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DOES SHAPE PREDICT PERFORMANCE? AN ANALYSIS OF
MORPHOLOGY AND SWIMMING PERFORMANCE IN GREAT
BASIN FISHES

by

John R. Aedo

A thesis submitted to the faculty of

Brigham Young University

in partial fulfillment of the requirements for the degree of

Master of Science

Department of Biology

Brigham Young University

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BRIGHAM YOUNG UNIVERSITY

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ABSTRACT

DOES SHAPE PREDICT PERFORMANCE? AN ANALYSIS OF MORPHOLOGY AND SWIMMING PERFORMANCE IN GREAT BASIN FISHES

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Master of Science

Swimming performance strongly influences fitness in aquatic organisms and is closely tied to external body morphology. Although this connection has been closely examined at the individual and species level, few studies have focused on this relationship as it pertains to functional group assemblages. Using functional groups based on similarities in habitat use and morphology, I test the hypothesis that swimming performance can be reliably predicted by functional group composition. I measured swimming performance as burst speed using a simulated predator attack and as prolonged speed using a step-endurance test in a laboratory flume. I measured morphology using geometric morphometric techniques. A difference in swimming behavior in four of the seven species was observed in the step-endurance test. Benthic species exhibited bracing behavior as an alternative to body-caudal fin (BCF) propulsion in the prolonged speed trials. Swimming performance exhibited a weak relationship with functional groups

based on habitat or morphology. Rather a species-based model was the best predictor of swimming performance. Although species exhibited variation in swimming performance, body size was the strongest predictor of absolute swimming performance across all models. Relative swimming performance (measured in body lengths·sec⁻¹) was negatively related to body size. The results of this study suggest that functional groups are not always reliable predictors of performance and they necessitate empirical testing to validate their effectiveness. This study also provides critical swimming performance data for previously unstudied Great Basin fishes which could be valuable for predicting fish passage through culverts, weirs and fish ladders.

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INTRODUCTION

Exploring the relationship between an organism's body shape and the way it performs in its environment is the central theme of ecomorphology (Motta et al 1995). This relationship is commonly examined in two distinct parts, as the effects of morphological variation on performance, and as effects of performance on resource use and fitness (Arnold 1983). The causal mechanisms associated with these two relationships are further mediated by unique behavioral differences that exist within and among species, and deserve consideration when examining ecomorphology (Garland et al. 1990; Irschick 2002). The results of these inquiries have helped ecologists understand the unique relationships that exist between morphology and the ability to perform specific ecological tasks such as feeding and predator avoidance which in turn, may have significant effects on growth, survival and reproduction (Arnold 1983; Plaut 2001).

Aquatic systems, and particularly lotic environments, provide a useful framework in which to conduct ecomorphological studies because of the diversity in body shape and microhabitat use exhibited by stream fishes. For example, aquatic ecologists have used the context of ecomorphology to make accurate predictions of swimming (Fisher & Hogan 2007), prey capture (Rincón et al. 2007) and predator avoidance (Dayton et al. 2005) as they relate to external shape characteristics. Morphological traits have been further used in an ecomorphological framework to draw connections with habitat use (Webb 1984; Douglas & Matthews 1992) and predator-prey interactions (Nannini & Belk 2006).

Among fishes, swimming ability has a major impact on organismal ecology, affecting prey capture (Rincón et al. 2007), predator evasion (Taylor & McPhail 1985), reproductive success (Videler 1993) and ultimately influencing evolutionary fitness (Kolok 1999; Reidy et al. 2000; Plaut 2001). Swimming performance in fish can be influenced by numerous factors including: locomotion type, body size, shape, physiology, temperature, and behavior (Beamish 1978; Videler and Wardle 1991; Hammer 1995). The influence of morphology on swimming performance has been shown to have a significant effect in aquatic vertebrates (Webb 1984; Blake 2004) and has become a focus of inquiry for both theoretical and applied studies (Hawkins & Quinn 1996; Ojanguren & Brana 2003; Rincón et al. 2007).

Biomechanical studies have shown that the optimal body profiles for maximal fast-start and continuous swimming performance are mutually exclusive (Webb and Skadsen 1980; Webb 1984; Wakeling 2006). Continuous, or prolonged speed is favored in taxa with a narrow caudal peduncle, a large anterior depth and mass, a high aspect ratio (large span, low chord) lunate (crescent shaped) tail and a relatively stiff streamlined anterior body (Hynes 1970; Webb 1982a, 1984). Burst speed is favored in species that can displace large amounts of water, including those with a large caudal fin, a flexible muscular body relative to body mass and a 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, Webb concluded that fish may therefore be classified as locomotor ‘generalists’ or ‘specialists’ and that this distinction results in the formation of morphologically derived swimming groups. While many efforts have focused on ecomorphological relationships in fish at the individual, population and community level (reviewed by Motta et al. 1995), few efforts have attempted to examine these relationships using functional group based estimates of performance derived from similarities in habitat use or from detailed morphological analysis (except Hawkins & Quinn 1996; Billman & Pyron 2005; Fisher & Hogan 2007).

