

Relationships among Swimming Ability, Current Velocity Association, and Morphology for Freshwater Lotic Fishes

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Abstract.—We determined swimming ability for 37 warmwater stream fishes in Texas and Louisiana and assessed relationships among swimming ability, habitat selection, and fish morphology. Mean absolute speeds (cm/s) were 17.8–81.9 cm/s for Cyprinidae, 50.9 cm/s for Characidae, 70.0 cm/s for Ictaluridae, 33.0 cm/s for Cichlidae, 40.0 cm/s for Percidae, 30.7–43.4 cm/s for Cyprinodontidae, 30.2 cm/s for Atherinidae, 15.7–18.6 cm/s for Poeciliidae, and 23.4–40.5 cm/s for Centrarchidae. Absolute swimming speeds were correlated ($P < 0.01$) to reported habitat descriptions (i.e., sloughs, lakes, streams, and rivers) of fishes. Absolute swimming speeds also were good predictors of spatial (i.e., runs, pools, and riffles) distributions of fishes from Independence Creek, Texas ($P = 0.03$), and Banita Creek, Texas ($P = 0.06$). Multivariate ordination of nine morphological attributes identified the linear combination of relative body depth, dorsal fin length, and caudal span width as an adequate predictor ($P < 0.01$) of swimming speed; however, several exceptions were noted. Understanding interactions between current velocity and swimming ability in fishes is critical to species conservation and to maintaining instream flow requirements for fishes.

Streamflow strongly influences spatial and temporal patterns in riverine fish assemblages at multiple scales (Schlosser 1985; Bain et al. 1988; Poff and Allan 1995). Spatially, fishes are distributed among current velocity and depth gradients within a stream reach (Angermeier 1987; Aadland 1993) and longitudinally among stream reaches (Kuehne 1962; Evans and Noble 1979). Temporally, occurrences and abundances of fishes fluctuate annually, which often are associated with low-flow and peak-flow events (Cross et al. 1985; Minckley and Meffe 1987). Consequently, fishes evolved numerous morphological (e.g., fin and body shape, higher proportion of red muscles) and behavioral traits through time, enabling some fish to be more fit at sustaining higher current velocities for exploiting food resources, reducing competition and predation, traversing large sections of streams during migration, and persisting in variable flow environments (Bone 1966; Gatz 1979; Taylor and McPhail 1985; Vogel 1994). Swimming speed, the maximum current velocity that a fish can withstand before being displaced downstream, is a measure of fitness associated with flowing environments and is used to infer habitat relationships and to explain patterns in fish morphology (Hawkins and Quinn 1996; Nelson et al. 2003; Ward et al. 2003).

Several studies have explored relationships among habitat selection, morphology, and swimming speed in freshwater fishes. Fishes with laterally compressed, deeper bodies and rounded caudal and paired fins generally select sluggish waters because their body and fin shapes are better suited for maneuvering than for speed (Alev 1969; Gosline 1971; Scarnecchia 1988). Fishes common to areas of high current velocity (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 (Hubbs 1941; Nursall 1958; Vogel 1994). Although these general trends are well established, morphological attributes, swimming speed, and habitat selection relationships are less evident when comparisons are made among congeners (Taylor and McPhail 1985; Shaefer et al. 1999; Ojanguren and Brana 2003). However, such studies typically assess these relationships with a truncated species pool (less than three species), which may limit detection of general patterns.

The purposes of this study were to assess relationships between swimming speed and habitat selection, specifically current velocity association, and between swimming speed and morphology of fishes from freshwater habitats in Texas and Louisiana. The objectives of this study were to determine swimming speed for a large number of obligate and facultative riverine fishes in Texas and Louisiana, to compare swimming speed to quantitative and qualitative measures of fish current velocity associations, and to compare swimming speed to morphological attributes of fishes. Fishes in the family Cyprinidae were primarily sought for this assessment because of their

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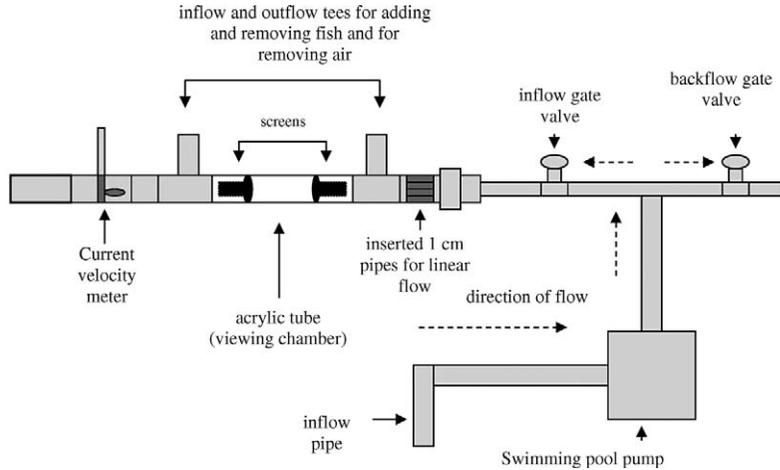


FIGURE 1.—Schematic diagram of the mobile swim tunnel used to determine swimming ability of various freshwater stream fishes in Texas and Louisiana from June through August 2003.

richness and abundance in freshwater streams of Texas and Louisiana (Conner and Suttkus 1986). The definition of swimming speed in this study closely resembles that of prolonged swimming speed used by Beamish (1978). Quantification of swimming speed and understanding its interrelationship with current velocity associations can provide useful information to explain spatial and temporal trends in fish occurrence and abundance, habitat partitioning among fishes, and potential impacts of instream flow modifications.

Methods

For this study, a swim tunnel was designed similar to that described by Brett (1964), but with minor modifications for mobility (Figure 1). A 1.5-hp (1 hp = 746 W) 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 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 of water in the acrylic tube was measured with a Marsh-McBirney Flow-Mate (model 2000) inserted behind the outflow tee. Plastic screens, 10 by 5 cm (mesh size 6 by 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 the swimming abilities of fish in the field, which avoided fish transportation, housing, and lengthy laboratory acclimation periods. Swimming abilities of fish determined by mobile swim

tunnels are consistent with those determined in controlled laboratory settings (Farrell et al. 2003; Lee et al. 2003) and probably provide an accurate assessment of fish capabilities (Bert and Simon 1981).

