

DISSERTATION

MITIGATION MEASURES FOR BARRIERS TO GREAT PLAINS FISH MIGRATION

Submitted by

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ABSTRACT

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The harsh, fluctuating environments of Great Plains streams present unique challenges to aquatic life. Great Plains streams historically supported a fish assemblage that was adapted to survive conditions such as high variability in flow and physicochemical characteristics and frequent changes in physical habitat. Despite the resistance and resilience of these fish species to the harsh conditions of Great Plains streams, many populations have declined in the face of human modifications that include changes in water chemistry, flow regulation, and fragmentation. Fragmentation, or the breaking of a continuous habitat into isolated segments, is a pervasive problem in Great Plains streams, and its reversal is essential to the conservation of Great Plains fishes. Although fragmentation is best reversed by removing structures that prevent fish movement, many of these structures are unlikely to be removed because of the benefits they provide to society. In these instances, fishways or fish ladders are also a viable option for ameliorating fragmentation. However, few recommendations exist for fishway design for small-bodied fishes, especially those of the Great Plains. Although the number of studies focusing on smaller fishes has increased in recent years, most fishway design recommendations are appropriate for salmonids or other large, economically important species such as clupeids.

The goal of this dissertation is to advance the science of fishway design for small-bodied, nonsalmonid fishes by reviewing existing information on small Great Plains fish swimming performance, developing a predictive swimming model for small Great Plains fishes, advancing rock ramp fishway design knowledge by evaluating the effects of substrate arrangement on fish

passage success, and evaluating fish passage success at two existing rock ramps in a Colorado stream.

The longitudinal fragmentation of streams is a pressing issue that can be ameliorated by installing fish ladders at barriers to fish movements. However, fish ladders must be designed using swimming performance of the target species, and studies of small-bodied fishes (defined as species with mean adult total length [TL] < 150 mm) are less common than studies of larger fishes. The review of swimming performance of small Great Plains fishes combined swimming studies, information from reviews, and unpublished data to summarize factors affecting small fish swimming performance and to identify generalities in the existing literature.

Performance in small-bodied fishes is affected by size, shape, behavior, environmental conditions, and physiological traits. Generalities are rare in the small fish swimming literature because few measured variables are common to all studies. Many small-bodied fishes can sprint at speeds of 50 cm/s or more, and the clear relationship between aerobic and anaerobic swimming ability for most species provides a means to estimate anaerobic swimming ability, which is more useful for fishway design, from the more-commonly measured aerobic swimming ability. Regression tree analysis of aerobic and anaerobic swimming data showed that performance was affected by taxonomy, and a summary of existing studies showed that swimming performance tends to increase between 5 and 30°C. This review can advance fishway design by making known swimming performance data more accessible and by identifying areas for future research.

The goal of the predictive swimming model study was to predict swimming performance of untested Great Plains fishes, because directly testing swimming performance of all species would be time-consuming and expensive. Species-specific swimming performance data are

essential to effective fishway design, but these data are lacking for most small-bodied fishes of the North American Great Plains. Models of maximum aerobic and sprint swimming ability were parameterized with 15 Great Plains species. Swimming abilities were measured in swimming flumes, and nine morphological and physiological variables were used as predictors. Random forest (RF) analyses were used in model construction because of their superior predictive power to regression models. The model for aerobic swimming explained 36% of the observed variation in the validation data set. The most important predictor variables were total length, weight, and percent red muscle at 50% of total length. The sprint model explained 47% of the observed variation in the validation data set. Total length, weight, and fish shape were the most important predictor variables. This study showed that swimming ability is best predicted with a combination of morphological and physiological variables. Although the RF models had limited precision, they can be used to predict swimming performance of untested Great Plains fish species when direct measurement of performance is not possible.

The goal of the rock ramp study was to estimate fish passage success over two substrate arrangements that produced different hydraulic conditions. Substrate arrangement on rock ramp fishways may affect passage success of small-bodied fishes, but few studies have been conducted to explore this. To help develop recommendations, a small model fishway (slope = 3%, flow = 0.026 m³/s) was constructed with two different substrate treatments: closely-spaced cobbles and widely-spaced cobbles. Hydraulic conditions were measured with an acoustic Doppler velocimeter, and passage success of three small-bodied fishes (longnose sucker *Catostomus catostomus*, longnose dace *Rhinichthys cataractae*, and johnny darter *Etheostoma nigrum*) were tested in 22-hour trials. Treatment-averaged values of velocity, Froude number, and energy dissipation factor did not vary between the two treatments. However, treatment-averaged values

showed that adding cobbles to a smooth ramp would increase small fish passage success, given their limited swim speeds and their preferences for lower Froude numbers. The range of individual point velocities and turbulence measurements differed between treatments. The median velocity in the closely-spaced treatment was 50% of the median velocity in the widely-spaced treatment. The widely-spaced cobble treatment had a higher range of velocities and more velocities that exceeded the sprinting abilities of the tested species than the closely-spaced treatment, indicating that closely-spaced cobbles on rock ramps provide more velocity refuges for ascending fish. Maps of hydraulic conditions showed that velocities in both treatments were highest around the cobbles in the center of the fishway and that the closely-spaced treatment had more variable flow fields but lower velocities than the widely-spaced treatment. There was no statistically significant difference between passage success over the closely-spaced and widely-spaced treatments for the three tested fish species, indicating that the higher turbulence in the closely-spaced treatment did not impede passage.

The field evaluation of two rock ramps was designed to advance the new science of designing rock ramp fishways for entire fish assemblages. Knowledge gained from field evaluations of existing fishway performance can greatly improve design, but these evaluations are rare, especially in systems without anadromous species. The movement of medium- and large-bodied fishes (TL > 100 mm) across rock ramps can be effectively measured with PIT tags. The goal of this study was to compare passage rates of PIT-tagged fishes across two structurally different fishways, one with a confined low-flow notch and a 4.5% slope and another that spanned the width of the river and had an 11.2% slope. Movement across the fishways was compared to movement at a single control site. Seven longnose dace *Rhinichthys cataractae*, 149 longnose sucker *Catostomus catostomus*, 368 brown trout *Salmo trutta*, and 527 rainbow

trout *Oncorhynchus mykiss* were tagged, and their movements past three sets of paired PIT tag antenna arrays were tracked in a 1-km section of a small Colorado stream for 14 months.

Antenna detection data that recorded fish movements were analyzed with a multi-state model in Program MARK, which generates transition probabilities and allows hypothesis testing. Model selection results indicated that fish were less likely to move across the steep fishway than the one with a lower slope and less likely to move longer distances (i.e., across more than one fishway/control site). These results, in combination with results from a small number of similar studies, provide more support that slopes of 5% or less increase passage rates of a wide variety of species and that fishway design specifications should be tailored to the resident fish assemblage.

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CHAPTER 1:

MITIGATION MEASURES FOR BARRIERS TO GREAT PLAINS FISH MIGRATION: INTRODUCTION AND EXPERIMENTAL APPROACH

INTRODUCTION

The streams of the western Great Plains have been intensively modified by agricultural and industrial land use for over a century, and as a result, these streams have lost many of the characteristics necessary to support robust fish assemblages. This dissertation focuses on evaluating methods to reverse one of the major alterations to western Great Plains streams: the loss of the longitudinal connectivity that is crucial to fish population persistence in a variable environment.

Streams of the North American Great Plains

The fishes inhabiting the western Great Plains of North America are subjected to unique environmental challenges produced by a semiarid climate with fluctuating environmental conditions. The highly variable climatic and physical conditions result in streams that can vary markedly within and between years in terms of water chemistry (Fausch and Bestgen 1997) and flow regime, producing a patchy environment where resource availability changes through space and time. Nevertheless, this region was historically home to a diverse fish fauna that developed highly mobile life histories (Dodds et al. 2004) to cope with the spatiotemporal variability of their environment. However, streams and rivers within this region have been extensively modified to supply water for irrigation, municipal use, and wastewater treatment and disposal needs (e.g., Strange et al. 1999). As a result, water chemistry and natural flow regimes have been altered. These modifications may increase or decrease spatial and temporal flow permanence and have caused losses of the spatial connectivity that is crucial to the persistence of

resident fish populations. Thus, a challenge facing fisheries biologists is devising approaches to restore the spatiotemporal connectivity to the streams and rivers of the western Great Plains. Doing so requires understanding of the climatic, physical, and ecological nature of the region, the ecology and swimming ability of the native fishes, and how fishway features such as slope and substrate arrangement affect passage success, in the laboratory and in the field (Figure 1-1).

The western Great Plains are bounded by the 100th meridian in the east and the Rocky Mountains in the west (Wohl et al. 2009), and are characterized by long, cold winters (minimum January temperature average: -19° C) followed by hot, dry summers (maximum average July temperature: 28-30° C). The region is semiarid. For example, the portion of the Missouri River Basin that flows through the Great Plains receives an average of 36 cm/year of precipitation, and the southwestern Great Plains (i.e., the Arkansas River, Red River, Canadian River and Little River basins) receive an average of 20 cm/year (Matthews et al. 2005). The timing and magnitude of precipitation events on the western Great Plains create a variable hydrograph in many of its streams.

Because Gulf Coast, Canadian, and Pacific air masses can all converge on the Great Plains, weather can be violent and unpredictable (Matthews et al. 2005). Much of the precipitation arrives with localized, intense thunderstorms, and flash flooding is common (Strange et al. 1999). In winter, portions of streams, including entire pools, may freeze completely (Labbe and Fausch 2000). Although blizzards do occur in winter, snowpack is not a reliable source of runoff because much of the snow sublimates (Wohl et al. 2009). During the hot, dry summers, streams are susceptible to dramatic flow reductions, intermittency, or complete drying (e.g., Falke et al. 2011). How these already-variable conditions will be altered by climate change should also be of concern to fisheries biologists.

Although the projected effects of climate change must be viewed in the context of anthropogenic changes to flow regimes (Graf 1999), stream conditions on the Great Plains are sensitive to climate (Covich et al. 1997; Brikowski 2008). For example, the duration of the monsoon season and the amount of precipitation delivered is dependent on sea surface temperatures, with El Niño years bringing a longer, wetter monsoon season to the Great Plains (Castro et al. 2001). Predictions for this region include increased incidence of drought, lower snowpack, increased storm intensity (IPCC 2007), and increased risk of drying in smaller streams (Covich et al. 1997). All of these factors would increase the already-high flow variability in Great Plains streams.

Great Plains Fishes: a Declining Assemblage

Fishes native to this ecosystem, collectively referred to as Great Plains fishes, have physiological and life history traits that allow them to survive in an environmentally, spatially, and temporally variable habitat. Adaptations such as small body sizes (ca. < 100 mm total length, TL) and short lifespans (ca. 1 – 2 years) (Fausch and Bestgen 1997) facilitate persistence in a constantly changing environment. Physiologically, many Great Plains fishes are able to tolerate harsh environmental conditions such as high salinity, hypoxia, high water temperatures, and sudden fluctuations in flow (Matthews 1987; Bramblett and Fausch 1991; Fausch and Bestgen 1997). Many species can recolonize empty habitats quickly after local extirpations caused by floods, drying, or harsh environmental conditions (Larimore et al. 1959; Scheurer et al. 2003; Falke et al. 2012). Despite the evolved resilience of these populations, many of the native fishes have declined in number and contracted in geographic range (Fausch and Bestgen 1997). For example, 29 of the 76 species native to the Platte River in Nebraska have decreased in abundance between 1945 and the present (Peters and Schainost 2005). In Colorado, 20 of 37

Great Plains fish species have been assigned a conservation status due to population declines or are extinct (Falke et al. 2011). In the South Platte River Basin, nearly half of the 29 native species have been extirpated or are listed as threatened, endangered, or of special concern (Table 1). These range contractions suggest that the physiological and life history traits that allow plains fishes to persist in unmodified streams do not necessarily allow them to thrive in anthropogenically altered streams.

Fragmentation: Effects on Fishes

While many factors have been cited as potential causes of the decline of plains fishes, including the altered flow regimes, physical habitat alterations, and degraded water quality associated with large-scale agricultural land use (Rabeni 1996; Fausch and Bestgen 1997; Galat et al. 2005; Matthews et al. 2005), perhaps the most pervasive anthropogenic disturbance of large and small Great Plains streams is fragmentation. Fragmentation is a common side effect of urban, industrial, and agricultural water use (Jackson et al. 2001). Instream structures such as culverts, water diversions, and dams impede or prevent movement of aquatic organisms, thereby dividing streams into a series of physically isolated segments. Fifty-two percent of North America's large river systems are moderately or strongly affected by fragmentation of their main stems, their tributaries, or both (Dynesius and Nilsson 1994). Extensive damming and water diversion is present on streams of the southwestern Great Plains (Matthews et al. 2005) and the Missouri River Basin (Galat et al. 2005). Even the relatively pristine Yellowstone River has three major cross-channel diversions that have altered upstream fish assemblages (Helfrich et al. 1999). This widespread change in stream connectivity could be a leading cause for the declines of Great Plains fishes (Aló and Turner 2005; Winston et al. 1991).

Connectivity, or the availability of continuous, unfragmented stream habitat is essential to the persistence of many lotic fish species (Fausch et al. 2002). Because the diverse habitats that supply spawning substrates, foraging opportunities, and seasonal refugia are spatially and temporally separate (Falke and Fausch 2010), survival of most Great Plains fishes depends on frequent movement. For example, the persistence of brassy minnow (*Hybognathus hankinsoni*) populations depends upon their ability to recolonize extirpated areas after desiccation or floods (Scheurer et al. 2003; Falke et al. 2010; Falke and Fausch 2010). The need for connectivity between habitat patches and the use of seasonally available habitats have also been documented for Arkansas darter *Etheostoma cragini* (Labbe and Fausch 2000; Groce et al. 2012). Fragmentation has been implicated in the extirpation of Great Plains fish species above barriers (Winston et al. 1991; Helfrich et al. 1999; Toepfer et al. 1999), less diverse fish assemblages above barriers (Guenther and Spacie 2006; Litvan et al. 2008a), and reduced population viability of the endangered Rio Grande silvery minnow, *Hybognathus amarus* (Alò and Turner 2005). Therefore, reestablishing connectivity is a key step in halting or reversing declines of the western Great Plains fish assemblage.

Reversing Fragmentation

Restoring connectivity to Great Plains streams would benefit numerous native fishes, including those that are threatened with basin-wide or regional extirpation, but resource managers in this region largely lack taxa-specific information on how this could be achieved. Urban and agricultural stream condition is driven by socioeconomic factors such as the need for flood control and consistent water delivery—this makes reversal of large-scale disturbances (e.g., altered flow regimes) unlikely. However, fish habitat quality varies at a more local scale, and allowing fish to move and therefore select habitats at this smaller scale may increase the ability

of these modified systems to support more robust, diverse, and persistent fish assemblages. The simplest method for restoring connectivity is the removal of instream structures, but reversing fragmentation by this means is often impractical given the benefits provided by those structures, including flood control, irrigation, and recreation. An alternate approach is the construction of structures that allow upstream and downstream movement of fishes. These structures are often referred to as fish ladders or fishways (Clay 1995). However, much of the past research aimed at developing fishway design criteria has been focused on salmonids, or at least on large-bodied fishes (Billman and Pyron 2005), so the available information may not be directly applicable to the majority of small-bodied Great Plains fishes.

STATEMENT OF PROBLEM AND EXPERIMENTAL APPROACHES

The goal of this dissertation is to advance the science of fishway design for small-bodied, nonsalmonid fishes by doing the following:

- Synthesizing existing information on small Great Plains fish swimming performance
- Developing a predictive swimming model for small Great Plains fishes
- Advancing rock ramp fishway design knowledge by evaluating the effects of roughness on fish passage success, and;
- Evaluating fish passage success at two existing rock ramps in a Colorado stream.

These four objectives address the lack of data that are needed to adapt fishway designs to small-bodied Great Plains fishes. The first objective involves summarizing what is known about Great Plains fish swimming and determining if generalities exist in the literature. The second involves determining whether it is possible to rapidly estimate swimming performance of an untested Great Plains fish species when lengthy swimming studies are not possible. The third

objective focuses on whether rough rock ramps hinder small fish passage through increased turbulence or facilitate it through reduced velocity. The fourth objective involves determining structural characteristics of rock ramps that affect passage rates of wild fish under natural conditions. The rationale for each of the four objectives is explained in further detail below, but the goal of this dissertation is to remove some of the guesswork associated with Great Plains fish passage so that fishway design for Great Plains species can approach the level of sophistication currently seen in salmonid fishway design.

In the past, fishways have been built primarily for passage of salmonids, which tend to be strong swimmers with the ability to leap over vertical obstacles. Studies of swimming performance in small, nonsalmonid fish have increased in the last 10 years, but there is still less available information on their swimming abilities and their needs with respect to fishways than there is for salmonids and other economically important fishes. Of the many types of fishways, rock ramp fishways, which are essentially artificial riffles, have shown the greatest promise in allowing passage of small-bodied fishes (Harris et al. 1998). For example, when riprap grade control structures in an Iowa stream were modified to allow fish passage, the index of biotic integrity used to measure the effects on the fish assemblage increased at seven of nine study sites (Litvan et al. 2008a). Some of the advantages of traditional rock ramps include effectiveness over a diversity of hydraulic conditions and the lack of confined entrances where predation or biotic interactions causing avoidance behaviors can occur (Bunt et al. 1998). However, several sources of uncertainty complicate attempts to design effective rock ramp fishways for use in Great Plains streams. These uncertainties exist because of limited data on the swimming performances of small Great Plains fishes, limited knowledge of how small Great Plains fishes

respond to hydraulic conditions such as roughness and turbulence, and a lack of field tests of rock ramp fishway effectiveness.

A Review of Existing Information on Small Great Plains Fish Swimming Performance

Small fish swimming ability has been tested for multiple reasons, but to date, no concerted effort has been made to integrate or synthesize the data into a single comprehensive source. Some studies have used swimming performance as a measure of comparative fitness between groups exposed to different levels of a contaminant (e.g., Bengtsson 1980; Periera et al. 2012), some have tested swimming performance to provide information to support fish passage studies (e.g., Adams et al. 2000; Bestgen et al. 2010), and others have examined how morphology affects swimming performance (e.g., Leavy and Bonner 2009). Critical swimming velocity (U_{CRIT} , Brett 1964) is a common laboratory measure of aerobic swimming performance. Critical swimming velocity information exists for approximately 17 native Missouri River Basin fishes (11 of which occur in Colorado), and sprinting abilities have been measured for 15 species, 5 of which occur in Colorado (Fausch and Bestgen 1997; Billman and Pyron 2005). However, the Missouri River supports 60 native fishes in Montana, and 110 species in Missouri. The South Platte River, a tributary to the Missouri River and one of Colorado's major rivers, supports 29 native species in Colorado (Fausch and Bestgen 1997, Table 1). Because studies on small fish swimming performance have varied with respect to goals and measurement endpoints, few generalities have emerged from the available literature on small-bodied fish swimming performance.

Chapter 2 of this dissertation presents a comprehensive review and synthesis of the current knowledge of the swimming abilities of small-bodied (adult TL \leq 150 mm) North American fishes and describes its shortcomings. This chapter also provides recommendations on

how to standardize studies to facilitate future meta-analyses and recommendations on how to move this body of knowledge past the descriptive stage that is typical of newer branches of science.

A Predictive Swimming Model for Small Great Plains Fishes

Although studying the swimming performance of every Great Plains fish is not feasible, given the large number of species present, it may be possible to construct a predictive model of fish swimming performance using easily measured morphological and physiological traits that could be used to predict the performance of otherwise untested species. Previous fish swimming studies have examined the relationship between shape and swimming performance in warmwater fishes (Billman and Pyron 2005; Aedo et al. 2009; Leavy and Bonner 2009). However, no study has integrated morphological and physiological traits to produce a predictive model that could estimate the performance of Great Plains fishes with unknown swimming abilities. Such a model would be useful in designing effective fishways and instream structures such as low-head diversion dams that permit upstream and downstream passage of a wide range of species. The goal of Chapter 3 of this dissertation is to present a modeling approach that predicts aerobic and anaerobic swimming ability as a function of fish morphology, relative percentages of red and white muscle in the axial muscle, and two simple hematological measurements.

A Laboratory Study of the Effects of Roughness on Fish Passage Success

Every rock ramp is unique—these structures differ with respect to slope, length, and the size and arrangement of substrate (A. Ficke, personal observation). Because the size and arrangement of the substrate affects velocity distributions and the size and orientation of turbulent eddies (e.g., Tritico and Cotel 2010), varying substrate size and orientation could have profound effects on passage success, particularly for small-bodied fishes that have not evolved in

turbulent environments. However, few studies have addressed the interactions between small-bodied fishes and hydraulic characteristics such as turbulence (Lacey et al. 2012). Therefore, the fourth objective of this dissertation was to test the effects of different substrate arrangements on an experimental rock ramp on the probability of upstream fish movement. The results of this test are presented in Chapter 4.

A Field Evaluation of Two Existing Rock Ramps in a Colorado Stream

Field evaluations of rock ramps are rare (e.g., Bernhardt et al. 2005), but testing their performance by estimating fish movement across them is a crucial step in improving fishway design for small-bodied species. Relating structural characteristics of rock ramps to fish passage success should help standardize design by determining what works and does not work under field conditions. A small number of studies have reported upstream passage rates and structural characteristics such as length and slope for one or more rock ramps (Santos et al. 2005; Litvan et al. 2008b; Franklin et al. 2012), but many rock ramps remain untested. Movement rates of wild fish were measured across two rock ramps that differed in slope and proportion of stream width used, and movement rates across these structures were compared to movement rates across a control site. The study reach was located in South Boulder Creek, Boulder County, Colorado. This mark-recapture study was designed to further explore the effects of rock ramp structural characteristics on fish passage success. It is described in Chapter 5 of this dissertation.

Table 1-1.—Fish species of the South Platte River drainage (from Fausch and Bestgen 1997). Fishes with a special listing status in Colorado are indicated: FT = federally threatened, SE = state endangered, ST = state threatened, and SC = species of special concern (Colorado Parks and Wildlife 2013).

Species	Extirpated in CO?	Status
Greenback cutthroat trout (<i>Oncorhynchus clarki stomias</i>)	No	ST, FT
River carpsucker (<i>Carpoides carpio</i>)	No	
Longnose sucker (<i>Catostomus catostomus</i>)	No	
White sucker (<i>C. commersonii</i>)	No	
Central stoneroller (<i>Campostoma anomalum</i>)	No	
Northern redbelly dace (<i>Chrosomus eos</i>)	No	SE
Lake chub (<i>Couesius plumbeus</i>)	No	SE
Red shiner (<i>Cyprinella lutrensis</i>)	No	
Brassy minnow (<i>Hybognathus hankinsoni</i>)	No	ST
Plains minnow (<i>H. placitus</i>)	No	SE
Common shiner (<i>Luxilus cornutus</i>)	No	ST
Hornyhead chub (<i>Nocomis biguttatus</i>)	Yes	n/a
Bigmouth shiner (<i>Notropis dorsalis</i>)	No	
Blacknose shiner (<i>N. heterolepis</i>)	Yes	
Sand shiner (<i>N. stramineus</i>)	No	
Suckermouth minnow (<i>Phenacobius mirabilis</i>)	No	SE
Fathead minnow (<i>Pimephales promelas</i>)	No	
Longnose dace (<i>Rhinichthys cataractae</i>)	No	
Creek chub (<i>Semotilus atromaculatus</i>)	No	

Table 1-1.—continued.

Species	Extirpated in CO?	Status
Black bullhead (<i>Ameiurus melas</i>)	No	
Channel catfish (<i>Ictalurus punctatus</i>)	No	
Stonecat (<i>Noturus flavus</i>)	No	SC
Plains topminnow (<i>Fundulus sciadicus</i>)	No	
Plains killifish (<i>F. zebrinus</i>)	No	
Green sunfish (<i>Lepomis cyanellus</i>)	No	
Orangespotted sunfish (<i>L. humilis</i>)	No	
Iowa darter (<i>Etheostoma exile</i>)	No	SC
Johnny darter (<i>E. nigrum</i>)	No	
Orangethroat darter (<i>E. spectabile</i>)	No	SC

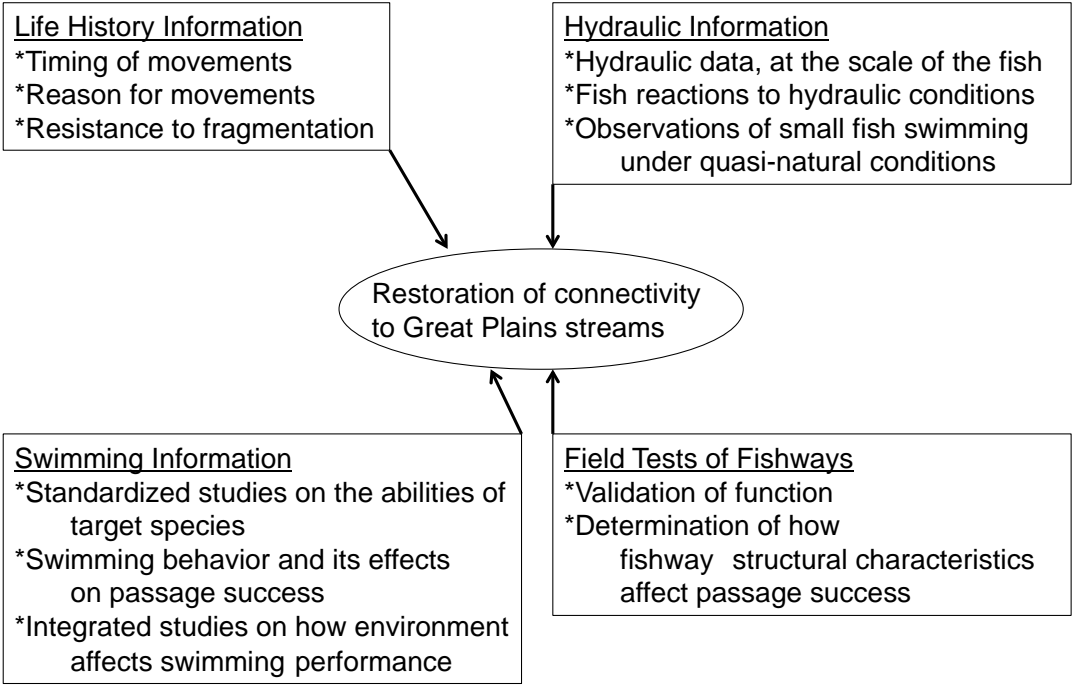


Figure 1-1.—Necessary elements to restore stream connectivity for Great Plains fishes.

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CHAPTER 2:
A REVIEW OF SWIMMING ABILITIES OF SMALL-BODIED NORTH AMERICAN
FISHES

INTRODUCTION

The North American continent supports a rich fish assemblage in a diverse array of habitats. Many of those fish populations, particularly those inhabiting the western Great Plains, persist through dynamic cycles of local extinction and recolonization (Larimore et al. 1959; Labbe and Fausch 2000; Fausch et al. 2002; Scheurer et al. 2003; Falke and Fausch 2010). These highly mobile populations are threatened in part because many North American streams are extensively fragmented by diversion dams (Bestgen and Platania 1991; Helfrich et al. 1999), culverts (Warren and Pardew 1998), and grade control structures (Litvan et al. 2008). This fragmentation has been implicated in the declines of many small-bodied fish populations (Winston et al. 1991; Alò and Turner 2005). Nevertheless, much of the infrastructure fragmenting these streams benefits society and is unlikely to be removed. When instream structure removal is not possible, longitudinal connectivity can be improved through other measures such as installing fish passage structures (fishways). Designing effective fishways requires swimming performance estimates for the target species, so that water velocities on the fishways do not exceed their abilities. In most Great Plains systems, the target species are small-bodied, nonsalmonid fishes.

Although the available swimming performance data for small Great Plains fishes has increased in recent years, knowledge about these species still lags behind what is known for salmonids. Early swimming performance studies focused on salmonids (e.g., Brett 1964), and

fishways have traditionally been designed to accommodate this highly mobile family of fishes. Salmonids are strong swimmers with well-developed swimming and jumping abilities (Stuart 1962; Kondratieff and Myrick 2006; Castro-Santos et al. 2013). However, most of the 900 fishes native to North America are not salmonids, and many are small, with typical adult sizes of 150 mm total length (TL) or less (Cross and Collins 1975; Page and Burr 1991). These smaller fishes often cannot ascend fishways designed for larger salmonids (Mallen-Cooper et al. 1999), because of their limited jumping ability and lower absolute swimming ability.

The need for swimming performance data that can be used to design fishways for small-bodied fishes has been the impetus for a number of recent studies. However, the specific focus on small-fish swimming ability, the factors that affect it, and the implications for conservation of these species is relatively new. As such, the current body of small-fish swimming literature offers few opportunities for synthesis for two main reasons. First, the *a priori* hypotheses and measured variables vary widely between studies. For example, some studies have focused on conservation measures (Toepfer et al. 1999; Adams et al. 2000; Scott and Magoulick 2008; Bestgen et al. 2010), while others have focused on life history, physiology, and the associated mechanisms underpinning performance (Garenc et al. 1999; Billman and Pyron 2005; Leavy and Bonner 2009). Because the foci of these studies are diverse, there are few measured variables that are common to all of them. Second, swimming performance can be measured with several different methods. These include incrementally increasing or “stepped” velocity tests used to estimate critical swimming velocity (U_{CRIT} , Brett 1964), constant acceleration tests, fixed velocity tests, and startle tests (Hammer 1995; Nelson et al. 2002). This disparate body of knowledge needs to be organized and synthesized to advance the science of swimming performance for small North American fish.

The goal of this review is to identify generalities in these fish swimming performance data and integrate existing studies so knowledge gaps can be identified. There have been no previous attempts to synthesize this knowledge, and the small-fish swimming literature consists of a large amount of heterogeneous information. This review consists of two parts: the main body of the paper, in which generalities in the small fish swimming literature are derived, and an appendix summarizing the studies that were found during the literature search but that were not used to synthesize the generalities presented in the main body of the paper. The appendix has three primary uses. First, it provides fish swimming information that can be used as a starting point in fishway design. Second, it will aid researchers and managers by summarizing swimming performance information in a single source to avoid redundancy in future research projects (i.e., through multiple tests of the same species). Third, it will allow researchers and managers to identify opportunities for future research.

METHODS

This synthesis includes a literature review and three data analyses. A combination of published and unpublished data was used in the review and the analyses. The methods used to collect these data are described below.

Data Collection

This synthesis relies largely on published data, which were collected through a literature search in the ProQuest Aquatic Sciences and Fisheries Abstracts and the Web of Science databases. The search terms “swimming performance” and “swimming ability” were combined with one of the following terms: physiology, hydraulics, temperature, toxicology, pollution, behavior, or morphology, for a set of 14 separate searches. Fifty-three published studies on the swimming performance of North American fishes with typical adult sizes of approximately 150

mm or less were incorporated into the review and the analyses. Small, nonsalmonid fishes were the focus of this review because of the relative lack of swimming performance information and because of the emerging understanding of the effects of fragmentation on these fishes. Small individuals of species with a typical adult TL greater than 150 mm were not included in this review, because the goal of this review was to focus on species that do not grow large enough to use traditional fishway designs. However, some studies involving larger taxa (e.g., salmonids) are presented to introduce concepts that have not been tested for small-bodied species.

Supplementary data

Swimming data for 16 North American species¹ are also presented in this report and incorporated into the analyses. These data were collected by the author for a laboratory study that examined the effects of physiological and morphological metrics on swimming performance. Though unpublished, the data were collected using established methods. Swimming performances were measured using constant acceleration tests (after Leavy and Bonner 2009). Fish were tested in Loligo Model 32 or Loligo Model 90 Swim Tunnels (Loligo Systems, Tjele, Denmark). After a one-hour acclimation period with a current of 5 cm/s, the velocity in the swim tunnel was increased by 5 cm/s every 5 s. Two measurements were recorded for each test. The first was gait transition velocity, where fish switched from steady swimming to intermittent burst or sprint swimming to maintain their position in the flume. Similar to critical swimming velocity, a gait transition speed (U_{TRANS}) represents a fish's maximum aerobic swimming ability (Peake 2008a) and a velocity that can be maintained for an extended interval (i.e., minutes to

¹black bullhead *Ameiurus melas*, stonecat *Noturus flavus*, brook stickleback *Culaea inconstans*, white sucker *Catostomus commersonii*, brassy minnow *Hybognathus hankinsoni*, creek chub *Semotilus atromaculatus*, fathead minnow *Pimephales promelas*, flathead chub *Platygobio gracilis*, longnose dace *Rhinichthys cataractae*, northern redbelly dace *Chrosomus eos*, suckermouth minnow *Phenacobius mirabilis*, plains killifish *Fundulus zebrinus*, plains topminnow *F. sciadicus*, green sunfish *Lepomis cyanellus*, Iowa darter *Etheostoma exile*, and Johnny darter *E. nigrum*

hours). The second measurement was the velocity at which the fish became exhausted and impinged on the rear screen of the swim tunnel. This maximum sprinting velocity (U_{MAX}) represents a conservative estimate of the fastest velocity that a species can attain; generally such velocities can be maintained for a minute or less. Median U_{TRANS} and U_{MAX} velocities for the 16 species are presented in the results and incorporated into the quantitative analyses described below.

Swimming data from fixed velocity tests (after Ficke et al. 2011) were also incorporated into this review. After a 1-hour acclimation period at 5 cm/s, the current velocity in the swim tunnel was increased to the fixed test velocity. The fish swam at this velocity until exhaustion, when it became impinged on the rear screen of the swimming chamber. Median endurance times of flathead chub (see footnote above for scientific names) and median endurance times and observed swimming behaviors of northern redbelly dace are presented in the section describing the effects of temperature on swimming performance.

Data Analyses

The goals and hypotheses of swimming performance studies of small-bodied fishes vary widely, so measurements and methods also vary widely between studies. The only variables common to all studies included in this review are species and a measure of swimming performance. Three exploratory analyses were conducted on this heterogeneous data set, which otherwise limited the range of possible analyses. The first explored the relationship between fish size and swimming ability across species, the second explored the relationship between aerobic and anaerobic swimming ability within a species, and the third examined how swimming performance varied by taxonomy.

The first analysis was designed to explore effects of total length on aerobic and anaerobic swimming performance. Although the positive effect of fish size is well-documented (Harvey 1987), particularly within species (Adams et al. 2000, Bestgen et al. 2010), the intent of this analysis was to determine whether this relationship was preserved across species and across studies with varying test conditions such as temperature. The data used in these analyses were obtained from 11 published studies and supplemented with mean swimming performance for one additional species (Ficke and Myrick, unpublished data). Analyses of standard length effects on swimming performance were not performed because most of these data came from two studies that incorporated length into their syntheses (Aedo et al. 2009; Leavy and Bonner 2009). Linear regression was used to test the relationship between total length and aerobic performance and the relationship between total length and anaerobic performance. Effects were considered statistically significant at $\alpha = 0.05$.

The relationship between aerobic and anaerobic swimming ability was analyzed for species for which maximum aerobic (U_{CRIT} or U_{TRANS}) and anaerobic (U_{MAX}) swimming ability data were available. If a clear relationship existed between aerobic and anaerobic performance, sprinting ability could be estimated for species that have been tested for U_{CRIT} . This would be useful for fishway design because U_{CRIT} is the most commonly reported measurement of swimming performance, whereas U_{MAX} is more applicable to fishway design. Paired aerobic and anaerobic performance data were available for 23 species, and the relationship between the two performance measures was analyzed with least-squares linear regression in JMP Pro 11 (SAS Institute 2013). The relationship between aerobic and anaerobic swimming performance was considered statistically significant at $\alpha = 0.05$.

The third analysis contained two parts and was designed to determine whether aerobic and anaerobic swimming performance varied by taxonomy. The first part focused on aerobic swimming performance, and the second focused on anaerobic swimming performance, but both analyses used the same independent variables. Family was used as the taxonomic predictor variable (n = 6 for the Aerobic analysis, n = 9 for the Anaerobic analysis).

The data used in the Aerobic analysis and the Anaerobic analysis were obtained from 12 published studies and supplemented with data on 16 species of fish tested at the Colorado State University Foothills Fishery Laboratory. The data were selected as follows to reduce “nuisance” variance that could mask potential relationships between swimming performance and the predictor variables. Fish length plays a major role in predicting swimming performance (see *Results*). However, because length in the published studies was variously reported as total length and standard length, and because length ranges were sometimes presented instead of mean lengths, the effect of fish length, generally considered a key variable in fish swimming performance, could not be added to the analysis. Therefore, only data collected from fish less than 100 mm TL were included, whereas those collected from larger fish were omitted.

Despite its importance in shaping swimming performance (See *Temperature Effects on Swimming Performance*), temperature was also omitted from the analyses because temperatures were inconsistently reported. Therefore, swimming performances could not be associated with a specific temperature. However, studies involving physiologically stressful temperatures or abrupt temperature changes were omitted from the Aerobic and Anaerobic analyses, because temperature stress reduces swimming performance (Hocutt 1973; Hammill et al. 2004). To reduce additional variation from temperature stress, studies were retained in the analysis if fish were tested at their acclimation temperatures and were tested at temperatures ranging from 15 to

33°C. Because test type can also influence performance measures (Hammer 1995, Plaut 2001), aerobic data were restricted to stepped velocity tests (i.e., those typically used to estimate U_{CRIT}), and anaerobic data were restricted to constant acceleration tests.

