THE UNIVERSITY OF TENNESSEE KNOXVILLE

Southeastern Fishes Council Proceedings

Volume 1 | Number 63 Article 1

March 2023

Morphological Differences Align with Habitat Partitioning Among Three Species of *Percina* (Percidae: Actinopterygii) in the Roanoke River, Virginia

Michael M. Calvert
Roanoke College

Steven L. Powers
Roanoke College, powers@roanoke.edu

Recommended Citation

Calvert, Michael M. and Powers, Steven L. (2023) "Morphological Differences Align with Habitat Partitioning Among Three Species of *Percina* (Percidae: Actinopterygii) in the Roanoke River, Virginia," *Southeastern Fishes Council Proceedings*: No. 63.
https://doi.org/10.7290/sfcp63eg0a
Available at: https://trace.tennessee.edu/sfcproceedings/vol1/iss63/1

Morphological Differences Align with Habitat Partitioning Among Three Species of *Percina* (Percidae: Actinopterygii) in the Roanoke River, Virginia

Abstract

The upper Roanoke River has three species of *Percina* (*P. nevisense,* Chainback Darter; *P. roanoka,* Roanoke Darter; and *P. rex,* Roanoke Logperch). Resource partitioning appears to be a key component of maintaining diverse fish assemblages with habitat and food partitioning cited as especially important in communities containing members of the same family. Some aspects of the diets of these species have been documented in the literature with only modest differences among them. Microhabitat data for adults of these species have also been published revealing differences in habitat occupied by each with *P. roanoka* living in the fastest, shallowest water and *P. nevisense* in the deepest, slowest water. In an effort to investigate morphological features that may be adaptations to these different microhabitats, 18 body measurements were taken from specimens of each species. Fineness ratios were calculated and compared among species. Natural-log transformed raw measurements were also included in a Principal Component Analysis (PCA). Measurements that loaded heavily in the PCA were tested for differences among species. Principal component (PC) two loaded heavily for body width, body depth, and dorsal fin height, while PC three loaded heavily for anal fin length and caudal fin depth. All of these measurements were different among at least two of the three species examined. The highest mean fineness ratio and thinnest body width was found in *P. nevisense.* The lowest fineness ratio and thickest body width was found in *P. roanoka* with *P. rex* having intermediate values. A taller spinous dorsal fin is found in *P. nevisense*, and a longer anal fin was found in *P. roanoka*. *Percina rex* had the largest caudal fin and smallest anal fin.

Keywords

Percidae, darters, fineness ratio, Percina roanoka, Percina nevisense, Percina rex

Cover Page Footnote

We thank the Roanoke College Biology Department for funding to purchase equipment used in this research. We also thank Robert Jenkins, Noel Burkhead, Jesse Thompson, and other past faculty, staff, and students of Roanoke College for collection of specimens used in this study. We thank Virginia Department of Wildlife Resources for the Scientific Collection Permit used to collect recent specimens examined in this work.

INTRODUCTION

The upper Roanoke River has six species of darter including three range restricted species of *Percina* (Bugas et al., 2019). This fauna includes *Percina nevisense,* Chainback Darter (Fig. 1); *Percina rex*, Roanoke Logperch (Fig. 2); and *Percina roanoka*, Roanoke Darter (Fig. 3). Maximum sizes for adults range from 55-115 mm SL. These species are all restricted to moderate gradient streams of the central Atlantic slope and may be found within the same stream reaches in the upper Roanoke (see Jenkins and Burkhead 1994 for dot distribution maps) in close proximity to one another. In addition to having similar ranges, other ecological similarities have also been documented for these species (Hobson 1979, Jenkins and Burkhead 1994, Rosenberger and Angermeier 2003, Spruill and Powers 2019)

Figure 1. *Percina nevisense* in the Roanoke River in Salem, VA on 20 February 2017.

Figure 2. *Percina rex* in the Roanoke River in Salem, VA on 12 May 2021.

Figure 3. *Percina roanoka* in the Roanoke River in Salem, VA on 14 May 2021.

Resource partitioning appears to be a key component of maintaining diverse fish assemblages, with habitat and food partitioning cited as especially important in communities containing members of the same family (Ross 1986). The diets of these species have been documented to varying degrees with all appearing to feed largely on aquatic insects (Jenkins 1977, Hobson 1979, Lee et al. 1980, Matthews et al. 1982, Jenkins and Burkhead 1994). Despite the lack of detailed diet information for all of these species, the research available suggests they do appear to feed on similar items. Therefore, it is likely spatial habitat partitioning plays a role in their coexistence as it has been cited as especially important in structuring stream fish assemblages (Grossman and Freeman 1987, Grossman et al. 1998, Matthews 1990).

Microhabitat data for these species have been published revealing modest differences habitat occupied by adults of each species. *Percina roanoka* appears to live in the fastest, shallowest water with mean current velocity of 0.318 m/s (SD = 0.114) and mean depth of 31.53 cm (SD = 7.93) (Spruill and Powers 2019). *Percina nevisense* occupies deeper and slower habitat than *Percina roanoka* with a mean current velocity at observation points of 0.17 meters per second (SD = 0.12), and a mean depth of 60.5 cm (SD = 16.7) (Powers and Whitlow 2018). Rosenberger and Angermeier (2003) reported mean bottom velocity for microhabitats occupied by adult *Percina rex* as 0.16 m/s (SD = 0.32) with the mean velocity of the water column as 0.63 m/s (SD = 0.70). Additionally, they reported a mean depth of 52.5 cm (SD = 12.7). Mean current velocities appear nearly identical among *P. nevisense* and *P. rex* at first glance. However, the measurement of current velocity 5 cm above the substrate by Powers and Whitlow (2018) is likely not equivalent to the bottom velocity reported by Rosenberger and Angermeier (2003) as current velocity of a stream cross section is near its minimum at the bottom and increases approaching the thalweg (Dodds and Whiles 2020). *Percina nevisense* is considered a benthic species while *P. rex* is considered hyperbenthic (Near 2002) further suggesting *P. nevisense* generally is immediately surrounded by water moving slower than the water around *P. rex.* Lastly, Powers and Whitlow (2018) quantified available habitat in their study reach of the Roanoke River in Salem including current velocity, depth, and substrate size. In numerous snorkel observations within this habitat quantified reach by S.L. Powers conducted during data collection for Powers and Whitlow (2018), Spruill and Powers (2019), and frequent informal observations, the regular observation of *P. rex* in habitats intermediate in current velocity and depth to those occupied by *P. nevisense* and *P. roanoka* further suggests adult *P. rex* generally inhabits intermediate habitats to those occupied by its congeners. However, given the similarities of the habitat variables noted above, some overlap in occupied habitat does appear common among these species.