Fish ranging from 20.0 to 80.0 mm standard length (SL) were collected with seines (1.2 × 2.4 m; 9.5-mm mesh) from streams in Texas and Louisiana from June through August 2003 (Table 1). Individuals longer than 80.0 mm SL were excluded from testing because of the physical restrictions of the swim tunnel (Brett 1964) and to minimize the influence of body length on swimming ability. Fish were collected with the seine in groups of three to five individuals and placed in a 44-L aerated container until testing. From the container, one individual at a time was captured randomly with a small dip net, immediately placed into the outflow tee, and gently guided into the acrylic tube. Initial current velocity was 0 cm/s in the acrylic viewing tube. Current velocity was increased 3–5 cm/s every 10 s until the fish stopped swimming because of fatigue, which was defined as the point at which an individual was impinged and unable to remove itself from the downstream screen for 4 s. Individuals that did not swim or that exhibited behavioral responses (i.e., oral grasping of the upper screen) were excluded. An individual was used only once. Following impingement, the final current velocity was recorded, and the fish was removed from the swim tunnel, anesthetized with tricaine methanesulfonate (80 mg/L), and preserved in a 10% formalin solution.

Dissolved oxygen (mg/L), oxygen saturation (%), and temperature (°C) of the stream near the water intake were measured every 2 h with an YSI model 60/10 multiprobe meter. Temperature and dissolved

TABLE 1.—Species and locations of freshwater fishes tested in the mobile swim tunnel from June through August 2003. All counties are in Texas; all parishes in Louisiana.

Species	Site
Cyprinidae	
Central stoneroller <i>Camptostoma anomalum</i>	Blanco River, Hays County
Red shiner <i>Cyprinella lutrensis</i>	Banita Creek, Nacogdoches County Yegua Creek, Washington County Canadian River, Hemphill County
Proserpine shiner <i>C. proserpina</i>	Independence Creek, Terrell County
Blacktail shiner <i>C. venusta</i>	San Marcos River, Hays County Blanco River, Hays County
Roundnose minnow <i>Dionda episcopa</i>	Independence Creek, Terrell County
Plains minnow <i>Hybognathus placitus</i>	Canadian River, Hemphill County Double Mountain Fork Brazos River, Fisher County Pease River, Foard County
Striped shiner <i>Luxilus chrysocephalus</i>	Little Sandy Creek, Sabine Parish
Ribbon shiner <i>Lythrurus fumeus</i>	Big Sandy Creek, Bastrop County
Redfin shiner <i>L. umbratilis</i>	Navasota River, Brazos County Banita Creek, Nacogdoches County
Speckled chub <i>Macrhybopsis aestivalis</i>	Kisatchie Falls, Natchidoches Parish Yegua Creek, Washington County Pease River, Foard County
Texas shiner <i>Notropis amabilis</i>	Independence Creek, Terrell County San Marcos River, Hays County Blanco River, Hays County
Emerald shiner <i>N. atherinoides</i>	Canadian River, Hemphill County
Blackspot shiner <i>N. atrocaudalis</i>	Banita Creek, Nacogdoches County
Red River shiner <i>N. bairdi</i>	Pease River, Foard County
Smalleye shiner <i>N. buccula</i>	Double Mountain Fork Brazos River, Fisher County
Ghost shiner <i>N. buchananii</i>	Yegua Creek, Washington County Navasota River, Brazos County
Sharpnose shiner <i>N. oxyrhynchus</i>	Double Mountain Fork Brazos River, Fisher County
Sabine shiner <i>N. sabiniae</i>	Banita Creek, Nacogdoches County
Silverband shiner <i>N. shumardi</i>	Yegua Creek, Washington County
Sand shiner <i>N. stramineus</i>	Blanco River, Hays County
Weed shiner <i>N. texanus</i>	Big Sandy Creek, Bastrop County
Mimic shiner <i>N. volucellus</i>	Big Sandy Creek, Bastrop County Blanco River, Hays County
Bullhead minnow <i>Pimephales vigilax</i>	Banita Creek, Nacogdoches County San Marcos River, Hays County
Creek chub <i>Semotilus atromaculatus</i>	Banita Creek, Nacogdoches County
Characidae	
Mexican tetra <i>Astyanax mexicanus</i>	Independence Creek, Terrell County
Ictaluridae	
Blue catfish <i>Ictalurus furcatus</i>	Yegua Creek, Washington County
Cyprinodontidae	
Blackstripe top minnow <i>Fundulus notatus</i>	Banita Creek, Nacogdoches County
Plains killifish <i>Fundulus zebrinus</i>	Independence Creek, Terrell County
Poeciliidae	
Largespring gambusia <i>Gambusia geiseri</i>	Spring Lake, Hays County
Sailfin molly <i>Poecilia latipinna</i>	Spring Lake, Hays County
Atherinidae	
Inland silverside <i>Menidia beryllina</i>	Lake Somerville, Lee County Yegua Creek, Washington County
Centrarchidae	
Redbreast sunfish <i>Lepomis auritus</i>	Blanco River, Hays County
Bluegill <i>Lepomis macrochirus</i>	Banita Creek, Nacogdoches County
Longear sunfish <i>Lepomis megalotis</i>	Banita Creek, Nacogdoches County
Largemouth bass <i>Micropterus salmoides</i>	Banita Creek, Nacogdoches County Independence Creek, Terrell County Spring Lake, Hays County
Percidae	
Rio Grande darter <i>Etheostoma grahami</i>	Independence Creek, Terrell County
Cichlidae	
Rio Grande cichlid <i>Cichlasoma cyanoguttatum</i>	Independence Creek, Terrell County

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; Ourrick and Cech 2000). Likewise, oxygen saturation greater than 70% has little effect on swimming performances of fishes (Beamish 1970). To minimize covariate influences on swimming ability, criteria for field testing were set for stream water temperatures that ranged between 20°C and 34°C and for oxygen saturation above 70%.

Swimming speed was defined as the mean current velocity (cm/s; absolute swimming speed) that individuals of a species could swim before fatigue. To further reduce the effect of body length on swimming ability, body lengths per second (BL/s; relative swimming speed) were calculated. Significant differences ($\alpha = 0.05$) in relative swimming speed among species were tested with an analysis of covariance (ANCOVA). Relative swimming speed was \log_{10} transformed to meet assumptions for homogeneity of variances and normality. Temperature (°C) and standard length were used as covariates. Fisher's least-significant-differences tests ($\alpha = 0.05$; Zar 1999) were used to detect differences between species. For all statistical tests, SAS statistical software (SAS Institute 2003) was used.

Qualitative habitat descriptions were obtained from Page and Burr (1991) for each species of fish tested. Habitat descriptions were given a score (1–5) according to reported water body (i.e., 1 = sloughs, 2 = lakes, 3 = headwater reaches, 4 = streams, 5 = small to large rivers) and mesohabitat (i.e., 1 = backwater areas, 2 = pools, 3 = springs, 4 = runs, 5 = riffles). Scores for water bodies and mesohabitat were multiplied to obtain an overall score for each species; low numbers described slow water habitats and high numbers described swift water habitats. For several species, habitat descriptions included multiple types of water body and mesohabitats; therefore, we independently assigned habitat scores without knowledge of species name or their swimming speed. Overall scores (one from each author) were averaged to obtain a final score for each species. Final scores were correlated (Peterson's correlation coefficients; Zar 1999) to absolute swimming speeds.

