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Comparative Swimming Performance of Five *Catostomus* Species and Roundtail Chub

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Abstract.—Decreased habitat connectivity and competition with nonnative species have led to declines of many freshwater fishes. An understanding of swimming performance can aid in the conservation of these fishes; however, acquiring sufficient numbers of rare and threatened species to perform swimming studies can be logistically challenging and ecologically costly. In order to determine whether swimming data for common sucker species may be substituted for that of similar but rare sucker species, we compared the swimming abilities of two rare western catostomid, Bluehead Sucker *Catostomus discobolus* and Flannelmouth Sucker *C. latipinnis*, as well as one catostomid with a less well understood status, Mountain Sucker *C. platyrhynchus*, with those of the common White Sucker *C. commersonii* and Longnose Sucker *C. catostomus*. We also examined Roundtail Chub *Gila robusta* because they are often included in conservation efforts involving Bluehead Sucker and Flannelmouth Sucker. The critical swimming velocities (*U*<sub>crit</sub>), standardized by body length, of Bluehead Sucker and Longnose Sucker differed significantly from those of White Sucker. However, there was no significant difference between the *U*<sub>crit</sub> of Mountain Sucker, Flannelmouth Sucker, and White Sucker. During constant acceleration trials, Bluehead Sucker exhibited the greatest swimming ability, reaching a mean maximum velocity of 4.56 ± 1.28 body lengths per second (BL/s; mean ± SD), followed by Mountain Sucker (3.56 ± 0.57 BL/s), White Sucker (3.28 ± 0.90 BL/s), Longnose Sucker (2.97 ± 0.31 BL/s), and Flannelmouth Sucker (2.22 ± 0.42 BL/s). Additionally, key behavioral differences in the swimming behaviors of the fishes studied were observed. We conclude that swimming performance data for common White Sucker should not be used in place of data for rarer species. Comprehensive swimming studies should be conducted on individual sucker species before implementing conservation strategies involving fish passageways or barriers.

The Rocky Mountain region of the western USA is home to a variety of native catostomid species. However, some species, including Bluehead Sucker *Catostomus discobolus*, Flannelmouth Sucker *C. latipinnis*, and Mountain Sucker *C. platyrhynchus* have experienced decreases in range and population size (Bezzerides and Bestgen 2002; Compton 2007; Schultz and Bertrand 2012). Bluehead Sucker and Flannelmouth Sucker, along with Roundtail Chub *Gila robusta*, are classified by the Wyoming Game and Fish Department as native species status 1 (NSS1), or rare species with declining and vulnerable habitat, and are thus the subjects of a range-wide conservation agreement between Arizona, Colorado, Nevada, New Mexico, Utah, and Wyoming state fisheries agencies (Utah Department of Natural Resources 2006). These species are regionally referred to as the “three species” and managed as a species group rather than individually (Utah Department of Natural Resources 2006). White Sucker *C. commersonii* is common throughout the region and has been introduced into many habitats that were formerly...
restricted to the above-mentioned species. Longnose Sucker *C. catostomus* is an uncommon introduced sucker in many of the regions’ watersheds.

Catostomid populations throughout North America face declines resulting from a variety of factors including decreased habitat connectivity and hybridization with introduced species (Cooke et al. 2005). Within the Rocky Mountain region, human impacts, such as land use, nonnative fish introductions, habitat fragmentation, and altered flow regimes, are probable reasons for observed declines (Bestgen and Propst 1989; Martinez et al. 1994; Propst and Gido 2004; Bestgen et al. 2006; Compton et al. 2008). Introductions of nonnative fishes can affect native catostomids through predation (e.g., Burbot *Lota lota*), competition (e.g., Longnose Sucker), and hybridization (e.g., White Sucker) (Sweet and Hubert 2010; Gardunio et al. 2011).

