

# Shape variation in a benthic stream fish across flow regimes

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**Abstract** Evolution of fish body shapes in flowing and non-flowing waters have been examined for several species. Flowing water can select for fish body shapes that increase steady swimming efficiency, whereas non-flowing water can favor shapes that increase unsteady swimming efficiency. Benthic stream fishes often use areas near the substrate that exhibit reduced or turbulent flow, thus it is unclear which swimming forms would be favored in such environments, and how shape might change across flow regimes. To test the relationship between fish body shape and flow regime in a benthic stream fish, we used geometric morphometric techniques to characterize lateral body shape in mountain sucker (*Catostomus platyrhynchus*) across flow rates, using stream gradient as an indicator of stream flow. Mountain suckers from low-flow environments were more streamlined, consistent with steady swimming body shapes, whereas mountain suckers from high flows had deeper bodies, consistent with unsteady swimming body shapes. In addition, smaller individuals tended to have more robust body shapes. These

patterns are opposite to those predicted for stream fishes in the mid-water column. The benthic stream environment represents a distinct selective environment for fish shape that does not appear to conform to the simple dichotomy of flowing versus non-flowing water.

**Keywords** Geometric morphometrics · Morphology · Flow · *Catostomus platyrhynchus* · Trade-off

## Introduction

In general, fish body shape predicts swimming performance in two distinct swimming modes termed steady and unsteady swimming (Webb, 1984; Blake, 2004; Langerhans & Reznick, 2007). Steady swimming is used during constant-speed movement and is facilitated by streamlined, fusiform bodies with high caudal aspect ratios. Unsteady swimming is used during rapid burst movements associated with abrupt changes in direction, and is facilitated by deep bodies and large caudal regions (Webb, 1984; Langerhans & Reznick, 2007). The distinct differences in shape that accompany these different swimming types generate a tradeoff between shapes that improve steady swimming and those that improve unsteady swimming (Blake, 1983, 2004; Webb, 1984; Langerhans & Reznick, 2007). Specific habitats can select for a

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swimming type and its corresponding body shape depending on the relative importance of that swimming type in the particular habitat. In complex habitats, for example, maneuverability is most important (favoring unsteady swimming morphology), whereas in open water habitats, cruising and straight-line swimming would be more beneficial (favoring steady swimming morphology; Langerhans & Reznick, 2007).

Predictions of body shape for fishes in flowing water (i.e., rivers and streams) can be derived from the same principles. Fishes that occupy flowing water are expected to exhibit a streamlined, fusiform shape and a small caudal aspect ratio similar to shapes of continuous fast-swimming fishes in open water (Langerhans & Reznick, 2007). For fishes that inhabit the mid-water column, flowing water habitats should correlate with shapes that maximize efficiency of steady swimming (McLaughlin & Grant, 1994; Langerhans et al., 2003; Sidlauskas et al., 2006; Langerhans & Reznick, 2007). While there are multiple observations to support this prediction, there are a few exceptions where fishes in non-flowing water exhibited more steady swimming body morphologies than the same species found in flowing water (Hendry et al., 2002; McGuigan et al., 2003; Krabbenhoft et al., 2009; Franssen et al., 2013). In these cases, it is likely that additional selective pressures other than flow drove the observed patterns (Krabbenhoft et al., 2009). Similarly, benthic stream fishes may not follow these same predictions because of their proximity to and use of the substrate to maintain position (Langerhans, 2008). Benthic fishes typically avoid swimming directly against the current by utilizing the boundary layer or by positioning themselves in microhabitats that typically experience low flow and less turbulence (Webb, 1989; Carlson & Lauder, 2011). This use of low-flow microhabitats may lessen the selective pressures caused by flow and in turn may change predictions on body morphology. Some have suggested that the “humped” morphology of some benthic riverine fishes (e.g., humpback chub, *Gila cypha* Miller) represents an adaptation to high flows (Miller, 1946; Moyle & Cech, 2004), however, these suggestions have been challenged (Portz & Tyus, 2004). It is not clear whether body shape of benthic stream fishes would covary with flow rates or not. We know of no studies that have empirically tested for intraspecific variation of body shape in benthic stream fishes across multiple flow rates.