Morphological differences associated with specific microhabitats have been documented for other species. This appears to be a complex process with all interactions of morphology and microhabitats occurring within the context of selection on the entire organism leaving specific interactions of morphology and microhabitat challenging to elucidate (Domenici 2003, Langerhans et al. 2007). This suggests precise microhabitat data and precise morphological data are necessary to tease apart partitioning that allows coexistence of these ecologically and morphologically similar syntopic species. As microhabitat data are documented in the literature discussed above, the objective of this study was to examine the morphology of each of these species and test for differences among them.

METHODS

Eighteen measurements of fins and distance between homologous landmarks on the body were taken using Fowler Pro Max (No. 614624) digital calipers from specimens of each species (*Percina nevisense*, n = 27; *Percina rex*, n = 27; *Percina roanoka*, n = 28) to quantify differences in body shape that are likely associated with habitat they occupy (Fig. 4). Specimens examined for this study were not sexed and are housed in the Roanoke College Ichthyological Collection identified in Table 1.

Table 1. Specimens examined in this study housed in the Roanoke College Ichthyological Collection. All specimens were collected in Virginia. Details of locality, date, and collectors and collection numbers are from specimen jar labels. Number of specimens examined (n) and range of standard length (SL) in mm of specimens examined are included.

Species	Virginia Locality and Collection Information	n	SL in mm
P. nevisense	Roanoke Co., Roanoke R. at Greenhill Park, 21 Oct 2010, SLP 10-10	2	56.8 - 67.8
P. nevisense	Franklin Co., Blackwater R. above Rt. 122 Bridge, 3 Feb 2007, REJ 2020	2	60.0 - 68.4
P. nevisense	Roanoke Co., Roanoke R. at Greenhill Park, 27 Jun 2011, REJ 2021	2	64.7 - 67.1
P. nevisense	Franklin Co., Pigg R. below dam at Rt. 713, 17 Feb 2007, REJ 2021	1	67.8
P. nevisense	Roanoke Co., Roanoke R. at Greenhill Park, 28 Jun 2010, SLP 10-15	1	73.4
P. nevisense	Franklin Co., Blackwater R., Don Riddle cabin, 26 Jan 2008, REJ 2026	4	52.2 - 73.4
P. nevisense	Franklin Co., Blackwater R. at Hwy 122, 16 Apr 2012, SLP 12-03	1	68.9
P. nevisense	Franklin Co., Snow Cr. at Laprade Mill, Rt. 858, 26 Jan 2008, REJ 2027	14	47.4 - 68.0
P. roanoka	Roanoke Co., Roanoke R. near and in Salem, collection date unknown	18	43.9 - 59.3
P. roanoka	Craig Co., Craig Cr. near Newcastle at Olds farm, 6 Sep 1982, REJ 954	10	44.2 - 61.2
P. rex	Roanoke Co., NF Roanoke R. at Ironto, 27 Mar 1981, NMB 532	1	118.5
P. rex	Roanoke Co., Roanoke R. near Rt. 612, 16 Apr 1982, NMB 739	3	84.2 - 114.0
P. rex	Roanoke Co., Roanoke R. off Rt. 639 5 Nov 1981, NMB 670	3	81.6 - 103.6
P. rex	Montgomery Co., SF Roanoke R. at Bonys Run, 16 Sep 1983, REJ 1039	4	88.3 - 100.8
P. rex	Pittsylvania Co., Leesville Reservoir, 24 Aug 1989, Mike Duval	1	102.9
P. rex	Montgomery Co., SF Roanoke R. at Bonys Run, 21 Sep 1968, REJ 297	4	94.4 - 98.8
P. rex	Salem City, Roanoke R. at Eddy St. bridge, 28 Mar 1982, NMB 722	2	103.6 - 103.7
P. rex	Montgomery Co., SF Roanoke R. at Bonys Run, 4 Oct 1982, REJ 956	1	102.5
P. rex	Salem City, Roanoke R. at 419 bridge in Salem, 25 Jun 1980, NMB 514	1	101.2
P. rex	Montgomery Co., SF Roanoke R. at Bonys Run, 30 Apr 1972, REJ 735	4	91.2 - 106.3
P. rex	Roanoke Co., Roanoke R. at Rt. 639 bridge, 28 March 1981, NMB 533	1	106.2
P. rex	Roanoke Co., Roanoke R. at Rt. 639 bridge, 14 April 1982, WHH 47	2	99.4 - 101.0

Measurements examined (with corresponding landmarks as noted in Fig. 4) were standard length (1–18), snout tip to origin of dorsal fin l (1–2), snout tip to origin of pelvic fin (1–4), spinous-dorsal fin origin to pelvic fin origin (2–4), pectoral fin length (3–7), width at pectoral fin (3–3), length of spinous-dorsal fin base (2–8), height of spinous dorsal fin (5–6), pelvic fin length (4–9), body depth (8–10), body width (maximum width below 8), length of soft-dorsal fin base (8–15), ventral caudal peduncle length (16–19), soft dorsal fin height (13–14), length of anal fin (11–12), depth of caudal peduncle (17–19), length of caudal fin (17–20), depth of caudal fin (20–21).