Problems with habitat fragmentation may be resolved by the removal or modification of instream barriers to allow unrestricted up- and downstream movements by the catostomids. Conversely, the creation of instream barriers may impede invasions of nonnative fish into critical catostomid habitat. To design effective fish passage structures or barriers, it is critical to understand the different swimming abilities of target fish species (Hyde 2007). Different species of fish exhibit a variety of endurance levels, maximum swimming speeds, and unique swimming behaviors that affect their ability to pass different barrier sizes and configurations. Unfortunately, studies that evaluate the swimming abilities of fish in relation to passage capability often require large numbers of fish (e.g., 240 individuals per species: Ficke et al. 2011). Collecting large numbers of sensitive species such as Bluehead Sucker and Flannelmouth Sucker may be infeasible due to the challenge of locating healthy populations. In such cases, one possible alternative is to use a more common and closely related species as a surrogate, provided the species have similar swimming performances.

Suitable surrogate species may be identified through swimming ability studies that require fewer fish (e.g., ≤20 individuals per species: this study) than complete, passage-focused studies. The critical swimming methodology (*U*$crit*) approach is a commonly used test of aerobic swimming endurance that uses a stepped velocity increase (Brett 1964; Beamish 1978). Because of its standardized methodology and frequent usage, this method is ideal for interspecific comparisons. The *U*$crit* does not, however, provide data that are directly applicable to fish passage or barrier design beyond a measurement of the maximum aerobic velocity a fish can maintain for a fixed amount of time. Comparisons using *U*$crit* can also require fewer fish to produce statistically meaningful values than other methods such as fixed velocity tests to compare aerobic swimming endurance (Hammer 1995). The constant acceleration test (CAT; Reidy et al. 1995) method is shorter in duration and estimates a maximum velocity that is closer to the maximum sprinting speed of the fish (Farrell 2008); the top velocity in a constant acceleration test could be considered a sprinting velocity and would be powered by the fast-glycolytic (anaerobic) muscles. The CAT approach is also useful in identifying swimming gait transitions (e.g., from steady swimming to unsteady or burst-and-glide swimming).

The availability of Bluehead Sucker, Flannelmouth Sucker, and Mountain Sucker held for a captive rearing study presented us with a unique opportunity to conduct swimming ability tests on rare catostomid species. Our primary research goal was to determine whether the swimming performance and behavior of the more common White Sucker and Longnose Sucker are interchangeable with those of Bluehead Sucker, Flannelmouth Sucker, and Mountain Sucker using *U*$crit* and CAT tests. The secondary goal of our study was to measure and compare the *U*$crit* of the “three species”—Bluehead Sucker, Flannelmouth Sucker, and Roundtail Chub—to determine whether they have similar swimming performances or whether one species’ swimming performance could be the driving factor when designing fish-passage structures.

**METHODS**

*Fish sources and care.*—The White Suckers we used were collected using two Smith-Root LR-24 backpack electrofishers on May 7, 2012, from Spring Creek (South Platte River watershed: UTM zone 13T, 493071 E, 4490414 N, NAD83) in Fort Collins, Colorado. Thirty-six White Suckers were transferred to a 416-L rectangular tank receiving constant flows of aerated well water at the Colorado State University Foothills Fisheries Laboratory (FFL). They were then tempered to the test temperature (8.0°C) from the stream temperature of Spring Creek (10.4°C) over 1 h. The fish were allowed to acclimate to the laboratory environment and study temperature for 25 d. The White Suckers were fed frozen bloodworms to satiation and were visually checked for signs of stress (abnormal coloration, behavior, or an unwillingness to feed) or disease daily. Several fish exhibited stress-indicative coloration and others did not respond to food for several days after being brought into the laboratory, but all fish appeared healthy and were actively feeding at least 2 weeks before we began conducting trials.

All other fishes used were provided by the Wyoming Game and Fish Department (WYGF). These fishes were part of an ongoing captive-holding and growth study being conducted by WYGF at the University of Wyoming Red Buttes Environmental Biology Laboratory (RBEBL); because this was their primary use, there was little emphasis on collecting fish of similar size. Longnose Suckers (n = 65) were collected by backpack electrofishing from the inlet of North Crow Reservoir (South Platte River watershed: UTM zone 13T, 484121 E, 4563317 N, NAD83) northeast of Laramie, Wyoming, on June 3, 2010. Mountain Suckers (n = 161) were collected by backpack electrofishing from Littlefield Creek (Little Snake River watershed: UTM zone 13T, 296466 E, 4591709 N, NAD83) near Rawlins, Wyoming. Bluehead Suckers (n = 50) were collected with trap nets from Ringhal Reservoir (Green River watershed: UTM zone 12T, 587468 E, 4556642 N, NAD83) near Green River, Wyoming, on August 10, 2010. Flannelmouth Suckers were...
collected from the Little Sandy River (Green River watershed: UTM zone 12T, 641532 E, 4684090 N, NAD83), also near Green River, Wyoming, on two occasions in 2011 (August 18, n = 6; October 1, n = 51) by backpack electrofishing. Roundtail Chub were collected from Muddy Creek (Little Snake River watershed: UTM zone 13T, 269755 E, 4590969 N, NAD83) on two occasions in 2011; 10 were collected on July 14, and 40 were collected on October 19.

