in 2005 and 2006. Values marked in bold are significant at alpha = .05.

	Mean (\pm SE)	Mean (\pm SE)	95% Confidence		t	df	p-value
	2005	2006	Lower	Upper			
Depth (m)	0.52 (0.03)	0.23 (0.02)	0.23	0.34	12.07	7	p \leq .001
Thalweg depth (m)	1.15 (0.18)	0.58 (0.08)	0.19	0.94	3.56	7	p \leq .01
Volume (m ³)	2007.28 (566.29)	741.91 (260.04)	361.09	2169.65	3.31	7	p \leq .01
Current Velocity (m/s)	.22 (.02)	.12 (.01)	0.05	0.14	5.30	7	p \leq .001
Temperature (C°)	24.43 (.99)	26.00 (.25)	-4.21	1.08	-1.40	7	p = .206

Table 7. Paired *t*-test (n = 8) results for temporal variability in biotic variables in 2005 and 2006. Values marked in bold are significant at alpha = .05.

	Mean (\pm SE)	Mean (\pm SE)	95% Confidence		t	df	p-value
	2005	2006	Lower	Upper			
Species Richness	6.75 (.52)	9.62 (.56)	-0.22	-0.09	-5.49	7	$p \leq$.001
# of juveniles /100m ²	0.61 (.22)	1.69 (.25)	-1.04	-0.29	-4.21	7	$p \leq$.01
# of adults /100m ²	1.36 (.64)	2.88 (1.21)	-0.74	-0.13	-3.41	7	$p \leq$.01
# of all fishes /100m ²	1.97 (.83)	4.57 (1.37)	-0.82	-0.23	-4.22	7	$p \leq$.01

Table 8. Jaccard similarity index and richness of replicated shoals in Little Uchee Creek in 2005 and 2005.

Shoal #	1	1/06'	5	5/06'	8	8/06'	10	10/06'
<u>Species List</u>								
<i>Anguilla rostrata</i>								1
<i>Campostoma pauciradii</i>	9	5	1					
<i>Cyprinella venusta</i>	5	1		17	6	9	2	4
<i>Ericymba buccata</i>	1	1						
<i>Hybopsis sp. winchelli</i>		1		7		1		
<i>Notropis texanus</i>		1	5	2				
<i>Semotilus thoreauianus</i>		3						
<i>Hypentelium etowanum</i>		3			6	1		1
<i>Moxostoma lachneri</i>	1					1		
<i>Ameiurus brunneus</i>	1	4		1		9		4
<i>Lepomis auritus</i>	2	5	2	3	5	10	3	4
<i>Lepomis cyanellus</i>	3							
<i>Lepomis gulosus</i>								1
<i>Lepomis macrochirus</i>	6	1	1			2		
<i>Lepomis megalotis</i>					1	2		2
<i>Micropterus cataractae</i>			1	1	2	3	2	1
<i>Micropterus punctulatus</i>		2						
<i>Percina nigrofasciata</i>	20	30	6	22	11	22	3	15
Richness	9	12	6	7	6	10	4	9
Jaccard similarity index		0.50		0.44		0.60		0.30

Table 9. Jaccard similarity index and richness of replicated shoals in Wacoochee Creek in 2005 and 2006.

Shoal #	18	18/06'	19	19/06'
<u>Species List</u>				
<i>Campostoma pauciradii</i>		2	1	6
<i>Cyprinella venusta</i>	25	25	1	3
<i>Ericymba buccata</i>			1	
<i>Hybopsis sp. winchelli</i>		2	3	
<i>Lythurus atrapiculus</i>	8			
<i>Notropis texanus</i>			2	1
<i>Moxostoma lachneri</i>	1	2	3	
<i>Ameiurus brunneus</i>	1	3	5	8
<i>Lepomis auritus</i>	1	2	4	2
<i>Lepomis cyanellus</i>	2	1	2	
<i>Lepomis macrochirus</i>	1		1	
<i>Micropterus punctulatus</i>		1		1
<i>Micropterus salmoides</i>			1	
<i>Percina nigrofasciata</i>	13	43		9
Richness	8	9	11	7
Jaccard similarity index		0.50		0.38

Table 10. Jaccard similarity index and richness of replicated shoals in Halawakee in 2005 and 2006.

Site#	27	27/06'	32	32S/06'
<u>Species List</u>				
<i>Lepisosteus oculatus</i>	1			
<i>Dorosoma cepedianum</i>	1			
<i>Campostoma pauciradii</i>		7	2	
<i>Cyprinella venusta</i>		3		6
<i>Hybopsis sp. winchelli</i>				3
<i>Notropis baileyi</i>	1			
<i>Cyprinus carpio</i>	2			1
<i>Hypentelium etowanum</i>			1	1
<i>Minytrema melanops</i>		2		
<i>Moxostoma lachneri</i>	5	2	3	1
<i>Ameiurus brunneus</i>		7	4	11
<i>Noturus leptacanthus</i>		1		
<i>Lepomis auritus</i>	15	7	3	6
<i>Lepomis cyanellus</i>			7	
<i>Lepomis macrochirus</i>	5	4	2	8
<i>Lepomis microlophus</i>	1			
<i>Lepomis miniatus</i>			4	
<i>Micropterus punctulatus</i>	2			12
<i>Micropterus salmoides</i>		2		
<i>Pomoxis nigromaculatus</i>	1			
<i>Perca flavescens</i>				1
<i>Percina nigrofasciata</i>	2	23		29
Richness	11	10	8	11
Jaccard similarity index		0.23		0.35

Table 11. Eigenvalues, percent, and cumulative variance for principal components for 2005

PC	Initial		Cumulative %
	Eigenvalues	% of Variance	
	Total		
1	5.29	31.12	31.12
2	2.70	15.91	47.03
3	2.22	13.07	60.11
4	1.81	10.64	70.75
5	1.66	9.77	80.52
6	1.05	6.21	86.74
7	.83	4.88	91.62
8	.51	3.01	94.64
9	.41	2.45	97.10
10	.23	1.40	98.50
11	.12	.73	99.24
12		.43	99.67
13		.23	99.90
14			99.99
15			99.99
16			100.00
17			100.00

Table 12. Eigenvalues, percent, and cumulative variance for principal components for 2006

PC	Initial		
	Eigenvalues Total	% of Variance	Cumulative %
1	5.390	31.70	31.70
2	3.444	20.25	51.96
3	2.189	12.87	64.83
4	1.687	9.92	74.76
5	1.170	6.88	81.64
6	.838	4.93	86.57
7	.806	4.73	91.31
8	.604	3.55	94.86
9	.315	1.85	96.72
10	.203	1.19	97.91
11	.145	.85	98.76
12	.120	.70	99.47
13		.35	99.82
14		.10	99.92
15			99.98
16			100.00
17			100.00

Table 13. Component loadings of environmental variables on principal components for 2005 and 2006. Variables in bold were used in regression analyses.

Environmental Variables	2005				2006			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
volume	0.92	-0.12	0.15	0.21	0.97	0.21		
depth	0.88				0.51	0.57	-0.12	0.21
area	0.84	-0.18	0.23	0.32	0.97		0.16	
thalweg depth	0.81	0.25	-0.31		0.44	0.59	0.51	0.13
width	0.72	-0.35	-0.42		0.69	0.46	-0.33	-0.11
length	0.69		0.43	0.28	0.87	-0.16	0.31	
velocity	0.68	0.36	0.38	-0.32	0.11	0.35	-0.35	-0.72
bedrock		-0.95	0.15	-0.16	0.13	0.95	0.10	
cobble	-0.10	0.78		-0.27		-0.74		-0.12
CV velocity		-0.35	0.88			0.23		0.91
CV width		0.11	0.84			-0.19	0.58	0.36
boulder	0.13	-0.15		0.91	0.31	-0.75		0.38
Simpson div.	0.18	0.52	0.13	0.76	-0.20	-0.90	0.13	0.17
Sand	0.24				-0.32		-0.33	-0.22
CV depth	-0.17	0.44	-0.12		0.15		0.93	
gravel	-0.12		-0.15		-0.19			-0.28
temperature	-0.38	0.22	0.12	0.30	-0.52	-0.26	0.30	

Table 14. ANOVA of PC variables selected from the principal component analysis for Little Uchee, Wacochee, and Halawakee Creek shoals. Values marked in boldface are significant at the alpha = .05 level.

2005		Sum of Squares	df	Mean Square	F	p
Volume (PC1)	Among Groups	0.74	2	0.37	1.094	0.36
	Within Groups	5.09	15	0.33		
	Total	5.83	17			
Bedrock (PC2)	Among Groups	0.05	2	0.02	1.572	0.24
	Within Groups	0.27	15	0.01		
	Total	0.33	17			
CV Velocity (PC3)	Among Groups	0.03	2	0.01	0.999	0.39
	Within Groups	0.25	15	0.01		
	Total	0.28	17			
Boulder (PC4)	Among Groups	0.03	2	0.01	3.294	0.07
	Within Groups	0.06	15	0.01		
	Total	0.09	17			
2006						
Volume (PC1)	Among Groups	1.97	2	0.98	4.604	0.02
	Within Groups	4.06	19	0.21		
	Total	6.03	21			
Bedrock (PC2)	Among Groups	0.05	2	0.02	0.964	0.40
	Within Groups	0.49	19	0.02		
	Total	0.54	21			
CV Depth (PC3)	Among Groups	0.02	2	0.01	0.517	0.60
	Within Groups	0.40	19	0.02		
	Total	0.42	21			
CV Velocity (PC4)	Among Groups	0.23	2	0.11	1.354	0.28
	Within Groups	1.63	19	0.08		
	Total	1.87	21			

Table 15. Bonferroni post-hoc analysis of selected principal components in 2006

Dependent Variable	(A) STREAM	(B) STREAM	Mean Difference	Std. Error	p
			(A-B)		
Volume (PC1)	Little Uchee	Wacoochee	.529	.21	.05
		Halawakee	.499	.21	.07
	Wacoochee	Little Uchee	-.529	.21	.05
		Halawakee	-.030	.21	1.00
	Halawakee	Little Uchee	-.499	.21	.07
		Wacoochee	.030	.21	1.00
Bedrock (PC2)	Little Uchee	Wacoochee	.101	.05	.25
		Halawakee	.082	.05	.46
	Wacoochee	Little Uchee	-.101	.05	.25
		Halawakee	-.018	.05	1.00
	Halawakee	Little Uchee	-.082	.05	.46
		Wacoochee	.018	.05	1.00
CV Depth (PC3)	Little Uchee	Wacoochee	.018	.07	1.00
		Halawakee	-.027	.07	1.00
	Wacoochee	Little Uchee	-.018	.07	1.00
		Halawakee	-.045	.07	1.00
	Halawakee	Little Uchee	.027	.07	1.00
		Wacoochee	.045	.07	1.00
CV Velocity (PC4)	Little Uchee	Wacoochee	.125	.09	.54
		Halawakee	.031	.09	1.00
	Wacoochee	Little Uchee	-.125	.09	.54
		Halawakee	-.093	.09	.97
	Halawakee	Little Uchee	-.031	.09	1.00
		Wacoochee	.093	.09	.97

Table 16. ANOVA of 2006 Environmental variables for shoals in Little Uchee, Wacoochee, and Halawakee creeks

		Sum of Squares	df	Mean Square	F	p
TEMP	Among Groups	.102	2	.051	.943	.407
	Within Groups	1.023	19	.054		
	Total	1.124	21			
DEPTH	Among Groups	.038	2	.019	1.168	.332
	Within Groups	.309	19	.016		
	Total	.348	21			
CVDEPTH	Among Groups	.022	2	.011	.517	.604
	Within Groups	.401	19	.021		
	Total	.423	21			
THALWEG	Among Groups	.083	2	.042	1.687	.212
	Within Groups	.470	19	.025		
	Total	.554	21			
VELOCITY	Among Groups	.010	2	.005	.230	.796
	Within Groups	.400	19	.021		
	Total	.410	21			
CVVELOCI	Among Groups	.233	2	.117	1.354	.282
	Within Groups	1.637	19	.086		
	Total	1.870	21			
WIDTH	Among Groups	.163	2	.082	2.037	.158
	Within Groups	.762	19	.040		
	Total	.925	21			
CVWIITH	Among Groups	.014	2	.007	.227	.799
	Within Groups	.590	19	.031		
	Total	.604	21			
LENGTH	Among Groups	.730	2	.365	3.656	.045
	Within Groups	1.897	19	.100		
	Total	2.627	21			
AREA	Among Groups	1.815	2	.907	4.978	.018
	Within Groups	3.463	19	.182		
	Total	5.278	21			
VOLUME	Among Groups	1.970	2	.985	4.604	.023
	Within Groups	4.065	19	.214		
	Total	6.035	21			
BEDROCK	Among Groups	.050	2	.025	.964	.399
	Within Groups	.498	19	.026		
	Total	.548	21			
BOULDER	Among Groups	.013	2	.007	.816	.457
	Within Groups	.155	19	.008		
	Total	.168	21			
COBBLE	Among Groups	.043	2	.022	2.314	.126
	Within Groups	.177	19	.009		
	Total	.220	21			
GRAVEL	Among Groups	.004	2	.002	.482	.625
	Within Groups	.087	19	.005		
	Total	.091	21			
SAND	Among Groups	.010	2	.005	.641	.538
	Within Groups	.155	19	.008		
	Total	.166	21			
SUBDIVER	Among Groups	.061	2	.030	.459	.639
	Within Groups	1.256	19	.066		
	Total	1.317	21			

Table 17. ANOVA of 2005 Environmental variables for shoals in Little Uchee, Wacoochee, and Halawakee creeks.