In addition to variability in swimming performance resulting from interspecific habitat and morphological differences, many fish exhibit allometric changes in body shape during growth which may be manifest as a differential rate of increase in swimming speed with an increase in body size (Ohlberger et al. 2006). The effect of body size on relative swimming performance is of particular interest as larger individuals experience competing forces associated with increased muscle mass and increased drag. Examining these changes as they relate to swimming allometry reveals inherent trade-offs and selective pressures that influence the association of form and function during the course of development (McHenry & Lauder 2006).

In this study, I explore the behavior, morphology, and swimming performance of seven naturally co-occurring stream fishes from the Great Basin. I test the hypothesis that swimming performance can be reliably predicted from functional groups based on similarities in habitat use and morphology. This hypothesis was tested by first, examining how swimming performance differed between benthic and mid-water stream fishes (habitat based functional groups). I then used morphological group-based

assemblages to examine how shape affected swimming performance independent of habitat use. Because morphology can influence fast start and continuous swimming in different manners, I used both burst and prolonged speed as swimming performance estimates. 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. Finally, I tested for allometric effects between body size and swimming performance to examine how somatic growth affects scaled swimming performance in temperate region stream fishes.

MATERIALS & METHODS

I measured morphology and swimming performance in 314 individuals from seven stream fish species in the Great Basin of the western USA, representing four families and six 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*), least chub (*Iotichthys phlegothonis*) and June sucker (*Chasmistes liorus*), 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. The results of swimming performance tests for all species are included in table 2.

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 1 for collection locations). All fish were collected and tested between 31 July 2007 and 23 October 2007 during low flow periods. Because of similar environmental conditions associated with the collection time (i.e. low water velocities, no extremes in temperature), all 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 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=5 mm). 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 *ad libitum*. Photoperiod was maintained at 12:12

ld. 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 were completed within one week following collection.

Laboratory water temperatures were maintained at $17.0^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ and near saturation with oxygen. This represents the mean water temperature of all sample sites during the collection period (range=14-20° C) and falls within the range of preferred temperatures for all species tested (Sigler and 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 ecomorphological relationships in stream fishes under conditions similar to what may be experienced in the wild by all taxa in this analysis.

Morphometric Analysis

I measured variation in body shape using geometric morphometric techniques. I 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, I used 18 landmarks at consistent locations across all species overlaid

onto the lateral view photograph of each individual (Fig. 1) using tpsDig2 (Rohlf 2006); 11 landmarks were designated as ‘sliding’ landmarks. These landmarks characterize morphological traits that are predicted to confer maximal burst and prolonged 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 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 (Fig. 1).

Burst Speed

Burst speed was measured using a simulated predator attack in a laboratory observation arena (Fig. 2). The arena consisted of a 100 cm x 100 cm white acrylonitrile-butadienestyrene (ABS) plastic octagonal arena with 15 cm high walls. The center of the arena contained a 20 cm diameter clear-plexiglass cylinder that receded into the bottom of the arena, constraining individuals to the center of the observation arena while acclimating previous to the simulated attack. The arena was completely enclosed on all sides except for one side that had two small 15 cm x 5 cm 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, 1.5 m 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 25 cm 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 $17.0^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$, 15 cm 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) 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 Inc. 1992-2005). The software electronically calculates the velocity of a moving object using the distance divided by time equation. 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 1 cm 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 $\text{m}\cdot\text{s}^{-1}$. Burst speed trials were always performed previous to prolonged speed trials.

Prolonged Speed

I 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 (20 cm tall x 20 cm wide x 80 cm long) connected to a downstream reservoir and an upstream flow conditioning section (Fig. 3). 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 4 cm long plastic grid with 7 mm diameter round openings on the upstream end, and a metal screen with 7 cm square openings on the downstream end. To reduce turbulence, all water passing through the pump was directed through a 30 cm long flow conditioning section consisting of a plastic honeycomb with 7 mm wide openings held in place by a 1mm 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 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.

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 $0.1 \text{ m}\cdot\text{s}^{-1}$ 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. All individuals were then preserved in 70% ethanol and stored in the laboratory.

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

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

where V_p is the highest velocity maintained for the full 5-min period ($\text{m}\cdot\text{s}^{-1}$), V_i is the velocity increment ($0.1 \text{ m}\cdot\text{s}^{-1}$), T_f is the elapsed time at the fatigue velocity, and T_i is the time between velocity increases (5 min.).

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 $\text{m}\cdot\text{s}^{-1}$) were used as the response variables in all three models. In the habitat use model, functional groups were delineated as either benthic or mid-water based on life-history information compiled for each species (Sigler and 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 redbreast shiner. In the 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 and Gorley 2006). Mean relative warps scores for each species, generated in tpsRelw were used as shape variables in the cluster analysis. The 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:

$$z=(x-\mu)/\sigma$$

where z is the standardized score, x is the raw score to be standardized (standard length of an individual, in mm), μ is the population mean and σ is 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) was 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 (z-score size=2) bodied individuals.