To explore relationships between absolute swimming speeds and in situ mean current velocity, current velocity information was obtained from published and unpublished studies that documented species distributions among current velocity gradients. Collectively, these studies encompassed a large geographic region that included upland streams in Louisiana (Peason

Ridge; Vernon, Natchitoches, and Sabine parishes; Williams et al. 2005), east Texas (Banita Creek, Nacogdoches County; Williams 2003), and west Texas (Independence Creek, Terrell County; Watson 2006). Reported mean current velocities for fishes, weighted by abundance, were correlated (Peterson's correlation coefficients) to absolute swimming speeds.

In the laboratory, morphological attributes of preserved fish were measured to the nearest 0.01 mm in length with a dissecting microscope and ocular micrometer, or to the nearest 0.001 g in weight with an electronic balance. Morphological attributes measured and considered important for defining swimming ability of fishes (Gatz 1979) were flatness index (ratio between maximum body depth and maximum body width), relative body depth (ratio between maximum body depth and standard length), relative peduncle length (ratio between caudal peduncle length and standard length), caudal peduncle flatness index (ratio between depth of peduncle at midpoint and width of peduncle at the same point), relative caudal span (ratio between caudal span and body depth), relative pectoral fin length (ratio between pectoral fin length and standard length), pectoral fin aspect ratio (ratio between length of pectoral fin and width of pectoral fin), relative dorsal fin (ratio between dorsal fin height and body depth), and relative weight (ratio between weight and length). Morphological attributes were transformed (z -scores) and those attributes that strongly segregated among families were identified with principal components analysis (PCA). Scores from PCA axis I and II 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 I and II.

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 ($F_{38, 373} = 20.9$, $P < 0.01$) among species. Standard length ($P < 0.01$) and water temperature ($P = 0.01$) were significant covariates; two-way and three-way interactions among treatment and covariate effects were not significant ($P > 0.05$; Table 3). Water temperatures ranged from 21.7°C to 33.4°C during all tests. Dissolved oxygen concentrations were greater than 70% of saturation during all tests, except on the Pease River, which had a concentration of 63% of

TABLE 2.—Mean relative (bl/s) and absolute (cm/s) swimming speeds \pm SE of various fishes in Texas and Louisiana from June through August 2003. Relative speeds sharing the same letter are not significantly different. Fisher's least-significant-differences tests ($\alpha = 0.05$).

Species	N	Mean relative speed (\pm SE)	Mean absolute speed (\pm SE)
Cyprinidae			
Emerald shiner	10	19.6 \pm 1.37 a	81.4 \pm 5.46
Silverband shiner	10	18.8 \pm 1.23 ab	79.4 \pm 6.02
Red shiner	16	17.2 \pm 1.20 ab	71.2 \pm 3.49
Sand shiner	18	15.7 \pm 0.68 abc	66.5 \pm 2.52
Proserpine shiner	10	15.7 \pm 1.25 abc	60.8 \pm 2.93
Texas shiner	29	15.3 \pm 0.77 abc	63.6 \pm 2.86
Speckled chub	11	14.7 \pm 1.28 abcd	61.9 \pm 4.40
Small-eye shiner	10	13.8 \pm 1.61 e	49.7 \pm 5.42
Central stoneroller	10	13.6 \pm 0.59 bcdef	62.9 \pm 2.77
Sharpnose shiner	10	13.4 \pm 0.87 defg	53.4 \pm 3.12
Blacktail shiner	19	13.4 \pm 0.65 abcdfgh	61.1 \pm 2.81
Ghost shiner	12	12.7 \pm 0.75 efgi	44.7 \pm 2.64
Sabine shiner	12	12.5 \pm 0.73 efgi	46.9 \pm 3.65
Plains minnow	32	12.4 \pm 0.78 efgi	61.1 \pm 3.57
Mimic shiner	15	12.3 \pm 0.88 egijk	43.6 \pm 3.71
Redfin shiner	13	12.3 \pm 0.81 efijkl	55.0 \pm 3.75
Ribbon shiner	11	11.6 \pm 1.74 egikmn	38.1 \pm 5.72
Red River shiner	10	10.4 \pm 0.99 egijklmn	45.6 \pm 4.96
Blackspot shiner	11	9.9 \pm 0.98 egijklmn	46.9 \pm 2.35
Weed shiner	7	9.4 \pm 1.21 egkmn	38.7 \pm 4.93
Striped shiner	10	9.3 \pm 0.89 ekmn	40.3 \pm 3.73
Bullhead minnow	12	7.9 \pm 0.49 ekmnopr	39.6 \pm 2.28
Creek chub	9	7.9 \pm 0.53 ekmnopr	44.2 \pm 1.61
Roundnose minnow	10	3.4 \pm 0.35 u	17.8 \pm 1.80
Characidae			
Mexican tetra	10	12.6 \pm 0.49 cdefghij	50.9 \pm 2.45
Ictaluridae			
Blue catfish	10	13.7 \pm 0.46 abcdf	70.0 \pm 1.86
Cyprinodontidae			
Plains killifish	10	12.0 \pm 1.12 efijklm	43.4 \pm 3.94
Blackstripe topminnow	10	5.5 \pm 0.69 qtu	30.7 \pm 3.69
Poeciliidae			
Largespring gambusia	7	6.8 \pm 0.67 qtu	15.7 \pm 1.36
Sailfin molly	5	5.5 \pm 1.03 tu	18.6 \pm 3.04
Atherinidae			
Inland silverside	9	8.0 \pm 0.92 opq	30.2 \pm 3.70
Centrarchidae			
Bluegill	4	8.1 \pm 0.39 egiklmnop	40.5 \pm 6.61
Red breast sunfish	5	7.5 \pm 0.66 nopqrs	35.4 \pm 1.89
Largemouth bass	8	7.3 \pm 0.78 opqst	23.4 \pm 2.40
Longear sunfish	5	5.7 \pm 0.79 oqstu	28.0 \pm 4.22
Percidae			
Rio Grande darter	4	11.1 \pm 0.25 defgijklmn	40.0 \pm 3.92
Cichlidae			
Rio Grande cichlid	8	8.7 \pm 0.50 emno	33.0 \pm 2.70

saturation. 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 ($r = 0.01$, $P > 0.05$) indicated that dissolved oxygen concentrations did not influence swimming ability of the fish tested in this study.

