

RELATIONSHIPS AMONG SWIMMING ABILITY, HABITAT USE, AND
MORPHOLOGY OF FRESHWATER FISHES FROM TEXAS AND LOUISIANA

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By

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ABSTRACT

**RELATIONSHIPS AMONG SWIMMING ABILITY, HABITAT USE,
AND MORPHOLOGY OF FRESHWATER FISHES FROM
TEXAS AND LOUISIANA**

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Relationships between swimming ability and both habitat selection and morphology were assessed for freshwater fishes from Gulf slope, Rio Grande, Red River,

and Canadian River drainages in Texas and Louisiana to better understand the influence that flow has on structuring fish assemblages. Swimming ability, relative (body lengths per second, $\text{bl}\cdot\text{s}^{-1}$) and absolute speeds ($\text{cm}\cdot\text{s}^{-1}$), were determined for 37 species from June through August 2003 in a mobile swim tunnel. Mean absolute ($\text{cm}\cdot\text{s}^{-1}$) speeds ranged from 31 to 84 $\text{cm}\cdot\text{s}^{-1}$ for Cyprinidae (N of species = 24), 50.9 $\text{cm}\cdot\text{s}^{-1}$ for Characidae ($N = 1$), 70 $\text{cm}\cdot\text{s}^{-1}$ for Ictaluridae, 33 $\text{cm}\cdot\text{s}^{-1}$ for Cichlidae, 40 $\text{cm}\cdot\text{s}^{-1}$ for Percidae, 31 to 43 $\text{cm}\cdot\text{s}^{-1}$ for Cyprinodontidae ($N = 2$), 30 $\text{cm}\cdot\text{s}^{-1}$ for Atherinidae ($N = 1$), 16 to 19 $\text{cm}\cdot\text{s}^{-1}$ for Poeciliidae ($N = 2$), and 23 to 41 $\text{cm}\cdot\text{s}^{-1}$ for Centrarchidae ($N = 4$). Mean relative ($\text{bl}\cdot\text{s}^{-1}$) speeds ranged from 3.4 to 19.6 $\text{bl}\cdot\text{s}^{-1}$ for Cyprinidae, 12.6 $\text{bl}\cdot\text{s}^{-1}$ for Characidae, 13.7 $\text{bl}\cdot\text{s}^{-1}$ for Ictaluridae, 8.7 $\text{bl}\cdot\text{s}^{-1}$ for Cichlidae, 11.1 $\text{bl}\cdot\text{s}^{-1}$ for Percidae, 5.5 to 12.0 $\text{bl}\cdot\text{s}^{-1}$ for Cyprinodontidae, 6.4 $\text{bl}\cdot\text{s}^{-1}$ for Atherinidae, 5.5 to 6.8 $\text{bl}\cdot\text{s}^{-1}$ for Poeciliidae, and 5.7 to 8.1 $\text{bl}\cdot\text{s}^{-1}$ for Centrarchidae. Absolute speeds ($\text{cm}\cdot\text{s}^{-1}$) were correlated with habitat current velocity from published and unpublished studies. In general, swimming ability explained longitudinal distributions of fishes with those having greater absolute speeds inhabiting areas of swifter currents (medium to large rivers) and those with lesser absolute speeds inhabiting areas of slower currents (springs, creeks, and small rivers) ($r^2 = 0.40$; $N = 37$; $P < 0.01$). Similarly, swimming ability primarily explained spatial (i.e., runs, pools, and riffles) distributions of fishes from Independence Creek ($r^2 = 0.51$, $N = 10$, $P = 0.03$), and Banita Creek ($r^2 = 0.70$, $N = 7$, $P = 0.06$). Morphological measurements (e.g. flatness index, relative body depth) that strongly segregated among families and within the Family Cyprinidae were identified with principle components analysis (PCA) and correlated (Peterson's correlation coefficients) with individual relative ($\text{bl}\cdot\text{s}^{-1}$) swimming speed. My results indicated that morphological attributes were a poor indicator of

swimming ability among families (PCA1: $r = -0.31$, $N = 412$, $P < 0.01$) (PCA 2: $r = 0.33$, $N = 412$, $P < 0.01$) and within Cyprinidae (PCA 1: $r = -0.34$, $N = 317$, $P < 0.01$) (PCA 2: $r = 0.08$, $N = 317$, $P = 0.17$). Overall, swimming abilities of fishes in part explain species distributions through time and space. However, other attributes (e.g., benthic orientation) were also deemed important in enabling fishes to persist in flowing environments. Understanding interactions between flow and fish assemblage structure is critical to species conservation and instream flow requirements for fish assemblages, especially obligate riverine specialists.

INTRODUCTION

Aspects of flow (e.g., depth and current velocity) strongly influence spatial patterns in riverine fish assemblages on multiple scales (Schlosser 1985; Bain et al. 1988; Poff and Allan 1995). Fishes are distributed longitudinally within a stream because of differences in habitat (i.e., flow regime) among reaches (Kuehne 1962; Harrel et al. 1967; Whiteside and McNatt 1972; Evans and Noble 1979). On a smaller scale, fishes are spatially distributed along current velocity and depth gradients among habitat types (i.e., pools, runs, and riffles) within a stream reach (Angermeier 1987; Gelwick 1990; Aadland 1993; Cantu and Winemiller 1997). In addition, peak flows affect spatial patterns in fish assemblages by differentially displacing species downstream (Cross et al. 1985; Minckley and Meffe 1987; Moyle and Light 1996).

Fishes expend energy to inhabit and persist in relatively high flow areas to exploit food resources, to migrate, to avoid competition, and to reduce predation (Edwards 1977; Taylor and McPhail 1985; Greenberg 1991; Freeman 1995; Schaefer et al. 1999; Dibble and Harrel 2000). Consequently, numerous morphological adaptations (i.e., fin shapes, body shapes, proportion of red muscles) are selected through evolutionary time, enabling some species to be more physically efficient at tolerating higher flow among multiple scales than others (Hora 1935; Hubbs 1941; Bone 1966; Lundberg and Marsh 1976; Gatz 1979; Vogel 1994; Schaarschmidt and Jurss 2003). As such, a species swimming ability,

the maximum current velocity that a fish can withstand before being displaced downstream, differs among fishes and is measured to infer habitat relationships, morphological divergence, and persistence in fluctuating flow regimes (Matthews 1985; Hawkins and Quinn 1996; Nelson et al. 2003; Ward et al. 2003). Also, quantification of swimming abilities and understanding of relationships among swimming ability and habitat selection can provide critical information in assessing flow regime needs (i.e., minimum flow requirements) of obligate and facultative riverine fishes.

Several studies have explored the relationships among habitat selection, morphology, and swimming ability in freshwater fishes. Fishes with laterally compressed deeper bodies and rounded caudal and paired fins generally select sluggish waters, as their body and fin shapes are better suited for maneuvering than speed (Aleev 1969; Gosline 1971; Scarnecchia 1988). Alternatively, fishes common in areas of high flow (i.e., run and riffle habitats) tend to have fusiform or dorsal ventrally flattened body shapes with long falcate pectoral and pelvic fins and forked caudal fins (Hora 1935; Hubbs 1941; Nursall 1958; Vogel 1994). Although general trends in morphology and habitat selection exist, correlations between congeners are often inconsistent among morphological attributes, swimming ability, and habitat selection (Taylor and McPhail 1985; Plaut 2000; Shaefer et al. 2000; Ojanguren and Brana 2003). However, such studies usually assess these relationships with a truncated species pool (< three species) which may limit detection of general patterns.

The purpose of this study was to assess relationships between swimming ability and habitat selection (reported current velocity selection of fishes in their naturally associated habitats), and between swimming ability and morphology (features among

families and within Cyprinidae that are important in discriminating swimming ability differences) of freshwater fishes from Gulf slope, Rio Grande, Red River, and Canadian River drainages in Texas and Louisiana. In particular, fishes Cyprinidae were sought for this assessment because of their richness and abundance in these drainages (Conner and Suttkus 1986), and so that a large number of species could be tested and used for these assessments. In addition, other fishes besides cyprinids were used when possible to provide insight into these relationships at an assemblage level and to increase the number of species tested. Swimming ability as used in this study closely resembles the definition of prolonged swimming speed used by Beamish (1978). It is a composite of both burst and sustained swimming ability and is defined as the absolute speed ($\text{cm}\cdot\text{s}^{-1}$) sustained between 20 seconds and 200 minutes, ending in fatigue of the fish.

