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**MORPHOLOGY AND
SWIMMING
PERFORMANCE OF
UTAH FISHES:
CRITICAL
INFORMATION FOR
CULVERT DESIGN IN
UTAH STREAMS**

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RESEARCH



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16. Abstract <p>This study provides burst and prolonged swimming performance information for 10 species of Utah fish to aid in culvert design. Additionally we explore the possibility of predicting swimming in Utah fishes based on similarities in habitat use and body shape. Unfortunately, habitat use and body shape appear to be weak predictors of swimming performance. Body size was the strongest predictor of swimming speed. With the exception of salmonids, most species were capable of swimming at comparable velocities for each size class. These results indicate that culvert design based on the relatively similar values of swimming performance for non-salmonids (approximately 1.3 ft/sec prolonged speed and 2.4 ft/sec burst speed for juveniles; 1.5 ft/sec prolonged speed and 3.3 ft/sec burst speed for mean-sizes; 1.9 ft/sec prolonged speed and 4.3 ft/sec burst speed for large individuals) will ensure that all species are able to traverse instream culverts. Salmonid-based estimates of swimming performance for culvert design may inhibit fish passage in the majority of native streamfishes by predicting swimming velocities well above their physical ability.</p>					
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1.0 EXECUTIVE SUMMARY

Historically, fish passage has received limited attention in the design and implementation of culverts. The limited number of streams in which fish passage is considered relies primarily on species by species estimates of swimming performance for salmonids. This study provides important swimming performance information for 10 species of Utah fish and evaluates the alternative of predicting swimming performance for suites of Utah fishes based on similarities in habitat use and body shape. Swimming performance was measured as burst speed using a simulated predator attack and as prolonged speed using a step-endurance test in a laboratory flume. Morphology was measured using geometric morphometric techniques. A difference in swimming behavior in nearly one half of the species tested was observed in the step-endurance test in which benthic species exhibited bracing behavior as an alternative to body-caudal fin (BCF) propulsion. Swimming performance exhibited only a weak relationship with predictive groupings based on habitat or morphology. Rather, a species-based model was the best predictor of swimming performance. Although individual species exhibited variation in swimming performance, body size was the strongest predictor of absolute swimming performance across all predictive models. With the exception of salmonids, most species were capable of swimming at equivalent velocities for each size class (approximately 1.3 ft/sec prolonged speed and 2.4 ft/sec burst speed for juveniles; 1.5 ft/sec prolonged speed and 3.3 ft/sec burst speed for mean-sizes; 1.9 ft/sec prolonged speed and 4.3 ft/sec burst speed for large individuals). These results indicate that culvert design based on the relatively similar values of swimming performance for non-salmonids will ensure that all species are able to traverse instream culverts. These results also indicate that culvert design based exclusively on swimming performance values for salmonids may greatly overestimate swimming capabilities for non-salmonids.

2.0 INTRODUCTION

Maintaining habitat connectivity in rivers and streams is an important factor in conservation of native stream fishes, especially where fish make seasonal migrations between spawning and rearing habitats (Shrank & Rahel 2004). The presence of impassible velocity barriers, such as some culverts creates non-natural obstructions and inhibits long term health of western stream species by creating water velocities greater than their maximum swimming ability, thus restricting regular movement within their range (Warren & Pardew 1998; Neraas & Spruell 2001). Barriers to movement created by impassible culverts can also result in genetic and demographic isolation leading to reduced genetic diversity which can potentially threaten long term population health (Laroche & Durand 2004; Wofford et al. 2005). Populations that show dispersal as an important part of their life history essentially become separated into isolated groups as a result of their inability to maneuver thorough high-velocities created by in-stream structures. Furthermore, barriers to movement may inhibit recovery of fish assemblages following disturbance (Winston et al. 1991; Detenbeck et al. 1992).

Traditional culvert design for fish passage has focused primarily on state and federally listed stream fishes, which are mainly comprised of migratory salmonids (i.e. trout, salmon, and char) (e.g. Peake et al. 1997; Gibson et al. 2005). However in the state of Utah, many non-salmonids also exhibit regular patterns of migration and dispersal as an essential part of their life history (Lindsey & Northcote 1963; Crist & Holden 1980; Decker & Erman 1992; Whitney & Belk 2000). Because of these regular movement patterns, population dynamics and long term health of these species are directly dependent upon unimpeded movement in western streams (Cowen et al. 2006; Coombs & Rodriguez 2007). To avoid negatively impacting populations of native stream fishes through habitat fragmentation and habitat loss, it is important to know the swimming performance of native Utah species in relation to conditions created by culvert placement.

There is a general expectation that swimming ability can be predicted by body form and size. Biomechanical studies have shown that the optimal body profiles for maximal fast-start and continuous swimming performance are mutually exclusive (Webb & Skadsen 1980; Webb 1984; Wakeling 2006). Continuous, or prolonged speed is favored in fishes with a narrow caudal peduncle, a large anterior depth and mass, a high aspect ratio (aspect ratio (A) = h^2/S , where h = height of tail and S =surface area of caudal blade), a lunate (crescent shaped) tail and a relatively stiff streamlined anterior body (Figure 1; Hynes 1970; Webb 1982a, 1984; Videler 1993). Burst speed is favored in species that can displace large amounts of

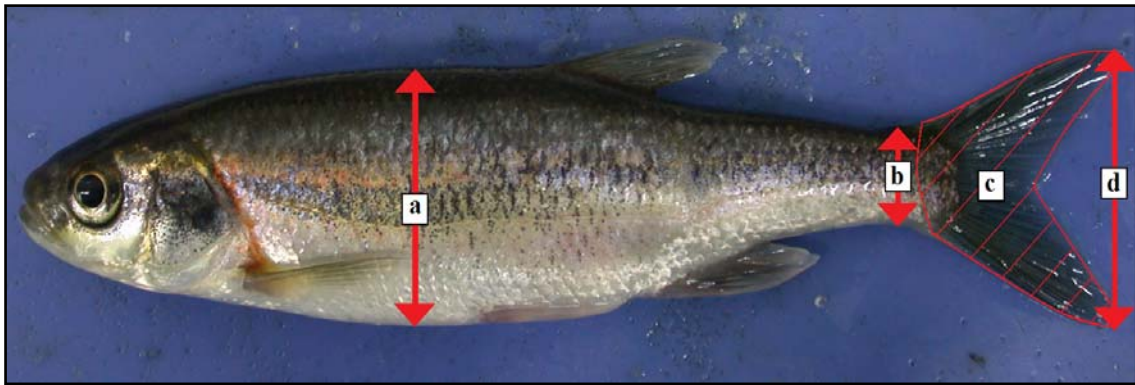


Figure 1. Photograph of redside shiner (*Richardsonius balteatus*) illustrating (a) anterior depth, (b) caudal peduncle depth, (c) surface area of caudal blade, and (d) height of tail.

water, including those with a large tail, a flexible muscular body relative to body mass, and large body depth around the caudal region (Webb 1982b, 1984). Consequently, inherent trade-offs between prolonged and burst swimming have been demonstrated in a large number of investigations (Lighthill 1975; Weihs 1972, 1973; Webb 1973, 1977). Webb (1984) recognized that many taxa do not necessarily specialize in either morphological strategy, but may take advantage of an intermediate strategy between the two body profiles. As a result of differing external morphologies and their influence on performance, design and implementation of a fish-friendly culvert should take into account not only the performance of all fish species present in given stream, but also upon their performance with regard to variation in size and morphology (body shape). Design and implementation of a fish friendly

culvert thus necessitates empirically testing swimming ability and swimming ability due to body shape.

While characterizing variation in size and morphology of fish in every Utah stream may be unreasonable, we may be able to identify general trends across all species. If we can successfully predict swimming ability from similarities in morphology and behavior, then species with unknown swim abilities may be reliably estimated from data on species similar in form and behavior (Chan 2001). Species may be assembled into functional groups that represent a general body form and behavior for that assemblage of species (Coffman et al. 2005). The expectation is that most of the variation in swim performance would be between, rather than among species within functional groups and that the trend with size would be consistent within groups. If such functional groups do indeed exist, it would make the design and installation of culverts more predictable and more standardized, thus streamlining the process and decreasing costs.

In this study, we explore the behavior, morphology, and swimming performance of seven naturally co-occurring stream fishes from the Great Basin, several of which are sensitive species (see Table 1). We test the hypothesis that swimming performance can be reliably predicted from functional groups based on similarities in habitat use and body shape. This hypothesis was tested by first, examining how swimming performance differed between benthic and mid-water stream fishes (habitat-based functional groups). We then used morphological group-based assemblages to examine how shape affected swimming performance independent of habitat use. Finally, we used a species-based model as a predictor of swimming performance. Because morphology can influence fast start and continuous swimming in different manners, we used both burst and prolonged speed as swimming performance estimates.

Table 1. Utah sensitive fish species list. Adapted from UDWR (2007).

Federal Candidate Species	
(None)	
Federally Threatened Species	
Lahontan Cutthroat Trout (introduced)	<i>Oncorhynchus clarkii henshawi</i>
Federally Endangered Species	
Humpback Chub	<i>Gila cypha</i>
Bonytail	<i>Gila elegans</i>
Virgin Chub	<i>Gila seminuda</i>
Colorado Pikeminnow	<i>Ptychocheilus lucius</i>
Woundfin	<i>Plagopterus argentissimus</i>
June Sucker	<i>Chasmistes liorus</i>
Razorback Sucker	<i>Xyrauchen texanus</i>
Conservation Agreement Species	
Bonneville Cutthroat Trout	<i>Oncorhynchus clarkii utah</i>
Colorado River Cutthroat Trout	<i>Oncorhynchus clarkii pleuriticus</i>
Virgin spinedace	<i>Lepidomeda mollispinis mollispinis</i>
Least Chub	<i>Iotichthys phlegethontis</i>
Roundtail Chub	<i>Gila robusta</i>
Bluehead Sucker	<i>Catostomus discobolus</i>
Flannelmouth Sucker	<i>Catostomus latipinnis</i>
Wildlife Species of Concern	
Northern Leatherside Chub	<i>Lepidomeda copei</i>
Southern Leatherside Chub	<i>Lepidomeda aliciae</i>
Desert Sucker	<i>Catostomus clarkii</i>
Yellowstone Cutthroat Trout	<i>Oncorhynchus clarkii bouvieri</i>
Bear Lake Whitefish	<i>Prosopium abyssicola</i>
Bonneville Cisco	<i>Prosopium gemmifer</i>
Bonneville Whitefish	<i>Prosopium spilonotus</i>
Bear Lake Sculpin	<i>Cottus extensus</i>

The general expectation was that functional groups consisting of benthic species would show dramatic differences in performance compared to groups consisting of mid-water species. We also provide an initial estimate of swimming performance for several previously unexamined Utah stream fishes.

3.0 RESEARCH METHODS

We measured morphology and swimming performance in 465 individuals from ten fish species in the Great Basin of the western USA, representing four taxonomic families (Cottidae, Catostomidae, Cyprinidae, Salmonidae) and nine genera. Swimming performance was quantified as burst and prolonged swimming speed in a laboratory setting. Shape was quantified using geometric morphometric techniques (Zelditch et al. 2004). Species tested included: mottled sculpin (*Cottus bairdi* Girard; n=52), mountain sucker (*Catostomus platyrhynchus* Cope; n=44), longnose dace (*Rhinichthys cataractae* Valenciennes; n=56), speckled dace (*Rhinichthys osculus* Girard; n=46), southern leatherside chub (*Lepidomeda aliciae* Jouy; n=45), redbelt shiner (*Richardsonius balteatus* Richardson; n=30), and brown trout (*Salmo trutta* L.; n=41). These taxa were selected because they all experience similar selective environmental pressures associated with cool, high gradient mountain streams, yet they exhibit a wide range of morphological diversity. Swimming performance tests were also completed for Bonneville cutthroat trout (*Oncorhynchus clarki utah* Suckley; n=53), least chub (*Iotichthys phlegethontis* Cope; n=55) and June sucker (*Chasmistes liorus* Jordan; n=34), but were excluded from this analysis due to the different selective environments in which least chub and June sucker occur (i.e. lentic systems), and the hatchery origin and narrow range of body sizes tested in Bonneville cutthroat trout (See Figure 2 for photos of species used).

4.0 DATA COLLECTION

4.1 Collection & Maintenance

Individuals used in this study were collected from four field locations in central Utah by means of electrofishing and then transported to a housing facility in aerated coolers (see Table 2 for collection locations). All wild fish were collected and tested between 31 July 2007 and 23 October 2007 during low flow periods. Hatchery individuals were tested through 15 Jan 2008. Because of similar environmental conditions associated with the collection time (i.e. low water velocities, no extremes in temperature), all wild individuals are assumed to be similarly physically conditioned.

Collected fish were housed in a laboratory facility on the campus of Brigham Young University, Utah. Prior to placing in aquaria, standard length (distance from the tip of the nose to the insertion of the caudal fin) of each fish was measured to the nearest mm. Individuals were housed in 55 gallon aquaria partitioned into four equal sections with plastic mesh (mesh size=0.016 ft). Each section housed one large and one small individual to ensure easy identification without the need of physically tagging individuals. Fish were kept in laboratory tanks and allowed to acclimate to laboratory conditions for at least 24 hours prior to the commencement of swimming trials. Fish were fed hatchery trout feed daily until satiated. A short day photoperiod of 12:12 ld was maintained throughout the entire experiment. Dechlorinated municipal water was changed weekly with the commencement of swimming trials for each species. To ensure that performance of collected individuals would reflect wild conditions, all tests for wild fish were completed within one week following collection.



Mottled sculpin (*Cottus bairdi*)



Mountain sucker (*Catostomus platyrhynchus*)



Longnose dace (*Rhinichthys cataractae*)



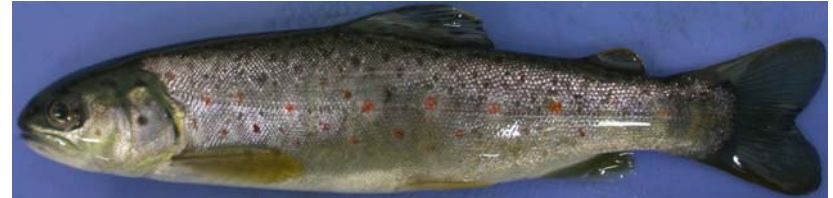
Speckled dace (*Rhinichthys osculus*)



Southern leatherside chub (*Lepidomeda aliciae*)



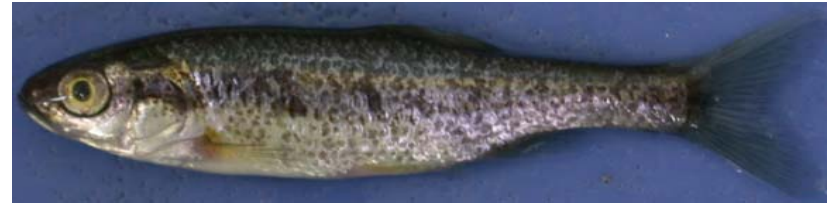
Redside shiner (*Richardsonius balteatus*)



Brown trout (*Salmo trutta*)



Bonneville cutthroat trout (*Oncorhynchus clarki utah*)-juvenile



Least chub (*Iotichthys phlegethontis*)



June sucker (*Chasmistes liorus*)

Figure 2. Species of Utah fish used in this study.