		Sum of Squares	df	Mean Square	F	p
TEMP	Among Groups	.200	2	.100	2.112	.156
	Within Groups	.709	15	.047		
	Total	.908	17			
DEPTH	Among Groups	.049	2	.024	.705	.510
	Within Groups	.518	15	.035		
	Total	.567	17			
CVDEPTH	Among Groups	.072	2	.036	.573	.576
	Within Groups	.939	15	.063		
	Total	1.011	17			
THALWEG	Among Groups	.037	2	.018	.449	.647
	Within Groups	.612	15	.041		
	Total	.648	17			
VELOCITY	Among Groups	.002	2	.001	.024	.976
	Within Groups	.476	15	.032		
	Total	.477	17			
CVVELOCI	Among Groups	.034	2	.017	.999	.391
	Within Groups	.254	15	.017		
	Total	.288	17			
WIDTH	Among Groups	.020	2	.010	.418	.666
	Within Groups	.359	15	.024		
	Total	.379	17			
CVWIDTH	Among Groups	.029	2	.014	.633	.545
	Within Groups	.342	15	.023		
	Total	.371	17			
LENGTH	Among Groups	.283	2	.141	.950	.409
	Within Groups	2.233	15	.149		
	Total	2.516	17			
AREA	Among Groups	.385	2	.193	.915	.422
	Within Groups	3.157	15	.210		
	Total	3.542	17			
VOLUME	Among Groups	.743	2	.371	1.094	.360
	Within Groups	5.090	15	.339		
	Total	5.833	17			
BEDROCK	Among Groups	.058	2	.029	1.572	.240
	Within Groups	.276	15	.018		
	Total	.333	17			
BOULDER	Among Groups	.030	2	.015	3.294	.065
	Within Groups	.067	15	.004		
	Total	.097	17			
COBBLE	Among Groups	.177	2	.089	4.056	.039
	Within Groups	.328	15	.022		
	Total	.505	17			
GRAVEL	Among Groups	.015	2	.007	2.490	.116
	Within Groups	.045	15	.003		
	Total	.059	17			
SAND	Among Groups	.130	2	.065	12.424	.001
	Within Groups	.078	15	.005		
	Total	.208	17			
SUBDIVER	Among Groups	.008	2	.004	.116	.891
	Within Groups	.543	15	.036		
	Total	.551	17			

Table 18. Standardized coefficients, representing the change in a dependent variable that result from a change of one standard deviation in an independent variable, for multiple regression of species richness and fish density against environmental principal components in 2005 and 2006. Significant coefficients are marked in bold. Significance test at alpha = .05. PC1 from 2005 and 2006 represented volume/size. PC2 from 2005 and 2006 represented proportion of bedrock. In 2005, PC3 represented CV of current velocity. PC3 and PC4 in 2006 represented CV of depth and current velocity, respectively. In 2005, PC4 represented proportion of boulder. r^2 values given with corresponding figures.

Dependent Variables	Year	Standardized Coefficients			
		PC1	PC2	PC3	PC4
Species Richness	2005	0.08	-0.40	0.57	-0.57
	2006	0.6	-0.31	0.18	0.45
Total # of fish /m ²	2005	-0.62	0.08	0.43	0.12
	2006	-0.58	0.04	0.16	0.04
Total # of juveniles /m ²	2005	-0.6	0.01	0.24	0.30
	2006	-0.49	-0.19	0.06	0.22
Total # of adults /m ²	2005	-0.57	0.18	0.48	-0.02
	2006	-0.32	0.17	0.2	-0.09
# of <i>C. pauciradii</i> (<80mm) /m ²	2005				
	2006	-0.64	-0.51	0.36	0.51
# of <i>C. pauciradii</i> density (>80mm) /m ²	2005	-1.08	0.02	0.3	0.44
	2006	-0.25	0.16	-0.53	0.09
# of <i>C. venusta</i> (>50mm) /m ²	2005	-0.04	0.77	0.1	-0.17
	2006	-0.34	0.59	0.09	-0.09
# of <i>P. nigrofasciata</i> (<60mm) /m ²	2005	-0.46	0.03	0.41	0.26
	2006	-0.53	0.09	-0.17	0.01

Table 19. Pearson correlations for shoal size (length/ area) and fish variables in 2005 and 2006. Significant coefficients are marked in bold. Linear regression significance test at alpha = .05.

	2005		2006	
	Length	Area	Length	Area
Richness	0.06	0.00	0.56	0.61
# of juv. <i>C. pauciradii</i> /m ²	-0.52	-0.52	-0.23	-0.35
# of adult <i>C. pauciradii</i> /m ²	-0.51	-0.63	-0.36	-0.39
# of adult <i>C. venusta</i> /m ²	-0.30	-0.34	-0.12	-0.21
# of juv. <i>L. auritus</i> /m ²	-0.32	-0.33	-0.17	-0.30
# of adult <i>L. auritus</i> /m ²	-0.46	-0.40	-0.55	-0.55
# of juv. <i>P. nigrofasciata</i> /m ²	-0.06	-0.15	-0.55	-0.54
# of adult <i>P. nigrofasciata</i> /m ²	-0.39	-0.51	-0.43	-0.41
# of juveniles /m ²	-0.37	-0.39	-0.40	-0.42
# of adults /m ²	-0.38	-0.48	-0.24	-0.23

Table 20. Component loadings of spatial variables on principal components combined for 2005 and 2006. Variables in bold were used in regression analyses.

Spatial variables		
	PC1	PC2
Proximity Index	0.915	
Distance to nearest neighbor	-0.901	
Distance to Chattahoochee		0.823
Link Magnitude		-0.787
% of variance	41.66	32.6
cumulative %	41.66	74.26

Table 21. Standardized coefficients, representing the change in a dependent variable that result from a change of one standard deviation in an independent variable, for multiple regression of species richness and fish density against spatial principal components. Significant coefficients are marked in bold. Significance test at alpha = .05. PC1 represented proximity index. PC2 represented link magnitude. r^2 values given with corresponding figures.

Dependent variables	Standardized Coefficients		
	Year	PC1	PC2
Species Richness	2005	0.26	-0.41
	2006	-0.57	0.12
Cyprinid density /m ²	2005	-0.06	-0.53
	2006	0.28	-0.56
Centrarchid density /m ²	2005	-0.5	-0.05
	2006	-0.24	0.48

Table 22. List of proximity ranges for species found in shoals in the Chattahoochee River Drainage.

Species	Mean Proximity		Proximity Range
	Index	SD	
<i>Camptostoma pauciradii</i>	11.48	9.37	0.47 - 32.61
<i>Cyprinella venusta</i>	12.19	8.34	0.47 - 32.61
<i>Ericymba buccata</i>	12.14	8.89	1.75 - 22.82
<i>Hybopsis sp. winchelli</i>	15.12	9.27	0.96 - 32.61
<i>Luxilus zonistius</i>	14.12	3.47	7.79 - 17.98
<i>Notropis baileyi</i>	1.69	0.73	0.96 - 2.48
<i>Notropis texanus</i>	14.86	9.40	4.11 - 32.61
<i>Semotilus thoreauianus</i>	8.68	5.07	4.11 - 14.13
<i>Hypentelium etowanum</i>	11.16	9.83	4.11 - 32.61
<i>Moxostoma lachneri</i>	10.51	9.68	1.75 - 32.61
<i>Ameiurus brunneus</i>	13.29	8.38	1.18 - 32.61
<i>Noturus leptacanthus</i>	6.58	6.29	0.96 - 14.97
<i>Lepomis auritus</i>	11.60	8.93	0.47 - 32.61
<i>Lepomis cyanellus</i>	11.34	8.25	1.75 - 22.82
<i>Lepomis macrochirus</i>	8.08	6.79	1.18 - 22.82
<i>Lepomis megalotis</i>	9.68	8.42	0.96 - 21.50
<i>Micropterus cataractae</i>	14.05	8.74	7.05 - 32.61
<i>Micropterus punctulatus</i>	12.13	7.80	0.47 - 22.82
<i>Percina nigrofasciata</i>	12.26	8.78	0.96 - 32.61

Table 23. Longitudinal succession of fish families in shoals for 2005 and 2006. (Upper = headwater sections, Middle = middle reaches of streams, Lower = lower reaches of streams)

	Upper	%	Middle	%	Lower	%
Little Uchee	Cyprinidae	43	Cyprinidae	36	Centrarcidae	43
	Centrarcidae	29	Centrarcidae	27	Cyprinidae	29
	Catostomidae	14	Catostomidae	18	Catostomidae	14
	Ictaluridae	7	Ictaluridae	9	Ictaluridae	7
	Percidae	7	Percidae	9	Percidae	7
Wacoochee	Cyprinidae	46	Cyprinidae	43		
	Centrarchidae	27	Centrarchidae	36		
	Ictaluridae	13	Ictaluridae	7		
	Catostomidae	7	Catostomidae	7		
	Percidae	7	Percidae	7		
Halawakee	Cyprinidae	34	Cyprinidae	34	Cyprinidae	34
	Catostomidae	20	Centrarchidae	33	Centrarchidae	33
	Centrarchidae	20	Catostomidae	13	Catostomidae	13
	Ictaluridae	13	Ictaluridae	13	Ictaluridae	13
	Percidae	13	Percidae	7	Percidae	7

Fig. 1. Shoal sites sampled in Little Uchee, Wacoochee, and Halawake Creeks in Alabama during summer 2005 and 2006.

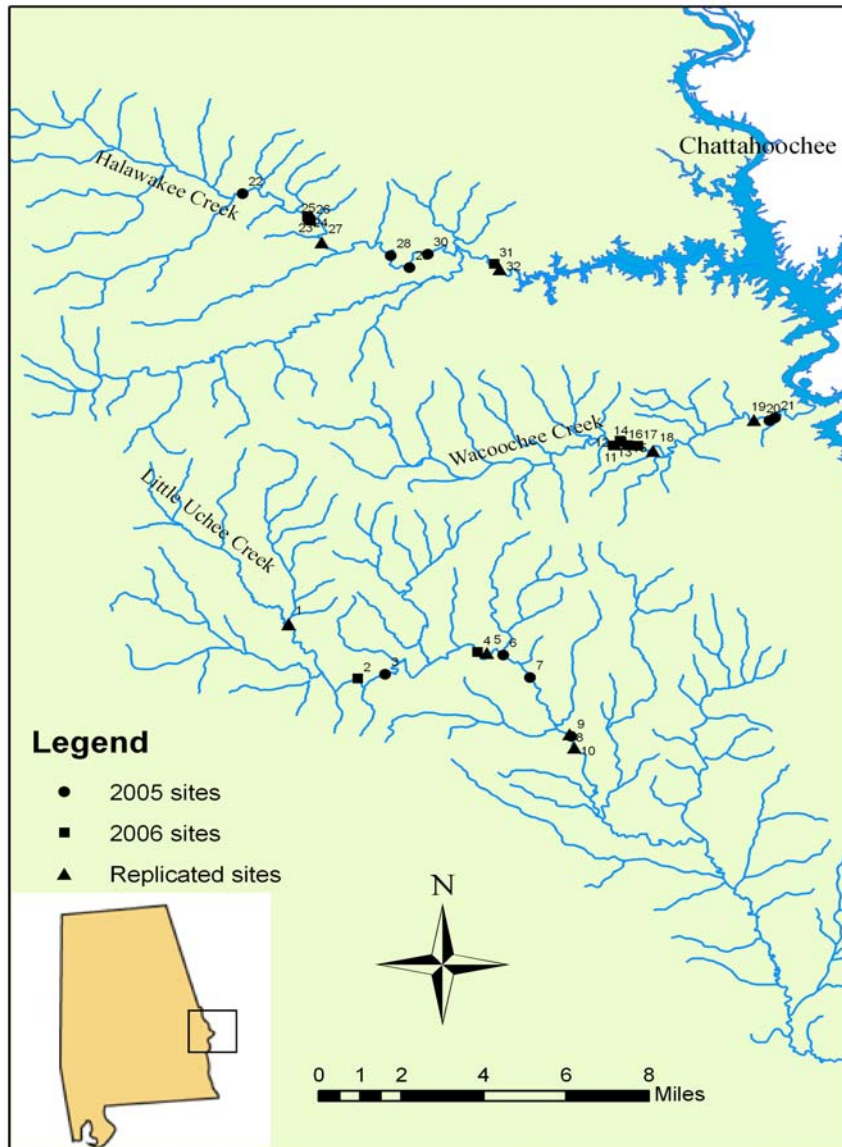


Fig. 2. Fish species composition from pool and shoals in Little Uchee Creek from 2005 and 2006.

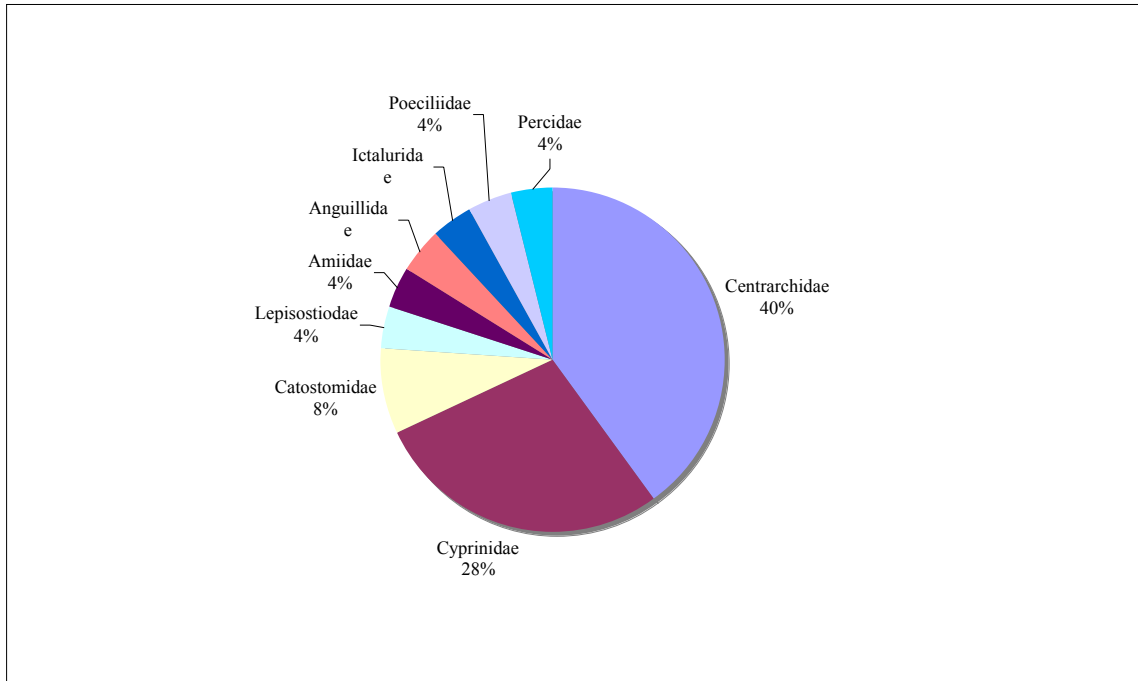


Fig. 3. Fish species composition from pool and shoals in Wacoochee Creek from 2005 and 2006.