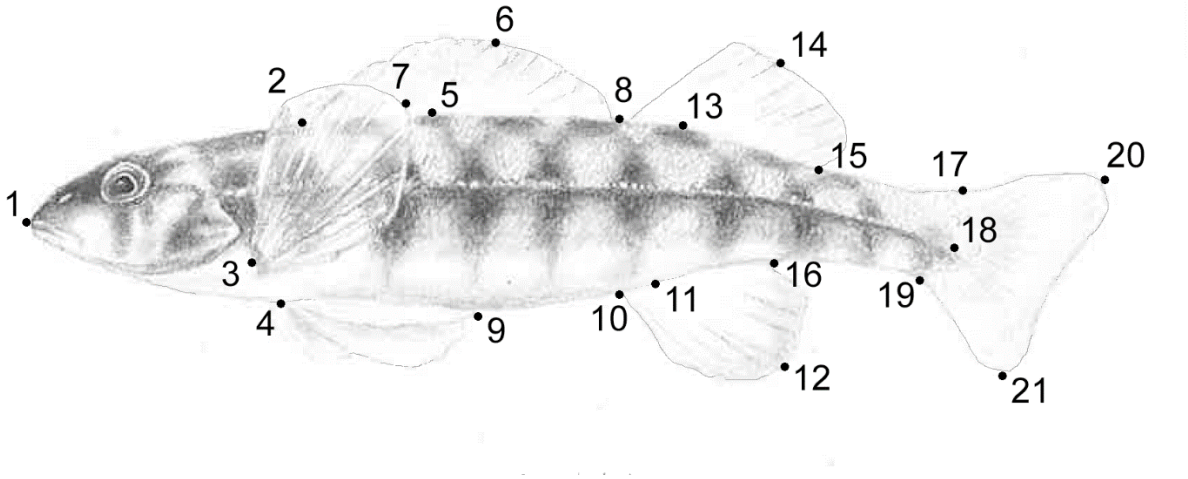

Figure 4. Landmarks used to take 18 standard and truss measurements from *Percina nevisense* (n = 27), *P. rex* (n = 27), and *P. roanoka* (n = 28) to quantifying morphological differences among species. Illustration by Charlotte Spaulding.

Following Armbruster and Page (1996), the 18 raw measurements were natural-log transformed in Excel 2016, and a principal component (PC) analysis of those transformed data was performed in Minitab 19 (Minitab LLC. State College, Pennsylvania) to quantify differences in shape of the species examined in this study. A correlation matrix was use in the PCA. Scatterplots of PC 2 and PC 3 scores were made in Minitab 19 and examined for morphological divergence among the species. Body measurements with absolute loading values > 0.3 were noted as most influential on PC scores and are labeled on Figure 5 and addressed in Results. All loading values for PC 2 and PC 3 are reported in Table 2. Body measurements that loaded heavily on PC 2 and PC 3 were further investigated for statistical differences among the species investigated. Fineness ratio was calculated for each specimen by the following formula (SL/body depth). Body width, dorsal fin height, anal fin length, and caudal fin depth are compared among species as a proportion of SL following Jenkins and Burkhead (1994). Fineness ratios, body width, dorsal fin height, anal fin length, and caudal depth among species were compared with Welch's ANOVA (alpha = 0.05) as it does not assume equal variance of samples. All statistical analyses and interval plots were done using Minitab 19.

RESULTS

Principal component 1 had nearly uniform loadings with all variables between 0.22 and 0.242. As noted in Armbruster and Page (1996), PC 1 captures size variation of specimens and accounted for 92.4% of the variation in our data, leaving PC 2 and PC 3 as functions of shape differences among the specimens examined accounting for 2.3% and 1.5% of the variation in the data, respectively. Figure 5 further illustrates the influence of size on PC 1 noting that *Percina rex* examined were 81.6-118.5 mm SL, *P. nevisense* were 47.4-73.4 mm SL, *P. roanoka* were 43.9-61.2 mm SL (Table 1).

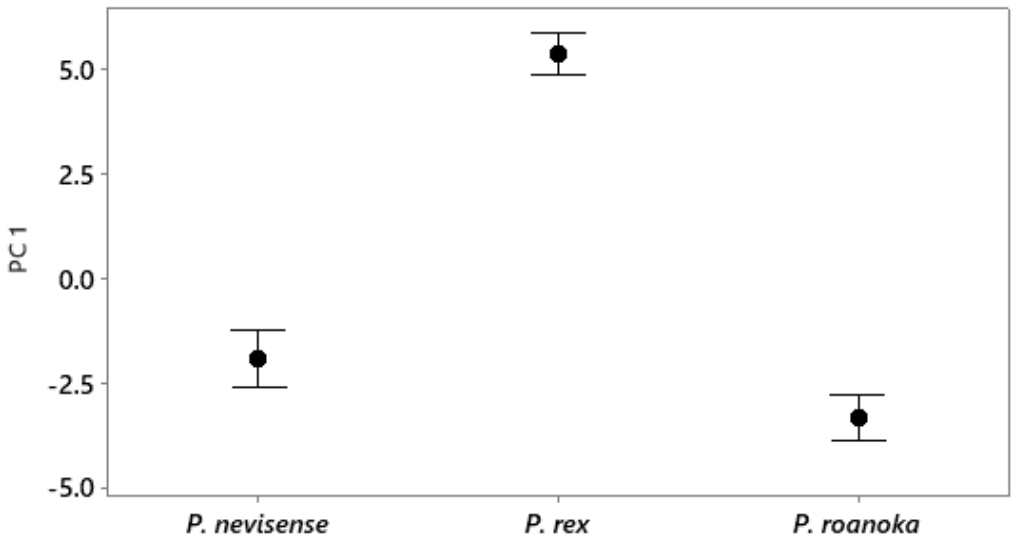

Figure 5. Plot of 95% confidence intervals of mean PC 1 scores of *Percina nevisense* (47.4-73.4 mm SL), *P. rex* (81.6-118.5 mm SL), and *P. roanoka* (43.9-61.2 mm SL).