To compare the three models I 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).

To test for allometric effects in relative performance within species, I calculated swimming performance slopes in relation to body size on log transformed data using ordinary least squares (OLS) regression. Two separate tests, one for burst swimming and one for prolonged swimming, were conducted for each species with log body size (SL in mm) used as the independent variable and log swimming performance (in body lengths·sec⁻¹) as the dependent variable. Swimming performance as measured in body lengths·sec⁻¹ factors out the absolute increase in swimming performance with size and reveals trends in relative swimming performance as body size changes. The isometric expectation is that relative swimming speed (relative to body length) would remain constant as size changes. Isometric effects would yield a near-zero slope and allometric effects would manifest as non-zero slope. Least squares regression was chosen so that slopes produced in the analysis would be comparable to other allometric equations.

RESULTS

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

groupings, one for each node at descending Euclidean distances (Fig. 4). 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 (*Cottus bairdi*), a salmonid group (*Salmo trutta*), a mid-water minnow group (*Lepidomeda aliciae* and *Richardsonius balteatus*) and a benthic minnow group (*Catostomus platyrhynchus*, *Rhinichthys cataractae* and *Rhinichthys osculus*). 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.

Swimming Performance & Behavior

Swimming tests were completed for 247 individuals with an approximately equal representation of swimming performance measures recorded for each of the seven species tested (Table 1). Critical swim velocity tests revealed a difference in swimming strategies among observed species. *Cottus bairdi*, *Catostomus platyrhynchus*, *Rhinichthys osculus* and *Rhinichthys cataractae* 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 *Cottus bairdi* 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. *Catostomus platyrhynchus* 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. *Rhinichthys osculus* and *Rhinichthys cataractae* exhibited various bending behaviors in an attempt to create a hydrofoil and maintain position in flowing water without continuously swimming. 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.

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 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 (Fig. 5). Prolonged speed swimming performance showed similar patterns of overlap with brown trout and mountain sucker outperforming the remaining six species at larger sizes (Fig. 6)

Swimming Allometry

In the burst speed analysis, mean slope for the relationship of body lengths per second swim speed over body length was significantly negative for all species except leatherside chub and speckled dace (Table 5). In the prolonged swimming speed analysis, swim speed in number of body lengths per second exhibited a significant negative slope for brown trout, mountain sucker, leatherside chub and mottled sculpin (Table 6).

DISCUSSION

Habitat-Based and Shape-Based Functional Groups

The ecomorphological hypothesis predicts that morphology is a strong predictor of performance and habitat use, and has accurately predicted niche relationships (Douglas & Matthews 1992), habitat use (Felley 1984; Casatti & Castro 2006) and feeding preferences in fish (Webb 1984). In this study, a two group habitat-based model consisting of benthic and mid-water stream fishes was used to predict swimming performance. At this predictive level, habitat-based functional groups are a means of producing groupings without actual functional data, and are based on known behavioral differences associated with habitat preference. Groupings consisted entirely of benthic or mid-water species and were expected to show dissimilar values for swimming performance, ultimately arising from unique differences in prey capture and microhabitat use by each functional group.

The morphologically-based groupings are a more robust way of producing functional groups and are based on empirical data. At this level, a total of four morphological groups are produced including: a sculpin group, a salmonid group, a

benthic minnow group and a mid-water minnow group. Each of the taxa within these groups exhibits strong similarities in both morphology and habitat use, likely resulting from common evolutionary histories. The sculpin group consists of a lie-in-wait feeder (Sigler and Sigler 1987) that moves very little throughout its life (Petty and Grossman 2004) and has a body shape that favors station holding (i.e. a flattened head and large pectoral fins) (Webb et al. 1996). *Cottus bairdi* shares some basic ecological traits such as feeding habits with benthic minnows, but have a much more recent freshwater invasion history compared with other species included in these analyses (Nelson 2006). The second morphological group included benthic minnows which also feed at the substrate level and expend very little energy in continuous swimming, but rather remain at the stream bottom foraging on aquatic vegetation and benthic invertebrates (Sigler & Sigler 1987). Beneficial morphological characteristics in this group are those that promote adherence to the substrate without the need to maintain continuous swimming for prey capture. The third shape group, which included all cyprinids, feed primarily on drifting aquatic organisms (Sigler & Sigler 1987) and benefit greatly by a body shape that allows them to maintain position upwards in the water column. They show signs of greater anterior depth that favors maneuverability (Rincón et al. 2007) and they tend to have slender caudal peduncles and a deeply forked tail that allows them to forage on suspended food drift (Webb 1984). Following the pattern of mid-water minnows, but also forming a distinct group is the salmonid group which closely resembles mid-water minnows in terms of habitat use and feeding but exhibits subtle differences in shape likely resulting from different evolutionary histories.