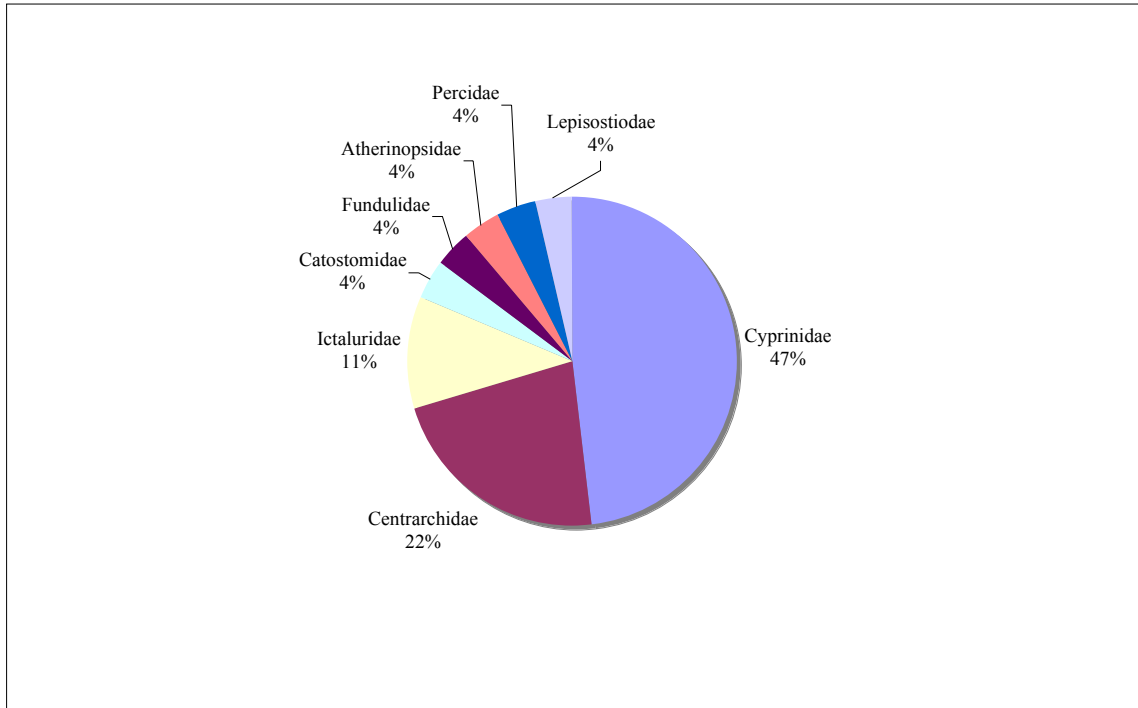


Fig. 4. Fish species composition from pool and shoals in Halawakee Creek from 2005 and 2006.

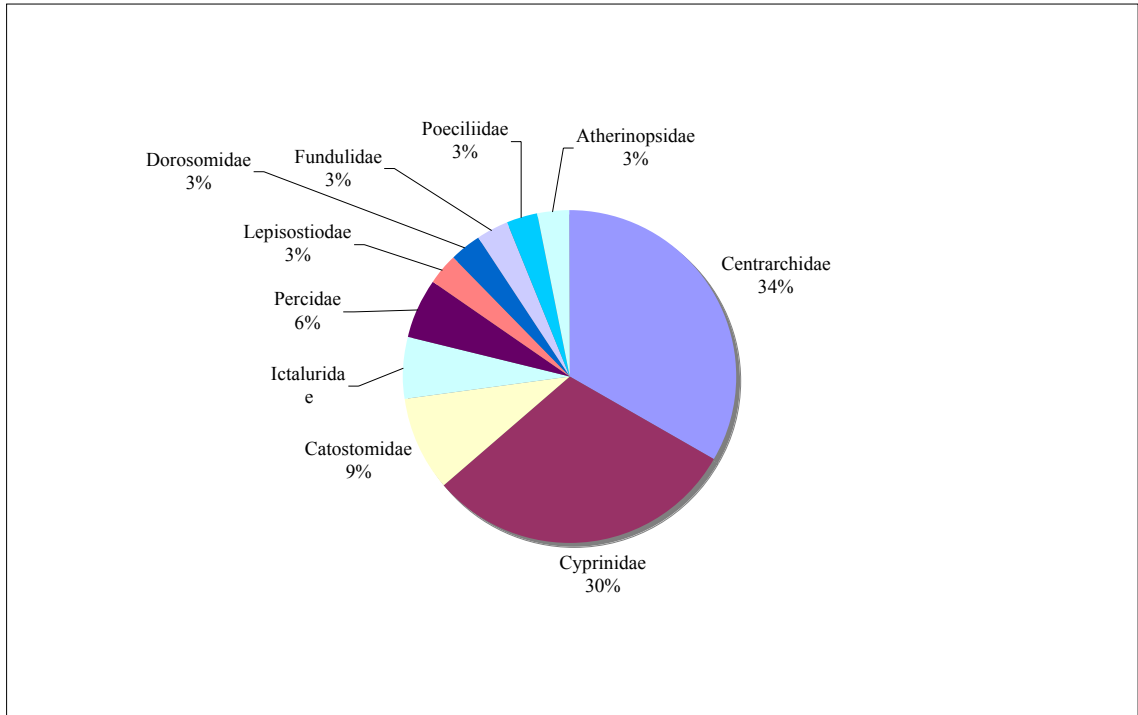


Fig. 5. Fish species composition of pool habitats in Little Uchee Creek in 2005.

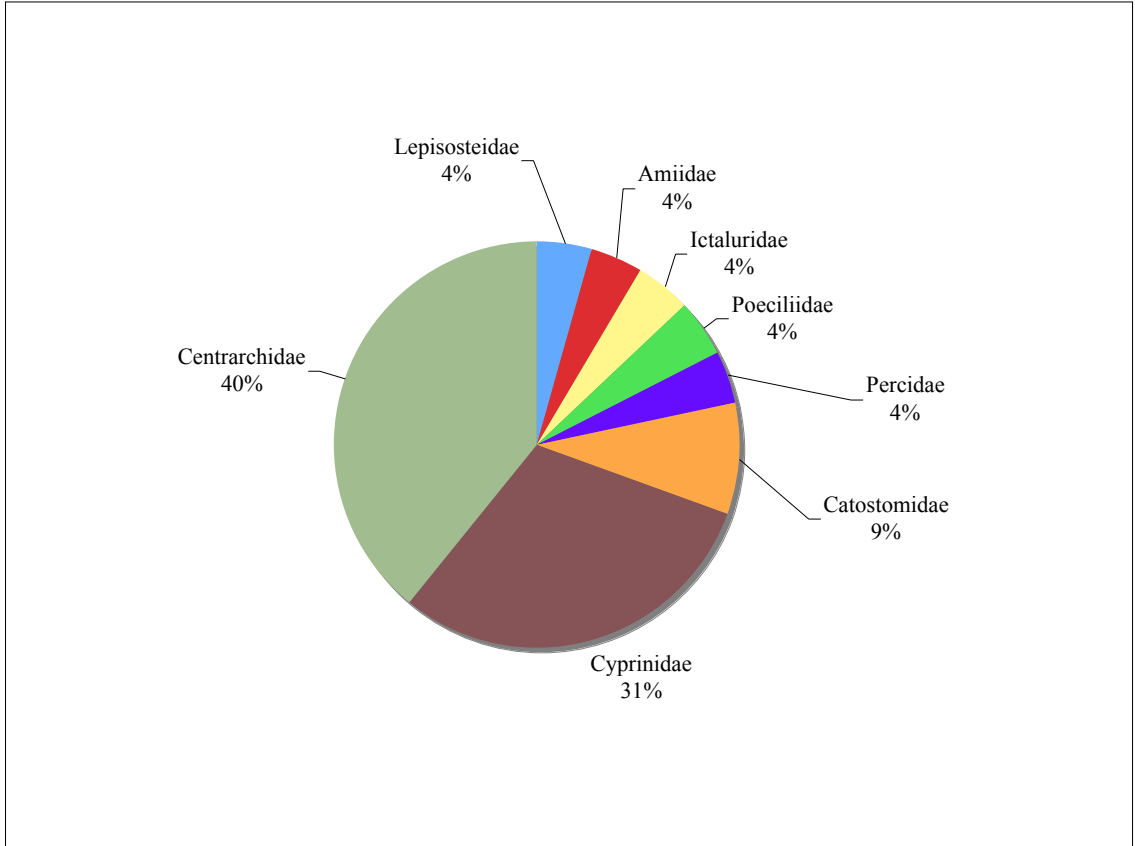


Fig. 6. Fish species composition of pool habitats in Wacochee Creek in 2005.

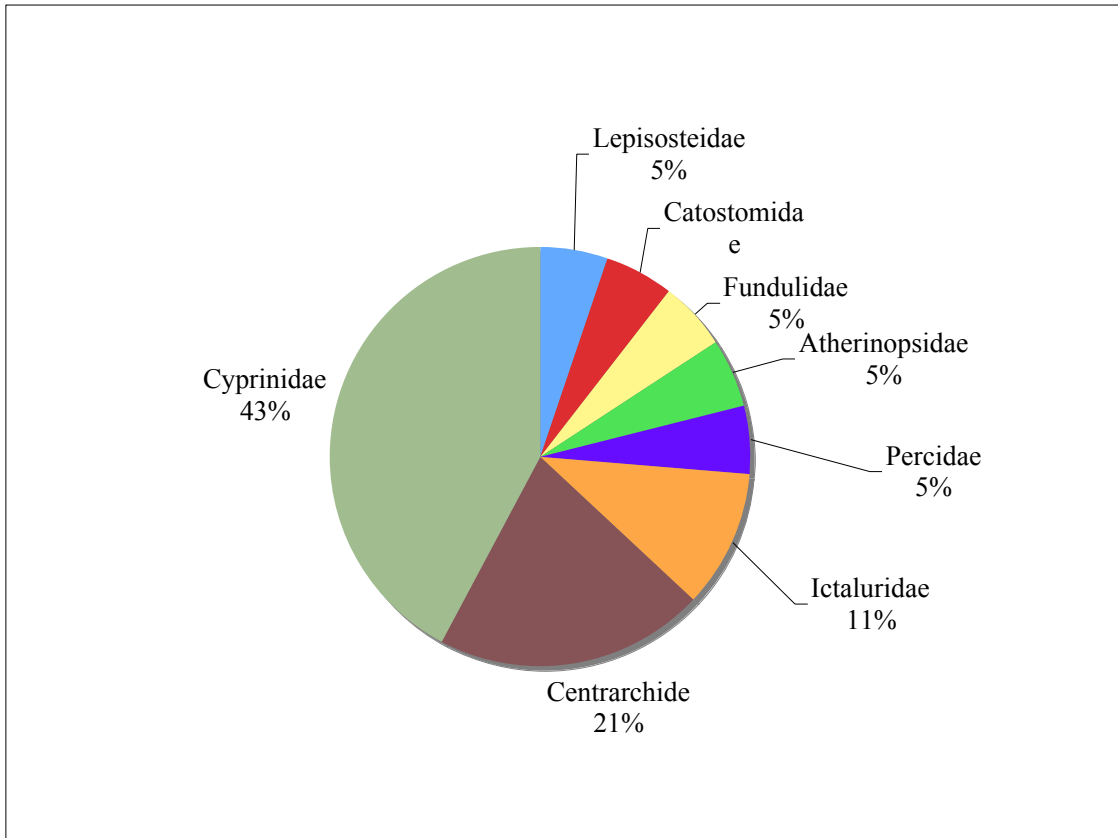


Fig. 7. Fish species composition of pool habitats in Halawakee Creek in 2005.

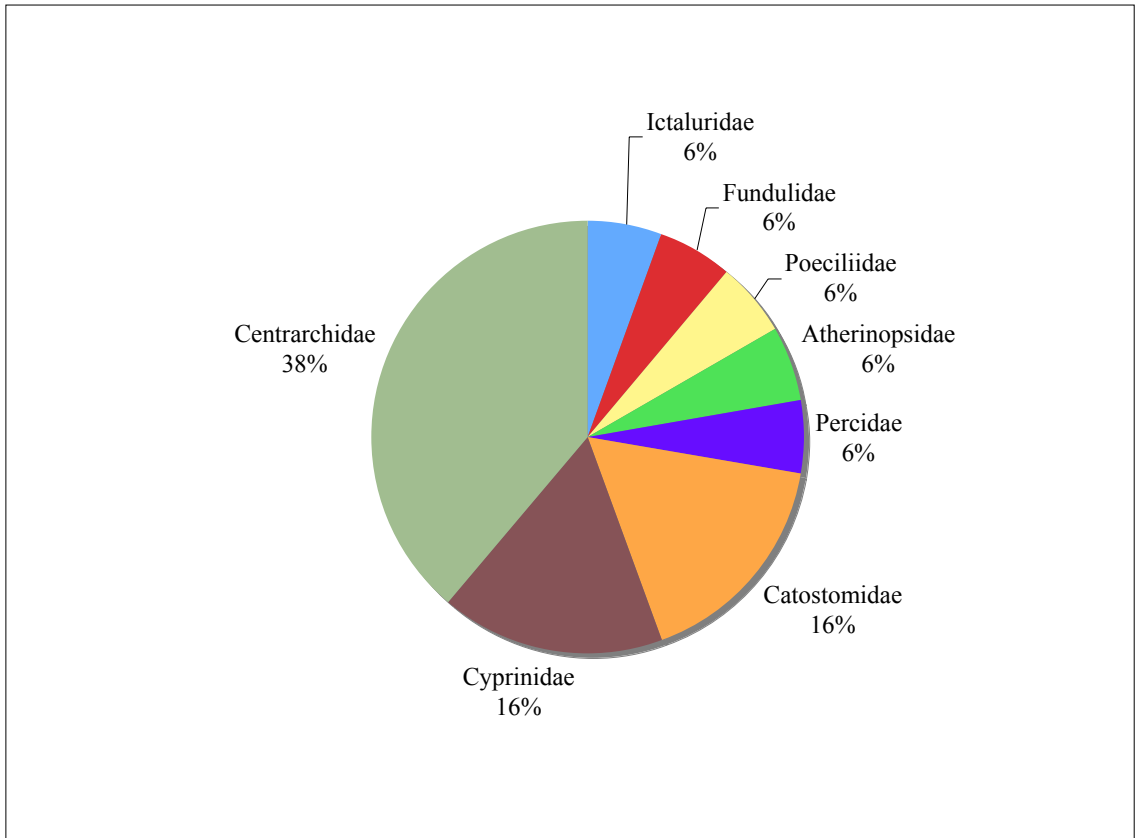


Fig. 8. Fish species composition of shoal habitats in Little Uchee Creek from 2005 and 2006.