Mean relative swimming speeds (\pm SE) ranged from 3.4 (± 0.35) to 19.6 (± 1.37) BL/s for Cyprinidae (24 species), 5.5 (± 0.69) to 12.0 (± 1.12) BL/s for Cyprinodontidae (2 species), 5.5 (± 1.03) to 6.8 (± 0.67) BL/s for Poeciliidae (2 species), and 5.7 (± 0.79) to 8.1 (± 0.39) BL/s for Centrarchidae (4 species). Among families with only a single species tested, mean relative swimming speeds (\pm SE) were 12.6 (± 0.49) BL/s for Characidae, 13.7 (± 0.46) BL/s

TABLE 3.—Mean standard length (mm) and temperature ($^{\circ}\text{C}$) \pm SE of various fishes in Texas and Louisiana from June through August 2003.

Species	N	Mean standard	Mean temperature ($^{\circ}\text{C}$)
Cyprinidae			
Emerald shiner	10	41.9 \pm 2.16	30.0 \pm 0.67
Silverband shiner	10	42.1 \pm 1.25	30.5 \pm 0.02
Red shiner	16	43.3 \pm 2.64	27.7 \pm 0.78
Sand shiner	18	42.7 \pm 0.95	28.4 \pm 0.54
Proserpine shiner	10	39.6 \pm 1.76	23.5 \pm 0.47
Texas shiner	29	42.2 \pm 1.14	23.4 \pm 0.24
Speckled chub	11	43.2 \pm 1.99	25.3 \pm 0.56
Smalleye shiner	10	36.3 \pm 1.01	32.9 \pm 0.11
Central stoneroller	10	46.3 \pm 1.09	28.2 \pm 0.17
Sharpnose shiner	10	39.9 \pm 0.62	32.9 \pm 0.13
Blacktail shiner	19	47.0 \pm 2.57	23.1 \pm 0.24
Ghost shiner	12	35.2 \pm 0.75	25.9 \pm 0.34
Sabine shiner	12	37.5 \pm 1.62	27.4 \pm 0.70
Plains minnow	32	51.1 \pm 2.57	28.7 \pm 0.66
Mimic shiner	15	35.3 \pm 0.93	27.8 \pm 0.07
Redfin shiner	13	45.1 \pm 1.67	29.0 \pm 0.69
Ribbon shiner	11	32.8 \pm 1.36	27.2 \pm 0.18
Red River shiner	10	44.2 \pm 2.25	25.8 \pm 0.37
Blackspot shiner	11	49.6 \pm 2.83	26.7 \pm 0.85
Weed shiner	7	41.3 \pm 1.01	27.3 \pm 0.06
Striped shiner	10	43.8 \pm 1.19	27.5 \pm 0.00
Bullhead shiner	12	50.2 \pm 1.83	23.4 \pm 0.12
Creek chub	9	57.1 \pm 2.69	28.5 \pm 1.36
Roundnose minnow	10	52.8 \pm 1.94	22.2 \pm 0.25
Characidae			
Mexican tetra	10	40.9 \pm 2.30	24.9 \pm 0.39
Ictaluridae			
Blue catfish	10	51.6 \pm 2.22	29.6 \pm 0.10
Cyprinodontidae			
Plains killifish	10	36.3 \pm 1.19	23.6 \pm 0.06
Blackstripe topminnow	10	55.7 \pm 1.35	28.3 \pm 0.77
Poeciliidae			
Largespring gambusia	7	23.4 \pm 2.44	22.7 \pm 0.00
Sailfin molly	5	34.9 \pm 2.38	22.7 \pm 0.00
Atherinidae			
Inland silverside	9	37.9 \pm 1.60	31.7 \pm 0.55
Centrarchidae			
Bluegill	4	49.7 \pm 1.86	25.3 \pm 1.93
Redbreast sunfish	5	48.4 \pm 3.06	26.7 \pm 0.00
Largemouth bass	8	32.4 \pm 1.72	24.2 \pm 0.86
Longear sunfish	5	48.5 \pm 1.34	24.4 \pm 0.50
Percidae			
Rio Grande darter	4	36.3 \pm 2.44	24.1 \pm 0.00
Cichlidae			
Rio Grande cichlid	8	38.7 \pm 3.42	25.6 \pm 0.00

for Ictaluridae, 8.0 (\pm 0.92) BL/s for Atherinidae, 11.1 (\pm 0.25) BL/s for Percidae, and 8.7 (\pm 0.50) BL/s for Cichlidae.

Mean absolute swimming speeds (\pm SE) ranged from 17.8 (\pm 1.80) to 81.4 (\pm 5.46) cm/s for Cyprinidae, 30.7 (\pm 3.69) to 43.4 (\pm 3.94) cm/s for Cyprinodontidae, 15.7 (\pm 1.36) to 18.6 (\pm 3.04) cm/s for Poeciliidae, and 23.4 (\pm 2.40) to 40.5 (\pm 6.61) cm/s for Centrarchidae. Among families with only a single

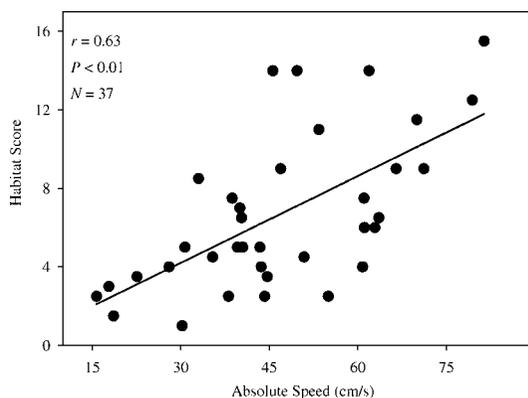


FIGURE 2.—Relationship between absolute speeds (cm/s) and habitat use, scored current velocity, (based on preferred habitat in Page and Burr [1991]) of fishes tested in the swim tunnel at various locations in Texas and Louisiana from June through August 2003. Higher habitat velocity scores indicate swifter currents.

species tested, mean absolute swimming speeds (\pm SE) were 50.9 (\pm 2.45) cm/s for Characidae, 70.0 (\pm 1.86) cm/s for Ictaluridae, 30.2 (\pm 3.70) cm/s for Atherinidae, 40.0 (\pm 3.92) cm/s for Percidae, and 33.0 (\pm 2.70) cm/s for Cichlidae. Emerald shiners had the fastest mean (\pm SE) absolute swimming speed (81.4 \pm 5.46 cm/s), whereas largespring gambusias had the slowest mean absolute swimming speed (15.7 \pm 1.36 cm/s; Table 2).

Current Velocity Associations

A positive association ($r = 0.63$; $N = 37$; $P < 0.01$) was found between absolute swimming speeds and habitat scores obtained from Page and Burr (1991) (Figure 2). In general, fishes reported to inhabit main channels of medium to large rivers were among the highest in mean (\pm SE) absolute swimming speeds (i.e., emerald shiner = 81.4 \pm 5.46; silverband shiner = 79.4 \pm 6.02, and blue catfish = 70.0 \pm 1.86 cm/s). Fishes reported to inhabit pool and run habitats in creeks and small to medium rivers were intermediate in mean absolute swimming speeds (i.e., blacktail shiner = 61.1 \pm 2.81, Sabine shiner = 46.9 \pm 3.65, and blackspot shiner = 46.9 \pm 2.35 cm/s). Fishes 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 (i.e., largespring gambusia = 15.7 \pm 1.36, roundnose minnow = 17.8 \pm 1.80, and sailfin molly = 18.6 \pm 3.04 cm/s).