The relationship between taxonomy and swimming performance was analyzed with a regression tree with 10-fold cross validation in JMP Pro 11 (SAS Institute 2013). This nonparametric method is useful in exploratory studies because it is resistant to outliers, it makes no assumptions about linearity or normality in the data set, and it is simple to interpret (Sutton 2005; SAS Institute 2012). In a regression tree analysis, data are partitioned into groups so that the sum of squared error for each group mean is minimized. Partitioning ceases when the amount of variation explained by the analysis does not increase with additional splits. This analysis identifies natural patterns in the data and can process categorical predictor variables, which makes it ideal for an analysis of the data on small fish swimming performance. Each split that separates the data into groups is assigned a p -value in JMP. Swimming abilities of different groups were considered statistically significant at $\alpha = 0.05$.

“Typical” Swimming Performances and Generalities

The goal of the literature review was to determine whether any generalities could be identified in the current literature on swimming performance of small North American fishes. The results from the 53 published studies from the literature search were synthesized to produce four broad generalities, which were supported by data from the analyses described above when applicable. These generalities are largely heuristic and provide opportunities for exploring underlying mechanisms and for more formal analyses in future studies. The identified generalities are presented in the results section, and studies that were located in the literature search but not incorporated into the synthesis are summarized in the appendix.

RESULTS

The small fish swimming literature is currently limited by a lack of standardization in measured variables. For example, every study reported standard or total length, not both. Some studies involved one or more temperatures that were held constant over time, and others involved ambient (i.e., fluctuating) temperatures that were reported as ranges. This data heterogeneity precluded the use of more complex meta-analyses and further syntheses. Nevertheless, a few broad generalities can be drawn.

Fish Size Affects Swimming Ability

Larger fish are faster, most of the time. Although experimental conditions such as test temperature varied in the studies used in this meta-analysis, total length still had a positive effect on swimming performance (Figure 2-1). The analysis of aerobic swimming performance showed that total length had a positive and statistically significant effect on aerobic swimming performance ($df = 12$, $p = 0.011$, $r^2 = 0.43$) and on anaerobic swimming performance ($df = 10$, $p = 0.023$, $r^2 = 0.45$). However, despite the pronounced effects of fish length on swimming performance, the majority of small-bodied fishes (< 150 cm TL) tested to date can achieve sprinting speeds of approximately 50 cm/s. Median sprinting ability of the 72 fishes included in this review was 62 cm/s, and the 25th percentile was 44 cm/s (Figure 2-2).

Aerobic versus Anaerobic Performance

As might be expected, there was a statistically significant relationship between aerobic and anaerobic swimming ability for the 23 studied species (linear regression, $df = 22$, $p < 0.001$, Figure 2-3). The relationship can be described with the following equation:

$$\text{Anaerobic} = 25.68 + (1.30 * \text{Aerobic}),$$

where Anaerobic = maximum anaerobic (sprint) swimming ability (cm/s) and Aerobic = maximum aerobic swimming ability (cm/s). This equation explained 42% of the variation in the data ($r^2 = 0.42$), and the anaerobic values predicted with the equation were within 20% of the measured values for 18 of the 23 studied species (Table 2-1), indicating that a clear and positive relationship exists between aerobic and anaerobic ability for most of the studied species.

Swimming Ability, Taxonomy, Swimming Mode, and Habitat Preference

Regression tree analysis results indicate that swimming ability varies between families. For aerobic performance, the regression tree model explained just over one-half of the variation in the data ($r^2 = 0.51$). The results of the Aerobic analysis indicate that the mean swimming ability of the slower group (Families Cyprinodontidae, Centrarchidae, Percidae) was 54% of the mean swimming ability of the faster group (Families Gasterosteidae, Osmeridae, and Cyprinidae, Figure 2-4).

The results of the Anaerobic analysis also indicate that taxonomy influences sprint swimming ability. The regression tree model explained nearly one-third of the variation in the data ($r^2 = 0.31$). The mean anaerobic performance of the slower group (Families Ictaluridae, Gasterosteidae, Cyprinodontidae, Poeciliidae, Atherinidae, Centrarchidae, Percidae, and Cichlidae) was 59% of the mean anaerobic performance of the faster group (Families Cyprinidae and Characidae, Figure 2-4).

Temperature Effects on Swimming Performance.

Few small-bodied fish species have been tested at multiple temperatures, and small sample sizes associated with each temperature and test type precluded a formal data analysis. However, data from 11 published studies and supplemental data (Ficke and Myrick, unpublished data) for two species made it possible to draw preliminary conclusions about the relationship

between temperature and swimming performance. Aerobic and anaerobic swimming performance increased between 5°C and 30°C for most of the tested species (Figure 2-5). However, delta smelt *Hypomesus transpacificus* U_{CRIT} was not significantly different between fish acclimated to 12°, 17°, or 21°C (Swanson et al. 1998). Similarly, although swimming performance of Mojave tui chub *Gila bicolor mohavensis* increased between 18°C and 24°C, it did not change between 24°C and 30°C (McClanahan et al. 1986). Likewise, fast-start swimming (i.e. volitional swimming trials involving a startle response) of eastern mosquitofish *Gambusia holbrooki* was approximately 102 cm/s at 26°, 30°, and 34°C, and fast-start speeds were lower outside of this optimal range (Wilson 2004).

DISCUSSION

Fish Size Affects Swimming Ability

Although larger fish tend to be faster than smaller ones, the positive effect of total length on swimming performance can be clouded by differences in morphology, behavior, and physiology. The positive relationship between TL and swimming performance is usually apparent in intraspecific studies (but see Colborne et al. 2011) but can become more diffuse in interspecific comparisons. For example, physiological and morphological differences between species can have pronounced effects on swimming performance (See *Taxonomy and Swimming Ability* for further detail).

Because many of the species tested to date can sprint at 50 cm/s or more, this velocity can be used as a starting point for fishway design, in the event that no other information is available for the target species. Still, because evidence exists that fish typically found in low-velocity habitats tend to be slower than those found in higher-velocity habitats (Leavy and Bonner 2009),

direct testing or modeling of target species' swimming ability is recommended whenever possible.

Aerobic versus Anaerobic Swimming Ability

The statistically significant, positive relationship between aerobic and anaerobic swimming ability in the 23 studied species indicates that fish with greater aerobic swimming performance also have greater anaerobic swimming ability. However, the regression equation that describes this relationship is relatively imprecise, and useful only to coarsely predict sprint speeds from U_{CRIT} or U_{TRANS} data. Anaerobic swimming speeds were underpredicted by as much as 33% and overpredicted by as much as 62% (Table 2-1). This equation could not be validated with external data because of the small number of species for which aerobic and anaerobic swimming data are available. Improving the predictive ability of this equation by incorporating new swimming performance data would reveal whether the relationship described by the regression analysis is general enough to be applied to other species.

Swimming Ability and Taxonomy

The regression tree analysis of small fish swimming data showed that ability varied with taxonomy. Taxonomic differences in swimming performance may be a reflection of how morphology and physiology vary across species. Several studies involving multiple small-bodied species have shown the importance of morphology in shaping performance. For example, fishes with more streamlined bodies tend to be faster than “stockier” or deeper-bodied fishes. Intraspecific studies of varying body forms have shown that deeper-bodied individuals have lower endurance than more streamlined individuals (threespine stickleback *Gasterosteus aculeatus*, Blake et al. 2005; bluegill *Lepomis macrochirus*, Colborne et al. 2011). Furthermore, studies of interspecific variation in morphology and swimming performance have shown that

more streamlined species tend to be faster than deep-bodied species and that large caudal fins and long, broad pectoral fins tend to be associated with higher swimming performance (Billman and Pyron 2005; Leavy and Bonner 2009). The relationship between morphology and swimming performance has also been demonstrated indirectly in the field. A study of channelized and unchannelized sections of an Iowa stream showed that less streamlined species such as centrarchids and ictalurids were absent from channelized sections (i.e., where higher water velocities are typical, Scarnecchia 1988).

Physiological differences between species may be another possible reason for the observed differences in swimming performance among families. For example, levels of the enzyme citrate synthase (CS) was positively correlated with aerobic swimming ability (measured as U_{CRIT}) of threespine stickleback (Schaarschmidt and Jürss 2003), and a study of large marine fish demonstrated that more active species tend to have higher levels of enzymes such as CS in their axial muscle (Gibb and Dickson 2002). However, no studies have been designed to link interspecific variation in enzymatic activity to swimming performance. Similarly, interspecific differences in muscle morphology could be an important factor in determining swimming performance. Fish use red (slow oxidative) muscle for aerobic swimming, and white (fast glycolytic) muscles for anaerobic, or sprint, swimming, and McLaughlin and Kramer (1991) demonstrated that fish with life histories involving more activities such as ranging and movement tended to have a higher percentage of red muscle than more sedentary species.

This generality should be considered preliminary because of the small number of species studied so far. For example, in the Anaerobic analysis, the performances of species in families Atherinidae and Characidae were both represented by single species with limited sprinting abilities, but other species in these families may be much faster.

Temperature Effects on Swimming Performance

Swimming performance appears to increase between 10 and 30°C for most of the species tested. However, the lack of large differences over a range of temperatures in some small fishes suggests that, like salmonids and large catostomids, (e.g., Brett 1964, Kolok et al. 1993), small fishes may have an “optimal temperature range”, over which swimming performance remains relatively constant. The reduction in swimming performance at suboptimal temperatures is likely related to physiological changes. At temperatures lower than the optimal range, changes in enzymatic activity (Hammill et al. 2004), reductions of muscle shortening velocities, and increases in muscle relaxation times tend to reduce swimming performance (Johnston and Temple 2002, Jones et al. 2008). The reduced performance of cyprinid red muscle at lower temperatures requires activating limited-endurance white muscle fibers at lower velocities (Jones 1982), leading to earlier fatigue and reduced endurance. This phenomenon has been observed in northern redbelly dace (mean TL = 54 ± 6 mm). Individuals acclimated to 10°C and 17.5°C used a combination of steady and burst swimming and fatigued quickly at 50 – 60 cm/s (median endurance ≤ 0.5 min) compared to individuals acclimated to 25°C and swimming at the same velocity (median endurance of 2.1 min, Ficke and Myrick, unpublished data). Swimming performance decreases at temperatures approaching the upper tolerance limits of a species, because higher energetic demands for resting metabolism reduce the scope for activity (Brett 1971; Kitchell et al. 1977). Increased resting metabolism at higher temperatures is caused by mechanisms such as decreased cardiac efficiency (Taylor et al. 1997), but these mechanisms have only been demonstrated for larger fishes.

Moving Forward towards Integrative Study

The summary above represents generalities based on a large amount of research, and may be useful in fishway development and to further the knowledge of the exercise physiology of small North American fishes. The most immediate practical use of the information in this review is the refinement of fishway design. The temperature dependence of swimming performance within some portion of a fish's thermal niche underscores the importance of developing fishways that not only work at a wide range of flows but that also account for the changing swimming performance of the target species with changing water temperature (i.e., seasonally). The temperature dependence of swimming performance also emphasizes the importance of considering the life history of target species in fishway design. For example, if a fish swims slowly at 10°C but does not move extensively at this temperature, it might not be necessary to design a fishway with velocities that accommodate its reduced ability at 10°C. However, given that the number of studies focused on the ecology of small North American fishes is still relatively small, the behavior and ecology of many small fishes remains unknown. Therefore, until more is known about the ecology of these fishes, fishways should be designed to allow passage under suboptimal conditions such as low temperatures whenever possible.

The second use of this information is to incorporate it into the design of more realistic studies of how fish swimming performance is shaped by the environment. For example, the effects of temperature on swimming performance are fairly well-documented (Brett 1964; Myrick and Cech 2000; Bestgen et al. 2010), but swimming performance is also affected by other environmental factors such as dissolved oxygen (reviewed in Beitinger et al. 2000), and photoperiod (Kolok 1991; Smiley and Parsons 1997). Swimming performance can also be reduced by a wide range of pollutants (see Appendix 2A). Currently, there is no clear picture of

how combined natural and anthropogenic stressors affect fish swimming ability, but a series of integrated studies could begin to address this.

Swimming performance studies of small North American fishes are increasing, but more congruence is needed before the science advances further. Creating a set of measurements common to all future studies would standardize them and allow for future meta-analyses. At a minimum, velocity, temperature, mean, maximum, and minimum fish total length, and test type should be reported for each study. A focus on integrative studies, instead of studies involving one manipulated factor such as temperature would produce results that would be more useful to managers seeking to conserve these species. Also, a focus on underlying mechanisms that drive swimming performance may provide further insight and allow better prediction of swimming performances of untested species.

Table 2-1.—Aerobic and sprint speeds of 23 North American fishes. Swimming data for species in bold were collected at the Colorado State University Foothills Fishery Laboratory (Ficke and Myrick, unpublished data). Predicted anaerobic speeds were obtained from the regression equation, and the percent error of the prediction is shown. Negative values in the prediction error column indicate that underprediction of sprint speeds, and positive values indicate overprediction.

Species	Aerobic speed	Sprint Speed	Predicted	Prediction
	(U_{TRANS}, cm/s)	(U_{MAX}, cm/s)	Sprint	Error
			Speed (cm/s)	
Black bullhead	34	64	70	+10%
Stonecat	54	62	96	+55%
White sucker	48	83	87	+5%
Brook stickleback	30	69	64	-7%
Blacknose dace	38	111	75	-32%
Brassy minnow	44	73	83	+14%
Central stoneroller	36	63	73	+16
Creek chub	53	88	94	+7%
Fathead minnow	39	90	76	-16%
Flathead chub	61	114	106	-7%
Longnose dace	44	78	83	+6%
Northern redbelly dace	40	72	77	+7%
Rio Grande silvery minnow	52	109	93	-15%
Suckermouth minnow	45	87	85	-3%
Topeka shiner	40	75	78	+4%
Banded killifish	25	88	59	-33%
Plains killifish	48	102	88	-13%

Table 2-1—continued.

Species	Aerobic speed	Sprint Speed	Predicted	Prediction
	(U_{TRANS}, cm/s)	(U_{MAX}, cm/s)	Sprint	Error
			Speed (cm/s)	
Plains topminnow	34	84	70	-17%
Bluegill	27	41	61	+51%
Green sunfish	41	79	79	< 1%
Longear sunfish	15	28	45	+62%
Iowa darter	38	70	75	+7%
Johnny darter	37	64	74	+17%

Table 2-2.—Summary of aerobic and anaerobic swimming ability by family. Species used to calculate mean swimming ability for each family were used in the regression tree analyses of taxonomic differences in swimming ability.

Family	Aerobic Ability (cm/s)		Anaerobic Ability (cm/s)	
	Species	Mean \pm SD	Species	Mean \pm SD
Cottidae	1	52.1	0	n/a
Ictaluridae	0	n/a	1	43.4
Gasterosteidae	1	32	0	n/a
Catostomidae	2	52.4 \pm 14.7	0	n/a
Cyprinidae	13	48.4 \pm 17.3	31	59.7 \pm 19.8
Osmeridae	1	37.9	0	n/a
Characidae	0	n/a	1	50.9
Cyprinodontidae	3	25.5 \pm 1.3	3	39.7 \pm 8.5
Poeciliidae	0	n/a	4	27.2 \pm 11.7
Atherinidae	0	n/a	1	30.2
Centrarchidae	3	18.3 \pm 7.8	4	38.6 \pm 8.7
Percidae	1	19.9	1	40
Cichlidae	0	n/a	1	33

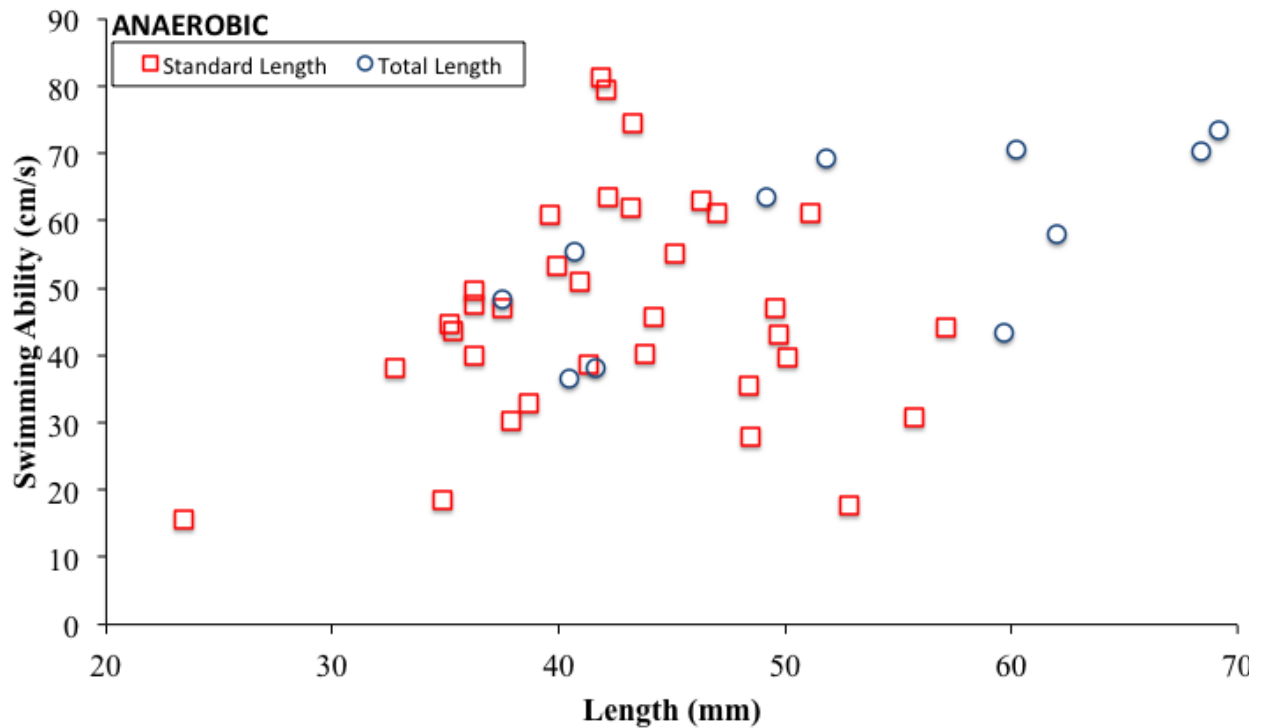
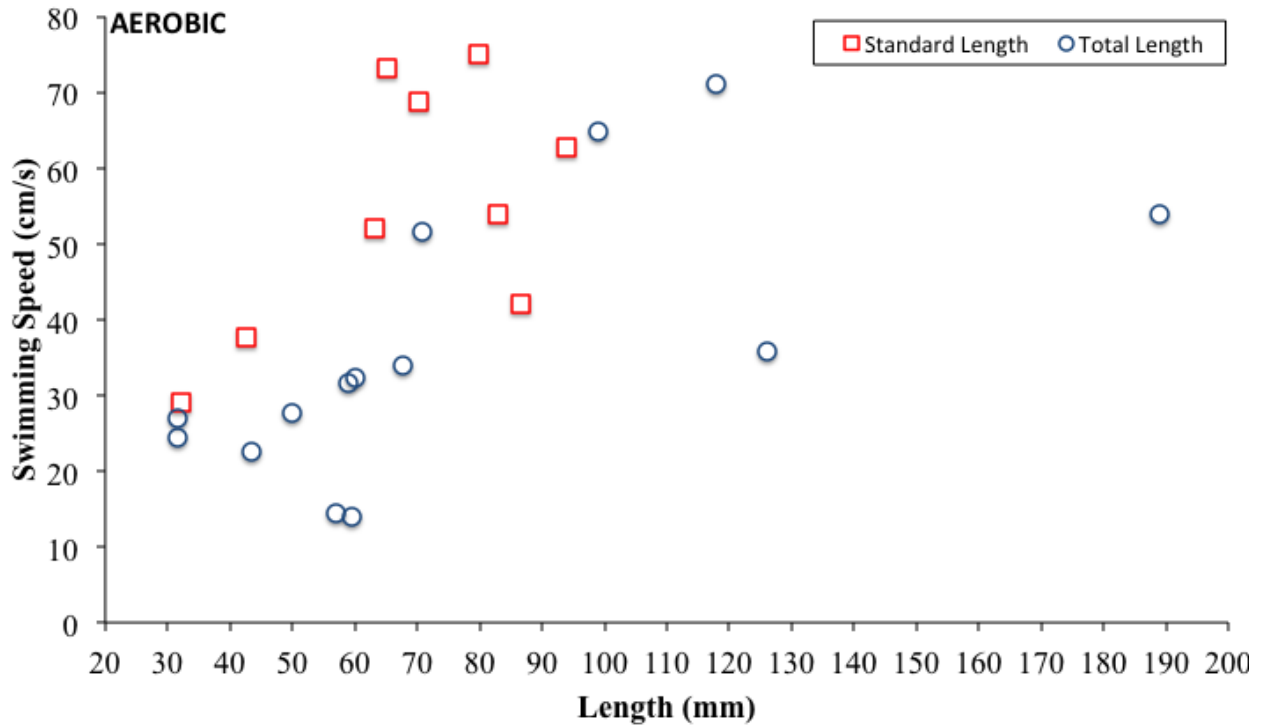


Figure 2-1.—Summary of relationships between aerobic swimming ability and length (top) and anaerobic swimming ability and length (bottom) in small North American fishes. Because of differences in how fish were measured, total length and standard length are distinguished on the graphs. Note the difference in x-axis scales between graphs.

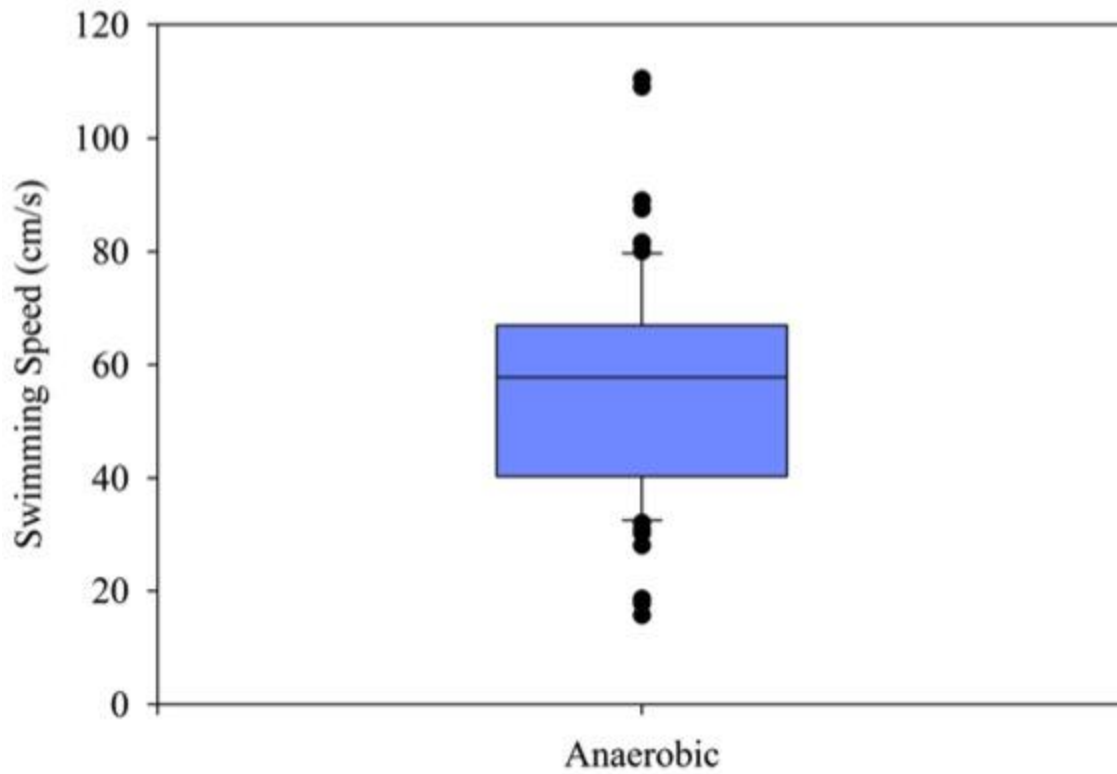


Figure 2-2.—Summary of known sprinting abilities of small-bodied North American fishes. Individual sprinting abilities of the 67 species included in this figure are listed in Appendix 2A.

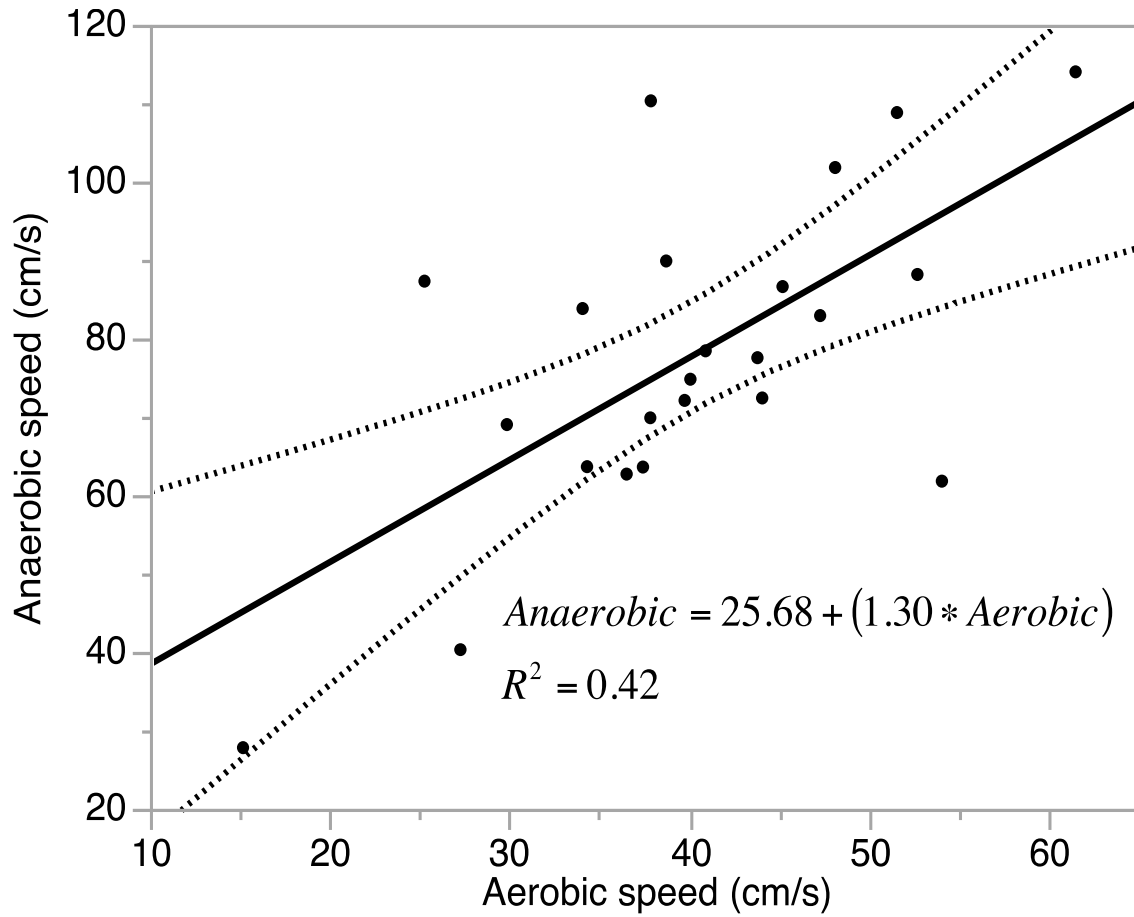


Figure 2-3.—Relationship between aerobic and anaerobic swimming performance of 23 small-bodied North American fishes. Each data point represents an individual species. The dashed lines represent 95% confidence limits for the regression line.

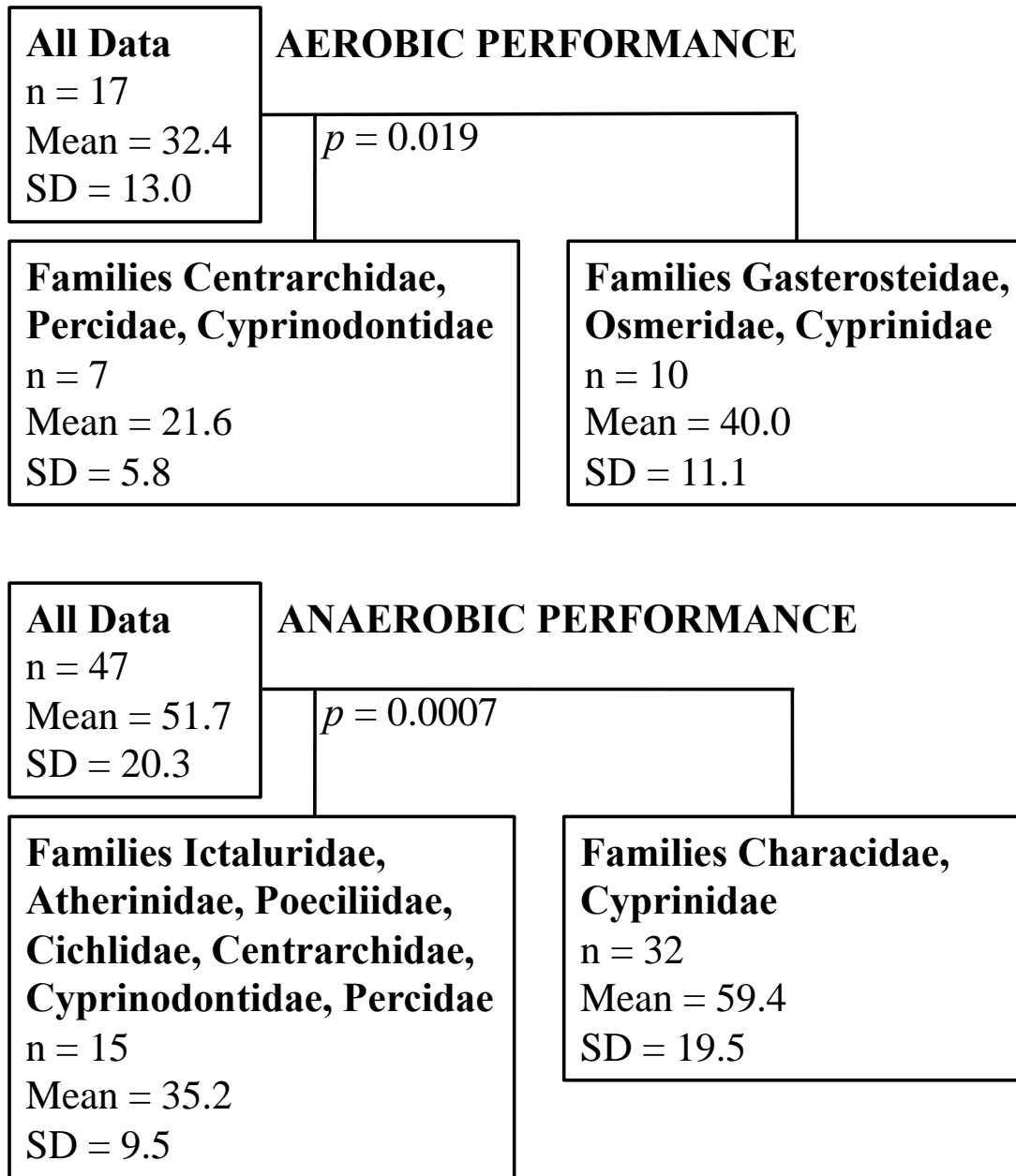


Figure 2-4.—Regression tree results for aerobic (top tree) and anaerobic (bottom tree) swimming performance as they relate to taxonomy. The *p*-values associated with each of the splits are shown, and *p*-values less than 0.05 indicate statistical significance (see text for details).

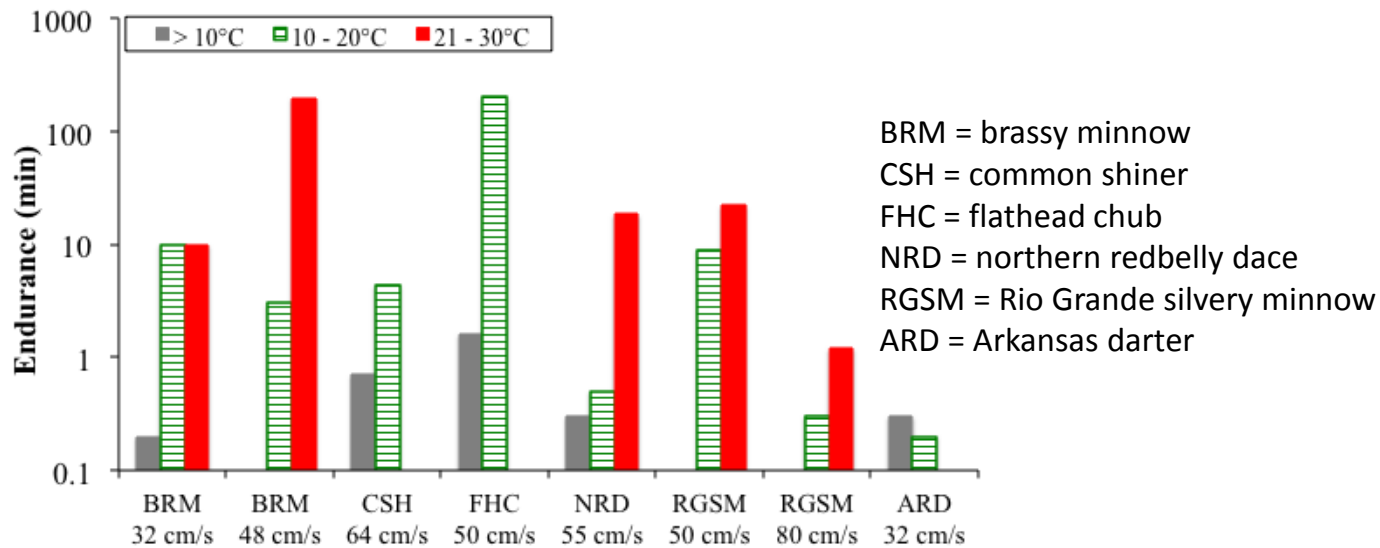
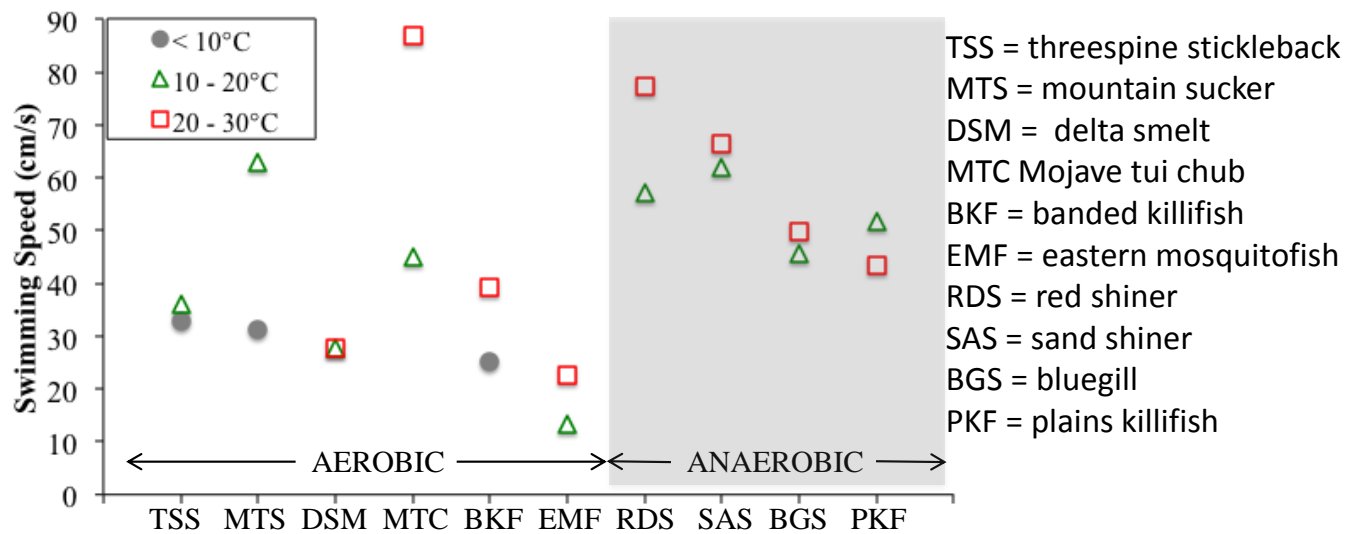


Figure 2-5.—Summary graph of available studies of temperature effects on swimming performance, separated by test type. Variable speed tests (top graph) are stepped velocity tests for calculation of UCRIT (aerobic) or constant acceleration tests (anaerobic). Fixed velocity tests are shown in the bottom graph.

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CHAPTER 3:
A PREDICTIVE MODEL OF SWIMMING ABILITY FOR SMALL-BODIED GREAT
PLAINS FISHES

INTRODUCTION

Stream fragmentation, or the breaking of a continuous series of habitat patches into many isolated segments, is a pervasive problem that has caused declines and local extinctions in many North American fish populations (Winston et al. 1991; Dynesius and Nilsson 1994; Fagan et al. 2002). As a result, restoring longitudinal connectivity to streams is an essential part of the effort to halt or reverse the decline of many stream fish populations. Although much of the infrastructure that blocks fish movement is unlikely to be removed because of the benefits it provides to society, retrofitting that infrastructure with fishways that fish can ascend is one possible means of restoring connectivity to fragmented systems.