Mountain sucker (*Catostomus platyrhynchus* Cope) is a common, benthic stream fish in rivers and streams of the intermountain western USA (Smith, 1966; Moyle, 2002; Wydoski & Wydoski, 2002). This species exhibits a typical streamlined body shape, has a reduced swim bladder, and spends most of its time in direct contact with the stream substrate (Smith, 1966; Hauser, 1969; Aedo, 2008). Mountain suckers occur in a wide variety of flow regimes ranging from fast-flowing mountain streams, to slower flowing streams, as well as ponds, lakes, and reservoirs (Hauser, 1969; Simpson & Wallace, 1982; Snyder, 1983; Decker, 1989). They prefer microhabitats with low water velocities, such as pools and backwaters, but they regularly move through and feed in higher velocity microhabitats such as riffles and runs (Moyle, 2002; Olsen & Belk, 2005). Because they commonly occur across a wide range of flow regimes, they provide a model system to test for covariation of body shape with flow rate.

In fast-flowing rivers and streams, the mid-water column habitat is characterized by relatively uniform flow rates and simple open habitats. In contrast, benthic environments in fast-flowing systems exhibit a complex arrangement of high and low flows and high and low turbulence (Hart et al., 1996; Hart & Finelli, 1999). In addition, large substrate elements create structural complexity and complex arrangements of refuge habitats (both from high flows and from predators; Harding et al., 1998). While benthic stream fishes will certainly encounter high flows as they traverse between areas of refuge, exposure to high flows may not be long enough to elicit steady swimming behaviors. As a consequence of these differences in complexity, unsteady or burst swimming efficiency may be more advantageous in flowing, benthic habitats as fish quickly navigate across areas of high flow (Langerhans & Reznick, 2007). In low (or no) flow benthic habitats, both steady and unsteady swimming may be equally advantageous. Based on differences in benthic habitats in high- and low-flow streams, we predicted that mountain sucker body shape would trend from a generalized, streamlined shape (i.e., narrower body depth dorsal-ventrally) in low-flow environments to a more robust body shape (i.e., deeper body depth dorso-ventrally) with a larger caudal area in high-flow habitats (predictions based on Langerhans & Reznick, 2007). We tested for variation in shape in mountain sucker according to these predictions across a wide range of flow regimes.

**Table 1** Collection location names, gradient (slope), gradient category, latitude and longitude coordinates, and number of mountain suckers sampled for each site

Site	Gradient (m/km)	Gradient category	Coordinates	<i>N</i>
1. Locomotive Springs, UT	2.3	Low	41°45' 112°50'	49
2. Muddy Creek, WY	3.4	Low	41°40' 110°40'	45
3. Sulfur Creek, WY	5.7	Low	41°00' 110°50'	48
4. Silver Creek, UT	8.5	Intermediate	40°50' 111°30'	50
5. Thistle Creek, UT	9.4	Intermediate	39°50' 111°30'	44
6. Toponce Creek, ID	10.0	Intermediate	42°50' 112°00'	49
7. Main Creek, UT	11.2	Intermediate	40°20' 111°30'	43
8. Sevier River (Panguitch), UT	11.8	High	37°50' 112°10'	49
9. Salina Creek, UT	15.7	High	38°50' 111°30'	49
10. Sevier River (Antimony), UT	20.3	High	39°00' 111°60'	49