Similar trends were observed between species absolute swimming speed and in situ current velocity associations (Figure 3). Absolute swimming speeds were positively associated with weighted estimates of mean current velocity at Independence Creek ($r = 0.68$,

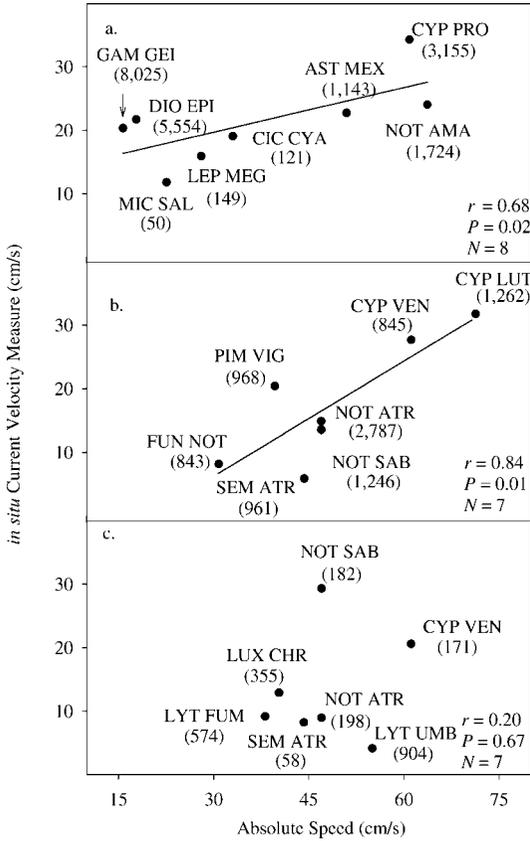


FIGURE 3.—Relationships between mean absolute speeds (cm/s) and mean habitat current velocities (cm/s) of abundant fishes at (a) Independence Creek (May 2002–October 2003), (b) Banita Creek (November 2001–October 2002), and (c) creeks on Peason Ridge (June 2001–August 2002). Abbreviations represent the first three letters of genus and species.

$N = 9, P = 0.03$) and Banita Creek ($r = 0.84, N = 7, P = 0.02$). Among the fishes of Independence Creek, the proserpine shiner is found in runs and flowing pools; estimated mean (\pm SE) habitat current velocity is 32 (± 0.6) cm/s (Watson 2006) with a mean absolute swimming speed of 60.8 (± 2.93) cm/s. Conversely, the largemouth bass is usually found in pools; estimated mean (\pm SE) habitat current velocity is 9 (± 1.7) cm/s with a mean absolute swimming speed of 23.4 (± 2.40) cm/s. Among the fishes of Banita Creek, the red shiner is a habitat generalist found in pools and runs; estimated mean (\pm SE) habitat current velocity is 32 (± 1.2) cm/s (Williams 2003) with a mean absolute swimming speed of 71.2 (± 3.49) cm/s. Conversely, the creek chub is usually found in shallow runs and pools in the headwater region; estimated mean (\pm SE) habitat current velocity is 6 (± 0.3) with a mean absolute swimming speed of 44.2 (± 1.61) cm/s.

However, deviations from fishes with increased swimming ability inhabiting areas of higher flows were observed. In Independence Creek, one outlier species (Rio Grande darter) was deleted from correlation analysis because measured mean absolute swimming speed was relatively slow (40.0 ± 3.92 cm/s), yet the species inhabits swift current velocities (46 ± 2.4 cm/s). Likewise, association between mean absolute swimming speed and estimated mean current velocity of habitat (Williams et al. 2005) was not significant ($r = 0.20, N = 7, P = 0.67$) for streams on Peason Ridge. Overall, absolute swimming speed was an adequate predictor of in situ current velocity associations, except for benthic-oriented fishes, such as the darters.

Morphology

The first two linear contrasts of morphological attributes explained 58% of the observed variation among the nine families (Figure 4) with the first PC axis (39% of total variation) primarily contrasting differences in relative body depth (PC loading = 0.48), flatness index (0.44), relative dorsal fin height (-0.43), and relative caudal span (-0.34). The second PC axis, primarily contrasting differences in relative pectoral fin length (-0.68) and pectoral fin aspect ratio (-0.64), explained 19% of total variation. Cichlidae and Centrarchidae were associated positively with PC I, which describes fishes with greater body depth, relatively shorter dorsal fin, and lesser caudal span (Figure 4). In contrast, Atherinidae, Cyprinidae, and Percidae were associated negatively with PC I, having a more streamlined body shape with relatively longer dorsal fin and greater caudal span. Percidae and Cichlidae were associated positively with PC II, having relatively longer and broader pectoral fins, whereas Atherinidae, Characidae, and Poeciliidae were associated negatively with PC II, having relatively shorter and more slender pectoral fins (Figure 4). Correlating individual PCA scores to species swimming speeds, PC I was inversely related to absolute swimming speed ($r = -0.31, N = 412, P < 0.01$), and PC II was directly related to absolute swimming speed ($r = 0.33, N = 412, P < 0.01$). Collectively, fishes with more streamlined body shapes, longer dorsal fins, greater caudal spans, and longer and broader pectoral fins tend to measure highest in swimming speed.

The first two linear contrasts of morphological attributes explained 53% of the observed variation within Cyprinidae (Figure 5), with the first PCA axis (32% of total variation) primarily contrasting differences in relative body depth (0.53), relative dorsal fin height (-0.51), and flatness index (0.40). The second PCA axis, primarily contrasting differences in pectoral fin aspect ratio (0.64) and relative pectoral fin length