Well-designed fishways require that the designer account for the swimming performances of target species (Mallen-Cooper et al. 1999), but such data are often unavailable for small-bodied fishes. Although swimming performance studies of small-bodied fishes have become more common in recent years, there is still less information available for these species than for salmonids. Critical swimming velocity (U_{CRIT} , the most common measure of maximum aerobic swimming ability, Brett 1964) data exist for approximately 17 native Missouri River Basin fishes (five of which occur in Colorado), and sprinting abilities have been documented for 15 species, seven of which occur in Colorado (Page and Burr 1991; Billman and Pyron 2005; Leavy and Bonner 2009). However, the Missouri River supports 60 native fishes in Montana, and 110 species in Missouri. The South Platte River, a tributary to the Missouri River and one of

Colorado's major rivers, supports 29 native species (Fausch and Bestgen 1997). Many of these species are economically unimportant, and direct tests of swimming performance are time-consuming and costly (e.g., Plaut 2001). For example, manufactured swim tunnels can cost up to \$30,000 (Loligo Systems Inc., Tjele, Denmark), and a substantial amount of time is required to collect, acclimate, and test the swimming performance of wild fishes. Therefore, it is infeasible to test every small-bodied fish in the Missouri River system, let alone in all Great Plains streams.

Because of the logistic difficulties of measuring swimming performance for a large number of individual species, a model predicting swimming performance that uses easily measured inputs would benefit managers responsible for providing swimming ability estimates for fishway design. Predicting swimming performance should be possible because it is a function of morphology and physiology. The body and fin morphology of fishes reflect their physical environment and their life history, and many studies have demonstrated the importance of morphology in swimming performance (Billman and Pyron 2005; Ohlberger et al. 2006; Fisher and Hogan 2007). For example, numerous studies have shown that a more streamlined morphology results in increased swimming ability within and between species. Fineness ratio, or the ratio of body length to body depth, caudal peduncle depth, and caudal fin area have all been linked to improved aerobic swimming performance (Taylor and McPhail 1985; Taylor and Foote 1991; Hawkins and Quinn 1996; Ohlberger et al 2006; Fisher and Hogan 2007), and fineness ratio has been linked to improved burst swimming performance (Billman and Pyron 2005). Traits such as enzymatic activity (Schaarschmidt and Jürss 2003), physiology (Ojanguren and Braña 2003), the ratio of red muscle to white muscle (McLaughlin and Kramer 1991), and hemoglobin concentration (Farlinger and Beamish 1978) also affect swimming performance.

To address this broader suite of potential factors, a combination of morphological and physiological measurements was used to develop a predictive swimming model for small-bodied fishes native to the western Great Plains, using a subset of the South Platte River fishes. The primary goal of this study was to build a model that predicts swimming performance of small-bodied fishes as a function of body shape and selected physiological measurements. This study is the first to integrate the known effects of morphology and physiological traits into a predictive swimming model. It was designed to increase knowledge about the factors affecting swimming performance and to predict the swimming performances of small-bodied target species when they cannot be measured. Predicted swimming abilities can be used to improve fishway designs for small-bodied species.

METHODS

Swimming performance data and selected morphological and physiological characteristics of 15 fish species were used to construct predictive swimming models. All data were collected at the Colorado State University Foothills Fishery Laboratory (FFL), and all experiments were conducted according to a protocol approved by the Colorado State University Animal Care and Use Committee (protocol #10-2259A).

Fish care

Wild fishes of the 15 species used in the study (Table 3-1) were collected via electrofishing from various sites in Colorado with the assistance of Colorado Parks and Wildlife personnel. These fish were transported to the FFL and held in 340-L round polyethylene tanks. The tanks received 5 – 10 L/min of air-saturated water, depending on stocking density, and the spray bars delivering the water were angled to produce a current of 0.05 to 0.10 m/s. Spray bar

direction was reversed once every 1 – 2 weeks to prevent fish from developing asymmetric musculature by swimming in round tanks in a single direction.

Fish were allowed to adjust to laboratory conditions and to recover from transport stress for one week. Afterwards, the temperature was adjusted by 2°C per day until it reached 20 ± 1°C. Water temperature was maintained within 1°C of the test temperature with electronic mixing valves (Asahi, Inc. Malden, Mass.). Fish were held at 20°C for at least 2 weeks before testing to allow acclimation (Lyytikäinen et al. 1997; MacNutt et al. 2004). All fish were maintained on a natural photoperiod. The timers used to control lighting were adjusted weekly to reflect the natural photoperiod for Fort Collins, Colorado (13T 494072, 4487697). Fish were fed bloodworms (Family Chironomidae), brine shrimp *Artemia spp.*, or commercial fish feeds *ad libitum* once daily.

Data Collection and Processing

Swimming performance was measured with a constant acceleration test (Drucker 1996; Reidy et al. 2000), wherein water velocity is increased at a constant rate until the fish is exhausted. Two velocities were recorded: the velocity at which the fish switched from steady swimming to intermittent burst swimming (the gait transition velocity, U_{TRANS}) and the velocity at which the fish became exhausted (the maximum test velocity, U_{MAX}). Like critical swimming velocity (U_{CRIT} , Brett 1964), the gait transition velocity is an estimate of maximum aerobic swimming capacity. However, gait transition velocity is a more precise estimate because it does not rely upon arbitrary selection of time intervals between velocity increases or the selection of an appropriate velocity increase or “step” (Peake 2008). The maximum test velocity, U_{MAX} , is an estimate of the sprint swimming ability of a fish. However, this value is an underestimate of a fish’s true sprinting ability because the fish tire during the test and because there is evidence that

laboratory tests underestimate swimming performance (e.g., Castro-Santos et al. 2013). The absolute swimming performance (cm/s) of individual fish was used in the data analyses, even though swimming performance can be scaled to fish size by using relative swimming performance (i.e., body lengths per second). Relative performance measures do not remove the influence of total length (TL) on swimming performance, because they also depend on fish size (e.g., Moyle and Cech 1988; Wakeling et al. 1999). Furthermore, absolute swimming performance measurements are more relevant to fish passage applications.

Fish were placed in Loligo Model 32 or Model 90 swim tunnels (Loligo Systems, Inc., Tjele, Denmark), depending on their size. Larger fish were tested in the Model 90 tunnels, so that the length of the swimming chamber was at least two times the total length of the fish (Reidy et al. 2000). Fish were afforded a 2-h acclimation period at a current of 5 cm/s. Trials began at 5 cm/s, and the current was increased by 5 cm/s every 5 s (e.g., Leavy and Bonner 2009). The time between velocity increases was set at 5 s to minimize underestimation of sprinting ability after pilot studies with a small number of plains topminnow indicated that velocities at exhaustion were 5 to 10 cm/s lower when velocity increases occurred every 10 seconds. Fish swam to exhaustion, defined as impingement on the rear screen of the swimming chamber. At the end of the swimming trial, fish were euthanized with MS-222 (250 mg/L, buffered to a neutral pH), weighed to the nearest 0.1 gram, and measured to the nearest millimeter. A total of 25 individuals was tested for each species, unless fewer than 25 individuals were collected during electrofishing efforts (Table 3-1). Morphology, hematology, and muscle measurements were collected as described below.

Fish morphology was described with landmark analyses (Rohlf and Marcus 1993) because this method separates morphological changes associated with an increase in size from

“local” changes at a small number of landmarks, and images used in landmark analysis can be scaled to remove size as a confounding factor. As a result, the total length of the fish can be analyzed as a separate variable. The landmark analyses followed a method described in Handelsman et al. (in preparation) and were conducted with the “tps” suite of morphological analysis programs (Rohlf 2009) and MorphoJ version 1.05f (Klingenberg 2011). The approach is described below.

First, a file containing a photograph of each specimen was created using tpsUtil, and landmarks were placed on digitized lateral photographs of individual fish (Figure 3-1) using Program tpsDIG (Rohlf 2009).

Landmarks were placed at fin insertions and inflection points between curves on the fish’s body (Rohlf and Marcus 1993). Program tpsRelw was used to scale the images of each specimen to the same length, regardless of species, so that total length could be analyzed as a separate variable. Program tpsRELW was also used to rotate the individual images so that they were all oriented at the same angle, and so differences in camera angle or position relative to the fish were not mistaken for true differences in shape (Rohlf and Marcus 1993; Rohlf 2009). Consensus shapes, the “typical” or average shape for each species, were also produced with tpsRELW. Program tpsRELW generates these shapes by calculating and plotting the average landmark locations for each species. Consensus shapes were generated to allow visual identification of interspecific morphological differences (Parsons et al. 2003; Langerhans 2004).

The landmark data for each scaled, aligned specimen were imported into MorphoJ, and Procrustes coordinates (i.e., x-y coordinates) were assigned to each landmark, so that the shape of each specimen could be described by a set of 15 x-y coordinate pairs. These x-y coordinates were used in a between-groups principal components analysis (PCA) in MorphoJ, where

individuals were grouped by species, and where each principal component (PC) described the interspecific differences in one or more landmark locations (e.g., Trapani 2003). To aid interpretation of interspecific shape differences, MorphoJ was also used to produce diagrams representing the landmark changes associated with the PCs. The size of the vector shown in the diagrams indicated the magnitude of the interspecific shape differences (see Results). The first two PCs from the between-groups PCA were used to assign species to “shape guilds”, or groups of similarly-shaped species. These shape guilds were developed with a k-means cluster analysis in Program JMP Pro 11 (SAS Institute 2013), where individuals that clustered closely on the principal components graph were assigned to the same shape guild. Shape guild was then used as a categorical variable in the analyses of swimming ability. The shape guilds were also analyzed with ANOVA and a Tukey’s test in Program JMP Pro 11 to determine whether UTRANS and/or UMAX varied significantly between guilds. Differences were considered statistically significant at $\alpha = 0.05$.

Shape guilds were based on two-dimensional profiles of individual fish, but cross-sectional shape has a large influence on drag (Webb 1998; Vogel 1994) and can therefore influence swimming performance. Width to depth ratio at 50% of total length was measured to differentiate between laterally compressed fishes, and more streamlined, cylindrical fishes. Caudal fin area can also have a large influence on swimming performance, but measuring it is difficult because caudal fin spread is dynamic during active swimming (C. Handelsman, Colorado State University, personal communication). However, caudal fin length has been used as a predictor variable in previous morphometric studies (e.g., Jónsson and Skúlason 2000; Hankison et al. 2006) so caudal fin length was used instead of area. Caudal fin length was divided by the total length of the fish to remove the influence of fish size from this predictor.

Hematological parameters affect oxygen delivery to exercising tissues (Olsen and Farrell 1996), so they have been measured in swimming performance experiments. Although many hematological tests are available, many of them require more blood than can be readily obtained from small fish (e.g., Gallagher et al. 1992). Therefore, hematological parameters measured in this study were limited to hematocrit and hemoglobin concentration, which are known to affect swimming ability (e.g., Lay and Baldwin 1999; Leonard and McCormick 1999). After fish were euthanized and photographed, blood was collected using caudal transection and small capillary tubes. Hematocrit was measured using centrifuged capillary tubes of whole blood. Hemoglobin concentration was measured using a QuantiChrom Hemoglobin Assay Kit (Bioassay Systems, Hayward, CA).

The proportions of red muscle and white muscle have been linked to fish activity or swimming ability (McLaughlin and Kramer 1991; Webb and Fairchild 2001), so these measurements were included in the predictive model as explanatory variables. Cross sections of euthanized fish were fixed in formalin for two weeks, stained with 1% toluidine blue (Koumoundouros et al. 2009) to improve contrast between red and white muscle, and photographed with a digital camera. The relative abundance of red and white muscle changes along a fish's length, with a greater proportion of red muscle closer to the tail (Wakeling et al. 1999), so the original study plan involved taking cross sections at 50% of TL and 75% of TL. However, because the small size of some of the fish made collecting and preserving cross sections difficult, only the cross sections at 50% of total length were used. Proportions of red and white muscle were digitally measured from photographs imported into ArcGIS (ESRI 2011). The total percentage of muscle at 50% of TL was also measured, because the body cavity of some species extended beyond 50% of TL. A species with a high proportion of muscle along a

large proportion of its length would have more muscle than a species with a large, elongated body cavity. Assuming that muscle mass affects swimming performance, the fish with more muscle would be expected swim faster.

Data Analyses

The predictive swimming models were constructed with two methods: random forest (RF, Cutler et al. 2007; Breiman 2001) and linear regression (LR). Random forest analyses are used primarily for prediction and rely on “machine learning”, where a statistical analysis package identifies patterns in the data in relation to the predictor variables. In a random forest analysis, a computer program constructs a regression tree using a randomly selected portion of the data set. This process is repeated multiple times, and the trees are averaged to produce a final predictive model. Random forest analyses are becoming more common in ecological studies (Lepak et al. 2012; Roberts et al. 2013). The RF models in this study were validated by dividing the data set. Eighty percent of the data were randomly selected and used to construct the model, and the remaining 20% were used to check its predictive value.

Least squares linear regression was used as an alternate method because it is simpler to interpret (e.g., Roberts et al. 2013) and commonly used in ecological studies. A correlation analysis was used to identify pairs of highly correlated variables (a correlation of 0.7 or greater, Tabachnick and Fidell 1996). When two variables were highly correlated, one was omitted from the analysis. A Box-Cox transformation of the predictor variable was successfully used to meet the assumption of normality for the analysis of UTRANS, and transformation was not necessary for the analysis of UMAX. The performances of the RF and LR analysis methods were compared by examining the R-squared values. The method that explained a higher proportion of

the observed variation in the data (as measured by the R-squared value) was used to develop the predictive swimming models.

The variables used in the predictive models for U_{TRANS} and U_{MAX} were: shape guild, total length, weight, width-to-depth ratio, caudal fin length, hematocrit, hemoglobin concentration, the percent of muscle at 50% of the fish's total length, and the proportion of red muscle at 50% of TL (U_{TRANS} analysis only), and the proportion of white muscle at 50% of TL (U_{MAX} analysis only). Because the proportions of red and white muscle at 50% TL add to 1.0, they are perfectly correlated and could not be used in the same analysis. The proportion of red muscle at 50% TL was used in the RF analysis of U_{TRANS} because the amount of red muscle has the potential to affect aerobic swimming performance (McLaughlin and Kramer 1991). The proportion of white muscle at 50% TL was used in the RF analysis of U_{MAX} because sprinting performance is powered by the larger, more powerful fibers found in white muscle (e.g., Rome et al. 1992; Jones 1982).

Although most of the RF analysis process relies on artificial intelligence, the following parameters can be adjusted to “tune” a model: the percentage of the model construction data points used to construct each individual tree, the number of predictor variables used to generate each tree, the minimum number of splits per tree, and the minimum number of remaining observations required to allow additional splitting (Hastie and Tibshirani 2009; Strobl et al. 2009). Models were refined by changing these settings slightly to maximize the amount of variation in swimming performance predictions that was explained by the models (see Appendix 3A).

RESULTS

Swimming Performance

Aerobic and anaerobic swimming performance varied by species. Mean U_{TRANS} values ranged from 30 cm/s for brook stickleback to 61 cm/s for flathead chub, and mean U_{MAX} values ranged from 65 cm/s for johnny darter to 114 cm/s for flathead chub (Table 3.2). The relationship between U_{TRANS} and U_{MAX} varied by species, with U_{TRANS} ranging from 43 to 61% of U_{MAX} . The intraspecific variation in U_{TRANS} and U_{MAX} also changed with species, but variation in U_{TRANS} was equal to or lower than the variation in U_{MAX} for all species.

Shape Guilds

The PCA analysis fit 15 principal components, and 75% of the interspecific variation in shape was described by the first two principal components (Figure 3-2). The first principal component represented interspecific differences in position and length of the dorsal fin, the location of the pectoral fin, and small changes in caudal peduncle shape and snout length. The second principal component represented interspecific differences in anal fin length, distance between the pectoral fin and the anal fin, and small changes in head thickness near the operculum (Figures 3-3 and 3-4). The fifteen tested species were grouped into the following shape guilds based on their PC1 and PC2 scores (Table 3-2, Figure 3-5): Cyprinidae and Catostomidae (CYP), Cyprinodontidae (CPR), Centrarchidae (SNF), Percidae and Gasterosteidae (PER), and Ictaluridae (ICT).

Aerobic (U_{TRANS}) swimming abilities and anaerobic (U_{MAX}) swimming abilities varied between the shape guilds. Fishes in the PER, CPR, and ICT guilds had significantly lower mean U_{TRANS} values than fishes in the CYP guild (ANOVA, 4 d.f., $p < 0.0001$). The PER and ICT guilds also had lower mean U_{MAX} values than fishes in the CYP and CPR guilds (ANOVA, 4

d.f., $p < 0.0001$). Mean U_{TRANS} and U_{MAX} performance in the SNF guild was not significantly different from any of the other guilds (Table 3-3). Mean swimming ability varied by guild, but the analyses indicated that guild alone explained a small proportion of the observed variation in swimming ability (see *Analysis Results*).

Physiological Characteristics

Although some physiological measurements were characterized by high intraspecific variation (Table 3-3), between-guild differences could be identified for others with less intraspecific variability. Mean hemoglobin concentrations ranged from 22 g/dL for fathead minnow to 36 g/dL for brassy minnow, but because of high intraspecific variation, mean hemoglobin levels were not significantly different by guild (ANOVA, $df = 4$, $p > 0.05$, Table 3-4). Mean hematocrit ranged from 35% for white sucker to 56% for plains topminnow. Although mean hematocrit values were higher in the CPR guild (52%) than in the remaining four guilds (46 – 48%), HCT did not vary significantly by guild (ANOVA, $df = 4$, $p > 0.05$, Table 3-4). Mean interspecific values for red muscle proportion at 50% of TL ranged from 0% for plains topminnow, brook stickleback, Iowa darter, and Johnny darter to 5% for brassy minnow and longnose dace. The percent red muscle at 50% of TL was significantly different between guilds (ANOVA, $df = 4$, $p < 0.0001$). Mean interspecific values for total proportion of muscle at 50% of TL ranged from 73% for fathead minnow to 99% for black bullhead. The CYP guild had the highest mean proportion of red muscle at 50% TL, and the CPR and SNF guilds had the lowest. The proportion of red muscle at 50% TL was significantly different between guilds (ANOVA, $df = 4$, $p < 0.0001$).

Analysis Results

Comparisons of the performances of random forest and linear regression methods indicated that the RF method was the most appropriate for predicting aerobic and anaerobic swimming ability. The adjusted R^2 values for the RF models were 41% and 47% for aerobic and anaerobic performance, respectively, and the adjusted R^2 values for the regression equations were 31% and 24% for aerobic and anaerobic performance, respectively. Because the RF analyses explained a higher proportion of the variation in aerobic and anaerobic ability, they are presented here. The regression equations are presented in Appendix 3A.

In the regression analysis of U_{TRANS} , The statistically significant predictors were the variable for the ICT shape guild, the proportion of red muscle at 50% of TL, TL, and the relative length of the caudal fin. The statistically significant predictors of U_{MAX} were the variable for the ICT shape guild and TL (Table 3-5). The regression expressions that solely included statistically significant variables did not provide appropriate estimates of swimming performance, but the global equations (i.e., with all variables included) could be useful if running RF models is not possible (see Appendix 3A).

The RF analyses indicated that total length was the most important predictor variable for both U_{TRANS} and U_{MAX} , but the remaining independent variables increased the predictive power of the models. For U_{TRANS} , the RF model explained 41% of the total variation in the model construction data and 36% of the total variation in the validation data. Total length (TL), the proportion of red muscle at 50% of TL, and weight were the most important predictors of aerobic performance (Table 3-6, Figure 3-6). These four predictors had a positive effect on aerobic performance. No single predictor variable accounted for more than 26% of the explained variation in the data.

For U_{MAX} , the RF model explained 48% of the total variation in the model construction data and 47% of the total variation in the validation data. Total length, weight, and shape guild were the most important predictors of anaerobic swimming performance (Table 3-6). Total length and weight had a positive effect on anaerobic performance. No single predictor variable accounted for more than 26% of the explained variation in the data (Figure 3-6).

DISCUSSION

This study resulted in the development of the first predictive swimming performance models for small-bodied Great Plains fishes, using a set of reproducible morphological and physiological measurements. The random forest swimming models successfully explained 41% and 48% of the observed variation in aerobic and anaerobic swimming performance of the tested species, respectively. These models provide a means to estimate swimming ability when direct measurements of performance are not possible (see Appendix 3A for details) and should prove useful to managers interested in fish passage and researchers interested in the interaction between the many variables that shape swimming performance. This study also showed that swimming performance is best predicted with a combination of morphological and physiological variables.

Importance of morphological and physiological predictors

Measures of fish size (i.e., total length and weight), physiology (proportion of red muscle at 50% TL) and fish morphology (shape guild) were the most important predictors of swimming performance of the 15 Great Plains fishes used in this study (Figure 3-6). Fish size has long been recognized as an important predictor of swimming performance, and total length has a positive effect on the swimming performance of many small-bodied fishes (e.g., Bestgen et al. 2010; Adams et al. 2000). For example, Aedo et al. (2009) studied 12 morphologically diverse Utah

fishes and found that total length was the only significant predictor of swimming performance. Interspecific variation in red muscle proportion was important in determining aerobic swimming performance—fishes with more red muscle tended to be faster than fishes with less red muscle. The results of this study are similar to those from a study by McLaughlin and Kramer (1991), where fishes with higher proportions of red muscle had higher typical activity levels than those with lower proportions of red muscle. Similarly, several studies have shown that morphology is important in determining swimming performance, though they acknowledge that other, non-morphological traits also shape swimming performance (e.g., Leavy and Bonner 2009; Billman and Pyron 2005).

The less important predictors of swimming performance were hemoglobin concentration, hematocrit, percent muscle at 50% TL and two morphological variables (caudal fin length and width-to-depth ratio at 50% TL). Individually, none of these predictors explains a large proportion of the observed variation in the predictive swimming models, but omitting them from the model decreased the predictive power. Hemoglobin concentration exhibited high intraspecific variability, and mean hemoglobin concentrations measured in this study were all higher than typical concentrations of < 15 g/dL (Gallaughier and Farrell 1998). Hematology has not been extensively studied in small Great Plains fishes, but high hemoglobin concentrations could be an evolutionary response to life in physicochemically variable environments (e.g., Richards and Mandic 2008; Richards 2011). The species included in this predictive swimming study also had high hematocrit values. Hematocrit values tend to be lower than 40% for most tested species (Peterson and Gilmore 1988; Gallaughier and Farrell 1998), but mean hematocrit values were over 40% for 13 of the 15 tested species in this study. High hematocrit values may be an evolutionary response to the constraints experienced by small-bodied fish in

physicochemically variable systems. However, collection of blood by caudal ligation or collection of blood after intense exercise could also have increased hematocrit values (e.g., Leonard and McCormick 1999; Gallagher et al. 1992). Measurement of hematocrit of the tested species after varying levels of exercise would provide more support for this hypothesis.

Whether individual predictor variables were morphological or physiological, most of them accounted for a small proportion of the explained variation. This reinforces the notion that swimming performance is shaped by multiple morphological and physiological factors and that inclusion of a comprehensive suite of variables increases the accuracy of a predictive swimming model. For example, a post-hoc analysis compared the performance of the full model with all nine predictor variables to the performance of a reduced model with the three top terms: total length, weight, and shape guild. Although the two models provided a similar fit to the training data, the full model provided a superior fit to the validation data (Figures 3-7 and 3-8), indicating better predictive ability. However, in the event that an untested species was rare enough that individuals could not be sacrificed for physiological measurements, morphological variables could be obtained from museum specimens or living specimens released immediately after measurement, and a rough approximation of swimming ability obtained.

Predictive value of RF models

The predictive power of the RF models could not be tested with other species, because published data required to run the RF models were unavailable for additional species. Therefore, graphs of the predicted versus observed values in the training and validation data sets were used to evaluate the predictive tendencies of the models. These indicated that the aerobic and anaerobic RF models tend to under-predict ability of slower swimmers and over-predict ability of faster swimmers (Figure 3-7). Because the primary goal of this study was to develop a

predictive swimming model that can be used in fishway design, overestimation of the swimming ability of the faster swimmers is undesirable. However, flume-based laboratory experiments tend to provide conservative estimates of fish swimming ability (e.g., Peake and Farrell 2006, Castro-Santos et al. 2013). Therefore, because the models were constructed with swimming performances measured in swimming flumes, over-prediction of the performance of faster swimmers by the models does not necessarily represent over-prediction of their swimming abilities under natural conditions.

One of the primary constraints of this predictive model may be the exclusive use of western Great Plains fishes in model development. Because swimming ability is a product of environmental conditions, regional differences in anaerobic and aerobic performances may occur, both within and between species. Fishes that frequent different habitats within a region have different swimming abilities (Leavy and Bonner 2009), and intraspecific variation in aerobic and anaerobic swimming ability is shaped by local habitat (e.g., Nelson et al. 2003, 2008), so regional changes in habitat type and availability may also affect swimming ability on a larger spatial scale. Furthermore, fish morphology can change over generations in response to a variety of environmental factors such as predation pressure (Taylor and McPhail 1985; Ghalambor et al. 2003) and the need to fulfill other functions such as feeding (Billman and Pyron 2005). Given that morphology has some influence on swimming performance, intraspecific variation in shape may complicate efforts to predict swimming performance on a regional scale. Therefore, environmental factors and regional morphological variation within species would curb the applicability of any predictive swimming model outside of the region in which it is developed.

A second reason for the modest predictive power of the RF models could be intraspecific, individual variation in swimming performance. Individual variation in swimming performance is both common (Bengtsson 1980; Kolok 1999) and repeatable over time (Kolok 1999; Nelson et al 2008). Swimming behaviors such as station holding (i.e., using pectoral fins as ailerons, Aedo et al. 2009, Underwood et al. 2014) and the use of the boundary layer or other low-velocity areas (Ward et al. 2003; Scott and Magoulick 2008) can all increase swimming performance in a swimming flume, but these behaviors are not exhibited by all species or all individuals within a species. As a result, differences in swimming behavior contribute to individual variation in performance.

Although individual variation in swimming performance can be modeled by fitting swimming performance data to a distribution (e.g., Haro et al. 2004), distributions cannot be modeled with a RF analysis (Mevin Hooten, Colorado State University, personal communication). Therefore, modeling individual variation was not possible, given that the goal of this study, to create predictive swimming models that can be used to provide estimates of aerobic and anaerobic ability for untested species, was best met with RF analyses. This study provides a means by which to estimate the “average” performance for an untested species. The values obtained from the RF model output can be adjusted accordingly for individuals of the species with reduced swimming ability due to physiological factors such as reproductive state or environmental factors such as lower water temperatures.

The RF models developed in this study can provide estimates of aerobic and anaerobic swimming performance for Great Plains fishes with unknown swimming abilities that cannot be directly measured. Estimated swimming performances can be used to establish appropriate fishway water velocities for small-bodied Great Plains fishes. Although direct measurement is

preferable, the RF models can be used to inform fishway design when a full-scale swimming performance study cannot be completed because of logistical constraints (e.g., limited availability of fish or time to conduct the studies).

Table 3-1.—Species, total length (TL) ranges, preferred position in the water column, and number of individuals used to develop the predictive swimming model. Habitat abbreviations are as follows: B = benthic, BP = benthopelagic, WC = water column, and S = surface-oriented.

Species (3-letter code)	Family	TL: Mean & Range (mm)	Sample Size	Habitat	Collection Site
Black bullhead <i>Ameiurus melas</i> (BBH)	Ictaluridae	69 (43 – 130)	12	B	Pawnee National Grassland, Weld County, CO
Brook stickleback <i>Culaea inconstans</i> (BSB)	Gasterosteidae	64 (54 – 73)	14	WC	Spring Creek, Fort Collins, CO
White sucker <i>Catostomus commersonii</i> (WHS)	Catostomidae	77 (68 – 85)	10	B	Spring Creek, Fort Collins, CO
Brassy minnow <i>Hybognathus hankinsoni</i> (BRM)	Cyprinidae	62 (55 – 70)	15	BP	CPW broodstock pond, Larimer County, CO
Creek chub <i>Semotilus atromaculatus</i> (CRC)		70 (50 – 83)	12	WC	Spring Creek, Fort Collins, CO
Flathead chub <i>Platygobio gracilis</i> (FHC)		102 (92 – 123)	25	BP	Fountain Creek, Colorado Springs, CO
Fathead minnow <i>Pimephales promelas</i> (FHM)		64 (56 – 70)	25	WC	Spring Creek, Fort Collins, CO
Longnose dace <i>Rhinichthys cataractae</i> (LND)		72 (59 – 105)	15	B	Spring Creek, Fort Collins, CO
Northern redbelly dace <i>Chrosomus eos</i> (RBD)		55 (41 – 64)	25	WC	West Plum Creek, CO
Suckermouth minnow <i>Phenacobius mirabilis</i> (SMM)		66 (51 – 88)	16	B	South Platte River, CO
Northern plains killifish <i>Fundulus zebrinus</i> (PKF)	Cyprinodontidae	58 (48 – 69)	17	S	Pawnee National Grassland, Weld County, CO
Plains topminnow <i>Fundulus sciadicus</i> (PTM)		57 (48 – 62)	25	S	Pawnee National Grassland, Weld County, CO
Green sunfish <i>Lepomis cyanellus</i> (GSF)	Centrarchidae	77 (49 – 98)	25	WC	Spring Creek, Fort Collins, CO

Table 3-1.—continued.

Species (3-letter code)	Family	Length: Mean & Range (mm)	Sample Size	Habitat	Collection Site
Iowa darter <i>Etheostoma exile</i> (IOD)	Percidae	49 (45 – 54)	15	B	Spring Creek, Fort Collins, CO
Johnny darter <i>Etheostoma nigrum</i> (JOD)		60 (50 – 74)	14	B	Cache la Poudre River, Larimer County, CO

Table 3-2.—Swimming performance and physiological traits of 15 species tested at the CSU Foothills Fishery Laboratory. Values are presented as means \pm standard deviations. Sample sizes for each species are identical to those listed in Table 1. Hb = hemoglobin concentration, HCT = hematocrit.

Species	Guild	TL (mm)	Weight (g)	U_{TRANS} (cm/s)	U_{MAX} (cm/s)	Hb (g/dL)	HCT (%)	Percent muscle @ 50% of TL (%)	Red Muscle @ 50% of TL (%)
Black bullhead	ICT	69.3 \pm 36.0	7.3 \pm 10.7	34.3 \pm 8.3	63.8 \pm 25.1	29.9 \pm 13.0	47 \pm 6	99 \pm 0.4	3 \pm 0.5
Brook stickleback	PER	64.1 \pm 4.7	1.9 \pm 0.3	29.8 \pm 8.5	69.2 \pm 15.9	22.1 \pm 9.6	53 \pm 8	90 \pm 11	0 \pm 0
White sucker	CYP	77.0 \pm 5.0	3.6 \pm 0.6	47.0 \pm 8.5	83.1 \pm 16.6	24.8 \pm 6.7	35 \pm 9	81 \pm 6	2 \pm 0.5
Brassy minnow	CYP	61.6 \pm 3.4	1.9 \pm 0.3	44.0 \pm 6.0	72.6 \pm 9.9	35.5 \pm 9.7	51 \pm 6	88 \pm 9	5 \pm 1.2
Creek chub	CYP	70.0 \pm 11.1	3.4 \pm 1.4	52.2 \pm 15.0	90.3 \pm 16.2	25.8 \pm 9.9	50 \pm 7	85 \pm 11	3 \pm 0.9
Flathead chub	CYP	101.6 \pm 6.6	8.7 \pm 1.5	61.4 \pm 16.4	114.2 \pm 16.1	31.7 \pm 12.0	48 \pm 5	88 \pm 7	4 \pm 1.0
Fathead minnow	CYP	63.7 \pm 4.2	2.6 \pm 0.6	38.7 \pm 7.3	90.1 \pm 18.8	21.8 \pm 10.8	55 \pm 8	73 \pm 5	1 \pm 0.4
Longnose dace	CYP	71.6 \pm 12.2	3.2 \pm 2.2	43.7 \pm 8.2	77.7 \pm 9.2	31.8 \pm 13.5	48 \pm 6	92 \pm 5	5 \pm 1.1
Northern redbelly dace	CYP	55.0 \pm 6.1	1.5 \pm 0.4	40.3 \pm 6.9	75.6 \pm 19.0	34.0 \pm 12.8	48 \pm 12	84 \pm 10	3 \pm 0.8

Table 3-2.—continued.

Species	Guild	TL (mm)	Weight (g)	U _{TRANS} (cm/s)	U _{MAX} (cm/s)	Hb (g/dL)	HCT (%)	Percent muscle @ 50% of TL (%)	Red Muscle @ 50% of TL (%)
Suckermouth minnow	CYP	67.1 ± 10.3	2.2 ± 1.0	44.7 ± 5.9	86.8 ± 13.4	32.2 ± 8.1	38 ± 8	93 ± 8	4 ± 4
Northern plains killifish	CPR	58.2 ± 6.0	1.7 ± 0.6	48.1 ± 14.6	102.0 ± 14.5	28.7 ± 8.7	45 ± 11	78 ± 4	3 ± 0.6
Plains topminnow	CPR	56.8 ± 2.7	1.7 ± 0.3	35.8 ± 6.7	79.1 ± 17.4	32.0 ± 44.6	56 ± 6	81 ± 5	0 ± 0
Green sunfish	SNF	75.4 ± 13.2	7.7 ± 3.3	40.8 ± 11.5	78.6 ± 19.3	30.3 ± 12.2	46 ± 9	80 ± 5	1 ± 0.2
Iowa darter	PER	48.8 ± 3.4	1.0 ± 0.1	37.8 ± 15.6	72.8 ± 21.7	36.1 ± 14.6	43 ± 9	92 ± 4	0 ± 0
Johnny darter	PER	60.4 ± 7.4	1.6 ± 0.8	37.4 ± 15.5	65.4 ± 20.5	33.0 ± 11.3	42 ± 14	97 ± 3	0 ± 0

Table 3-3.—The mean maximum aerobic and anaerobic swimming speeds for shape guilds established from the 15 tested species. The 95% confidence intervals are shown in parentheses. Superscript letters represent ANOVA results and indicate whether swimming performance was significantly different between guilds.

Shape Guild	Aerobic Velocity, U_{TRANS} (cm/s)	Anaerobic Velocity, U_{MAX} (cm/s)
Cyprinidae and Catostomidae, CYP	46.5 (44.5 – 48.7) ^A	90.3 (86.7 – 93.9) ^A
Cyprinodontidae, CPR	40.1 (36.7 – 43.5) ^B	87.2 (81.5 – 93.0) ^A
Centrarchidae, SNF	40.7 (36.6 – 44.9) ^{AB}	84.3 (75.6 – 93.0) ^{AB}
Percidae and Gasterosteidae, PER	34.9 (30.6 – 39.2) ^B	67.6 (61.5 – 73.7) ^B
Ictaluridae ICT	34.2 (29.0 – 39.5) ^B	63.8 (47.9 – 79.8) ^B

Table 3-4.—Physiological traits for shape guilds established from the 15 tested species. Values are presented as means \pm standard deviations. Different superscript letters in each column indicate significant between-group differences as identified with ANOVA (4 df, $p < 0.0001$ for all tests where differences were identified) and Tukey tests. No letters are present for hemoglobin or hematocrit, because no between-group differences were identified.

Shape Guild	Hemoglobin (g/dL)	Hematocrit (%)	Percent muscle @ 50% of TL (%)	Red Muscle @ 50% of TL (%)
Cyprinidae and Catostomidae, CYP	29.6 (\pm 11.7)	48 (\pm 10)	85 (\pm 10) ^B	4 (\pm 2.1) ^A
Cyprinodontidae, CPR	30.9 (\pm 35.1)	52 (\pm 9)	80 (\pm 5) ^C	0 (\pm 0) ^B
Centrarchidae, SNF	29.8 (\pm 13.0)	46 (\pm 9)	80 (\pm 5) ^{BC}	0 (\pm 0) ^B
Percidae and Gasterosteidae, PER	30.1 (\pm 12.9)	46 (\pm 11)	93 (\pm 7) ^A	1.2 (\pm 1.7) ^C
Ictaluridae, ICT	29.9 (\pm 13.1)	47 (\pm 6)	99 (\pm 0.4) ^A	3.2 (\pm 0.5) ^A

Table 3-5.—Statistically significant predictors of aerobic and anaerobic swimming performance as determined by least-squares linear regression. Predictor variables were tested with t-tests (d.f. = 1). Beta estimates for each variable are shown, whether or not it was statistically significant (see Appendix 3A for details). Shape guild variables were analyzed as “dummy variables”, where the guild that included the tested species was assigned a value of 1.0 and the remaining guilds were assigned a value of zero. “n/a” for Group 5 indicates that if a fish belonged to this guild, all of the group dummy variables were zero. “n/a” for red or white muscle indicates that it was not used in the regression analysis.

Predictor Variable	Aerobic, U_{TRANS}		Anaerobic, U_{MAX}	
	p-value	β estimate	p-value	β estimate
Group 1, ICT	> 0.0082	-8.25	0.0236	-12.00
Group 2, CYP	> 0.05	2.96	> 0.05	4.51
Group 3, PER	> 0.05	2.64	> 0.05	-1.78
Group 4, SNF	> 0.05	2.04	> 0.05	-2.22
Group 5, CPR	n/a	n/a	n/a	n/a
TL	< 0.0001	0.28	< 0.0001	0.49
Hemoglobin	> 0.05	2×10^{-5}	> 0.05	1×10^{-6}
Hematocrit	> 0.05	13.60	> 0.05	12.56
Percent muscle at 50% TL	> 0.05	0.05	> 0.05	-0.28
Proportion red muscle at 50% TL	0.0091	1.13	n/a	n/a
Proportion white muscle at 50% TL	n/a	n/a	> 0.05	-0.74
Caudal fin length, scaled to TL	0.0043	162.19	> 0.05	16.43
Width-to-depth ratio at 50% TL	> 0.05	12.74	> 0.05	12.45

Table 3-6.—Best predictors from random forest analyses in JMP. The R-Squared value is the percentage of total variation in the validation data that is explained by the model. Terms per split is the number of randomly-chosen predictor variables used to generate each split in a tree, and total terms is the total number of predictor variables used in the models.

