Habitat Partitioning and Associated Morphological Differences Among Three Species of Catostomidae (Teleostei: Actinopterygii) in the South Fork Roanoke River, Virginia

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ABSTRACT

The upper Roanoke River has 11 species of Catostomidae including *Moxostoma ariommum,* Bigeye Jumprock; *Moxostoma cervinum,* Blacktip Jumprock; and *Thoburnia rhothoeca,* Torrent Sucker. 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. The diets of these species have been documented in previous work revealing only modest differences among them. Snorkeling observations and subsequent quantification of microhabitat were conducted to illuminate habitat partitioning among these morphologically and ecologically similar species. *Thoburnia rhothoeca* inhabited the shallowest, fastest water, over the smallest substrate, and *Moxostoma ariommum* inhabited the deepest, slowest water, over the largest substrate, with *M. cervinum* intermediate for all habitat variables. In an effort to correlate morphological adaptations to these different microhabitats, 22 body measurements were included in a Principal Component Analysis revealing a bigger eye for *M. ariommum* and more fusiform bodies for *T. rhothoeca* and *M. cervinum* consistent with findings in other species inhabiting faster waters. Other correlations among morphology and microhabitat were less clear.

Keywords: *Moxostoma, Thoburnia,* suckers, snorkel observations

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INTRODUCTION

The upper Roanoke River has 11 species of Catostomidae including several highly range restricted species (Bugas et al., 2019). This diverse fauna includes *Moxostoma ariommum,* Bigeye Jumprock; *Moxostoma cervinum,* Blacktip Jumprock; and *Thoburnia rhothoeca,* Torrent Sucker. These species are all less than 200 mm standard length and restricted to small or medium sized high to moderate gradient streams of the central Atlantic slope. They can also 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 including the same seine haul (S.L. Powers, personal observation). In addition to having similar ranges and habitats, other ecological similarities have been documented for these species (Jenkins and Burkhead, 1994; Tarasidis and Powers, 2014; Thompson et al., 2015)

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 in previous work with *T. rhothoeca* feeding mostly on detritus and Chironomidae, but also feeding on other Diptera as well as Ephemeroptera and Trichoptera (Tarasidis and Powers, 2014). *Moxostoma cervinum* feed largely on Chironomidae, while also ingesting Ephemeroptera, Trichoptera, and Acari (Thompson et al., 2015). *Moxostoma ariommum* have a varied diet including Ephemeroptera, Trichoptera, and other Diptera in addition to large numbers of Chironomidae (Jenkins and Burkhead, 1994). As these differences in diet are modest, it is unlikely they alone are responsible for the resource partitioning allowing the coexistence of these species in small streams like the South Fork Roanoke River. Habitat partitioning has been cited as especially important in structuring stream fish assemblages (Grossman and Freeman, 1987, Grossman et al., 1998).

While the diets of these species have been documented in previous studies, detailed investigations into their specific microhabitats are largely lacking. Additionally, investigations of morphological adaptation to specific microhabitats facilitating this partitioning is completely lacking for these species. Morphological changes associated with specific microhabitats have been documented for other species, but 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 accompanied by precise morphological data are necessary to tease apart partitioning that allows coexistence of these ecologically and morphologically similar syntopic species. Therefore, the objective of this study was to examine the microhabitat and morphology of each species for evidence of resource partitioning and morphological adaptation to their specific microhabitats.

METHODS

Snorkeling observations occurred from 2018 to 2020 in June and July to quantify microhabitat of each species. The study site was in the South Fork Roanoke River in Montgomery County, VA 7.6 km SSE of Shawsville upstream of Allegheny Springs Road near Camp Alta Mons

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(37° 06' 03.04" N, 80° 14' 59.29" W). At this locality, the stream is less than 15 m wide with maximum depth less than 1.5 m at normal summer flows. All observations were made with flows between 50 and 100 cubic feet per second on the stream flow gauge (Station Number 02053800) maintained by the United States Geologic Survey on the South Fork Roanoke River near Shawsville, VA (https://waterdata.usgs.gov/va/nwis/current/?type=flow). In addition to avoiding high flows, periods of high turbidity were also avoided for snorkeling due to difficulty in observation of study species and subsequent data collection.