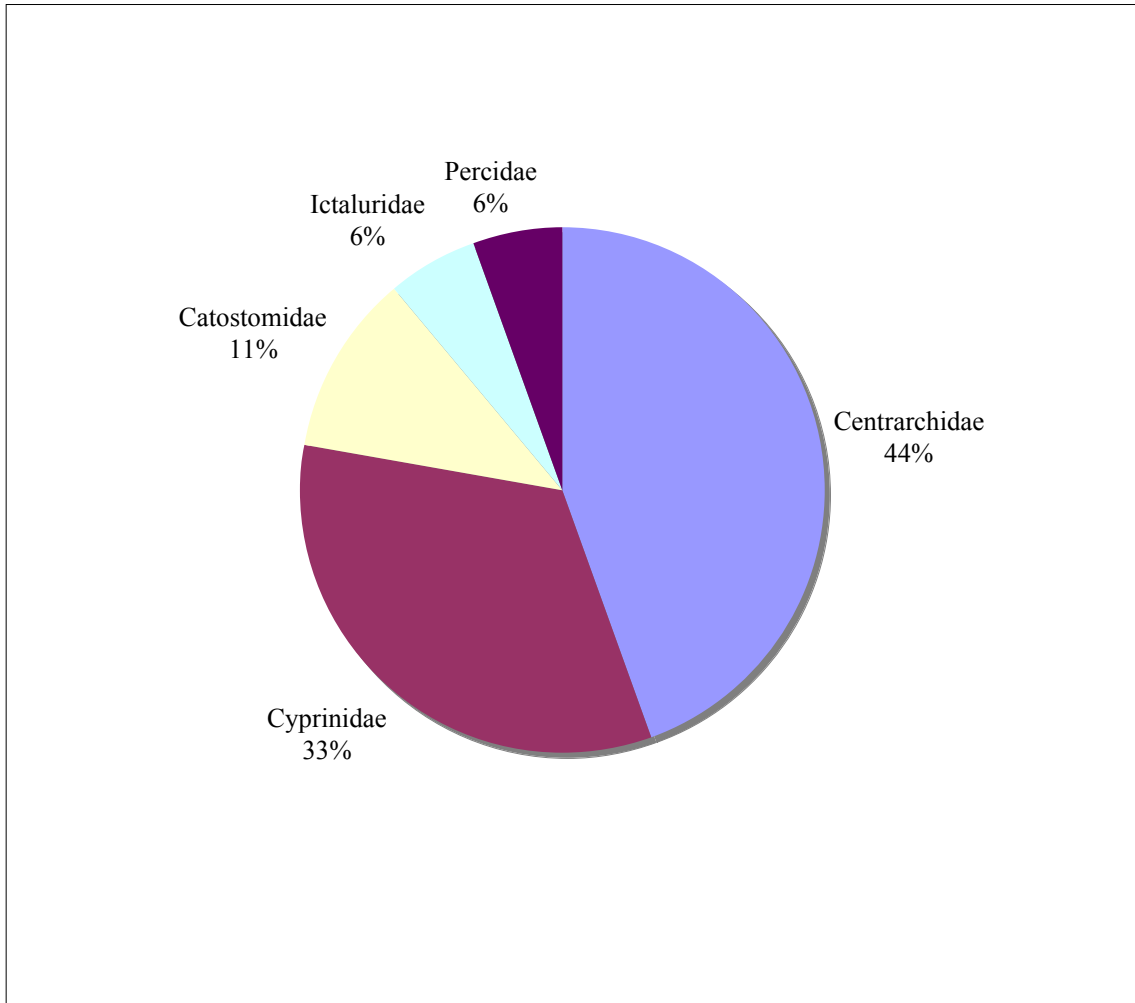


Fig. 9. Fish species composition of shoal habitats in Wacochee Creek from 2005 and 2006.

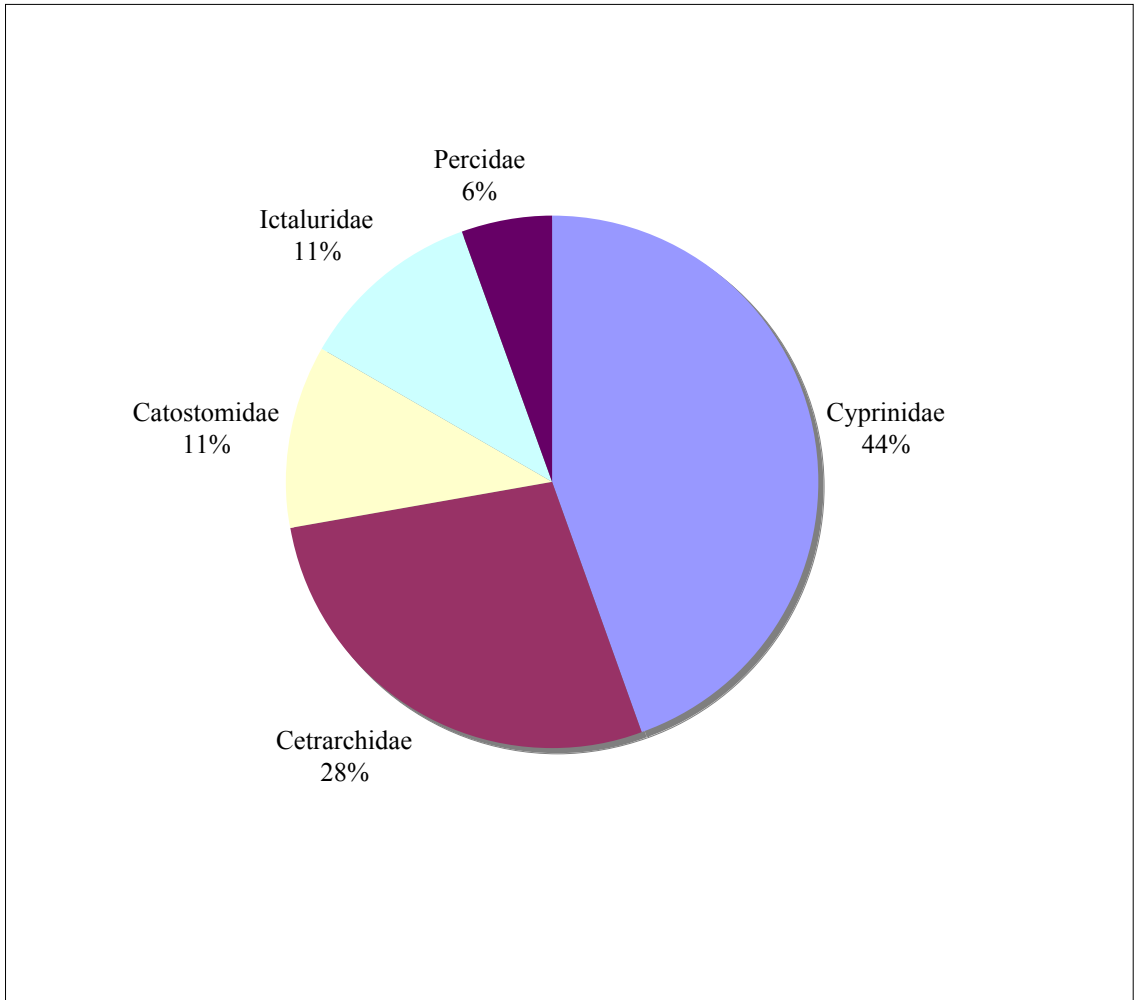


Fig. 10. Fish species composition of shoal habitats in Halawakee Creek from 2005 and 2006.

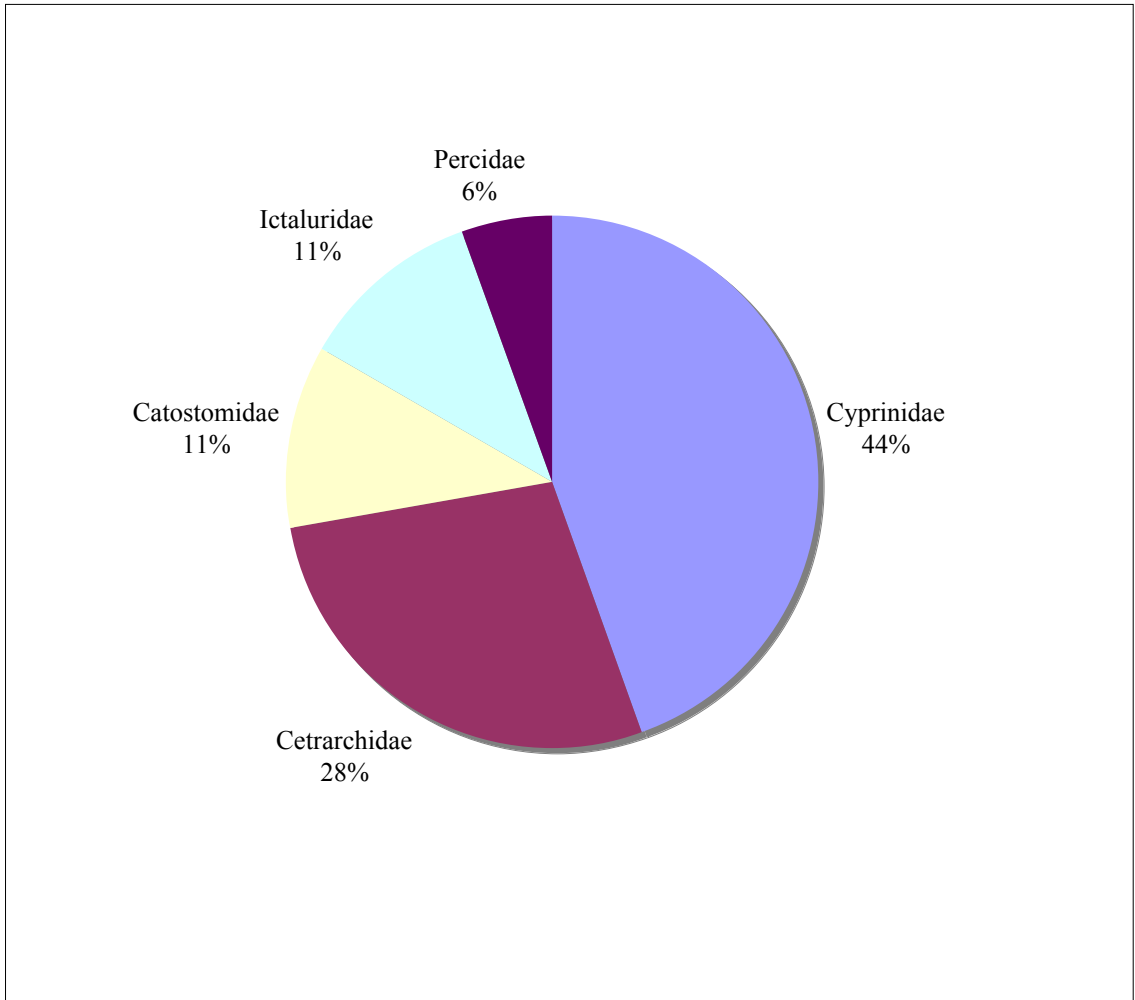


Fig. 11. Uchee Creek gauge from July 2004 – Jan 2007.

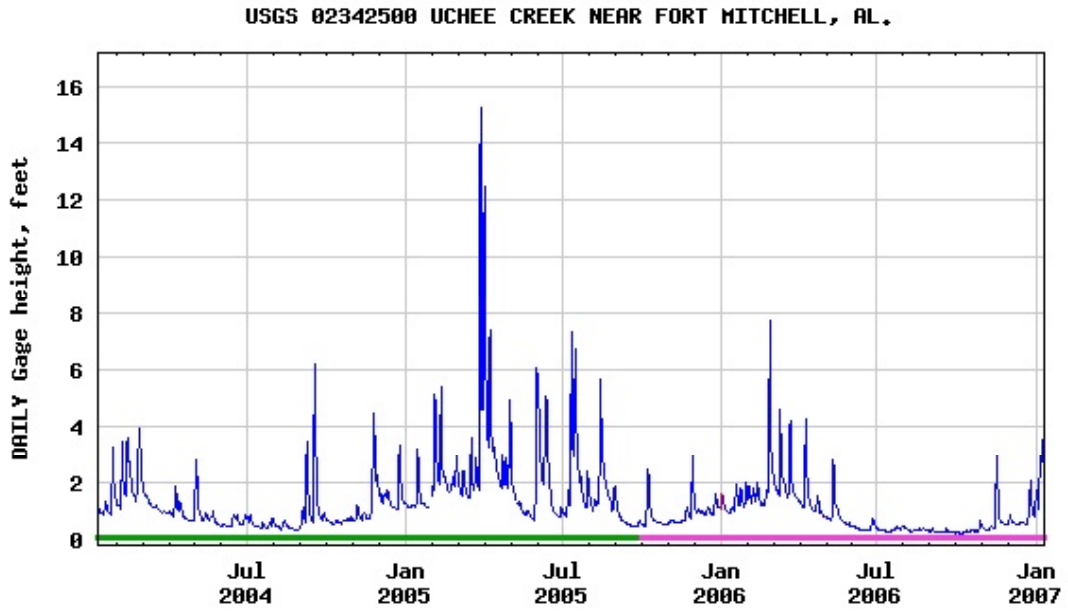


Fig. 12. Principal component analysis plots of environmental variables of shoals in 2005

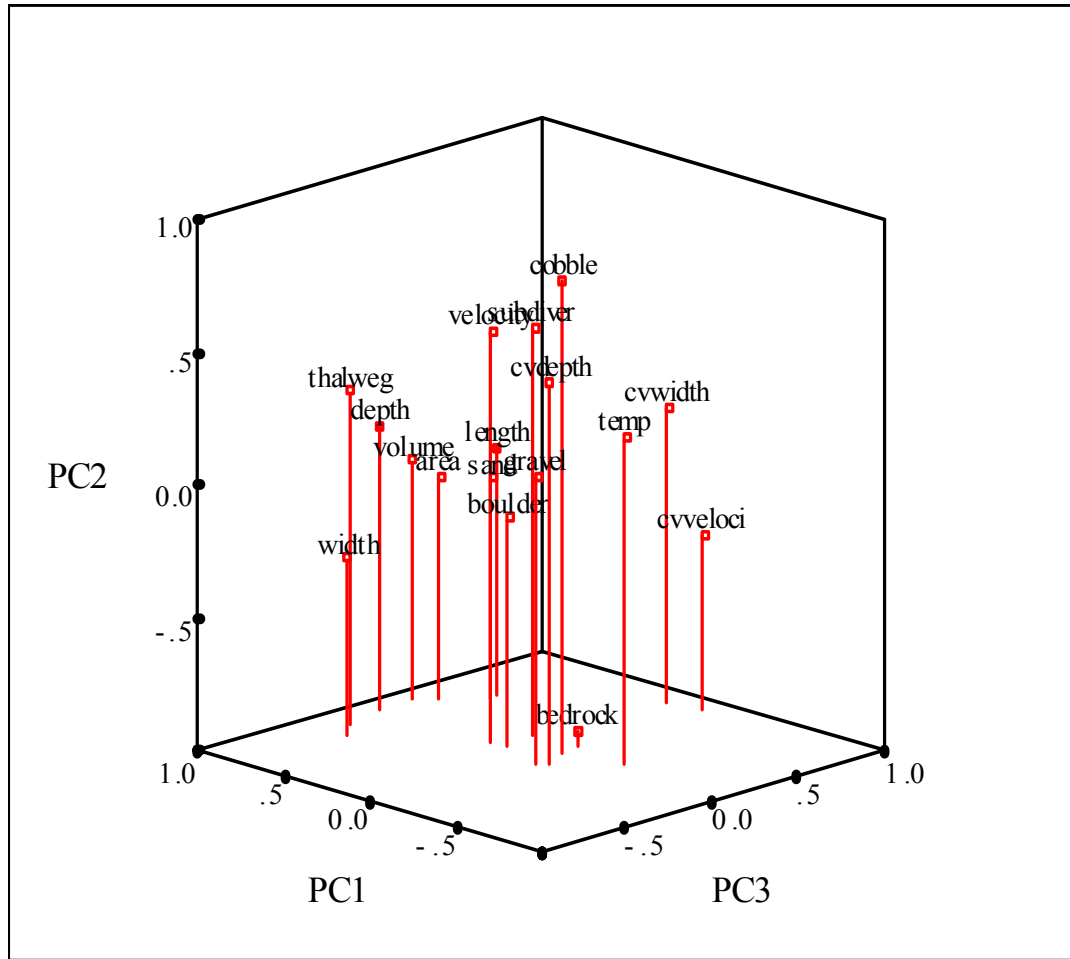


Fig. 13. Principal component analysis plots of environmental variables of shoals in 2006