After collection, all fish were transported directly to the RBEBL in purpose-built fish-hauling tanks. Before transport, hauling tanks were filled with water from a hatchery or dechlorinated municipal water source. The use of water from these sources reduced the likelihood of transporting invasive invertebrates, vertebrates, plants, or disease pathogens in water from the collection site. Water in the hauling tank was kept cool and ice was added, when necessary, to maintain a temperature similar to that at RBEBL. Salt was dissolved in the stocking tanks (1% NaCl concentration by water weight) to reduce hauling stress and as a prophylactic treatment for external parasites. All fish were initially held in 1.2-m-diameter circular tanks; however, Longnose Suckers and Mountain Suckers were moved to separate 0.6-m-diameter tanks on June 7, 2011, and held at initial densities of 20.7 and 6.4 kg/m³, respectively. The Bluehead Suckers were moved to a 4.6-m-long rectangular tank shortly after entering the laboratory and were held at a density of 1.6 kg/m³. The Flannelmouth Suckers were split into two 1.2-m-diameter circular tanks and held at a density of 7.9 or 9.5 kg/m³. The Roundtail Chub were held in a 0.6-m-diameter circular tank. All fish were held at low densities and the holding arrangement was determined by available circular tanks at RBEBL. All fish were monitored for signs of stress and disease throughout the time they were held in the laboratory. It is important to note that the original collection of all species other than the White Sucker was done for an unrelated study, and thus there was no emphasis placed on collecting a wide range of total lengths, as was done for the White Sucker.

The suckers used were identified upon capture by personnel experienced in catostomid fish identification using meristic counts and morphometric characteristics to phenotypically identify the fish to species. Additionally, Bluehead Suckers from Ringdal Reservoir, Flannelmouth Suckers from Little Sandy Creek, and Roundtail Chub from Muddy Creek have been analyzed for genetic purity during previous studies (Douglas and Douglas 2007a, 2007b; Gelwicks et al. 2009). Bluehead Suckers from Ringdal Reservoir are isolated from White Suckers and are 100% genetically pure. While hybridization of Flannelmouth Suckers with White Suckers from Little Sandy Creek does occur, it was determined that phenotypic identification, when compared with genotypic identification, was correct for 99% of Bluehead Suckers and 86% for Flannelmouth Suckers (Gelwicks et al. 2009). Also, the accuracy of these identifications for a subsample of the suckers held for this study was confirmed genetically using high-throughput DNA sequencing and analysis of genetic clustering (E. Mandeville, University of Wyoming, personal communication). Based on the genetic analyses, visual identification was found to be 100% accurate for the fish we used for the swimming trials.

The water source at the RBEBL is a natural spring supplying water that ranges between 6.1°C and 7.8°C, and all tanks were supplied by this source. All suckers at the RBEBL were offered a daily diet consisting of algae wafers, algae cultures on Plexiglas plates, and two pellet diets specifically formulated for June Sucker Chasmistes liorus and Razorback Sucker Xyrauchen texanus at the U.S. Fish and Wildlife Service’s Bozeman Fish Technology Center, Bozeman, Montana. They are commercially produced by Skretting USA (Tooele, Utah) and are the primary diets for hatchery-reared June Suckers and Razorback Suckers. Roundtail Chub were offered daily rations of June Sucker and Razorback Sucker pellets and frozen bloodworms.