Observation and subsequent habitat data collection followed Spruill and Powers (2019). Snorkeling observations were made moving downstream. Data were collected for all three species on the same days. At the point of first sighting of an individual of each target species, a 5 cm diameter galvanized steel marker numbered and painted fluorescent green was placed on the substrate. At each marker, water depth and the diameter of five representative rocks within 10 cm of the marker were measured with a meter stick. Bedrock greater than 1 m across was recorded as 100 cm. The identification of the target species and all habitat data were recorded on a dive slate. Current velocity approximately 5 cm above the substrate was measured with a JDC Electronics FloWatch FW450 flowmeter. For depth and velocity, a total of 30, 35, and 36 observations were made for *M. ariommum, M. cervinum,* and *T. rhothoeca,* respectively. For substrate, the diameters of the five representative rocks at each observation point were summed and divided by five to find the mean value for substrate diameter. That mean value for each observation point was used for analyses. No attempt was made to quantify all available habitat. Equal variances were not assumed for habitat data, therefore a Welch's one-way analysis of variance (ANOVA) was conducted to test for differences in occupied habitat among species for each measured habitat variable with alpha levels of 0.05. Minitab 19 (Minitab LLC. State College, Pennsylvania) was used to calculate descriptive statistics, statistical analyses, and generate interval plots.

Twenty-two measurements were taken using Fowler Pro Max (No. 614624) digital calipers from specimens (n = 10) of each species to quantify differences in body shape (Fig. 1). Fineness ratio was calculated for each specimen by dividing standard length (SL) by the body depth at the dorsal fin origin. Fineness ratios among species were compared with a Welch's ANOVA. Following Armbruster and Page (1996), the 22 raw measurements were natural-log transformed in Excel 2016, and a principal component (PC) analysis of those transformed data was performed in Minitab 19 to quantify differences in shape of the species. Size variation of specimens was accounted for in PC 1, leaving PC 2 and PC 3 as functions of shape differences. Scatterplots of PC 2 and PC 3 scores were examined for morphological differences among the species. Body measurements with absolute Eigenvector values of > 0.3 were considered especially influential on PC scores and are reported after the measurements in Results.