## Materials and methods

### Sampling design

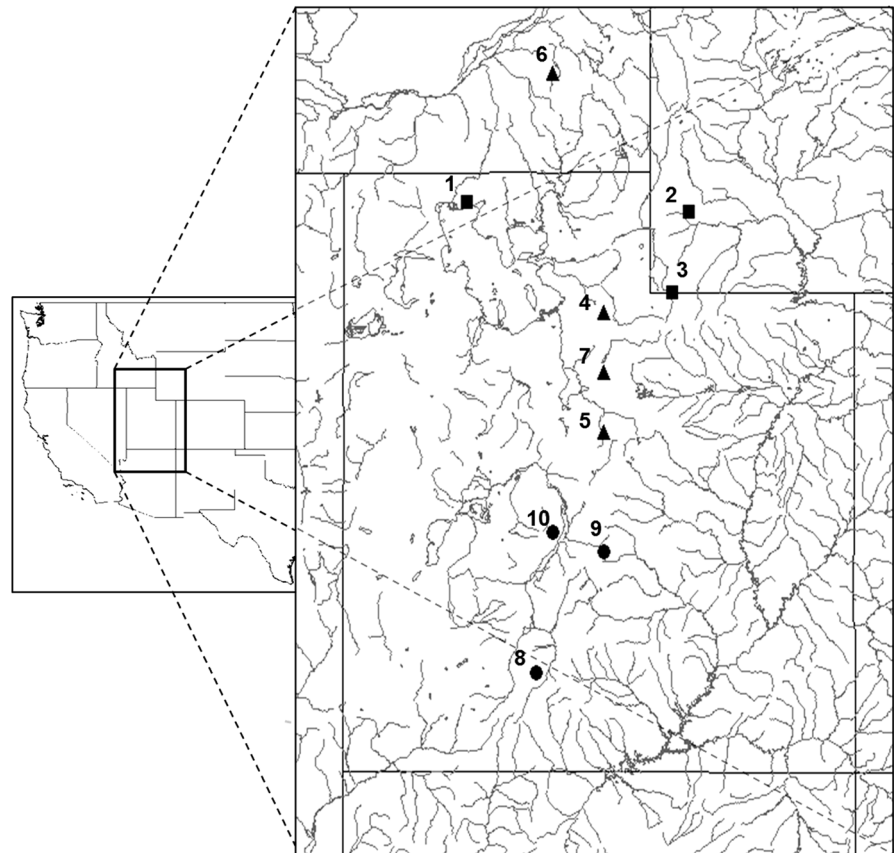
We collected approximately 50 adult mountain suckers from each of ten locations in Utah, Idaho, and Wyoming (Table 1, Fig. 1) for a total of 476 fish collected. Fish ranged in size from about 110 to 190 mm SL, but the full range of size variation was not found in each location. Fish were collected during low-flow conditions in July and August. Flows can vary depending on the season, with higher flows in the spring, and lower flows in late summer through the fall. Body shape is a response to the average selective environment over many generations, not to the flow rate of a specific microhabitat at a specific time of year. Thus, we assumed stream gradient would give a better representation of this overall selective environment than short-term measurements of water velocity. Locations were selected based on availability of mountain suckers and appropriate gradients. Whereas the two lower gradient categories are somewhat mixed in their latitudinal distribution, the highest gradient

category is localized in the lowest latitudes. Thus, latitude is partially confounded with gradient category. However, there are no predictive hypotheses for the effect of latitude on fish morphology, but there are predictions for morphology across different flow regimes. Thus, although our sample partially confounds latitude, we interpret our results as a response to gradient. Specimens were anesthetized using MS-222, and placed in a small tank filled with water. Using a Panasonic AG-EZ1 digital video camera, we recorded video images of the lateral side of each fish, and selected a still photo from the video to use in morphometric analysis. Mountain sucker are considered sexually monomorphic except for the difference in length of the anal fin (Smith, 1966; Sigler & Sigler, 1996). Anal fin length was not included in the analysis, so we did not differentiate between sexes in the analysis.