Table 2. Summary of sample sizes and collection locations for species used in the study. N represents sample size and SE indicates standard error of the mean.

Species	N _{total}	Collection location	Mean Standard Length (mm)	Range (mm)	SE
Mottled sculpin	52	Diamond Fork, UT	63.3	29-86	1.56
Mountain sucker	44	Soldier Creek, UT	93.91	43-150	4.82
Longnose dace	56	Soldier Creek, UT	65.18	35-91	2.33
Speckled dace	46	Salina Creek, UT	69.96	46-86	1.65
Southern leatherside chub	45	Soldier Creek, UT	83	39-107	2.57
Redside shiner	30	Fish Creek, UT	79.8	34-112	3.14
Brown trout	41	Diamond Fork, UT	98.23	76-116	1.43
Bonneville cutthroat trout	53	Little Dell & Manning Meadows Hatcheries, UT	54.67	39-70	1.26
Least chub	55	Wahweap Hatchery-Big Water, UT	32.24	21-47	0.77 6
June sucker	34	Fisheries Experiment Station-Logan, UT	86.56	26-205	10.3 2

Laboratory water temperatures were maintained at $17.0^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ ($62.6^{\circ}\text{F} \pm 0.9^{\circ}\text{F}$) and near saturation with oxygen. This represents the mean water temperature of all sample sites during the collection period (range= $14\text{-}20^{\circ}\text{C}$) ($57.2^{\circ}\text{-}68^{\circ}\text{F}$) and falls within the range of preferred temperatures for all species tested (Sigler & Sigler 1987). While swimming performance is clearly optimized for certain taxa at different temperatures (Beamish 1978; Lee et al. 2003), the temperature values at which individuals were tested reasonably simulate conditions at which these taxa all co-occur. This analysis provides a starting point for understanding shape and performance relationships in stream fishes under conditions similar to what may be experienced in the wild by fishes used in this analysis.

4.2 Morphometric Analysis

We measured variation in body shape using geometric morphometric techniques. We generated shape variables for each individual using the thin-plate spline approach in the tpsRelW morphometric software (Rohlf 2007). Geometric morphometric techniques quantify variation in shape by comparing the spatial relationships between a set of user-defined landmarks and allows visualization of this variation through thin plate spline diagrams. The shape variables that quantify this variation, also known as relative warps scores, describe individual variation against a mean or group-averaged shape (Zelditch et al. 2004). In total, we used 18 landmarks at consistent locations across all species overlaid onto the lateral view photograph of each individual (Figure 3) using tpsDig2 (Rohlf 2006); 11 landmarks were designated as ‘sliding’ landmarks. These landmarks characterize morphological traits that are predicted to confer maximal burst and

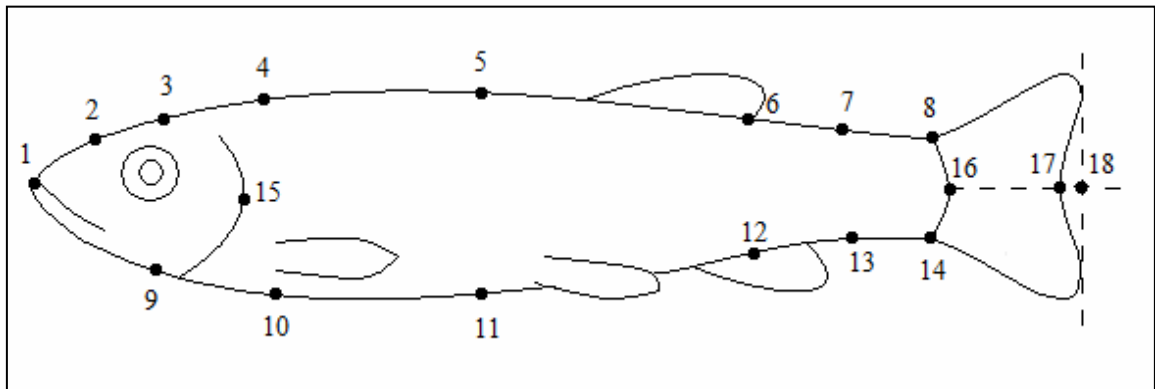


Figure 3. Locations of 18 landmarks used for geometric morphometrics. Full landmarks include: (1) tip of the snout, (8) dorsal insertion of the caudal fin, (14) ventral insertion of the caudal fin, (15) longest point of the operculum, (16) lateral insertion of the caudal fin, (17) fork of the tail, (18) projected total length. Landmarks 2-7 and 9-13 were designated as semi-landmarks. Semi-landmarks represent shape at proportional distances between full landmarks.

swimming performance (Webb 1984). Landmarks 1-5 and 9-11 characterize relative anterior body depth and length, landmarks 6-8 and 12-14 describe the depth and length of prolonged the caudal peduncle region, landmarks 16-18 quantify tail size and fork depth, and landmark 15 characterizes head size relative to the anterior body shape.

4.3 Burst Speed

Burst speed was measured using a simulated predator attack in a laboratory observation arena (Figure 4). The arena consisted of a 3.28 ft x 3.28 ft white acrylonitrile-butadienestyrene (ABS) plastic octagonal arena with 0.49 ft high walls. The center of the arena contained a 0.66 ft diameter clear-plexiglass cylinder that receded into the bottom of the arena, constraining individuals to the center of the observation arena while acclimating and previous to the simulated attack. The arena was completely enclosed on all sides except for one side that had two small 0.49 ft x 0.16 ft doors that allowed the mock predator to be projected into the arena towards the tested individual. The observation arena was situated within a larger 300 gallon, 4.92 ft diameter circular poly-vinyl chloride (PVC) tank suspended by a platform of ABS plastic. Adjacent to the observation arena and also situated within the larger circular tank was the mock-predator platform. The mock predator platform consisted of a 0.82 ft polycarbonate model representing the anterior portion of an adult brown trout (*Salmo trutta*) and was situated adjacent to the observation arena and attached to the platform by an aluminum runner which allowed the mock predator to slide freely into the observation arena. A white cloth covering the observation arena eliminated outside disturbances and premature startling of acclimating fish. Water was maintained at $17.0^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ ($62.6^{\circ}\text{F} \pm 0.9^{\circ}\text{F}$), 0.4 ft depth, and near saturation with oxygen.

For each burst swimming trial, a single individual was introduced into the clear confinement cylinder in the center of the tank, and allowed to acclimate for 15 minutes. After the acclimation period, the cylinder was lowered to the level of the bottom of the arena and the mock-predator was rapidly propelled through the arena doors towards the test subject. Test fish were always facing the arena doors before the mock attack was initiated. Burst speed response was recorded directly from above using a high speed digital video camera (Phantom v4.2, Vision Research, Wayne, NJ, USA) at $200 \text{ frames}\cdot\text{sec}^{-1}$. Burst speed was measured with the aid of the Phantom Camera Control software v 8.4 (Vision Research, Wayne, NJ, USA). The software electronically calculates the velocity of a moving object using the distance divided by time equation.

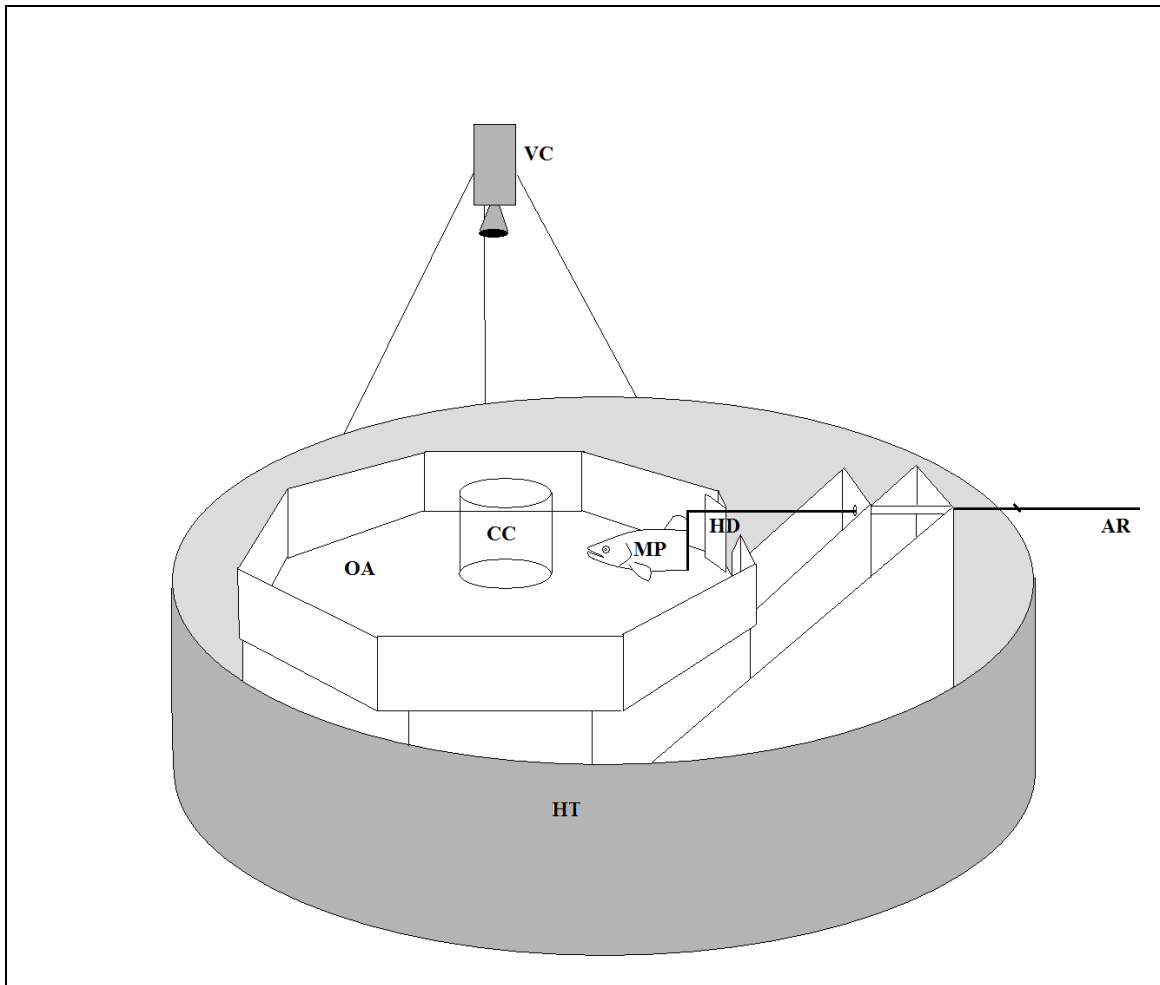


Figure 4. Three-dimensional representation of observational tank used to measure burst speed. VC, video camera; OA, observation arena; CC, confinement cylinder; MP, mock predator; HD, hinged doors; AR, aluminum runner.

Time is measured by multiplying the inverse of the framing rate by the number of frames recorded from start to finish of a user-defined video recorded event. Distance is calculated by indicating a two-point distance from the starting and ending position of the measured object set to a user-defined distance scale. A 0.033 ft square grid drawn on the bottom of the arena was used as a length reference to create the distance scale.

Burst speed was estimated using the insertion of the dorsal fin as a reference point relative to the swimming performance of the whole individual. The insertion of the dorsal fin acts as a center of mass and reduces the variation in swimming performance due to undulations of the tail and head of the fish. Burst speed occurs in three distinct stages (Weihs

1973). Stage one consists of a unilateral contraction of muscles, bending the fish into a C-shape. Stage two consists of a strong propulsive stroke of the tail, projecting the fish forward and ends when the tail stroke reaches maximum exertion on the opposite side of the body. Stage three consists of a gliding or continuous swimming behavior. Burst speed was measured from the end of stage one to the end of stage two, measured in $\text{ft}\cdot\text{s}^{-1}$. Burst speed trials were always performed previous to prolonged speed trials.

4.4 Prolonged Speed

We measured prolonged swimming speed using a step endurance test in a Blazka-type swimming chamber (Brett 1964). Step endurance tests are a convenient way of quantifying critical swim velocity by progressively testing over a range of water velocities, and require smaller sample sizes in comparison to fixed velocity tests (Hammer 1995). The swim chamber for the experiment consisted of a clear acrylic rectangular observation area (0.66 ft tall x 0.66 ft wide x 2.62 ft long) connected to a downstream reservoir and an upstream flow conditioning section (Figure 5). An impeller-powered 7½ HP motor situated between the reservoir and flow conditioning section cycled water through the observation area. Each test fish was restricted to the observation area by a 0.13 ft long plastic grid with 0.023 ft diameter round openings on the upstream end, and a metal screen with 0.23 ft square openings on the downstream end. To reduce turbulence, all water passing through the pump was directed through a 0.98 ft long flow conditioning section consisting of a plastic honeycomb with 0.023 ft wide openings held in place by a 0.003 ft wide opening wire mesh. Following the flow conditioning section, water passes through a contraction section which reduces the cross-sectional area and accelerates the flow into the observation section. During all trials, water was maintained at $17.0^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ and near saturation with oxygen. Water velocities were controlled by specifying the shaft frequency of the pump using a GE model AF-300 inverter. Average water velocity in the swim chamber was measured by averaging the velocity measurements of nine equally spaced quadrants across a cross section of the observation area measured using a Swoffer model 3000 flow meter.