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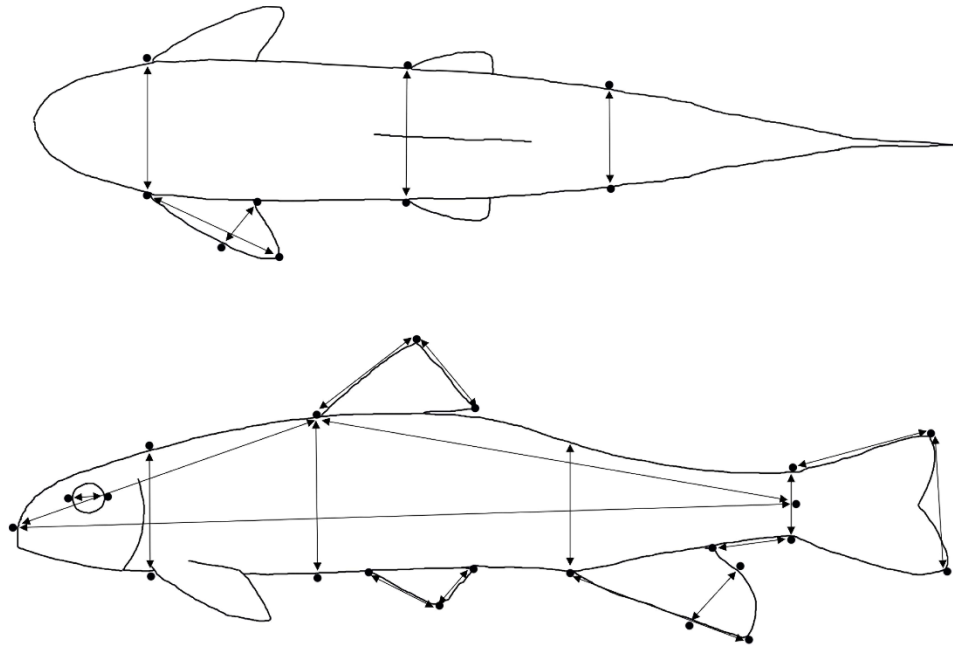
FIGURE 1: Twenty-two measurements taken from *Moxostoma ariommum*, *M. cervinum*, and *Thoburnia rhothoeca* for the principal component analysis quantifying morphological differences among species.
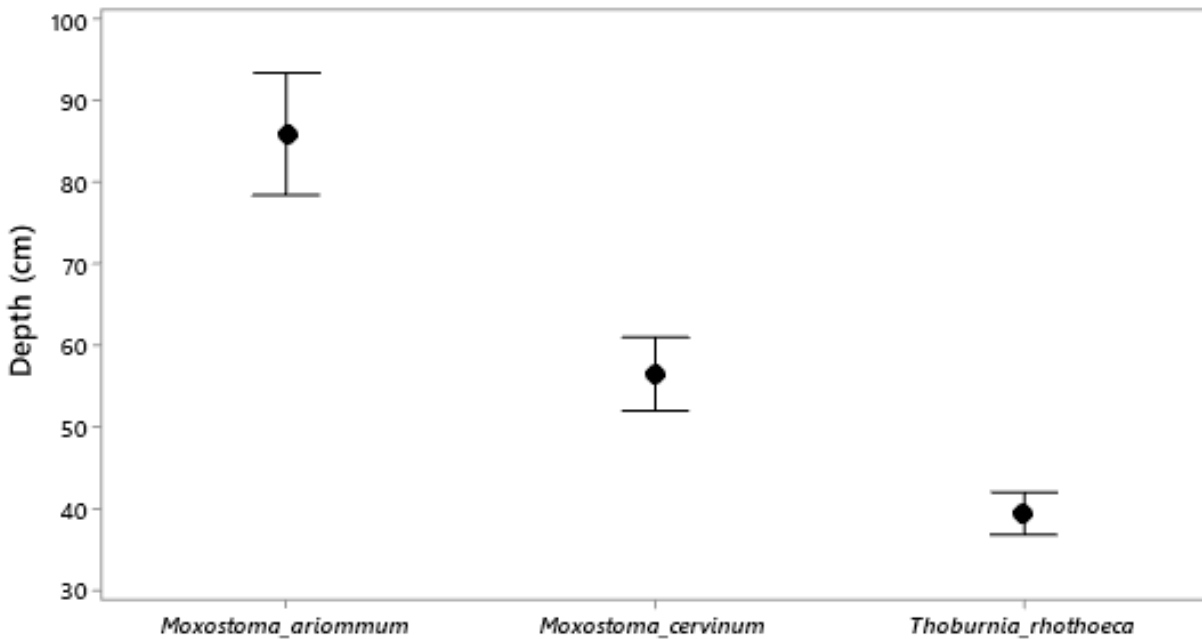
RESULTS