MATERIALS AND METHODS

Assessment of swimming ability

Several apparatuses (i.e., fish wheels, circular tanks, and swim tunnels) are used to assess swimming ability of fishes; however, swim tunnels tend to be the most common (Bainbridge and Brown 1958; Vogel and LaBarbera 1978; Videler and Wardle 1991). For this study, a swim tunnel was designed similar to that of Brett (1964), but with minor modifications for mobility (Figure 1). A 1.5 horsepower swimming pool pump, powered by a portable generator, pumped water from the stream through a 91-cm long and 8-cm diameter clear acrylic tube (viewing chamber). Six, 1-cm polyvinyl chloride (PVC) tubes were placed inside the inflow tee to provide rectilinear flow through the acrylic tube, which was confirmed with dye injection. Two gate valves that divert water either through the acrylic viewing tube or through the backflow exit were used to control flow rate. Current velocity flowing through the acrylic tube was measured with a Marsh-McBirney Flow-Mate (Model 2000) current velocity meter inserted behind the outflow tee. Plastic screens, 10 cm by 5 cm (6 mm x 6 mm), were placed on the upper and lower ends of the viewing chamber to prevent fish from escaping the viewing area.

Portability of the swim tunnel allowed for testing of swimming abilities in the field while avoiding fish transportation, housing, and lengthy acclimation periods in the laboratory, a necessity to test a large number of species and individuals within a relatively short time. Swimming abilities of fish determined by mobile swim tunnels are

consistent with those conducted in controlled laboratory settings (Lee et al. 2003; Farrell et al. 2003) and likely provide a more accurate assessment of fish capabilities (Berst and Simon 1981).

Fish ranging from 20 to 80 mm in standard length (SL) were collected with seines (1.2 x 2.4 m; 9.5 mm mesh) from streams in Texas and Louisiana from June through August 2003 (Table 1). Individuals >80 mm in SL were excluded from testing because of physical restrictions of the swim tunnel (Brett 1964). In groups consisting of three to five individuals, fish were placed in a 44-L aerated container until testing. One individual at a time was captured with a small dip net, immediately placed into the outflow tee, and gently guided into the acrylic tube. Initial current velocity was $0 \text{ cm}\cdot\text{s}^{-1}$ in the acrylic viewing tube. Current velocity was increased 3 to $5 \text{ cm}\cdot\text{s}^{-1}$ every 10 seconds until the fish stopped swimming because of fatigue. Here, fatigue was defined as the point at which an individual was impinged and unable to remove itself from the downstream screen for four seconds. Individuals that did not swim or exhibited behavioral responses (i.e., oral grasping of the upper screen) were excluded. Individuals were only used once. Following impingement, the final current velocity was recorded, and the specimen was removed from the swim tunnel, anaesthetized with tricaine methanesulfonate ($80 \text{ mg}\cdot\text{l}^{-1}$), and preserved in 10% formalin.

Dissolved oxygen ($\text{mg}\cdot\text{l}^{-1}$), oxygen saturation (%), and temperature ($^{\circ}\text{C}$) of the stream near the water intake were measured every two hours with an YSI Model 60/10 multi-probe meter. Temperature and dissolved oxygen concentrations affect swimming ability in fishes (Brett 1964; Beamish 1970; Parsons and Smiley 2003) although significant effects of temperature on swimming performances are not always detected

when fish are within their thermal tolerances (Jones et al. 1974; Myrick and Cech 2000). Likewise, oxygen saturation has little effect on swimming performances of fish if >70% (Beamish 1970). To minimize covariate influences on swimming ability, criteria for field testing were set for stream water temperatures that ranged between 20 and 34°C and for oxygen saturation >70%.

Swimming ability for each species used was defined as the average current velocity ($\text{cm}\cdot\text{s}^{-1}$; absolute swimming speed) that individuals of that species could swim before fatigue. To eliminate size effect on swimming ability, body lengths per second ($\text{bl}\cdot\text{s}^{-1}$; relative swimming speed) were also calculated and averaged for each species. Differences ($\alpha=0.05$) in relative swimming speed among species were tested with an analysis of covariance. Temperature (°C) and oxygen saturation (%) were used as covariates. Fisher's least significant differences tests (Zar 1999) were used to detect differences between species. For all statistical tests, SAS (SAS Institute, Gary, IN) was used.

Absolute swimming speed correlated to habitat use

Habitat descriptions were obtained from Page and Burr (1991) for each species tested. Habitat descriptions were given a score (1 to 5) according to reported water body (i.e., sloughs, lakes, headwater reaches, streams, small to large rivers) and mesohabitats inhabited (i.e., backwater areas, pools, springs, runs, and riffles). Scores for water bodies and mesohabitats were multiplied to obtain an overall score for each species, with low numbers describing slow water habitats and high numbers describing swift water habitats. For several species, habitat descriptions included multiple types of water body and

mesohabitats; therefore, two biologists independently assigned habitat scores without knowledge of species name or their swimming speed. Overall scores (one from each biologist) were averaged to obtain a final score for each species. For example, *Notropis shumardi* are found in pools and runs of large turbid rivers (Page and Burr 1991).

Biologist #1 gave *N. shumardi* a score of 10 (five for large river and two for pools and runs) whereas biologist #2 gave *N. shumardi* a score of 15 (five for large river and three for pools and runs), resulting in a habitat description final score of 12.5 for *N. shumardi*. Final scores were correlated (Peterson's correlation coefficients; Zar 1999) to absolute swimming speeds.

To explore relationships between absolute swimming speeds and habitat use (e.g., current velocity) at the assemblage level, fish assemblage data and current velocity information were obtained from published and unpublished studies (Bonner in press; Williams 2003; Williams et al., In press) that documented species distributions among current velocity gradients. Collectively, these studies document a large spatial distribution of fishes from upland streams in Louisiana (Peason Ridge Wildlife Management Area; Vernon, Kistachie, and Sabine Parishes) to east Texas (Banita Creek, Nacogdoches County) and west Texas (Independence Creek, Terrell County). Reported average current velocities for species, weighted by abundance, were correlated (Peterson's correlation coefficients; Zar 1999) to absolute swimming speeds. Species not abundant and those of the assemblage not tested here were excluded from the correlation analyses.

Quantification of fish morphology

In the laboratory, morphological attributes of preserved fish were measured (to the nearest 0.01 mm; nearest 0.0001 g in weight). Morphological attributes measured and considered important to defining swimming ability of fishes (Gatz 1979) were flatness index (maximum body depth/maximum body width), relative body depth (maximum body depth/standard length), relative peduncle length (caudal peduncle length/standard length), caudal peduncle flatness index (depth of peduncle at midpoint/width at the same point), caudal span/body depth, relative pectoral fin length (pectoral fin length/standard length), aspect ratio of the pectoral fin (length of pectoral fin/width of pectoral fin), dorsal fin height/body depth, and weight/length. Morphological attributes were transformed (z-scores) and those attributes that strongly segregated among families were identified with principle components analysis (PCA). Scores from PCA axis 1 and 2 were correlated (Peterson's correlation coefficients) with individual relative swimming speed (grouped by family) to assess relationships between body morphology and relative swimming speed. Likewise, morphological attributes that strongly segregated within Cyprinidae were determined similarly with individual relative swimming speed per species correlated to species scores for PCA 1 and 2.

RESULTS

Swimming speeds

Relative and absolute swimming speeds were determined for 412 individuals representing 37 species and 9 families (Table 2). Relative swimming speeds differed ($F_{1,374}=29.46$, $P < 0.01$) among species with temperature ($^{\circ}\text{C}$) a significant covariate ($P < 0.01$). Relative swimming speeds were slightly positively correlated ($r^2 = 0.07$) to higher temperatures (Figure 2). Mean relative swimming speeds (\pm SE) ranged from 3.4 (± 0.35) to 19.6 (± 1.37) $\text{bl}\cdot\text{s}^{-1}$ in Cyprinidae ($N = 24$), 5.5 (± 0.69) to 12.0 (± 1.12) $\text{bl}\cdot\text{s}^{-1}$ in Cyprinodontidae ($N = 2$), 5.5 (± 1.03) to 6.8 (± 0.67) $\text{bl}\cdot\text{s}^{-1}$ in Poeciliidae ($N = 2$), and 5.7 (± 0.79) to 8.1 (± 0.39) $\text{bl}\cdot\text{s}^{-1}$ in Centrarchidae ($N = 4$). For families with only a single species tested, mean relative swimming speeds (\pm SE) were 12.6 (± 0.49) $\text{bl}\cdot\text{s}^{-1}$ for Characidae, 13.7 (± 0.46) $\text{bl}\cdot\text{s}^{-1}$ for Ictaluridae, 6.4 (± 0.92) $\text{bl}\cdot\text{s}^{-1}$ for Atherinidae, 11.1 (± 0.25) $\text{bl}\cdot\text{s}^{-1}$ for Percidae, and 8.7 (± 0.50) $\text{bl}\cdot\text{s}^{-1}$ for Cichlidae.