Predictive Ability of Functional Groups on Swimming Performance

Of the three predictive models, habitat-level functional groups produced the poorest fit with swimming performance data. The lack of correspondence in the prolonged swimming tests is particularly interesting, given the difference in swimming behavior between the two groups. Swimming trials revealed that when subjected to high water velocities, benthic species including *Cottus bairdi*, *Catostomus platyrhynchus*, *Rhinichthys osculus* and *Rhinichthys cataractae* all maintain position by direct contact with the substrate in an attempt to brace. However, taxa in this group were able to maintain position at the same velocities as mid-water species without any exhaustive physical effort. Similar holding behaviors have been observed in several species, including oral suctioning by loricariidae (Gerstner 2007), oral grasping in cyprinids (Adams et al. 2003), fin-positioning by cyprinids (Facey & Grossman 1992) and juvenile salmonids (Arnold et al. 1991) and body positioning by *Cottus bairdi* (Webb et al. 1996). 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 taxa 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 is a violation of the first part of the ecomorphological hypothesis which predicts that morphological variation would have a direct effect on performance. Benthic species are able to overcome what seems to be disadvantageous

morphology for prolonged swimming through unique bracing behaviors. This behavior-mediated performance further illustrates the need to account for unique behavioral adaptations when examining form and function relationships in ecomorphological studies (Garland et al. 1990; Irschick 2002).

Morphologically-based functional groups were somewhat more successful than habitat-based functional groups at predicting swimming performance, but were still not 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 and 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.

By and large, variation in swimming performance due to body size was much greater than interspecific variation in swimming performance. 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 a single group model with size as a predictor variable may adequately predict performance in temperate region stream fishes.

Overall, the inability to find any reliable correspondence between functional groups in either the habitat-based or shape-based models demonstrates the necessity of empirically testing performance of taxa within functional groups. Functional groups have been used to make a variety of ecological predictions (Fox and Brown 1993; Bengtsson 1998). However, without empirically testing the validity of these predictions as they relate to performance, they may be of limited application or utility.

Allometric Effects

The rate of increase in swim speed, as demonstrated in body lengths·sec⁻¹ are generally negatively correlated with body size. Least squares regression produced significant negative slopes for most taxa in burst and prolonged swimming tests. The slopes produced in these tests are indicative of negative allometric effects for all species examined. As body size increases in fish, the effects of drag increase allometrically, resulting in the observed negative slopes. These negative slopes are likely a product of the exponential growth in drag associated with increased surface area which increases with the square and volume which increases to the third power. Thus, swimming performance relative to body size is greatest in juvenile and small bodied individuals.

Conservation Applications

Reliably predicting swimming performance has valuable management implications (Peake et al. 1997). Swimming performance is an important variable in the design and implementation of in-stream barriers to movement such as culverts, weirs and dams (Warren and Pardew 1998). Fish that rely upon stream connectivity often become fragmented by these barriers because swimming performance was not properly accounted for in the design stages, and swim speeds are generally well below the water velocities created by these obstacles (Gibson et al. 2005). The results of my swimming performance tests highlight the need to consider swimming behavioral type when designing for fish passage. As reported above, benthic species rely on a bracing behavior and interacting with the substrate to maintain position during high water velocities. Fish passage efforts will be greatly enhanced by designing for substrate that maximizes

holding ability in benthic fishes. Furthermore, the success of fish passage may be increased by taking into account the swimming performance values reported in this study. 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 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. Additionally, in both the burst and prolonged speed tests, body size proved to be the most reliable predictor of swimming performance. Fish passage models that allow for passage of small bodied fish will effectively allow movement in a stream for all species and size classes.

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Tables

Table 1. 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
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
June sucker	34	Fisheries Experiment Station-Logan, UT	86.56	26-205	10.32
Southern leatherside chub	45	Soldier Creek, UT	83.00	39-107	2.57
Least chub	55	Wahweap Hatchery-Big Water, UT	32.24	21-47	0.78
Longnose dace	56	Soldier Creek, UT	65.18	35-91	2.33
Mottled sculpin	52	Diamond Fork, UT	63.30	29-86	1.56
Mountain sucker	44	Soldier Creek, UT	93.91	43-150	4.82
Redside shiner	30	Fish Creek, UT	79.80	34-112	3.14
Speckled dace	46	Salina Creek, UT	69.96	46-86	1.65