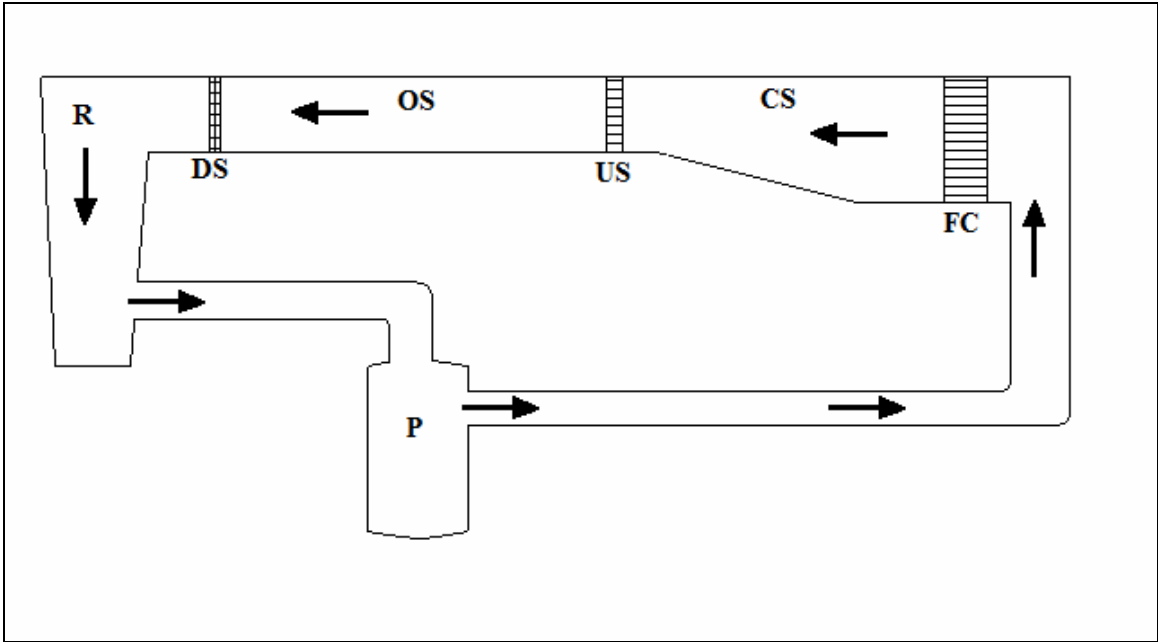


Figure 5. Representation of the swimming chamber used for prolonged swimming performance tests. FC, flow conditioner; CS, confinement section; US, upstream screen; OS, observation section; DS, downstream screen; R, Reservoir; P, pump. Arrows indicate current directions.

Trials were initiated by placing an individual in the observation section for 15 min without flow. After this acclimation period, water velocities were increased by $0.33 \text{ ft}\cdot\text{s}^{-1}$ every 5 min until the fish could no longer maintain position and became impinged on the downstream metal screen. Several successive taps on the fish's caudal peduncle with a plastic rod were employed to encourage individuals resting on the metal screen to continue swimming. When an individual would no longer respond to stimulation following impingement, the swimming trial was terminated, the water velocity returned to zero and the time at fatigue and velocity at fatigue recorded (Beamish 1978; Hammer 1995). Individual fish were then promptly euthanized with an overdose of MS-222, placed on their right side in a dissection tray and digitally photographed for morphometric analysis.

Critical swimming velocity, or the velocity at which fish become fatigued (U_{crit} , measured in $\text{ft}\cdot\text{s}^{-1}$) was calculated using the following formula (Brett 1964):

$$U_{\text{crit}} = V_p + (T_f/T_i)V_i \quad (1)$$

where:

V_p = the highest velocity maintained for the full 5-min period ($\text{ft}\cdot\text{s}^{-1}$)

V_i = the velocity increment ($0.33 \text{ ft}\cdot\text{s}^{-1}$)

T_f = the elapsed time at the fatigue velocity (in min)

T_i = the time between velocity increases (5 min)

5.0 DATA EVALUATION & STATISTICAL ANALYSIS

An analysis of covariance (ANCOVA) using the SAS statistical analysis software series (SAS 1987) was employed to test the hypothesis that swimming performance can be predicted by functional group association. The analysis was conducted using three models based on the following functional groups: 1) habitat use groups, 2) morphological groups, or 3) individual species. All three models were carried out first using burst speed and then prolonged speed data as response variables, for a total of six ANCOVA tests. Log-transformed swimming performance speeds (in $\text{ft}\cdot\text{s}^{-1}$) were used as the response variables in all three models. In the 1) habitat use model, functional groups were delineated as either benthic or mid-water based on life-history information compiled for each species (Sigler & Sigler 1987). The benthic species group consisted of mountain sucker, longnose dace, mottled sculpin and speckled dace while the mid-water group consisted of brown trout, leatherside chub and reidside shiner. In the 2) morphological model, a cluster analysis was performed to group fish according to similarities in shape using Euclidean distances, processed with the PRIMER 6 software package (Clarke & Gorley 2006). Mean relative warps scores for each species, generated in tpsRelw were used as shape variables in the cluster analysis. The 3) species model was void of any *a priori* group predictions and provides a standard for comparison for functional groupings based strictly on swimming performance values. To correct for inherent size differences among individuals and groups, a standardized measure of body size (Z-score) was used as a covariate in the analysis. The Z-scores were calculated using the formula:

$$z=(x-\mu)/\sigma \quad . \quad (2)$$

where:

z = the standardized score

x = the raw score to be standardized (standard length of an individual, in mm)

μ = the population mean

σ = the population standard deviation.

The use of z-score size provides a standardized estimate of size across all taxa where the mean size for one species may differ greatly from another due to inherent differences in body size. Because the sample sizes and ranges of collected individuals do not provide an accurate representation of the actual wild population characteristics, both the population means and standard deviations used to calculate z-score sizes were taken from previous studies that contained accurate size distributions for the taxa used in this analysis (Hepworth 2006; Houston & Belk 2006; Beavers 2008). Due to a particularly narrow sample size range in brown trout, swimming performance data for burst and prolonged speed for larger individuals from similar performance tests (Magnan 1929; Blaxter & Dickson 1959; Peake et al. 1997) were included in the analyses (n=43). To illustrate differences in swimming performance among species, least squares means estimates of swimming performance at three standardized sizes were calculated and plotted. The three size classes used represent small (z-score size= -2), mean (z-score size=-0.5) and large bodied individuals (z-score size= 2).

To compare the relative performance of each of the three models, we used a model selection procedure based on Akaike Information Criteria (AIC). AIC scores were compared among the three models and the model with the lowest AIC score was chosen as the best fitting (reviewed by Johnson & Omland 2004).

6.0 RESULTS

6.1 Morphological Analysis

Morphological analysis using tpsRelw generated a total of 32 relative warps scores for each individual, with 99% of the observed variation explained in the first 17 relative warps. The cluster analysis produced a total of six possible morphological

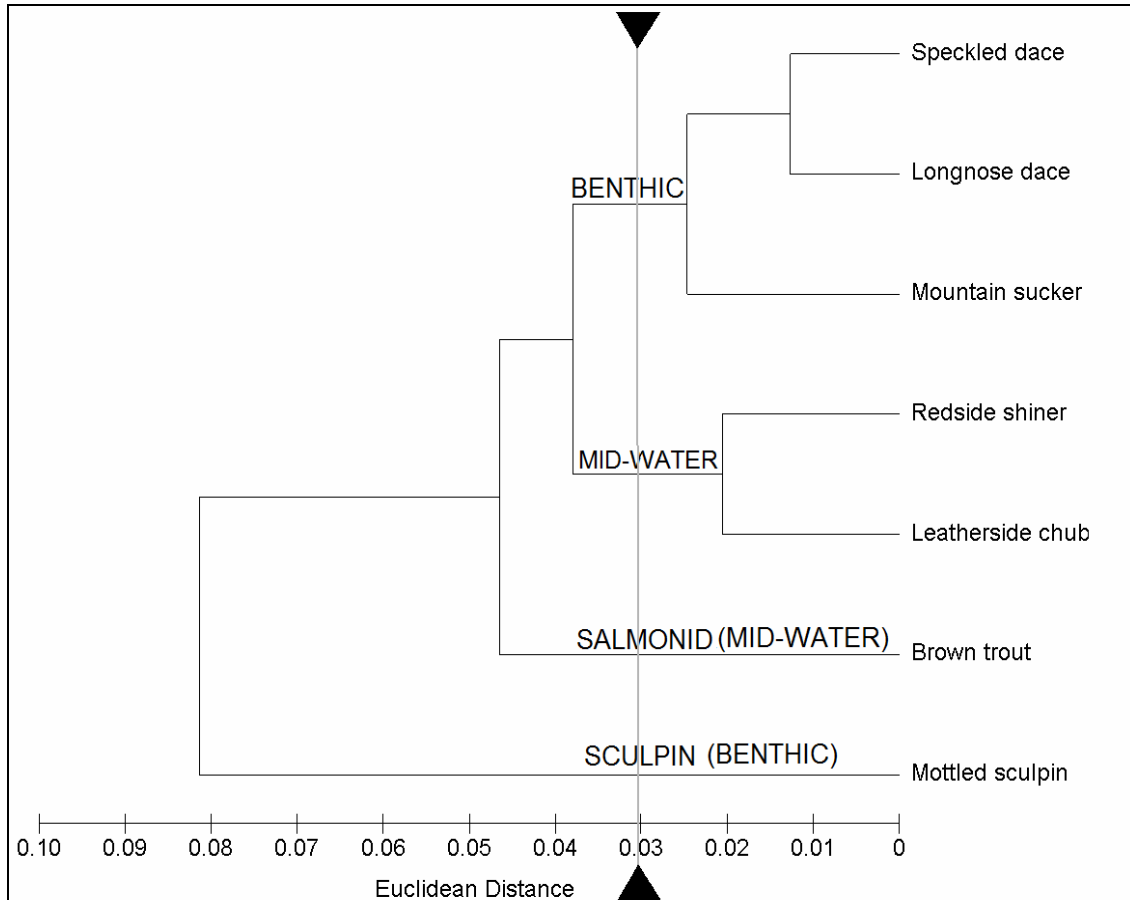


Figure 6. Cluster analysis of morphological and habitat relationships of seven stream fishes from the Great Basin. Triangle and line represents the level of similarity used for the morphological groupings.

groupings, one for each node at descending Euclidean distances (Figure 6). The grouping produced at a Euclidean distance of 0.03 consists of four distinct assemblages that strongly correspond to habitat use and taxonomy and was used as the predictive morphological group for the ANCOVA. Groupings produced at this level consist of a sculpin group (mottled sculpin), a salmonid group (brown trout), a mid- water minnow group (leatherside chub and reidside shiner) and a benthic minnow group (mountain sucker, speckled dace and longnose dace). While there are five other approximations of shape groups available for these taxa, the four group model was selected because of its biological significance in preserving the habitat similarities among species within each morphological group, yet adequately accounts for the morphologic variation associated with these groups.

6.2 Swimming Performance & Behavior

Swimming tests for the species used in the analysis were completed for 247 individuals with an approximately equal representation of swimming performance measures recorded for each of the seven species tested. (Appendix A contains graphical results of the raw swimming performance data for all ten species, as well as a table of basic descriptive statistics for each swimming test. No inferences in this report are made based on these results and are intended only as a means of preserving important data.) Critical swim velocity tests revealed a difference in swimming strategies among observed species. Mottled sculpin, mountain sucker, speckled dace and longnose dace exhibited bracing behaviors in response to high water velocities. Thus, reported U_{crit} values for this species should instead be considered as critical holding velocities, or slip speed velocities (Rimmer et al. 1985). Bracing behavior in mottled sculpin was comprised of an absence of caudal fin movement and a lateral extension of pectoral fins at an angle to promote a net downward force to ‘anchor’ the fish to the bottom of the flume. Mountain sucker exhibited a burst and hold strategy whereby individuals will alternate between a short burst of swimming followed by an oral gripping behavior on the bottom of the swimming chamber in an attempt to maintain their position. Speckled dace and longnose dace exhibited various bending behaviors in an attempt to create a hydrofoil and maintain position in flowing water without continuously swimming (Figure 7). The remaining species exhibited direct swimming and all values associated with these species should be considered as true measures of critical

swim velocity (U_{crit}). Unlike tests for critical swimming velocity, burst speed tests revealed no unique swimming behavior in any of the species tested.



Figure 7. Bracing behavior exhibited by longnose dace (*Rhinichthys cataractae*) in the prolonged swimming trials.

6.3 Predictive Ability of Functional Groups on Swimming Performance

Of the three models tested, AIC scores were lowest for the species model for both burst and prolonged swimming speed (Table 3). In this model, species, standardized body size, and their interaction were significant predictors of both burst and prolonged speed (Table 4). All species and groups showed a great deal of overlap in burst speed swimming performance at all sizes, with the exception of brown trout which consistently had the highest burst speed across all sizes (Figs. 8-10). Prolonged speed swimming performance showed similar patterns of overlap with brown trout and mountain sucker outperforming the remaining six species at larger sizes in the species model (Figs. 11-13).

Table 3. Comparison of AIC scores for the three predictive models of swimming performance.

Model	AIC Score
Burst Speed	
Habitat Use Level	76.1
Morphological Group Level	-19.4
Species Level	-35.3
Prolonged Speed	
Habitat Use Level	55.2
Morphological Group Level	-7.2
Species Level	-16.8

Table 4. Results of ANCOVA tests for the species-based model of swimming performance for burst and prolonged speed tests.

	<u>Prolonged Speed</u>				<u>Burst Speed</u>		
	df	F-stat	p-value		df	F-stat	p-value
Species Level				Species Level			
Group	6, 151	19.12	< 0.001	Group	6, 204	28.76	< 0.001
Size	6, 151	140.55	< 0.001	Size	6, 204	142.83	< 0.001

7.0 CONCLUSION

Of the three predictive models, habitat-level functional groups produced the poorest fit with swimming performance data. The lack of correspondence observed in the prolonged swimming tests is particularly interesting, and highlights the difference in swimming behavior between the two groups. Swimming trials revealed that when subjected to high water velocities, benthic species, including mottled sculpin, mountain sucker, speckled dace and longnose dace all maintain position by direct contact with the substrate in an attempt to brace. Utilizing bracing, benthic species were able to maintain position at the same velocities as mid-water species without exhaustive physical effort. Bracing behavior has many inherent benefits including food capture, predator avoidance and habitat selection while concurrently allowing fish to expend minimal energy in the process (Arnold et al. 1991; Billman & Pyron 2005). Such divergence in behavior is perhaps attributed to dissimilarity in habitat use. Those species that feed at the benthic level share the same bracing behavior in flowing water and do not necessitate the same continuous swimming behavior as mid-water species. Bracing behavior appears to be a means of equalizing the ability to maintain position in moving water and illustrates the need to account for unique behavioral adaptations when examining form and function relationships (Garland et al. 1990; Irschick 2002).

Shape-based functional groups were somewhat more successful than habitat-based functional groups at predicting swimming performance, but still did not exhibit the best model fit. Examination of the least squares means for the species represented by each functional group revealed various degrees of overlap across the tested range of sizes with the exception of brown trout. This lack of connection between morphological grouping and swimming performance may be representative of other factors that have an influence on performance independent of shape. As a result, clear relationships between form and function often are not plainly manifest (Baker et al. 1995; Cech & Massingill 1995; Nannini & Belk 2006). Overall, these results suggest that functional groups based purely on morphology may not necessarily serve as reliable predictors of swimming performance.

Species-based models were the most reliable predictors of swimming performance in both swimming tests and exhibited the lowest AIC scores among all three models. Least squares means estimates for each performance test revealed broad overlap in swimming performance among species, and species-specific relationships between body size and swimming performance. In burst swimming tests, brown trout had higher swimming speeds than all other species at the mean and large body sizes. However, all other taxa exhibited a high degree of overlap over the entire range of body sizes. Prolonged speed tests showed similar patterns of overlap in performance. This lack of wide ranging interspecific differences in swimming performance may be indicative of some minimum performance criteria for inhabiting certain hydrologic regimes that may be fairly consistent across groups of stream fishes (Poff & Allan 1995). All taxa used in this analysis have to cope with the same seasonal variation in water velocities, and as a result all converge on a narrow range of values for swimming performance.