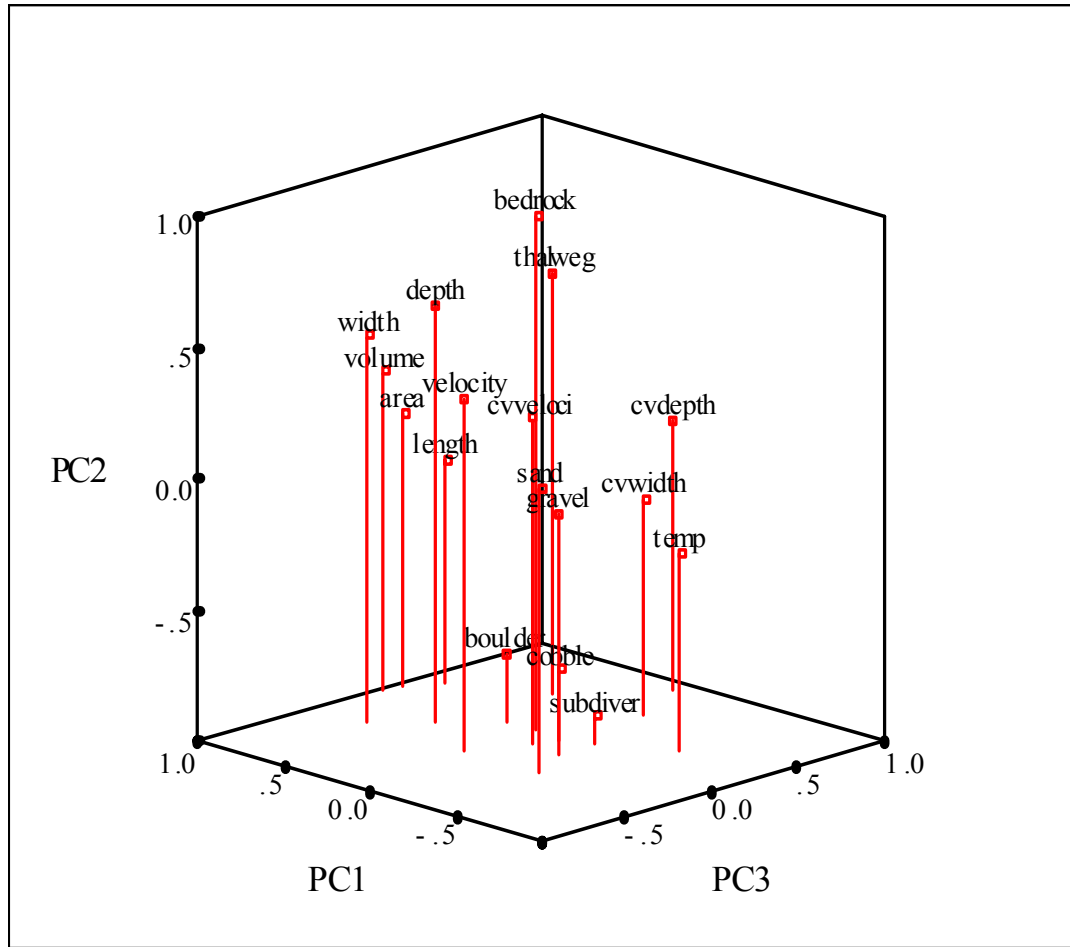


Fig. 14. Linear relationship of species richness and CV of current velocity of shoals in 2005. Significant at alpha = 0.05 ($r^2 = .15$)

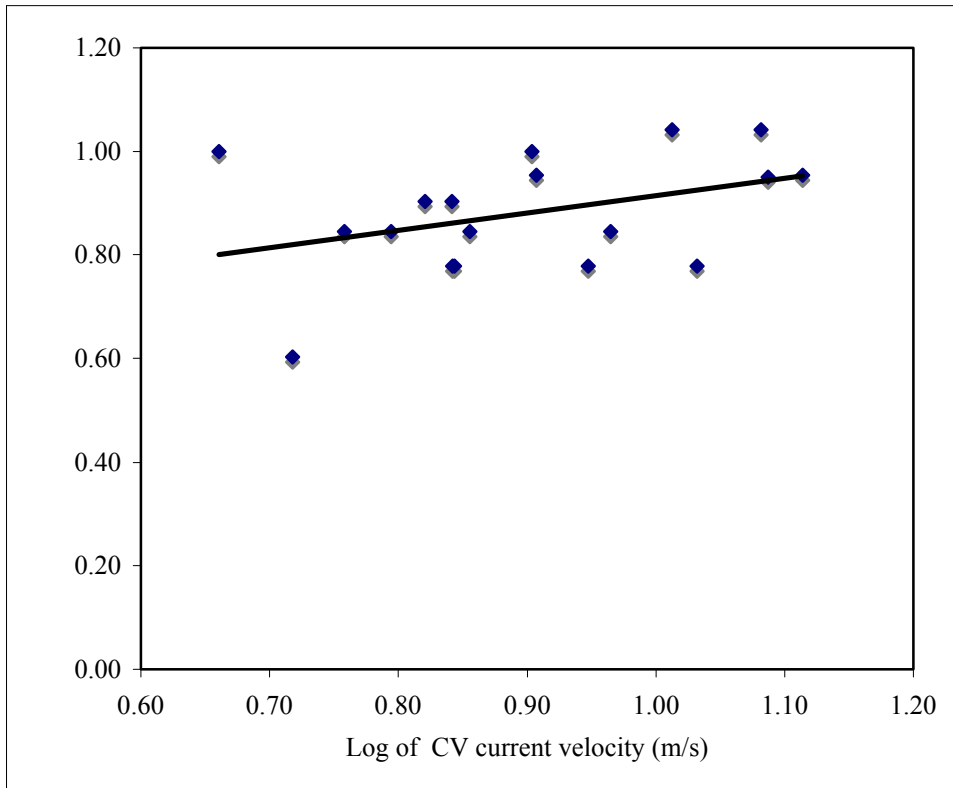


Fig. 15. Linear relationship between species richness and proportion of boulder in shoals in 2005. Significant at $\alpha = 0.05$ ($r^2 = 0.27$)

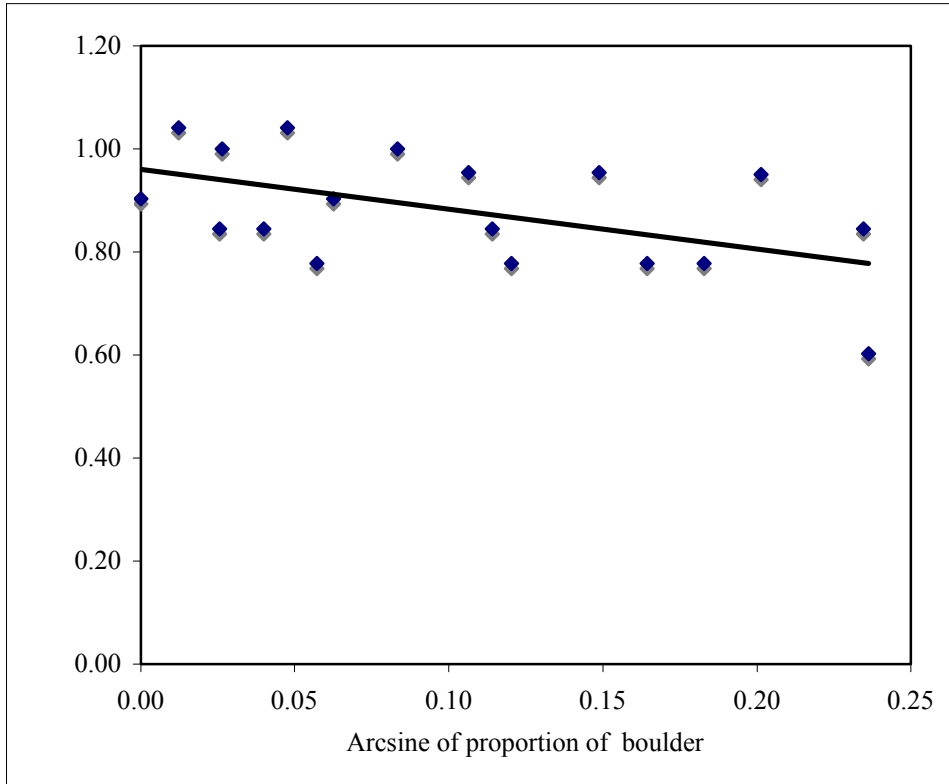


Fig. 16. Linear relationship of the total fish density/m² and shoal volume in 2005. Significant at alpha = 0.05 ($r^2 = 0.33$)

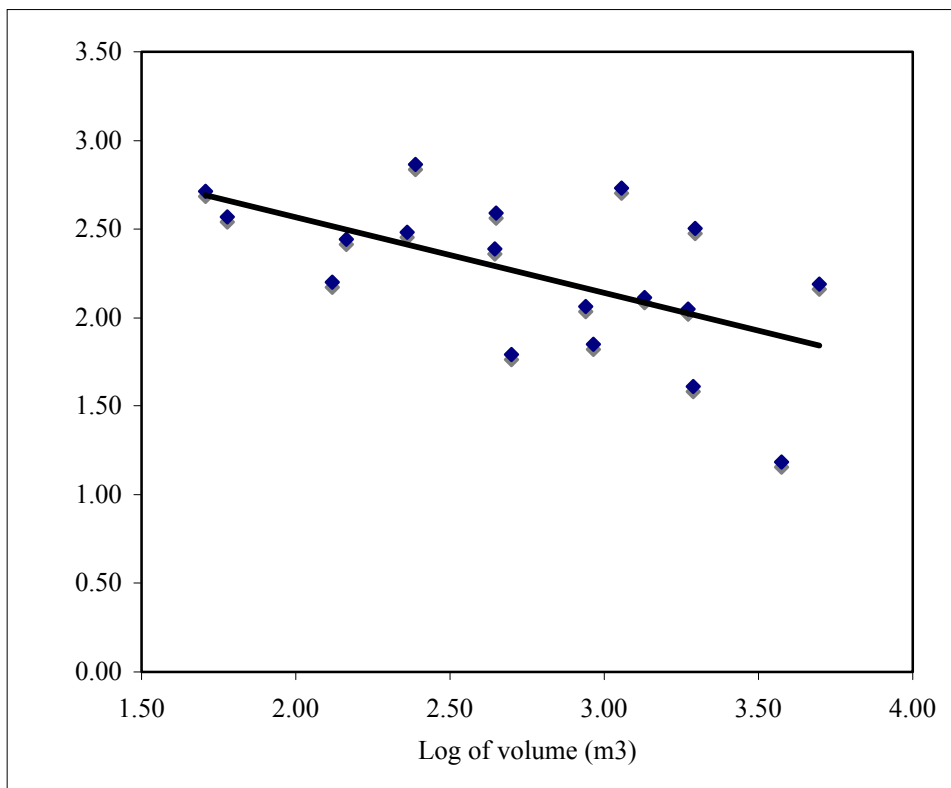


Fig. 17. Linear relationship between juvenile fish density/m² and shoal volume in 2005. Significant at alpha = 0.05 ($r^2 = 0.19$)

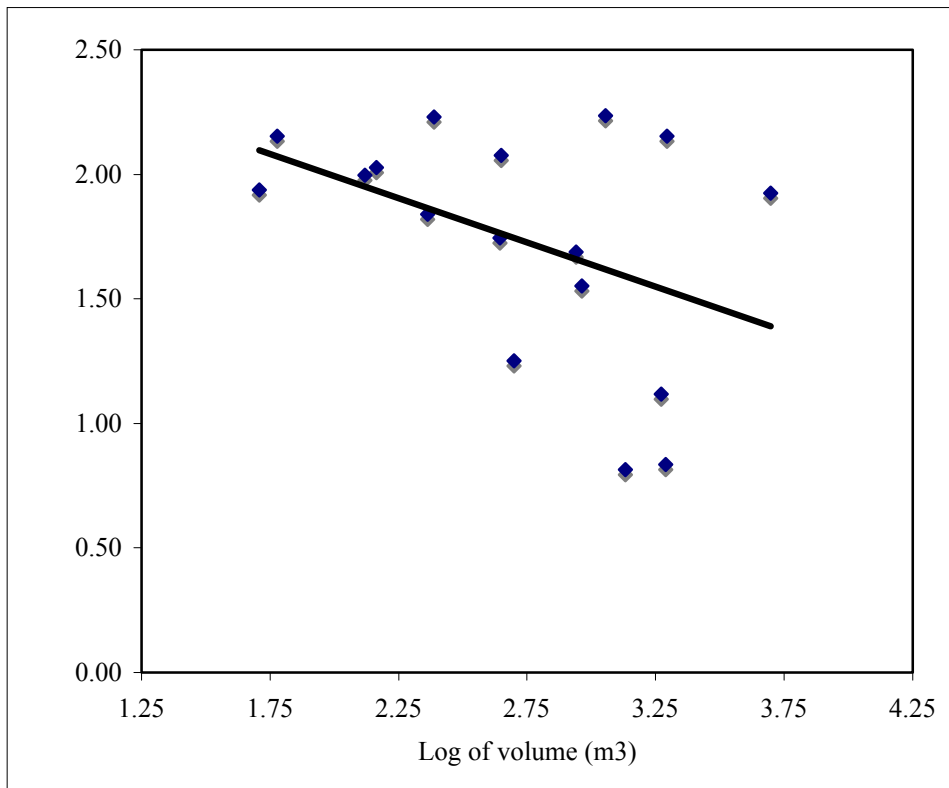


Fig. 18. Linear relationship between adult fish density/m² and shoal volume in 2005. Significant at alpha = 0.05 ($r^2 = 0.30$)