Table 2. Summary of swimming performance data for species used in the study. SL represents standard length in mm, SE indicates standard error and N indicates sample size. Predictive equations for burst and prolonged speed (y) are provided and are calculated as swimming performance in $\text{m}\cdot\text{s}^{-1}$. 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 (m/s)	N_{burst}	Burst Speed Equation	SE	R^2	Mean Prolonged Speed (m/s)	$N_{\text{prolonged}}$	Prolonged Speed Equation	SE	R^2
Brown trout	1.37	31	$y=0.0112(\text{SL})+0.292$	0.06	0.103	0.50	17	$y=0.0025(\text{SL})+0.262$	0.02	0.23
Bonneville cutthroat trout	1.21	47	$y=0.0107(\text{SL})+0.623$	0.03	0.145	0.39	42	$y=0.0072(\text{SL})-0.005$	0.01	0.63
June sucker	1.53	29	$y=0.0037(\text{SL})+1.206$	0.06	0.435	0.42	27	$y=0.0009(\text{SL})+0.331$	0.02	0.45
Southern leatherside chub	1.20	38	$y=0.0137(\text{SL})+0.142$	0.06	0.437	0.54	22	$y=0.0052(\text{SL})+0.132$	0.04	0.34
Least chub	0.87	50	$y=0.0036(\text{SL})+0.757$	0.03	0.009	0.29	50	$y=0.0059(\text{SL})+0.092$	0.01	0.30
Longnose dace	1.20	27	$y=0.0085(\text{SL})+0.650$	0.06	0.242	0.73	15	$y=0.0068(\text{SL})+0.284$	0.06	0.24
Mottled sculpin	1.17	46	$y=0.0052(\text{SL})+0.845$	0.03	0.100	0.52	25	$y=0.003(\text{SL})+0.338$	0.03	0.06
Mountain sucker	1.48	25	$y=0.0088(\text{SL})+0.718$	0.09	0.415	0.63	15	$y=0.0056(\text{SL})+0.247$	0.04	0.65
Redside shiner	1.32	29	$y=0.0076(\text{SL})+0.740$	0.06	0.165	0.75	19	$y=0.0082(\text{SL})+0.148$	0.05	0.68
Speckled dace	1.34	21	$y=0.0143(\text{SL})+0.391$	0.07	0.299	0.69	20	$y=0.009(\text{SL})+0.059$	0.03	0.47

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 both burst and prolonged speed tests.

	Prolonged Speed				Burst Speed		
	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
Group x Size	6, 151	8.78	< 0.001	Group x Size	6, 204	8.19	< 0.001

Table 5. Results of least squares regression for burst swimming speed relative to body size. Log-transformed values were used for both body size (standard length in mm) and swimming performance (body lengths·sec⁻¹). Negative values for slope indicate negative allometric effects with swimming performance. P-values indicate the probability of slope differing from zero. Standardized equations are provided for comparison to other allometric equations. BL indicates body lengths and SL indicates standard length (in mm)

Species	Slope	p-value	Standardized Allometric Equation
Brown trout	-0.354	<0.001	Burst Speed (BL/sec.)=70.11·SL ^{-0.354}
Mountain sucker	-0.456	0.001	Burst Speed (BL/sec.)=129.51·SL ^{-0.456}
Leatherside chub	-0.042	0.794	Burst Speed (BL/sec.)=18.28·SL ^{-0.042}
Longnose dace	-0.566	0.001	Burst Speed (BL/sec.)=193.54·SL ^{-0.566}
Mottled sculpin	-0.719	<0.001	Burst Speed (BL/sec.)=364.27·SL ^{-0.719}
Redside shiner	-0.604	0.001	Burst Speed (BL/sec.)=232.93·SL ^{-0.604}
Speckled dace	-0.241	0.357	Burst Speed (BL/sec.)=54.49·SL ^{-0.241}

Table 6. Results of least squares regression for prolonged swimming speed relative to body size. Log-transformed values were used for both body size (standard length in mm) and swimming performance (body lengths·sec⁻¹). Negative values for slope indicate negative allometric effects with swimming performance. P-values indicate the probability of slope differing from zero. Standardized equations are provided for comparison to other allometric equations. BL indicates body lengths and SL indicates standard length (in mm).

Species	Slope	p-value	Standardized Allometric Equation
Brown trout	-0.191	<0.001	Prolonged Speed (BL/sec.)=12.34·SL ^{-0.191}
Mountain sucker	-0.305	0.041	Prolonged Speed (BL/sec.)=33.35·SL ^{-0.305}
Leatherside chub	-0.421	0.032	Prolonged Speed (BL/sec.)=42.12·SL ^{-0.421}
Longnose dace	-0.295	0.316	Prolonged Speed (BL/sec.)=37.19·SL ^{-0.295}
Mottled sculpin	-0.616	0.036	Prolonged Speed (BL/sec.)=103.07·SL ^{-0.616}
Redside shiner	-0.081	0.501	Prolonged Speed (BL/sec.)=14.40·SL ^{-0.081}
Speckled dace	-0.076	0.692	Prolonged Speed (BL/sec.)=13.38·SL ^{-0.076}