Predicted Metric	Terms per Split	Total Terms	Top Terms	R-Squared
Maximum aerobic speed (U_{TRANS})	2	9	weight, red muscle at 50% TL, TL	36%
Maximum anaerobic speed (U_{MAX})	6	9	weight, TL, shape guild	47%

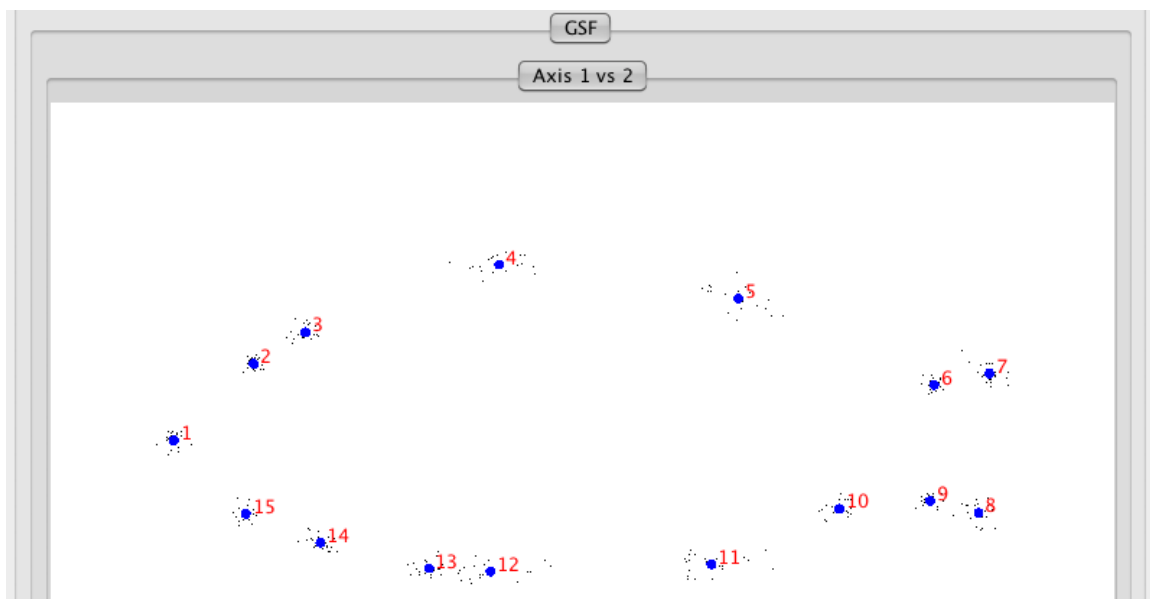


Figure 3-1.—Top: Screenshot of a digitized green sunfish (*Lepomis cyanellus*) specimen in MorphoJ. Caudal fin landmarks were omitted from the analysis (see text for details). Bottom: consensus locations of landmarks for all green sunfish specimens are shown in blue, and individual landmarks for each analyzed specimen are shown in black.

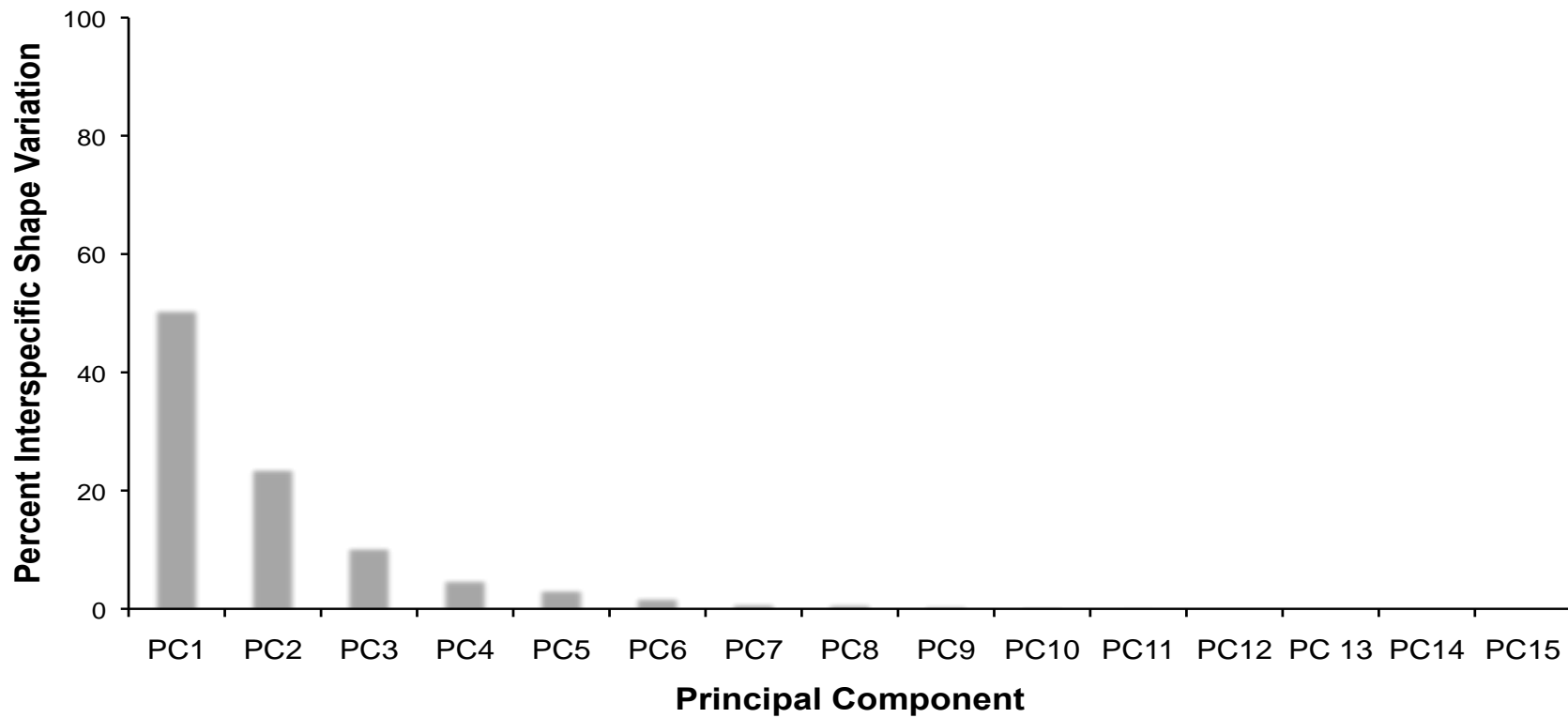


Figure 3-2.—The fifteen principal components generated by the between-groups PCA in MorphoJ. The first two principal components explained 75% of the interspecific variation in shape.

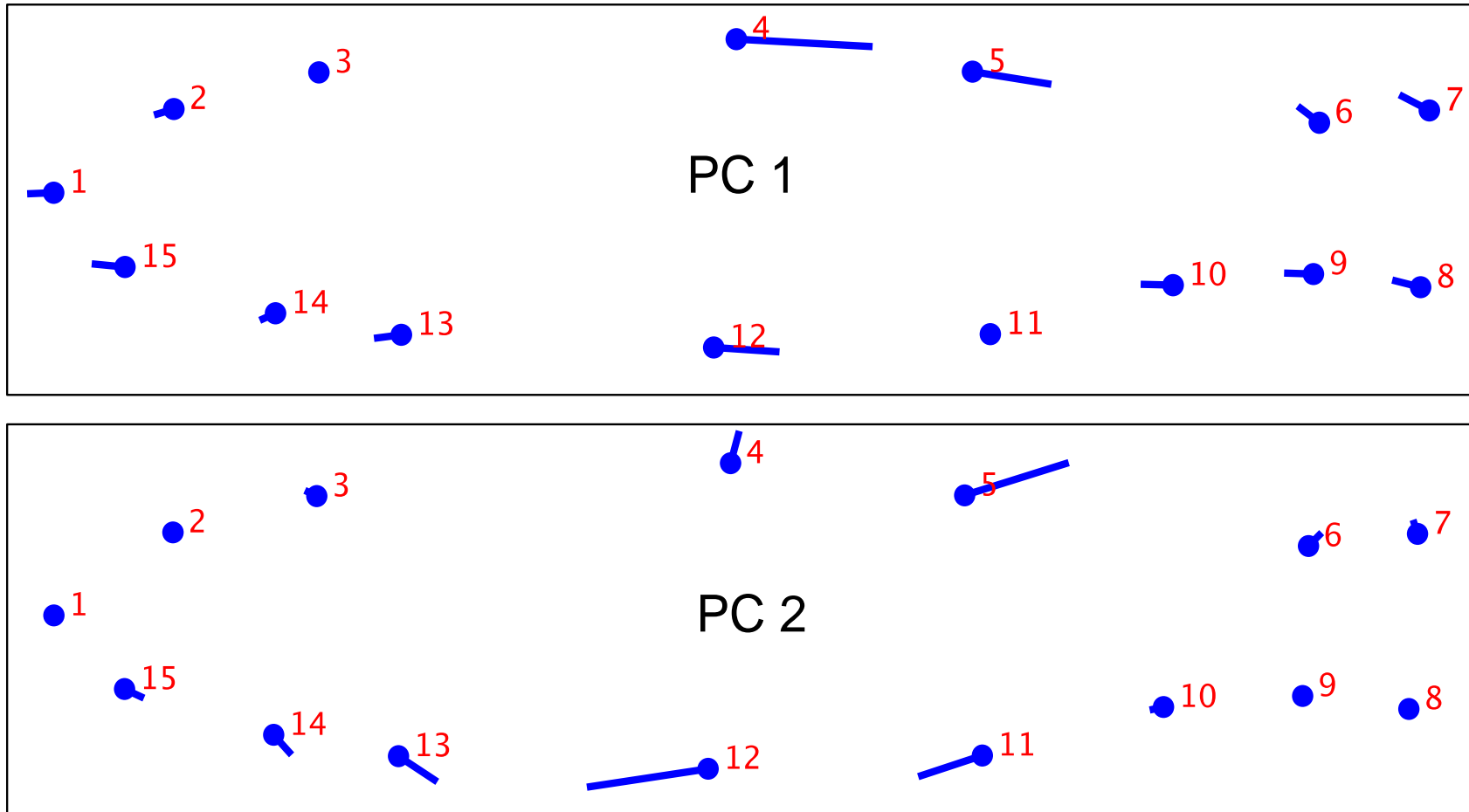


Figure 3-3.—The landmark changes represented in the first two principal components used to distinguish species-specific differences in shape. Longer vectors indicate larger differences in landmark locations between species. Landmarks representing dorsal fin length and position (landmarks 4 and 5) and pectoral fin position (landmark 12) varied most by species. Smaller changes involved snout bluntness (landmarks 1 and 15) and caudal peduncle thickness (landmarks 6 – 10). For PC 2, anal fin length (landmark 12) and distance between the front of the anal fin and the pectoral fin insertion point (landmark 13) had the most variation. Smaller changes involved dorsal fin length and body depth near the dorsal fin (landmarks 4 and 5) and variation in head thickness near the operculum (landmarks 13-15).

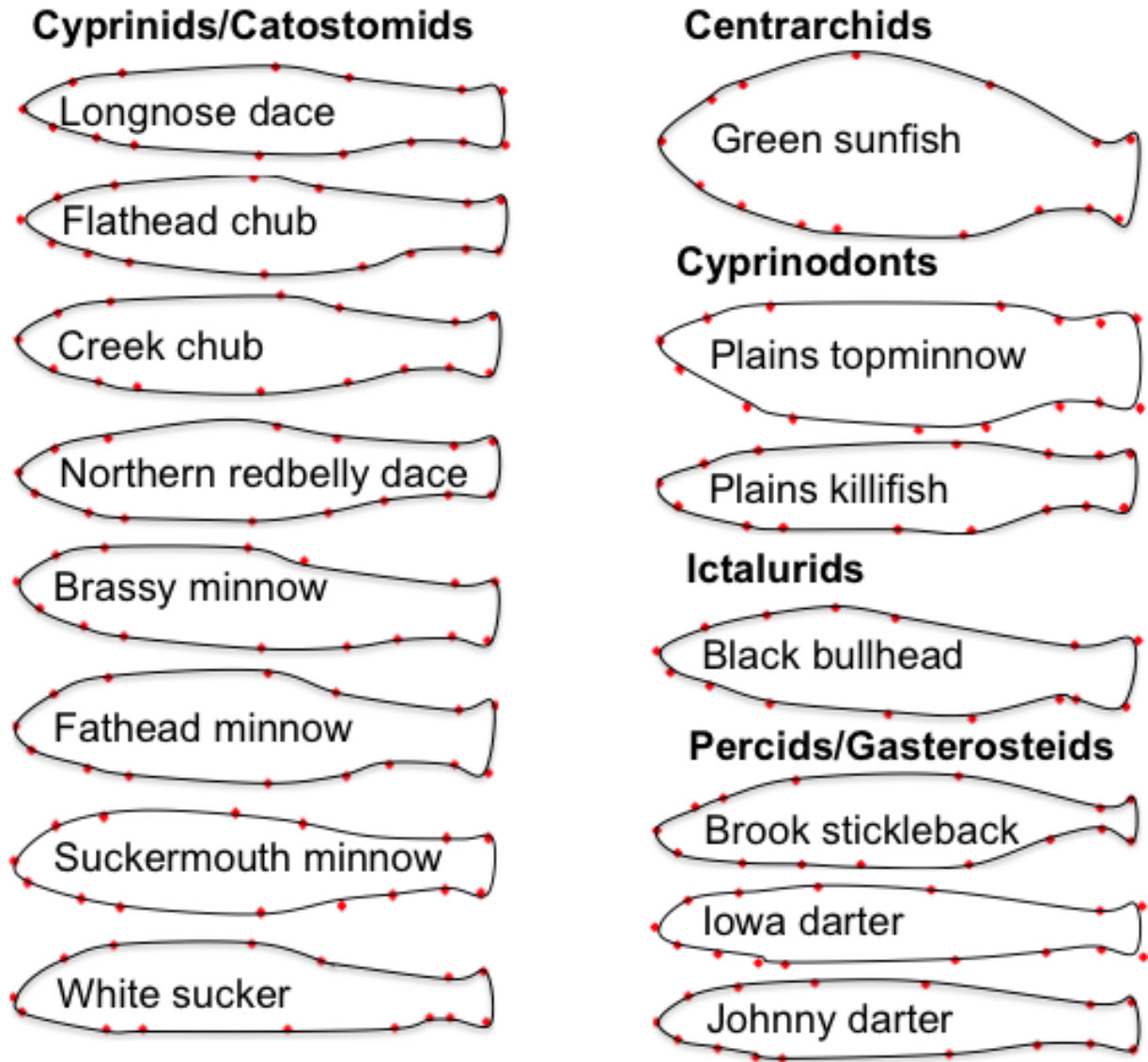


Figure 3-4.—Species-specific consensus shapes from the tpsRelw program. The fifteen tested species were grouped into guilds based on shape similarity. Consensus shapes were scaled to the same length to highlight changes in body shape.

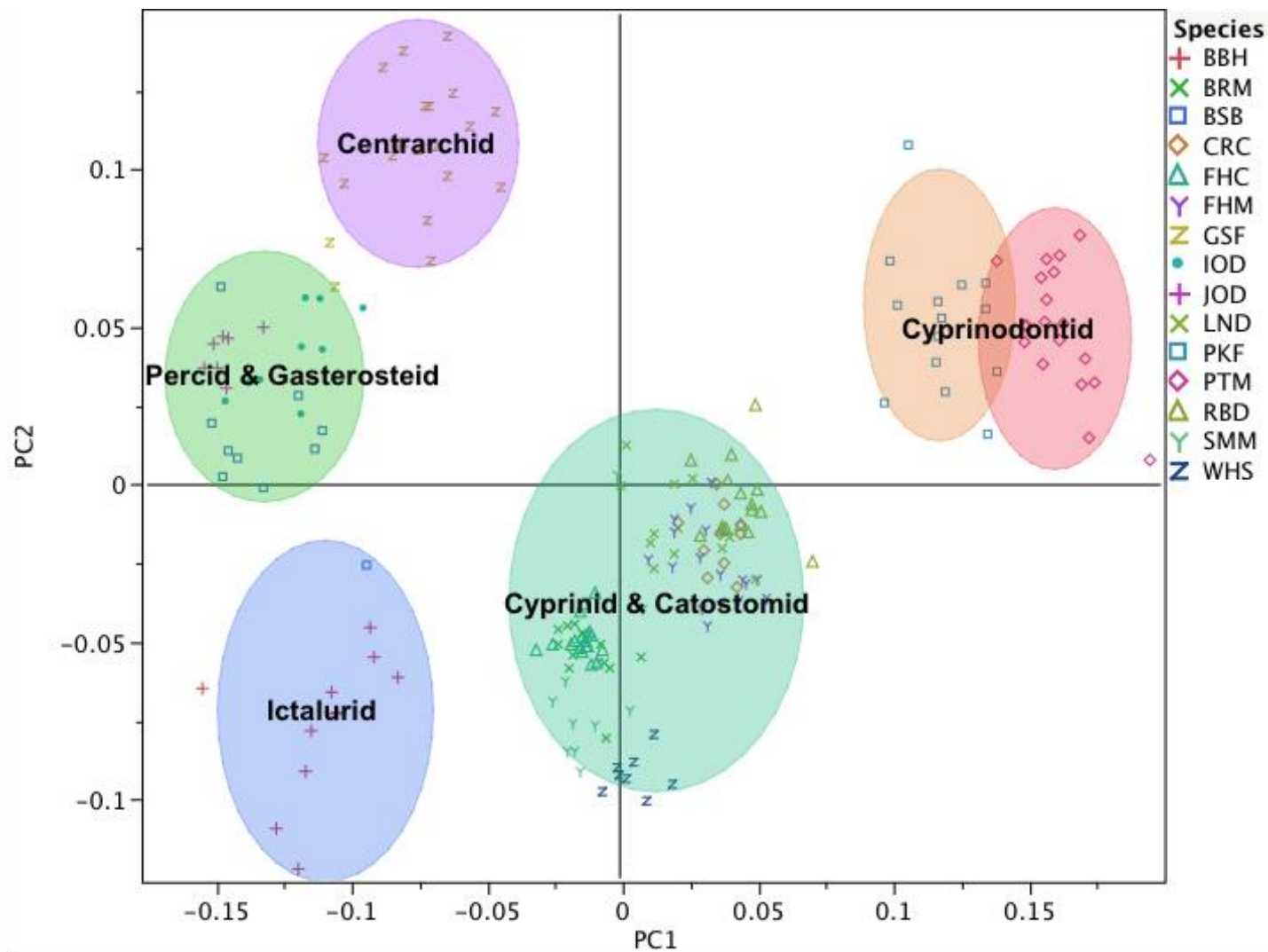


Figure 3-5.—Shape guilds as determined by k-means cluster analysis for the fifteen tested species, based on the first two principal components from a between-groups PCA. The shapes are 95% confidence ellipsoids generated in JMP Pro 11. Although northern plains killifish and plains topminnow separated into two groups in the analysis, these two groups were combined because of their distance from the remaining groups in multivariate space.

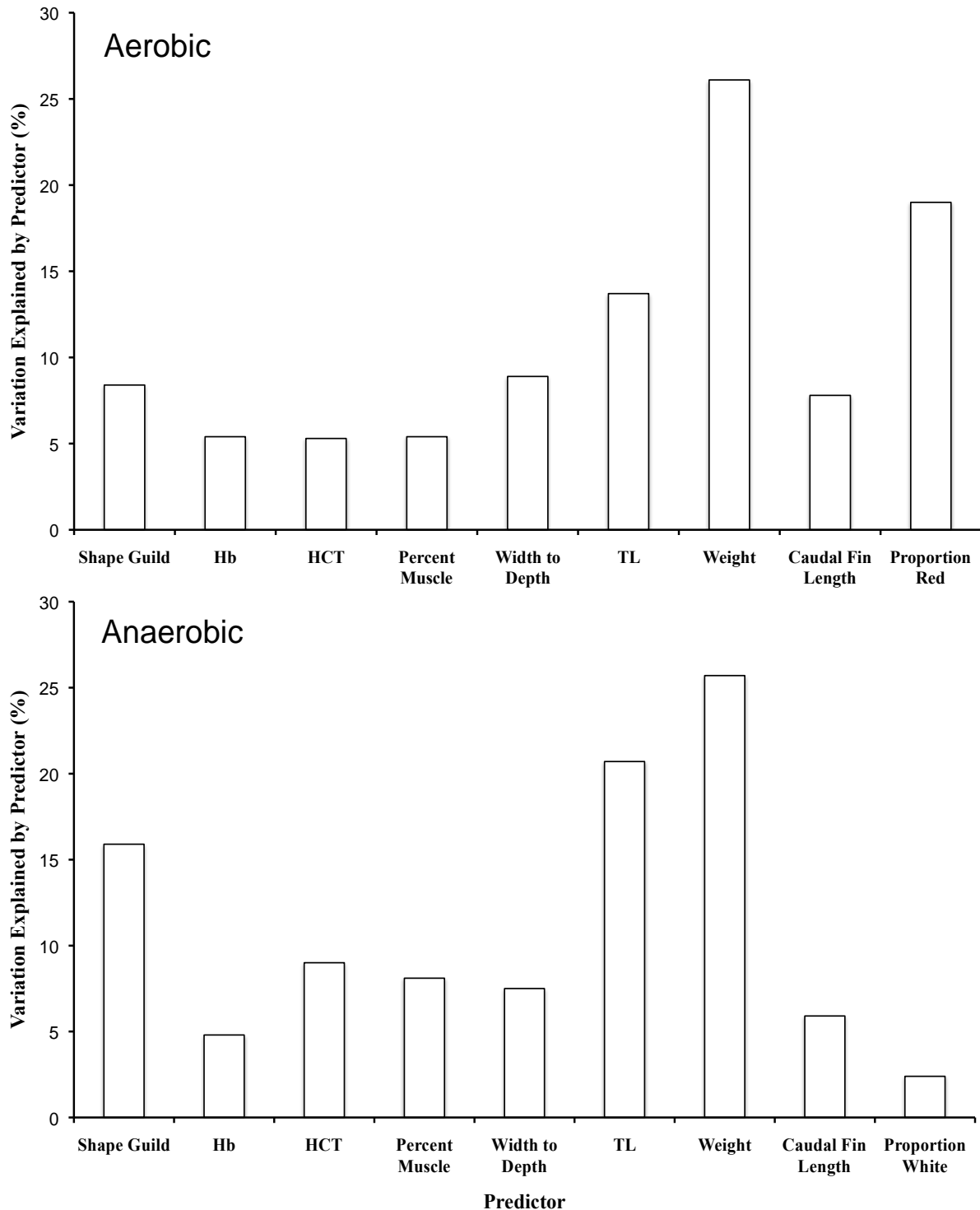


Figure 3-6.— Percent of explained variation in aerobic (top) and anaerobic (bottom) swimming endurance attributable to each predictor variable. “Shape Guild” refers to the morphological groups (see Figure 3-4). “Proportion Red” and “Proportion White” refer to the proportion of the muscle at 50% of TL that is red or white muscle, respectively.

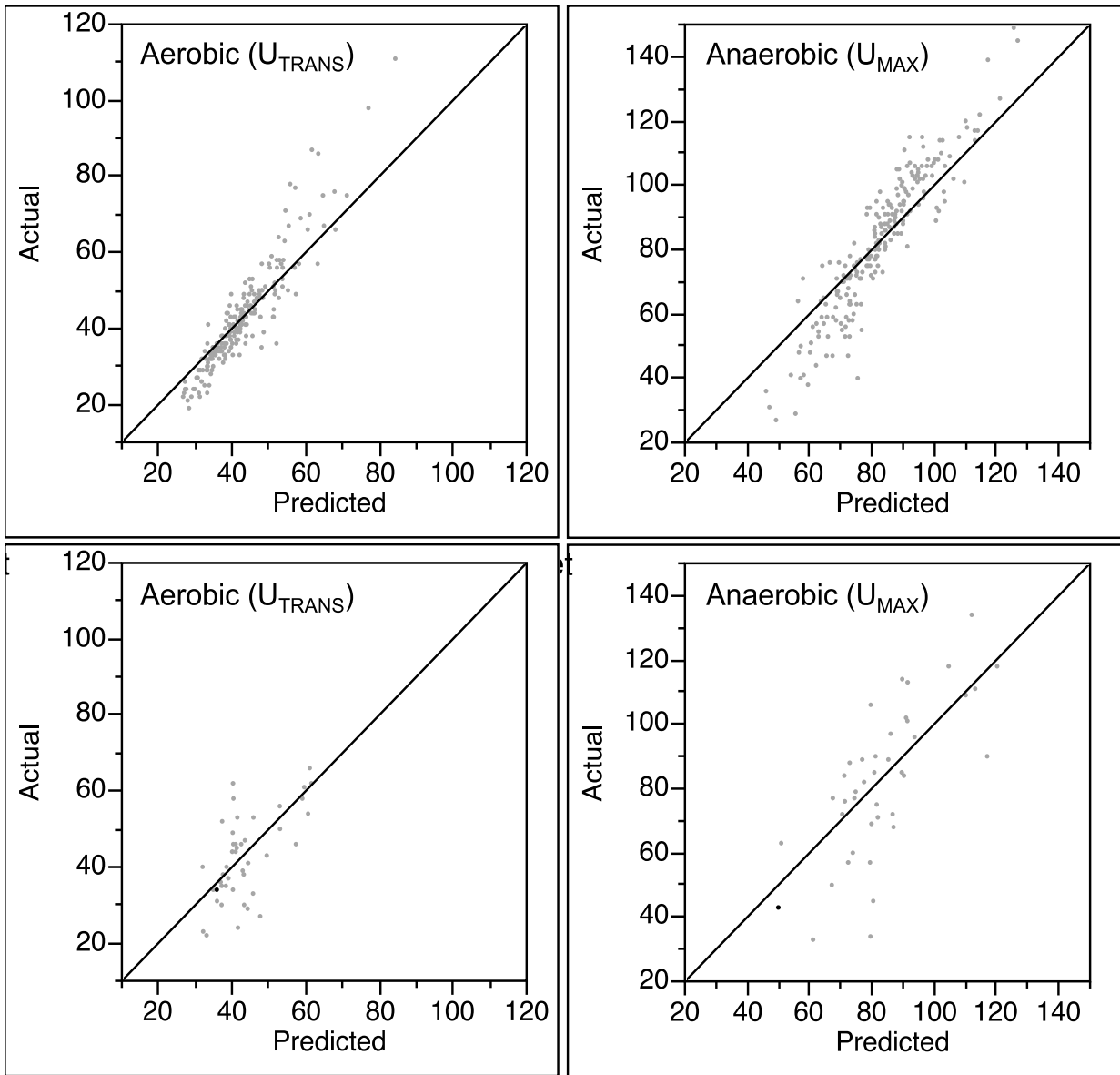


Figure 3-7.— Actual (i.e., measured) versus predicted (i.e., RF model output) values of aerobic (top and bottom left) and anaerobic (top and bottom right) swimming performance. The training portion ($n = 217$) and the validation portion ($n = 53$) of the data set are represented by the top and bottom panels, respectively.

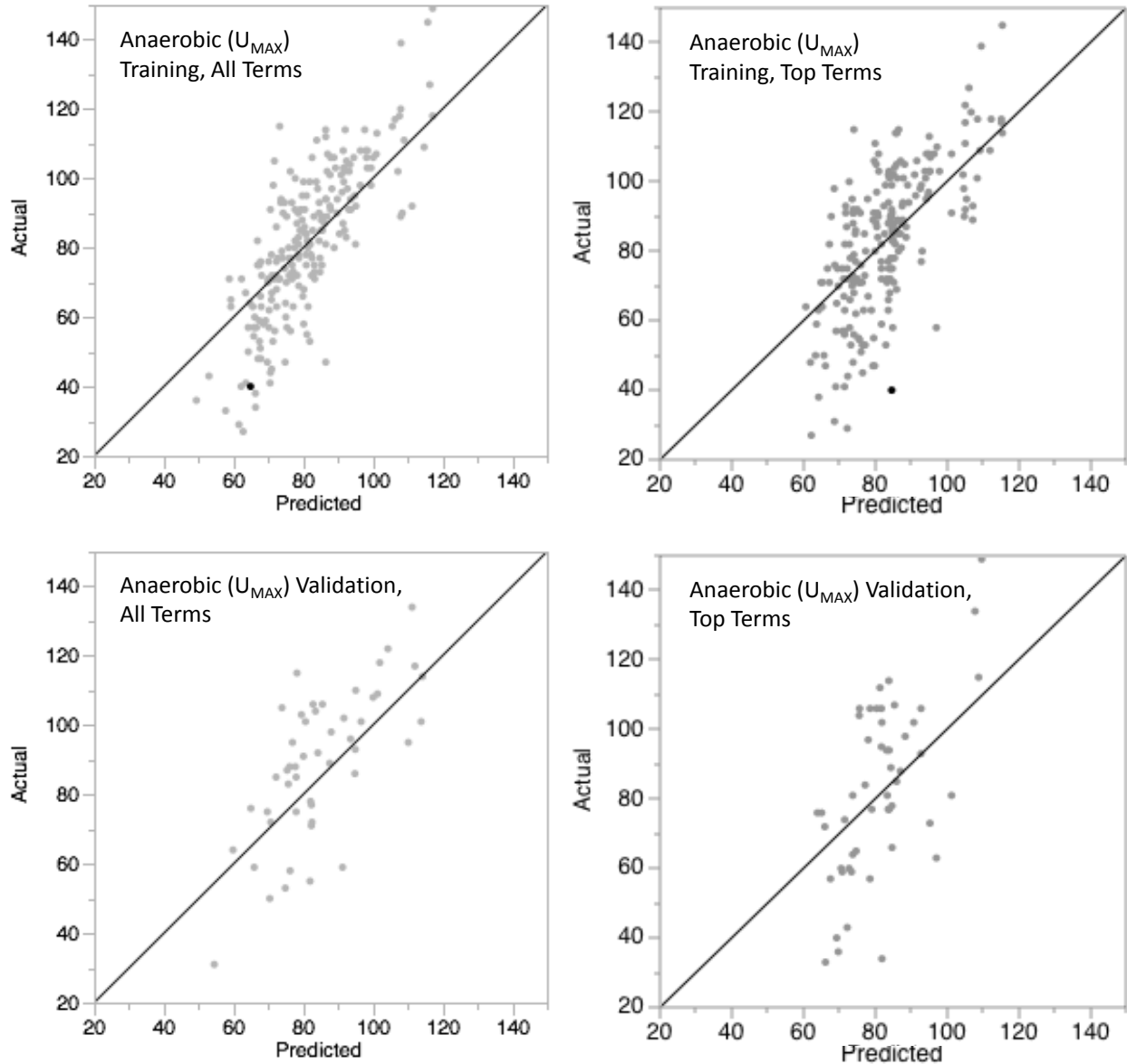


Figure 3-8.—Comparison of predictive power of the full RF models and the reduced RF models (i.e., with top terms only), as shown by actual versus predicted plots. The graphs on the left represent the full models, and those on the right represent the reduced models. The training portion ($n = 217$) and the validation portion ($n = 53$) of the data set are represented by the top and bottom panels, respectively.

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CHAPTER 4:
THE EFFECTS OF SUBSTRATE ARRANGEMENT ON HYDRAULIC CONDITIONS AND
FISH PASSAGE SUCCESS IN A MODEL ROCK RAMP FISHWAY

INTRODUCTION

Fragmentation of streams by barriers such as dams, culverts, and road crossings can cause extirpations of small-bodied fish populations (Winston et al. 1991; Warren and Pardew 1998). As a result, fishery biologists and managers have worked to restore longitudinal connectivity in streams. When removal of the infrastructure that fragments streams is not a realistic option, fish passage can be facilitated with properly designed fishways. Of the many different fishway types, rock ramps may be the most useful in situations involving small-bodied fishes.

Rock ramp fishways, which resemble artificial riffles, have shown promise in allowing passage of large and small-bodied fishes (Harris et al. 1998). For example, when riprap grade control structures in an Iowa stream were modified to allow fish passage, the percentage of fish² released below a structure and recaptured above it increased from 0.6% to 13.1% (Litvan et al. 2008). Two advantages of traditional rock ramps are their diverse depths and velocities, which can allow passage of species with varying swimming abilities (Clay 1995; Harris et al. 1998).

Despite the interest in using rock ramps to facilitate passage of small-bodied fishes, there is little information to guide designers working in smaller streams and with smaller species.

Rock ramps vary widely in their width, length, and slope, and their substrate type, placement, and spacing. For example, perturbation boulder rock ramps are defined as having small spaces

² Black bullhead *Ameiurus melas*, yellow bullhead *A. natalis*, channel catfish *Ictalurus punctatus*, and creek chub *Semotilus atromaculatus*.

in between the roughness elements and create a turbulent, straight channel, whereas rock weir ramps can incorporate rows of submerged boulders that cause flows to meander or that block flow and create a pool-and-weir configuration (Mooney 2007). There are recommendations for the design of rock ramps on large rivers and for spacing of boulder-sized roughness elements (e.g., FAO/DVWK 2002), but there is little available information for small streams and small-bodied species.

Regardless of fishway type, the traditional approach to designing fishways focuses primarily on velocity. Biologists have assumed that if the measured swimming performance of a fish exceeds the design velocity of the fishway, then that fish will be able to ascend the fishway (e.g., Starrs et al. 2011). This approach was refined by Peake et al. (1997), who used multiple measures of endurance at varying velocities to develop acceptable combinations of fishway distance and water velocity. Although hydraulic variables such as turbulence are known to affect fish swimming performance in some cases (Tritico and Cotel 2010), these variables are often not considered in rock ramp design, probably due to the limited knowledge of how fish respond to turbulence and hydraulic roughness. For example, swimming performance data are often obtained from swimming flumes, where simplified hydraulic conditions do not mimic hydraulics in natural systems (Webb et al. 2010). Little is known about how turbulence affects fish passage success, and there are few recommendations for substrate placement in small rock ramp fishways. Therefore, the effects of turbulence, as controlled by substrate arrangement, on the passage success of small-bodied fishes warrants study.

Although the efficiency of a rock ramp can be tested under laboratory or field conditions, studies focused on small fishes are best performed in the laboratory. Monitoring small-bodied fish movement under natural conditions presents inherent difficulties such as problems with

reading visual implant elastomer (VIE) tags and uncertainty in capture probabilities (Curtis 2006; Ficke and Myrick 2009). Although passive inductive transponder (PIT) tags and small sonic tags can provide more accurate information because of high detection probabilities, the potential for greater spatial resolution, and the ability to pinpoint the timing of movement, their field use is limited to fishes larger than 60 mm standard length (Archdeacon et al. 2009). Tests of volitional swimming in open channels are less artificial than swimming flume tests, because fish may perform better in open channels (Haro et al. 2004). Such tests also are useful for describing behaviors such as refuging in low-velocity areas (Peake 2008a; Scott and Magoulick 2008), refusal to swim to exhaustion (Voukoun and Watrous 2009), and even willingness to enter the test sections, all of which can affect passage success under field conditions.

A few laboratory studies have advanced our knowledge of how hydraulic parameters such as velocity and turbulence affect fish performance, but such studies are mostly limited to large fishes. The abilities of five nonsalmonid fishes to navigate rock ramps with known hydraulic parameters have been measured under laboratory conditions (Rio Grande silvery minnow *Hybognathus amarus* Bestgen et al. (2010); blueback herring *Alosa aestivalis* and American shad *A. sapidissima* Haro et al. (2008); Maquarie perch *Macquaria australasia* Starrs et al. (2011); shovelnose sturgeon *Scaphirhynchus platorhynchus* White and Mefford (2002), Table 4-1). These experiments all involved detailed hydraulic measurements and measurements of fish performance. Bestgen et al. (2010) and Mefford and White (2002) compared upstream movement rates at different levels of bed roughness, and Haro et al. (2008) compared upstream passage success in a perturbation boulder fishway versus a rock weir fishway that created a meandering channel between submerged rock vanes. However, no attempts have been made to

link substrate arrangement, the resulting hydraulic conditions, and passage success of small-bodied species in a laboratory setting.

This study had two goals. The first was to determine how changing the substrate on a rock ramp affected hydraulic conditions such as velocity and turbulence. The second was to determine the effects of these hydraulic conditions on upstream passage success of three native Colorado fishes: longnose sucker (*Catostomus catostomus*), longnose dace (*Rhinichthys cataractae*), and johnny darter (*Etheostoma nigrum*). The first study hypothesis was that adding cobble to a rock ramp would cause significant decreases in velocity and increases in turbulence. This hypothesis was tested to demonstrate whether there is a clear benefit to adding roughness elements to grade control structures in urban streams to allow fish passage. The second hypothesis was that the increased turbulence in the treatment with the highest roughness would not offset the benefits of lower velocity, and that all three species would move upstream more often in the rougher treatment. This hypothesis was tested to confirm the benefit of lower velocity for ascending fishes, even when turbulence is increased.

METHODS

Experimental Apparatus

An experimental rock ramp fishway was constructed at the Colorado State University Engineering Research Center (ERC) to allow testing of substrate arrangements in an apparatus long enough to mimic a real fishway. This model fishway mimicked a low-flow notch, which confines stream flows to a small percentage of the channel width at base flow (Figure 4-1). A trapezoidal channel was used, so that a variety of depths and velocities were available to ascending fishes.