Mean absolute swimming speeds ranged from 17.8 (± 1.80) to 81.4 (± 5.46) $\text{cm}\cdot\text{s}^{-1}$ for Cyprinidae, 30.7 (± 3.69) to 43.3 (± 3.94) $\text{cm}\cdot\text{s}^{-1}$ for Cyprinodontidae, 15.7 (± 1.36) to 18.6 (± 3.04) $\text{cm}\cdot\text{s}^{-1}$ for Poeciliidae, and 22.6 (± 2.40) to 40.5 (± 3.30) $\text{cm}\cdot\text{s}^{-1}$ for Centrarchidae. For families with only a single species tested, mean absolute swimming speeds (\pm SE) were 50.9 (± 2.45) $\text{cm}\cdot\text{s}^{-1}$ for Characidae, 70.0 (± 1.86) $\text{cm}\cdot\text{s}^{-1}$ for Ictaluridae, 30.2 (± 3.70) $\text{cm}\cdot\text{s}^{-1}$ for Atherinidae, 40.0 (± 1.96) $\text{cm}\cdot\text{s}^{-1}$ for Percidae, and 33.0 (± 2.70) $\text{cm}\cdot\text{s}^{-1}$ for Cichlidae. *Notropis atherinoides* had the fastest mean (\pm SE)

absolute swimming speed ($81.4 \pm 5.46 \text{ cm}\cdot\text{s}^{-1}$) whereas *Gambusia geiseri* had the slowest mean absolute swimming speed ($15.7 \pm 1.36 \text{ cm}\cdot\text{s}^{-1}$, Figure 3).

Water temperatures ranged from 21.7 °C to 33.4 °C during all tests. Dissolved oxygen concentrations were >70% of saturation during all tests, except on the Pease River which had levels of 63%. While using the swim tunnel, turbulence created as the water passed through the swimming pool pump increased the dissolved oxygen concentration in the immediate area of the river. Diagnostic plot and correlation between dissolved oxygen concentrations and relative swimming speeds ($r^2 = 0.01$, $P > 0.05$) indicated that dissolved oxygen concentrations did not influence swimming ability of fish tested in this study.

Habitat use

A positive correlation ($r^2 = 0.40$; $N = 37$; $P < 0.01$) existed between absolute swimming speeds and habitat scores obtained from Page and Burr (1991, Figure 4). In general, species (i.e., *Notropis atherinoides*, *Notropis shumardi*, and *Ictalurus furcatus*) reported to inhabit main channels of medium to large rivers were among the highest in mean (\pm SE) absolute swimming speeds (81.4 ± 5.46 , 79.4 ± 6.02 , and $70.0 \pm 1.86 \text{ cm}\cdot\text{s}^{-1}$, respectively). Species (i.e., *Cyprinella venusta*, *Notropis sabiniae*, and *Notropis atrocaudalis*) reported to inhabit pool and run habitats in creeks and small to medium rivers were intermediate in mean absolute swimming speeds (61.0 ± 1.86 , 47.0 ± 3.65 , and $47.0 \pm 2.35 \text{ cm}\cdot\text{s}^{-1}$, respectively). Likewise, species (i.e., *Gambusia geiseri*, *Dionda episcopa*, and *Poecilia latipinna*) reported to inhabit backwater, run, and pool habitats in springs, headwater areas, creeks, and small streams were among the lowest in mean

absolute swimming speeds (15.7 ± 1.36 , 17.8 ± 1.80 , and 18.6 ± 3.04 $\text{cm}\cdot\text{s}^{-1}$, respectively).

At the assemblage scale, similar trends between species absolute swimming speed and habitat were found (Figure 5). Absolute swimming speeds were strongly correlated with weighted estimates of mean current velocity at Independence Creek ($r^2 = 0.51$, $N = 10$, $P = 0.03$) and Banita Creek ($r^2 = 0.70$, $N = 7$, $P = 0.06$). In Independence Creek, estimated mean (\pm SE) current velocity is $32.0 (\pm 0.60)$ $\text{cm}\cdot\text{s}^{-1}$ for *Cyprinella proserpina* (T. Bonner, unpublished data), which inhabits runs and flowing pools and measured $60.8 (\pm 2.93)$ $\text{cm}\cdot\text{s}^{-1}$ in mean absolute swimming speed. Correspondingly, estimated mean current velocity is $8.5 (\pm 1.68)$ $\text{cm}\cdot\text{s}^{-1}$ for *Micropterus salmoides*, which inhabits pools in Independence Creek and measured $22.6 (\pm 2.40)$ $\text{cm}\cdot\text{s}^{-1}$ in mean absolute swimming speed. In Banita Creek, estimated mean current velocity is $31.8 (\pm 1.20)$ $\text{cm}\cdot\text{s}^{-1}$ for *Cyprinella lutrensis* (Williams 2003), a habitat generalist that inhabits pools and runs in lower reaches of Banita Creek and measured 71.2 ± 3.49 $\text{cm}\cdot\text{s}^{-1}$ in mean absolute swimming speed. Correspondingly, estimated mean current velocity is $5.9 (\pm 0.33)$ $\text{cm}\cdot\text{s}^{-1}$ for *Semotilus atromaculatus*, which inhabits headwater reaches of Banita Creek and measured 44.2 ± 1.61 $\text{cm}\cdot\text{s}^{-1}$ in mean absolute swimming speed.

Deviations from fishes with increased swimming ability inhabiting areas of higher flows were observed however. In Independence Creek, one outlier species (*Etheostoma grahami*) was deleted from correlation analysis because measured mean absolute swimming speed was relatively slow (40.0 ± 1.96 $\text{cm}\cdot\text{s}^{-1}$), yet the species inhabits swift current velocities (45.6 ± 2.39 $\text{cm}\cdot\text{s}^{-1}$). Likewise, correlation between mean absolute swimming speed and estimated mean current velocity of habitat (Williams in press) was

not significant ($r^2 = 0.04$, $N = 7$, $P = 0.67$) for streams on Peason Ridge Wildlife Management Area.

Morphology

Linear contrasts of morphological attributes explained 58% of the observed variation among the nine families with the first PCA axis (39% of total variation) primarily contrasting differences in body depth (PCA loading = 0.48), flatness index (0.44), dorsal fin height (-0.43), and caudal span (-0.34), and the second axis (19% of total variation) primarily contrasting differences in relative length (-0.68) and aspect ratio (-0.64) of the pectoral fin. Cichlidae and Centrarchidae were associated positively with PCA axis 1, which describes fish with greater body depth, relatively shorter dorsal fin, and lesser caudal span (Table 3, Figure 6). In contrast, Atherinidae, Cyprinidae, and Percidae were associated negatively with PCA axis 1, having a more streamlined body shape with relatively longer dorsal fin and greater caudal span. Percidae and Cichlidae were associated positively with PCA axis 2, having relatively longer and broader pectoral fins whereas Atherinidae, Characidae, and Poeciliidae were associated negatively with PCA axis 2, having relatively shorter and slender pectoral fins (Table 3, Figure 7). Correlating individual PCA scores to species swimming speeds, PCA axis 1 was inversely related to absolute swimming speed ($r = -0.31$, $N = 412$, $P < 0.01$) and PCA axis 2 was directly related to absolute swimming speed ($r = 0.33$, $N = 412$, $P < 0.01$). However, strength of relationships was weak at the family level.

Linear contrasts of morphological attributes explained 53% of the observed variation within Cyprinidae with the first PCA axis (32% of total variation) primarily

contrasting differences in body depth (0.53), dorsal fin height (-0.51), flatness index (0.40), and caudal span (-0.31), and the second axis (21% of total variation) primarily contrasting differences in aspect ratio (0.64) and relative length of the pectoral fin (-0.60). *Cyprinella lutrensis* and *Semotilus atromaculatus* were associated positively with PCA axis 1, describing deeper bodied fish with shorter dorsal fins and caudal fin span. *Macrhybopsis aestivalis* associated negatively with PCA axis 1, its body shape is streamlined with a longer dorsal fin and greater caudal span. *Cyprinella venusta*, *Lythrurus fumeus*, and *Notropis shumardi* were associated positively with PCA axis 2, having relatively shorter and slender pectoral fins. In contrast *Macrhybopsis aestivalis*, *Notropis bairdi*, *Notropis stramineus*, and *Dionda episcopa* associated negatively with PCA axis 2, having relatively longer pectoral fins. Correlating individual PCA scores to species swimming speeds, PCA axis 1 was inversely related to absolute swimming speed ($r = -0.34$, $N=317$, $P < 0.01$) and PCA axis 2 was directly related to absolute swimming speed ($r = 0.08$, $N=317$, $P = 0.17$). However, strength of relationships within the Cyprinidae was weak.