Swimming protocol.—All swimming trials (at both the RBEBL and FFL) were conducted in the same 90-L swim tunnel (model 90, Loligo Systems, Tjele, Denmark). In both locations, the swim tunnel was supplied with air-saturated, flow-through water (ca. 0.5–1.0 L/min) from the same source that supplied the fish-holding tanks. Water velocity in the swim tunnel is directly related to the frequency output of the variable speed motor, as displayed on the digital motor controller. We calibrated the flume prior to conducting swimming trials by measuring the water velocity as a function of motor controller output and developed a calibration curve that allowed repeatable velocity settings.

A random catostomid species was selected daily for all catostomid $U_{crit}$ and CAT trials conducted at the RBEBL. The swim tunnel was disinfected overnight with Virkon Aquatic (Western Chemical) prior to each swimming session involving a different species to prevent disease transmission between species. The $U_{crit}$ trials were conducted with 18 Bluehead Suckers (13.1–37.4 cm TL), 13 Flannelmouth Suckers (25.6–34.4 cm TL), 18 Longnose Suckers (12.7–35.8 cm TL), 22 Mountain Suckers (9.7–16 cm TL), 20 White Suckers (10.6–26.5 cm TL), and 20 Roundtail Chub (11.5–25.9 cm TL). Ten constant acceleration trials using each species were also conducted.

For each trial, a fish was selected at random from the appropriate holding tank and measured (SL, FL, and TL in centimeters, wet weight in grams). The fish was then placed in the swim tunnel, an opaque black screen was placed over the forward portion of the swim chamber to provide cover and encourage rheotaxis, and the velocity was set to 0.5 body lengths per second (BL/s; based on TL) for $U_{crit}$ trials, or 10 cm/s for CAT experiments. Velocity increases were started after the >1-h recovery period. For $U_{crit}$ trials, the velocity was increased by 0.5 BL/s every 10 min. Velocity steps were related to fish TL to account for the varied size distributions among the different species (Table 1). For the constant acceleration trials, fish were first subjected to an immediate velocity increase from 10 to 40 cm/s, and then the velocity was subsequently increased by 4 cm/s every 24 s, producing an acceleration rate of 10 cm·s⁻¹·min⁻¹.
All fish were kept under constant remote observation during the trials for proper swimming behavior using a video camera and monitor. Fish often “cheated” by resting against the rear mesh of the swim chamber. When this occurred, the current was either momentarily reversed or pulsed (rapid upwards increase of 10–15 cm/s for <10 s) and returned to the test velocity to encourage the desired swimming behavior. If fish were able to hold a static, nonswimming position at lower velocities through fin and mouth placement the behavior was allowed, as it is a natural behavior employed by some species in flowing environments. Trials were terminated when the fish either became impinged on the rear mesh, or would no longer hold position in the swim chamber without resting against the rear mesh, after four consecutive attempts to restore normal swimming or holding behavior with the techniques described above.

The numbers of fish tested per species for the $U_{\text{crit}}$ study on Bluehead Sucker, Flannelmouth Sucker, Longnose Sucker, Mountain Sucker, and Roundtail Chub. Identical lowercase letters indicate equivalences between the five catostomid species, while identical uppercase letters indicate equivalences among Bluehead Suckers, Flannelmouth Suckers, and Roundtail Chub. Values are means ± SDs.

### ANOVA $P$-value comparison

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**Data analyses.—** All individual $U_{\text{crit}}$ values were calculated using

$$U_{\text{crit}} = U_i + \left( \frac{T_i}{T_{ii}} \right) U_{ii}$$

Brett (1964), where $U_i$ is the highest velocity that the fish was able to maintain for the whole time increment, $U_{ii}$ is the velocity increment (0.5 BL/s), $T_i$ is the time elapsed at the terminal velocity increment, and $T_{ii}$ is the time increment between velocity steps (10 min). Relative $U_{\text{crit}}$ estimates (i.e., length-adjusted $U_{\text{crit}}$) were created for each fish by dividing the $U_{\text{crit}}$ by the TL of individual fish. Comparisons of both of these values were then made among all sucker species and among Bluehead Sucker, Flannelmouth Sucker, and Roundtail Chub.

All statistics were calculated using JMP version 5.0 (SAS Institute, Cary, North Carolina). Differences in TL, wet weight, and monitor.