Figures

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

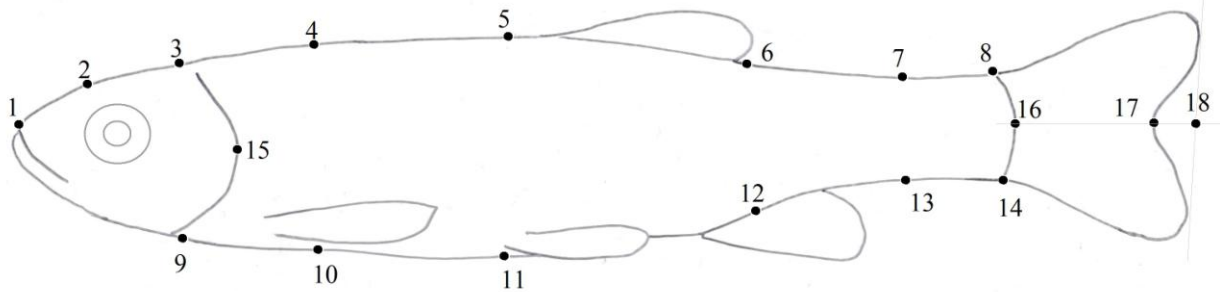


Fig. 2. Three-dimensional representation of observational tank used to measure burst speed. VC, video camera; OA, observation arena; CC, confinement cylinder; MP, mock predator; HD, hinged doors; AR, aluminum runner.

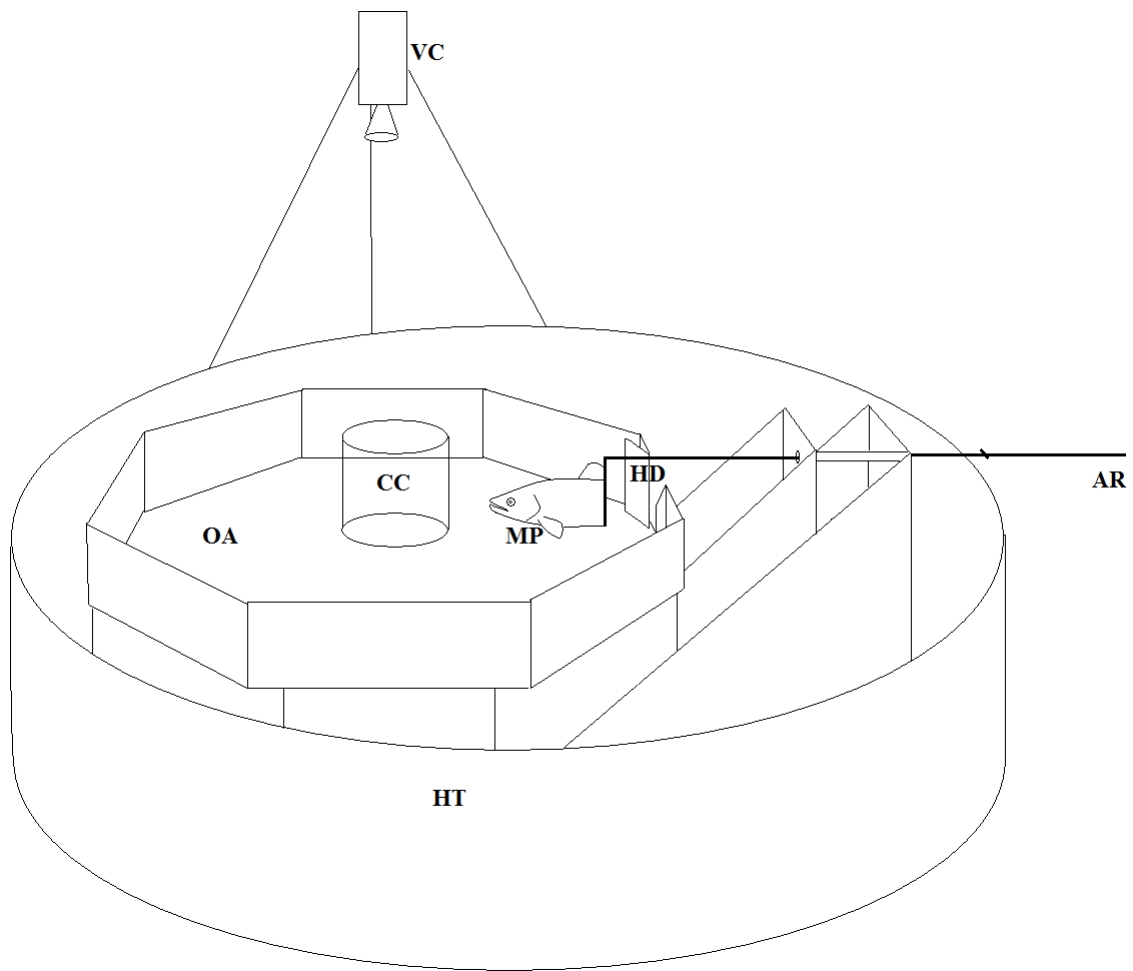


Fig. 3. Representation of the swimming chamber used for prolonged swimming performance tests. FC, flow conditioner; CS, confinement section; US, upstream screen; OS, observation section; DS, downstream screen; R, Reservoir; P, pump. Arrows indicate current directions.