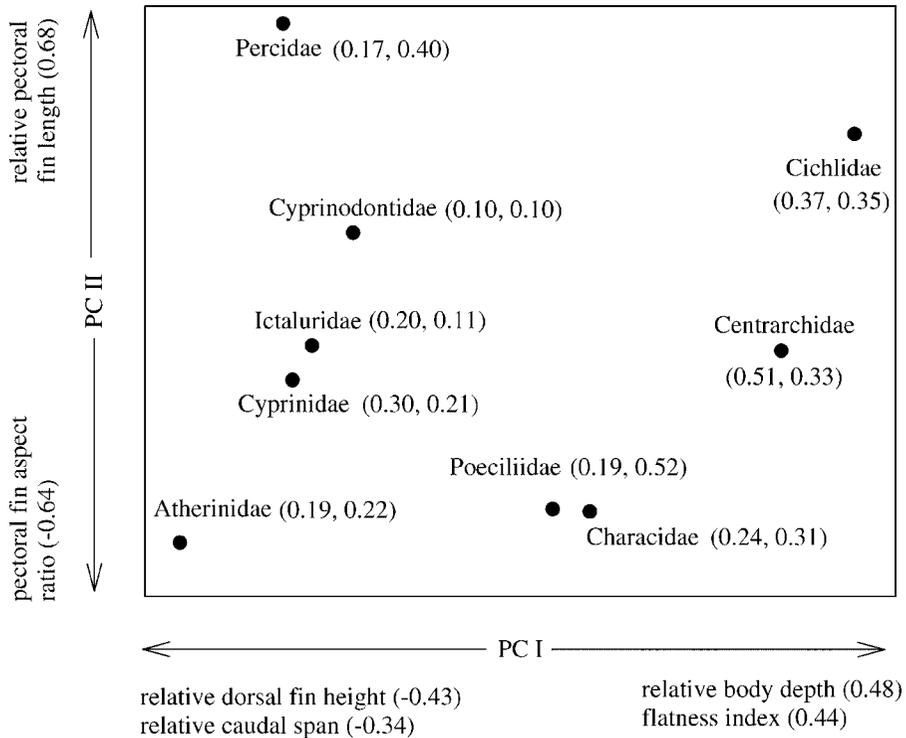


FIGURE 4.—Plot of mean principal component scores for PCA I and II obtained from morphometric attributes deemed important in swimming ability among nine families. Numbers in parentheses indicate standard errors (PC 1, PC 2).

(-0.60), explained 21% of total variation. Red shiner and creek chub were associated positively with PC I, describing deeper-body cyprinids with shorter dorsal fins. Speckled chub associated negatively with PC I; its body shape is streamlined with a relatively longer dorsal fin. Blacktail shiners, ribbon shiners and silver-band shiners were associated positively with PC II, having relatively shorter and more slender pectoral fins. In contrast, speckled chub, Red River shiners, sand shiners, and roundnose minnows associated negatively with PC II, having relatively longer pectoral fins. Correlating individual PCA scores to species swimming speeds, PC I was inversely related to absolute swimming speed ($r = -0.34$, $N = 317$, $P < 0.01$), and PC II was not associated with absolute swimming speed ($r = 0.08$, $N = 317$, $P = 0.17$). With only PC I having a significant association with swimming speed, cyprinids with relatively streamlined bodies, long dorsal fins, and wider caudal spans tend to measure highest in swimming ability.

Discussion

Fishes tested herein differed in relative and absolute swimming speeds, with swimming speeds partially explaining large-scale and small-scale patterns in fish

occurrence and abundance. In part, swimming speed explained the longitudinal distributions of fishes. Fishes with greater swimming speeds inhabit medium to large rivers, whereas those with lesser swimming speeds inhabit springs, creeks, and small rivers. Likewise, this association, in part, explained smaller-scale spatial segregation of fishes. Fishes with greater swimming speeds inhabit runs, riffles, and flowing pools, whereas those with slower swimming speeds inhabit pools and backwater habitats. However, swimming speed, or more specifically the musculature and physiological processes that enable higher swimming speeds (Schaarschmidt and Jurs 2003), do not account for all patterns in spatial distributions related to flow.

Fish behavior also influences species persistence in swift water and might be independent of swimming speed capabilities. Oral grasping and biting and holding onto vegetation or other debris are examples of behavioral responses that may enable fishes 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 red shiners, blacktail shiners, redbfin shiners, sand shiners, roundnose minnows, and creek chub. Within the swim tunnel, oral grasping of

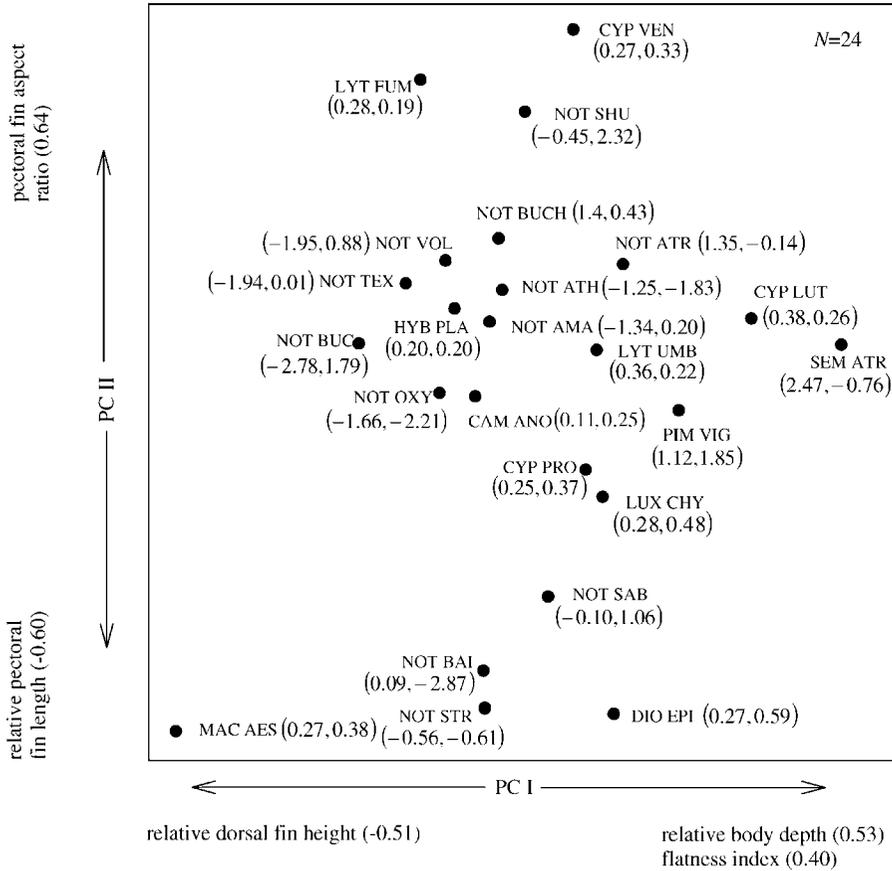


FIGURE 5.—Plot of mean principal component scores for PCA I and II obtained from morphometric attributes deemed important in swimming ability among Cyprinidae collected from various locations in Texas and Louisiana from June through August 2003. Species abbreviations represent the first three letters of genus and species. Numbers in parentheses indicate standard errors (PC 1, PC 2).

the intake screen allowed red shiners to withstand current velocities up to 129 cm/s before fatigue. Other behaviors that improve a fish’s capability for withstanding high current velocities include the exploitation of velocity refuges and the adjustment of the the body and fin position relative to substrate (Minckley and Meffe 1987; Adams et al. 2000; Ward et al. 2003). Use of benthic habitats and positioning of fins may explain the disparity between absolute swimming speed and habitat current velocity for fish such as the Rio Grande darter where current velocity is measured at the standard 60% of depth but the fish resides in interstitial spaces of cobble and gravel substrate.