In general, variation in swimming performance due to body size was much greater than variation in swimming performance due to species differences. This result is not surprising, due to a combination of increased muscle power and lateral surface area exhibited in larger individuals (Goolish 1989) which may have a greater effect on performance than behavior or morphology alone. As body size increases, the volume of muscle mass also increases allowing fish to achieve higher speeds during prolonged swimming (Beamish 1978). Large body size is also a main contributing factor to the displacement of large amounts of water in fast-starts (Webb & Weihs 1986), an observation consistent with earlier predictions for burst speed swimming. Based on these results, it would seem that body size or size class alone may adequately predict swimming performance for Utah stream fishes.

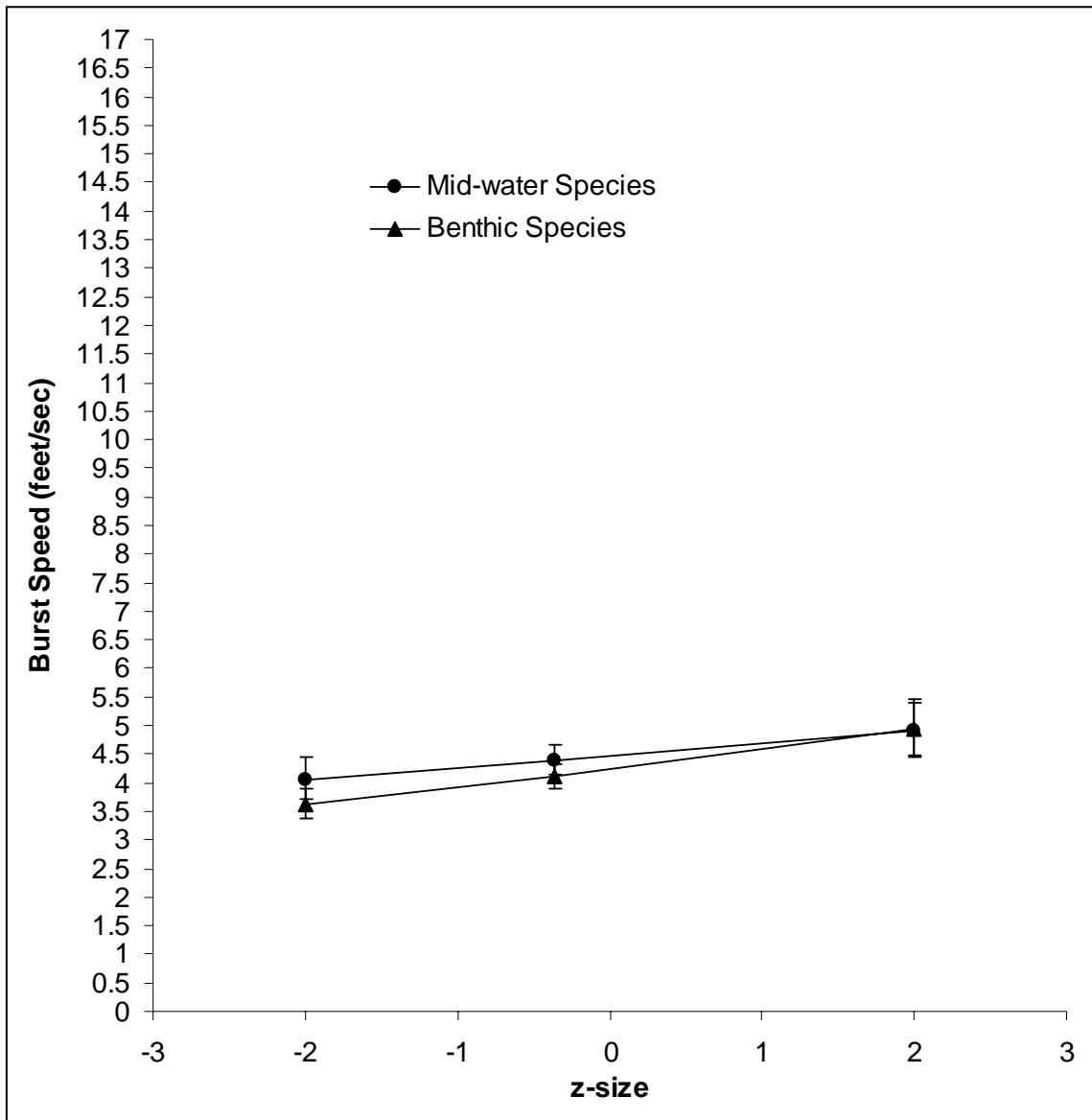


Figure 8. Back transformed least squares means estimates of burst speed swimming performance for benthic and mid-water species at small ($z\text{-size}=-2$), mean ($z\text{-size}=-0.5$) and large ($z\text{-size}=2$) body sizes. Error bars indicate ± 2 standard errors.

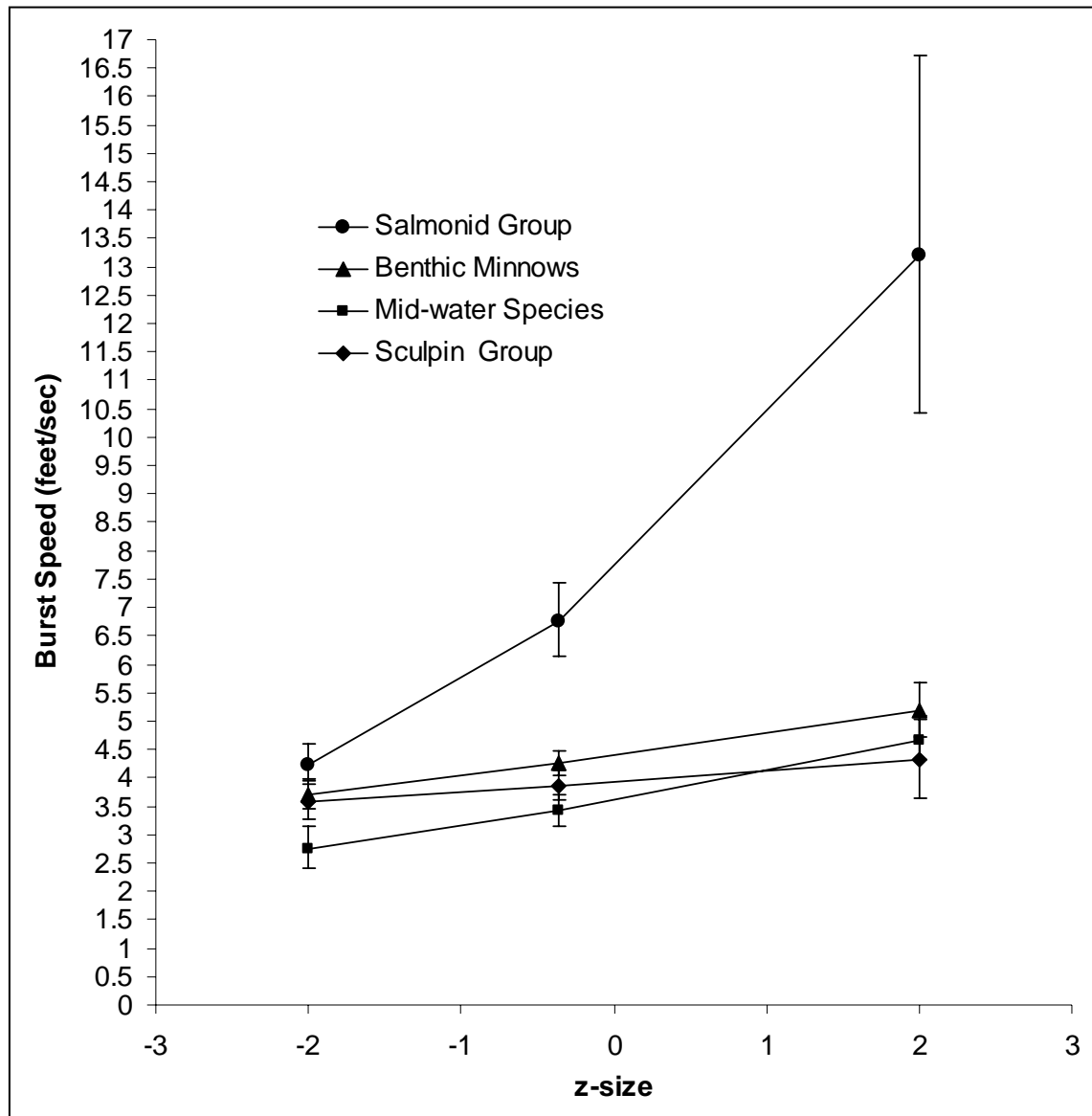


Figure 9. Back transformed least squares means estimates of burst speed swimming performance for morphological groups at small ($z\text{-size}=-2$), mean ($z\text{-size}=-0.5$) and large ($z\text{-size}=2$) body sizes. Error bars indicate ± 2 standard errors.

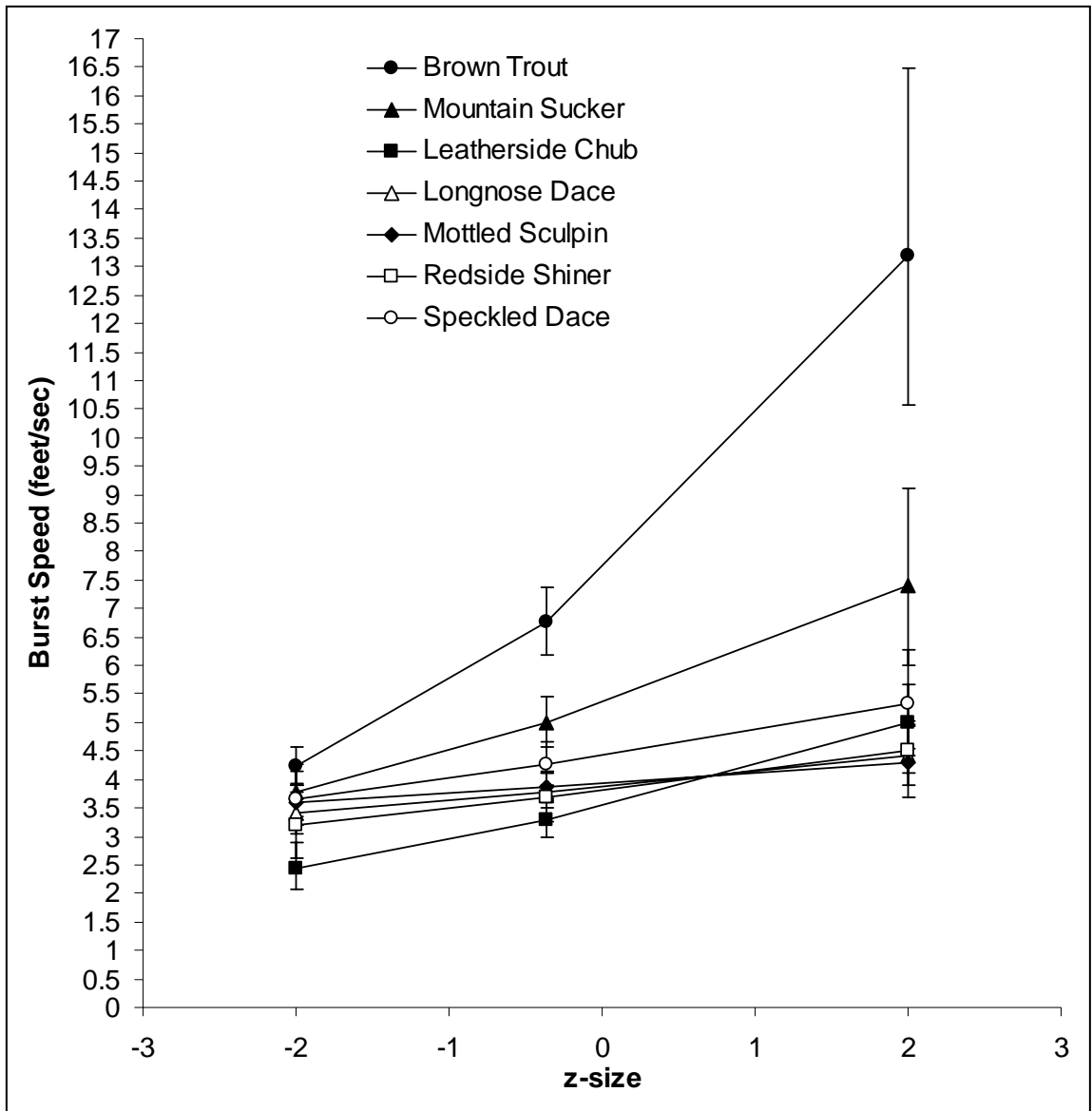


Figure 10. Back transformed least squares means estimates of burst speed swimming performance for individual species at small ($z\text{-size}=-2$), mean ($z\text{-size}=-0.5$) and large ($z\text{-size}=2$) body sizes. Error bars indicate ± 2 standard errors.