DISCUSSION

This study demonstrated that selected fishes from western Gulf slope, Rio Grande, Red River, and Canadian River drainages differed in relative and absolute swimming speeds. Correspondingly, swimming speeds were strongly associated with reported habitats of the fishes. This association, in part, explains longitudinal distributions of fishes with those fishes with greater swimming speeds inhabiting medium to large rivers whereas those with lesser swimming speeds inhabiting springs, creeks, and small rivers. Likewise, this association, in part, explains spatial segregation of a fish assemblage among habitat types with those fish with greater swimming speeds inhabiting runs, riffles, and flowing pools whereas those with lesser swimming speeds inhabiting pools and backwater habitats. However, swimming speed or more specifically musculature and physiological processes that enable higher swimming speeds (Schaarschmidt and Jurss 2003) do not account for all patterns in freshwater fish spatial distributions related to flow.

Fish behavior also influences species persistence in swift water, and is usually independent of swimming speed capabilities. Oral grasping, biting and holding onto vegetation or other debris, is one behavioral response that may enable fishes such as those in Cyprinidae to maintain position in swift currents (Adams et al. 2000; Adams et al. 2003; Ward et al. 2003). In this study, oral grasping was observed in *Cyprinella lutrensis*, *C. venusta*, *Lythrurus umbratilis*, *Notropis stramineus*, *Dionda episcopa*, and

Semotilus atromaculatus. Within the swim tunnel, oral grasping of the intake screen allowed *C. lutrensis* to withstand current velocities up to $129 \text{ cm}\cdot\text{s}^{-1}$ before fatigue. Other behaviors that improve capabilities to withstand high current velocities include the use of benthic or shoreline habits to exploit velocity refuges among sand ridges, gravel and cobble substrates, and vegetation, create negative lift by adjusting angles of pectoral fins, lowering or arching of body position relative to substrate, and use of pectoral, pelvic and anal fins to adhere to interstitial spaces of substrate (Meffe 1984; Matthews 1985; Minckley and Meffe 1987, Webb 1989; Arnold et al. 1991; Adams et al. 2000; Ward et al. 2003). Use of benthic habitats and use of fins may explain the disparity between absolute swimming speed and habitat current velocity of *Etheostoma grahami* in Independence Creek. Nevertheless, swimming speed seems to be the best predictor among all possible factors that affect a species selection of current velocity.

In this study, swimming speeds of fishes did not provide insight into responses of fish to flood events or in areas where flows are altered because of impoundments. Fishes reported to be highly susceptible to downstream displacement during high flow events includes several species or genera with relatively low absolute swimming speeds (i.e., *Gambusia*, *Poecilia*, *Micropterus*, *Lepomis*, and *Pimephales*), but also includes several species or genera with relatively high absolute swimming speeds (*Cyprinella*, *Ictalurus*, Meffe 1984; Minckley and Meffe 1987; Schultz et al. 2003). Thus, swimming speed is not a strong predictor of flood-adapted species. Instead, these results support Meffe (1984) and Ward et al. (2003) conclusions that species persistence during high flow events includes behavioral adaptations, especially for species that did not measure high in swimming speeds. Likewise, swimming speeds do not adequately predict which species

will be more abundant after reduction in flows following impoundments and dewatering, presumably because lower peak flows no longer displace invasive species downstream. Fishes reported to increase in abundance following alterations to flow regime include those genera with low swimming speeds (i.e., *Lepomis*, *Micropterus*, *Menidia*, *Pimephales*, *Gambusia*), but also those species or genera with high swimming speeds (*Cyprinella lutrensis*, *Notropis atherinoides*, *Notropis stramineus*, and *Ictalurus*, Minckley and Meffe 1987; Winston et al. 1991; Platania 1991; Anderson et al. 1995; Bonner and Wilde 2000). Consequently, this study indicates swimming speeds were not consistent in predicting downstream displacement or invasive attributes of fishes.

Morphological characteristics deemed important in defining swimming ability in fish (Gatz 1979) were not strongly correlated with swimming speeds of fish observed in this study. Principal component analyses segregated families and species within Cyprinidae primarily by body shape, shape and size of pectoral and caudal fins, and dorsal fin height. Body depth and size and shape of fins are reported to be important correlates with swimming speeds in other studies (Matthews 1985, Schaefer 1999, Plaut 2000, Hawkins and Quinn 2003). Similar to these studies, families of fishes with higher swimming speeds were generally more streamlined with longer pectoral fins and height of dorsal and caudal fins exceeding body depth, than those with lower swimming speeds. However, there were some notable exceptions that weakened the correlation among families. For example, *Menidia beryllina* is a highly streamlined fish with a low swimming speed; however, this body shape evolved in pelagic coastal waters for surface feeding and not under flowing conditions (Hubbs et al. 1991). Also, *Astyanax mexicanus*

is a short, deep body fish with relatively short pectoral fins, but had a high swimming speed.

Among Cyprinidae, four species ranked lowest in relative swimming speeds generally had higher body depth to length ratio and shorter pectoral fins, which is consistent with expectations. However, numerous exceptions existed including the five species ranked highest in relative swimming speeds being intermediate in relative body depth, dorsal fin height, and caudal span. Our findings support those of Felley (1984) who did not detect differences in relationships between morphology and habitat selection by 21 *Notropis* species within Cyprinidae. However, when incorporating morphological attributes associated with diet and feeding, Douglas and Matthews (1992) detected relatively strong relationships between habitat use (i.e., current velocity, substrate, and depth) and morphology.

Information on species swimming abilities, especially absolute swimming speeds, also has applied implications. Numerous road crossings bisect streams throughout Gulf slope, Rio Grande, Red River, and Canadian River drainages of Texas and Louisiana, and other streams throughout North America. Usually, smaller road crossings are equipped with concrete or metal culverts that artificially accelerate current velocity through the crossing. These culverts restrict movement of numerous fishes including darters, minnows, topminnows, and sunfish (Warren and Pardew 1988; Schaefer et al. 2002). Consequently, streams become fragmented, altering the ecological and biological importance of flowing waters to the resident fishes including predator avoidance, food acquisition, thermal refugia, reproduction, recolonization, and recruitment (Metsker 1970; Berra and Gunning 1972; Peterson and Bailey 1993; Freeman 1995; Schlosser

1995; Warren and Pardew 1998; Schaefer et al. 2002). Absolute swimming speeds reported here provide current velocity guidelines for properly designing and constructing culvert systems that do not impede fish movement upstream during normal and above normal flows. In general, culvert systems need to be sufficiently wide to maintain flows through the culvert less than the resident species absolute swimming speeds in areas where spring discharge or extended precipitation runoff keep flows elevated for prolonged periods, especially during spring and early summer during the height of reproduction activities.

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TABLES AND FIGURES

Table 1. Species and locations of freshwater fishes tested in the mobile swim tunnel from June through August 2003.

Family	Species	Site
Cyprinidae	<i>Campostoma anomalum</i>	Blanco River, Hays County, TX
	<i>Cyprinella lutrensis</i>	Banita Creek, Nacogdoches County, TX
		Yegua Creek, Washington County, TX
		Canadian River, Hemphill County, TX
		Independence Creek, Terrell County, TX
	<i>Cyprinella proserpina</i>	San Marcos River, Hays County, TX
	<i>Cyprinella venusta</i>	Blanco River, Hays County, TX
	<i>Dionda episcopa</i>	Independence Creek, Terrell County, TX
	<i>Hybognathus placitus</i>	Canadian River, Hemphill County, TX
		Double Mountain Fork Brazos River, Fisher County, TX
		Pease River, Foard County, TX
	<i>Luxilus chrysocephalus</i>	Little Sandy Creek, Vernon Parish, LA
	<i>Lythrurus fumeus</i>	Big Sandy Creek, Bastrop County, TX
		Navasota River, Brazos County, TX
	<i>Lythrurus umbratilis</i>	Banita Creek, Nacogdoches County, TX
		Kisatchie Falls, Vernon Parish, LA
	<i>Macrhybopsis aestivalis</i>	Yegua Creek, Washington County, TX
		Pease River, Foard County, TX
	<i>Notropis amabilis</i>	Independence Creek, Terrell County, TX
		San Marcos River, Hays County, TX
		Blanco River, Hays County, TX
	<i>Notropis atherinoides</i>	Canadian River, Hemphill County, TX
	<i>Notropis atrocaudalis</i>	Banita Creek, Nacogdoches County, TX
	<i>Notropis bairdi</i>	Pease River, Foard County, TX
	<i>Notropis buccula</i>	Double Mountain Fork Brazos River, Fisher County, TX
	<i>Notropis buchanani</i>	Yegua Creek, Washington County, TX
		Navasota River, Brazos County, TX
	<i>Notropis oxyrhynchus</i>	Double Mountain Fork Brazos River, Fisher County, TX
	<i>Notropis sabiniae</i>	Banita Creek, Nacogdoches County, TX
	<i>Notropis shumardi</i>	Yegua Creek, Washington County, TX
	<i>Notropis stramineus</i>	Blanco River, Hays County, TX
<i>Notropis texanus</i>	Big Sandy Creek, Bastrop County, TX	
<i>Notropis volucellus</i>	Big Sandy Creek, Bastrop County, TX	
	Blanco River, Hays County, TX	
<i>Pimephales vigilax</i>	Banita Creek, Nacogdoches County, TX	
	San Marcos River, Hays County, TX	
<i>Semotilus atromaculatus</i>	Banita Creek, Nacogdoches County, TX	

Table 1. Continued.