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holding temperatures, and trial temperatures among species were compared among species with one-way ANOVA. Linear models were used to test for species, fish length (using TL), and interaction effects on absolute $U_{\text{crit}}$ and the relative $U_{\text{crit}}$ across the different catostomid species and for the “three species.” When significant differences ($P < 0.05$) were indicated, Tukey’s post hoc analyses were used to identify treatment means that were significantly different from others.

We plotted fish TL versus absolute and relative $U_{\text{crit}}$ and used linear regression to fit lines to the resulting plots. The same approach was used to illustrate the relationship between the five sucker species’ TL and their gait transition velocities. Finally, we graphically compared the relationship between TL and the $U_{\text{crit}}$ and $U_{\max}$ of the five sucker species using this same approach, albeit with logarithmic lines of best fit.

Videos of the critical swimming trials were analyzed to identify gait transitions. The transitions and endpoints of interest were the maximum station-holding velocity ($U_{\text{SH-max}}$), maximum aerobic swimming velocity (the transition from steady to burst swimming; $U_{\text{A-max}}$), and maximum (impingement) velocity ($U_{\text{max}}$). The $U_{\text{SH-max}}$ was identified as the highest velocity at which fish could maintain position without any backward slippage, to account for exploratory and velocity-refuge-seeking behaviors that occurred throughout earlier portions of the trial. Each of these transition velocities were then plotted against TL. Analyses of variance and Tukey’s analyses were also used to compare the fish lengths (TL), wet weight, holding temperatures, and trial temperatures of the CAT trials. We observed an interesting behavior in some species wherein the high-friction surface of the lips was used to aid station-holding ability. We refer to this behavior as mouth holding. To provide a quantitative measure of this behavior among species, the total time that the behavior was employed and the maximum velocity at which it was effective were also recorded.

**RESULTS**

**Critical Swimming Speed**

*Catostomid comparison.*—Bluehead Sucker, Flannelmouth Sucker, Longnose Sucker, and Mountain Sucker all exhibited significantly different critical swimming velocities across a range of sizes (Table 1; Figure 1), and differences in the way that critical swimming velocity changed with size, as shown by the varying slopes of the regression lines in Figure 1. The effects of species ($P < 0.0001$) and TL ($P = 0.0057$) on $U_{\text{crit}}$ were both significant; however, the interaction effect between species and TL on $U_{\text{crit}}$ was not significant. Similarly, the effects of species ($P < 0.0001$) and TL ($P < 0.0001$) on relative $U_{\text{crit}}$ were again significant, but the interaction was not. There were significant differences in both test and holding temperatures among the five sucker species, though they were all within 0.5°C of each other (Table 1). There were significant differences in both TL and wet weight among all five species (Table 1).
All suckers, with the exception of Flannelmouth Sucker, showed definite length versus $U_{\text{crit}}$ relationships, wherein larger fish achieved higher absolute $U_{\text{crit}}$, but lower relative $U_{\text{crit}}$ (Figure 1). However, the effect of TL on $U_{\text{crit}}$ was only significant for Bluehead Sucker ($P = 0.0500$), Mountain Sucker ($P = 0.0229$), and White Sucker ($P = 0.0004$). The effect of TL on the relative $U_{\text{crit}}$ (BL/s) was significant for Bluehead Sucker ($P < 0.0001$), Flannelmouth Sucker ($P = 0.0407$), and Longnose Sucker ($P = 0.0003$). There was an apparent, but not significant, negative relationship between $U_{\text{crit}}$ and TL for Flannelmouth Sucker (Figure 1). Based on the TL versus relative $U_{\text{crit}}$ linear relationship least-squares means, only Bluehead Sucker and Longnose Sucker were significantly better swimmers than White Sucker, while Flannelmouth Sucker and Mountain Sucker did not significantly differ from any other species (Table 1).

Three-species comparison.—When comparing Bluehead Sucker, Flannelmouth Sucker, and Roundtail Chub, there was a significant species effect on both $U_{\text{crit}}$ ($P < 0.0001$) and relative $U_{\text{crit}}$ ($P < 0.0001$). Among all three species, there was only a significant length (TL) effect on relative $U_{\text{crit}}$ ($P < 0.0001$; Table 1). The interaction effect was not significant for either model. As with the catostomid $U_{\text{crit}}$ comparison, there were significant differences in TL, wet weight, and both holding and test temperatures among all species (Table 1).