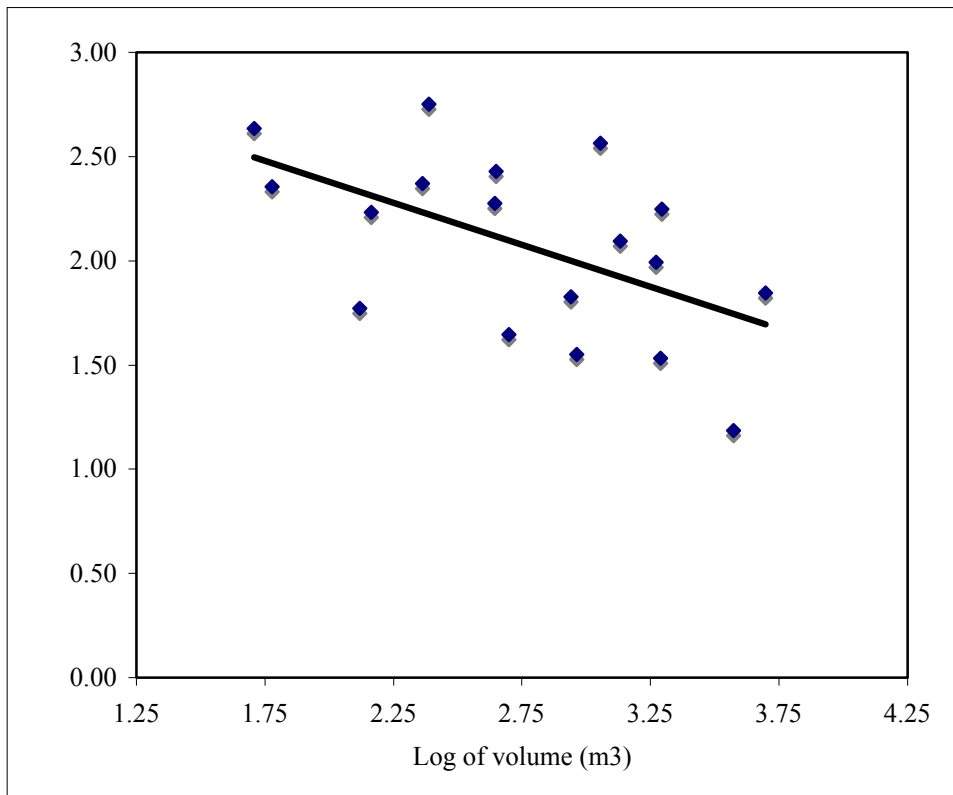


Fig. 19. Linear relationship between number of adult *C. pauciradii*/m² and shoal volume in 2005. Significant at alpha = 0.05 ($r^2 = 0.66$)

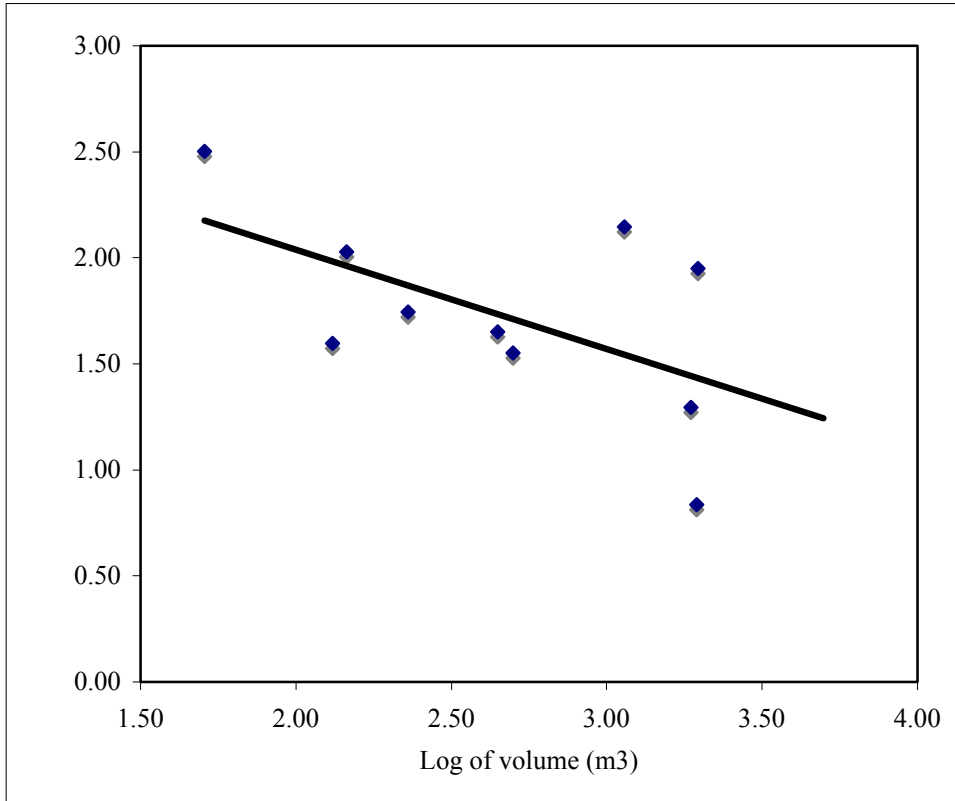


Fig. 20. Linear relationship between number of adult *C. venusta*/m² and the proportion of bedrock in 2005. Significant at alpha = 0.05 ($r^2 = 0.32$)

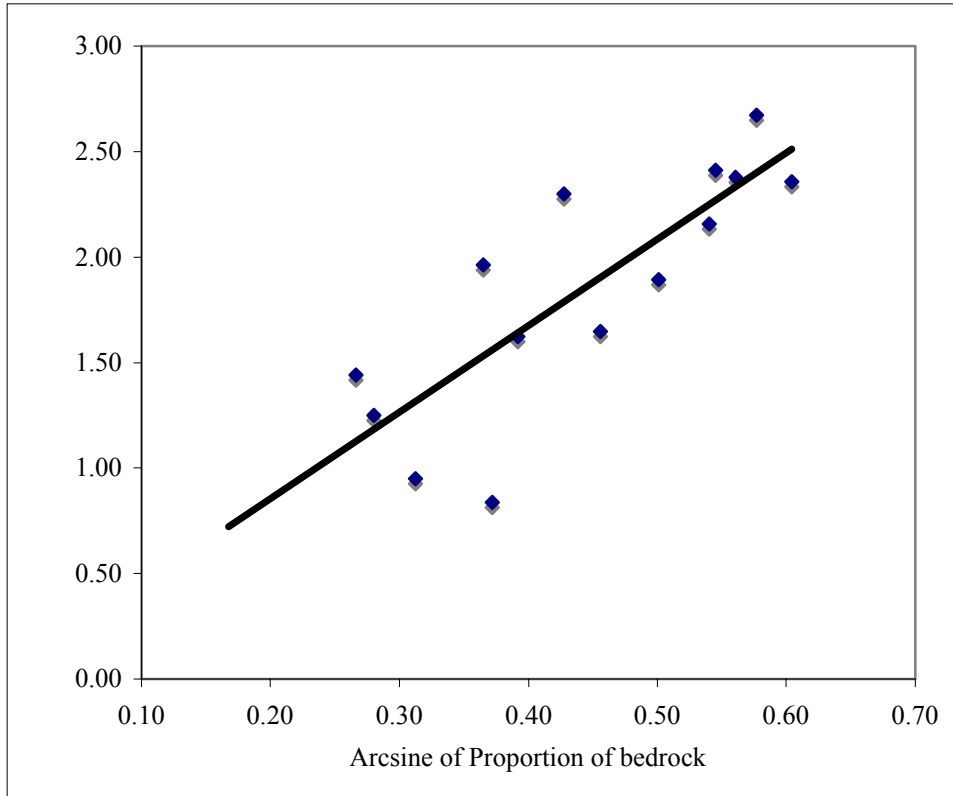


Fig. 21. Linear relationship between number of cyprinids/m² and shoal volume in 2005. Significant at alpha = 0.05 ($r^2 = 0.41$)

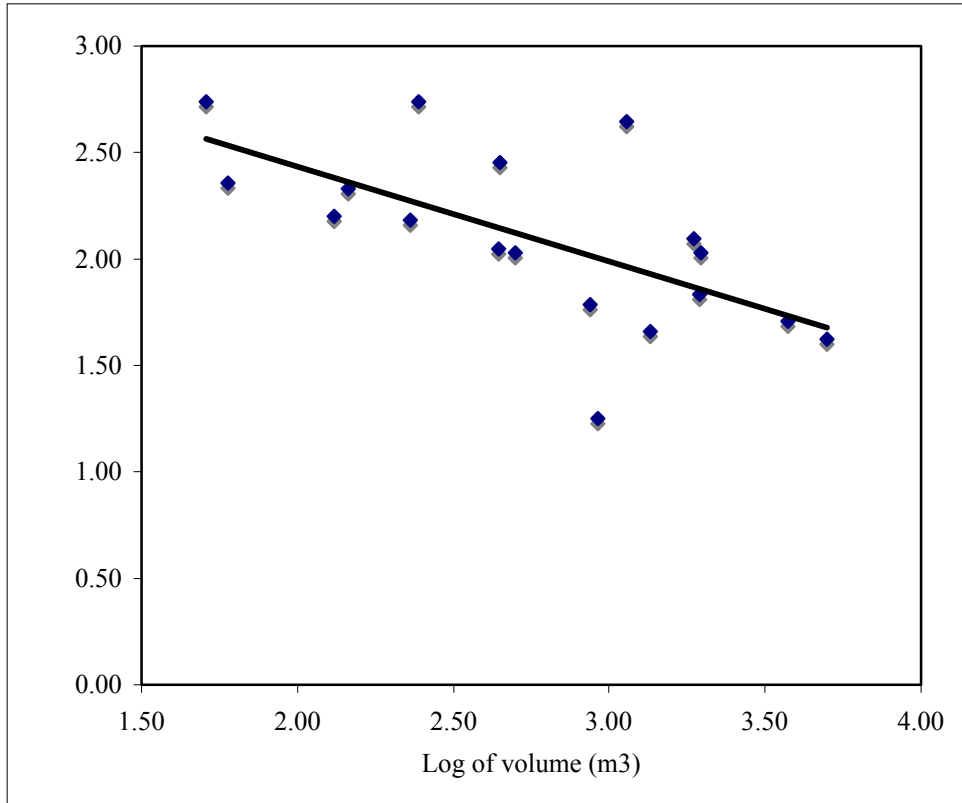


Fig. 22. Linear relationship between species richness and shoal volume in 2006. Significant at alpha = 0.05 ($r^2 = 0.30$)

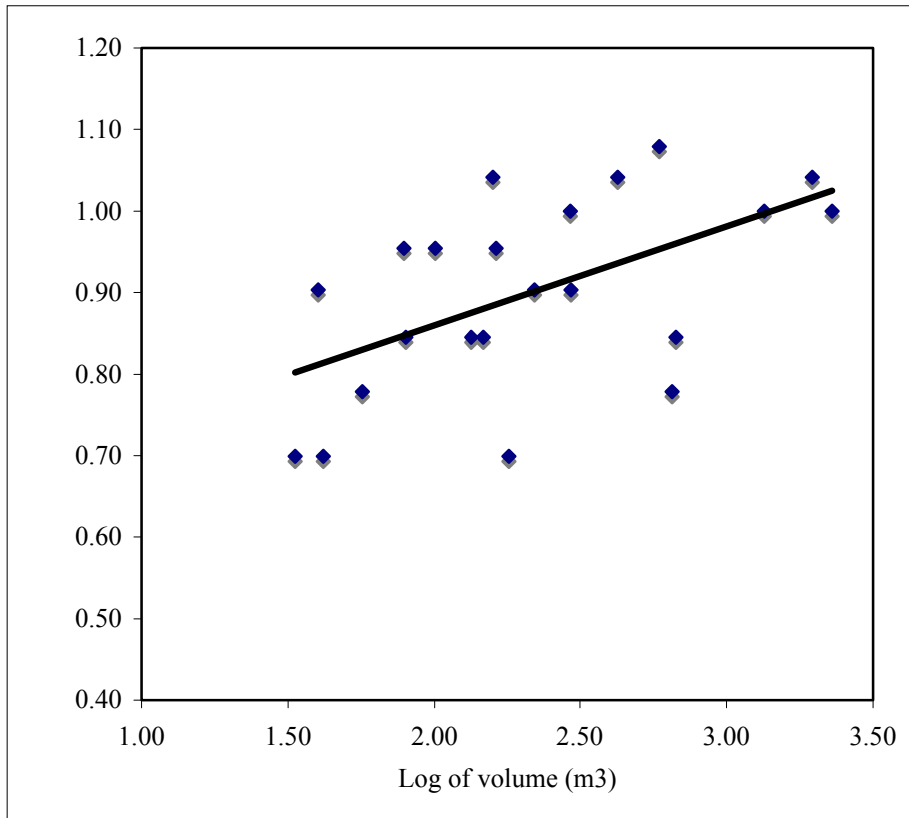


Fig. 23. Linear relationship between number of juvenile *P. nigrofasciata*/m² and shoal volume in 2006. Significant at alpha = 0.05 ($r^2 = 0.34$)