The rock ramp was 10.1 m long and constructed inside an 18.3-m long x 1.2-m wide by 1.2-m high flume (Figure 4-2). Water was delivered to the upstream end of the flume by a Cascade 880 RPM mixed flow pump with a maximum capacity of 0.7 m³/s (11,000 gpm). From downstream to upstream, the model fishway consisted of three sections: the tailrace, the main body of the fishway, and the upstream holding/fish collection area. In the tailrace, a screen was constructed of 1.9-cm diameter PVC pipe and 0.3 cm plastic mesh and placed 2 m from the fishway entrance to create a quiescent downstream holding area for fish. Cobble substrate was placed in the tailrace to provide resting locations and cover. Water depth was set to 0.2 m by placing a board immediately downstream of the screen. Upstream of the main body of the fishway, a screen was constructed in the same manner as the downstream screen; the screen was located 2 m from the rock ramp exit to confine ascending fish to the test section. The upstream holding area was 0.61 m deep and also had low velocity and cobble substrate to provide resting opportunities and cover. On the rock ramp, roughness elements were placed in a chevron formation based on the perturbation boulder design (Figure 4-2). The cobbles were 10 – 15 cm in diameter (rather than large boulders) due to the smaller ramp size and the small size of the subject fish.

Hydraulic Design

Rock ramp water velocities are variable, but velocities are high enough in localized areas that small-bodied fishes must sprint to ascend them. Low-flow measurements of multiple points on rock ramps in two streams located in the Rocky Mountain foothills (Spring Creek, Fort Collins, Colorado, and the St. Vrain River, Longmont, Colorado) indicate that water velocities between roughness elements such as boulders or cobbles range from 0.2 to 0.7 m/s. (A. Ficke, unpublished data). However, water velocities on segments of these ramps without roughness

elements were often ≥ 1.0 m/s. The model fishway was designed to produce an average water velocity of 0.64 m/s at a flow of 0.026 m³/s, because many small-bodied fishes are forced to sprint at this speed (Bestgen et al. 2010; Billman and Pyron 2005; Leavy and Bonner 2009; Ficke et al. 2011; Ficke et al. unpublished data). The experimental rock ramp was built on a 3.0% slope. The velocity and slope were chosen for two reasons. First, a slope of 3% has been recommended for passage of “weaker” (i.e., smaller) fishes (Aadland 2010). Second, the selected velocity of 0.64 m/s is similar to those observed on rock ramps in the field. Average water depths were 0.1 m, and the width of the water surface was 0.3 m.

The ramp dimensions and the flow (0.026 m³/s) did not differ between treatments. Instead, hydraulic conditions were altered by changing the arrangement of the substrate within the experimental rock ramp. Two different substrate treatments were used: a closely-spaced treatment with cobbles spaced so that they were approximately one diameter apart from one another, and a widely-spaced treatment where half of the cobbles from the closely-spaced treatment were removed (Figure 4-2).

Data Collection: Hydraulics

Detailed measurements were taken with a Vectrino Acoustic Doppler Velocimeter (ADV, Nortek AS, Rud, Norway) to characterize the hydraulics of each substrate treatment. In turbulent systems, it is difficult to obtain data without a large amount of “noise” (Martin et al. 2002). The ADV settings were adjusted to balance the need for clear data points and the need to collect sufficient data points to properly characterize velocity and turbulence for both treatments. The sampling rate of the ADV was 50 Hz, the recording time for each sample was 60 seconds (Natalie Youngblood, Engineering Research Center, Colorado State University, personal communication), and data points were retained if the signal-to-noise ratio was 15 or greater for

all four vectors and the correlations were greater than 40 percent for all four vectors (Martin et al. 2002). Data collected with the ADV were analyzed in MATLAB (Mathworks, Natick, Massachusetts) to provide single values of hydraulic variables at each measuring location.

A total of 55 and 46 sampling points were collected for the closely-spaced and widely-spaced treatments, respectively. These sampling points varied in depth and location along the cross section, so that variability in velocity and turbulence was captured for each treatment. The close spacing of the rocks in the first treatment limited the number of locations where hydraulic measurements could be taken, and the turbulence in both treatments limited the number of locations where correlations and signal-to-noise ratios were high enough to retain the data points. As a result, it was not always possible to collect data points at multiple locations within a single transect (Figure 4-3). However, data were collected at multiple locations and depths within each treatment.

Data Collection: Fish Passage Trials

Longnose sucker *Catostomus catostomus*, longnose dace *Rhinichthys cataractae*, and johnny darter *Etheostoma nigrum* were collected from the Cache la Poudre and Big Thompson rivers for use in fish passage trials. These species are widespread in Colorado, and are an important part of the fish assemblage in many streams (Woodling 1985). Furthermore, the effects of turbulence on these species' ability to navigate rock ramps is unknown. This set of three species provided a comparison of a moderately-sized fast swimming fish (longnose sucker), a small-bodied fast swimming fish (longnose dace), and a small-bodied, slow swimming fish (johnny darter) (Ficke et al. 2011, also see Chapter 2, Appendix 2A).

Johnny darter and longnose dace were tested in groups of 10 individuals, and longnose suckers were tested in groups of three to five individuals, due to limited availability (Table 4-2).

Six trials (after Bestgen et al. 2010) were conducted with johnny darter and longnose dace for each substrate type. Only five longnose sucker trials were conducted for the closely-spaced treatment, and three for the widely-spaced substrate, because fewer individuals of this species were captured during collection efforts. New fish were used for each trial.

Fish were placed in the downstream holding section at the beginning of each trial and allowed 22 hours to move up the fishway to the upstream holding area. At the end of each experiment, each fish was removed from the apparatus, weighed (g) and measured (total length, TL, in mm). The location of each individual (downstream holding area, rock ramp, or upstream holding area) was also recorded, so that the effect of total length on passage success could be analyzed. Of all the individuals tested, only four fish were collected on the rock ramp (i.e., as opposed to an upstream or downstream holding chamber) at the end of the trial. These individuals were omitted from the data analysis to permit the use of a binary outcome (i.e., successful or unsuccessful passage). As with Bestgen et al. (2010), direct observations of fish behavior were not possible on the ramp, but fish were periodically observed in the downstream holding area to ensure that they were attempting to move upstream. Fish placed in the downstream holding area required no additional stimulus besides running water to attempt upstream movement, which matched fish behavior in previous studies on jumping performance over artificial waterfalls (Kondratieff and Myrick 2005, 2006; Brandt et al. 2005).

Fish were considered to have successfully negotiated the ramp if they were found in the upstream holding area at the end of the trial. This was a conservative estimate of success, because fish that successfully moved upstream and returned downstream before the end of the trial were considered unsuccessful. However, a motion-activated camera validated that few individuals returned downstream after ascending the ramp. This camera was placed at the

upstream edge of the rock ramp, where the water surface was tranquil and fish movements were easily detected.

Data Analyses: Hydraulics

The closely-spaced and widely-spaced treatments were compared using two sets of values: treatment-averaged values and data ranges based on individual point data. Average values for velocity and depth for the closely-spaced and widely-spaced treatments were used to calculate Manning's n , the Froude number (Fr), turbulent kinetic energy (TKE), and the energy dissipation factor (EDF). Data collected at individual points with the ADV were used to calculate the observed range of values for velocity and TKE. The individual data points were also used produce plan (i.e., overhead) view and cross-sectional velocity maps to show spatial variation in velocity. The treatment-averaged values, the observed ranges, the spatially explicit analyses, and the dependent and independent variables used in the calculations are described in detail below.

Treatment-averaged values

Hydraulic variables that are presented as single averages for the closely-spaced and widely-spaced substrate treatments provided a basis for comparison between the two substrate treatments and a theoretical smooth ramp. The smooth ramp was not constructed or measured, but it was modeled to test whether adding cobbles to a ramp increased its useability for fishes by decreasing challenging hydraulic conditions. Average values of velocity, Froude number, Manning's n , and energy dissipation factor (EDF) were calculated for the two measured substrate treatments and the theoretical smooth ramp. Froude number is a measure of whether flow is tranquil or rapid and is calculated with the following equation:

$$Fr = V / \sqrt{h * g} \quad (\text{Equation 1})$$

where V = velocity in the upstream-downstream direction, h = water depth, and g = 9.81 m/s². A Froude number > 1.0 indicates rapid flow (Knighton 1998).

Manning's roughness (n) is a measure of resistance to flow due to roughness in an open channel. It is calculated with the following equation:

$$n = R^{2/3} * S^{1/2} / V \quad (\text{Equation 2})$$

where R = the hydraulic radius of the channel, S = channel slope, and V = velocity in the upstream-to-downstream direction (Knighton 1998). Treatment-averaged values of Manning's roughness and Froude number were estimated with a normal depth calculator (Ponce 2014). Normal depth is attained when the downward momentum of the water moving over a stable bed has balanced with the physical features of the channel to reach a depth that will not change in a longitudinal direction, unless the morphology of the channel changes. The normal depth calculation is iterative. The calculation uses equation 1 and equation 2 and adjusts Manning's n until calculated depths match the average measured depth (obtained during collection of ADV data) in the channel. Average velocity, Froude number and Manning's n were compared between treatments to determine how they were affected by the closely-spaced and widely-spaced substrate.

Energy dissipation factor is a measure of turbulence for which maximum allowable values have been established for selected species. Energy dissipation factor is calculated with the following equation:

$$EDF = \gamma QS / A \quad (\text{Equation 3})$$

where γ = the unit weight of water (998 kg/m³), Q = flow (m³/s), S = the slope of the ramp, and A = the cross-sectional area of the flow (m²). The recommended EDF maxima for rock ramps are 34.3 kg-m/m³·sec for salmonids (D. Laiho, Boulder County Parks and Open Space, personal communication) and 15.7 kg-m/m³·sec for clupeids, (*Alosa* spp.; Haro et al. 2008; Larinier and Travade 2002). The EDF was calculated for each treatment using the measurements of flow, slope, and cross-sectional area and compared to the literature-based recommendations.

Range of values within each treatment

Velocities and calculations of TKE from individual ADV measurement points were recorded and presented as a range of values for each treatment. Turbulent kinetic energy is a measure of turbulence that accounts for velocity changes in the x, y, and z directions. It is calculated with the following equation:

$$TKE = 1/2 \left(\sqrt{\sum v_{x,i}^2 / n_x} + \sqrt{\sum v_{y,i}^2 / n_y} + \sqrt{\sum v_{z,i}^2 / n_z} \right) \quad (\text{Equation 4})$$

where v_x , v_y , and v_z = water velocity in the x, y, and z directions, and n_x , n_y , and n_z = the number of velocity measurements taken in the x, y, and z directions (Rodi 1980, Silva et al. 2012). The range of values for both velocity and TKE were compared between treatments to determine whether the variability in velocity and turbulence differed between the closely-spaced and widely-spaced substrate arrangements.

Velocity Ranges and Detailed spatial mapping of velocity

Velocity in the upstream-downstream direction (V_x) was analyzed with a Wilcoxon test in JMP Pro 11 (SAS Institute 2013) to determine if velocities varied significantly between substrate treatments. Because the velocity data were not normally distributed, this nonparametric

test was used. The velocity distributions of the two treatments were considered significantly different at $\alpha = 0.05$.

Plan or overhead view and cross-sectional velocity maps were also created for both treatments. Plan view maps were created by averaging velocities taken in the following locations: mid-channel, beside the cobbles placed in mid-channel, at the base of the side slopes, and on the side slopes. Cross-sectional velocity maps were created for two cross sections from each treatment using Surfer 8.0 (Golden Software, Golden, Colorado). Additional cross sections were not mapped because the difficulties associated with collecting data from this model fishway prevented collection of sufficient data points at other cross sections. Because cobbles were present in the center of the channel in both cross sections from the closely-spaced treatment and absent from the center of the channel in both cross sections from the widely-spaced treatment (Figure 4-3), the mapped cross sections represent the changes in velocity distributions that resulted from removal of the rocks placed in the center of the channel.

Data Analyses: Fish Passage Trials

The probability of successful upstream movement was modeled using a logit function with a binomial distribution. The probability of successful passage (defined as movement of an individual into an upper chamber or holding area) was modeled as a function of treatment (i.e., substrate arrangement), and fish total length. The effect of substrate arrangement was tested with a general linear model and a logit link function in JMP Pro 11. We could not assume that behavior of each individual fish was unaffected by the behavior of the other fish in the trial (e.g., Ficke et al. 2011; Kondratieff and Myrick 2006). Therefore, each trial group was considered as a single experimental unit, with the substrate arrangement as the predictor variable and the proportion of successful finishers in a trial as the dependent variable. The importance of total

length in upstream passage success of individual fish was analyzed with logistic regression in JMP Pro 11. Success rates were analyzed separately for the three species because of differences in their swimming abilities, and within each species, the effects of total length on passage success were analyzed separately for each substrate type. Predictor variables in the analyses were considered statistically significant at $\alpha = 0.05$.

The range of velocities observed in each treatment were compared to known swimming abilities of the three fish species (see Chapter 3) to determine whether fish were more likely to encounter excessive velocities in one treatment than in the other. Velocity plan view and cross-section maps of both treatments were qualitatively examined to identify any high-velocity areas that could inhibit passage of the three species.

RESULTS

Treatment Hydraulics

Treatment-averaged values showed few differences between the closely-spaced and widely-spaced substrate arrangements, but indicated that the addition of cobbles had a large effect on hydraulic conditions. Average velocity, Froude number, and EDF were similar between the closely-spaced and the widely-spaced cobble treatments, but both treatments had lower values for all three parameters than would be expected on a smooth ramp (i.e. without cobbles, Table 4-1). Comparison of model output for a smooth ramp and model output for the treatments showed that the addition of cobbles to a smooth ramp would result in a 31 – 34% reduction in average velocity, a 37 – 41% reduction in Froude number, and a 31 – 36% reduction in energy dissipation factor (Table 4-3).

Although treatment-averaged hydraulic variables were similar between the substrate arrangements, the treatments differed with respect to the range of velocity and TKE measured

throughout the treatment, spatial distribution of velocity, and the complexity of the flow fields in representative cross sections. The observed ranges of velocity were similar between treatments (Figure 4-4), but the closely-spaced cobble treatment had a lower median velocity (0.32 m/s) and a lower range of velocities (- 0.11 – 1.07 m/s) than the widely-spaced treatment (0.64 m/s, - 0.09 – 1.28 m/s). Similarly, treatment-averaged values of TKE were similar, but the closely-spaced treatment had a slightly higher median TKE and a wider observed range of values (0.03, < 0.001 – 0.49) than the widely-spaced treatment (0.02, < 0.001 – 0.40).

Between-treatment differences were also apparent in the plan view and cross section maps. The plan views show that velocities in both treatments were highest at the bottom of the side slope, on either side of the mid-channel cobbles (Figure 4-5), but the averaged mid-channel velocity for locations downstream of cobbles was lower in the closely-spaced treatment than in the widely-spaced treatment. Shallow water submerged the cobbles that were attached to the side slope in the closely-spaced treatment, but not all of the cobbles on the side slopes were completely submerged in the widely-spaced cobble treatment. Cross-section maps showed that the closely-spaced treatment was deeper and characterized by more spatially variable velocities than the widely-spaced treatment. For example, for the cross sections at 6.1 and 6.3 m from the top of the rock ramp, velocities to the left of the center cobbles in the closely-spaced cross sections range from zero to 1.0 m/s, but velocities in the same area in the widely-spaced treatment ranged from 0.35 to 1.0 m/s (Figure 4-6). These maps also show that removal of the rocks in the center of the channel caused high velocities to occur closer to the bottom of the channel than in the closely-spaced treatment.

Fish passage trials

Longnose suckers had the highest rate of passage success (mean success rates = 88 and 92%) in both substrate treatments, followed by longnose dace with moderate rates of success (mean success rates = 31 and 38%). Johnny darters had the lowest rates of passage success (mean success rates = 5 and 0%). The success rates for all three species were more variable between trials in the closely-spaced treatment than in the widely-spaced treatment (Table 4-4). Logistic regression analysis showed that there was no statistically significant difference between passage success in the closely-spaced and the widely-spaced treatments for any of the three species. Total length did not affect passage success of longnose sucker or johnny darter in the closely-spaced or widely-spaced substrate treatment, or longnose dace in the widely-spaced substrate treatment. Total length had a statistically significant effect on upstream passage success for longnose dace in the closely-spaced substrate treatment (Table 4-4), but the effect was negative.

DISCUSSION

Hydraulic modeling and analysis of treatment-averaged variables identified few differences between the closely-spaced and widely-spaced cobble treatments, but the modeling results did demonstrate that increasing roughness by adding cobbles led to a marked decrease in average velocity, Froude number, and EDF. Examination of the observed range of values of velocity and TKE and the velocity maps identified differences between treatments. The median velocity in the closely-spaced cobble treatment was half that of the widely-spaced treatment, and the range of velocities was lower in the closely-spaced cobble treatment. Longnose sucker and longnose dace moved upstream successfully in both treatments, but johnny darter only moved upstream in the closely-spaced treatment. These results indicate that while representing

hydraulic conditions in a fishway with average or median values provides a starting point for design and validation, the variability and spatial arrangement of hydraulic variables is more important in determining whether the fishway will function as desired.

The modeled values of the treatment-averaged variables (velocity, Fr, and EDF) show the benefit of adding cobble to fishways, because modeled values of all three variables were lower in both treatments than they would have been on a smooth ramp. No measures of passage success are available for the rock ramp with no cobble, because trials were not run without cobbles. However, the modest to low success rates of longnose dace and johnny darter when median velocities were lower than their known swimming abilities suggest that if median or average ramp velocities exceed the measured sprinting abilities of the test species, little to no upstream passage would occur.

The decrease in velocity with the addition of cobbles caused a decrease in Fr and EDF, both of which can potentially affect fish passage success. A decrease in Fr should also increase fish passage success, based on the results of a study of fishes native to the South Platte River in Nebraska (Yu and Peters 1997). This study involved sampling fish with pre-positioned electrofishing grids and demonstrated that the 24 species sampled showed strong preferences for habitats with $Fr < 0.3$. The occurrence of higher Fr in fishways could result in reduced passage success or avoidance of the fishway. The addition of cobble to the ramp also resulted in a 31 and 33% decrease in EDF for the closely-spaced and widely-spaced cobble treatments, respectively, from the estimated non-cobble condition. The energy dissipation factor for both cobble treatments was less than $20 \text{ kg}\cdot\text{m}/\text{m}^3\cdot\text{sec}$, which is below the maximum recommendation for salmonids and slightly above the maximum recommendation for American shad *Alosa sapidissima* ($15.68 \text{ kg}\cdot\text{m}/\text{m}^3\cdot\text{sec}$, Haro et al. 2008). An energy dissipation factor of less than 20

kg-m/m³·sec allowed some passage success of the small fishes used in this experiment, so the criterion for American shad might serve as an approximate guideline for fishways designed for small species accustomed to some turbulence, at least until more taxa-specific values are derived.

Importance of Substrate Arrangement and Spatially Explicit Velocities

One of the most important revelations of this study was that two different substrate arrangements produced different median velocities and velocity ranges in a rock ramp, even though both treatments were designed with the same velocity, slope, flow and ramp dimensions. This has important implications for the passage of small fishes, even though passage rates were similar between treatments for the three tested species. The median maximum sprinting velocities of longnose dace and johnny darter were estimated to be 0.7 m/s under laboratory conditions, and the median maximum sprinting speed of longnose sucker was 0.8 m/s (Ficke and Myrick unpublished data). As a result, a fish in the widely-spaced treatment was more likely to encounter velocities that exceeded its sprinting ability than one tested in the closely-spaced treatment (Figure 4-4). This indicates that a rock ramp with design velocities that approach the sprinting ability of small fishes can be made more passable by adding cobbles that mimic the closely-spaced treatment (i.e., spacings of approximately one diameter apart). Although an average or design velocity is a good starting point for fishway design, fish will seek lower velocities when they are available, so spatially explicit velocity data are important in design. Spatially explicit data can be used to identify “trouble spots” in fishways, where fish may not be able to ascend. For example, the plan view velocity maps indicated that the areas immediately downstream of cobbles in the center of the channel provided slower water velocities in the closely-spaced treatment than in the widely-spaced treatment and that the highest velocities occurred immediately on either side of the centerline cobbles in both treatments (Figure 4-5).

The cross section maps showed the effects of removing cobbles from the center of the channel. The widely-spaced treatment provided a more uniform flow field, but higher velocities were more common and closer to the bottom than in the closely-spaced treatment (Figure 4-6).

Species-Specific Effects of Turbulence on Success

Turbulence is known to reduce the swimming performance of fishes, likely because of the increased cost of maintaining position in the water column (e.g., Tritico and Cotel 2010). Turbulence had a negative effect on passage time of Iberian barbel *Luciobarbus bocagei* in an experimental pool-type fishway (Silva et al. 2011), and higher turbulence, in combination with high velocities and lack of refuge in an experimental vertical slot fishway prevented upstream passage of Rio Grande silvery minnow *Hybognathus amarus* (Bestgen et al. 2010). The results of these studies provide a possible explanation for why passage success was modest for longnose dace and nearly zero for johnny darter, even though their sprinting abilities were higher than the median velocities of either treatment. However, the fact that passage varied little between treatments for any of the three tested fish species suggests that the higher TKE values in closely-spaced cobble treatment (Figure 4-4) were not an impediment to upstream passage. Turbulent kinetic energy values in both treatments ranged from < 0.01 to 0.19 , compared to a modeled range of 0.03 to 0.21 in the St. Vrain River, a stream that transitions from the mountains to the plains on the Colorado Front Range (Kolden 2013). Maintaining fishway turbulence at levels similar to what could be encountered in a fish's natural environment may help ensure passage success.

Multiple hydraulic characteristics of fishways determine fish passage success, but they are interrelated, which necessitates considering all of them in fishway design. Hydraulics can be altered by changing design features such as slope or substrate arrangement, but designs that

focus on a single hydraulic variable may not facilitate fish passage. For example, velocity can be altered by changing hydraulic roughness, slope, or the cross-sectional shape of the channel. In this experiment, velocity was controlled by increasing roughness with the addition of cobbles, which produced hydraulic conditions that increased the probability of successful passage. High roughness (Manning's $n = 0.05$) reduced water velocities to speeds compatible with swimming abilities of longnose dace and johnny darter, but this high roughness could produce high turbulence that could be problematic for species that are not accustomed to it, even in the low-velocity resting areas behind the cobbles. Using design slopes of less than 3% for small-bodied fishes may increase passage success by decreasing the number of roughness elements required to retard water velocity and therefore the turbulence intensity in the rock ramp.

Table 4-1.—Studies involving rock ramp hydraulics and fish passage success. All fish lengths are total length unless specified.

Species	Length Range	Methods & Reference
Shovelnose sturgeon <i>Scaphirhynchus platorhynchus</i>	250 – 350 mm fork length	Direct observation of fish passage success and behavior at variable velocities and four bottom substrate types (White and Mefford 2002).
Blueback herring <i>Alosa aestivalis</i>	> 200 mm	Rock weir versus perturbation boulder rock ramp, 1:20 slopes. Side-by-side ramps in a laboratory setting, passage success measured with PIT antennae (Haro et al. 2008).
American shad <i>A. sapidissima</i>		
Rio Grande silvery minnow <i>Hybognathus amarus</i>	53 – 88 mm	Measured passage success over different-sized substrates in a laboratory flume, measured passage success through a vertical slot and a rock ramp fishway in the laboratory (Bestgen et al. 2010).
Macquarie perch <i>Macquaria australasia</i>	79 – 261 mm	Direct tests of swimming performance, hydraulic measurements on rock ramp in Cotter River, Australian Capital Territory, Australia. Passage success inferred by comparing measured swimming ability to hydraulics (Starrs et al. 2012).

Table 4-2.—Description of sample sizes, individual lengths, and number of trials for each substrate for the three species tested in the rock ramp study. Lengths are reported as a mean with the range in parentheses.

Species	Sample size	Total length (mean and range, mm)	Trials, Closely- spaced	Trials, Widely- spaced
Longnose sucker, <i>Catostomus catostomus</i>	37	154 (93 – 251)	5	3
Longnose dace, <i>Rhinichthys cataractae</i>	117	64 (47 – 98)	6	6
Johnny darter, <i>Etheostoma nigrum</i>	120	56 (42 – 73)	6	6

Table 4-3.—Treatment-averaged hydraulic variables obtained from a normal depth calculation. Roughness estimate for the smooth channel (i.e., no cobbles) taken from Chow (1959). V = velocity in the upstream-downstream direction, Fr = Froude number, and EDF = energy dissipation factor.

Treatment	V (m/s)	Manning's n	Fr (dimensionless)	EDF (kg-m/m ³)
No Cobbles (estimated)	0.91	0.032	1.03	28.0
Closely-spaced cobbles	0.63	0.049	0.65	19.4
Widely-spaced cobbles	0.60	0.052	0.61	18.7

Table 4-4.—Measured upstream passage success rates of each species in the closely-spaced and widely-spaced cobble treatments and results of logistic regression analyses of substrate arrangement and fish total length effects on passage success. Success is reported as percentage of individuals from all trials that ascended the ramp, with the range of success rates for the separate trials in parentheses. Statistical significance of substrate arrangement was determined with chi-square tests with one degree of freedom. For each species, statistical significance of total length was determined with chi-square tests with one degree of freedom. Total length was tested separately for each substrate type.

Species	Success, Closely- spaced	Success, Widely- spaced	TL (mm), Widely- spaced	TL (mm), Closely- spaced	Substrate Arrangement
Longnose sucker, <i>Catostomus</i> <i>catostomus</i>	88% (60 – 100)	92% (75 – 100)	p = 0.6589	p = 0.8228	p = 0.7312
Longnose dace, <i>Rhinichthys</i> <i>cataractae</i>	31% (0 – 70)	38% (20 – 50)	p = 0.0007	p = 0.1674	p = 0.3494
Johnny darter, <i>Etheostoma</i> <i>nigrum</i>	5% (0 – 30)	0% (0 – 0)	no success	p = 0.5654	p = 0.1350



Figure 4-1.—The model rock ramp constructed at the Colorado State Engineering Research Center (left photo) and an example of a low-flow notch in a fishway in a small Colorado stream (right photo). The low-flow notch in the fishway is 21.3 m long and has a slope of 4.5%. The model rock ramp fishway was constructed in a 1.2-m wide flume, and average water depths were 0.11 m.

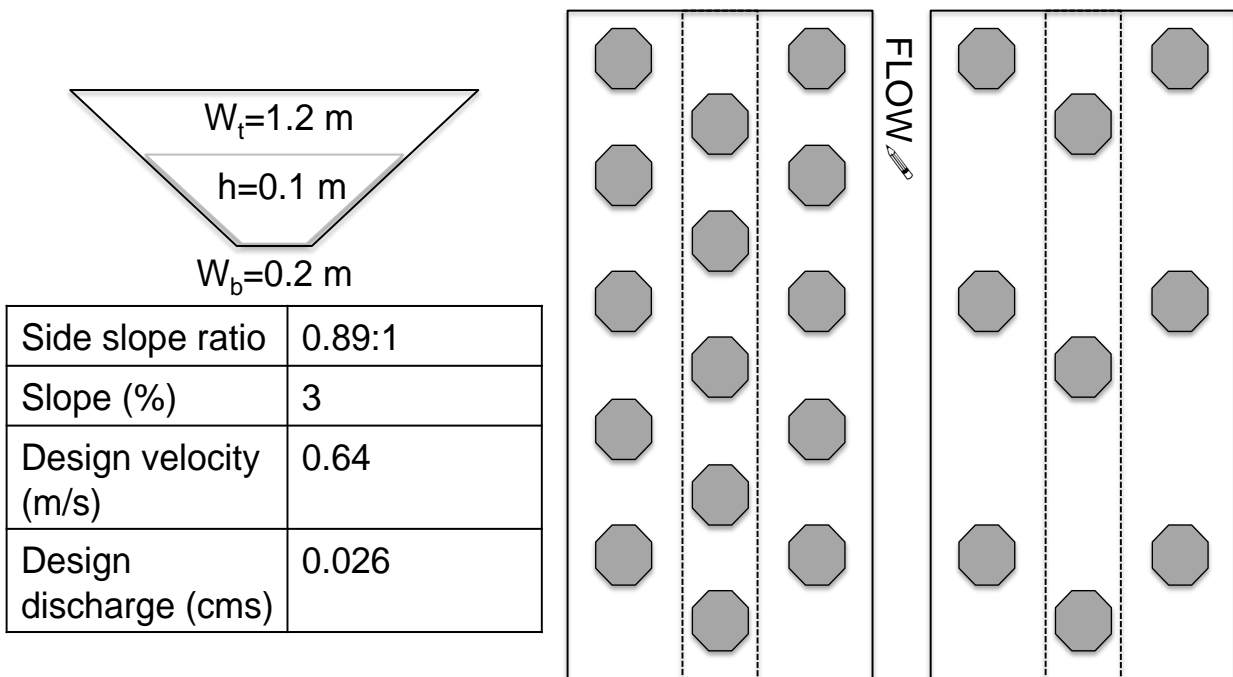
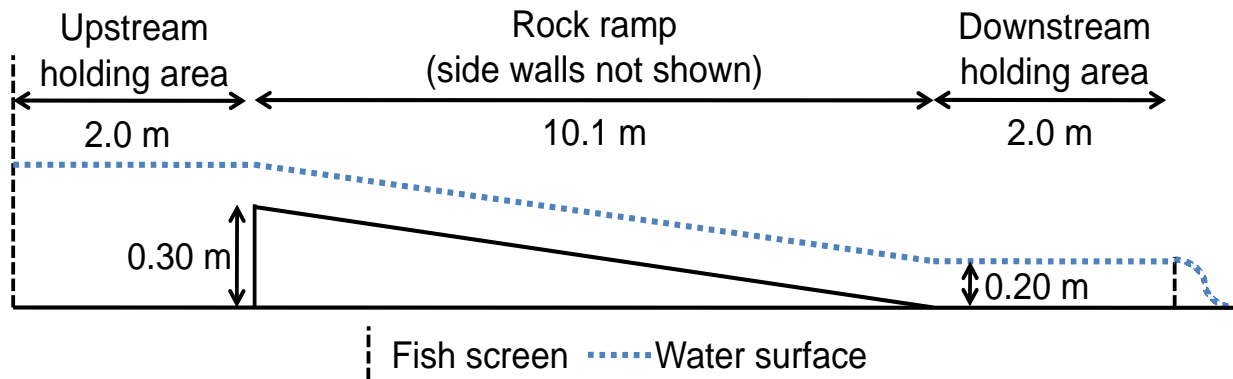


Figure 4-2.—Top: the experimental rock ramp constructed at Colorado State University’s Engineering Research Center. Bottom: cross-sectional design parameters and plan view of substrate placement. Both treatments used cobbles that were 10 to 15 cm in diameter. Two treatments were tested; a closely-spaced cobble treatment where cobbles were glued to the ramp approximately one diameter apart from one another (left), and a widely-spaced cobble treatment, with half of the cobbles removed (right).

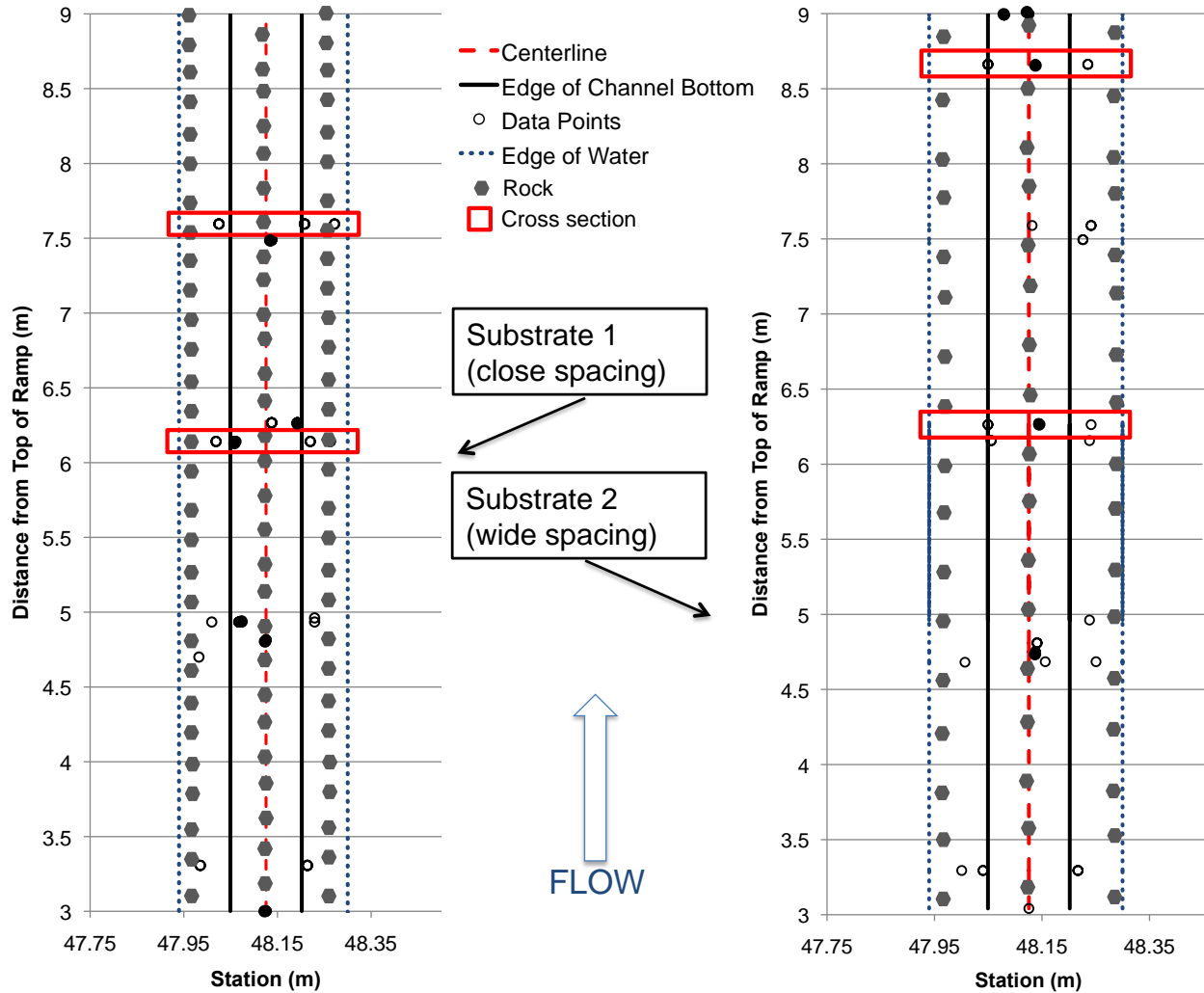


Figure 4-3.—Data points collected in each substrate treatment with the acoustic Doppler velocimeter. “Station” is a measure of distance across the rock ramp. Locations of cross sections used to compare flow fields between treatments are shown. Filled data points indicate that multiple measurements were taken at different depths at a single x-y location.

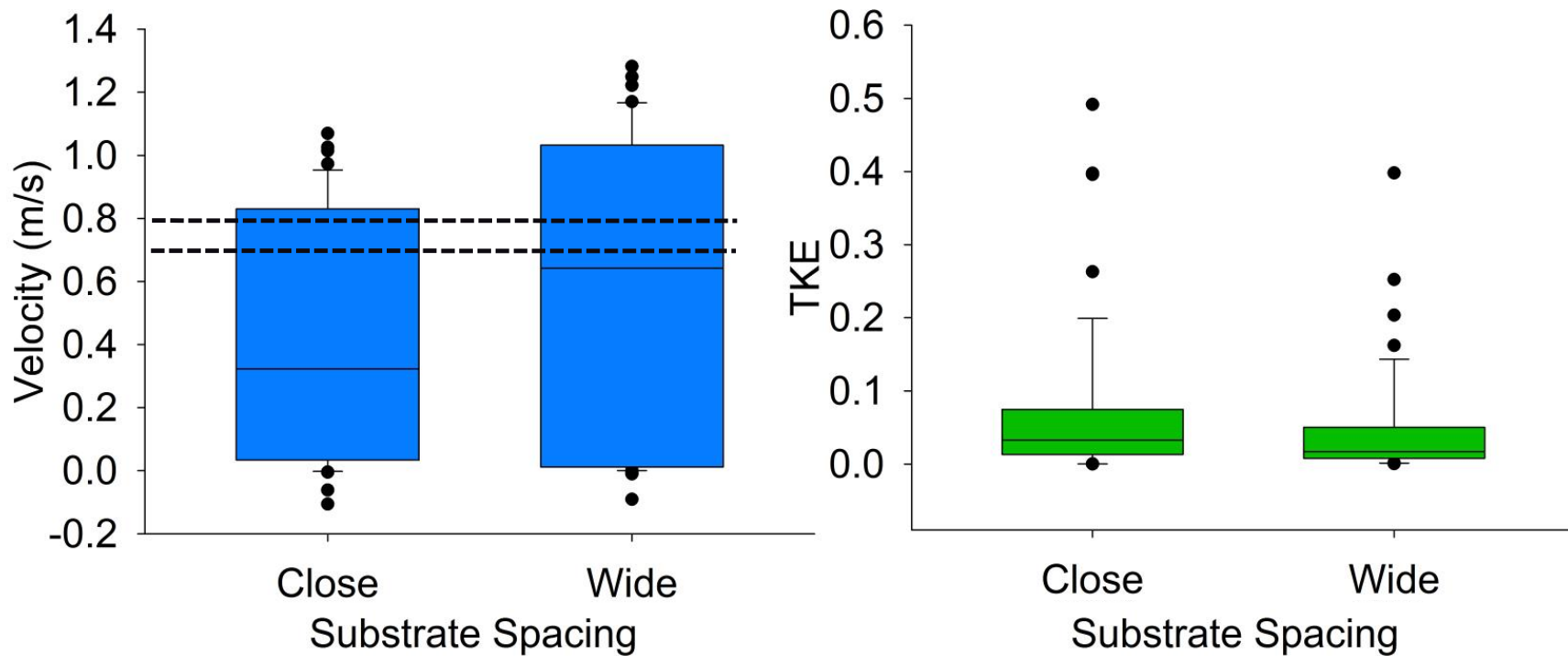


Figure 4-4.—Box plots showing the range of velocities and TKE measurements in the closely-spaced and widely-spaced cobble treatments. The bottoms and tops of the boxes represent the 25th and 75th percentiles of the observed values, respectively, and the line inside the boxes represents the median values. The dashed lines in the velocity graph show the median sprinting ability of longnose dace and johnny darter (lower dashed line) and longnose sucker (upper dashed line) measured under laboratory conditions (see discussion for details).