Similar to the suckers studied, except for Flannelmouth Sucker, Roundtail Chub showed a significant positive relationship between TL and $U_{\text{crit}}$ ($P = 0.0500$), and a significant negative relationship between TL and the relative $U_{\text{crit}}$ ($P < 0.0001$). Bluehead Sucker appeared to again have the highest overall relative $U_{\text{crit}}$, and Roundtail Chub the lowest. Based on the least-squares means generated from the linear relationships between TL and relative $U_{\text{crit}}$, Bluehead Sucker were significantly faster swimmers than Roundtail Chub; however, Flannelmouth Sucker were not significantly different from either species (Table 1).

### Constant Acceleration

The constant acceleration experiments provide information on the maximum relative swimming velocities of the five sucker species. The fastest of the sucker species was the Bluehead Sucker, followed by the Mountain Sucker, White Sucker, Longnose Sucker, and the Flannelmouth Sucker (Table 2). Interestingly, while the Bluehead Sucker was also the fastest species in the critical swimming velocity trials, the order of the remaining species is different. The three major swimming categories used by the suckers were station holding, steady (aerobic) swimming, and burst-and-glide (anaerobic or unsteady) swimming. For all fish, all transition velocities appeared to increase with TL; however, the relationships were not significant (Figure 2). The transitions did not always follow the expected trend wherein fish would move from station holding to steady swimming, to burst-and-glide swimming, and finally become impinged at the $U_{\text{max}}$. Bluehead Sucker and Mountain Sucker transitioned from steady to burst-and-glide swimming at velocities lower than the $U_{\text{crit}}$, while, according to the relationship between TL and $U_{\text{crit}}$, Flannelmouth Sucker reached $U_{\text{max}}$ before $U_{A_{\text{max}}}$. For White Sucker, the trend appears as expected for smaller fish, but then is essentially reversed for larger fish. We also noted that the relative $U_{\text{max}}$ was always higher than the relative $U_{\text{crit}}$ for fish of similar size (Figure 3).

The constant acceleration trials showed distinct differences in swimming behavior among the five sucker species. Station holding was used more frequently by Bluehead Sucker, Flannelmouth Sucker, and Longnose Sucker than by Mountain Sucker and White Sucker, but Mountain Sucker used station holding more frequently than White Sucker (Table 3). Also, two different types of station holding were observed. Fish either used simple fin placement and body form to maintain position on the swimming chamber floor or walls, or they used the high friction surface of their lips and possibly suction to increase their ability to maintain a static position. Bluehead Sucker used mouth holding most frequently and at much higher velocities than other species (Table 3). The other sucker species tested used limited mouth holding, with the notable exception of White Sucker, which was not observed to employ the behavior (Table 3).

### DISCUSSION

This comparative study on the aerobic and anaerobic swimming performance of catostomid fishes found in the

<table>
<thead>
<tr>
<th>Species</th>
<th>Proportion of fish that exhibited station holding</th>
<th>Proportion of fish that exhibited mouth holding</th>
<th>Mean $\pm$ SD percentage of whole trial spent mouth holding</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bluehead Sucker</td>
<td>1.0</td>
<td>1.0</td>
<td>45.0 $\pm$ 21.1</td>
</tr>
<tr>
<td>Flannelmouth Sucker</td>
<td>0.9</td>
<td>0.5</td>
<td>3.6 $\pm$ 5.2</td>
</tr>
<tr>
<td>Longnose Sucker</td>
<td>0.9</td>
<td>0.8</td>
<td>4.2 $\pm$ 2.9</td>
</tr>
<tr>
<td>Mountain Sucker</td>
<td>0.7</td>
<td>0.7</td>
<td>8.7 $\pm$ 8.6</td>
</tr>
<tr>
<td>White Sucker</td>
<td>0.2</td>
<td>0.0</td>
<td>0 $\pm$ 0</td>
</tr>
</tbody>
</table>
FIGURE 2. Constant acceleration trial gait transition velocities (grey circles = maximum station-holding velocity, grey squares = steady swimming to burst swimming transition velocity, and solid triangles = impingement velocity) plotted against TL for Bluehead Sucker, Flannelmouth Sucker, Longnose Sucker, Mountain Sucker, and White Sucker (BHS, FMS, LNS, MTS, and WHS, respectively). Lines represent linear lines of best fit.
U.S. Intermountain region revealed substantial species-level differences in aerobic and anaerobic swimming ability and in swimming behavior. These interspecific differences suggest that natural resource managers should carefully evaluate whether data from one sucker species could be used as a surrogate for another species. This approach might work when substituting performance data from a slower species, like White Sucker, for that of a faster species, like Bluehead Sucker, when designing a fish passage structure, but the same substitution might be ill-advised when designing a velocity barrier.