In the multivariate analysis of body shape, loadings of all variables on PC 2 and PC 3 are presented in Table 2. Of note, PC 2 loaded heavily for body width below junction of dorsal fins (maximum width below 8 in Fig. 4) (-0.54), spinous dorsal fin height (5–6 in Fig. 4) (0.49), and body depth (8–10 in Fig. 4) (-0.42). Principal component three loaded heavily for anal fin length (11–12 in Fig. 4) (0.68) and caudal fin depth (20–21 in Fig. 4) (0.40). As a result, these measurements were investigated further for statistical differences among species.

Table 2. Measurements used in the principal component (PC) analysis of body shape of *Percina nevisense*, *P. roanoka*, and *P. rex* and the loadings of each for PC 2 and PC 3.

Measurement in PCA	Loading on PC2	Loading on PC3
standard length (1-18)	0.112	-0.198
snout tip to origin of dorsal fin l (1-2)	0.152	-0.229
snout tip to origin of pelvic fin (1-4)	0.014	-0.149
spinous-dorsal fin origin to pelvic fin origin (2-4)	-0.117	-0.060
pectoral fin length (3-7)	-0.008	0.035
width at pectoral fin (4-9)	-0.102	0.118
spinous dorsal fin height (5-6)	0.485	-0.002
length of spinous-dorsal fin base (2-8)	0.069	-0.227
body depth (8-10)	-0.417	0.146
length of soft-dorsal fin base (8-15)	0.183	-0.239
anal fin length (11-12)	0.189	0.678
soft dorsal fin height (13-14)	0.212	0.196
ventral caudal peduncle length (16-19)	-0.085	-0.104
depth of caudal peduncle (17-19)	-0.234	0.088
length of caudal fin (17-20)	0.203	-0.175
caudal fin depth (20-21)	0.016	0.404
width at pectoral fin (3-3)	-0.125	-0.149
body width (max below 8)	-0.541	-0.070

The scatterplot of PC 2 and PC 3 reveal that *Percina nevisense* has minimal overlap with *P. rex* or *P. roanoka* with the former generally having higher PC 2 scores and lower PC 3 scores than the latter two. There is low to moderate overlap among *P. rex* and *P. roanoka* with *P. rex* having generally higher PC 2 and lower PC 3 scores than *P. roanoka* (Fig. 6).

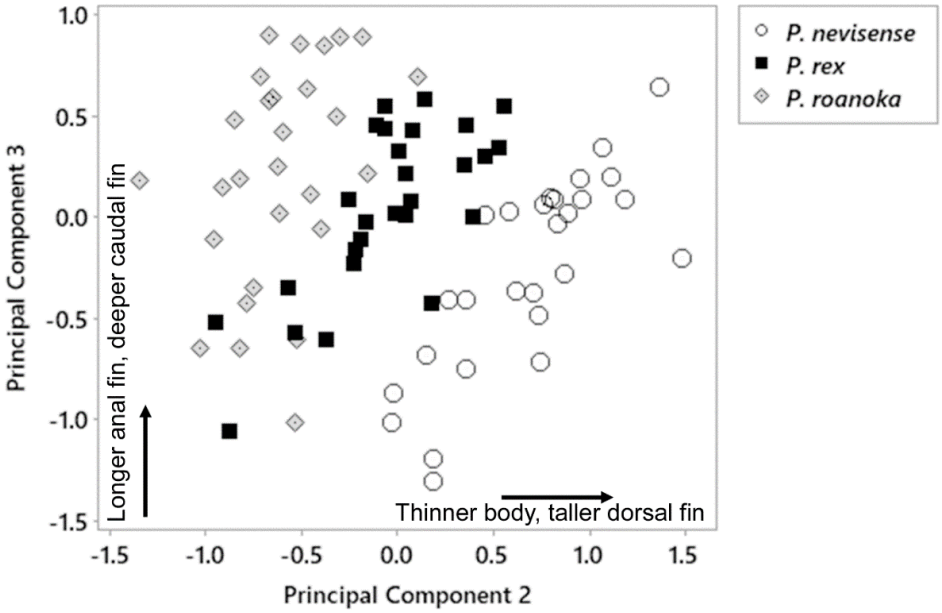

Figure 6. Scatterplot of Principal Component (PC) scores of 18 natural-log transformed body measurements of *Percina nevisense* (n = 27), *P. rex* (n = 27), and *P. roanoka* (n = 28).

Mean fineness ratios (Fig. 7) were not equal among species ($P < 0.001$) with the highest mean fineness ratio of 7.13 (SE = 0.06) found in *Percina nevisense*. The lowest mean fineness ratio of 5.38 (SE = 0.07) was found in *P. roanoka*. An intermediate mean fineness ratio of 6.34 (SE = 0.08) was found in *P. rex*.