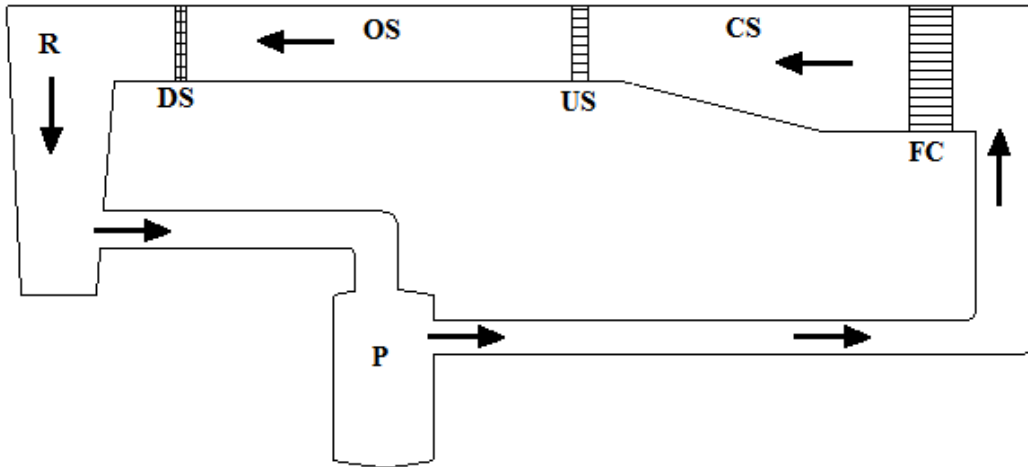


Fig 4. Cluster analysis of morphological and habitat relationships of seven stream fishes from the Great Basin. Triangle and line represents the level of similarity used for the morphological grouping.