The experiments showed that the five sucker species tested represent a continuum of aerobic swimming ability, with Bluehead Sucker reaching the highest aerobic velocities when tested at temperatures of 7.5–8.0°C, followed by Flannelmouth Sucker,
Longnose Sucker, Mountain Sucker, and White Sucker. While we did observe significant differences among holding and test temperatures, the temperature ranges were small (0.5°C and 0.2°C, respectively), and were probably not biologically significant. The differences between the five species are such that they could be placed into three overlapping groups: the fast-swimming Bluehead Sucker and Flannelmouth Sucker, the medium-speed Flannelmouth Sucker, Longnose Sucker, and Mountain Sucker, and the slow-swimming Mountain Sucker and White Sucker. This overlapping performance illustrates the challenge with using performance data from one sucker species when designing an instream barrier or passage structure for another species.

The designer of a fish passage structure could use a conservative approach and substitute data from one of the “slow-swimming” species, like a White Sucker, to establish design criteria for a structure designed to pass a fast-swimming species, like a Bluehead Sucker. The designer could be fairly confident that Bluehead Sucker in the same size range as the White Sucker (10.6–26.5 cm TL) from which the performance data were gathered would be capable of successfully passing the structure. Conversely, trying to use the same data to design an instream fish barrier would not be recommended, because of the substantial difference in performance between the two species, and because one generally wants to prevent passage of 100% of the target species, not just the average member of that species. However, fish trying to negotiate a potential barrier tend to use their fast-glycolytic or anaerobic muscles, so it is important that those values also be considered.

In terms of anaerobic swimming or sprinting ability, the study also showed a continuum of top velocities among the five species, though the order was somewhat different. Therefore, from a barrier design point of view, using performance data from one of the slower species (e.g., Flannelmouth Sucker) to establish critical barrier velocities might result in a barrier that fails to prevent the upstream movement of a faster species. This is because they can either achieve a higher sprinting velocity or can maintain an equivalent velocity for a longer period of time (endurance at velocities above aerobic levels was not quantified in this study). Not only do the different sucker species have different aerobic and anaerobic swimming abilities, they also display different swimming behaviors, which would further complicate any attempts to use data interchangeably between species.

The swimming behaviors of the five species of sucker were notably different, and again formed a continuum from species wherein all individuals used some form of station-holding behavior (Bluehead Sucker) to White Sucker, where only 20% of tested fish used station-holding behavior. Interestingly, more than 50% of the individual fish in every sucker species tested except White Sucker used station-holding behavior and perhaps gained some energetic advantage by doing so. Fishes that can hold their position in the swimming flume without using their trunk musculature to do so presumably expend less energy than those that use active swimming to maintain position. Thus, one possible reason for the relatively poor performance of the White Sucker in the critical swimming velocity experiments relative to the other species is simply that, unlike the other species, most of the White Suckers swam continuously and thus expended their aerobic energy more quickly. This may also explain why Bluehead Suckers were able to clearly outperform the other four species, given that they spent an average of 45% of their time using station-holding behaviors. From a management standpoint, these differences in swimming behavior deserve consideration when designing passage and barrier structures. Fish that use station holding would be more capable of ascending an instream structure because they would be able to use nonswimming behaviors to hold their position to rest, whereas species that swim continuously would find the same ascent more energetically costly and might fatigue before successfully completing passage.