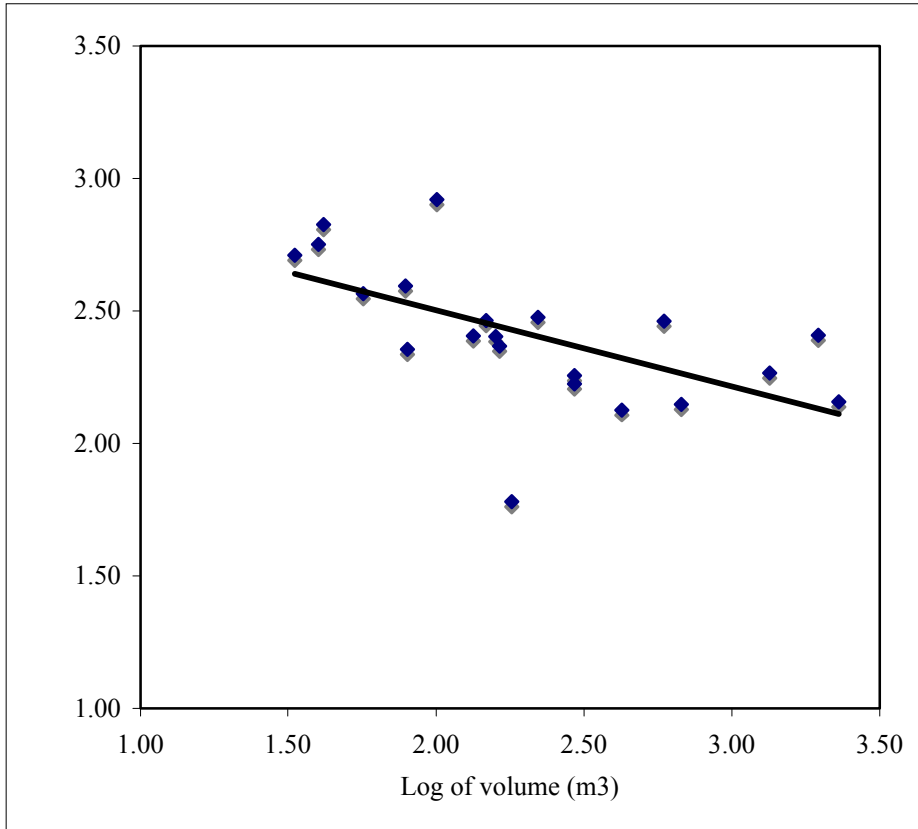


Fig. 24. Linear relationship between number of cyprinids/m² and shoal volume in 2006. Significant at alpha = 0.05 ($r^2 = 0.28$)

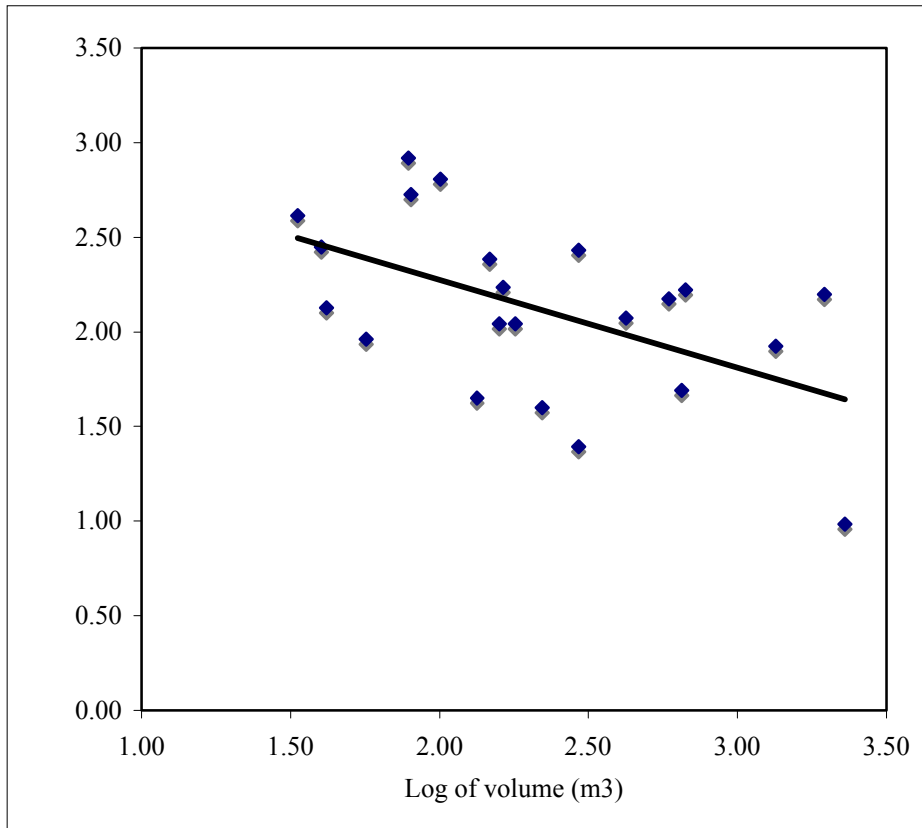


Fig. 25A. Species-area relationship for shoals in 2005.

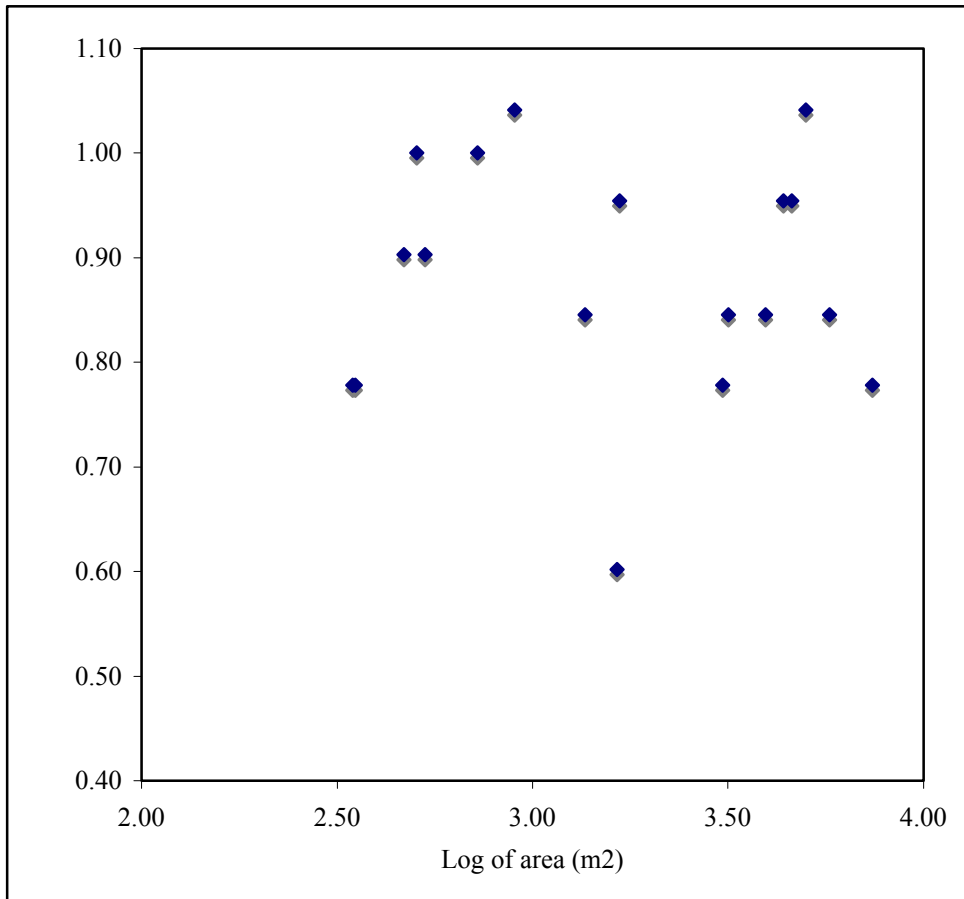


Fig. 25B. Species-area relationship for shoals in 2006. Significant at alpha = 0.05 ($r^2 = 0.40$)

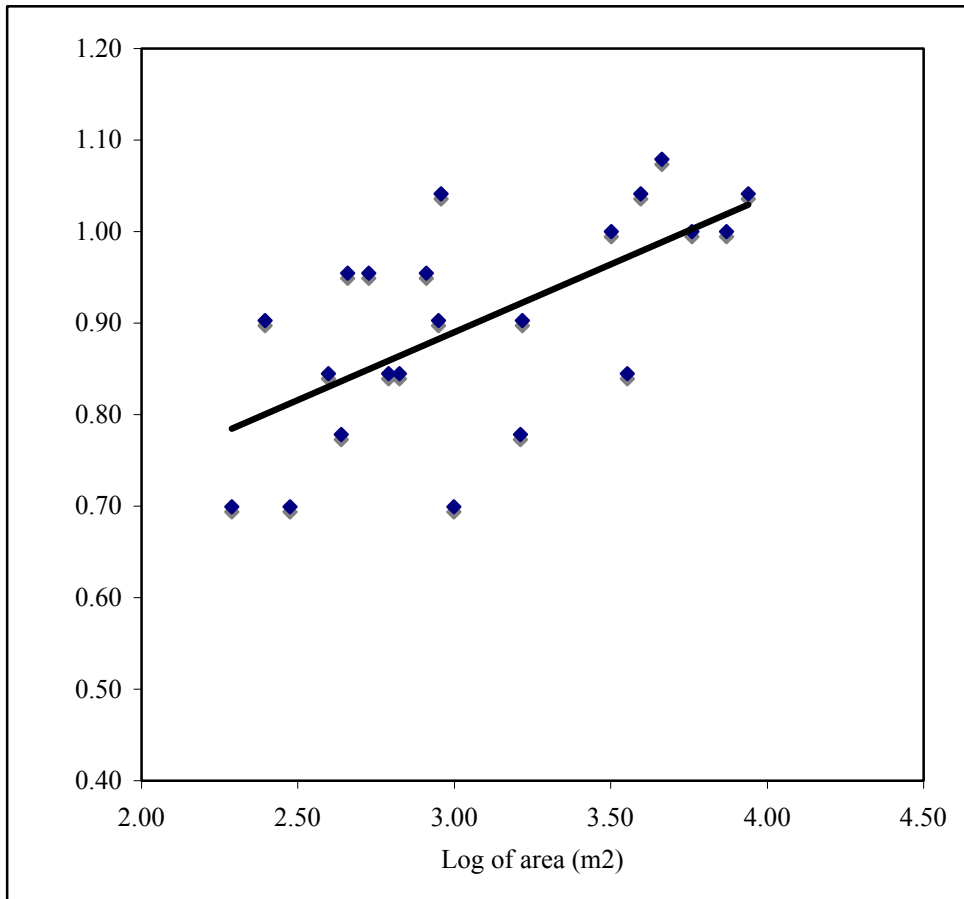


Fig. 26. Linear relationship between density of *C. pauciradii*/m² and CV of current velocity in 2006. Significant at alpha = 0.05 ($r^2 = 0.51$)

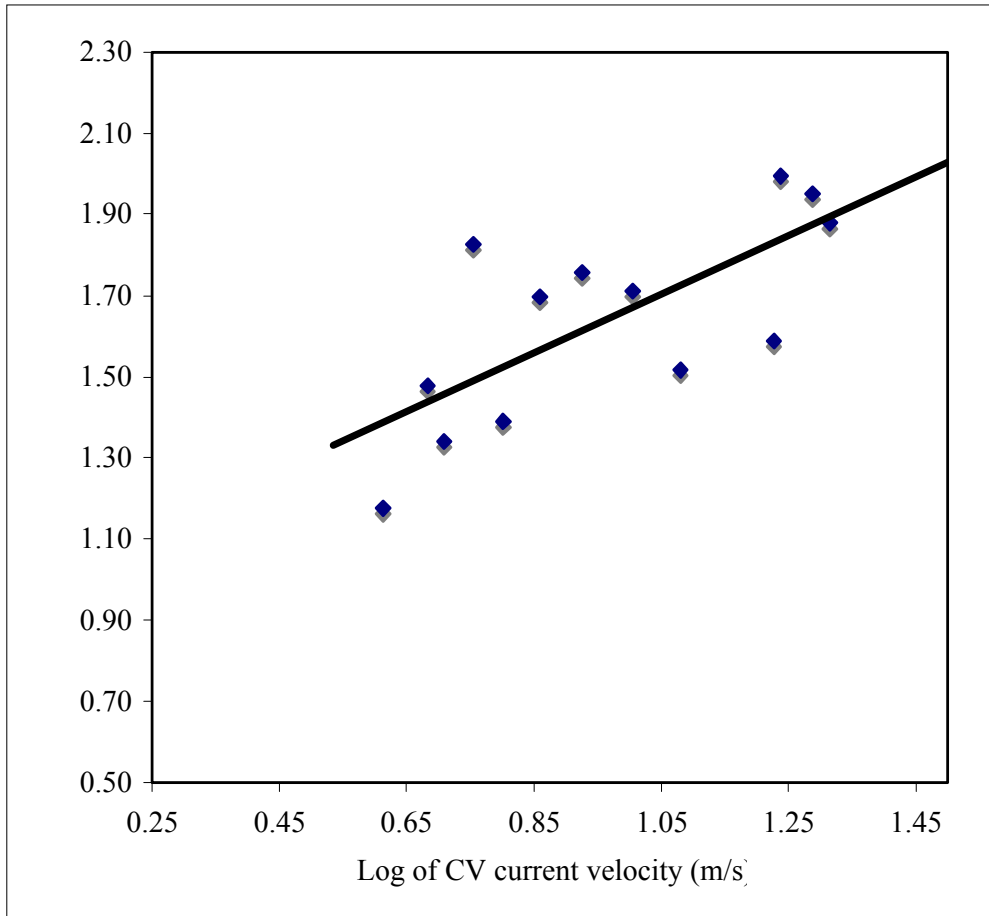


Fig. 27. Size and spatial distribution of shoal habitats in Little Uchee Creek.

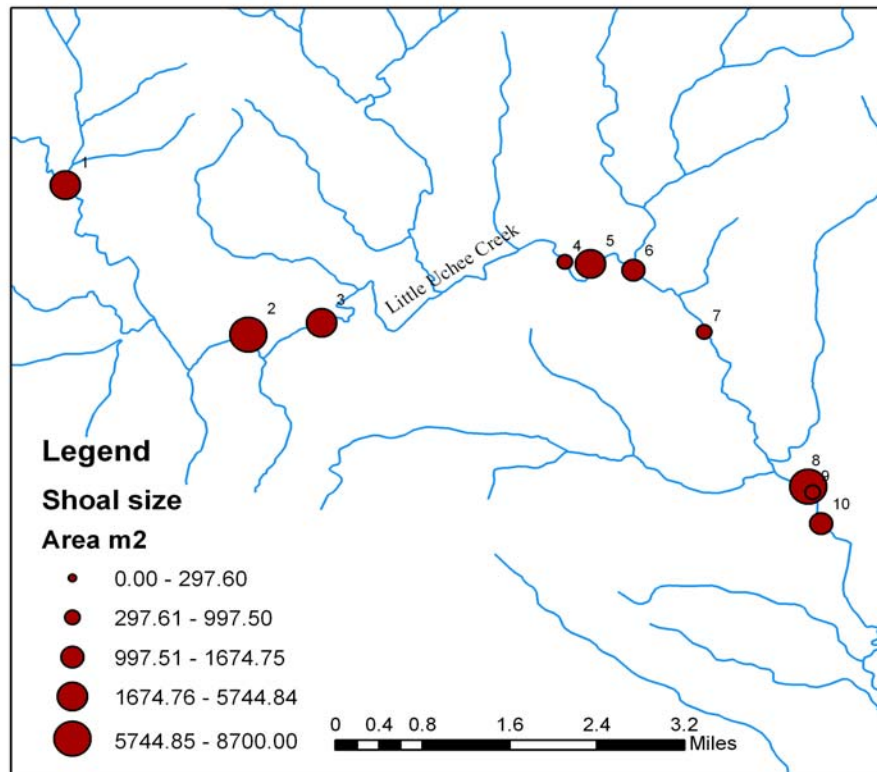


Fig. 28. Size and spatial distribution of shoal habitats in Wacooshee Creek.