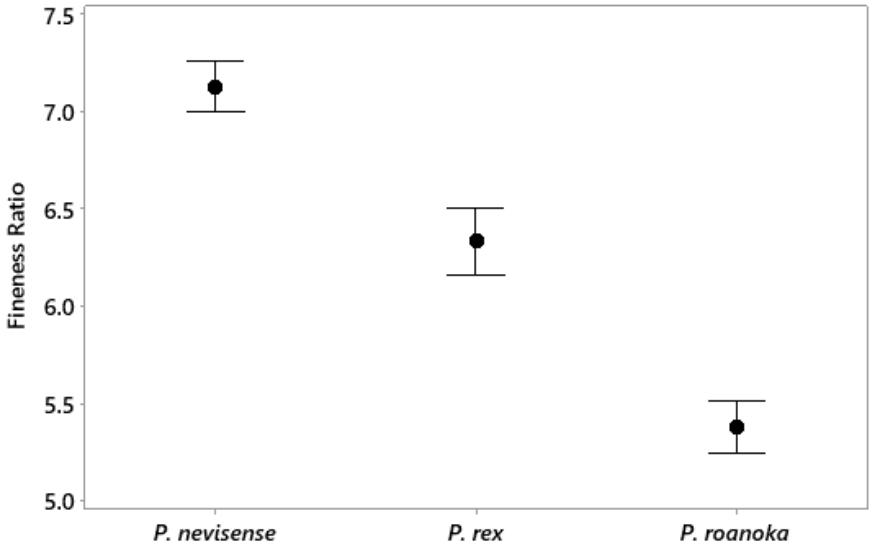

Figure 7. Plot of 95% confidence intervals of mean fineness ratio of *Percina nevisense* (n = 27), *P. rex* (n = 27), and *P. roanoka* (n = 28).

Mean body widths as a proportion of SL (Fig. 8) were not equal among species ($P < 0.001$) with the lowest body width of 0.083 (SE = 0.002) found in *Percina nevisense*. The highest mean body width of 0.114 (SE = 0.002) was found in *P. roanoka*. An intermediate mean body width of 0.098 (SE = 0.002) was found in *P. rex*.

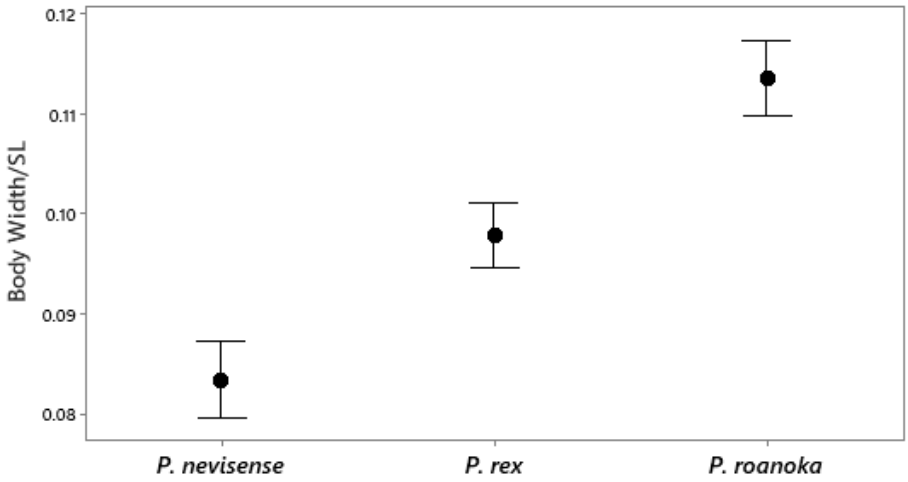

Figure 8. Plot of 95% confidence intervals of body width as proportion of SL of *Percina nevisense* (n = 27), *P. rex* (n = 27), and *P. roanoka* (n = 28).

Mean dorsal fin heights as a proportion of SL (Fig. 9) were not equal among species ($P < 0.001$) with the lowest dorsal fin height of 0.077 (SE = 0.002) found in *Percina rex*. The highest mean dorsal fin height of 0.090 (SE = 0.002) was found in *P. nevisense.* An intermediate mean dorsal fin height of 0.085 (SE = 0.002) was found in *P. roanoka*.

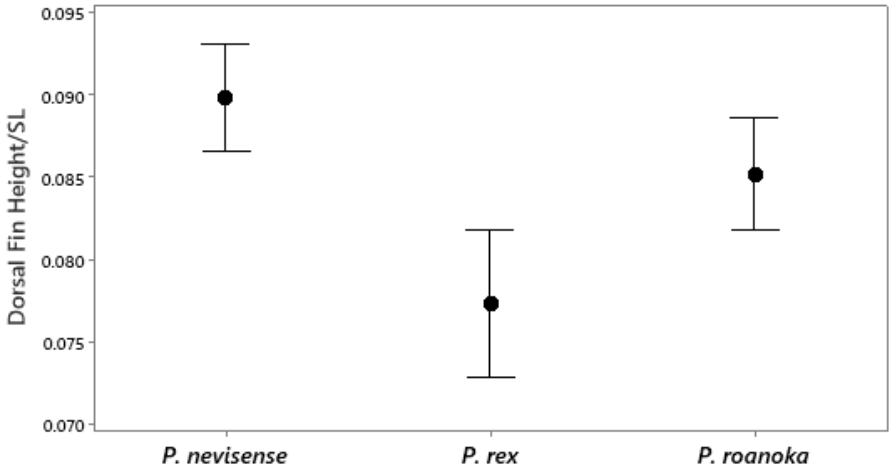

Figure 9. Plot of 95% confidence intervals of dorsal fin height as a proportion of SL of *Percina nevisense* (n = 27), *P. rex* (n = 27), and *P. roanoka* (n = 28).

Mean anal fin lengths as a proportion of SL (Fig. 10) were not equal among species ($P < 0.001$) with the highest anal fin length of 0.113 (SE = 0.003) found in *Percina roanoka*. The lowest mean anal fin length of 0.092 (SE = 0.002) was found in *P. rex.* An intermediate mean anal fin length of 0.099 (SE = 0.003) was found in *P. nevisense*.