### Morphometric analysis

Of the 476 images taken, 11 were unusable (e.g., poor focus of image, poor angle of fish) and were excluded from analysis. We digitized 13 landmarks (tpsDig2; Rohlf, 2005) on photos from 465 fish as follows: (1) anterior tip of the snout, (2) center of the eye, (3) junction of the opercular flap with the ventral outline, (4) semilandmark midway between points 1 and 6, (5) semilandmark midway between points 3 and 8, (6) anterior insertion of the dorsal fin, (7) semilandmark located at the posterior insertion of the dorsal fin (we made this a semilandmark between points 6 and 10 because the posterior insertion of the dorsal fin is not always easily identified in live fish with relaxed fin positions), (8) anterior insertion of the pelvic fin, (9) anterior insertion of the anal fin, (10) semilandmark located on the dorsal outline at the narrowest part of the caudal peduncle, (11) semilandmark located on the ventral outline at the narrowest part of the caudal peduncle, (12) dorsal insertion of the caudal fin, and (13) ventral insertion of the caudal fin (Fig. 2). A semilandmark is mathematically fixed in one direction and thus only retains variation in the axis perpendicular to the line between the two landmarks where it is placed (Bookstein, 1996; Perez et al., 2006). We used tpsRelw to generate shape variables called relative warps. Relative warps result from a principal components analysis of the partial warps and uniform components (Rohlf, 2003). We used the first 15 relative warps in our statistical analyses, which accounted for 97% of shape

**Fig. 1** Map of collection sites in Idaho, Wyoming, and Utah. *Squares* represent the lowest gradients, *triangles* represent intermediate gradients, and *circles* represent the highest gradients. Numbers reference locations from Table 1

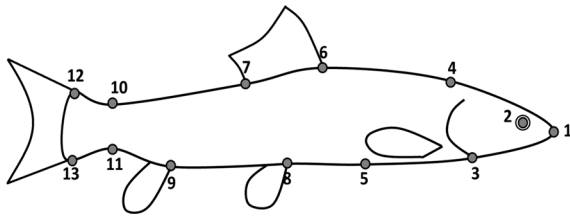


variation, and we plotted the first two relative warps on a thin-plate spline representation to visualize differences between individuals of different sizes and from different gradients.

We analyzed shape variation using a multivariate mixed model in an analysis of variance framework. Multivariate mixed models give us the benefits of a mixed model by allowing us to include both fixed effects (e.g., flow category) and random effects (e.g., collection location), while still allowing us to incorporate all shape variables simultaneously (multivariate analysis). We divided gradients into high, intermediate, and low categories and treated gradient category as a fixed effect in our model (we define low gradient as below 7 m/km, intermediate gradient as between 7 and 11.5 m/km, and high gradient as above 11.5 m/km). Centroid size was standardized within locations by converting it to a z-score, and was included in the model as a covariate. Relative warps are repeated measures on the same individual, so we

treated both individuals and collection location as random effects.

For purposes of analysis, the multivariate response variable matrix is converted to a single vector and variables are treated as repeated measures in the mixed model. This vectorization process of our response variable matrix (the ordered relative warps) necessitates the use of an index variable as a fixed categorical effect in the model that indexes the order of the response variables (Wesner et al., 2011; Hassell et al., 2012). This is similar to including a time variable in a repeated measures analysis that signifies the order of sampling events (Wesner et al., 2011). We also included interactions between our index variable and the other fixed effects. Main effects by themselves test whether shape varies between levels of the main effect on average across all relative warps. Because principal components (i.e., relative warps) are orthogonal and independent, it is unlikely that main effects by themselves will differ because of arbitrary differences



**Fig. 2** Location of landmarks used for geometric morphometric analysis on *Catostomus platyrhynchus*

**Table 2** Results of mixed repeated measures MANCOVA analyzing shape variation in mountain sucker, *Catostomus platyrhynchus*

Effect	df	F	P
Type 3 tests of fixed effects			
Index variable	14, 2583	0.11	1
Gradient category	2, 11.8	11.16	<b>0.0019</b>
Centroid size	1, 2673	3.45	0.0632
Centroid size × gradient	2, 2673	5.79	<b>0.0031</b>
Gradient × index variable	28, 3631	10.21	<b>&lt;0.0001</b>
Centroid size × index variable	14, 2583	9.55	<b>&lt;0.0001</b>
Centroid size × gradient × index variable	28, 3631	1.69	<b>0.0134</b>

Significant effects are bolded

among relative warps in the direction of effects. The interaction of the main effects and the index variable thus provides a better test of the hypothesis that at least some aspects of shape (i.e., relative warps) vary across the different levels of the main effect. Shape variation was visualized with thin-plate spline transformations using tpsRelw (Rohlf, 2003), and we plotted mean shape at relatively large and relatively small sizes by gradient category.