Family	Species	Site
Characidae	<i>Astyanax mexicanus</i>	Independence Creek, Terrell County, TX
Ictaluridae	<i>Ictalurus furcatus</i>	Yegua Creek, Washington County, TX
Cyprinodontidae	<i>Fundulus notatus</i>	Banita Creek, Nacogdoches County, TX
	<i>Fundulus zebrinus</i>	Independence Creek, Terrell County, TX
Poeciliidae	<i>Gambusia geiseri</i>	Spring Lake, Hays County, TX
	<i>Poecilia latipinna</i>	Spring Lake, Hays County, TX
Atherinidae	<i>Menidia beryllina</i>	Lake Somerville, Lee County, TX
		Yegua Creek, Washington County, TX
Centrarchidae	<i>Lepomis auritus</i>	Blanco River, Hays County, TX
	<i>Lepomis macrochirus</i>	Banita Creek, Nacogdoches County, TX
	<i>Lepomis megalotus</i>	Banita Creek, Nacogdoches County, TX
	<i>Micropterus salmoides</i>	Banita Creek, Nacogdoches County, TX
		Independence Creek, Terrell County, TX
		Spring Lake, Hays County, TX
Percidae	<i>Etheostoma grahami</i>	Independence Creek, Terrell County, TX
Cichlidae	<i>Cichlasoma cyanoguttatum</i>	Independence Creek, Terrell County, TX

Table 2. Mean relative ($\text{bl}\cdot\text{s}^{-1}$) and absolute ($\text{cm}\cdot\text{s}^{-1}$) swimming speeds \pm SE, and minimum and maximum standard length (mm) of various fishes in Texas and Louisiana from June through August 2003. Superscripts indicate significant differences between fishes ($P<0.05$) by analysis of covariance.

Family	Species	N	Relative Speed ($\text{bl}\cdot\text{s}^{-1}$)	Absolute Speed ($\text{cm}\cdot\text{s}^{-1}$)	Standard Length (mm)	
			Mean \pm SE	Mean \pm SE	Minimum	Maximum
Cyprinidae	<i>Notropis atherinoides</i>	10	19.6 \pm 1.37 ^a	81.4 \pm 5.46	37.0	59.7
	<i>Notropis shumardi</i>	10	18.8 \pm 1.23 ^a	79.4 \pm 6.02	35.2	49.9
	<i>Cyprinella lutrensis</i>	16	17.2 \pm 1.20 ^{ab}	71.2 \pm 3.49	30.1	62.3
	<i>Notropis stramineus</i>	18	15.7 \pm 0.68 ^{bc}	66.5 \pm 2.52	37.2	48.1
	<i>Cyprinella proserpina</i>	10	15.7 \pm 1.25 ^{bcd}	60.8 \pm 2.93	32.2	47.8
	<i>Notropis amabilis</i>	29	15.3 \pm 0.77 ^{bc}	63.6 \pm 2.86	31.7	57.2
	<i>Macrhybopsis aestivalis</i>	11	14.7 \pm 1.28 ^{cde}	62.0 \pm 4.40	26.1	51.8
	<i>Notropis buccula</i>	10	13.8 \pm 1.61 ^{cedf}	49.7 \pm 5.42	30.1	40.5
	<i>Campostoma anomalum</i>	10	13.6 \pm 0.59 ^{def}	62.9 \pm 2.77	43.3	55.1
	<i>Notropis oxyrhynchus</i>	10	13.4 \pm 0.87 ^{def}	53.4 \pm 3.12	36.1	43.8
	<i>Cyprinella venusta</i>	19	13.4 \pm 0.65 ^{def}	61.1 \pm 2.81	22.1	78.2
	<i>Notropis buchanani</i>	12	12.7 \pm 0.75 ^{efg}	44.7 \pm 2.64	31.9	44.0
	<i>Notropis sabiniae</i>	12	12.5 \pm 0.73 ^{efgh}	47.0 \pm 3.65	36.1	43.1
	<i>Hybognathus placitus</i>	32	12.4 \pm 0.78 ^{fg}	61.1 \pm 3.57	31.9	75.3
	<i>Notropis volucellus</i>	15	12.3 \pm 0.88 ^{efgh}	43.6 \pm 3.71	30.6	41.6
	<i>Lythrurus umbratilis</i>	13	12.3 \pm 0.81 ^{efgh}	55.0 \pm 3.75	38.5	60.3
	<i>Lythrurus fumeus</i>	11	11.6 \pm 1.74 ^{fghjk}	38.1 \pm 5.72	27.9	45.1
	<i>Notropis bairdi</i>	10	10.4 \pm 0.99 ^{ghjkl}	45.6 \pm 4.96	35.1	57.7
<i>Notropis atrocaudalis</i>	11	9.9 \pm 0.98 ^{hijklm}	47.0 \pm 2.35	23.8	57.9	

Table 2. Continued.

Family	Species	N	Relative Speed (bl·s ⁻¹)		Standard Length (mm)	
			Mean ± SE	Mean ± SE	Minimum	Maximum
Cyprinidae	<i>Notropis texanus</i>	7	9.4 ± 1.21 ^{ijklmno}	38.7 ± 4.93	35.7	44.0
	<i>Luxilus chrysocephalus</i>	10	9.3 ± 0.89 ^{klmn}	40.3 ± 3.73	37.4	48.9
	<i>Pimephales vigilax</i>	12	8.0 ± 0.49 ^{lmnopq}	39.6 ± 2.28	40.8	62.7
	<i>Semotilus atromaculatus</i>	9	7.9 ± 0.53 ^{lmnopq}	44.2 ± 1.61	38.2	64.8
	<i>Dionda episcopa</i>	10	3.4 ± 0.35 ^r	17.8 ± 1.80	45.2	61.9
Characidae	<i>Astyanax mexicanus</i>	10	12.6 ± 0.49 ^{efgh}	50.9 ± 2.45	34.3	58.7
Ictaluridae	<i>Ictalurus furcatus</i>	10	13.7 ± 0.46 ^{cdef}	70.0 ± 1.86	39.2	61.4
Cyprinodontidae	<i>Fundulus zebrinus</i>	10	12.0 ± 1.12 ^{efghij}	43.4 ± 3.94	31.0	31.0
	<i>Fundulus notatus</i>	10	5.5 ± 0.69 ^{pqr}	30.7 ± 3.69	48.9	61.5
Poeciliidae	<i>Gambusia geiseri</i>	7	6.8 ± 0.67 ^{nopq}	15.7 ± 1.36	20.7	26.8
	<i>Poecilia latipinna</i>	5	5.5 ± 1.03 ^{pr}	18.6 ± 3.04	30.7	41.8
Atherinidae	<i>Menidia beryllina</i>	9	6.4 ± 0.92 ^{lmnopq}	30.2 ± 3.70	30.5	42.5
Centrarchidae	<i>Lepomis macrochirus</i>	4	8.1 ± 0.39 ^{klmnopq}	40.5 ± 3.30	44.3	75.3
	<i>Lepomis auritus</i>	5	7.5 ± 0.66 ^{lmnopq}	35.4 ± 1.89	39.4	56.0
	<i>Micropterus salmoides</i>	8	7.3 ± 0.78 ^{mnpq}	22.6 ± 2.40	27.5	41.6
	<i>Lepomis megalotus</i>	5	5.7 ± 0.79 ^{opqr}	28.0 ± 4.22	44.4	75.3
Percidae	<i>Etheostoma grahami</i>	4	11.1 ± 0.25 ^{efghijklm}	40.0 ± 1.96	30.5	42.3
Cichlidae	<i>Cichlasoma cyanoguttatum</i>	8	8.7 ± 0.50 ^{klmnop}	33.0 ± 2.70	26.3	51.0

Table 3. Loadings and % variance (from principal component analysis) explained by morphometric data of the first two axes among Family and within the Family Cyprinidae of fishes tested in a mobile swim tunnel at various locations in Texas and Louisiana from June through August 2003. Variables in bold are the main components of each axis.