Current velocity was not equal among species (P < 0.001; mean for *Moxostoma ariommum* = 0.18 m/s, SE = 0.02; mean for *Moxostoma cervinum* = 0.25 m/s, SE = 0.02; mean for *Thoburnia rhothoeca* = 0.54 m/s, SE = 0.03; Fig. 2). Depth of water observed in was not equal among species (P < 0.001; mean for *Moxostoma ariommum* = 85.93 cm, SE = 3.67; mean for *Moxostoma cervinum* = 56.51 cm, SE = 2.22; mean for *Thoburnia rhothoeca* = 39.4 cm, SE = 1.28; Fig. 3). Substrate size also was not equal among species (P < 0.001; mean for *Moxostoma ariommum* = 39.07 cm, SE = 5.71; mean for *Moxostoma cervinum* = 14.95 cm, SE = 1.66; mean for *Thoburnia rhothoeca* = 9.9 cm, SE = 0.69; Fig. 4).
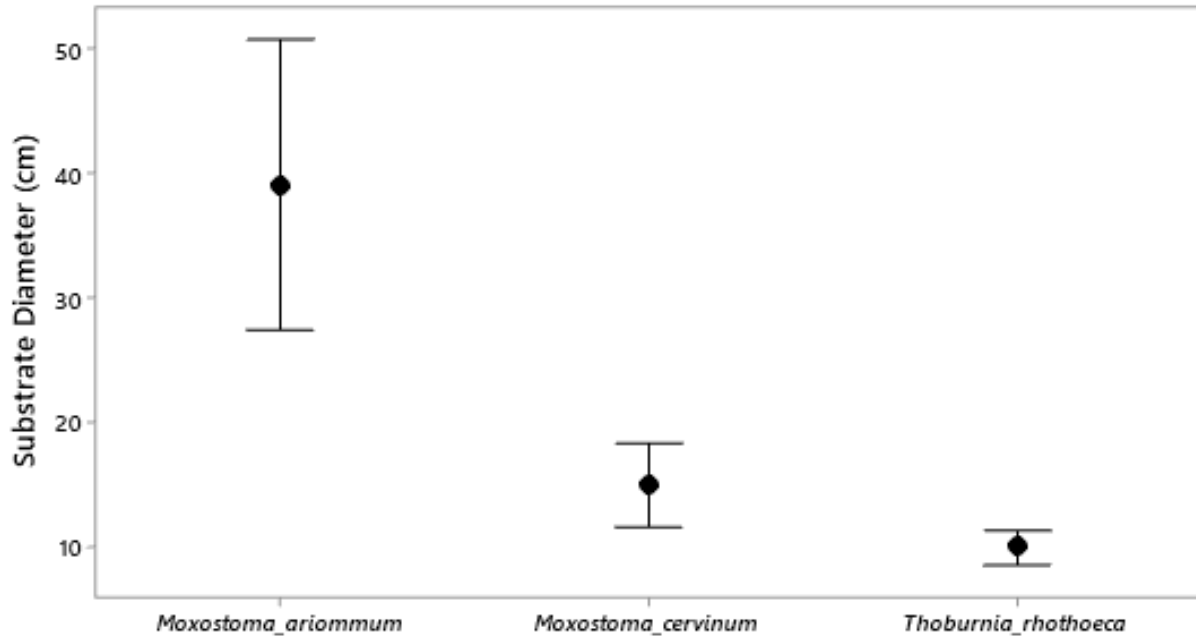
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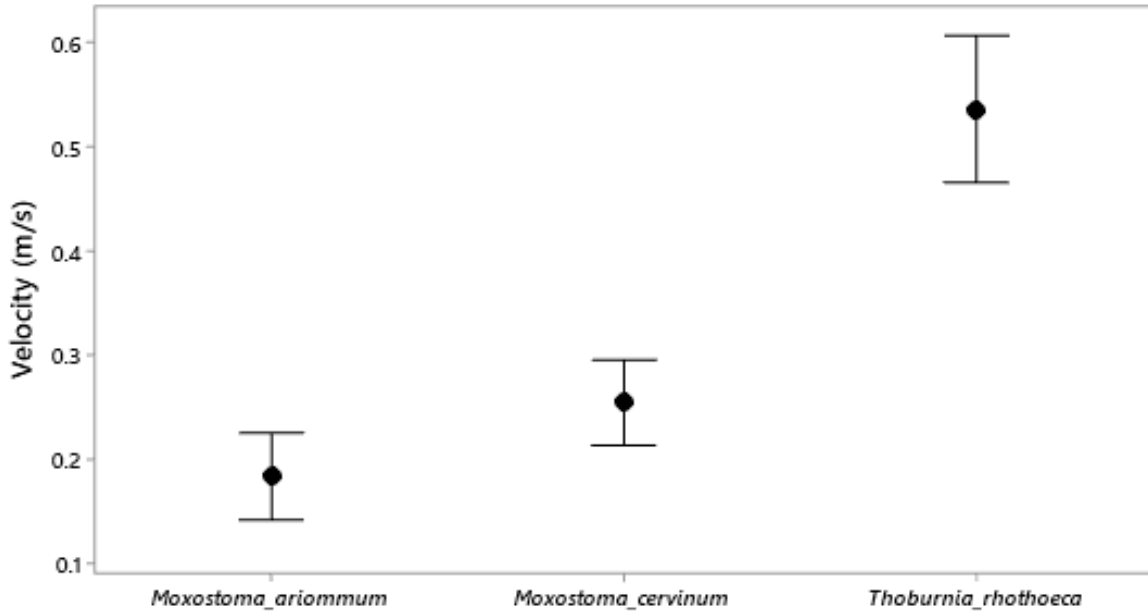
FIGURE 2: Plot of 95% confidence intervals of mean velocity of water occupied for *Moxostoma ariommum* (n = 30), *M. cervinum* (n = 35), and *Thoburnia rhothoeca* (n = 36) in the South Fork Roanoke River in Montgomery County, Virginia.