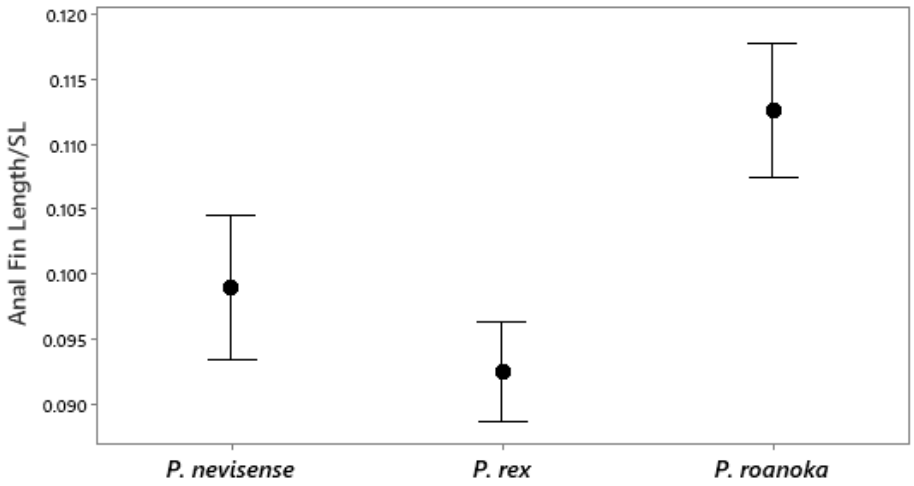

Figure 10. Plot of 95% confidence intervals of anal fin length as a proportion of SL of *Percina nevisense* (n = 27), *P. rex* (n = 27), and *P. roanoka* (n = 28).

Mean caudal fin depths as a proportion of SL (Fig. 11) were not equal among species ($P < 0.001$) with the highest caudal fin depth of 0.213 (SE = 0.004) found in *Percina rex*. The lowest mean caudal fin depth of 0.177 (SE = 0.005) was found in *P. nevisense.* An intermediate mean caudal fin depth of 0.195 (SE = 0.007) was found in *P. roanoka*.

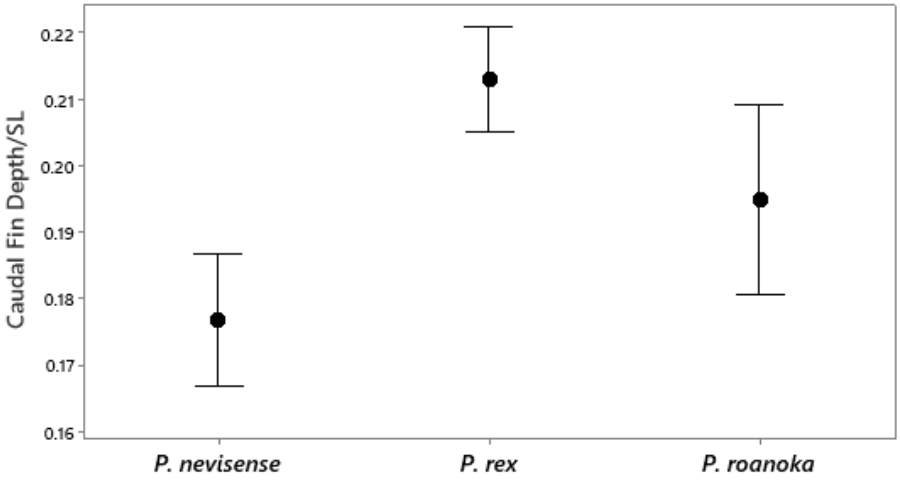

Figure 11. Plot of 95% confidence intervals of caudal fin depth as a proportion of SL of *Percina nevisense* (n = 27), *P. rex* (n = 27), and *P. roanoka* (n = 28).

DISCUSSION

The minimal to moderate overlap of the polygons formed by each of these species in Figure 6 indicate morphological differences among them in a coarse examination of their body shapes. More detailed analyses of these morphological differences further illustrate their contrasting morphologies as there are statistical differences among at least two of the three species for all five of the variables compared with ANOVA. These morphological differences appear to be associated with some of the habitat differences documented in Rosenberger and Angermeier (2003), Powers and Whitlow (2018), and Spruill and Powers (2019).

With a mean fineness ratio of 5.38, *Percina roanoka* appears to be the closest of the three species to 4.5 which is generally considered the optimum for endurance swimming (Webb 1975, Walker et al. 2013). As these fast waters inhabited by *P. roanoka* likely exert strong selective pressures on body shape, it is not surprising *P. roanoka* most closely resembles this optimally efficient body shape. The highest mean fineness ratio among species examined was in *P. nevisense* which appears to inhabit the slowest water of the *Percina* found in the upper Roanoke River. Higher fineness ratios are common in fishes utilizing burst-and-coast swimming patterns (Chung 2009). The coast phase of burst-and-coast swimming can result in substantial energetic savings over continuous swimming (Videler and Weihs 1982, Wu et al. 2007). This energetic savings appears greatest when fish are swimming at less than maximum speeds (Videler and Weihs 1982), and therefore would be expected to maximize efficiency while swimming in slower currents like those inhabited by *P. nevisense*. Walker et al. (2013) further illustrated slender bodies and higher fineness ratios likely maximize the reduction in drag in laminar flows and transitional flows while more robust bodies provide optimal hydrodynamic efficiency in more turbulent flows. Given the highly turbulent waters in the riffle habitat inhabited by *P. roanoka* and the slower and likely more transitional flows occupied by *P. nevisense*, the more elongate body of the latter may help maximize the conservation of energy while swimming at less than maximum speed in the slower water it inhabits. A similar pattern of higher fineness ratios of fishes associated with slower water was recently noted in Powers and Spruill (2021). Page (1983) also documented deeper bodies in riffle dwelling darter species in comparison to those living in slower water habitats. Cyprinidae also show a similar pattern with Langerhans et al. (2007) documenting a more fusiform body associated with increased water flows. Body widths also show a similar pattern to fineness ratios with *P. roanoka* having the thickest body, *P. nevisense* the thinnest, and *P. rex* intermediate further illustrating the trend of more robust bodies in faster water currents.