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 include several species or genera with relatively low

absolute swimming speeds (i.e., *Gambusia*, *Poecilia*, *Micropterus*, *Lepomis*, and *Pimephales*), as well as several species or genera with relatively high absolute swimming speeds (i.e., *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 the conclusions of Meffe (1984), Ward et al. (2003), and Scott and Magoulick (2008) 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 impoundment 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 genera with low swimming speeds (i.e., *Lepomis*, *Micropterus*, *Meni-*

dia, *Pimephales*, *Gambusia*), but also species or genera with high swimming speeds (i.e., red shiner, emerald shiner, sand shiner, and *Ictalurus*) (Minckley and Meffe 1987; Platania 1991; Winston et al. 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 among fishes (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 (Schaefer et al. 1999; Ojanguren and Brana 2003). In this study, 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. There were some notable exceptions that weakened the correlation among families. For example, the inland silverside 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, Mexican tetra a short, deep-bodied fish with relatively short pectoral fins, had a high swimming speed. These exceptions were attributed to analogous selection of body morphologies among fishes.

Among Cyprinidae, the four species that 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; for example, the five species that ranked highest in relative swimming speeds were intermediate in relative body depth, dorsal fin height, and caudal span. Our findings support those of Felley (1984) and Wood and Bain (1995), who did not detect relationships between morphology and habitat selection (i.e., current velocity) within Cyprinidae. Similar morphological features among species may have diverse functions and weaken ecomorphological relationships (Felley 1984). 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.

Absolute swimming speeds reported here also provide guidelines for assessing potential impacts of

instream impediments. Road crossings equipped with concrete or metal culverts can temporarily, partially, or completely impede fish movement by artificially accelerating current velocities (Metsker 1970; Bates 2003). Restricted movements associated with road crossings are documented for several warmwater fishes, including cyprinids, fundulids, and centrarchids (Warren and Pardew 1998; Schaefer et al. 2002). Consequently, streams become fragmented, altering the ecological and biological importance of flowing waters to the resident fishes in the areas of predator avoidance, food acquisition, thermal refugia, reproduction, recolonization, and recruitment (Schlosser 1985; Warren and Pardew 1998; Schaefer et al. 2002). National, state, and local guidelines are available to assess existing culverts (Clarkin et al. 2005) and aid the design of new culverts to provide passage for aquatic species (Bates 2003). Results of this study provide additional specifications for culvert designs by identifying current velocities that impede fish movement.

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References

- Aadland, L. P. 1993. Stream habitat types: their fish assemblages and relationship to flow. *North American Journal of Fisheries Management* 13:790–806.
- Adams, S. R., J. J. Hoover, and K. J. Killgore. 2000. Swimming performance of the Topeka shiner (*Notropis topeka*) an endangered midwestern minnow. *American Midland Naturalist* 144:178–186.
- Adams, S. R., G. L. Adams, and J. J. Hoover. 2003. Oral grasping: a distinctive behavior of cyprinids for maintaining station in flowing water. *Copeia* 2003:851–857.
- Aleev, Y. G. 1969. Function and gross morphology in fish. Israel Program for Scientific Translations, Jerusalem.
- Anderson, A. A., C. Hubbs, K. O. Winemiller, and R. J. Edwards. 1995. Texas freshwater fish assemblages following three decades of environmental change. *Southwestern Naturalist* 40:314–321.
- Angermeier, P. L. 1987. Spatiotemporal variation in habitat selections by fishes in small Illinois streams. Pages 52–60 in W. J. Matthews and D. C. Heins, editors. *Community and evolutionary ecology of North American stream fishes*. University of Oklahoma Press, Norman.
- Bain, M. B., J. T. Finn, and H. E. Booke. 1988. Streamflow