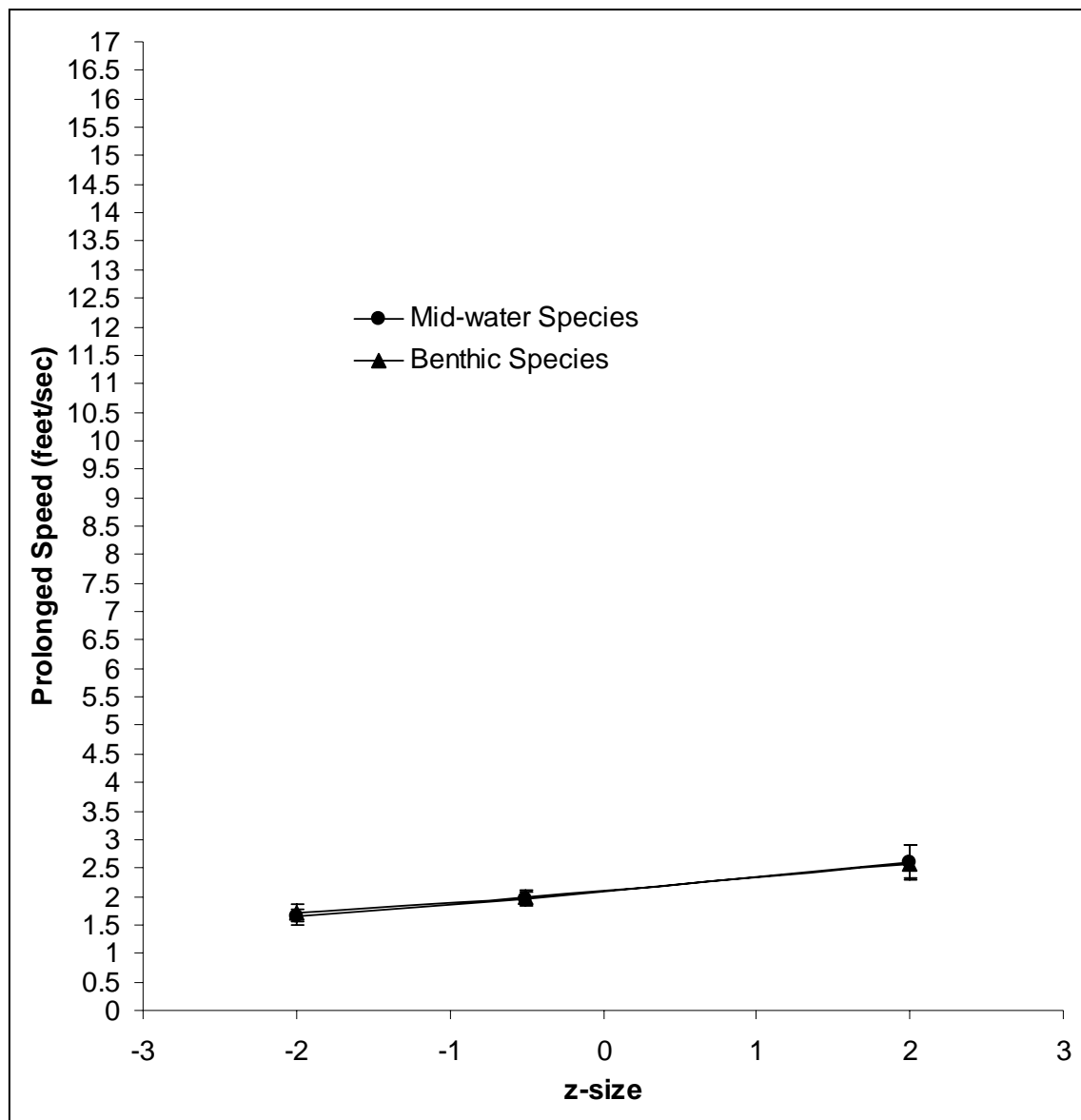


Figure 11. Back transformed least squares means estimates of prolonged speed swimming performance for benthic and mid-water species at small ($z\text{-size}=-2$), mean ($z\text{-size}=-0.5$) and large ($z\text{-size}=2$) body sizes. Error bars indicate ± 2 standard errors.

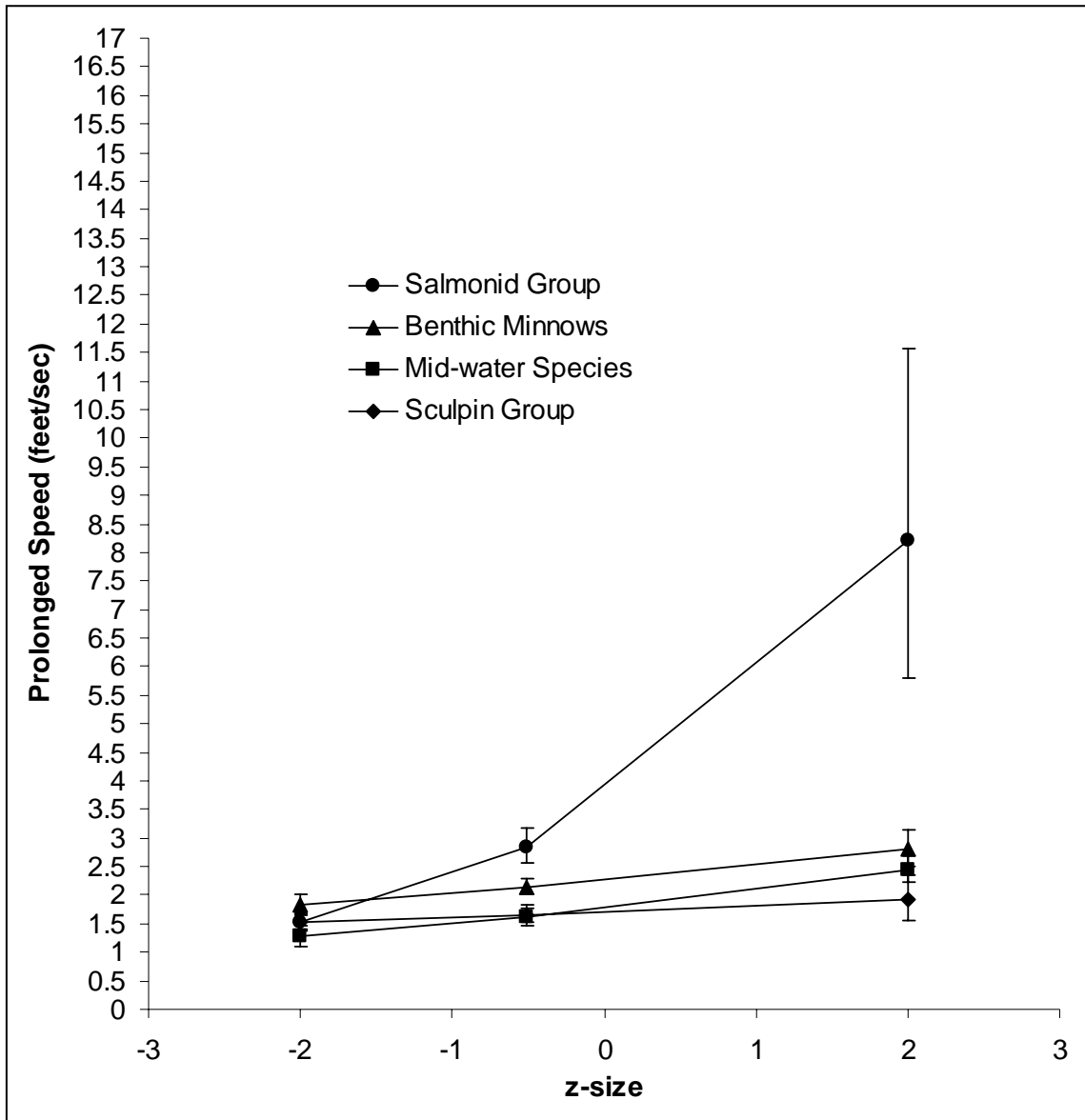


Figure 12. Back transformed least squares means estimates of prolonged speed swimming performance for morphological groups at small ($z\text{-size}=-2$), mean ($z\text{-size}=-0.5$) and large ($z\text{-size}=2$) body sizes. Error bars indicate ± 2 standard errors.

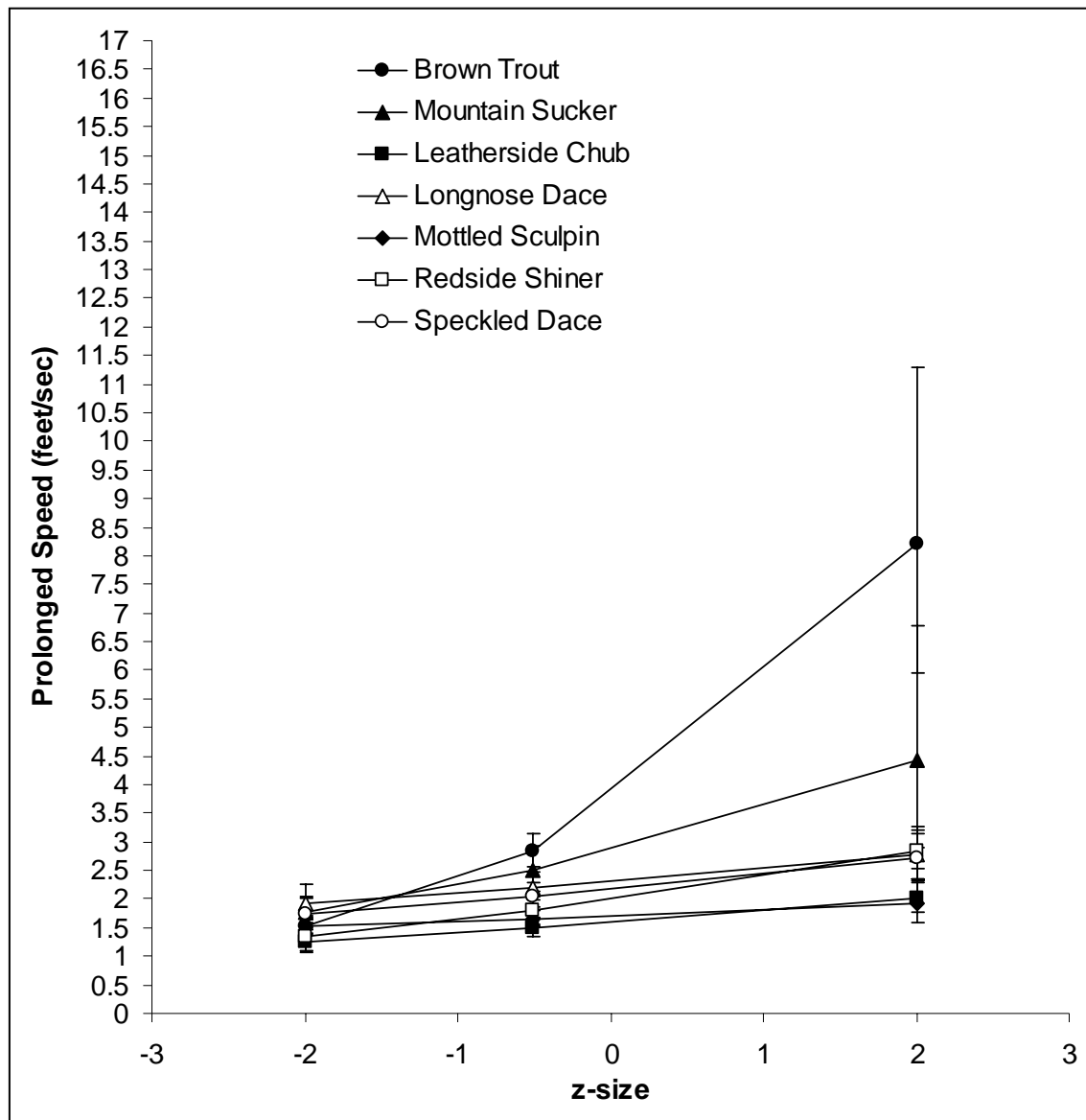


Figure 13. Back transformed least squares means estimates of prolonged speed swimming performance for individual species at small ($z\text{-size}=-2$), mean ($z\text{-size}=-0.5$) and large ($z\text{-size}=2$) body sizes. Error bars indicate ± 2 standard errors.

8.0 RECOMMENDATIONS

Among the fish tested in this study, swimming performance values did not differ much between species, which simplifies prediction of swimming performance to an extent. The similarities in swimming speeds observed in the burst and prolonged speed tests suggest that fish passage structures need only be designed for a single group of fish, as opposed to the hypothesized need for multiple shape-based or habitat-based assemblages. Perhaps even more important than group designation in swimming speed prediction is the fact that most of the variation in swimming performance was due to differences in body size. Because body size provided the most reliable predictor of swimming performance across all models, it should be considered the most important variable when designing for fish passage in Utah culverts.

Graphical results from the least squares estimates of swimming performance for each species and size class (Figs. 10 & 13) show that the majority of Utah fishes fall within a similar range of swimming performance (see Table 5 for a numerical summary of the results). Although most values for swimming performance were relatively similar across all species, optimizing fish passage in culverts based on performance values for the absolute weakest swimmer will buffer for variation in swimming performance in species with slightly higher performance values. The weakest small-bodied fish were capable of burst speeds of 2.4 feet/sec and prolonged speeds of 1.3 feet/sec; mean sized fish were capable of burst speeds of 3.3 ft/sec and prolonged speeds of 1.5 m/s; and large sized fish swam at 4.3 ft/sec burst speed and 1.9 ft/sec prolonged speed. While the physical design of culverts is beyond the scope of this report, using swimming performance values for the small-bodied, weakest swimmers will ensure successful passage in culverts for all fish, regardless of species designation or body size. Furthermore, because fish alternate between burst and prolonged speed efforts (Beamish 1978), culvert design should be based on swimming performance values for both modes

Table 5. Table of back-calculated swimming speeds for 3 size classes of Utah fish. Size classes include juvenile, mean and large body sizes. Mean swimming speeds (in feet/sec.) are reported along with the upper (UCL) and lower (LCL) 95% confidence intervals.

Species	Burst Speed			Prolonged Speed		
	LCL	Mean speed (ft/sec)	UCL	LCL	Mean Speed (ft/sec)	UCL
Brown trout						
Juveniles	3.914	4.236	4.585	1.397	1.517	1.647
Mean size	6.188	6.758	7.380	2.568	2.844	3.149
Large	10.573	13.201	16.483	5.941	8.196	11.308
Mountain sucker						
Juveniles	3.366	3.791	4.269	1.574	1.782	2.017
Mean size	4.568	4.988	5.447	2.134	2.500	2.928
Large	6.008	7.394	9.100	2.894	4.423	6.762
Leatherside chub						
Juveniles	2.066	2.442	2.887	1.060	1.264	1.507
Mean size	2.989	3.277	3.592	1.352	1.505	1.677
Large	4.411	4.996	5.659	1.775	2.022	2.304
Longnose dace						
Juveniles	3.060	3.402	3.783	1.656	1.931	2.252
Mean size	3.492	3.784	4.100	1.977	2.208	2.466
Large	3.908	4.406	4.968	2.346	2.767	3.263
Mottled sculpin						
Juveniles	3.283	3.585	3.915	1.373	1.526	1.697
Mean size	3.621	3.866	4.126	1.521	1.661	1.813
Large	3.683	4.308	5.038	1.574	1.914	2.328
Redside shiner						
Juveniles	2.616	3.207	3.932	1.096	1.358	1.682
Mean size	3.272	3.686	4.153	1.564	1.790	2.049
Large	4.106	4.501	4.934	2.533	2.852	3.210
Speckled dace						
Juveniles	3.196	3.646	4.158	1.465	1.735	2.055
Mean size	3.894	4.264	4.670	1.848	2.051	2.276
Large	4.536	5.339	6.283	2.339	2.717	3.157

of swimming. The duration of burst swimming velocities is generally thought to not exceed 20 seconds (Beamish 1978). Prolonged speed however, is a continuous effort used to describe swimming speeds maintained from 20 sec. up to 200 min. and results in fatigue (Beamish 1978).

Designing fish passage for all individuals is crucially important. Seasonal and daily movement of fishes in Utah streams is strongly influenced by patterns of life history unique

to each species and should have a strong influence in culvert design. While limited information on movement patterns exists for many of the species in this analysis, existing life history information indicates that many species make daily and seasonal migrations both up and downstream (see Table 6 for a review of the species tested in this study). Furthermore, recent mark-recapture studies conducted on Utah streams indicate that both salmonids and non-salmonids exhibit regular upstream and downstream movement, even where traversing a culvert is necessary (Beavers 2008).