## Results

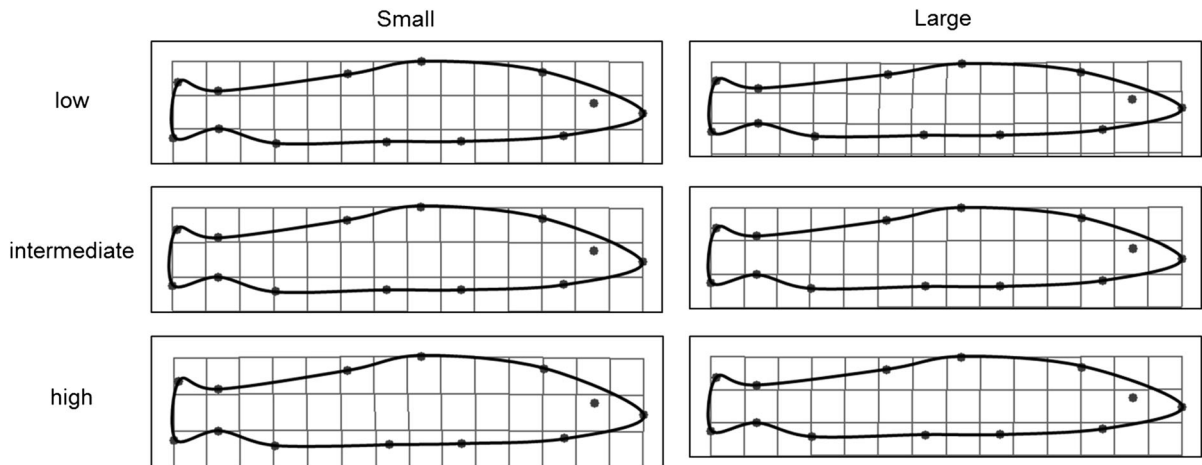
Body shape of mountain sucker is significantly affected by gradient (gradient by index variable interaction), and by centroid size (centroid size by index variable interaction), as well as by the interaction between gradient and centroid size (gradient, centroid size, and index variable interaction; Table 2). Mountain suckers from low-flow environments tended

to exhibit a more streamlined body, whereas, those from high-flow environments were more robust and had deeper bodies (Fig. 3). Smaller mountain suckers exhibited overall deeper bodies compared to larger mountain suckers (Fig. 3). The significant gradient by centroid size by index variable interaction indicates that the shift from low-flow phenotypes to high-flow phenotypes exhibited a similar pattern in both large and small individuals, but the phenotype at intermediate flows was more similar to low-flow phenotypes in small individuals and more similar to high-flow phenotypes in large individuals (Fig. 4).