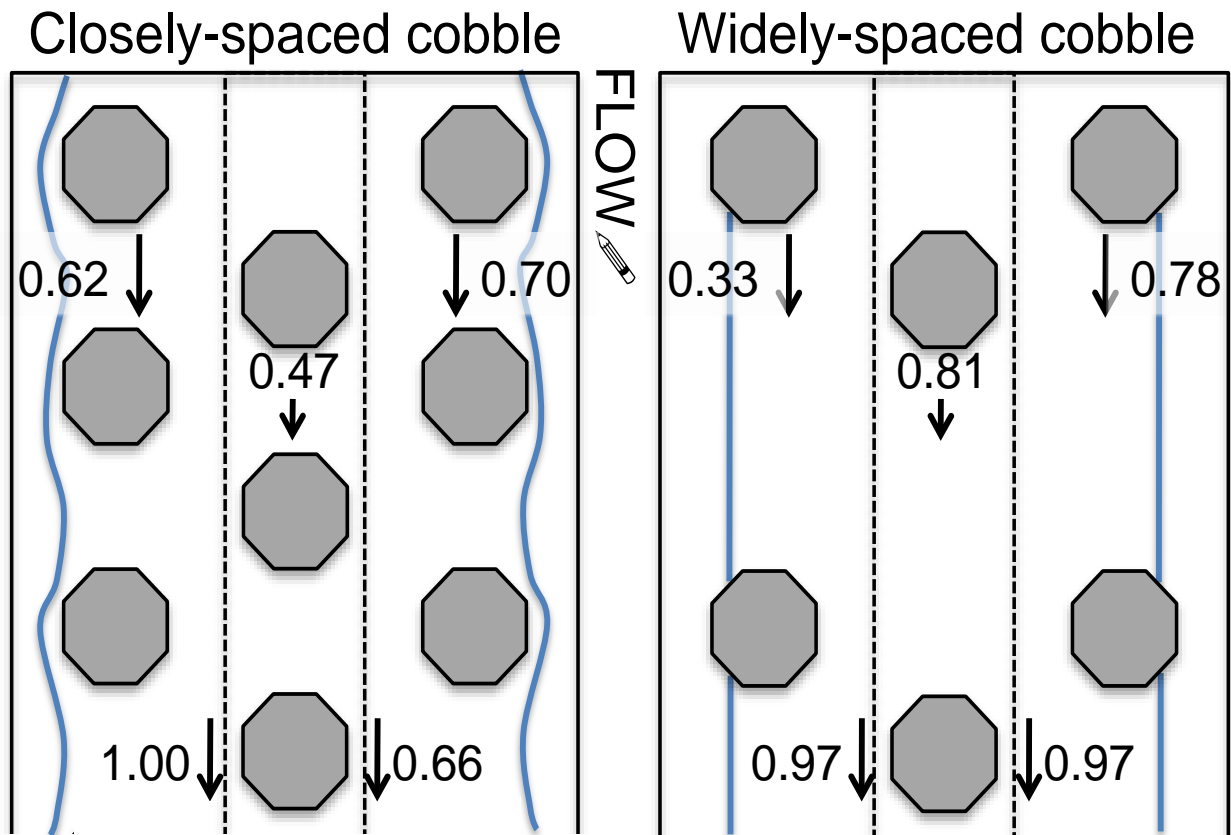


Figure 4-5.—Averaged velocities (m/s) in the downstream direction in specific areas of the rock ramp. The specific areas were: mid-channel, beside the cobbles placed in mid-channel, at the base of the side slopes, and on the side slopes. Areas to the right and the left of the dashed lines represent the side slopes of the model fishway.

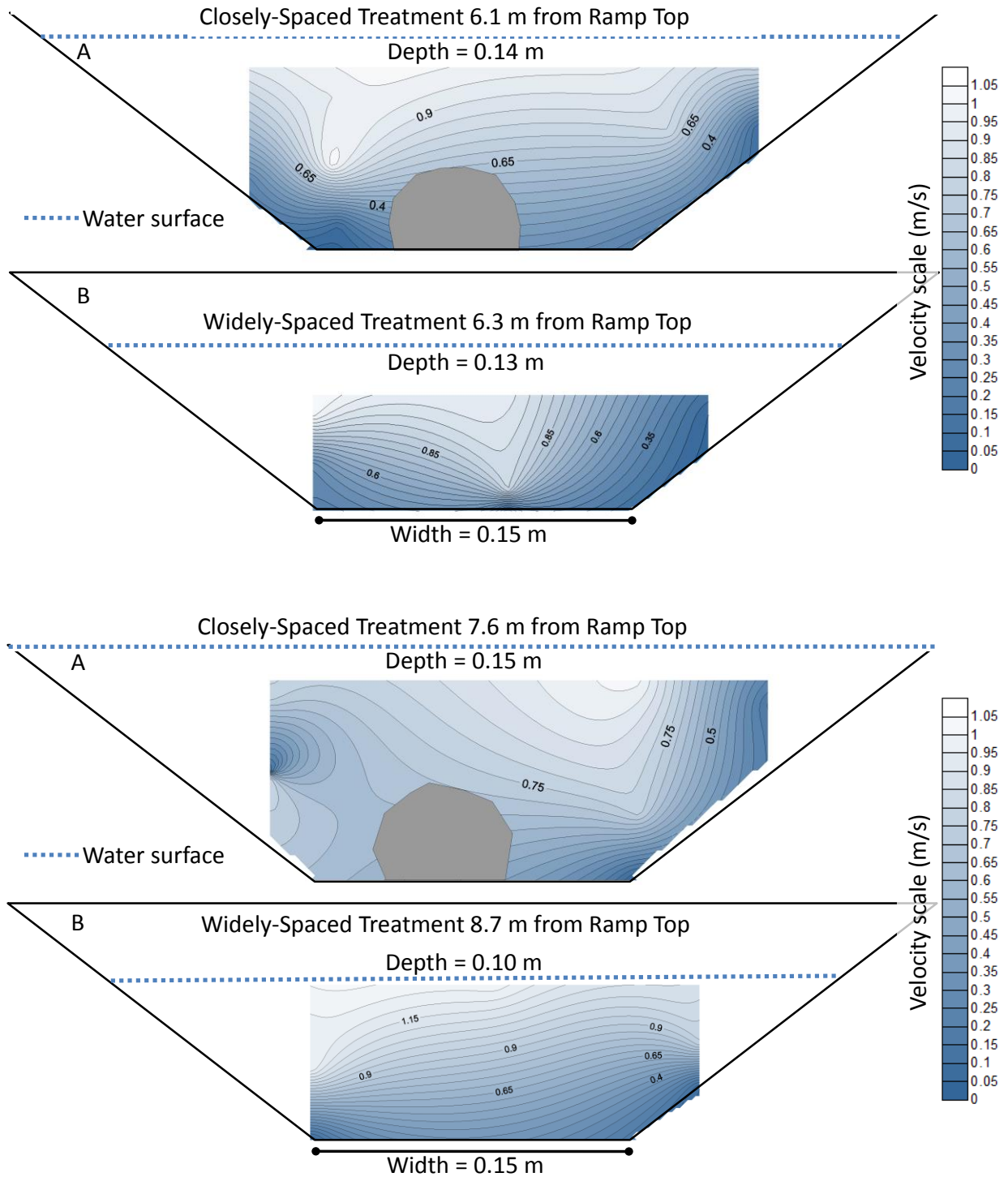


Figure 4-6.—Comparison of cross sections from the closely-spaced (A) and the widely-spaced (B) cobble treatments. Four cross sections had sufficient data points for contour mapping. Cobbles were present in the center of the channel in the closely-spaced treatment cross sections and absent from the center of the channel in the widely-spaced treatment cross sections. Trapezoids have been added to show the extent of the water. The trapezoids are not completely filled because the graphing program used to represent the cross sections (Surfer 8.0) does not extrapolate beyond the measured data range.

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CHAPTER 5:
FISH PASSAGE OVER TWO ROCK RAMP FISHWAYS WITH DIFFERENT DESIGN
FEATURES

INTRODUCTION

Fish populations in many North American streams are highly fragmented (Dynesius and Nilsson 1994) because instream structures such as culverts, grade control structures, and dams prevent or impede movement. Reversing fragmentation is a common goal of stream restoration projects (Bernhardt et al. 2005), but many instream structures are unlikely to be removed because they benefit society. Therefore, resource managers often consider the installation of fishways at such structures the most practical way of reducing fragmentation. Ideally, fishways are designed to accommodate the swimming performance of the target species or fish assemblage, but design recommendations have traditionally focused on economically important clupeids and salmonids. Other species, particularly those that are not game fish, have received less attention.

Fortunately, researchers are moving away from the traditionally studied fishes, leading to several recent fish passage studies that have focused on resident riverine and nonsalmonid fishes instead of anadromous fishes and salmonids (Peter 1998; Mallen-Cooper et al. 1999; Haro et al. 2004; Castro-Santos 2005; Bestgen et al. 2010; Silva et al. 2012). Some studies have tested fishway efficiency for nonsalmonid fishes in the field (e.g., Katopodis et al. 1991; Bunt et al. 1999; Bunt et al. 2001), but most of them have involved passage through laboratory flumes or rock ramp prototypes (Haro et al. 2004; Castro-Santos 2005; Bestgen et al. 2010; Silva et al. 2012). Because laboratory study results are not always directly applicable to natural streams,

evaluation of existing fishways is necessary to ground-truth laboratory studies and to identify key structural and hydraulic characteristics that affect passage success in the field.

There are three main classes of fishways: pool-and-weir, vertical slot, and rock ramp (Clay 1995). Although rock ramp fishways have shown promise in allowing upstream passage of fishes (Harris 1998; Litvan et al. 2008), their effectiveness has not been extensively studied. Design guidelines have been proposed for rock ramps (FAO/DVWK 2002; Mooney et al. 2007), but there is wide variation in rock ramp characteristics such as the size and placement of roughness elements (i.e. cobbles and boulders), length, and slope. Existing rock ramps thus show lots of variation in design, and, as with many stream restoration projects, few are monitored after construction to measure their effectiveness (Bernhardt et al. 2005; Roscoe and Hinch 2010). Therefore, studies that identify the rock ramp characteristics that aid or hinder fish passage success are sorely needed. The growing number of rock ramp structures in urban streams in the Rocky Mountain Region offers an opportunity to compare passage success across rock ramps with different characteristics.

Monitoring upstream fish movements over rock ramps is challenging because, unlike pool-and-weir and vertical slot fishways, rock ramps often lack confined entrances and exits. Repeated sampling of fishes given small, subcutaneous tags (visual implant elastomer [VIE] or visual implant alphanumeric [VI-alpha] tags) has been used to infer movement rates across rock ramps (Litvan et al. 2008). Although studies using this method are suitable for fishes ≥ 50 mm in length (Sutphin et al. 2007), analysis of movement data can be hindered by low capture probabilities and difficulty in identifying uniquely tagged individuals (Ficke et al 2009; Curtis et al. 2006).

Generally speaking, fish movements through fishways are best monitored with a mark-recapture approach using continuous monitoring technology (Calles and Greenberg 2012; Franklin et al. 2012). Passive integrated transponder (PIT) tags can be monitored with antennae and have been used extensively to monitor fish movement through fishways or over potential instream obstacles (Castro-Santos et al. 1996; Nunalee et al 1998; Zydlewski et al 2001; Compton et al. 2008; Stuart 2008). Detecting movement of PIT-tagged fish with stationary antennae at stream cross-sections removes much of the uncertainty of studies that employ serial sampling to re-locate tagged individuals. The antennae detect tags with high efficiency, and fish movement past fixed locations is monitored constantly instead of during discrete sampling events (Zydlewski et al. 2006). The goal of this study was to apply PIT tag technology to measure fish movement across two rock ramp fishways of dissimilar design in a highly modified segment of a Colorado foothills stream.

METHODS

Study Area

The study site, located on South Boulder Creek, Colorado, encompassed just over 1.0 km of stream and two instream rock ramps (Figure 5-1). The downstream structure is the McGinn fishway (UTM 13S 481124, 4425654) and upstream one is the South Boulder fishway (UTM 13S 484932, 4424718). The McGinn fishway is approximately 0.9 km downstream of the South Boulder fishway. These structures were chosen because they differed in slope, width, ramp length, and substrate type. The McGinn fishway (Figure 5-2) is a 21.3-m long sculpted concrete fishway with a 1.5-m wide confined low-flow notch and a slope of 4.5%. The South Boulder fishway is 10.4 m long and spans the width of the stream (9.1 m). This fishway has an unconfined low-flow notch and a slope of 11.2%. A control site was also established

approximately halfway between the two fishways at a small row of boulders spanning the stream (Figure 5-1). Although most of the habitat in the study area consisted of riffles or runs, this “boulder vane” had pools upstream and downstream of it, as did the diversion structures. This site was chosen as a control because the habitat on either side of the boulder vane was similar to the habitat on either side of the two fishways. The choice of this control location reduced the probability that differences in movement rates could be attributed to habitat differences between the control location and the fishway sites. Furthermore, based on the results of an earlier study (Ficke and Myrick 2009), a small boulder vane with no vertical drop such as this one would not impede movement of the fish species in the study segment. The control site was included in the study design because no information was available on fish movement rates in South Boulder Creek. Movements across the control site provided “baseline” rates to which movements across the fishways could be compared. The study area was divided into three sections to facilitate data collection and analysis. Location A was between the site bottom and the McGinn fishway, Location B was between the McGinn fishway and the control site, and Location C was between the control site and the South Boulder fishway (Figure 5-1, see Model Construction for details).

Monitoring movement of fishes in this 1-km stream section also allowed collection of data on movements over longer distances than earlier studies that focused on a single structure. The length of the segment also may have reduced high emigration rates from the study area. Such high rates are often reported in studies focused on shorter stream segments (see Ficke and Myrick 2009 for a review).

This study was designed to test the hypothesis that fish movement rates were affected by a combination of season, structure gradient, and distance. Specifically, the McGinn fishway, the downstream, low-slope fishway, would allow fish passage rates similar to those across a control

reach for most of the year, but upstream passage rates would be lower than at the control structure during spring runoff, because water velocities would be high in the confined low-flow notch. In contrast, the high slope of the South Boulder fishway would reduce passage rates compared to the control reach throughout the year, but the seasonal pattern of movement would be similar to that observed at the control reach. Specifically, upstream passage rates at the South Boulder fishway were expected to be higher during spring runoff, when water spread across the structure. Distance was also believed to affect movement in that fish would be more likely to move short distances (i.e., over a single fishway or the control site) instead of over multiple sites.

Tagging

Fish were collected in the study segment in May 2010, August 2010, October 2010, March 2011, and May 2011. During each sampling trip, a single pass was made from the site bottom to the site top with two Smith-Root LR-24 backpack electrofishing units in a side-by-side arrangement. For all five sampling occasions, electrofishing the entire study reach took two days. On the second day, electrofishing resumed at the stopping point from the first day. Twenty-nine percent of the fish were captured and tagged downstream of the McGinn fishway, 43% were captured and tagged between the McGinn fishway and the control site, and 28% were captured and tagged between the control site and the South Boulder fishway. Once tagged, fish were released in the middle of the segment in which they were captured. Tagged fish recaptured during subsequent electrofishing efforts were noted but not included in the model used to analyze movement rates.

Captured fish were anesthetized in an oxygenated bath containing high concentrations of CO₂ (3 mg/L), until gill ventilation rate slowed and the fish lost equilibrium. Anesthetized fish were weighed to the nearest 0.1 g and measured in mm (total length, TL). Brown trout *Salmo*

trutta, rainbow trout *Oncorhynchus mykiss*, longnose dace *Rhinichthys cataractae*, and longnose sucker *Catostomus catostomus* meeting minimum length and weight requirements were tagged with a 23-mm half-duplex PIT tag (Oregon RFID, Portland, Oregon). Fish selected for tagging weighed at least 20 g so that tags would not exceed 2% of the fish's body weight (Brown et al. 1999). Minimum TL for tagging was 118 mm for trout, 100 mm for longnose dace, and 150 mm for longnose sucker.

To tag fish, a 5 mm incision was made in the body wall of the fish posterior to the pectoral fin. A PIT tag was then gently inserted into the incision, which was closed with non-absorbable Ethicon monofilament sutures (Roussel et al. 2000) and a $\frac{3}{8}$ -circle cutting needle (Summerfelt and Smith 1990). A single suture tied with an instrument knot was used to close the incision, and all equipment was disinfected in 80% ethanol before each surgery. Processed fish were placed in a recovery bath containing Polyqua™, which replaces a fish's protective slime coat after handling (Swanson et al. 1996) and later transferred to a live car until the end of the day.

Post-tagging survival was measured in two trials. During the first two marking occasions, a subset of the captured fish ($n = 20$) were held in a live car in the stream overnight and released the following day to measure mortality. Four fish died after the first marking occasion (80% survival), but overnight survival was 100% after the second occasion.

A key assumption of tagging is that the tags do not affect the behavior or biology of the tagged organism (Guy et al. 1996). At the beginning of the mark-recapture study, it was not known whether PIT tags were appropriate for the nonsalmonid resident fishes in the study segment of South Boulder Creek. Although previous studies indicated that PIT tags would not reduce swimming performance or increase mortality rates in trout (Brown et al. 1999; Newby et

al. 2007; Roussel et al. 2000), there were few comparable studies on nonsalmonid fishes. However, a companion laboratory study showed that the 23-mm tags used in South Boulder Creek did not affect swimming performance of white sucker (*Catostomus commersonii*), creek chub (*Semotilus atromaculatus*), or flathead chub (*Platygobio gracilis*) and that tag retention rates were 100% after 30 days (Ficke et al. 2012).

Antenna Placement and Construction

Six pass-through PIT tag antennas (Figure 5-3) were placed in South Boulder Creek in May 2010 and maintained through July 2011. Antenna pairs were installed so that one antenna was immediately upstream and the other was immediately downstream of each of the two fishways, with an additional pair of antennae installed in the same manner at the control site (Figure 5-1). Each pass-through antenna was constructed with 8-gauge speaker wire attached to 6.35 mm (¼ inch) aircraft cable suspended over the stream. The wire that ran along the bottom of the stream was fed through 19 mm (¾ inch) diameter flexible sprinkler conduit and anchored to the substrate with Duckbill earth anchors spaced 0.6 m to 1.2 m apart. Antenna tuners, readers, and software were purchased from Oregon RFID. Each antenna reader was powered by two 12-V deep-cycle marine batteries that were exchanged weekly. The batteries were housed in metal boxes insulated with 19 mm (¾ inch) closed-cell foam insulation. During winter, a 30-watt solar charging kit composed of two small panels and a voltage controller was connected to each pair of batteries to extend the operating time. All antennae operated continuously, except during marking occasions, when they were turned off to prevent the current from the backpack electrofisher from damaging the antenna readers. The control antennae were damaged twice by cattle but were repaired within two days both times.

Each PIT tag reader had an internal clock that recorded detection times, making it possible to distinguish between upstream and downstream movement. Detection probability, the probability that a tagged fish is detected when it passes through an antenna, was measured at each antenna using methods explained in Compton (2007). Detection probability was measured weekly because fish swimming speeds and streamflow affect antenna performance (Zydlowski et al. 2006).

Data Analyses

The goal of this study was to compare movement rates across the control site to movement rates across the two fishways. Movement data were analyzed with Program MARK (White and Burnham 1999), a collection of software that can produce maximum likelihood estimates of population abundance and demographic rates such as survival, capture probabilities, and movement probabilities. Estimates are derived from the tag recapture data that describe individual detection histories at the six antennae in the study area.

A multi-state mark-recapture (MSMR) model was used to analyze the movement data. These models provide estimates of apparent survival (ϕ), capture probability (p), and transition probability (Ψ , the probability that an animal will move from one location to another in a specified time frame). A MSMR model also allows estimation of survival, capture probability, and transition probability that change in response to time and/or location (Lebreton et al. 2009). Multi-state mark-recapture models can be used to analyze movements of fish detected with PIT tag antennae (Horton et al. 2011, Fetherman et al. in press), but the models must be modified to accommodate unique characteristics of PIT tag detection data. The MSMR model in Program MARK was modified to estimate transition probability before survival, to estimate transition

probability within instead of between time periods, and to accommodate multiple marking events within a single time period (See Appendix 5A for details).

The study was separated into six time intervals, each of which was at least one month long. Estimation of movements over shorter time periods (i.e. week-long or month-long) is possible when large numbers of detections occur, but the low number of movements in this study made it necessary to establish the following seasonal time periods: Spring 2010 (May only), Summer 2010 (Jun – Aug), Fall 2010 (Sep – Nov), Winter 2011 (Dec – Feb), Spring 2011 (Mar – May), and Summer 2011 (June and July only). Although it is traditional to estimate transition probabilities between time periods (Williams et al. 2002), transition probabilities were estimated within the time periods because of their length.

A typical assumption in mark-recapture analyses is that marking and releasing an animal is an instantaneous procedure that occurs at the beginning of a time period (Williams et al. 2002), which was not always the case in this study. For example, in summer 2010, individuals were marked in the third month in the time period (August), but in fall 2010, individuals were marked in the second month (October), so marked animals were at large for varying times in the first time period after they were marked. Because the difference in length of the first time period can affect survival probabilities, detection probabilities, and transition probabilities (Williams et al. 2002), a “timing covariate” was added to the model. Individuals marked and released in the first month of a time period received the same covariate, individuals marked in the middle month of a time period received the same covariate, and individuals marked in the last month of a time period all received the same covariate.

Model Construction

The models constructed in Program MARK contained three states that represented physical locations in the stream. From downstream to upstream, Location A was downstream of the McGinn fishway, location B was between the McGinn fishway and the control site (near the middle of the study reach), and location C was between the control site and the South Boulder fishway (Figure 5-1 and 5-4). The model also contained six states that represented known upstream movements across the structures and the control site. Movement state D represented an upstream movement across the McGinn fishway, movement state E represented an upstream movement across the control site, and movement state F represented a movement across the South Boulder fishway. Movement G represented an upstream movement across the McGinn fishway and the control site in a single time period, movement H represented upstream movement across the control site and the South Boulder fishway in a single time period, and movement I represented upstream movement across the McGinn fishway, the control site, and the South Boulder fishway in a single time period (Figure 5-4).

The multi-state model was structured so that a fish in a given physical location (states A, B, and C) would have to move through a movement state (states D – I) before reaching another physical location. Movement states (D – I) represent a movement between two physical states (A, B, and C) detected by the paired antennae. These movement states were necessary because a fish was detected while it moved from one physical state to another, not when it was recaptured in a new location during subsequent sampling events. The model was structured so that an individual that moved over one or multiple fishways and/or control sites ‘entered’ the appropriate movement state and then transitioned into the appropriate physical state prior to the next time period. For example, a marked fish released in location A (below the McGinn fishway) and detected by both antennae at the fishway would transition into state D during the

first occasion of the time period and would transition into state B during the “dummy” occasion of the same time period. The capture history representing this movement would be AD B0 or AD 00, depending on whether or not the fish was detected in location B after it moved there (See Appendix 5A for details). Combinations of locations and transition probabilities that were not physically possible were fixed at zero. Downstream movements were not addressed in this model because upstream movement rates were of primary concern. Downstream movements were compared qualitatively between structures but were not included in the multi-state model analysis.

Model Validation

Because this application of MSMR models is unusual (but see Horton et al. 2011, Fetherman et al., in press), it was necessary to verify that model parameters were identifiable and nonbiased (see citations in Bailey et al. 2010). Toward that end, a “perfect” set of capture histories was generated using the estimated values of ϕ , p , and ψ from South Boulder Creek in the software GENMSS (J. Hines, U.S. Geological Survey, personal communication). These generated capture histories were then analyzed in program MARK to test model structure. The estimates of the survival, capture, and transition probabilities estimated by MARK were identical to the parameters used to generate the capture histories in GENMSS, indicating that the models in program MARK were constructed properly.

Model Development and Testing of Hypotheses

A set of 106 models (Appendix A) was constructed to measure the influence of structure type (i.e., the control site and the two fishways), distance, and timing covariates on transition probabilities in South Boulder Creek. The study hypotheses were tested by building models that varied with respect to the variables included and their relationships. Survival probability was

always fixed at 1.0 in the first occasion of each period, but in the “dummy” occasion, it was modeled as constant over time (\cdot), varying in spring, summer, fall, and winter (“season”), or differing between spring/summer and fall/winter (“winter”). The effects of the timing covariates (“cov”) on survival, capture probability, and transition probability were also tested in the model selection process. Capture probability in the first occasion of each time period (p_{D-I}) was set at 1.0, because it was assumed that a fish passing over the paired antennae would always be detected. Capture probability in the “dummy” occasion (p_{A-C}), which represented the probability that a fish was detected at a single antenna (i.e., in a physical location but not moving between physical locations) was modeled with the same structures ([\cdot], [season], [winter], and [cov]) that were used for survival. Likewise, transition probabilities in the first occasion of the time period were also modeled in the same manner to test for seasonal changes in the probability of movement.

Four additional transition probability configurations were constructed to test the importance of structure type and distance in controlling fish movement: (1) a “null” model where all transition probabilities were equal, to represent the possibility that fish were equally likely to move over one or more fishways or the control sites (i.e., no distance or structure effect, Table 5-1), (2) a “distance only model” where probability of movement across one, two, or three antenna pairs varied but structure type did not influence transition probabilities, (3) a “structure only” model where transition probabilities varied over the three structures (the control reach, the McGinn fishway, and the South Boulder fishway) and (4) a “distance and structure” model where movement was influenced by both factors, allowing all six transition probabilities to be estimated uniquely.

The multi-state model with the largest number of parameters (i.e., ϕ [season], p_{D-I} [fixed], p_{A-C} [season], ψ [season*structure*distance]) was used to estimate overdispersion using the median \hat{c} approach in Program MARK (Cooch and White 2012). The parameter \hat{c} measures the model fit to the data, with a value of 1.0 being ideal. The resulting \hat{c} value was greater than 1.0 (see Results), so QAICc was used to rank candidate models (after Cooch and White 2012). Survival, detection probability in the physical locations, and transition probabilities were estimated with model averaging to account for model uncertainty (Burnham and Anderson 2002).

RESULTS

Tagging Results

Of the 1,051 fish that were tagged, 355 (34%) were detected in a subsequent time period (Table 5-2). Thirty-nine percent of the fish detected ($n = 138$) moved upstream across at least one pair of antennae (Table 5-3), and the remaining individuals were detected by a single antenna. Only two fish made separate upstream movements in different time periods. The remaining fish moved upstream during a single time period, and no further movement was detected in subsequent time periods

All three larger species (brown trout, rainbow trout, longnose sucker) were able to move across both fishways, and one longnose dace moved upstream across the steeper South Boulder fishway. No longnose dace were detected moving upstream past the McGinn fishway.

Movements were rare from December through February at both fishways and at the control site (Figure 5-5). Movement at the control site occurred throughout most of the year, with more movement detected in the spring and summer; the timing of peak movement varied by species. The seasonal pattern of movement across the McGinn fishway was similar to the

control site in that detected movements were higher in the spring than in the fall, but detected movements from mid-April to mid-May were lower at McGinn than at the control site. The seasonal pattern of movement across the South Boulder fishway was similar to that of the control site, but fewer movements were detected.

The PIT tag antenna arrays detected 77 fish moving downstream across at least one pair of antennae, so movement was biased in an upstream direction in the study reach. The total number of downstream movements was highest at the McGinn fishway, intermediate at the control reach, and lowest over the South Boulder fishway (Figure 5-6).

MARK Analysis Results

Tests of the multi-state model with the largest number of parameters produced evidence of overdispersion in the multi-state mark-recapture data ($\hat{c} = 3.11$). However, the model results are reported with confidence, because the AICc model rankings were similar to the QAICc model rankings, indicating an adequate fit to the data (Cooch and White 2012). The top ranked models were identical using AICc or QAICc, so only QAICc rankings are presented here. A total of 13 models had a QAICc weight greater than 0.01, and the two top models had a combined weight of 0.52 (Table 5-4).

Seasonal variation in parameters and importance of timing covariates

Survival probability estimates ranged from 37.1% (Spring 2011 to Summer 2011) to 99.8% (Winter 2011 to Spring 2011) and differed between all four seasons (the [season] model structure, Table 5-5). The [season] model structure was present in all 13 of the models with QAICc weight of 0.01 or more, indicating that constant survival over time [.] or survival that differed between spring/summer and winter/fall [winter] were not likely. Timing covariates were associated with survival in four of the 13 top models, indicating that survival between the

first and second time periods depended on whether the fish was marked in the first, second, or third month of the first time period. However, the models where survival depended on the timing covariates had low QAIC_c weights, suggesting that the timing of marking was of limited importance. Capture probability in the physical states varied from 42.5% (Fall 2010 to Winter 2010) to 52.4% (Summer 2010 to Fall 2010, Table 5-5). Capture probabilities were constant over time in the top model [·], but the [winter] and [seasonal] model structures were present in the remaining top models. The varying model structures and the small changes in capture probability estimates indicate that capture probability changes slightly between seasons. Timing covariates were present in two of the top models, but these models had low QAIC_c weight (Table 5-4), indicating that capture probabilities in the physical states (i.e. between time periods) were largely unaffected by the timing of marking.

The probability of movement (measured by transition probabilities) changed over time in all of the weighted models. The [winter] model structure (i.e. different movement in spring/summer than in fall/winter) appeared in the five top models and in 10 of the 13 weighted models (Table 5-4). In the remaining three models, movement differed in all four seasons. The model structures indicate that movement rates were seasonal but that substantial differences did not occur from March through August or from September through February. As with capture probability, the timing covariates were only associated with transition probabilities in one model with a low QAIC_c weight, indicating that movement was unaffected by the timing of marking within a time period.

Model-averaged estimates indicated that the probability of all movements except those across the McGinn fishway only (ψ^{AD}) and movements across the McGinn fishway, the control site, and the South Boulder fishway (ψ^{AI}) were lower in fall and winter than in other seasons.

Movement across the McGinn fishway only was similar between seasons, and movement across the McGinn fishway, the control site, and the South Boulder fishway was low in spring 2010, winter 2011, and summer 2011 and zero in the remaining time periods.

Distance, fishway type, and transition probabilities

Model selection results supported the hypothesis that both distance and structure influenced movement in the study reach (Table 5-4). The “distance and structure” model configuration, where all six transition probabilities were unique, was present in 10 of the 13 weighted models. The “distance only” model configuration was present in three models that had a combined QAIC weight of 0.03, indicating limited support in the data for the “distance only” hypothesis. The “structure only” and “null” hypotheses were not supported by the data.

Comparisons of model-averaged estimates of movement across a single structure indicated that movement across the South Boulder fishway was lower than movements across the control or McGinn sites (Figure 5-7, Figure 5-8). Estimates of movement across the South Boulder fishway (11% slope) were lowest in fall 2010 and roughly equal (but still low) in the remaining time periods, indicating that upstream passage was not facilitated by high flows in spring. Movement across the McGinn fishway was similar to movement across the control site within most time periods (i.e., the confidence intervals for estimates between the two sites overlapped). Movement across the McGinn fishway was higher in fall 2010 than in any other time period, but the confidence intervals for movement estimates at each time period all overlapped (Figure 5-7), indicating that passage in spring was not inhibited by high water velocities in the confined low-flow notch. Estimates of movement also showed that long distance movements that required a fish to pass over multiple structures are rare (Figure 5-8).

DISCUSSION

This study demonstrated that rates of fish passage on a fishway with 4.5% slope were similar to passage rates over a control site and that passage rates over a steeper fishway (11% slope) were lower. The study also showed that fishways with steep slopes (up to 11%) still allow some passage of the four species studied, but at reduced rates. The lowest transition probabilities were associated with movements across multiple pairs of antennae and movements across the steep South Boulder fishway. Based on these results, the high slope of the South Boulder fishway was more of an impediment to fish passage than the confined low-flow notch in the McGinn fishway.

The estimated movement rates in South Boulder Creek varied slightly with season. Individual fish movements in South Boulder Creek did exhibit distinct seasonal patterns (Figure 5-6), so the lower seasonal variation in transition probabilities is probably a function of the long time periods used in the analysis and the relatively small number of fish that crossed the paired antenna. Other studies of fish movement have shown that large numbers of individuals move within a short time for a variety of reasons, including seeking winter habitat (Grabowski and Isely 2006), spawning (Gowan and Fausch 1996), or ranging during floods (Albanese et al. 2004). Nevertheless, the seasonal variation in movement that would be expected at the McGinn fishway if the confined low-flow notch impeded fish passage at high flows (i.e., lower movement rates in spring and summer) was not detected in the transition probability estimates or in the data on individual fish movements.

This study showed that steeper fishway slopes can inhibit fish passage. Although field evaluations of rock ramps are uncommon (Franklin et al. 2012), a review of the existing literature lends support to these results. Santos et al. (2005) documented successful upstream

movement of eight species³ across a 6-m wide × 26-m long ramp with a 3.8% slope in Portugal. High passage efficiency was inferred because more individuals were detected moving through the fishway than were captured during electrofishing efforts immediately downstream of the fishway. Two comparative studies in North America measured passage success across rock ramps of varying slopes. The first found that alewife *Alosa pseudoharengus* (TL > 200 mm) passage across a 32-m long ramp with a 4.2% slope was 94%, but passage across two consecutive rock ramps with an overall slope of 7.1% was lower (73% and 64%, Franklin et al. 2012). The second study compared movement rates of four species⁴ across three rock ramps that were modified after the beginning of the study. Modifications involved reductions in slope from 7 – 8% to approximately 5% and grouting of downstream riprap or removal of a vertical drop. This increased ramp lengths from 13 – 14 m to 20 – 36 m. After modification, movement rates over one or more of these structures increased from less than 2% to 14% (Litvan et al. 2008). The results of these studies are similar to the results from South Boulder Creek in that movement rates were lower for ramps with a slope > 5%. However, Franklin et al. (2012) warned that specific local hydraulics are also important in determining passage success, because alewife passage through some engineered fishways with extremely high slopes (e.g., 26%) was nearly 100%.

Although slope has been discussed in the limited number of field studies involving fish passage across rock ramps, other aspects of these structures have received less attention. For example, substrate size on the ramp bottom is important in determining passage success (e.g., Bestgen et al. 2010), but this has not been examined in comparative field studies. A study of an

³ sea lamprey *Petromyzon marinus*, brown trout *Salmo trutta*, striped mullet *Mugil cephalus*, Iberian barbel *Barbus bocagei*, Iberian red roach *Chondrostoma arcasii*, Iberian nase *Chondrostoma polylepis*, Iberian chub *Squalius carolitertii*, and European eel *Anguilla anguilla*.

⁴ Yellow bullhead *Ameiurus natalis*, black bullhead *Ameiurus melas*, channel catfish *Ictalurus punctatus*, and creek chub *Semotilus atromaculatus*

8-m wide \times 220-m long rock ramp showed that only 15% of Rio Grande silvery minnow (*Hybognathus amarus*) that entered the fishway successfully moved upstream (Archdeacon and Remshardt 2012). Slope was not reported, but water velocities measured within the ramp were generally less than 50 cm/s, which are well within the swimming ability of Rio Grande silvery minnow (Bestgen et al. 2010). Substrate size in the rock ramp was not reported but may have influenced passage success. Rio Grande silvery minnow movement success in a laboratory test varied with substrate size, presumably due to boundary layer thickness and near-bed turbulence (Bestgen et al. 2010). The size of the bed substrate and the size and placement of roughness elements (i.e., cobbles or boulders that fish can use as velocity refuges) on rock ramps designed for small fishes deserves further study, both in the laboratory and the field.

Cross-sectional ramp dimensions may also be important in determining the passage success of small-bodied species. The results of this study do not support the hypothesis of reduced passage through a confined low-flow notch at high flows. However, species other than those included here might have difficulties with the hydraulic conditions produced in a rock ramp where water may not spread across the width of the stream as flows increase. The effect of slope on fish passage success masked any potential effects of the confined low-flow notch in the South Boulder Creek study. However, laboratory or field studies that compared fish passage success across structures with the same slope but different cross-sectional shape characteristics such as side-slope angle and width-to-depth ratio would further efforts to optimize rock ramp design for small-bodied species.

Calculating transition probabilities requires the estimation of two parameters: survival and detection probability (Cooch and White 2012). The uncertainty associated with the estimates of survival and detection probability in the physical states contributes to the

uncertainty in the transition probability estimates. Despite the uncertainty surrounding the accuracy of the transition probability estimates, the significantly lower movement rates across the South Boulder fishway and over long distances support the hypothesis that steep slopes, long distances, or a combination of the two reduce movement rates in the study segment of South Boulder Creek. The use of a single antenna on each side of the two fishways and the control site and the assumption that the detection probability at the antenna pairs was 100% likely led to conservative estimates of movement. However, estimates at all three sites were affected by the same antenna configurations and detection probability assumptions. Therefore, these limitations did not affect the ability to test hypotheses by comparing movement rates within the study area.