The results of these swimming performance tests also highlight the need to consider swimming behavioral type when designing for fish passage. As reported above, benthic species use the substrate to maintain position through bracing without the need of continuous swimming and likely to seek the lower velocities created by the irregularities of a stream bottom. Because nearly one-half of the species present in a given stream may use the substrate to maintain position and migrate in upstream, accounting for substrate type in culvert design may be nearly as important as the critical swimming velocities of stream fishes. In this study, the bottom layer of the laboratory flume was devoid of any normal obstructions or substrate that may be encountered in an intermountain stream (i.e. cobbles, woody debris and vegetation). Test fish relied solely upon the friction between their body and the plexiglass flume. As a result, estimates for holding velocity reported herein may be lower than actual holding velocities exhibited in the field where friction may be higher and fish may be able to use interstitial spaces between cobbles to avoid high water velocities and maintain position without continuously swimming. Given this bracing behavior, additional research into how fish use the substrate and interstitial spaces during upstream movement is recommended.

The results of swimming performance tests also highlight the ineffectiveness of water velocity estimates traditionally used in culvert design. As demonstrated in both burst and prolonged speed tests, the salmonid group outperformed all other species. Fish passage models however, have traditionally been established using salmonid-based

Table 6. Summary of movement patterns exhibited by fish species used in this study.

Species	Seasonal or spawning migration	Fry Movement	Juvenile Movement	Diel movement	Other movement	Reference
Bonneville cutthroat trout (<i>Oncorhynchus clarki utah</i>)	Mid-April to July (Mostly upstream). Post-spawn migration in late spring (downstream)			Limited movement (median = 39 m) occurring during low-light periods of the day	Infrequently in Fall and Winter Sporadic movement in the Summer.	Hilderbrand & Kershner (2000); Shrank & Rahel (2004)
Brown trout (<i>Salmo trutta</i>)	October to December (Upstream) to nearest acceptable riffle area			Moderate movement during low-light periods of the day. Also moves to surface at low light.		Sigler & Sigler (1987); Young (1999)
June sucker (<i>Chasmistes liorus</i>)	May to Mid-June on descending leg of spring runoff (upstream)	Mid-June (Downstream)				Whitney & Belk (2000)
Least chub (<i>Lotichthys phlegethontis</i>)	April to August (from springs to marshes and back)				Regular movement between springs, marshes and streams seeking optimal water quality	Crist & Holden (1980)
Longnose dace (<i>Rhinichthys cataractae</i>)	Early June to July				Moves into deeper water during mid-summer to avoid high water temperatures	Sigler & Sigler (1987)
Mottled sculpin (<i>Cottus bairdi</i>)	Feb to May				Very limited in movement in Spring-Fall (1-4 m)	Brown & Downhower (1982); Petty & Grossman (2004)
Mountain sucker (<i>Catostomus platyrhynchus</i>)	June and July	Mid-June	Seeks shallow quiet waters.			Sigler & Sigler (1987)
Redside shiner (<i>Richardsonius balteatus</i>)	May to June (Upstream)	Mid to late June (downstream)		In lakes, they move into shallow water during the day and deeper water at night		Lindsey & Norhtcote (1963); Sigler & Sigler (1987)
Southern leatherside chub (<i>Lepidomeda aliciae</i>)	June to August	Congregates near brushy areas and close to shore.				Sigler & Sigler (1987)
Speckled dace (<i>Rhinichthys osculus</i>)	Spawn in June/July. Males congregate in small area.	Congregate in warm shallows of streams near large rocks.		Moves at night, spending the day among rocks in shallow water or in slightly deeper areas.		Sigler & Sigler (1987)

models of swimming performance (Peake et al. 1997). Efforts to maintain habitat connectivity for all species may be hindered because design for water velocities was much greater than the threshold swimming performance of non-salmonid species. Because non-salmonids all have very similar values for burst and prolonged speed, designing fish passage for all species would be better suited by merely designing for all species at a non-salmonid level.

Fish passage efforts will be greatly enhanced by taking into account the swimming performance values reported in this study. Because of the similarities in performance and environments exhibited in the Utah stream fishes examined in this study, species from similar environments not included in this analysis are expected to perform in a similar manner and reported performance values may potentially be used as a surrogate for other Utah stream fishes.

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APPENDIX: SWIMMING PERFORMANCE RESULTS

Appendix A contains graphical results of the raw swimming performance data for all ten species, as well as a table of basic descriptive statistics for each swimming test. No inferences in this report are made based on these results and are intended only as a means of preserving important data.

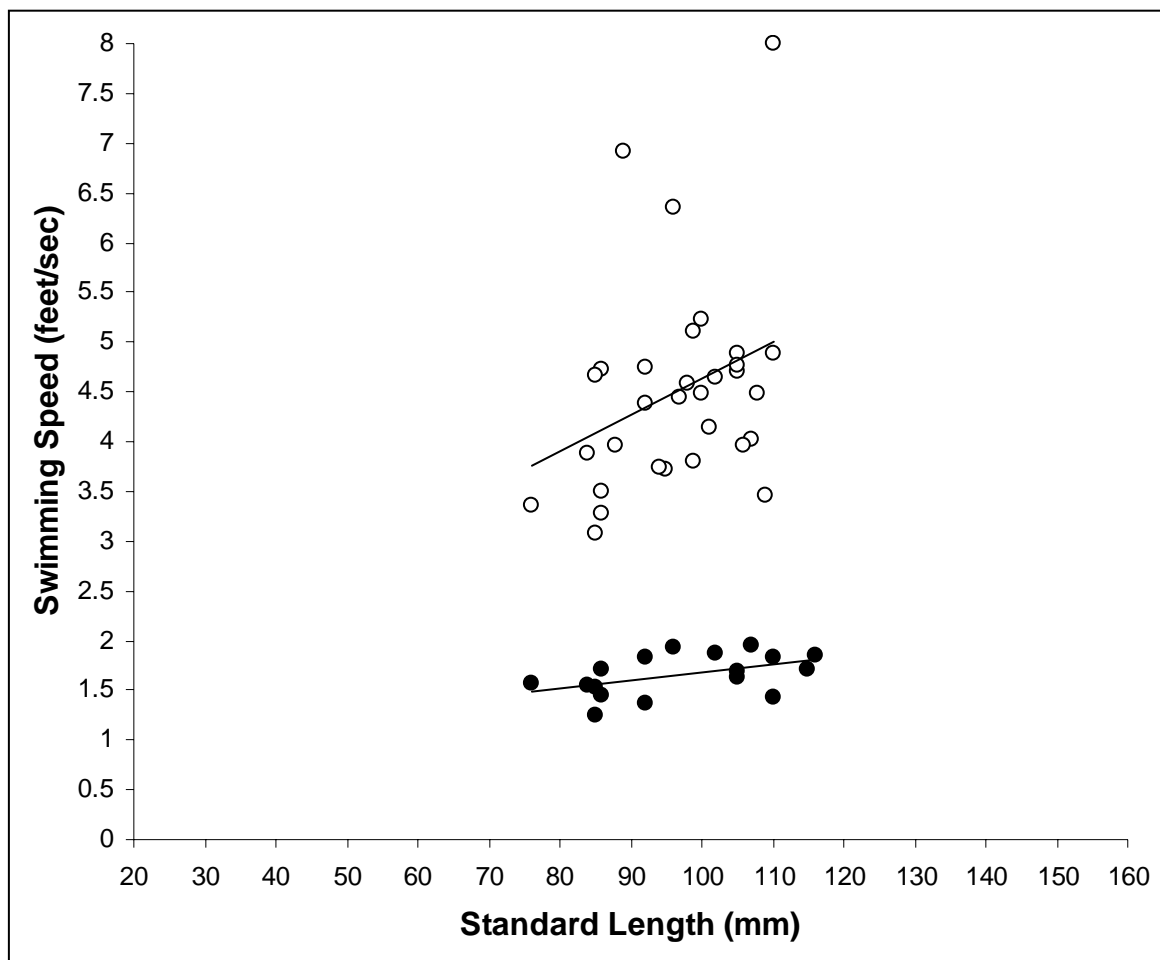


Figure 14. Results of swimming performance tests for brown trout (*Salmon trutta*) for burst (○, $R^2=0.103$) and prolonged (●, $R^2=0.229$) speed swimming.

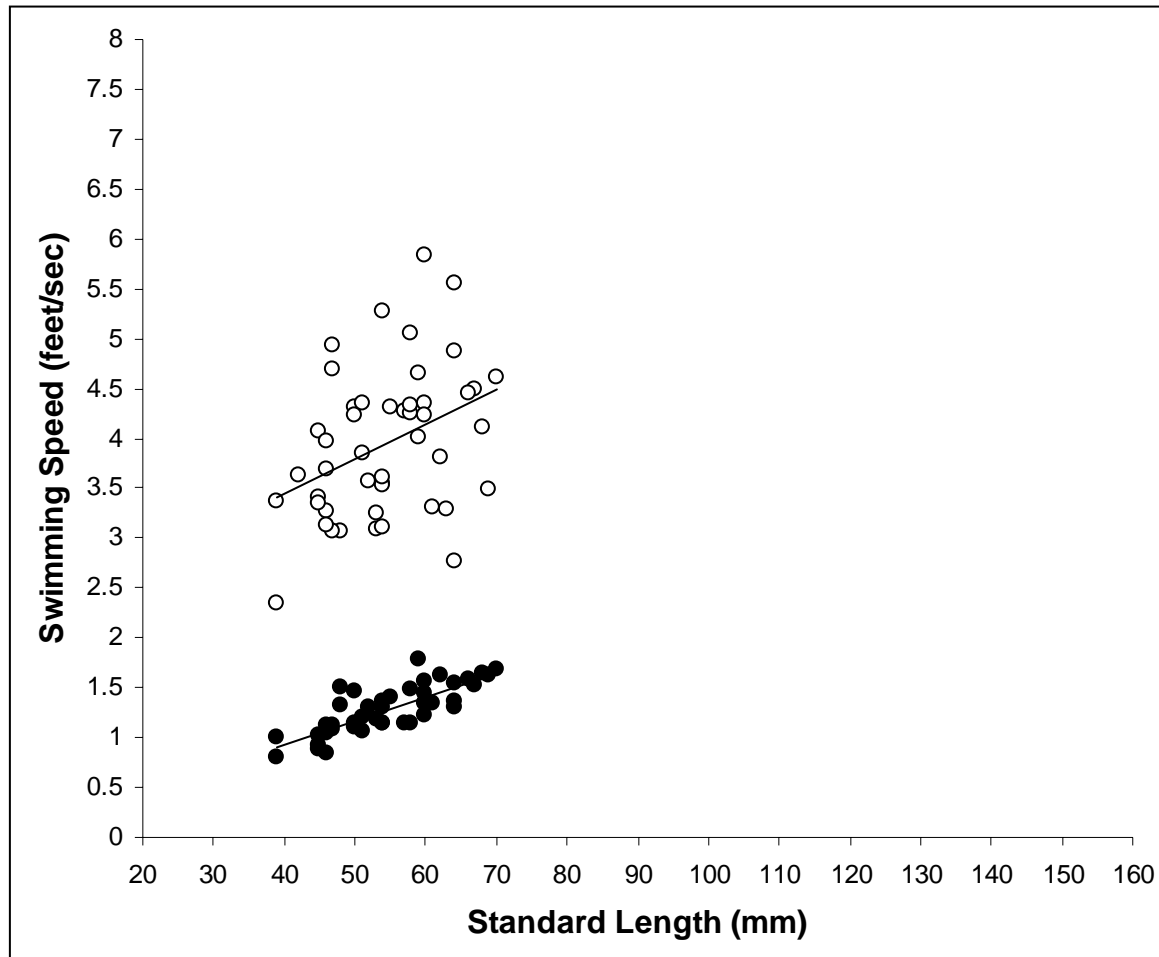


Figure 15. Results of swimming performance tests for Bonneville cutthroat trout (*Oncorhynchus clarki utah*) for burst (○, $R^2=0.146$) and prolonged (●, $R^2=0.630$) speed swimming.

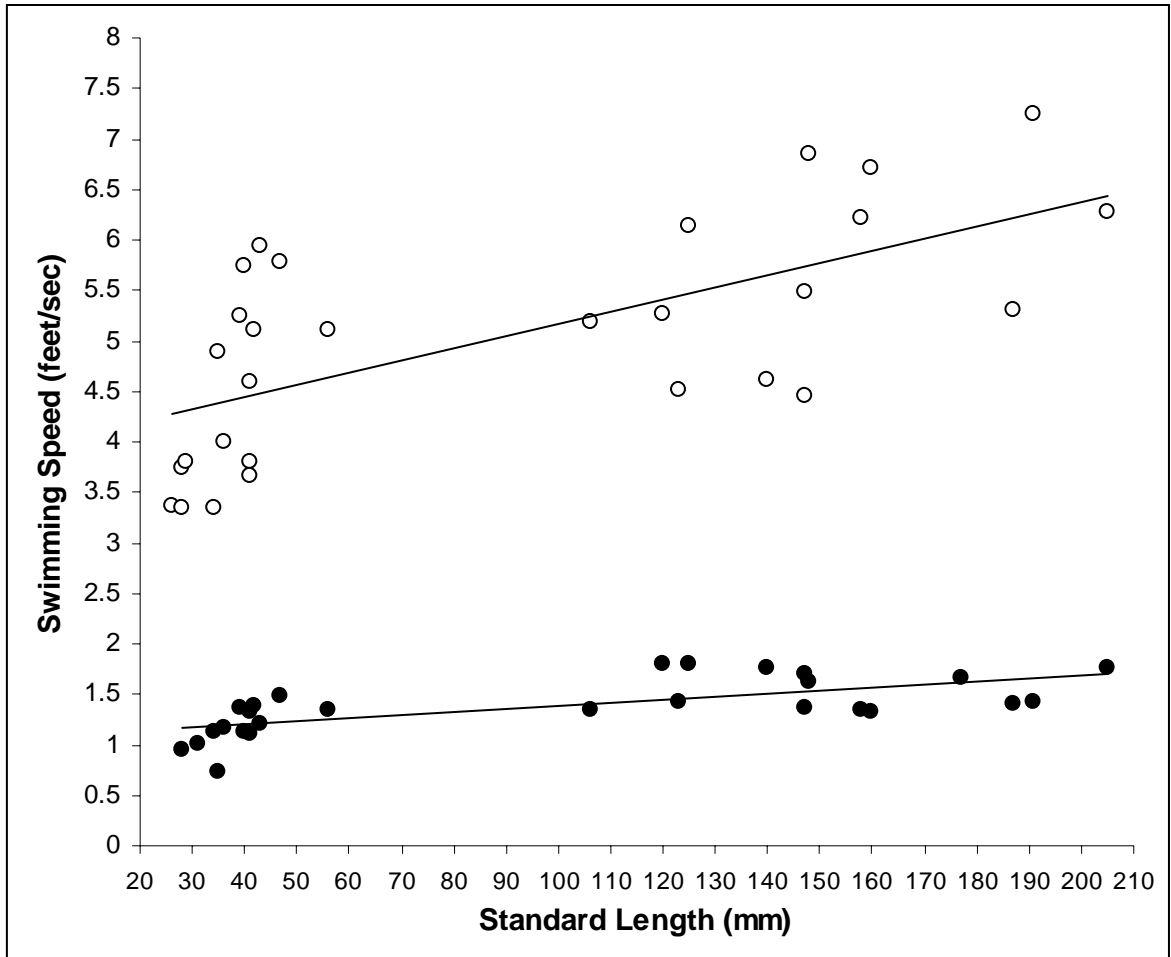


Figure 16. Results of swimming performance tests for June sucker (*Chasmistes liorus*) for burst (○, $R^2=0.435$) and prolonged (●, $R^2=0.454$) speed swimming. Note: scale of x-axis differs from other swimming performance figures in appendix.