Additionally, the highest dorsal fin height of *P. nevisense* compared to *P. rex* and *P. roanoka* appears to reflect adaption to the current velocities they inhabit. A similar pattern was documented by Istead et al. (2015) finding dorsal fins in Centrarchidae reduced by faster flowing water. Brinsmead and Fox (2002) also found larger fins in Centrarchidae in lake environments than in streams. The smaller dorsal fin of the faster water inhabitant *P. roanoka* likely reduces drag helping it swim more efficiently. The smallest dorsal fin of the species examined found in *P. rex* does not fit this pattern but this may not be surprising due to the use of a wide range of habitats as documented by Rosenberger and Angermeier (2003). Additionally, *P. rex* is unique among these species as hyperbenthic (Near 2002). As current velocity generally increases with distance from the substrate (Dodds and Whiles 2020), the smaller dorsal fin may aid in that increased current.

The longer anal fin length of *Percina roanoka*, the species found in the fastest water, may be used to hold station. Matthews (1985) suggested the larger paired fins of *P. roanoka* allow for better grasping of the substrate than those of *Etheostoma flabellare*, Fantail Darter which has a lower critical current speed and thus is likely adapted to the slower currents they inhabit (Matthews et al. 1982). As the anal fin also contacts the substrate in benthic, riffle dwelling darters, increased size of this structure may provide an increased contact with the substrate thus helping *P. roanoka* conserve energy in the faster waters it inhabits in comparison to the those inhabited by its congeners in the upper Roanoke River. While *P. rex* has the smallest anal fin length of the species examined in this study despite being found in generally intermediate currents, it is also the only one of these species categorized as hyperbenthic rather than benthic (Near 2002). Therefore, an enlarged anal fin would not be beneficial to holding station, but would likely increase drag.

The smaller caudal fin depth of *P. nevisense* is also consistent with living in slower current. Greater caudal fin depths in *P. roanoka* and *P. rex* likely help them swim more effectively in the challenging environment of faster waters. The greatest caudal depth in *P. rex* may also be attributed to its nature as a hyperbenthic species (Near 2002) as current velocity increases with distance from the substrate (Dodds and Whiles 2020). Langerhans (2008) proposed a model of phenotypic differences of fishes with higher flows corresponding to higher aspect ratio caudal fins as an adaptation to swimming in those faster waters. Fast currents are likely especially influential on morphology and even fish assemblages as a whole with less hydrodynamically efficient species being completely absent from habitats with especially fast currents (Scarnecchia 1988).

As it appears there is greater similarity in habitat for *Percina nevisense* and *P. rex* (Rosenberger and Angermeier 2003, Powers and Whitlow 2018) than the habitat occupied by *P. roanoka* (Spruill and Powers 2019), we should expect a greater similarity in fineness ratios among *P. nevisense* and *P. rex.* The difference among *P. nevisense* and *P. rex* is smaller than the difference in fineness ratios of *P. rex* and *P. roanoka*. A similar but very slight difference in body width among the three species further suggests the adaptive nature of their body shapes. The amount of overlap in the scatterplots of PC 2 and PC 3 scores does not, however show this same pattern. *Percina nevisense* has no overlap with *P. rex* or *P. roanoka*, but there is some overlap among *P. rex* and *P. roanoka* in the scatterplot presented in Figure 5. Additionally, the fins of *P. rex* do not appear to be intermediate in size among these species (Figs. 9-11). The lack of intermediacy in *P. rex* for these characters may be attributed to the wide variety of habitats inhabited by *P. rex* as noted by Rosenberger and Angermeier (2003). Additionally, *P. rex* is unique among these species as a hyperbenthic rather than benthic species (Near 2002) likely causing it to interact with its environment somewhat differently than its syntopic congeners. The larger maximum size and hyperbenthic nature of *P. rex* may also mean it is less likely to experience the boundary layer escape from current noted by Carlson and Lauder (2011) further complicating how these three species interact with one another and their environments. As suggested by Domenici (2003) and Langerhans et al. (2007), the interactions between morphology and habitat are complex with selection working on individuals within the context of behavior and physiological characteristics where different taxonomic groups are likely to display different trends. Therefore, it is not surprising that our data show a mosaic pattern of relationships between divergent morphologies and the habitats each species occupies.

The differences in morphology documented here, the divergent habitats with which *P. nevisense, P. rex,* and *P. roanoka* are associated (Rosenberger and Angermeier 2003, Powers and Whitlow 2018, Spruill and Powers 2019), and the modest diet differences among them (Jenkins 1977, Hobson 1979, Lee et al. 1980, Matthews et al. 1982, Jenkins and Burkhead 1994) likely contribute to their resource partitioning and the maintenance of the diverse assemblage of *Percina* in the upper Roanoke River drainage consistent with the summary of other taxa provided by Ross (1986). Future study using more detailed habitat data collected with consistent methods within the same reach of stream at the same time may help provide greater clarity on this topic. As there is minimal published information on the diets of these species, greater work in this area would also likely be helpful in elucidating how these species persist and interact in the upper Roanoke River.