FIGURE 3: Plot of 95% confidence intervals of mean depth of water occupied for *Moxostoma ariommum* (n = 30), *M. cervinum* (n = 35), and *Thoburnia rhothoeca* (n = 36) in the South Fork Roanoke River in Montgomery County, Virginia.

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FIGURE 4: Plot of 95% confidence intervals of mean substrate diameter below *Moxostoma ariommum* (n = 30), *M. cervinum* (n = 35), and *Thoburnia rhothoeca* (n = 36) in the South Fork Roanoke River in Montgomery County, Virginia.

Mean fineness ratios were not equal among species (P < 0.001; mean for *Moxostoma ariommum* = 5.36, SE = 0.13; mean for *Moxostoma cervinum* = 5.04, SE = 0.08; mean for *Thoburnia rhothoeca* = 4.63, SE = 0.04). In the multivariate analysis of body shape, principal component two loaded heavily for eye width (-0.61), body width at pelvic fin origin (0.33), body width at anal fin origin (0.32), and body depth at dorsal fin origin (0.30). Principal component three loaded heavily for dorsal fin height (0.61) and caudal peduncle length (-0.47). The scatterplot of PC 2 and PC 3 reveal that *Moxostoma ariommum* has no overlap with *T. rhothoeca* or *M. cervinum* on PC 2 with the former having lower PC 2 scores than the latter two. There is minimal overlap among the latter two species along PC 3 with *T. rhothoeca* having higher PC 3 scores than *M. cervinum* (Fig. 5).
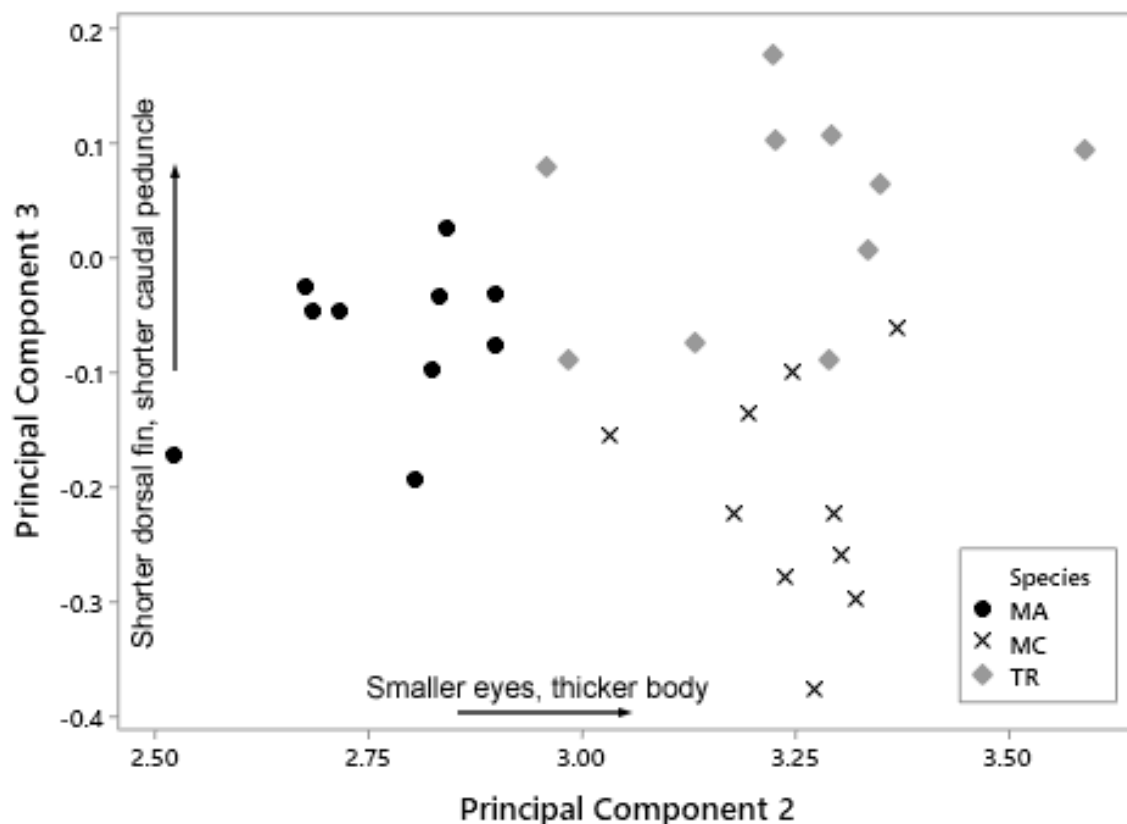
FIGURE 5: Scatterplot of Principal Component (PC) scores of 22 natural-log transformed body measurements of *Moxostoma ariommum* (MA), *M. cervinum* (MC), and *Thoburnia rhothoeca* (TR).