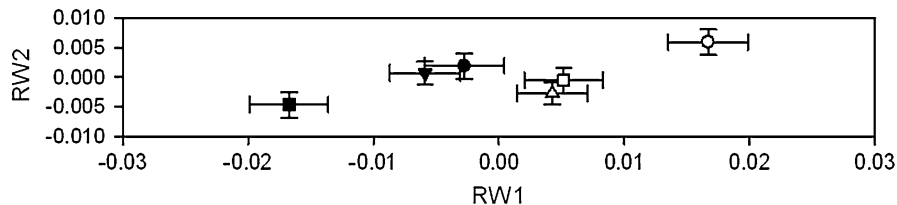
## Discussion

More robust bodies in higher flows can be interpreted as an adaptation for unsteady swimming performance in a structurally complex habitat. Mountain suckers typically avoid fast flows even in high gradient environments and are usually found in pools and pool-run edge habitats or behind obstructions like rocks and logs (Hauser, 1969; Moyle, 2002). They persist in intermittent streams with little to no flow during mid-summer (Carter & Hubert, 1995). In addition, mountain suckers may ameliorate the effects of flow by using boundary layers created by uneven substrates and “bracing” against the substrate. Such bracing behavior has been observed in several other species, including fin bracing in cyprinids (Blake, 2006), salmonids (Arnold et al., 1991), percids (Carlson & Lauder, 2010), and loricariids (Blake, 2006), oral suctioning in loricariids (Blake, 2006), and body arching in plaice, rays (Webb, 1989), and percids (Carlson & Lauder, 2010). Mountain suckers exhibit fin bracing and body arching to maintain position on the substrate (Aedo, 2008). By avoiding flow through habitat selection, use of the near substrate boundary layer, and bracing behavior, unsteady swimming may increase in importance for mountain suckers in high flow. A deeper body and a larger caudal region may allow for more effective movement through turbulent and high velocity patches between suitable habitats.

Our results could be interpreted to suggest that a more robust body is adaptive to maintaining position within the boundary layer. Robust bodies in fishes of the Colorado River, particularly the humpback chub (*Gila cypha*), have been suggested as an adaptive trait for benthic fishes in swift waters. Miller (1946)



**Fig. 3** Shape outlines of mountain sucker representing thin-plate spline transformations at  $3\times$  magnification based on least squares means of size and gradient category on relative warps 1 and 2



**Fig. 4** Least squares means ( $\pm 1$  SE) for relatively small (*open symbols*) and relatively large (*closed symbols*) mountain sucker from high gradient (*circles*), intermediate gradient (*triangles*), and low gradient (*squares*) streams. Relative warp 1 accounts

for 33.75% and relative warp 2 accounts for 14.45% of the variation (axes are scaled to represent percent variation explained)

proposed that the large nuchal hump directly posterior to the head produced negative lift to push the fish toward the boundary layer (Moyle & Cech, 2004). The more robust bodies of mountain suckers in high flow could act similarly, helping the fish maintain position on the substrate where flow is slower and more stable.

While this explanation seems reasonable, it has not been experimentally tested. Portz and Tyus (2004) challenged this assumption in the humpback chub by specifically testing drag and lift for fish with and without nuchal humps. Fish with nuchal humps tended to have greater drag and substantial positive lift in higher velocities, which would make it more difficult to maintain position in the boundary layer. Mountain suckers with deeper bodies could face similar problems in fast flows. Thus, robust bodies in higher flow likely do not aid in generating negative lift.

It should be noted that our results may indicate a plastic response to flowing water. Recent research by

Franssen et al. (2013) investigated plasticity in body morphology in a cyprinid species. They found flow-induced phenotypic plasticity in body morphology; fish from flowing and non-flowing environments both showed similar morphologies when raised in flowing environments. However, these morphologies were opposite what they had found in natural populations, where fish from flowing environments were deeper bodied than fish from non-flowing environments. If our results are indicative of a plastic response to flow, this plastic response may still be adaptive. Future research should investigate whether the patterns in mountain suckers continue when fish from high- and low-flow environments are raised in a common environment.

Shape was not consistent across sizes; smaller individuals tended to have a more robust body than larger individuals. Adult fish are typically better swimmers than juveniles. Though our samples consisted entirely of adults, larger adults may simply be

better swimmers than smaller individuals, and thus adaptations for unsteady swimming are less important. Another possible explanation for this difference could be a change in habitat preference between older and younger individuals. While large mountain suckers are typically found in swift waters, smaller individuals prefer calmer, shallower areas (Sigler & Sigler, 1996). Larger individuals thus may have a greater need for steady swimming morphologies compared to smaller individuals (viz., they are exposed to and must swim against current more frequently). Smaller individuals also tend to be better able to utilize the boundary layer (Carlson & Lauder, 2011) and would have a lesser need for body shape that would enhance steady swimming.