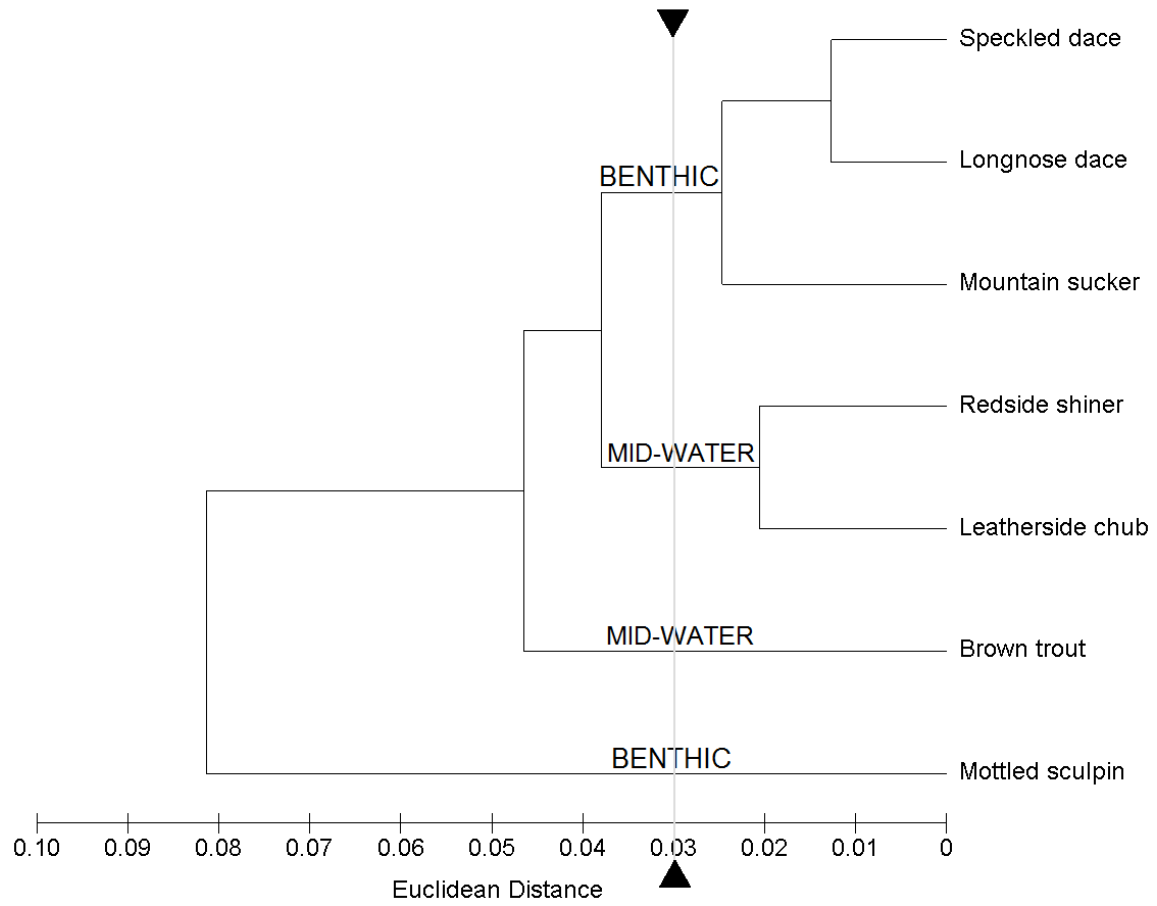


Fig 5. Least squares means estimates of burst speed swimming performance at small (z -size=2), mean (z -size=-0.5) and large (z -size=2) body sizes. Error bars indicate ± 2 standard errors.

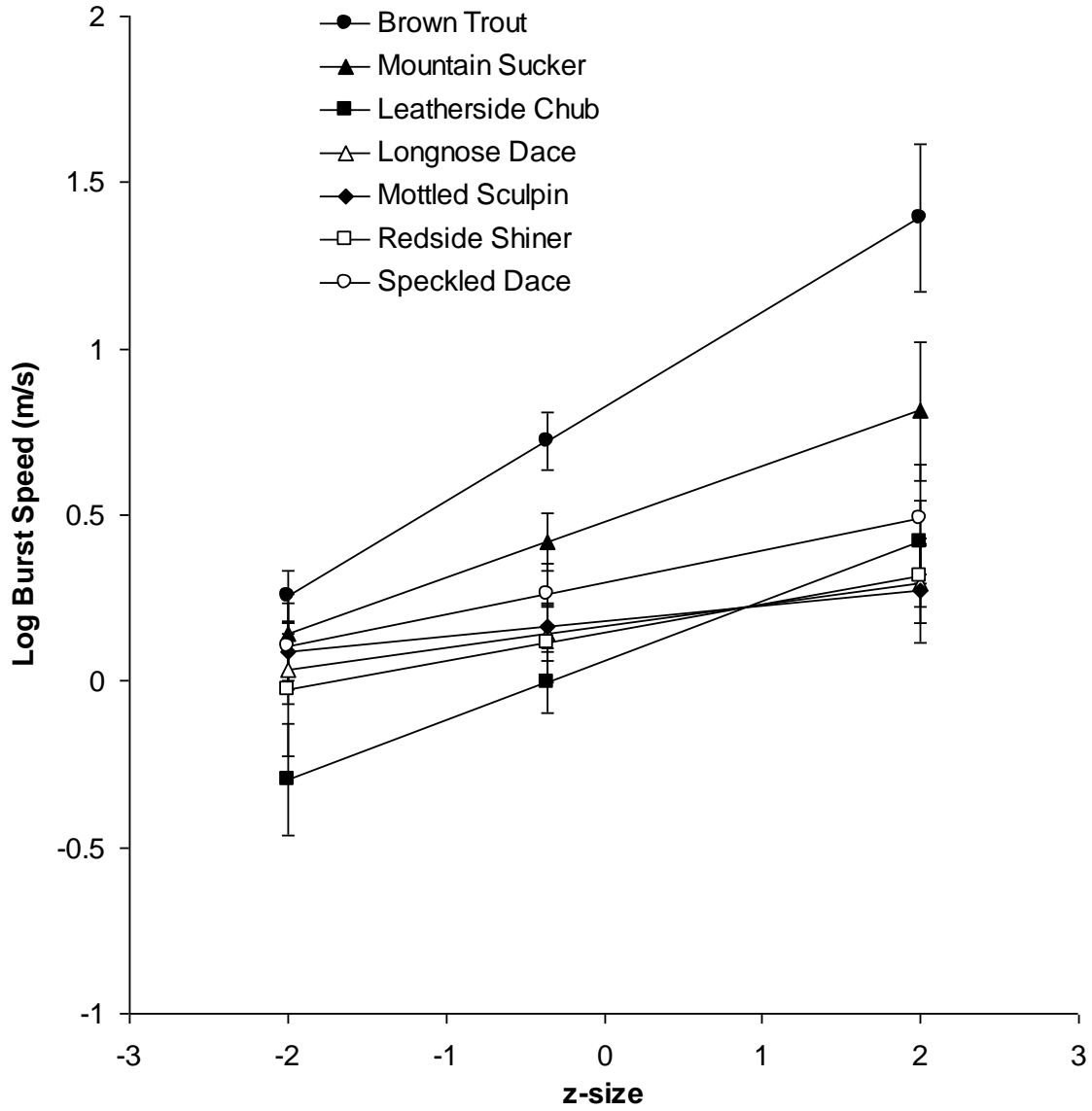


Fig 6. Least squares means estimates of prolonged speed swimming performance at small (z-size=2), mean (z-size=-0.5) and large (z-size=2) body sizes. Error bars indicate ± 2 standard errors.