Attributes	Family		Cyprinidae	
	PCA1	PCA2	PCA1	PCA2
Weigth to Length	0.303	0.295	0.327	- 0.258
Dorsal Fin to Body Depth	- 0.426	0.143	- 0.511	0.025
Flatness Index	0.439	- 0.033	0.400	0.169
Relative Body Depth	- 0.484	0.119	0.526	- 0.073
Relative Peduncle Length	0.091	0.036	0.095	- 0.201
Peduncle Flatness Index	0.338	- 0.049	0.258	0.243
Caudal Span to Body Depth	- 0.342	- 0.120	- 0.312	0.161
Aspect Ratio Pectoral Fin	0.215	- 0.636	- 0.219	0.640
Relative Pectoral Fin Length	- 0.115	0.675	- 0.147	- 0.603
% Variance explained	39.3	18.6	31.6	21.4

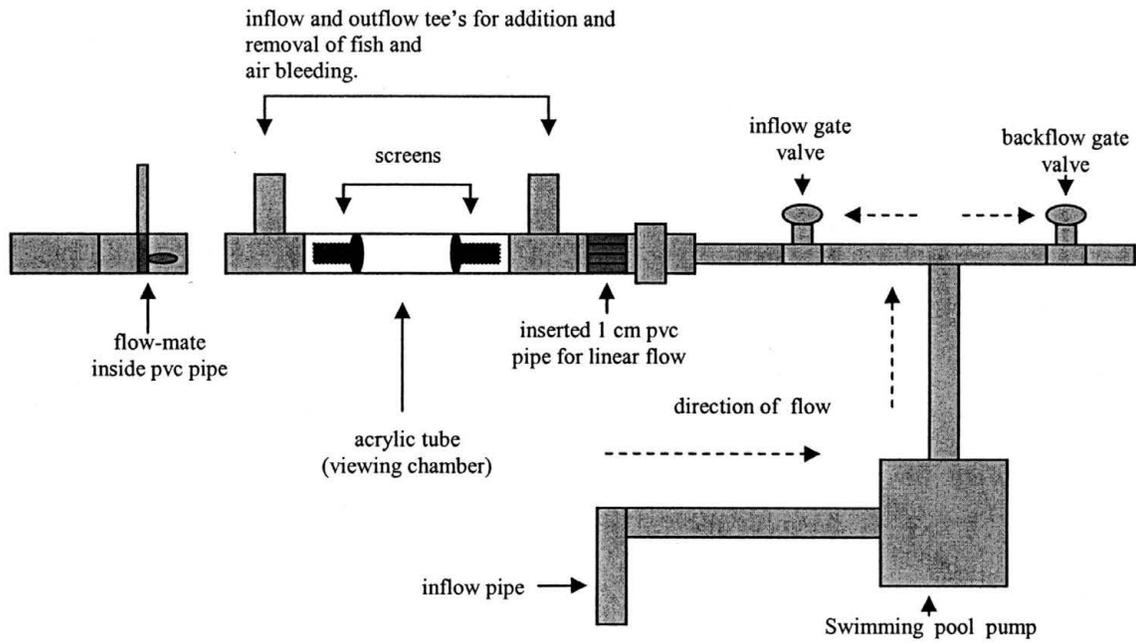


Figure 1. Schematic diagram of the mobile swim tunnel used to determine swimming ability of various freshwater stream fishes in Texas and Louisiana from June through August 2003.

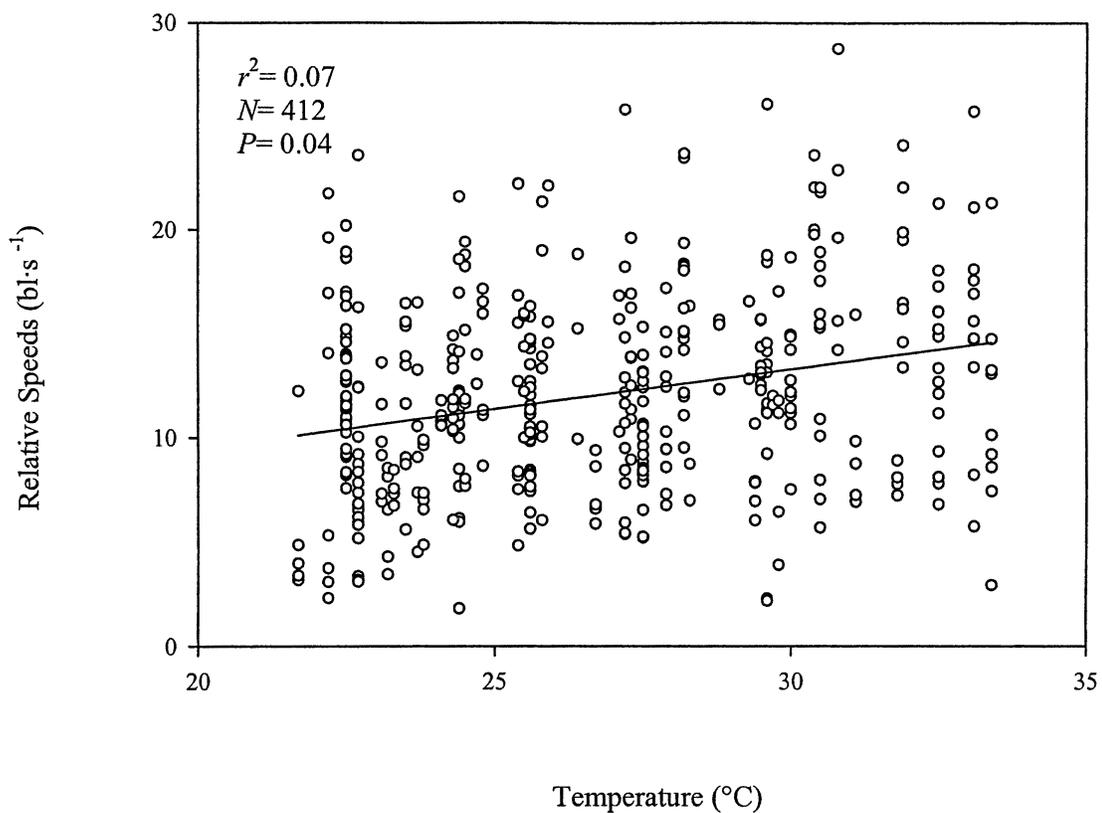


Figure 2. Relative speeds (bl·s⁻¹) of freshwater stream fishes and temperature (°C) at each testing location in Texas and Louisiana from June through August 2003.