## Conclusion

Flow is a good predictor of body morphology for fishes that swim in the mid-water column. Our results indicate that flow can also predict body morphology for benthic fishes, but these predictions may differ from those for mid-water column fishes. Mountain sucker from low-flow environments exhibited more streamlined body shapes consistent with steady swimming morphologies, whereas mountain suckers from high-flow environments exhibited deeper bodies consistent with unsteady swimming morphologies. Avoidance of high flows by benthic fishes through bracing behavior may increase unsteady swimming importance as fish traverse structurally complex benthic environments. Further research should address the adaptive nature of this shape change including examining whether deeper bodies help to generate negative lift.

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## References

- Aedo, J. R., 2008. Does Shape Predict Performance? An Analysis of Morphology and Swimming Performance in Great Basin Fishes. Brigham Young University, Provo, UT.
- Arnold, G. P., P. W. Webb & B. H. Holford, 1991. The role of the pectoral fins in station-holding of Atlantic salmon parr (*Salmo salar* L.). *Journal of Experimental Biology* 156: 625–629.
- Blake, R. W., 1983. Functional design and burst-and-coast swimming in fishes. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 61: 2491–2494.
- Blake, R. W., 2004. Fish functional design and swimming performance. *Journal of Fish Biology* 65: 1193–1222.
- Blake, R. W., 2006. Biomechanics of rheotaxis in six teleost genera. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 84: 1173–1186.
- Bookstein, F. L., 1996. Landmark methods for forms without landmarks: localizing group differences in outline shape. Paper presented at the Proceedings of the 1996 Workshop on Mathematical Methods in Biomedical Image Analysis (MMBIA '96).
- Carlson, R. L. & G. V. Lauder, 2010. Living on the bottom: kinematics of benthic station-holding in darter fishes (Percidae: Etheostomatinae). *Journal of Morphology* 271: 25–35.
- Carlson, R. L. & 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.
- Carter, B. & W. A. Hubert, 1995. Factors influencing fish assemblages of a high-elevation desert stream system in Wyoming. *Great Basin Naturalist* 55: 169–173.
- Decker, L. M., 1989. Coexistence of two species of sucker, *Catostomus*, in Sagehen Creek, California, and notes on their status in the Western Lahontan Basin. *Great Basin Naturalist* 49: 540–551.
- Franssen, N. R., L. K. Stewart & J. F. Schaefer, 2013. Morphological divergence and flow-induced phenotypic plasticity in a native fish from anthropogenically altered stream habitats. *Ecology and Evolution* 3: 4648–4657.
- Harding, J. M., A. J. Burky & C. M. Way, 1998. Habitat preferences of the rainbow darter, *Etheostoma caeruleum*, with regard to microhabitat velocity shelters. *Copeia* 1998: 988–997.
- Hart, D. D. & C. M. Finelli, 1999. Physical–biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics* 30: 363–395.
- Hart, D. D., B. D. Clark & A. Jasentuliyana, 1996. Fine-scale field measurement of benthic flow environments inhabited by stream invertebrates. *Limnology and Oceanography* 41: 297–308.
- Hassell, E. M. A., P. J. Meyers, E. J. Billman, J. E. Rasmussen & M. C. Belk, 2012. Ontogeny and sex alter the effect of predation on body shape in a livebearing fish: sexual dimorphism, parallelism, and costs of reproduction. *Ecology and Evolution* 2: 1738–1746.
- Hauser, W. J., 1969. Life history of the mountain sucker, *Catostomus platyrhynchus*, in Montana. *Transactions of the American Fisheries Society* 98: 209–215.
- Hendry, A. P., E. B. Taylor & J. D. McPhail, 2002. Adaptive divergence and the balance between selection and gene flow: lake and stream stickleback in the misty system. *Evolution* 56: 1199–1216.