LITERATURE CITED

Armbruster, J.W., and L.M. Page. 1996. Redescription of *Aphanotorulus* (Teleostei: Loricariidae) with the description of one new species, *A. ammophilus*, from the Rio Orinoco Basin. *Copeia* 1996:379-389.

Brinsmead, J., and M.G. Fox. 2002. Morphological variation between lake- and stream-dwelling rock bass and pumpkinseed populations. Journal of Fish Biology 61:1619-1638.

Bugas, P.E., Jr., C.D. Hilling, V. Kells, M.J. Pinder, D.A. Wheaton, and D.J. Orth. 2019. Field guide to the freshwater fishes of Virginia. Johns Hopkins University Press. Baltimore, Maryland.

Carlson, R.L. and G.V. Lauder. 2011. Escaping the flow: boundary layer use by the darter *Etheostoma tetrazonum* (Percidae) during benthic station holding. Journal of Experimental Biology 214:1181-1193.

Chung, M-H. 2009. On burst-and-coast swimming performance in fish-like locomotion. Bioinspiration & Biomimetics 4:036001

Dodds, W.K., and M. Whiles. 2020. Freshwater Ecology: Concepts and Environmental Applications of Limnology. Third Edition. Academic Press. San Diego, California.

Domenici, P. 2003. Habitat, body design and the swimming performance of fish. *In:* Vertebrate Biomechanics and Evolution. V.L. Bels, J.P. Gase and A. Casinos. Eds. BIOS Scientific Publishers Ltd. Oxford, England.

Grossman, G.D., and M.C. Freeman. 1987. Microhabitat use in a stream fish assemblage. Journal of Zoology 212:151-176.

Grossman, G.D., Ratjczak, R.E., Jr., Crawford, M., and M.C. Freeman. 1998. Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. Ecological Monographs 68:396-420.

Hobson, J.F. 1979. Life history aspects of a percid fish, *Percina crassa roanoka*, the piedmont darter. Bios 3:148-157.

Istead, A.E., S. Yavno, and M.G. Fox. 2015. Morphological change and phenotypic plasticity in response to water velocity in three species of Centrarchidae. Canadian Journal of Zoology 93:879-888.

Jenkins, R.E. 1977. Roanoke Logperch, *Percina rex* (Jordan and Evermann) 1889. Status Report to the Office of Endangered Species, U.S. Fish and Wildlife Service, Washington, D.C.

Jenkins, R.E., and N.M. Burkhead. 1994. Freshwater Fishes of Virginia. American Fisheries Society. Bethesda, Maryland.

Lee, D.S., C.R. Gilbert, C.H. Hocutt, R.E. Jenkins, D.E. McCallister, and J.R. Stauffer. 1980. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh, North Carolina.

Langerhans, R.B., L.J. Chapman, and T.J. DeWitt. 2007. Complex phenotype-environment associations revealed in an East African cyprinid. Journal of Evolutionary Biology 20:1171-1181.

Langerhans, R.B. 2008. Predictability of Phenotypic Differentiation across Flow Regimes in Fishes. Integrative and Comparative Biology 48(6):750-768.

Matthews, W.J. 1985. Critical current speeds and microhabitats of the benthic fishes *Percina roanoka* and *Etheostoma flabellare*. Environmental Biology of Fishes 12:303-308.

Matthews, W.J. 1990. Spatial and temporal variation in fishes of riffle habitats: a comparison of analytical approaches for the Roanoke River. The American Midland Naturalist 124:31-45.

Matthews, W.J., J.R. Bek, and E. Surat. 1982. Comparative ecology of the darters *Etheostoma podostemone*, *E. flabellare* and *Percina roanoka* in the upper Roanoke River drainage, Virginia. *Copeia* 1982:805-814.

Near, T.J. 2002. Phylogenetic relationships of *Percina* (Percidae: Etheostomatinae). *Copeia* 2002:1-14.

Page, L.M. 1983. Handbook of Darters. T.F.H. Publications, Neptune City, New Jersey.

Powers, S.L. and P. Whitlow. 2018. Microhabitat of the Chainback Darter, *Percina nevisense* (Actinopterygii: Percidae) in the upper Roanoke River in Salem, VA. *Banisteria* 50:10-14

Powers, S.L., and D.R. Spruill. 2021. Habitat Partitioning and Associated Morphological Differences Among Three Species of Catostomidae (Teleostei: Actinopterygii) in the South Fork Roanoke River, Virginia. Virginia Journal of Science 72:1-11.

Rosenberger, A. and P.L. Angermeier. 2003. Ontogenetic shifts in habitat use by the endangered Roanoke Logperch (*Percina rex*). Freshwater Biology 48:1563-1577.

Ross, S.T. 1986. Resource partitioning in fish assemblages: a review of field studies. *Copeia* 1986:352-388.

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.

Spruill, D.R., and S.L. Powers. 2019. Microhabitat Comparison of *Percina roanoka* (Roanoke Darter) and *Percina nevisense* (Chainback Darter) in the Roanoke River. Virginia Journal of Science 70:1-7.

Videler, J.J., and D. Weihs. 1982. Energetic advantage of burst-and-coast swimming of fish at high speeds. Journal of Experimental Biology 97:169-178.

Walker, J.A., M.E. Alfaro, M.M. Noble, and C.J. Fulton. 2013. Body fineness ratio as a predictor of maximum prolonged-swimming speed in coral reef fishes. PLoS ONE 8(10): e75422.

Webb, P.W. 1975. Hydrodynamics and energetics of fish propulsion. Bulletin of Fisheries Research Board of Canada 190:1-158.

Wu, G., Y. Yang, and L. Zeng. 2007. Kinematics, hydrodynamics and energetic advantages of burst-and-coast swimming of koi carps (*Cyprinus carpio* koi). Journal of Experimental Biology 210:2181-2191.