- regulation and fish community structure. *Ecology* 69:382–392.
- Bates, K. 2003. Design of road culverts for fish passage. Washington Department of Fish and Wildlife Report, Olympia.
- Beamish, F. W. H. 1970. Oxygen consumption of largemouth bass, *Micropterus salmoides*, in relation to swimming speed and temperature. *Canadian Journal of Zoology* 48:1221–1228.
- Beamish, F. W. H. 1978. Swimming capacity. Pages 101–172 in W. S. Hoar and D. J. Randall, editors. *Fish physiology*, volume 7. Academic Press, New York.
- Berst, A., and R. Simon. 1981. Proceedings of the international stock concept symposium. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1457–1914.
- Bone, Q. 1966. On the function of the two types of ourotomal muscle fibre in elasmobranch fish. *Journal of Marine Biology* 46:321–349.
- Bonner, T. H., and G. R. Wilde. 2000. Changes in the Canadian River fish assemblage associated with reservoir construction. *Journal of Freshwater Ecology* 15:189–198.
- Brett, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *Journal of Fisheries Research Board of Canada* 21:1183–1225.
- Clarkin, K., A. Conner, M. J. Furniss, B. Gubernick, M. Love, K. Moynan, and S. Wilson Musser. 2005. National inventory and assessment procedure for identifying barriers to aquatic organism passage at road–stream crossings. U.S. Forest Service, National Technology and Development Program Report, Washington, D.C.
- Conner, J. V., and R. D. Suttus. 1986. Zoogeography of freshwater fishes of the western gulf slope. Pages 413–456 in C. H. Hocutt and E. O. Wiley, editors. *The zoogeography of North American freshwater fishes*. Wiley, New York.
- Cross, F. B., R. E. Moss, and J. T. Collins. 1985. Assessment of dewatering impacts on stream fisheries in the Arkansas and Cimarron Rivers. Kansas Fish and Game Commission, Nongame Wildlife Contract 46, Topeka.
- Douglas, M. E., and W. J. Matthews. 1992. Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. *Oikos* 65:213–224.
- Evans, J. W., and R. L. Noble. 1979. The longitudinal distribution of fishes in an east Texas stream. *American Midland Naturalist* 101:333–343.
- Farrell, A. P., C. G. Lee, K. Tierney, A. Hodaly, S. Clutterham, M. Healey, S. Hinch, and A. Lotto. 2003. Field-based measurements of oxygen uptake and swimming performance with adult Pacific salmon using a mobile respirometer swim tunnel. *Journal of Fish Biology* 62:64–84.
- Felley, J. D. 1984. Multivariate identification of morphological–environmental relationships within the Cyprinidae (Pisces). *Copeia* 1984:442–455.
- Gatz, A. J. 1979. Ecological morphology of freshwater stream fishes. *Tulane Studies in Zoology and Botany* 21:91–124.
- Gosline, W. A. 1971. Functional morphology and classification of teleostean fishes. University Press of Hawaii, Honolulu.
- Hawkins, D. K., and T. P. Quinn. 1996. Critical swimming velocity and associated morphology of juvenile coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead trout (*Oncorhynchus ourkiss*), and their hybrids. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1487–1496.
- Hubbs, C. L. 1941. The relation of hydrological conditions of speciation in fishes. Pages 182–195 in *A symposium on hydrobiology*. University of Wisconsin Press, Madison.
- Hubbs, C. R., J. Edwards, and G. P. Garrett. 1991. An annotated checklist of the freshwater fishes of Texas, with keys to identification of species. *Texas Journal of Science Supplement* 43:1–56.
- Jones, D. R., J. W. Kiceniuk, and O. S. Bamford. 1974. Evaluation of the swimming performance of several fish species from the Mackenzie River. *Journal of the Fisheries Research Board of Canada* 31:1641–1647.
- Kuehne, R. A. 1962. A classification of streams, illustrated by fish distribution in an eastern Kentucky creek. *Ecology* 43:608–614.
- Lee, C. G., A. P. Farrell, A. Lotto, M. J. MacNutt, S. G. Hinch, and M. C. Healey. 2003. The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *Journal of Experimental Biology* 206:3239–3251.
- Meffe, G. K. 1984. Effects of abiotic disturbance on coexistence of predator–prey fish species. *Ecology* 65:1525–1534.
- Metsker, H. E. 1970. Fish versus culverts: some considerations for resource managers. U.S. Forest Service, Engineering Technical Report ETR-7700-5 USDA, Washington, D.C.
- Minkley, W. L., and G. K. Meffe. 1987. Differential selection by flooding in stream–fish communities of the arid American Southwest. Pages 93–104 in W. J. Matthews and D. C. Heins, editors. *Community and evolutionary ecology of North American stream fishes*. University of Oklahoma Press, Norman.
- Nelson, J. A., P. S. Gotwalt, and J. W. Snodgrass. 2003. Swimming performance of blacknose dace (*Rhinichthys atratulus*) mirrors home-stream current velocity. *Canadian Journal of Fisheries and Aquatic Sciences* 60:301–308.
- Nursall, J. R. 1958. The caudal fin as a hydrofoil. *Evolution* 12:116–120.
- Ojanguren, A. F., and F. Brana. 2003. Effects of size and morphology on swimming performance in juvenile brown trout (*Salmo trutta* L.). *Ecology of Freshwater Fish* 12:241–246.
- Ourrick, C. A., and J. J. Cech. 2000. Swimming performances of four California stream fishes: temperature effects. *Environmental Biology of Fishes* 58:289–295.
- Page, L. M., and B. M. Burr. 1991. Peterson's field guide to freshwater fishes. Houghton Mifflin Company, New York.
- Parsons, G. R., and P. Smiley. 2003. The effect of environmental changes on swimming performance of the white crappie. *Journal of Freshwater Ecology* 18:89–96.
- Platania, S. P. 1991. Fishes of the Rio Chama and upper Rio Grande, New Mexico, with preliminary comments on their longitudinal distribution. *Southwestern Naturalist* 36:186–193.
- Poff, N. L., and J. D. Allan. 1995. Functional organization of

- stream fish assemblages in relation to hydrological variability. *Ecology* 76:606–627.
- SAS Institute. 2003. Statistical Analysis System, version 9.1. SAS Institute, Cary, North Carolina.
- Scarnecchia, D. L. 1988. The importance of streamlining in influencing fish community structure in channelized and unchannelized reaches of a prairie stream. *Regulated Rivers: Research and Management* 2:155–166.
- Schaarschmidt, T., and K. Jurss. 2003. Locomotory capacity of Baltic Sea and freshwater populations of the threespine stickleback (*Gasterosteus aculeatus*). *Comparative Biochemistry and Physiology Part A* 135:411–424.
- Schaefer, J. F., W. L. Lutterschmidt, and L. G. Hill. 1999. Physiological performance and stream microhabitat use by the centrarchids *Lepomis megalotus* and *Lepomis macrochirus*. *Environmental Biology of Fishes* 54:303–312.
- Schaefer, J. F., E. Marsh-Matthews, D. E. Spooner, K. B. Gido, and W. J. Matthews. 2002. Effects of barriers and thermal refugia on local movement of the threatened leopard darter, *Percina pantherina*. *Environmental Biology of Fishes* 57:1–10.
- Schlosser, I. J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. *Ecology* 66:1484–1490.
- Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. Pages 392–401 in J. L. Nielsen and D. A. Powers, editors. *Evolution and the aquatic ecosystem*. American Fisheries Society, Symposium 17, Bethesda, Maryland.
- Schultz, A. A., O. E. Maughan, and S. A. Bonar. 2003. Effects of flooding on abundance of native and nonnative fishes downstream from a small impoundment. *North American Journal of Fisheries Management* 23:503–511.
- Scott, M. K., and D. D. Magoulick. 2008. Swimming performance of five warmwater stream fish species. *Transactions of the American Fisheries Society* 137:209–215.
- Taylor, E. B., and J. D. McPhail. 1985. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon *Oncorhynchus kisutch*. *Canadian Journal of Fisheries and Aquatic Sciences* 42:2029–2033.
- Vogel, S. 1994. *Life in moving fluids*. Princeton University Press, Princeton, New Jersey.
- Ward, D. L., A. A. Schultz, and P. G. Matson. 2003. Differences in swimming ability and behavior in response to high water velocities among native and nonnative fishes. *Environmental Biology of Fishes* 68:87–92.
- Warren, M. L., Jr., and M. G. Pardew. 1998. Road crossings as barriers to small-stream fish movement. *Transactions of the American Fisheries Society* 127:637–644.
- Watson, J. M. 2006. Patterns and habitat associations of a desert spring fish assemblage and responses to a large-scale flood. Master's thesis. Texas State University–San Marcos.
- Williams, C. S. 2003. Cyprinid assemblage structure along physical, longitudinal, and seasonal gradients and life history and reproductive ecology of the Sabine shiner. Master's thesis. Texas State University–San Marcos.
- Williams, L. R., T. H. Bonner, J. D. Hudson, III, M. G. Williams, C. S. Williams, and T. R. Leavy. 2005. Interactive effects of environmental variability and military training on stream biota of three headwater drainages in western Louisiana. *Transactions of the American Fisheries Society* 134:192–206.
- Winston, M. R., C. M. Taylor, and J. Pigg. 1991. Upstream extirpation of four minnow species due to damming of a prairie stream. *Transactions of the American Fisheries Society* 120:98–105.
- Wood, B. M., and M. B. Bain. 1995. Morphology and microhabitat use in stream fish. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1487–1498.
- Zar, J. H. 1999. *Biostatistical analysis*, 4th edition. Prentice Hall, Upper Saddle River, New Jersey.