DISCUSSION

The habitat data suggest *T. rhothoeca, M. cervinum,* and *M. ariommum* occupy different microhabitats despite occupying the same stream reach within our study site. All three habitat variables appear to be important in habitat partitioning for these catostomids that share many ecological characteristics. *Thoburnia rhothoeca* occupies the fastest, shallowest water, with the smallest substrate. The mean value of 9.9 cm diameter and relatively small standard error of substrate for *T. rhothoeca* suggests this habitat is mostly cobble. This quantified microhabitat of fast, shallow water over cobble is consistent with the riffle habitat reported by Matthews (1990) for *T. rhothoeca*. *Moxostoma ariommum* occupies the slowest, deepest water over the largest substrate. This substrate is mostly bedrock consistent with habitat descriptions in Jenkins and Burkhead (1994) for *M. ariommum*. *Moxostoma cervinum* appears to inhabit habitat intermediate between that occupied by *T. rhothoeca* and *M. ariommum*. Collectively, these analyses can be interpreted as *T. rhothoeca* primarily occupying riffle habitat, *M. cervinum* occupying run habitat nearest the base of riffles, and *M. ariommum* occupying slower run habitat over bedrock substrate.

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While the differences in habitat appear to be quite clear, associated morphological differences among these species are not necessarily as clear. With a fineness ratio of 4.63, *T. rhothoeca* appears very similar to the optimum for endurance swimming of 4.5 (Walker et al., 2013). The highest fineness ratio among species examined was in *M. ariommum* which inhabited the slowest water. Higher fineness ratios are common in burst-and-coast swimming patterns (Chung 2009). These burst-and-coast swimming patterns are often associated with maximizing sensory perception in fishes (Ashraf et al., 2020). With *M. ariommum* having a much larger eye than the other two species examined, the high fineness ratio and large eye may be associated with one another.