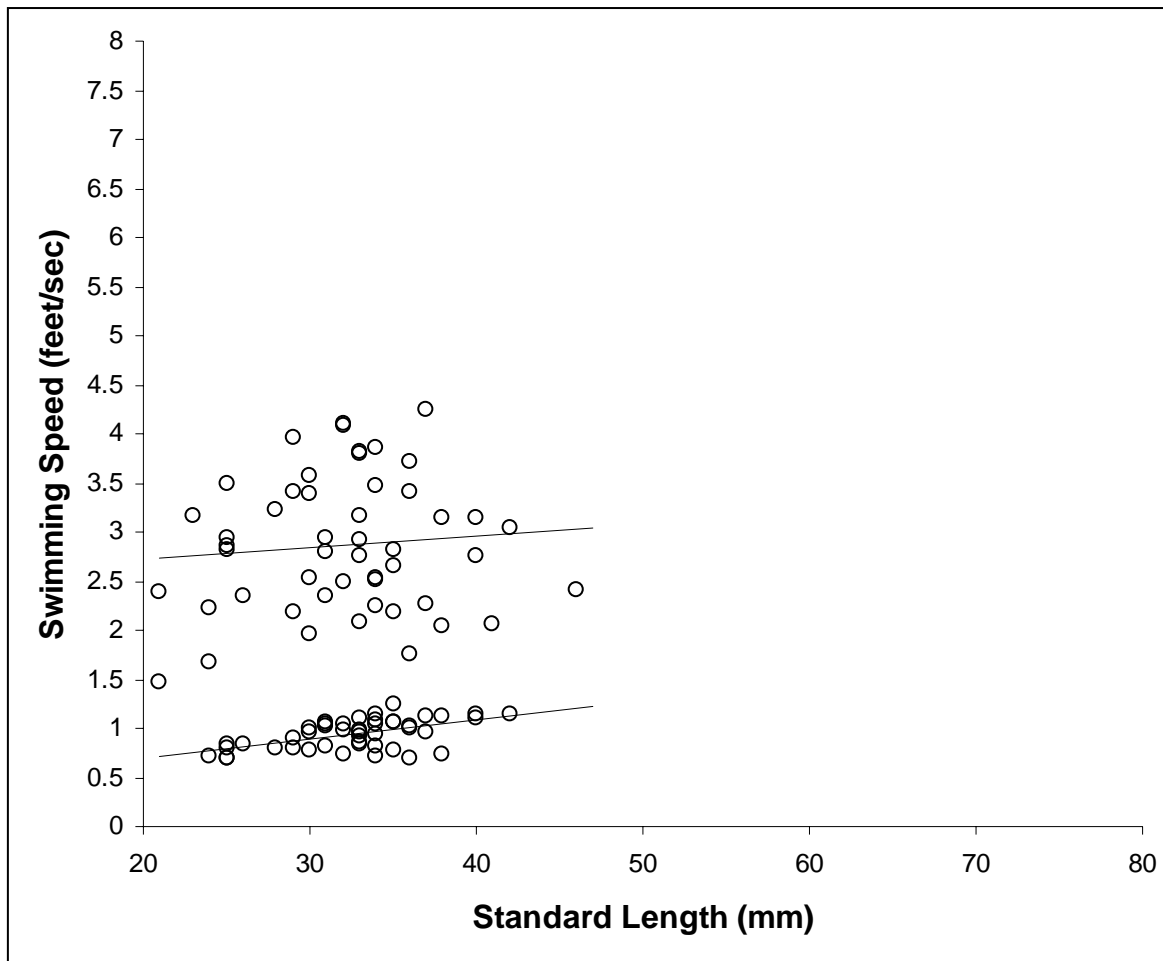


Figure 17. Results of swimming performance tests for least chub (*Lotichthys phlegethontis*) for burst (\circ , $R^2=0.009$) and prolonged (\bullet , $R^2=0.30$) speed swimming. Note: Scale of x-axis differs from other swimming performance figures in appendix.

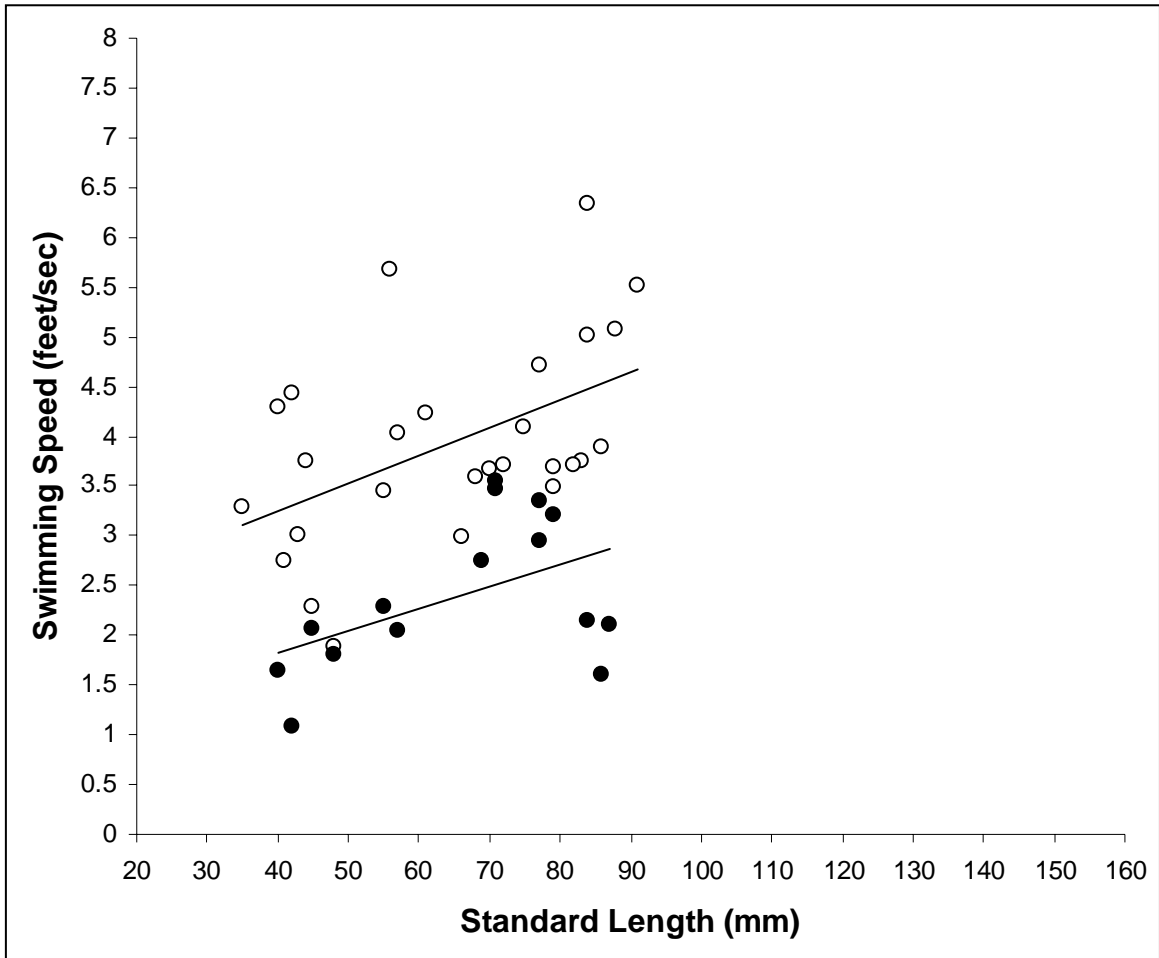


Figure 18. Results of swimming performance tests for longnose dace (*Rhinichthys cataractae*) for burst (\circ , $R^2=0.242$) and prolonged (\bullet , $R^2=0.238$) speed swimming.

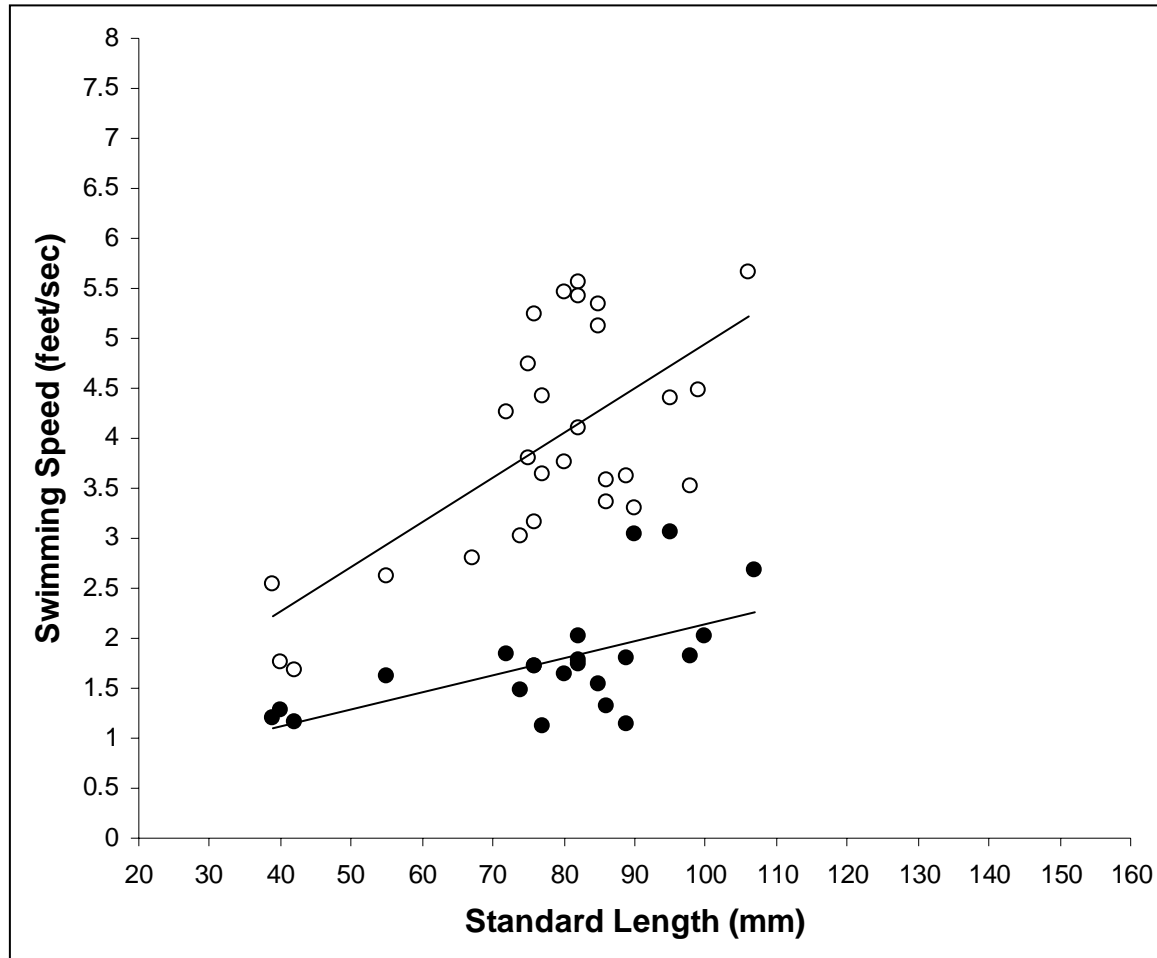


Figure 19. Results of swimming performance tests for southern leatherside chub (*Lepidomeda aliciae*) for burst (○, $R^2=0.437$) and prolonged (●, $R^2=0.335$) speed swimming.

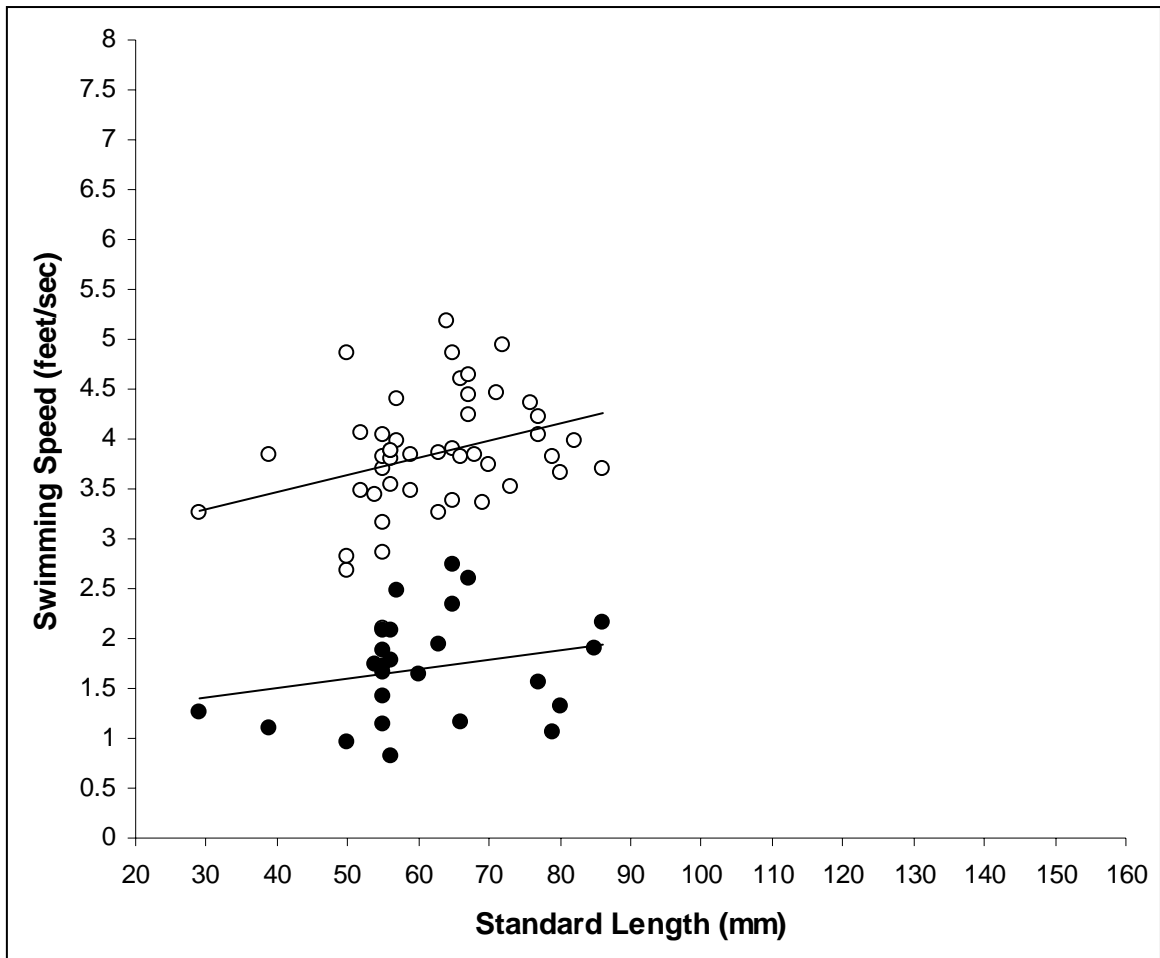


Figure 20. Results of swimming performance tests for mottled sculpin (*Cottus bairdi*) for burst (○, $R^2=0.10$) and prolonged (●, $R^2=0.603$) speed swimming.