- Krabbenhof, T. J., M. L. Collyer & J. M. Quattro, 2009. Differing evolutionary patterns underlie convergence on elongate morphology in endemic fishes of Lake Waccamaw, North Carolina. *Biological Journal of the Linnean Society* 98: 636–645.
- Langerhans, R. B., 2008. Predictability of phenotypic differentiation across flow regimes in fishes. *Integrative and Comparative Biology* 48: 750–768.
- Langerhans, R. B. & D. N. Reznick, 2007. Ecology and evolution of swimming performance in fishes: predicting evolution with biomechanics. In Domenici, P. & B. G. Kapoor (eds), *Fish Locomotion: An Eco Ethological Perspective*. Science Publisher, Enfield: 200–248.
- Langerhans, R. B., C. A. Layman, A. K. Langerhans & T. J. Dewett, 2003. Habitat-associated morphological divergence in two neotropical fish species. *Biological Journal of the Linnean Society* 80: 689–698.
- McGuigan, K., C. E. Franklin, C. Moritz & M. W. Blows, 2003. Adaptation of rainbow fish to lake and stream habitats. *Evolution* 57: 104–118.
- McLaughlin, R. L. & J. W. A. Grant, 1994. Morphological and behavioral differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow-running vs fast-running water. *Environmental Biology of Fishes* 39: 289–300.
- Miller, R. R., 1946. *Gila cypha*, a remarkable new species of cyprinid fish from the Colorado River in Grand Canyon, Arizona. *Journal of the Washington Academy of Sciences* 36: 409–415.
- Moyle, P. B., 2002. *Inland Fishes of California*. University of California Press, Berkeley, CA.
- Moyle, P. B. & J. J. Cech, 2004. *Fishes: An Introduction to Ichthyology*, 5th ed. Pearson Prentice Hall, Upper Saddle River, NJ.
- Olsen, D. G. & M. C. Belk, 2005. Relationship of diurnal habitat use of native stream fishes of the eastern Great Basin to presence of introduced salmonids. *Western North American Naturalist* 65: 501–506.
- Perez, S. I., V. Bernal & P. N. Gonzalez, 2006. Differences between sliding semi-landmark methods in geometric morphometrics, with an application to human craniofacial and dental variation. *Journal of Anatomy* 208: 769–784.
- Portz, D. E. & H. M. Tyus, 2004. Fish humps in two Colorado River fishes: a morphological response to cyprinid predation? *Environmental Biology of Fishes* 71: 233–245.
- Rohlf, F. J., 2003. tpsRelw Relative Warps Analysis, Version 1.36. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, NY.
- Rohlf, F. J., 2005. tpsDig, Digitize Landmarks and Outlines, Version 2.05. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, NY.
- Sidlauskas, B., B. Chernoff & A. Machado-Allison, 2006. Geographic and environmental variation in *Bryconops* sp. cf. *melanurus* (Ostariophysi: Characidae) from the Brazilian Pantanal. *Ichthyological Research* 53: 24–33.
- Sigler, W. F. & J. W. Sigler, 1996. *Fishes of Utah: A Natural History*. University of Utah Press, Utah.
- Simpson, J. C. & R. L. Wallace, 1982. *Fishes of Idaho*. University Press of Idaho, Moscow.
- Smith, G. R., 1966. Distribution and Evolution of the North American Catostomid Fishes of the Subgenus *Pantosteus*, Genus *Catostomus*. University of Michigan, Museum of Zoology, Miscellaneous Publications 129.
- Snyder, D. E., 1983. Identification of catostomid larvae in Pyramid Lake and the Truckee River, Nevada. *Transactions of the American Fisheries Society* 112: 333–348.
- Webb, P. W., 1984. Body form, locomotion, and foraging in aquatic vertebrates. *American Zoologist* 24: 107–120.
- Webb, P. W., 1989. Station-holding by three species of benthic fishes. *Journal of Experimental Biology* 145: 303–320.
- Wesner, J. S., E. J. Billman, A. Meier & M. C. Belk, 2011. Morphological convergence during pregnancy among predator and nonpredator populations of the livebearing fish *Brachyrhaphis rhabdophora* (Teleostei: Poeciliidae). *Biological Journal of the Linnean Society* 104: 386–392.
- Wydoski, R. G. & R. S. Wydoski, 2002. Age, growth, and reproduction of mountain suckers in Lost Creek Reservoir, Utah. *Transactions of the American Fisheries Society* 131: 320–328.