Urban streams may have space constraints that force designers to use high slopes (D. Laiho, Boulder County Parks and Open Space, personal communication). Furthermore, reduced slopes are associated with higher construction costs (Litvan et al. 2008). As a result, even if fishways are installed in urban systems, they may still restrict upstream or downstream movement. The question of “How much fish passage is enough?” is outside the scope of this study, but it is a pressing question. The biological implications of restricted fish passage are less clear than the implications of completely blocked migration, and few studies have estimated the amount of intra-population movement needed to maintain viability in fragmented environments (but see Alò and Turner 2005, Labonne and Gaudin 2006, Schick and Lindley 2007). As fishway installation continues in urban streams, structures that restrict movement may become as common or more common than complete barriers. Striking a balance between space restrictions, financial limitations, and the physiological abilities of the resident fish assemblage remains a major challenge in fishway design.

Table 5-1.—Varying relationships between transition probabilities designed to test competing hypotheses in Program MARK.

Hypothesis	Transition Probability Structure
“Null”	$\psi^{AD} = \psi^{AG} = \psi^{AI} = \psi^{BE} = \psi^{BH} = \psi^{CF}$
Distance Only	$\psi^{AD} = \psi^{BE} = \psi^{CF}; \psi^{AG} = \psi^{BH}; \psi^{AI}$
Structure Only	$\psi^{AD} = \psi^{AG}; \psi^{BE}; \psi^{CF} = \psi^{BH}; \psi^{AI}$
Structure and Distance	$\psi^{AD}; \psi^{AG}; \psi^{AI}; \psi^{BE}; \psi^{BH}; \psi^{CF}$

Table 5-2.— Summary of number of fish tagged and the proportion that were detected again in South Boulder Creek from May 2010 through July 2011. Longnose sucker summary includes one white sucker × longnose sucker (*Catostomus commersonii* × *C. catostomus*) hybrid.

	Longnose dace	Longnose sucker	Brown trout	Rainbow trout
Length range (mm)	104 - 140	112 – 296	118 - >500	120 – 525
Total number tagged	7	149	368	527
Total number recaptured	4 (57%)	86 (57%)	127 (35%)	138 (26%)

Table 5-3.—Summary of detected upstream movements in South Boulder Creek from May 2010 through July 2011. Longnose sucker summary includes one white sucker × longnose sucker (*Catostomus commersoni* × *C. catostomus*) hybrid.

Movement	Longnose	Longnose	Brown	Rainbow
	dace	sucker	trout	trout
McGinn only	0	7	25	21
Control only	1	20	14	16
South Boulder only	0	3	4	5
McGinn + control	0	0	2	3
Control + South Boulder	1	1	3	7
McGinn, control, + South Boulder	0	0	0	5

Table 5-4.— Top models in MARK, evaluated with QAICc selection. Seasonal model structures vary as follows: “Season” = parameter varies with the four seasons, “winter” = parameter varies between spring/summer and fall/winter, “cov” = parameter varies with timing covariates, “.” = parameter constant over time. Additional factors affecting Ψ are: D = distance, S = structure/fishway type. Models with QAICc weight > 0.01 are not shown.

Model Rank	Model Description	log (L)	K	QAICc	Δ QAICc	w_i
1	$\phi(\text{season})p(.)\Psi(\text{winter}*D*S)$	-1601.32	15	1060.08	0	0.28
2	$\phi(\text{season})p(\text{season})\Psi(\text{winter}*D*S)$	-1592.30	18	1060.42	0.33	0.24
3	$\phi(\text{season}*cov)p(\text{season})\Psi(\text{winter}*D*S)$	-1587.72	20	1061.57	1.48	0.13
4	$\phi(\text{season})p(\text{winter})\Psi(\text{winter}*D*S)$	-1601.22	16	1062.06	1.98	0.10
5	$\phi(\text{season}*cov)p(\text{winter})\Psi(\text{winter}*D*S)$	-1596.62	18	1063.19	3.11	0.06
6	$\phi(\text{season})p(\text{winter})\Psi(\text{season}*D*S)$	-1585.21	22	1064.06	3.98	0.04
7	$\phi(\text{season})p(\text{season})\Psi(\text{season}*D*S)$	-1576.80	25	1064.83	4.75	0.03
8	$\phi(\text{season}*cov)p(\text{season}*cov)\Psi(\text{season}*D*S)$	-1586.80	22	1065.09	5.00	0.02
9	$\phi(\text{season})p(\text{season})\Psi(\text{season}*D)$	-1607.76	16	1066.27	6.19	0.01
10	$\phi(\text{season})p(.)\Psi(\text{winter}*D*S*cov)$	-1591.92	21	1066.32	6.24	0.01
11	$\phi(\text{season}*cov)p(\text{winter}*cov)\Psi(\text{winter}*D*S)$	-1595.21	20	1066.38	6.30	0.01
12	$\phi(\text{season})p(.)\Psi(\text{winter}*D)$	-1627.10	10	1066.50	6.42	0.01
13	$\phi(\text{season})p(\text{season})\Psi(\text{winter}*D)$	-1617.76	13	1066.58	6.50	0.01

Table 5-5.—Seasonal variation in survival probability and capture probability for tagged fishes in South Boulder Creek. Estimates were obtained with model averaging in Program MARK.

Season	Survival Probability (%)	Capture Probability (%)
Spring 2010 – Summer 2010	37.6 (± 7.0)	43.2 (± 8.0)
Summer 2010 – Fall 2010	85.2 (± 10.3)	52.4 (± 9.5)
Fall 2010 – Winter 2010	63.7 (± 8.4)	42.5 (± 6.8)
Winter 2010 – Spring 2011	99.8 (± 1.0)	49.1 (± 7.0)
Spring 2011 – Summer 2011	37.1 (± 7.0)	43.1 (± 8.0)



Figure 5-1.—The South Boulder Creek study segment. The two fishways are 0.9 km apart. McGinn Diversion (downstream) has a lower slope (4.5%) and a confined low-flow notch; South Boulder Ditch Diversion (upstream) has a higher slope (11.2%) and an unconfined low-flow notch. Locations A, B, and C refer to stream sections below the McGinn fishway, between the McGinn fishway and the control site, and between the control site and the South Boulder fishway, respectively. The circles indicate fish release locations after tagging.



Figure 5-2.—The McGinn fishway (top) and South Boulder fishway (bottom). Although water overtops the entire McGinn structure at high flows, the low-flow notch shown in the photo (top right) is characterized by high velocities during high flows.

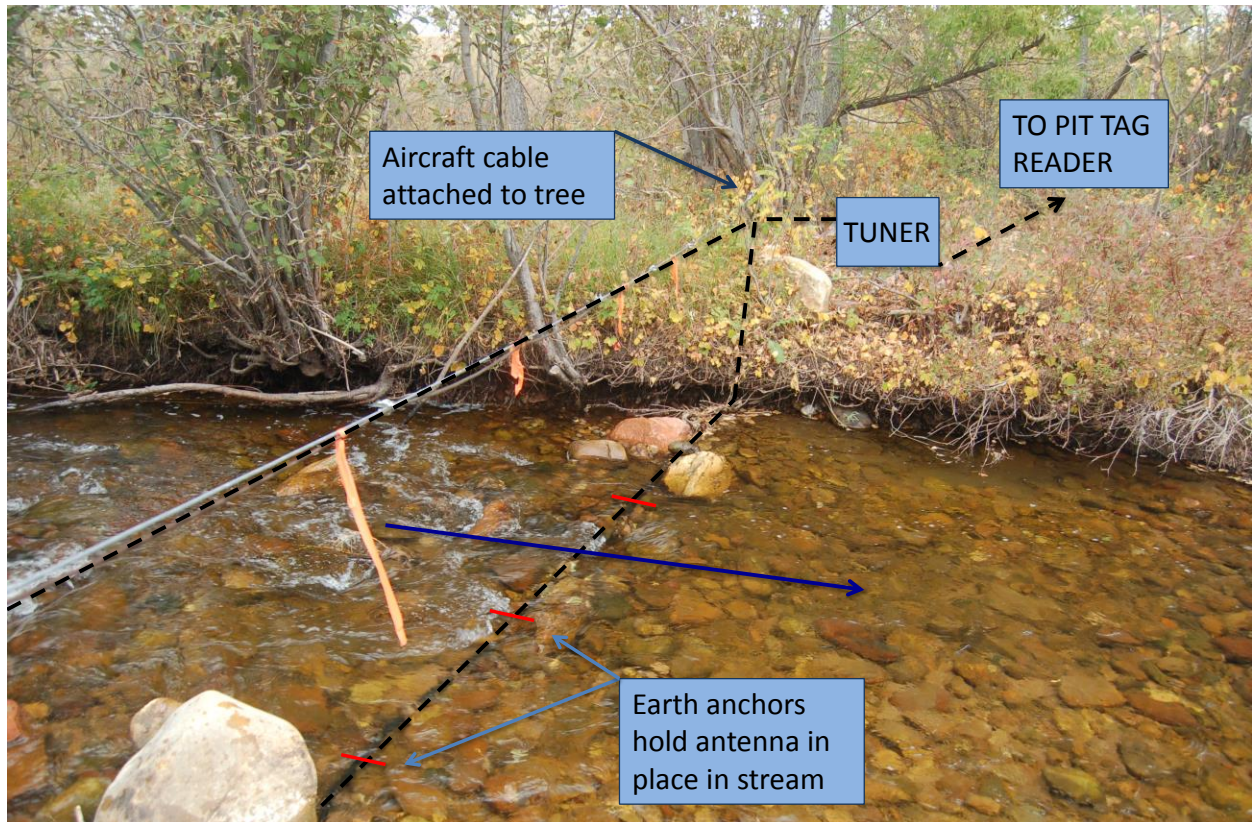


Figure 5-3.—Diagram of a pass-through antenna for reading PIT tags. Dashed line shows antenna suspended from aircraft cable and anchored to stream bed. When a tagged fish crosses the plane of the antenna (indicated by solid blue arrow), the antenna transmits a signal to the reader, and the reader stores the unique number of the tag and the time at which the tag was read.

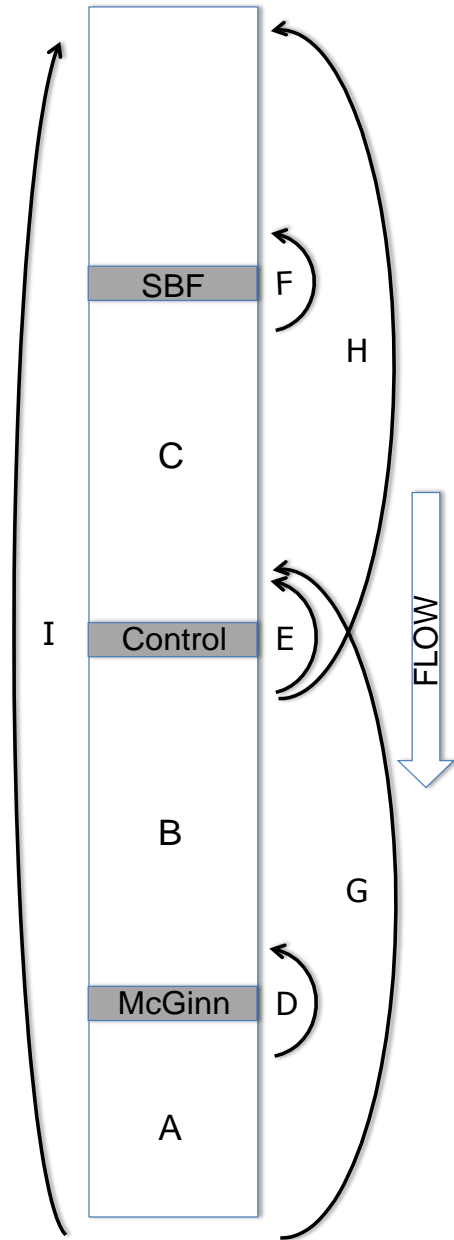


Figure 5-4.—Diagram of model states: physical states (A – C) and the movement states (D – I) used in a multi-state model to quantify the importance of distance and rock ramp structures on fish movement probabilities in South Boulder Creek. SBF = South Boulder fishway.

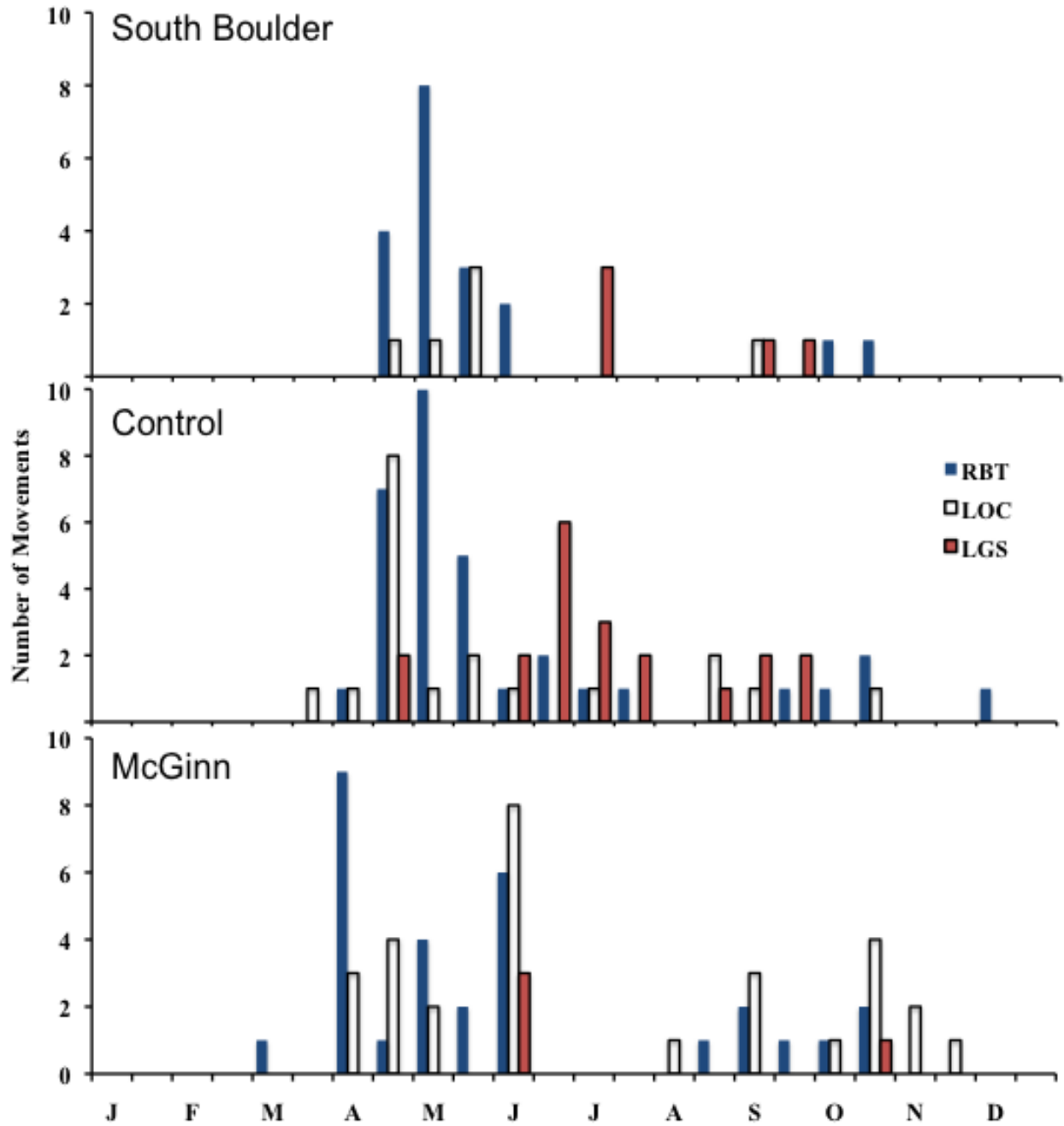


Figure 5-5.—Temporal patterns of fish movement among months. Figure represents the total number of individuals detected moving upstream across the McGinn fishway (bottom), the control site (middle), and the South Boulder fishway (top). Detections for May, June, and July are combined values from 2010 and 2011. RBT = rainbow trout, LOC = brown trout, and LGS = longnose sucker.

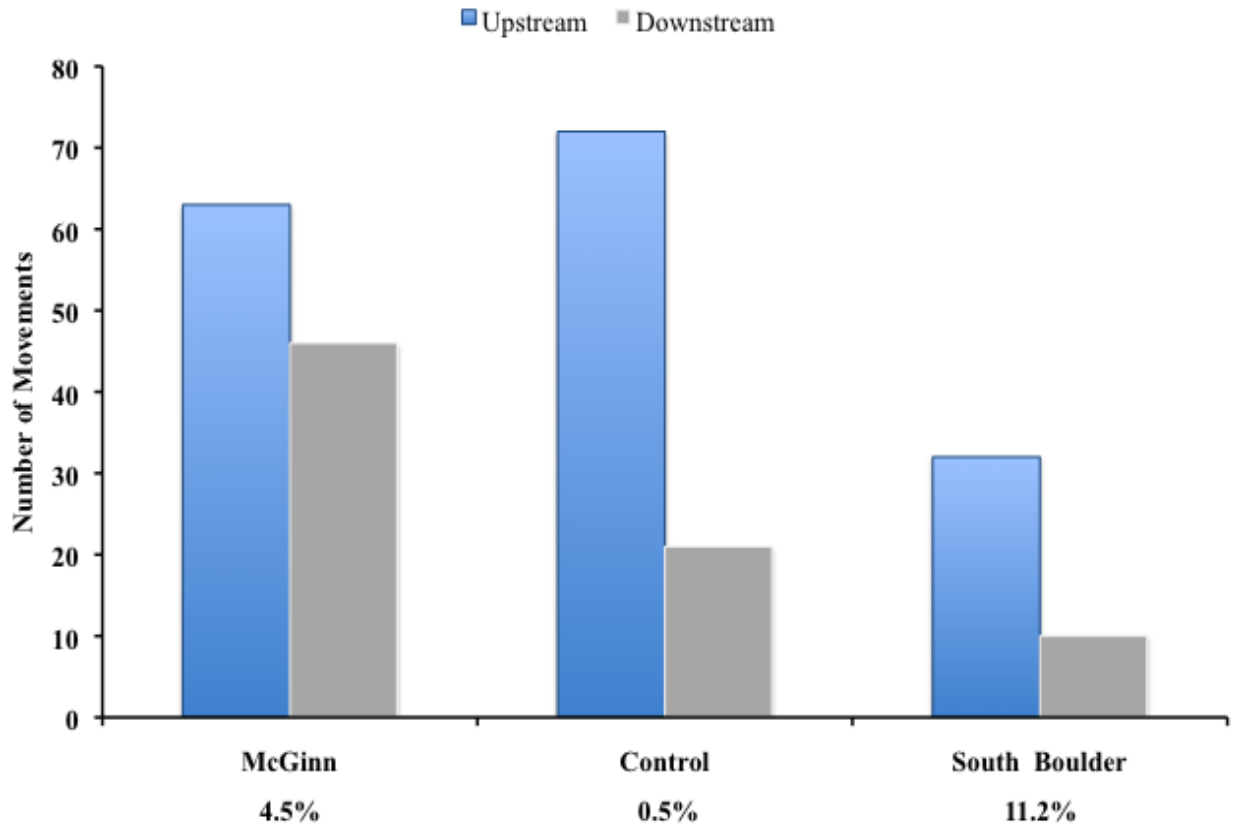


Figure 5-6.—Total number of detected upstream and downstream movements for all tagged species in South Boulder Creek. Fishway slopes and streambed slope (control site only) are presented below the site names.

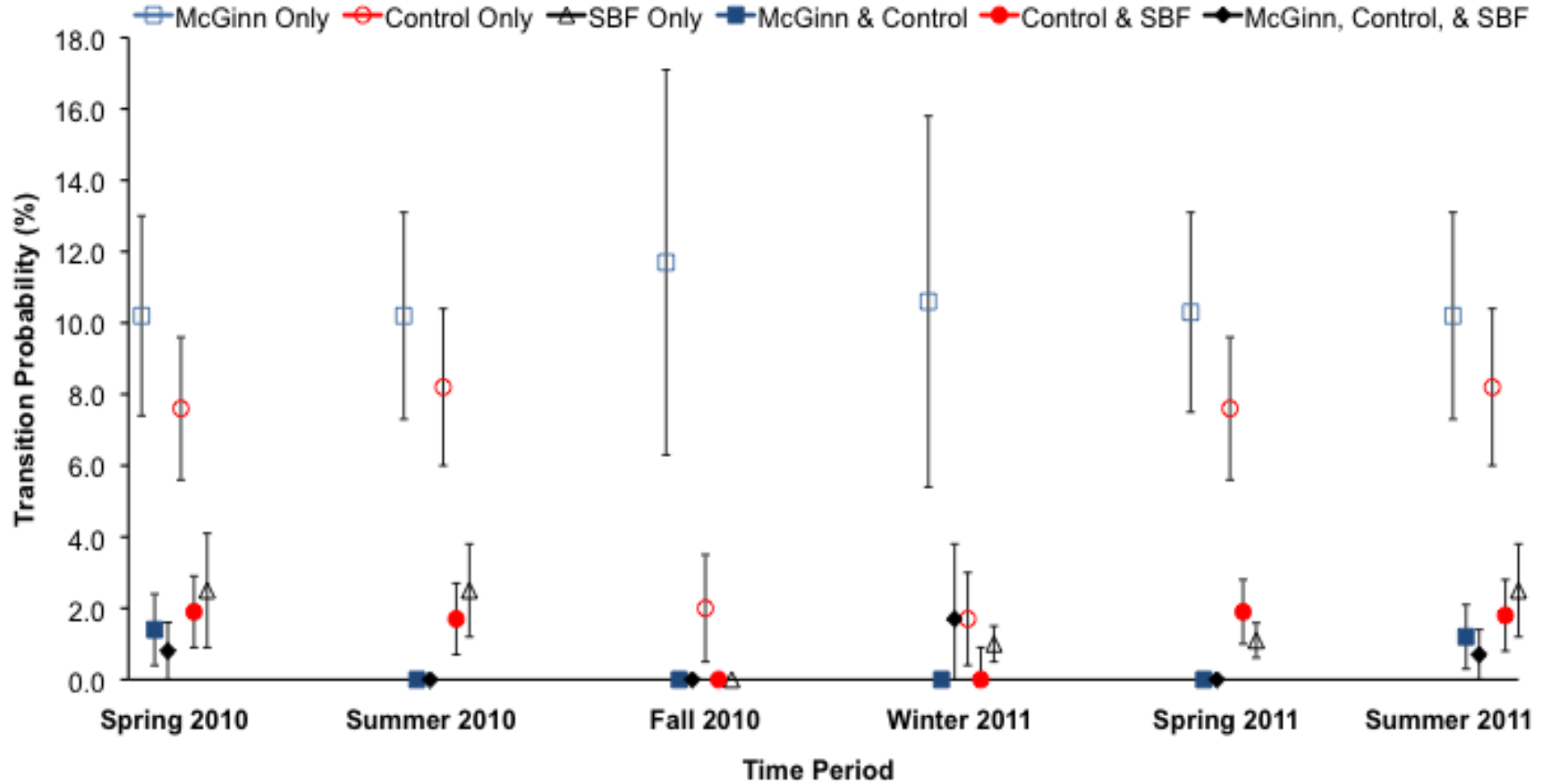


Figure 5-7.—Model-averaged estimates of upstream transition probabilities (in percent, with 95% C.I.) for each seasonal time period, May 2010 – July 2011. Zero values with no confidence intervals represent very low estimates (< 0.1%). Transition probabilities were estimated using all species combined. SBF = South Boulder fishway. Transition probabilities within each seasonal time period are staggered on the graph for clarity.

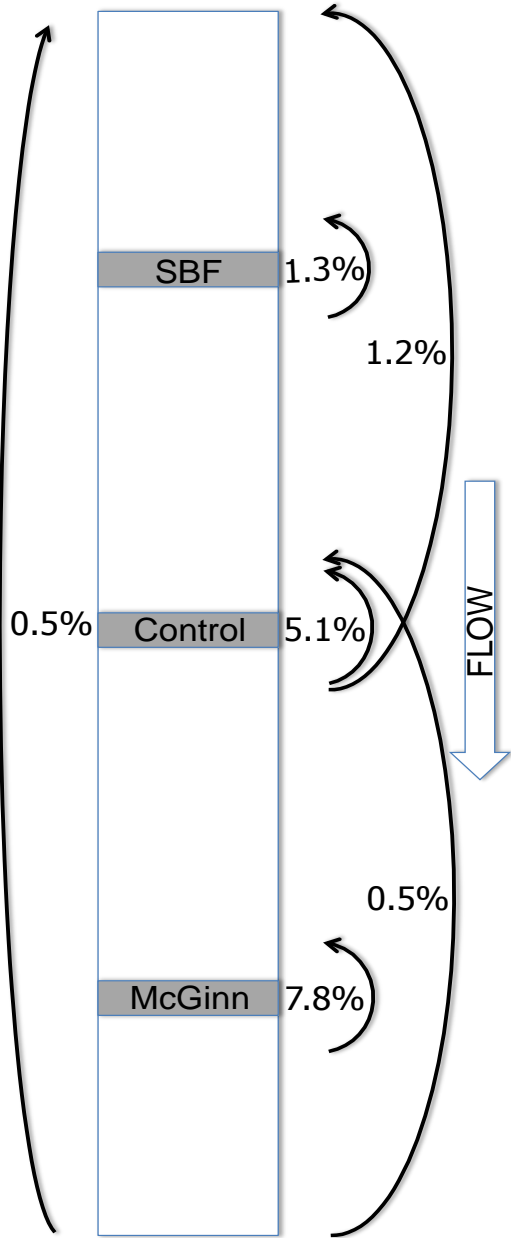


Figure 5-8.—Movement estimates for South Boulder Creek, averaged over the study period. SBF = South Boulder fishway.

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APPENDIX 2A

SUMMARY OF STUDIES OMITTED FROM REVIEW AND SYNTHESIS

The summaries that follow were not included in the synthesis because they were outside the scope of the paper. However, they are included in this appendix for three reasons. First, one of the purposes of this review was to compile information on swimming performance of small North American fishes so that it could be more easily accessed by managers and researchers. Second, these summaries will prevent redundancy in future research. Managers interested in swimming performance data can examine this appendix to determine whether their target species have been the subjects of prior studies. Third, it is hoped that the summaries below will allow researchers to generate testable hypotheses for future studies and syntheses on small fish swimming performance.

Ontogeny and Swimming Performance

Within species, an increase in total length (TL) is usually correlated with increased swimming endurance in most cases (but see Colborne et al. 2011). Unlike absolute swimming velocity (i.e. measured in cm/s), relative swimming ability (i.e., measured in body lengths per second) tends to decrease as fish size increases. This is may be in part due to investment in reproduction. For example, a small number of studies demonstrated that gravid female fish exhibit reduced swimming performance. Mean U_{CRIT} in female western mosquitofish *Gambusia affinis* immediately before parturition was 20% lower than mean U_{CRIT} of the same individuals before onset of pregnancy (Plaut 2002). The author concluded that the reduction in swimming performance was a function of energetic investment in reproduction, not a change in shape. Garenc et al. (1999) studied ontogenetic changes in swimming performance and concluded that the faster relative abilities of juvenile fish occur because the investment in reproduction by adults

detracts from enzymatic activity and the amount of muscle protein present in the body. Studies of small-bodied tropical (Trinidadian guppy *Poecilia reticulata*) and marine (Atlantic silverside *Menidia menidia*) fishes suggest that a limited energy budget requires tradeoffs between swimming performance and other critical functions such as reproductive investment and growth (Ghalambor et al. 2003, Ghalambor et al. 2004). Although their bioenergetics have not been studied in detail, small North American fishes are probably subject to similar energetic constraints.

Toxicants and Swimming Performance

Swimming performance, often using the critical swimming velocity approach, has been employed as an endpoint in a number of toxicology studies, many of which have focused on salmonids (e.g., Little and Finger 1990; Tudorache et al. 2010; Kennedy and Picard 2012) or zebrafish *Danio rerio* (e.g., Sárria et al. 2011; Marit and Weber 2012; Pereira et al. 2012). A limited number of studies have focused on small North American fishes as well.

Toxicology studies involving small-bodied fishes have focused on a wide variety of compounds, varying measures of swimming performance, and different life stages. However, the studied toxicants generally appear to reduce swimming performance. For example, a 2009 study examined the effects of endocrine disrupting compounds (EDCs) on the fast-start performance of larval fathead minnows *Pimephales promelas*. Although the effects varied depending on the life stage (embryo or larvae) at the time of exposure and the type of EDC used in the test, the fast-start performance of larval fathead minnows was reduced, causing an increased reaction time to the stimulus (McGee et al. 2009). Similarly, benthic lake chubsuckers *Erimyzon sucetta* given a 100-day exposure to sediments contaminated with coal ash exhibited reduced swimming performance compared to control fish. Exposed fish subjected to a startle

response sprinted 30% to 100% slower (i.e., they refused to swim) than control fish, and the mean U_{CRIT} for exposed fish was only half that of control fish (47.9 ± 3.62 versus 24.0 ± 4.3 cm/s, Hopkins et al. 2003). Kolok et al. (1998) exposed fathead minnows to sediment known to be contaminated with a mixture of heavy metals and hydrocarbons and reported that the U_{CRIT} decreased by 24% when fish were re-tested following 10 day of exposure. Fathead minnows held in aquaria containing uncontaminated sediment or no sediment (i.e., controls) experienced no reduction in mean U_{CRIT} over the same 10-d period. These studies highlight the fact that fish in polluted water are likely to exhibit poorer swimming performance than those in less impacted systems, yet this may not extend to all species.

In contrast to the work cited above, some studies suggest that some fishes can acclimate to, or are unaffected by, some polluted environments. For example, spottail shiners *Notropis hudsonius* collected from a site exposed to uranium mill effluent had similar mean U_{CRIT} values to fishes collected from a reference site (4.5 ± 0.28 L/s versus 4.2 ± 0.35 L/s, respectively; Goertzen et al. 2012). Stepped velocity tests were used to examine swimming performance of bluegill exposed to varying concentrations of the surfactant alkyl benzene sulfonate for 30 days. Mean and median swimming endurances of the exposed groups did not vary significantly from the control group (Lemke and Mount 1963). Similarly, bluegill exposed to fluorine did not exhibit reduced swimming performance until exposed to lethal concentrations (reviewed in Little and Finger, 1990). Thus it is fair to conclude that the ability of fish to maintain similar swimming performance after exposure to pollutants in natural systems will vary by species and the characteristics of the pollutant mixtures.

Experiments with salmonids have shown that mechanisms by which heavy metals reduce swimming performance depend upon the metal being studied. For example, at chronically toxic

concentrations, copper reduces swimming performance through a reduction in metabolic scope because of a diversion of available energy to metabolizing excess amounts of the metal (reviewed in Grosell 2012). On the other hand, aluminum causes changes in gill morphology that reduce oxygen transfer efficiency in addition to burdening a fish with the energetic cost of repairing damaged gills (Wilson 2011). A limited number of studies on small-bodied fishes have elucidated additional mechanisms by which swimming performance can be reduced. A study of larval delta smelt showed that responses to copper exposure may go beyond higher resting metabolic costs. This study included volitional (i.e. voluntary) swimming tests of individuals exposed to one of several concentrations of copper (0 – 213 µg/L) for a period of 96 hours. Though the relationship was not statistically significant, mean swimming speeds were reduced by copper concentrations, and the use of molecular biomarkers indicated that copper exposure disrupted neuromuscular, digestive, and immune functions (Connon et al. 2010). Similarly, the pesticide Bifenthrin affects transcription of genes that control neuromuscular function and energy metabolism in larval fathead minnows (Beggel et al. 2011a), and exposure to complex uranium mill effluent reduces enzymatic activity that controls swimming performance in adult fathead minnows (Goertzen et al. 2011).

Although toxicity in natural systems is mediated by environmental conditions and the presence of other pollutants (Newman and Clements 2008; Beggel et al. 2011b), it is not surprising that toxicants reduce swimming performance. As a result, fishways constructed in polluted streams may be less effective if water velocities are derived from swimming performances data on fish tested in clean water. Accommodating for reduced swimming performance in polluted waters could be accomplished by conducting field tests of swimming performance using mobile flumes and fish captured at potential fishway sites.

Parasite Infections and Swimming Performance

Most studies of parasitism or disease and swimming performance have focused disproportionately on salmonids (e.g., Barber et al. 2000; Wagner et al. 2005; Powell et al. 2008; Nendick et al. 2011). Generally, the effects of disease and/or parasitism appear to be nonlinear (i.e., threshold effects are common), and effects on swimming performance vary by parasite in salmonids. However, the effects of parasites or disease on swimming performance of small-bodied fishes are relatively unexplored. A single study found that fathead minnow *Pimephales promelas* exhibited reduced activity in response to a severe infection of a brain-encysting parasite (Shirakashi and Goater 2002). Given the larger relative size of some parasites to their hosts (e.g., the parasitic copepod *Lernaea cyprinacea*), it is likely that changes in hydrodynamic drag will result in reduced swimming performance.

Swimming flumes and quasi-natural apparatus: which to use?

Swimming performance has been traditionally measured with swimming flumes, but newer studies involving apparatus with more natural flow conditions (e.g., raceways, smooth ramps, and rock ramps) suggest that swimming flumes underestimate true swimming performance. This is likely because fish reduce swimming effort when they cannot maintain forward progress against a current within the confines of a swimming chamber (Peake and Farrell 2006) and because the simple hydraulic conditions that are created by design in a swimming flume do not allow fish to exploit the variable velocity fields that would be present under natural conditions (Liao et al. 2003; Haro et al. 2004). However, swimming flumes do provide a means for direct and conservative measurement of swimming performance. Conservative measures of performance are useful in fishway design because they provide a “safety factor” to ascending fishes. For example, if the optimum swimming performance of a

fish is used in design, the resulting fishway may not be useable to fish moving at suboptimal temperatures, fish that are gravid, or fish that are living in a polluted system.

In addition to providing a means to directly measure swimming performance, flumes also allow the observation of swimming behaviors. Swimming behaviors are important because they allow fish to cope with challenging conditions such as floods (Ward et al. 2003; Schwartz and Herricks 2005), so may also allow small fish to ascend fishways with challenging conditions like high water velocities or high turbulence. While some studies of swimming behavior in salmonids (e.g., Tudorache et al. 2008, 2011) and other large bodied fishes including clupeids *Alosa spp.*, northern pike *Esox lucius*, white sucker *Catostomus commersonii* (Haro et al. 2004, Castro-Santos 2005), and smallmouth bass *Micropterus dolomieu* (Peake and Farrell 2004) have been successfully conducted in quasi-natural apparatus, swimming behaviors of small fishes have been observed almost exclusively in swimming flume studies.

Swimming behaviors are diverse in small-bodied fishes. Gait-switching behaviors, where fish alternate between steady (i.e., aerobic) and unsteady (i.e., anaerobic or burst) swimming gaits at moderate speeds (Peake and Farrell 2004), have been reported in brassy minnow and common shiner (Ficke et al. 2011). Species such as speckled dace *Rhinichthys osculus* Ward et al. (2003), sculpin *Cottus spp.* (Webb et al. 1996; Aedo et al. 2009), darters *Etheostoma spp.*, *Percina roanoka* (Matthews 1985; Ficke et al. 2011), suckers *Catostomus spp.* (Myrick and Cech 2000; Underwood et al. 2014), and flathead chub *Platygobio gracilis* (Ficke and Myrick, unpublished data) can use their pectoral fins as ailerons to maintain position on the substrate without swimming. Speckled dace *Rhinichthys osculus*, longnose dace *R. cataractae* (Aedo et al. 2009) and fantail darters *Etheostoma flabellare* (Matthews 1985) were reported to bend their bodies to simulate a hydrofoil in order to maintain position without swimming. Oral

grasping has been documented in 11 cyprinid and one small catostomid species *Catostomus platyrhynchus* (Adams et al. 2000, 2003; Young et al. 2004; Aedo et al. 2009; Underwood et al. 2014). The experiments that revealed these behaviors were all conducted in swimming flumes, where small fish could be easily observed.

Adding structural complexity to flumes has revealed additional swimming behaviors and the reactions of fish to more hydraulically complex environments. Some species of small-bodied fishes have been observed seeking and selecting lower velocities when a velocity gradient is available. Scott and Magoulick (2008) used a smooth flume and a flume roughened with cobbles to study swimming ability and behavior of five warmwater fishes. The authors found that some fishes sought velocity refuges in each of the experimental treatments. Cardinal shiners *Luxilus cardinalis* and longear sunfish *Lepomis megalotis* selected lower-than-average velocities in the smooth flume, and orangethroat darters *Etheostoma spectabile* and green sunfish *L. cyanellus* selected lower-than-average velocities in the roughened flume (Scott and Magoulick 2008). Studies involving swimming flumes containing simple structures such as small cylinders have also shown behavioral responses to variable flows. Although fish can exploit velocity refuges to save energy (Sutterlin and Waddy 1975), high levels of turbulence reduce swimming performance, especially if vortices are large relative to the fish and/or vertically oriented (Lupandin 2005; Tritico and Cotel 2010; Silva et al. 2012). For example, the diameter and orientation of eddies affected swimming ability and behavior of creek chub *Semotilus atromaculatus* (Tritico and Cotel 2010). The critical swimming velocity of 53 ± 1.8 cm/s was reduced by as much as 22% by the turbulence created by placing 25-mm diameter cylinders into the experimental flume. Smaller cylinders did not reduce swimming performance as much as the 25-mm cylinders, and placing the large cylinders horizontally, so they created vertical

disturbances in the flow field, had a greater negative effect on performance than cylinders placed vertically. Turbulence may reduce swimming performance because fish must work harder to maintain position in less uniform flow. For example, river chub *Nocomis micropogon* seeking refuge from high velocities behind cylinders replaced swimming behaviors with “balancing” behaviors such as the use of median and paired fins (Webb 1998).