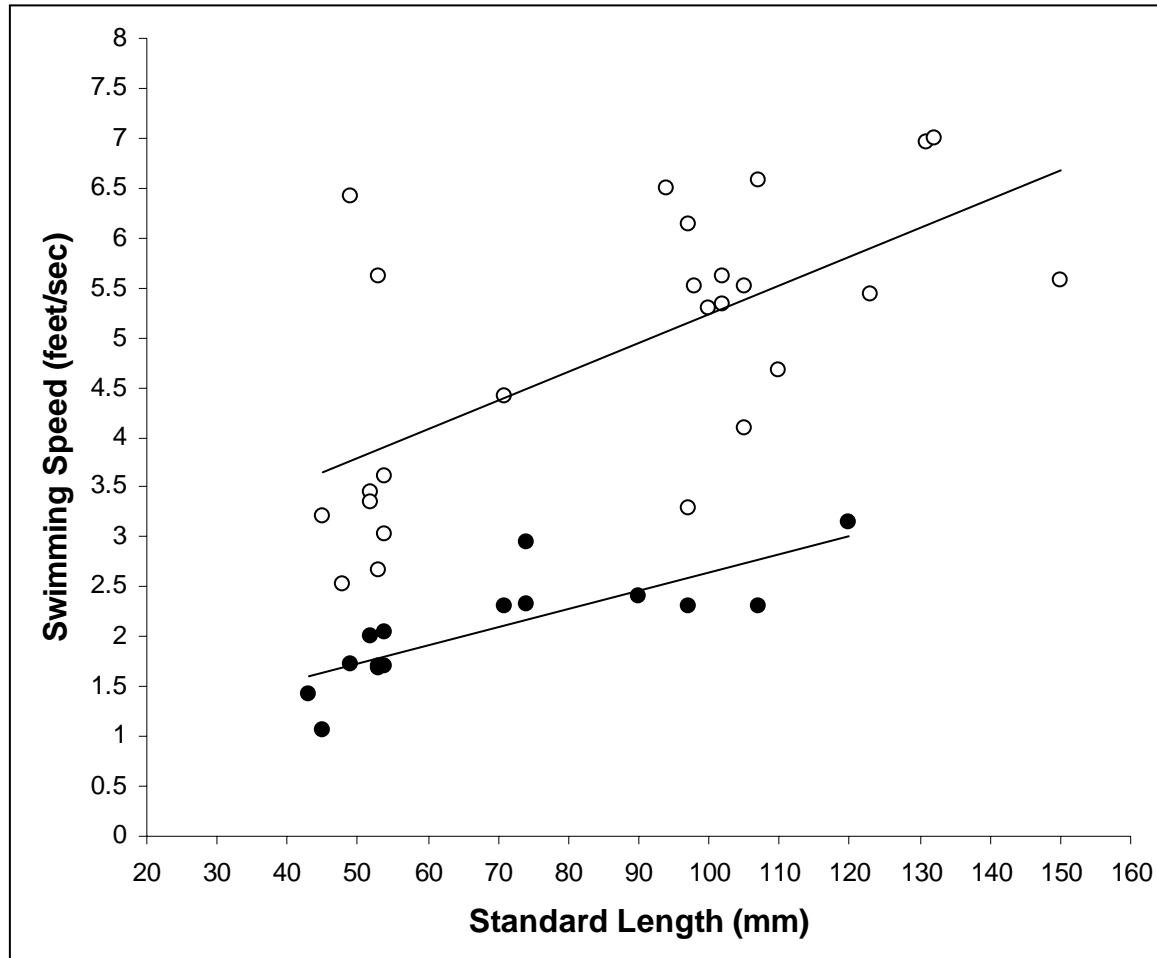


Figure 21. Results of swimming performance tests for mountain sucker (*Catostomus platyrhynchus*) for burst (○, $R^2=0.415$) and prolonged (●, $R^2=0.647$) speed swimming.

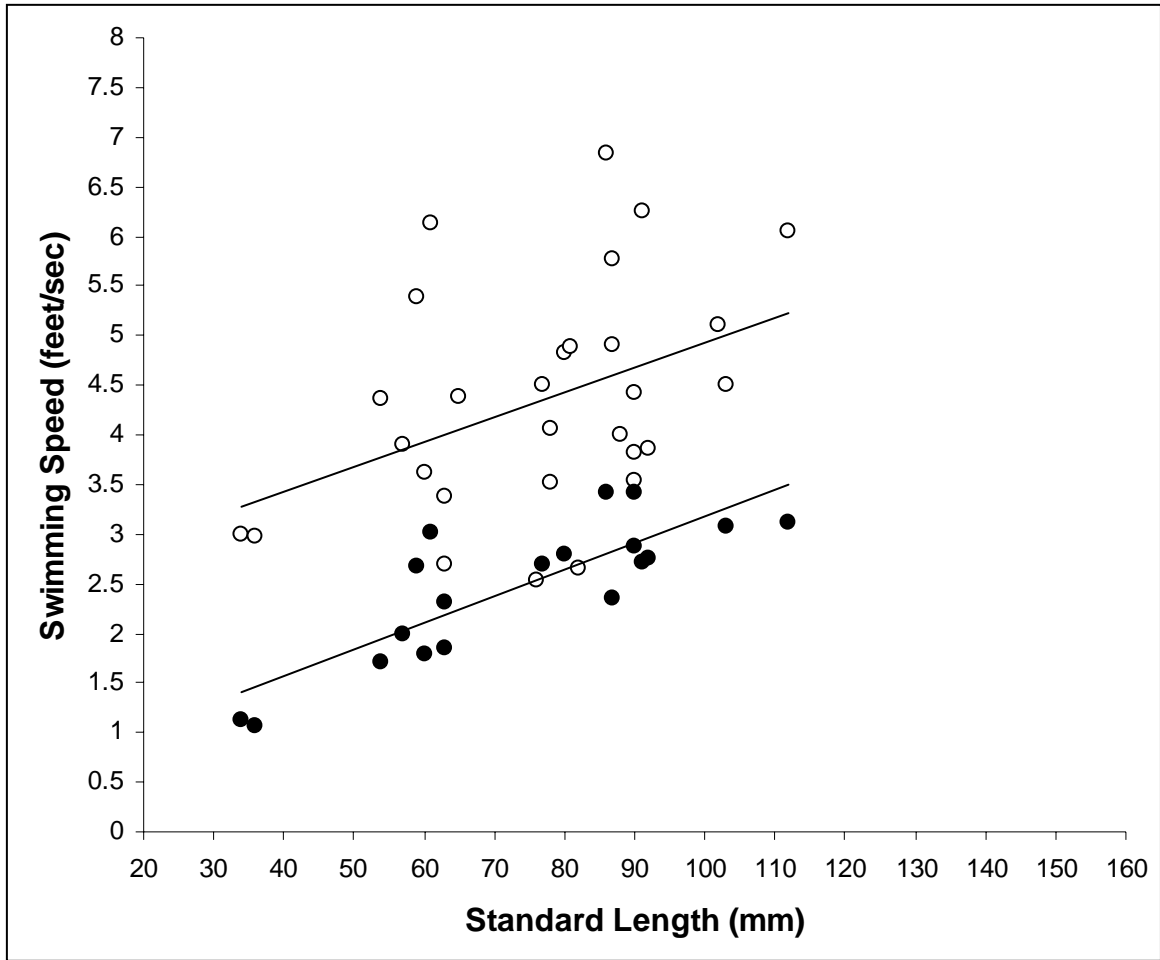


Figure 22. Results of swimming performance tests for redside shiner (*Richardsonius balteatus*) for burst (\circ , $R^2=0.165$) and prolonged (\bullet , $R^2=0.681$) speed swimming.

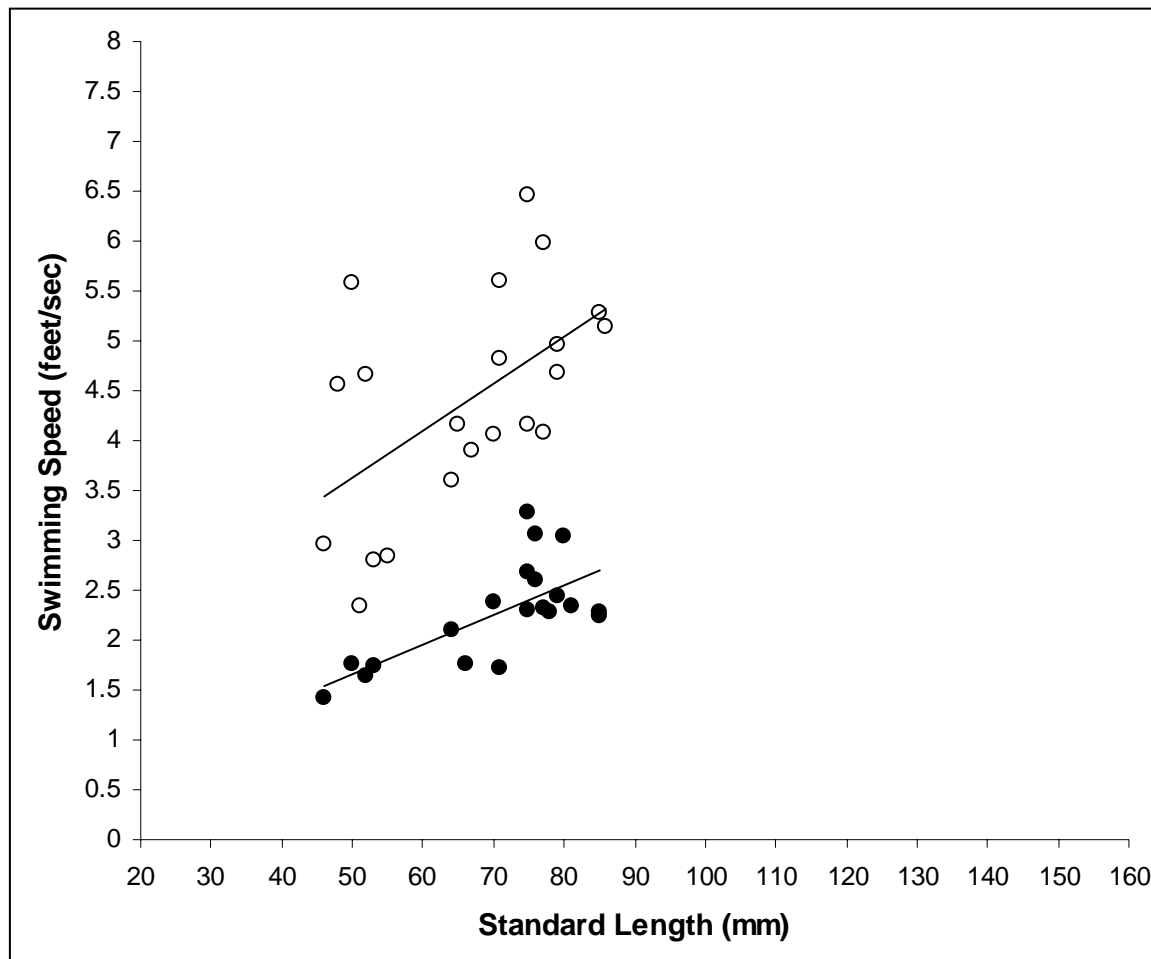


Figure 23. Results of swimming performance tests for speckled dace (*Rhinichthys osculus*) for burst (○, $R^2=0.30$) and prolonged (●, $R^2=0.474$) speed swimming.

Table 7. Summary statistics of raw swimming performance data for species used in the study. SL represents standard length in inches, SE indicates standard error and N indicates sample size. Linear regression equations for burst and prolonged speed (y) are provided and are calculated as swimming performance in ft·s⁻¹. Due to the narrow range of body size samples for brown trout and Bonneville cutthroat trout, predictive equations should not be extrapolated beyond the range of body sizes used in this analysis.

Species	Mean Burst Speed (ft/s)	N _{burst}	Burst Speed Regression Equation	SE	R ²	Mean Prolonged Speed (ft/s)	N _{prolonged}	Prolonged Speed Regression Equation	SE	R ²
Brown trout	4.495	31	y=0.037(SL)+0.958	1.008	0.103	1.640	17	y=0.008(SL)+0.858	0.192	0.229
Bonneville cutthroat trout	3.953	47	y=0.035(SL)+2.043	0.696	0.145	1.280	42	y=0.024(SL)-0.017	0.150	0.63
June sucker	5.026	29	y=0.012(SL)+3.957	0.850	0.435	1.378	27	y=0.003(SL)+1.086	0.204	0.454
Southern leatherside chub	3.937	38	y=0.045(SL)+0.466	0.861	0.437	1.772	22	y=0.017(SL)+0.434	0.461	0.335
Least chub	2.861	50	y=0.012(SL)+2.482	0.691	0.009	0.951	50	y=0.020(SL)+0.301	0.129	0.297
Longnose dace	3.937	27	y=0.028(SL)+2.132	0.892	0.242	2.395	15	y=0.022(SL)+0.931	0.689	0.238
Mottled sculpin	3.839	46	y=0.017(SL)+2.772	0.585	0.10	1.706	25	y=0.010(SL)+1.110	0.522	0.06
Mountain sucker	4.856	25	y=0.029(SL)+2.357	1.098	0.415	2.067	15	y=0.018(SL)+0.809	0.340	0.647
Redside shiner	4.331	29	y=0.025(SL)+2.426	1.068	0.165	2.461	19	y=0.027(SL)+0.485	0.407	0.681
Speckled dace	4.396	21	y=0.047(SL)+1.281	0.945	0.299	2.264	20	y=0.029(SL)+0.193	0.375	0.474