The functional significance of the larger eye of *M. ariommum* is not easily explained. Jenkins and Burkhead (1994) suggest it allows for greater detection of predators. The occupation of slower water by *M. ariommum* may make them more susceptible to predation especially over bedrock substrate with fewer crevices to hide from predators. Modest dietary differences exist among the study species (Jenkins and Burkhead, 1994; Tarasidis and Powers, 2014; Thompson et al., 2015); these differences may also be associated with contrasting eye sizes. *Moxostoma ariommum* appear to rely somewhat less heavily on chironomids and detritus than *T. rhothoeca* and *M. cervinum* and more heavily on larger aquatic insect nymphs. The large eye may be associated with increased reliance on sight feeding for those larger and more motile food items. Similarly, *Moxostoma lacerum* was hypothesized to use its large eye as an adaptation for sight feeding (Miller and Evans, 1965) on aquatic snails (Fink and Humphries, 2010) in slower run habitats (Jenkins and Burkhead, 1994) like those inhabited by *M. ariommum*. Mean eye size has been documented as inversely associated with depth in most fishes, but this relationship does not appear to be clearly linear. There is some evidence that a greater relative eye investment (i.e. size) is associated with dimly lit environments (Caves et al., 2017). As *M. ariommum* is a benthic fish in the deepest water of the species investigated in this study, it may inhabit more dimly lit waters than *M. cervinum* or *T. rhothoeca* possibly explaining the larger eyes of the former. Additionally, Caves et al. (2017) found increased acuity in more complex habitats. The larger substrate size beneath *M. ariommum* may represent a more complex habitat than inhabited by *M. cervinum* or *T. rhothoeca.*

The increased width and depth near the center of the body of *T. rhothoeca* and *M. cervinum* in comparison to *M. ariommum* may be associated with the contrasting current velocities inhabited by them. Langerhans et al. (2007) document a more fusiform body associated with increased water flow for Cyprinidae. The greater body depth and width near the middle of the body of *T. rhothoeca* and *M. cervinum* compared to *M. ariommum* suggest a similar phenomenon in Catostomidae with these more fusiform bodied species occupying the fastest water within our study site.

The smaller dorsal fin of *T. rhothoeca* compared to *M. cervinum* is consistent with the findings of Istead et al. (2015) who found dorsal fins in Centrarchidae reduced by faster flowing water. The smaller dorsal fin likely reduces drag helping to reduce exertion needed in the fast water inhabited by *T. rhothoeca.* However, this trend in a reduced dorsal fin did not extend to *M. ariommum* which inhabits the slowest water of all species examined in this study and has largely overlapping values for PC 3 scores with *T. rhothoeca.* The interaction between dorsal fin size and current velocity is likely complex as other authors investigating the influence of current velocity

on dorsal fin size found a direct relationship between them rather than an inverse relationship (Paez et al., 2008; Leavy and Bonner, 2009).

Variation in caudal peduncle length with variation in water flow has been documented with different authors reporting contrasting relationships in different species as Foster et al. (2015) reported a shortened caudal peduncle in response to faster water in *Goodea atripinnis,* Blackfin Goodea (Goodeidae) but the opposite in *Chirostoma jordani,* Mesa Silverside (Atherinopsidae). Istead et al. (2015) reported longer caudal peduncles for three species of Centrarchidae reared in faster waters. However, all of these species have very different gross morphologies than our study species and likely have vastly different overall hydrodynamics than the Catostomidae investigated in this study. Additionally, caudal peduncle length loaded heavily on PC 3 largely segregating *T. rhothoeca* and *M. cervinum.* As these two species occupy much more similar habitats than that of *M. ariommum,* we should expect differences among them to be more nuanced. This leaves the generally inverse relationship between caudal peduncle length and current velocity occupied difficult to clearly explain with any certainty.

As suggested in 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, habitats, and diets of these syntopic catostomid species. Collectively, these differences likely contribute to their resource partitioning and the maintenance of the diverse assemblage of catostomids in the Roanoke River drainage consistent with the summary of other taxa provided by Ross (1986). Additionally, increased sample sizes may lead to different findings.

ACKNOWLEDGMENTS

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