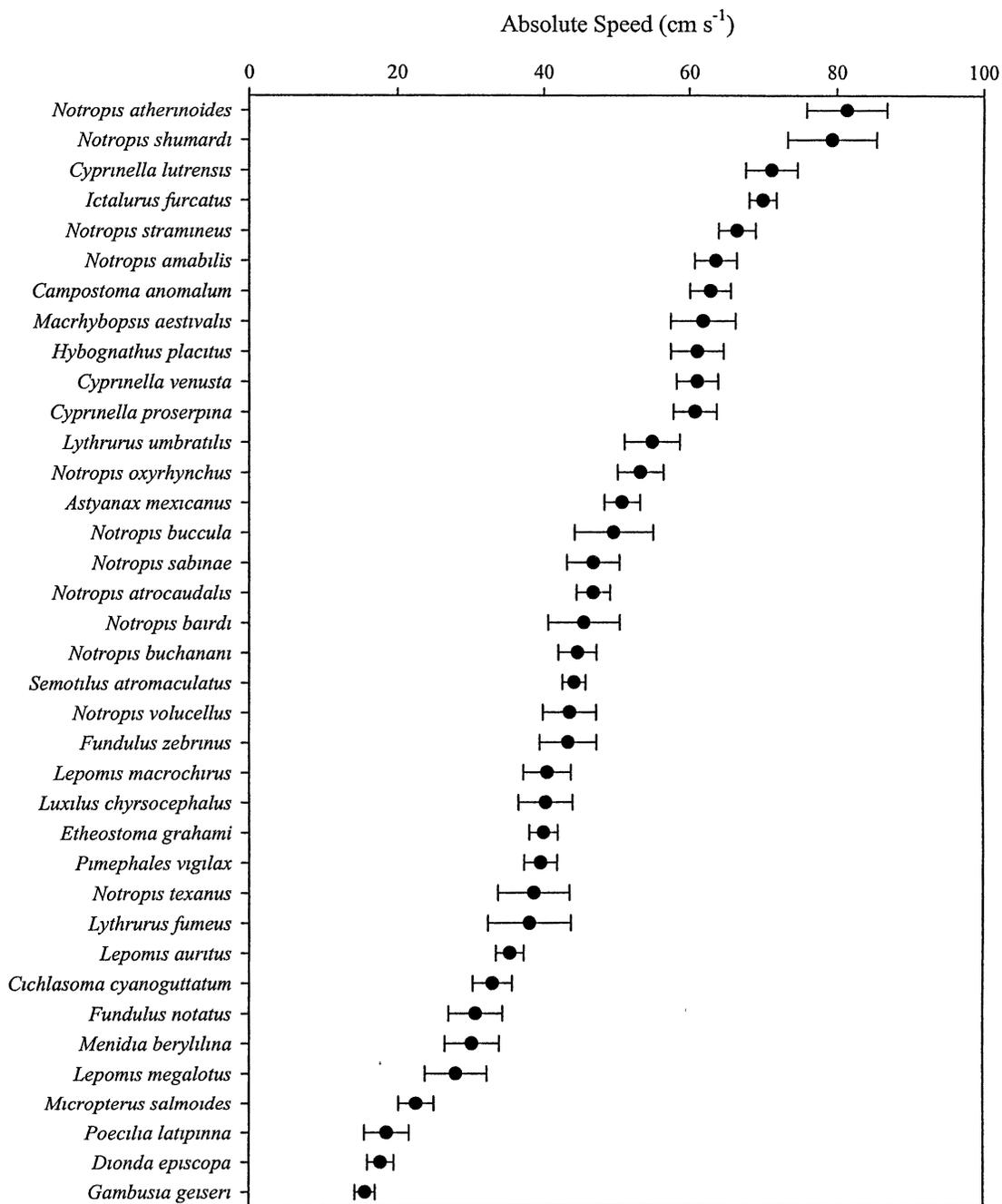


Figure 3. Absolute speeds ($\text{cm}\cdot\text{s}^{-1}$) \pm SE of various freshwater fishes in Texas and Louisiana from June through August 2003.

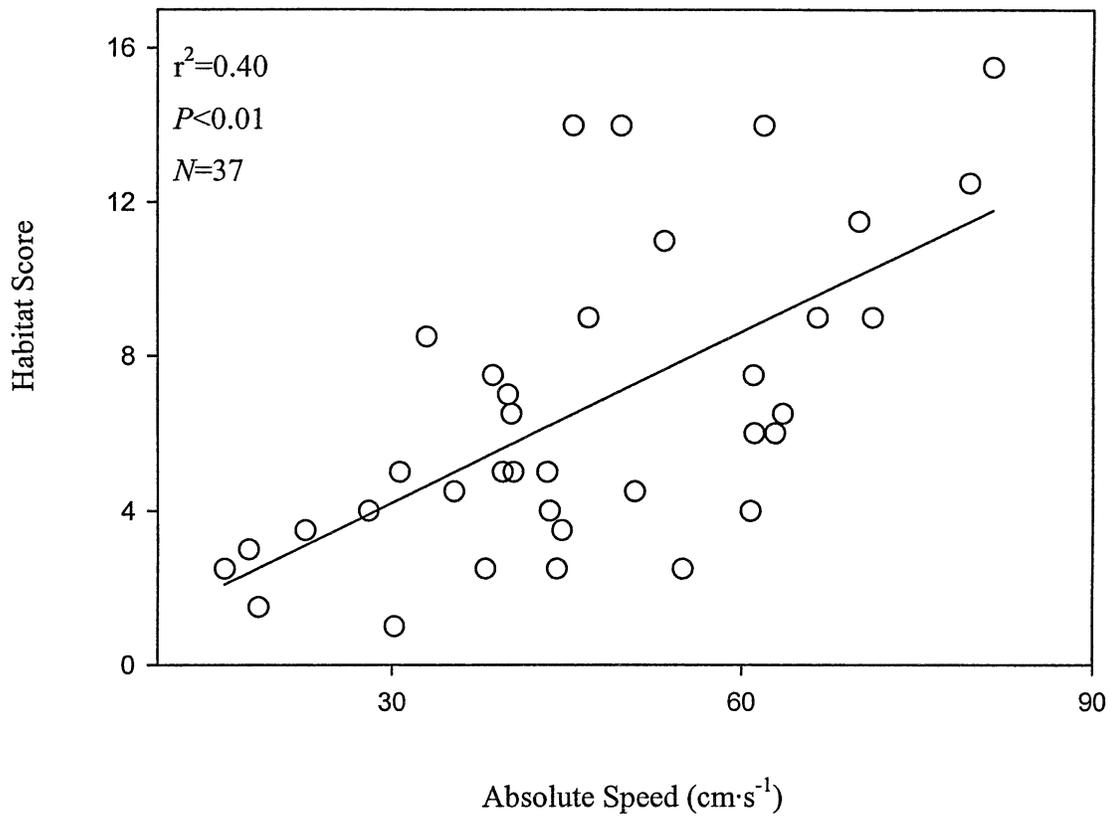


Figure 4. Relationship between absolute speeds ($\text{cm}\cdot\text{s}^{-1}$) and habitat use, scored current velocity, (based on preferred habitat in Page and Burr (1991)) of fishes tested in the swim tunnel at various locations in Texas and Louisiana from June through August 2003. Higher habitat velocity scores indicate swifter currents.

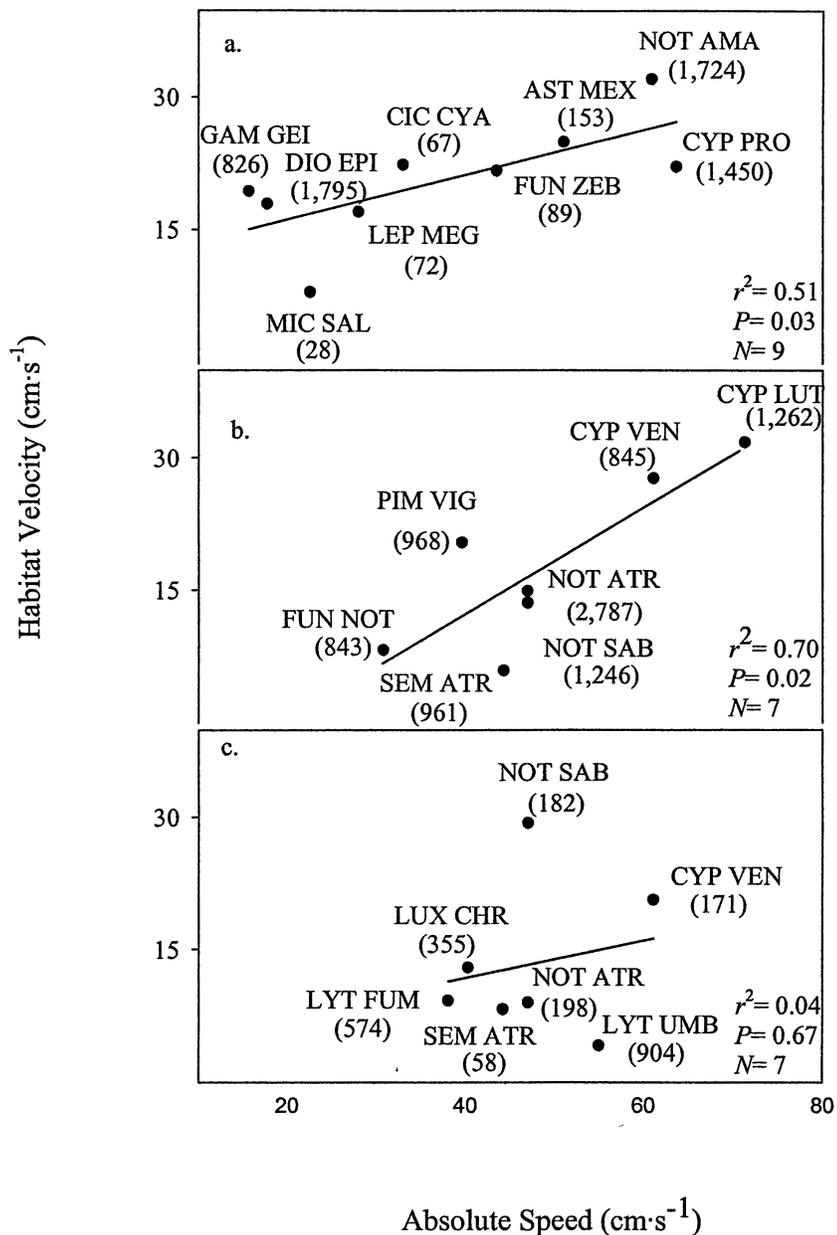


Figure 5. Relationships between mean absolute speeds ($\text{cm}\cdot\text{s}^{-1}$) and mean habitat current velocities ($\text{cm}\cdot\text{s}^{-1}$) of abundant fishes at (a) Independence Creek (May 2002-October 2003), (b) Banita Creek (November 2001- October 2002), and (c) creeks on Peason Ridge Wildlife Management Area (June 2001- August 2002). Abbreviations represent the first three letters of genus and species.