When viewed individually, the five sucker species generally showed the expected relationships between swimming performance and fish size, where larger fish reached higher absolute swimming velocities, while smaller fish reached higher relative swimming velocities. The one exception to this was the Flannelmouth Sucker, which did not show a significant positive relationship between TL and critical swimming velocity. This likely results from the lack of a wide range of tested sizes (TL range, 25.6–34.4 cm) rather than representing the first documented case of length-independent swimming ability. The different slopes of the regression lines showing the relationship between fish size and relative swimming ability provide further evidence for the contention that sucker swimming ability cannot be readily interchanged between species. Species such as the Bluehead Sucker show a much more rapid decline in performance than do species like White Sucker, though the reason for this difference is not known.

Our results compare favorably with data from other sources. Ficke et al. (2012) measured mean relative \( U_{\text{crit}} \) values ranging from 1.8 to 2.5 BL/s for White Suckers 90–158 mm TL, acclimated to 15°C and also from Spring Creek in Fort Collins, Colorado. The performance of White Suckers of similar size used in this study falls within the same range, suggesting that \( U_{\text{crit}} \) is a repeatable measure for this species. Flannelmouth Suckers from 105 to 123 mm TL swum at 10°C had a mean \( FV_{50} \) (velocity at which 50% of individuals cannot swim for a full 30 min) of 38.3 cm/s (Ward et al. 2002). This value is similar to the \( U_{\text{crit}} \) for Mountain Suckers of the same size that we evaluated. This suggests that smaller Flannelmouth Suckers also have a higher \( U_{\text{crit}} \) than smaller White Suckers. Ward et al. (2003) used a swimming procedure with a stepwise increase in velocity similar to the CAT trials used in our study and found that the average maximum velocity reached for Bluehead Suckers 61.5–81.5 mm TL was 86.62 cm/s. This velocity corresponds well with the predicted values for impingement velocity of 60–80-mm fish that we measured.

The so-called “three species” (Bluehead Sucker, Roundtail Chub, and Flannelmouth Sucker) co-occur in parts of the upper
Colorado River system and are often the subject of multispecies management efforts, so comparisons of their swimming abilities are appropriate. Bluehead Sucker was the fastest species, followed by the Flannelmouth Sucker and the Roundtail Chub when relative aerobic swimming ability was compared. As one might expect, the two sucker species were able to use station holding during the \( U_{\text{crit}} \) experiments, while the Roundtail Chub swam continuously and did not attempt to do so. Myrick and Cech (2000) reported a similar phenomenon in a study comparing the swimming performance of Sacramento Suckers \( C. \) and Roundtail Chub under one set of environmental conditions. Temperature is directly linked to swimming performance, and fish generally have a temperature range where performance is maximized (Beamish 1978; Batty and Blaxter 1992). If these fishes had been tested at higher temperatures (within the species’ preferred thermal ranges) it is likely that swimming velocities and stamina would also have increased. For instance, Ward et al. (2002) found a 40% increase in the swimming ability of Flannelmouth Suckers between 10°C and 20°C. However, Myrick and Cech (2000) reported that the critical swimming velocities of 19–20-cm TL Sacramento Suckers tested at 10, 15, and 20°C were temperature independent and point out that of the fishes tested in their study Sacramento Suckers occupy the widest elevational and latitudinal gradients and thus may have a broader thermal range over which their swimming performance is optimized.

Our results may also have been influenced by the unavoidable necessity of using fish that had been held under laboratory conditions for different time intervals prior to testing. The swimming performance of certain catostomids can decrease in association with long periods of time between the time when the fish are captured and the swimming tests are conducted (Ward et al. 2002). However, because White Suckers spent the shortest amount of time (25 d) in the laboratory prior to study yet still exhibited relatively poor swimming ability compared with other species that were held for much greater amounts of time (1–2 years), we remain confident in the trends observed wherein White Sucker critical swimming velocity was consistently lower than that of the other sucker species.

While our study does provide useful information on the relative abilities of the five tested sucker species and Roundtail Chub, it should be viewed as a pilot study. A more thorough evaluation of swimming performance should be conducted on each of the five sucker species to better inform fishway or barrier design. This future study should combine measurements of swimming endurance at fixed velocities (fixed velocity tests) with tests of fish performance in scaled-down fishways so that the effects of fish behavior can be integrated with their swimming performance. Additionally, this study should be conducted on all life stages and sizes of the target species. At a minimum, this type of study should be conducted for the White Sucker if designing structures for passage of all of these suckers is the main objective for future conservation work.

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