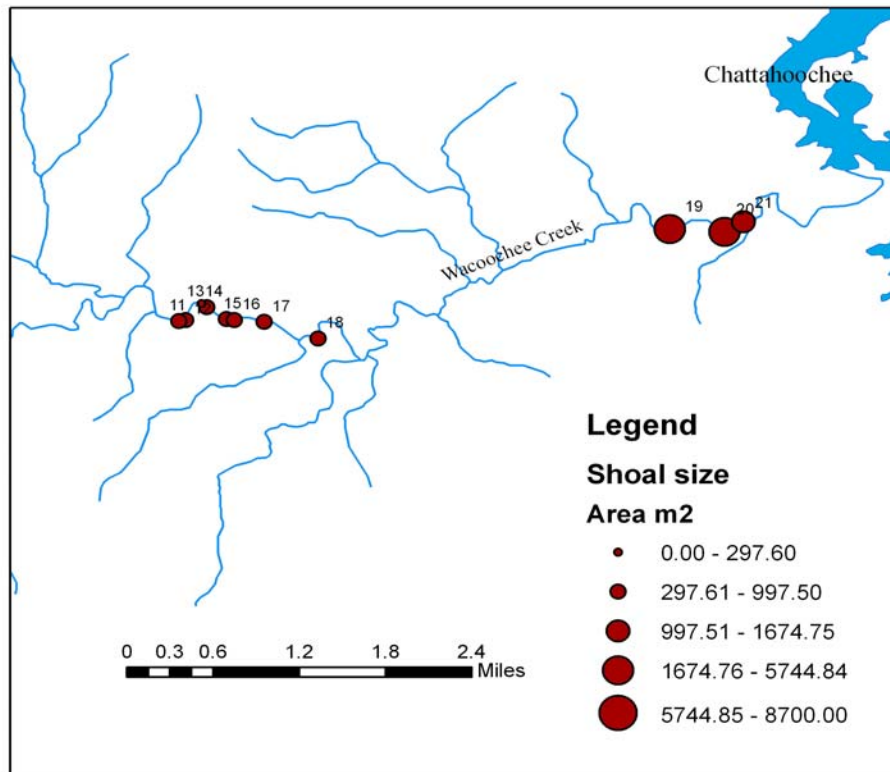


Fig. 29. Size and spatial distribution of shoal habitats in Halawakee Creek.

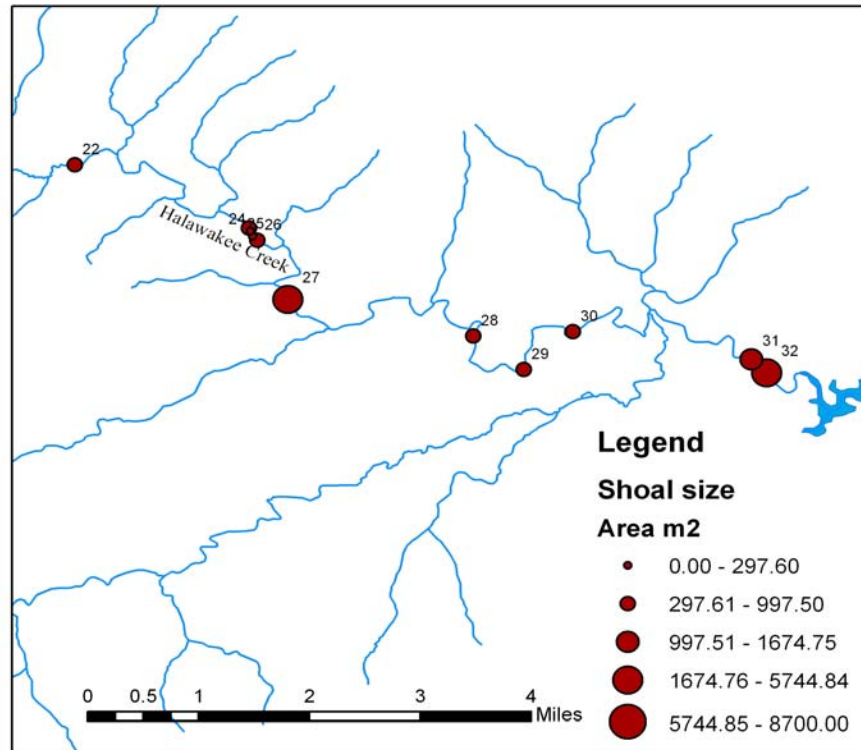


Fig. 30. Linear relationship between species richness and proximity index in 2006. Significant at alpha = 0.05 ($r^2 = 0.31$)

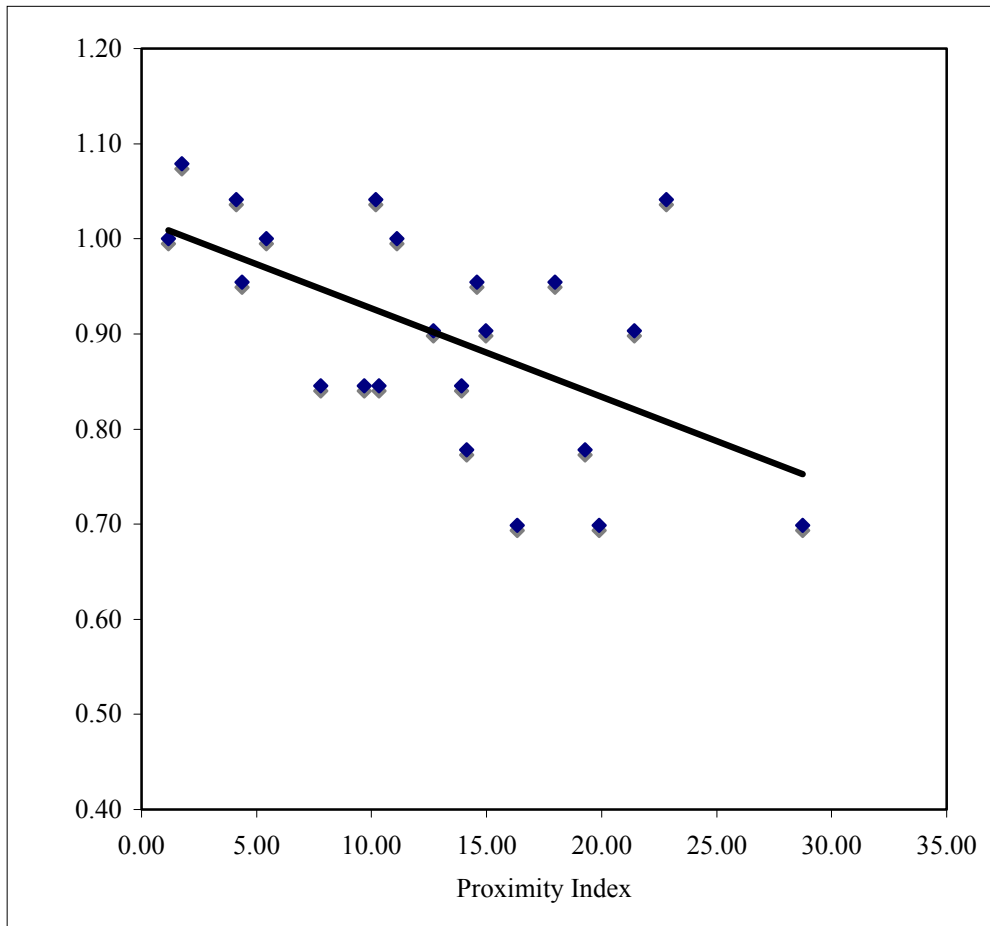


Fig. 31. Linear relationship between the number of cyprinids/m² and link magnitude in 2005. Significant at alpha = 0.05 ($r^2 = 0.28$)

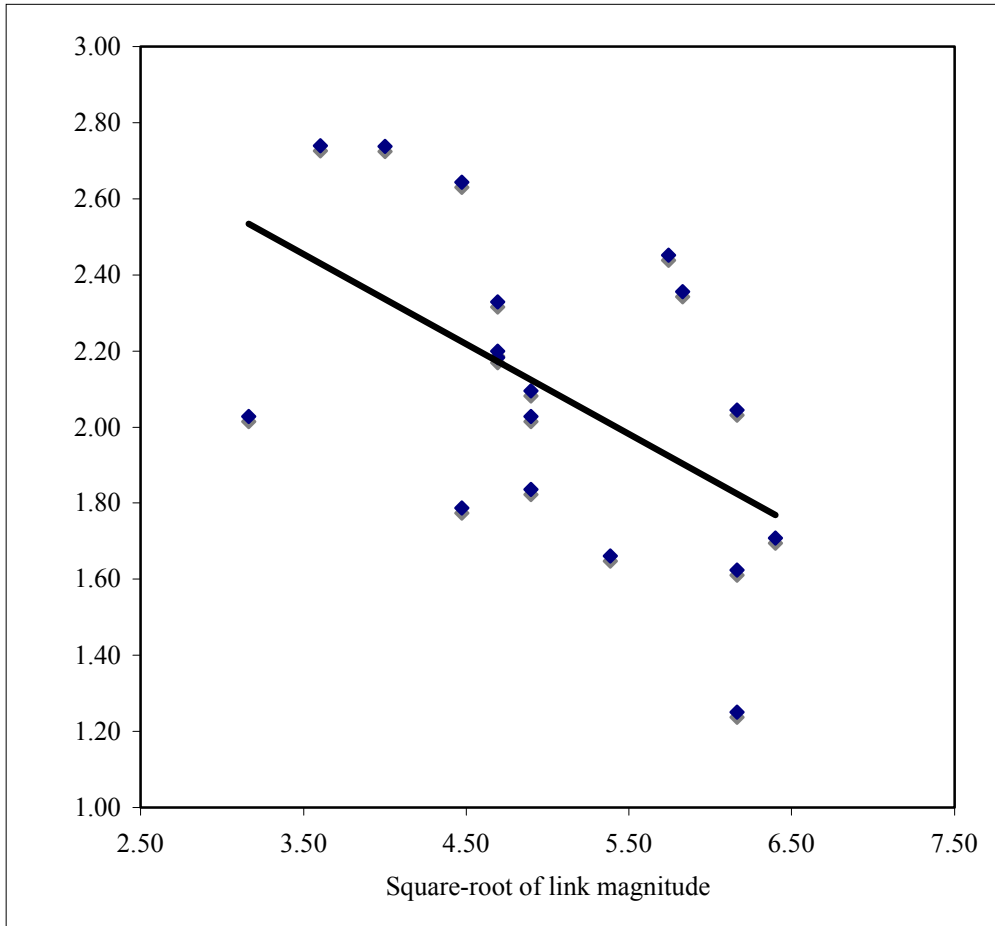


Fig. 32. Linear relationship between the number of cyprinids/m² and link magnitude in 2006. Significant at alpha = 0.05 ($r^2 = 0.26$)

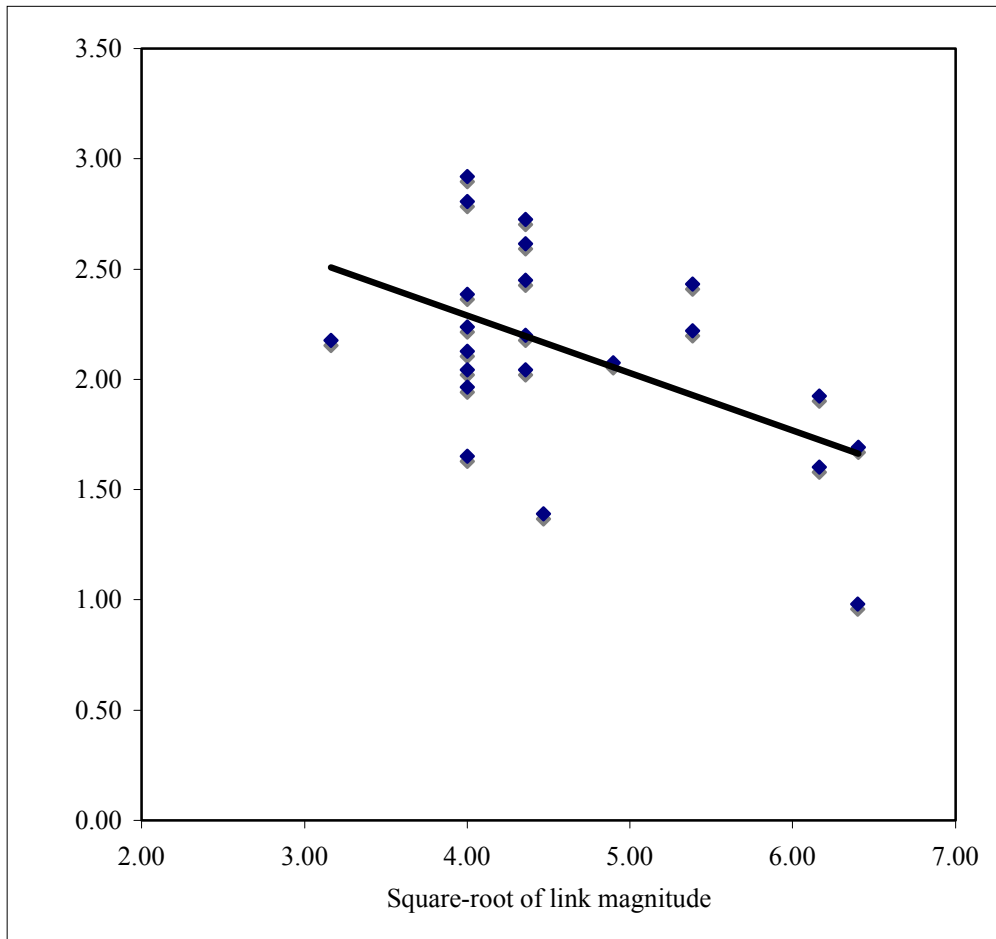


Fig. 33. Linear relationship between the number of centrarchids and link magnitude in 2006. Significant at $\alpha = 0.05$ ($r^2 = 0.18$)