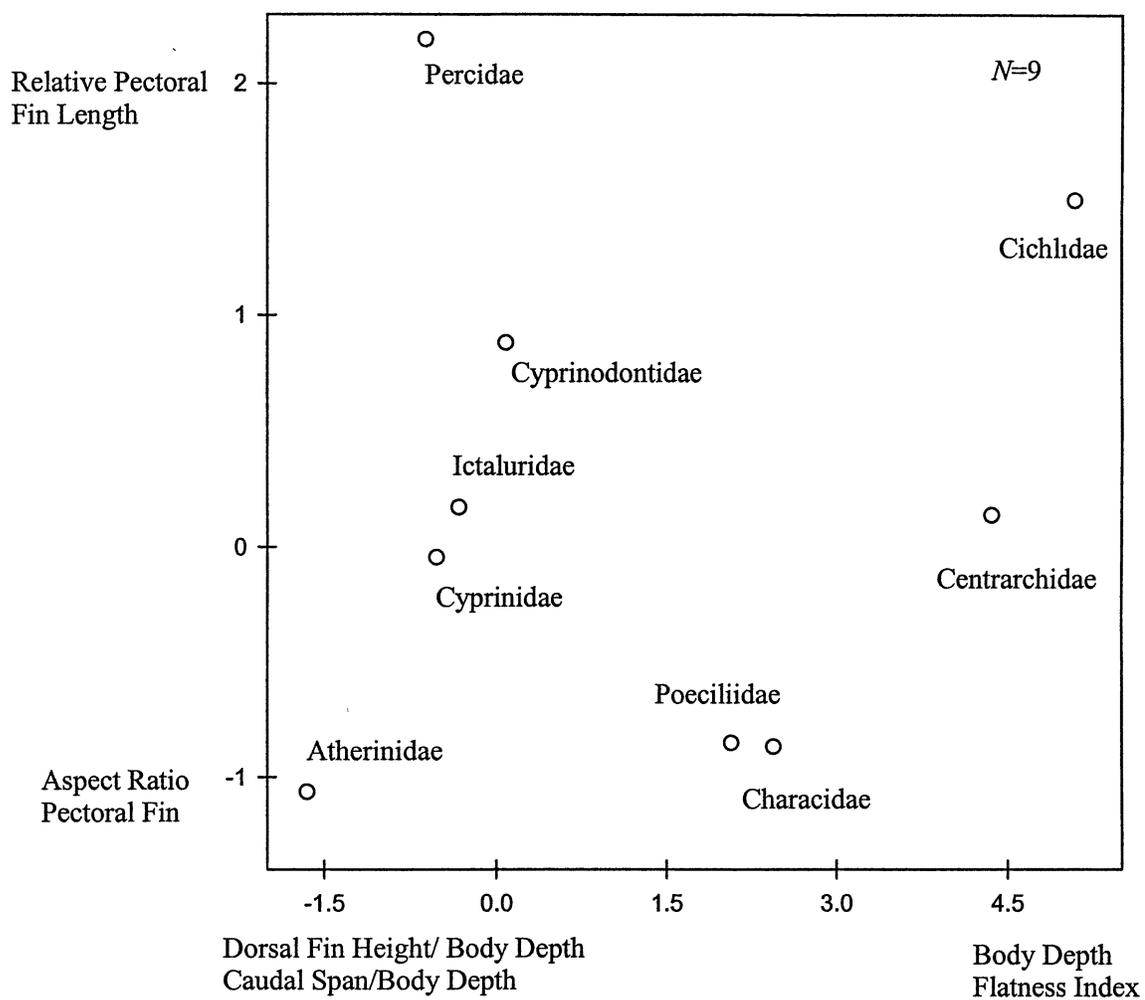


Figure 6. Plot of mean principal component scores for PCA # 1 and 2 obtained from morphometric attributes deemed important in swimming ability among nine families.

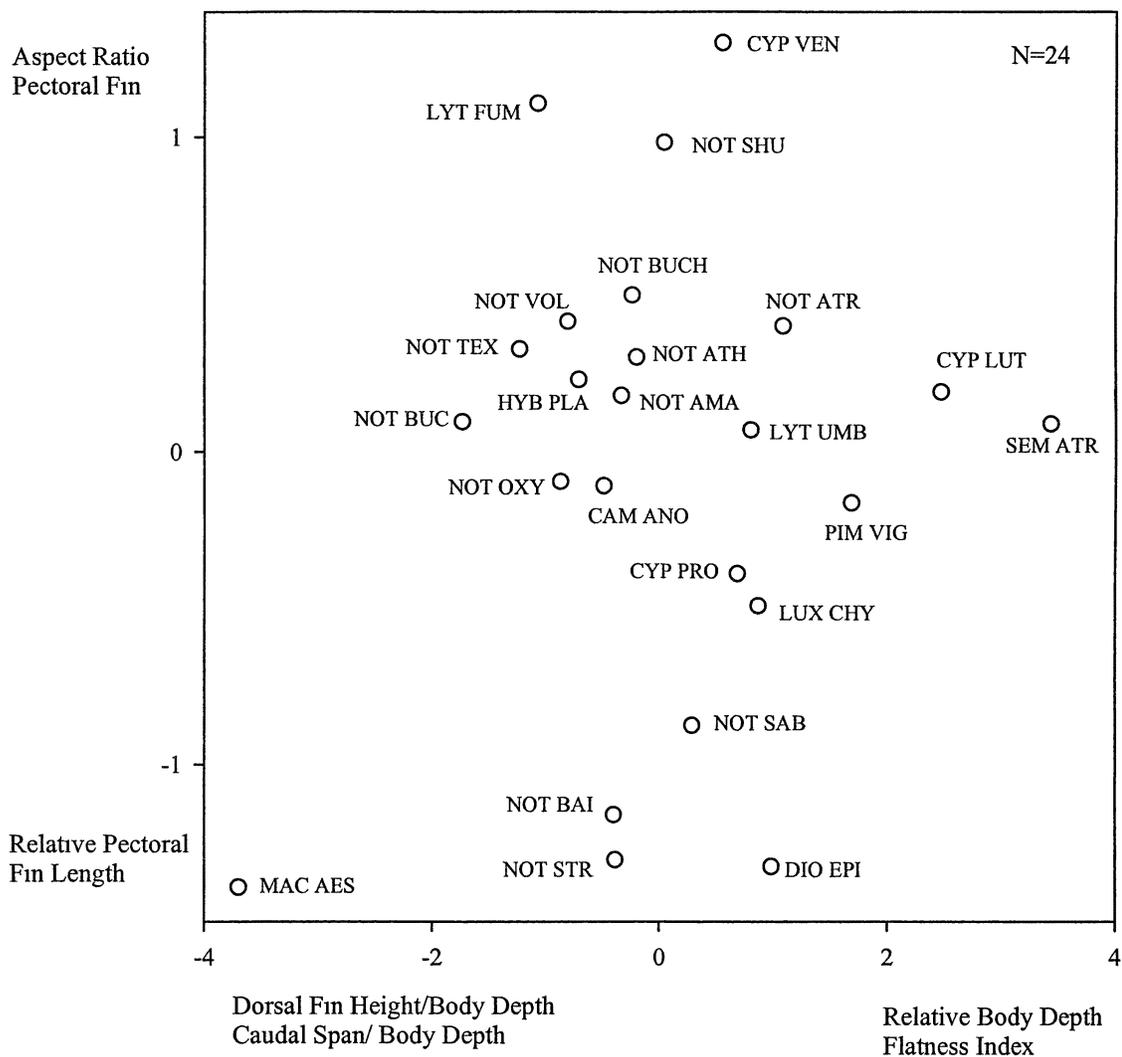


Figure 7. Plot of mean principal component scores for PCA # 1 and 2 obtained from morphometric attributes deemed important in swimming ability among Cyprinidae collected from various locations in Texas and Louisiana from June through August 2003. Species abbreviations represent the first three letters of genus and species.

VITA

Tracy Renee Leavy was born in Rochester, New York, on September 2, 1971, the daughter of Jean Leavy-Ells and Charles Ells. She received the degree of Bachelor of Science in Marine Science from Long Island University-Southampton in 1996. During the following year she was employed as a Laboratory/Aquaculture Assistant at Cospers Environmental Services in Bohemia, New York. In 1997, she was accepted into the US Peace Corps and served for two years as an Aquaculture Extension Agent in Timongolo, Cameroon, West Africa. In April 2000, she was employed as a Biological Research Technician (Fisheries) for US Fish and Wildlife Service and in October 2000 as a Fishery Biologist for US Geological Service, Biological Resources Division in Reno, Nevada. In 2002, she entered the Graduate College of Texas State University-San Marcos.

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