While apparatus such as raceways, smooth ramps, and rock ramps present fish with hydraulic conditions that are more similar to those in a natural stream or a fishway, it is difficult to observe small fish under these conditions (e.g., Bestgen et al. 2010). The spatial position of larger fishes within a raceway or model fishway can be tracked with PIT tags, if the apparatus is fitted with multiple readers (i.e., Castro-Santos et al. 1996), but spatial positions of fishes that are too small (ca. < 70 – 80 mm) to receive PIT tags cannot be tracked in this manner.

Although individual small fish can be observed in an apparatus with a smooth water surface (e.g. Goettel 2013), the irregular surface that is typical in a semi-natural setting such as a rock ramp prevents tracking of individuals (e.g., Bestgen et al. 2010). Fish can be subcutaneously marked with visual implant elastomer (VIE) marks, and fluorescent lighting can be used to illuminate the marks, but the fluorescent lighting does not make the VIE marks visible to an observer looking at an irregular water surface (A. Ficke, unpublished data). Furthermore, much of the software designed to track small fishes (e.g., DanioTrack, Loligo Systems, Tjele, Denmark) requires a mostly tranquil water surface. The recent technology of dual frequency identification sonar (DIDSON, Sound Metrics, Bellevue, Washington) has been used to track fish behavior when fish cannot be directly observed (Patrick et al 2014). However, turbulence can prevent detection of fish, especially if they are small (Holmes et al. 2005), so the utility of

DIDSON in an apparatus designed to mimic a turbulent system such as a rock ramp needs to be empirically tested.

Fish could be tracked in quasi-natural conditions either with new technology or with a novel application of an existing methodology. Underwater cameras have been used to track fishes at discrete locations such as fishways (Negrea et al. 2014) and mouths of commercial fishing nets (Underwood 2012) and have been towed behind slow-moving boats (Cooke and Bunt 2004). Multiple cameras could be placed in a “representative” section of a rock ramp (i.e., a row of cobbles or boulders) where hydraulics could be modeled or measured. Alternatively, fish pathways could be analyzed using a methodology developed by Hughes and Kelly (1996). The original methodology required one side camera and one overhead camera, which cannot be used to track fish through an irregular water surface. A possible solution would be to build a flume with semi-opaque, colored Plexiglas (to minimize disturbance to the fish). Cameras could be placed on the side and the underside of the flume to record fish locations over time, and pathways chosen by individual fish could be mapped using digitizing and video analysis methods described in Hughes and Kelly (1996).

Flumes are useful for studies requiring tight control of velocity (i.e., to detect small changes in swimming performance in a manipulative experiment) and providing conservative estimates of performance for fishway design. However, the advantage of quasi-natural apparatus such as model rock ramps is that their hydraulic conditions more closely resemble those in natural systems. Much of the guesswork in designing fishways for small North American fishes could be removed by designing integrative studies that involve the use of flumes and quasi-natural apparatus.

Table 2A.—Published swimming performances of small-bodied North American fishes. Velocities were determined by one of three tests (shown as footnotes below): 1.) critical swimming velocity tests, 2.) fixed velocity tests, 3.) constant acceleration tests, or 4.) fast-start tests in still water.

Species	Aerobic or prolonged speed (cm/s)	Sprint or burst speed (cm/s)	Temperature (°C)	Reference
Family: Cottidae				
<i>Cottus cognatus</i>	n/a	77 ± 22 ₄	15	(Webb 1978)
<i>C. bairdi</i>	63.3 ₁	117 ₄	17	(Aedo 2009)
Family: Ictaluridae				
<i>Ameiurus melas</i>	n/a	43.4 ± 2.1 ₃	17.5	(Prenosil 2014)
<i>Noturus flavus</i>	52.1 ± 4.5 ₃	61.9 ± 4.7 ₃	20	(Ficke and Myrick, unpublished data)
Family: Gasterosteidae				
<i>Gasterosteus aculeatus</i>	44.5 ₂	53.5 ₂	15	(Blake 2005)
	28 – 36 ₁	n/a	5 – 15	Reviewed in Peake 2008b
Family: Catostomidae				
<i>Catostomus platyrhynchus</i>	62.8 ₁	148 ₄	17	(Aedo et al. 2009)
	31.2 ₁	n/a	8	(Underwood et al. 2014)
<i>Chasmistes liorus</i>	42.1 ₁	152.4 ₄	17	(Aedo et al. 2009)
Family: Cyprinidae				
<i>Agosia chrysogaster</i>	n/a	73.5 ₁	20	(Ward et al. 2003)
<i>Campostoma anomalum</i>	n/a	67 ₂	20.4	(Billman and Pyron 2005; Scott and Magoulick 2008; Leavy and Bonner 2009)
	n/a	62.9 ± 2.77 ₃	21.7 – 33.4	
	35.5 (±2.52) – 37.4 (±8.40) ₁	n/a	20 – 22	
<i>Chrosomus eos</i>	15 – 40 ₂	60 – 75 ₂	10 – 25	(Mee et al. 2011; Ficke and Myrick, unpublished data)
<i>Clinostomus elongatus</i>	n/a	67 ₂	20.4	(Billman and Pyron 2005)
<i>Cyprinella lutrensis</i>	n/a	57.3 (±2.6) – 71.2 (±3.49) ₃	17.5 – 33.4	(Ward et al. 2003; Leavy and Bonner 2009; Prenosil 2014)

Table 2A.—continued.

Species	Aerobic or prolonged speed (cm/s)	Sprint or burst speed (cm/s)	Temperature	Reference
<i>Cyprinella lutrensis</i>	n/a	77.5 ₃	20	(Leavy and Bonner 2009)
<i>Cyprinella proserpina</i>				
<i>Cyprinella spiloptera</i>	n/a	60.8 ± 2.93 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
	40.2	n/a	30	(Hocutt 1973)
<i>Cyprinella venusta</i>	n/a	61.1 ± 2.81 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Dionda episcopa</i>	n/a	17.8 ± 1.8 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Ericymba buccata</i>	n/a	67 ₂	20.4	(Billman and Pyron 2005)
<i>Hybognathus amarus</i>	51.5 ₁	100 – 118	15 – 23	(Bestgen et al. 2010)
<i>Hybognathus hankinsoni</i>	16 – 48 ₂	32 – 64 ₂	10 – 25	(Ficke et al. 2011)
<i>Hybognathus placitus</i>	n/a	61.1 ± 3.57 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Hypomesus transpacificus</i>	27.6 ± 5.1 ₁	n/a	12 – 21	(Swanson et al. 1998)
<i>Iotichthys phlegethontis</i>	29.0 ₁	87.2 ₄	17	(Aedo et al. 2009)
<i>Lepidomeda aliciae</i>	53.9 ₁	120.1 ₄	17	(Aedo et al. 2009)
<i>Luxilus cardinalis</i>	31.7 (± 2.38) – 26.48 (± 4.59) ₁	n/a	20 – 22	(Scott and Magoulick 2008)
<i>Luxilus chrysocephalus</i>	n/a	67 ₂	20.4	(Billman and Pyron 2005; Leavy and Bonner 2009)
	n/a	40.3 ± 3.73 ₃	21.7 – 33.4	
<i>Luxilus cornutus</i>	n/a	67 ₂	20.4	(Webb 1978; Billman and Pyron 2005; Ficke et al. 2011)
	48 ₂	64 ₂	10 – 17.5	
	n/a	114 ± 14 ₄	15	
<i>Lythrurus fumeus</i>	n/a	38.1 ± 5.72 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Lythrurus umbratilis</i>	n/a	55.0 ± 3.75 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Macrhybopsis aestivalis</i>	n/a	61.9 ± 4.40 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Margariscus margarita</i>	n/a	67 ₂	20.4	(Billman and Pyron 2005)

Table 2A.—continued.

Species	Aerobic or prolonged speed (cm/s)	Sprint or burst speed (cm/s)	Temperature	Reference
<i>Meda fulgida</i>	50.6 – 86.0 ₁	n/a	20	(Ward et al. 2003; Ward and Hilwig 2004)
<i>Notropis oxyrhynchus</i>	75.3	53.4 ± 3.12 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Notemigonus crysoleucas</i>	38 – 47 ₁	n/a	21 – 23	(Beecham et al. 2007)
<i>Nocomis biguttatus</i>	n/a	67 ₂	20.4	(Billman and Pyron 2005)
<i>Notropis amabilis</i>	n/a	63.6 ± 2.86 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Notropis atherinoides</i>	n/a	81.4 ± 5.46 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Notropis atrocaudalis</i>	n/a	46.9 ± 2.35 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Notropis bairdi</i>	n/a	45.6 ± 4.96 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Notropis buccula</i>	n/a	49.7 ± 5.42 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Notropis buchanani</i>	n/a	44.7 ± 2.64 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Notropis topeka</i>	30 – 40 ₂	40 – 75 ₂	20	(Adams et al. 2000)
<i>Pimephales notatus</i>	n/a	67 ₂	20.4	(Billman and Pyron 2005)
<i>Pimephales promelas</i>	n/a	67 ₂	20.4	(Ward et al. 2003; Billman and Pyron 2005)
	n/a	69.11 ₃		
<i>Pimephales vigilax</i>	n/a	39.6 ± 2.28 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Platygobio gracilis</i> > 100 mm	71.0 ± 15.1 ₁	n/a	20	(Ficke et al. 2012)
<i>Platygobio gracilis</i> < 100 mm	25 – 60 ₂	70 – 90 ₂	10 – 17.5	(Ficke and Myrick, unpublished data)
<i>Pogonichthys macrolepidotus</i>	63.0 (±4.9) – 66.5 (±6.0) ₁	n/a	19	(Sutphin et al. 2007)
<i>Rhinichthys atratulus</i>	n/a	67 ₂	20.4	(Billman and Pyron 2005; Nelson et al. 2003, 2008)
	30.87 (±1.64) – 46.12 (±12.63) ₁	80 – 160	20	
<i>Rhinichthys cataractae</i>	73.2 ₁	67 ₂ – 120.1 ₄	17 – 20.4	(Billman and Pyron 2005; Aedo et al. 2009)

Table 2A.—continued.

Species	Aerobic or prolonged speed (cm/s)	Sprint or burst speed (cm/s)	Temperature	Reference
<i>Rhinichthys osculus</i>	68.9 ₁	70.4 – 133.8 ₄	17 – 20	(Ward et al. 2003; Aedo et al. 2009)
<i>Richardsonius balteatus</i>	75.0 ₁	132.0 ₄	17	(Aedo et al. 2009)
<i>Semotilus atromaculatus</i>	n/a	67 ₂	20.4	(Billman and Pyron 2005; Leavy and Bonner 2009)
	n/a	44.2 ± 1.61 ₃	21.7 – 33.4	
<i>S. atromaculatus</i> (>100 mm)	35.9 ± 10.8 ₁	n/a	20	(Ficke et al. 2012)
Family: Osmeridae				
<i>Osmerus mordax</i>	30.1 – 45.6 ₁	n/a	10	Reviewed in Peake 2008b
Family: Characidae				
<i>Astyanax mexicanus</i>	n/a	50.9 ± 2.45 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
Family: Cyprinodontidae				
<i>Cyprinodon pecosensis</i>	24.3 (±4.02) ₁ – 36.3 (±1.2)	n/a	21 – 23	(Kodric-Brown and Nicoletto 1993; Rosenfield et al. 2004)
<i>Cyprinodon variegatus</i>	26.9 ± 3.45 ₁	n/a	21 – 23	(Rosenfield et al. 2004)
<i>Fundulus diaphanus</i>	25.2 – 35.7 ₁	85 – 90 ₄	10 – 35	Reviewed in Peake 2008b
<i>Fundulus notatus</i>	n/a	30.7 ± 3.69 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Fundulus sciadicus</i>	n/a	45 – 55 ₂	10 – 25	(Ficke and Myrick, unpublished data)
	n/a	40.7 ± 1.1 ₃	17.5	(Prenosil 2014)
<i>Fundulus zebrinus</i>	n/a	43.4 (±3.94) – 51.8 (±1.7) ₃	21.7 – 33.4	(Leavy and Bonner 2009; Prenosil 2014)
Family: Poeciliidae				
<i>Gambusia affinis</i>	n/a	37.5(±1.2) – 38.5 ₃	20	(Ward et al. 2003)
<i>Gambusia geiseri</i>	n/a	15.7 ± 1.36 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Gambusia holbrooki</i>	13.5 (± 0.2) – 22.6 (± 0.9) ₁	n/a	18 – 30	(Hammill et al. 2004)
<i>Poecilia latipinna</i>	n/a	18.6 ± 3.04 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Poeciliopsis occidentalis</i>	n/a	36.5 ₃	21.7 – 33.4	(Leavy and Bonner 2009)

Table 2A.—continued.

Species	Aerobic or prolonged speed (cm/s)	Sprint or burst speed (cm/s)	Temperature	Reference
Family: Atherinidae				
<i>Menidia beryllina</i>	n/a	30.2 ± 3.70 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
Family: Centrarchidae				
<i>Lepomis auritus</i>	n/a	35.4 ± 1.89 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Lepomis cyanellus</i>	11.41 (±5.77) – 13.89 (±0.59) ₁	46.2 – 49.2 ± 1.9 ₃	17.5 – 22	(Ward et al. 2003; Scott and Magoulick 2008; Prenosil 2014)
<i>Lepomis macrochirus</i>	n/a	40.5 (±6.61)– 45.7 (±1.5) ₃	21.7 – 33.4	(Schaefer et al. 1999; Jones et al. 2008; Leavy and Bonner 2009)
	27.24 (±1.14) ₁	n/a	22	
<i>Lepomis megalotis</i>	n/a	28.0 ± 4.22 ₃	21.7 – 33.4	(Schaefer et al. 1999; Scott and Magoulick 2008; Leavy and Bonner 2009)
	14.4 (±0.18) – 15.74 (±5.77) ₁	n/a	20 – 22	
Family: Percidae				
<i>Etheostoma caeruleum</i>	n/a	89 ± 13 ₄	15	(Webb 1978)
<i>Etheostoma cragini</i>	16 ₂	32 ₂	10 – 17.5	(Ficke et al. 2011)
<i>Etheostoma grahami</i>	n/a	40.0 ± 3.92 ₃	21.7 – 33.4	(Leavy and Bonner 2009)
<i>Etheostoma spectabile</i>	17.25 (±4.49) – 22.49 (±3.02) ₁	n/a	20 – 22	(Scott and Magoulick 2008)
<i>Percina pantherina</i>	12 – 42 ₂	60 ₂	n/a	(Toepfer et al. 1999)
Family: Cichlidae				
<i>Cichlasoma cyanoguttatum</i>	n/a	33.0 ± 2.70 ₃	21.7 – 33.4	(Leavy and Bonner 2009)

APPENDIX 3A:

PREDICTING SWIMMING PERFORMANCE OF UNTESTED GREAT PLAINS FISHES

Random Forest Method

This appendix describes the method used to predict swimming performance of untested fish species of the western Great Plains. Because RF analyses rely upon machine learning, the steps are fairly simple but will vary with the statistical program used. The following steps describe how this analysis can be run in JMP Pro 11.

Two predictive swimming models were developed in the study described in the main body of this paper: one for aerobic ability, and one for anaerobic ability. If the user would like to develop new models or refine the existing ones, it would be necessary to collect novel U_{TRANS} and U_{MAX} data using constant acceleration tests. However, predicting swimming performance of an untested species with the existing models requires only the following predictor variables: Shape Guild (see text for details), TL, weight, width-to-depth ratio at 50% TL, hemoglobin concentration, hematocrit, percentage of muscle at 50% TL, proportion of red muscle at 50% TL, and proportion of white muscle at 50% TL.

The steps below describe how to predict swimming performance of an untested species using the models developed in this study.

1. Open the data set used to construct the model (available upon request⁵) and add all known variables for the untested species. Because all of the predictor variables explain a fairly low proportion of the observed variation in aerobic and anaerobic swimming ability, it is strongly recommended that all of the predictor variables be

⁵ Email Ashley Ficke at ashleyduncanficke@gmail.com for the data set used in model construction.

included in the model, despite the additional effort associated with obtaining the physiological measurements.

2. Import the data set into JMP Pro 10. From the drop-down menu in JMP, choose “Analyze > modeling > partition”. This will open a window that provides options for multiple partition-based analyses.
 - a. In the lower left corner, check the “missing value categories” box, so that new entries (i.e., those without swimming ability measurements) will be included in the analysis.
 - b. Choose “Bootstrap Forest” from the drop-down menu labeled “Method”
 - c. Enter 0.2 in the “Validation Portion” box to separate the model construction and validation portions of the data set.
3. Select the dependent and independent variables, and add them to the “Y, Response” and “X, Factor” boxes, respectively. Hit “OK”, and a new window will appear. This new window allows the user to select additional analysis options.
 - a. Number of trees in the forest: The recommendation from Cutler et al. (2007) is to choose a number between two and 500. In JMP, enter 500, and check the “Early Stopping” box at the bottom of the window. This option stops the program from producing additional trees once the error no longer decreases with the addition of more trees. This error stabilized at a relatively small number of trees in the original analysis (< 30 for both aerobic and anaerobic).
 - b. Number of terms sampled per split: This is the number of predictor variables sampled to produce a split in the tree (i.e. a new partition in the data). JMP

allows the user to select a range of values, so that the analysis will be run once for each number, and the analysis with the highest R-squared value will be selected. Enter “2” into this box, check the “Multiple Fits over number of terms”, and enter “8” into the “Max Number of terms” box. This provides the maximum allowable range of terms sampled per split per Cutler et al. (2007).

- c. Bootstrap sample rate: This is the proportion of the model construction data sampled for each tree. Cutler et al. (2007) recommends a range of 0.6 – 0.7.
 - d. Minimum splits per tree: This controls the size of the tree, but the model is likely not sensitive to this per Cutler et al. (2007). Changing this number had little effect on the predictive power of the models, so the minimum splits per tree was left at JMP defaults ($n = 5$).
 - e. Minimum size split: This is the minimum number of observations needed to produce a split or partition in the tree. This value also had little effect on the predictive ability of the model, so it was left at the JMP default level ($n = 10$).
4. Hit “OK”, and allow the RF model to run. This can take a few minutes. Once the model finishes running, check the R-squared value for the model construction and validation portions of the data. The R-squared value for the validation portions of the data set should be close to 40% for aerobic ability and anaerobic ability. If this is not the case, re-run the model after adjusting “Bootstrap sample rate”, “Minimum splits per tree”, and “Minimum size split”.
 5. Once a satisfactory RF model has been developed, click on the red arrow at the top left corner of the RF report produced by JMP. Select “Plot actual by predicted” and examine the graph to ensure an acceptable model fit. Select “Column contributions”

to obtain relative measures of importance for each predictor variable. The sum of squared error for a given variable, divided by the total sum of squared error provides the amount of variation explained by that variable.

6. Finally, select the red arrow at the top left corner of the report again, and select “Save Columns > Save Predicteds”. This command generates a new column of predicted swimming abilities for each row, including those with missing values.

Regression Method

This section describes the use of the developed regression equation to predict swimming performance. It also contains information on predictive ability of the full regression equation, the regression equation containing only statistically significant variables, and the RF models. This information will allow the user to decide whether it the ease of use of the regression method outweighs its lower predictive power.

The full regression equation for predicting aerobic swimming ability is:

$$U_{TRANS}^{-0.4} = 0.37 + 0.18(ICT) - 0.009(CYP) - 0.0006(PER) - 0.006(SNF) - 5 * 10^{-8}(Hb) - 0.03(HCT) - 0.0001(M_{50}) - 0.002(RM_{50}) - 0.027(WD_{50}) - 0.0005(TL) - 0.39(CFin),$$

where ICT, CYP, PER, and SNF are the shape guilds (input = 1 if fish belongs to guild, 0 otherwise), Hb = hemoglobin concentration (mg/dL), HCT = hematocrit ($0 < n < 1$), M_{50} = the percent of muscle at 50% of TL (%), RM_{50} = the proportion of the muscle at 50% TL that is red muscle (%), WD_{50} = the width-to-depth ratio of the fish at 50% of TL ($0 < n < 1$), TL= total length (mm), and CFin= the length of the caudal fin divided by the total length of the fish ($0 < n < 1$). Although many of these terms were not statistically significant, they are all included

above, because the regression equation that only included significant predictors had poor predictive value (Table 3A-1).

The full regression equation for predicting anaerobic swimming ability is:

$$U_{MAX} = 125.39 - 12.02(ICT) + 4.51(CYP) - 1.78(PER) - 2.22(SNF) + 0.000001(Hb) + 12.56(HCT) - 0.28(M_{50}) - 0.74(WM_{50}) + 12.45(WD_{50}) + 0.49(TL) + 16.43(Cfin),$$

where ICT, CYP, PER, and SNF are the shape guilds (input = 1 if fish belongs to guild, 0 otherwise), Hb = hemoglobin concentration (mg/dL), HCT = hematocrit ($0 < n < 1$), M_{50} = the percent of muscle at 50% of TL (%), RM_{50} = the proportion of the muscle at 50% TL that is red muscle (%), WD_{50} = the width-to-depth ratio of the fish at 50% of TL ($0 < n < 1$), TL = total length (mm), and CFin = the length of the caudal fin divided by the total length of the fish ($0 < n < 1$). Although many of these terms were not statistically significant, they are all included above, because the regression equation that only included significant predictors had poor predictive value (Table 3A-1).

The predictive abilities of the random forest and regression models were compared by examining predicted versus actual values for U_{TRANS} and U_{MAX} for each individual fish. The percentage of predictions that were within 20% of the measured values was used to compare model performance. External data were not available to test predictive ability, so the same data used in model construction were used to compare model performance. The random forest model had a similar percentage of predictions within 20% of the measured U_{TRANS} values than the full regression model, but the range of error was greater in the random forest model (Table 3A-1). The random forest model performed better than the full regression model in predicting U_{MAX} , with a higher percentage of predictions within 20% of actual values and a smaller range of error. Although the full regression models do not predict swimming performance as accurately as the

RF models, they are easy to use and require no specialized computer programs. Therefore, they may be a viable alternative for predicting swimming performance when the RF models cannot be used.

Table 3A-1: Comparison of predictive value of full regression equation, regression equation with statistically significant predictors only, and RF models. Predictive ability was compared by determining the range of error and the proportion of predictions that were within the range of -20% to + 20% of the actual value for each method.

Method	Aerobic		Anaerobic	
	Error Range	Percent within 20% of actual value	Error Range	Percent within 20% of actual value
Regression, significant predictors	-72% to +19%	19%	+18% to +458%	< 1%
Regression, full model	-59% to +71%	66%	-100% to +160%	65%
Random Forest model	-49% to +108%	67%	-35% to +121%	76%

APPENDIX 5A:

DETAILS ON MARK MULTI-STATE MARK RECAPTURE MODEL CONSTRUCTION

FITTING THE MARK MODEL TO DETECTIONS AT PAIRED ANTENNAE

Analyzing movement of PIT-tagged fishes with paired antennae is unique in that movement is not inferred when a fish is tagged in one location in a given time period (t) and recaptured in another location in a subsequent time period ($t + 1$). Instead, a fish has moved if it is detected at pair of antennae in a relatively short period of time (24 hours, in this case), and inference of movement does not depend on the fish's detection in the new location. By default, Program MARK calculates survival before calculating a transition probability (“the survive then move” paradigm, Lebreton and Pradel 2002; Cooch and White 2012), but because movement in this study was detected when a live fish swam across a pair of antenna, survival probability would have to be 100% if it were estimated before movement. As a result, “dummy” occasions were constructed, so that a single time period is represented with a pair of variables. In the first occasion of a time period, transition probabilities were estimated, and survival was fixed at 1.0. In the second “dummy” occasion, survival to the next time period (ϕ) and detection probabilities within the physical locations (p_A, p_B, p_C) were estimated (Figure 5A-1). Constructing capture histories with two occasions for each time period allowed estimation of transition probability before survival, and separation of detections at a pair of antennae (i.e., successful movement across a structure) from detections at a single antennae (i.e., no movement across a structure, but animal detected in physical location). Transition probability was estimated between the “real” and “dummy” occasions in a time period, so it could be considered as having been estimated within, not between time periods.

Capture Histories and Detections at a Single Antenna

The MSMR model in Program MARK requires individual capture histories. Multi-state capture histories are combinations of letters and zeros that describe the animal's location throughout the study. The capture histories were structured to accommodate the “dummy” time period described above by describing a single time period with a pair of letters/zeros. For example, a fish with a capture history of “00 A0 AD 00 B0” would have been marked and released in location A in the second time period and would have moved to location B (through movement state D) in the third time period. It would not have been detected in location B (i.e., at a single antenna) during the fourth time period, but it would have been detected in the fifth. Capture histories were constructed for each tagged fish from the data recorded during its initial marking and from subsequent detections at the antennae in South Boulder Creek. Successful upstream movement of an individual fish across a fishway (or the control site) was defined by the detection of the fish at the downstream and upstream antennae at the fishway (or the control site) within a 24-hour period. If a fish was detected at a single antenna only, it was assumed that the fish did not move upstream past the structure. On the rare occasion that a fish was detected in an upstream location without having been detected moving across the appropriate antenna pair, the fish was removed from the study. Detections at a single antenna allowed estimation of capture probabilities (in the physical states) and survival in the “dummy” occasion of each time period.

Constraining the MARK Model to Reflect Reality

Biologically, some transitions among the nine location and movement states (A-I) were impossible, and were thus fixed to zero. In addition, several transitions were fixed at 1.0. The fixed transition probabilities included:

- Transitions directly from one physical location to another (e.g., state A to state B):
These could not occur in the model because a fish must move from one physical location, through a movement state, to the ending location corresponding to the movement state. For example, for a fish that moved from location A to location B within a time period, ψ^{AB} was fixed at zero, estimation of ψ^{AD} occurred in the first occasion of the time period ψ^{DB} was fixed at 1.0 in the dummy occasion of the same time period.
- Transitions from one physical location to a movement state that is associated with a different starting physical location: Transition probabilities were tied to specific starting and ending locations. For example, individuals in location A can only transition to movement states D, G, and I, because all other transition states begin in locations B or C. Therefore, ψ^{AD} , ψ^{AG} , and ψ^{AI} can be estimated, and $\psi^{AE} = \psi^{AF} = \psi^{AH} = 0$ (Figure 5A-1).
- All transitions involving two movement states (e.g., transition D to transition E, $\psi^{DE}=0$): A fish cannot go from one movement state to another movement state. Instead, it transitions to a movement state in the first occasion of the time period and transitions to the appropriate physical location in the second occasion of the time period. Multiple movements within the same time period were represented with a single movement state. For example, the transition probability for a fish moving between physical locations A and C in a single time period is represented by ψ^{AG} (first occasion in time period) and ψ^{GC} (fixed at 1.0, second or “dummy” occasion in time period), because a fish that moves from location A to transition state G must end up in location C.

- Detection probability at individual antennae exceeded 95 percent during all field tests of antenna performance, and a preliminary MARK analysis indicated that models where the capture probabilities in the movement states (i.e., p_D , p_E , p_F , p_G , p_H , p_I) were not fixed had no support from the data. Therefore, the detection probability of fish passing the antenna pairs was fixed at 1.0.

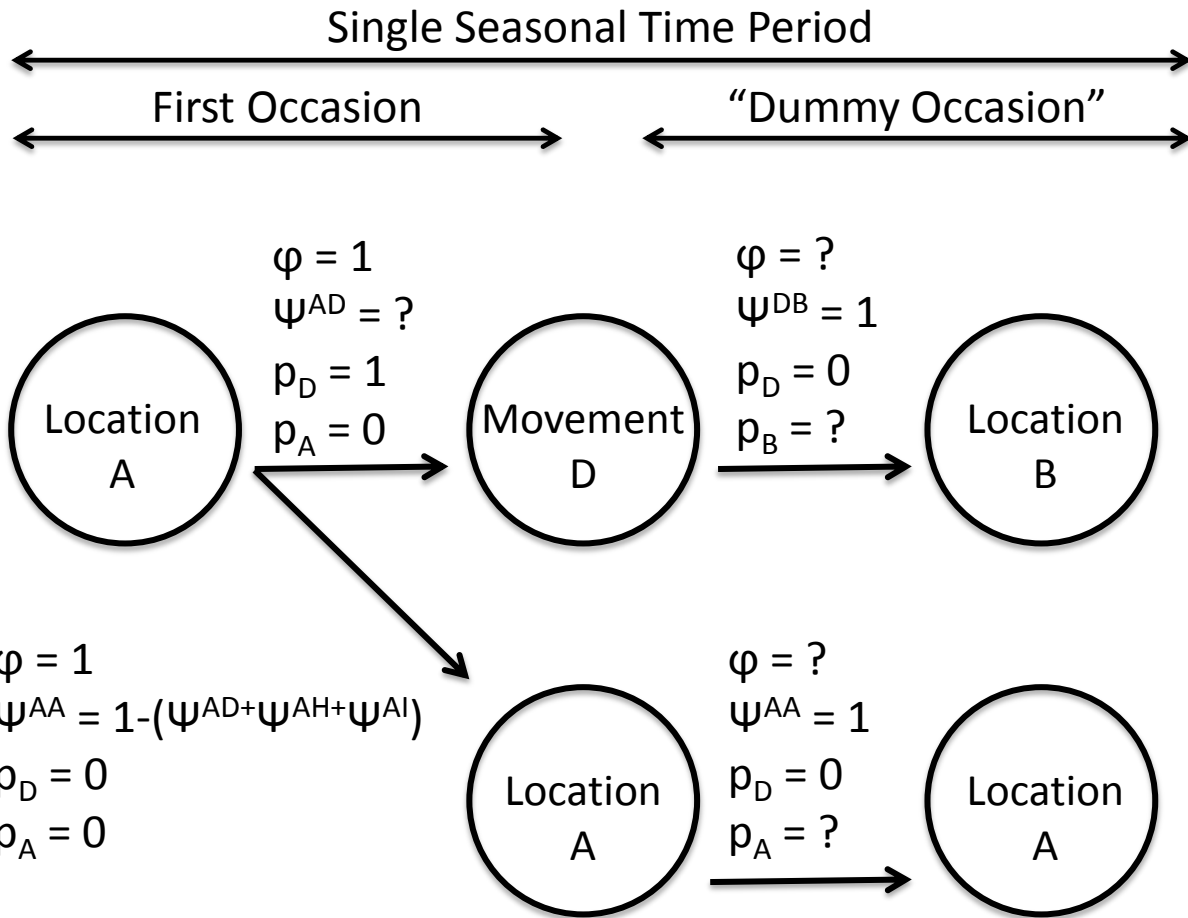


Figure 5A-1.—Conceptual diagram of the model used to represent a fish in Location A at the beginning of a time period, t . During the first occasion of the time period, the probability that the fish moves within the time period (ψ^{AD} , ψ^{AG} , or ψ^{AI}) is estimated. During this occasion, survival probability (ϕ) and the probability that a moving fish is detected at the antenna pairs it crosses (p_D , p_G , and p_I) were fixed at 1.0. Survival and capture probabilities within the physical states (p_A , p_B , and p_C) were fixed at zero and estimated in the “dummy” occasion. In the “dummy” occasion, survival between time periods (ϕ) and capture probabilities within each location (p_A , p_B , and p_C) were estimated. Capture probabilities in the movement state (p_D , p_G , and p_I) were fixed at zero, because they were already assigned the fixed value of 1.0 in the first occasion of the time period. Transitions from a movement state to the appropriate location (ψ^{DB} , ψ^{GC}) were fixed at 1.0.

APPENDIX 5B:

FULL LIST OF MODELS RUN IN PROGRAM MARK

Table 5B-1.—Full list of models run in Program MARK. Num. Par. = number of model parameters. Abbreviations for model effects are as follows: Season = varies with all four seasons, d = varies by distance, S = varies by structure/fishway, winter = varies between spring/summer and fall/winter, cov = varies depending on when the individual was tagged during the first time period.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Par	QDeviance	-2log(L)
{s(season)p(fixed)T(d*S*winter)}	1060.083	0	0.27937	1	15	1029.7831	3202.625
{s(season)p(fixed*season)T(d*S*winter)}	1060.416	0.3331	0.23651	0.8466	18	1023.988	3184.603
{s(season*cov)p(fixed*season)T(d*S*winter)}	1061.567	1.4847	0.13298	0.476	20	1021.0414	3175.439
{s(season)p(fixed*winter)T(d*S*winter)}	1062.064	1.9813	0.10374	0.3713	16	1029.7242	3202.442
{s(season*cov)p(fixed*winter)T(d*S*winter)}	1063.189	3.1065	0.0591	0.2115	18	1026.7615	3193.228
{s(season)p(fixed*winter)T(d*S*season)}	1064.062	3.9795	0.0382	0.1367	22	1019.4277	3170.42
{s(season)p(fixed*season)T(d*S*season)}	1064.833	4.7505	0.02598	0.093	25	1014.0166	3153.592
{s(season*cov)p(fixed*season*cov)T(d*S*winter)}	1065.086	5.0034	0.02289	0.0819	22	1020.4516	3173.605
{s(season)p(fixed*season)T(d*season)}	1066.269	6.1867	0.01267	0.0454	16	1033.9296	3215.521
{s(season)p(fixed)T(d*S*winter*cov)}	1066.319	6.2359	0.01236	0.0442	21	1023.7396	3183.83
{s(season*cov)p(fixed*winter*cov)T(d*S*winter)}	1066.383	6.3002	0.01197	0.0428	20	1025.8569	3190.415
{s(season)p(fixed)T(d*winter)}	1066.501	6.4178	0.01129	0.0404	10	1046.3636	3254.191
{s(season)p(fixed*season)T(d*winter)}	1066.582	6.4995	0.01083	0.0388	13	1040.3553	3235.505
{s(season)p(fixed*winter)T(d*S*winter*cov)}	1067.652	7.5691	0.00635	0.0227	21	1025.0729	3187.977
{s(season)p(fixed*winter)T(d*season)}	1068.263	8.1804	0.00468	0.0168	13	1042.0362	3240.733
{s(season)p(fixed*winter)T(d*winter)}	1068.491	8.4086	0.00417	0.0149	11	1046.3269	3254.077
{s(season)p(fixed*cov)T(d*S*winter*cov)}	1069.233	9.1506	0.00288	0.0103	23	1022.5407	3180.102
{s(winter)p(fixed*season)T(d*S*winter)}	1069.564	9.4813	0.00244	0.0087	17	1035.1815	3219.414

Table 5B-1.—continued.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Par	QDeviance	-2log(L)
{s(season*cov)p(fixed*winter)T(d*S*winter*cov)}	1069.62	9.5372	0.00237	0.0085	24	1020.8666	3174.895
{s(season)p(fixed)T(S*winter)}	1069.947	9.8643	0.00201	0.0072	12	1045.7526	3252.291
{s(winter)p(fixed*season)T(d*S*season)}	1070.268	10.1854	0.00172	0.0062	23	1023.5755	3183.32
{s(season)p(fixed*season)T(S*winter)}	1070.286	10.2031	0.0017	0.0061	15	1039.9862	3234.357
{s(season*cov)p(fixed*cov)T(d*S*winter*cov)}	1070.564	10.4809	0.00148	0.0053	24	1021.8103	3177.83
{s(season*cov)p(fixed*season*cov)T(d*S*winter*cov)}	1071.482	11.399	0.00094	0.0034	28	1014.4597	3154.97
{s(season*cov)p(fixed)T(d*S*winter)}	1071.508	11.4255	0.00092	0.0033	16	1039.1685	3231.814
{s(.)p(fixed*season)T(d*S*winter)}	1071.919	11.8366	0.00075	0.0027	16	1039.5795	3233.092
{s(season)p(fixed*winter)T(S*winter)}	1071.922	11.839	0.00075	0.0027	13	1045.6948	3252.111
{s(season*cov)p(fixed*cov)T(d*S*winter)}	1072.088	12.0052	0.00069	0.0025	18	1035.6601	3220.903
{s(.)p(fixed*season)T(d*S*season)}	1072.143	12.0605	0.00067	0.0024	22	1027.5087	3195.552
{s(season)p(fixed*season)T(S*season)}	1072.156	12.0734	0.00067	0.0024	20	1031.6302	3208.37
{s(season*cov)p(fixed*winter*cov)T(d*S*winter*cov)}	1072.842	12.759	0.00047	0.0017	26	1019.9592	3172.073
{s(season)p(fixed*winter)T(S*season)}	1073.391	13.3087	0.00036	0.0013	18	1036.9636	3224.957
{s(.)p(fixed*season)T(d*season)}	1073.965	13.8819	0.00027	0.001	14	1045.7026	3252.135
{s(winter)p(fixed*season)T(d*winter)}	1075.061	14.9785	0.00016	0.0006	12	1050.8668	3268.196
{s(.)p(fixed*season)T(d*winter)}	1077.14	17.0572	0.00006	0.0002	11	1054.9756	3280.974
{s(summerfall)p(fixed*season)T(S*winter)}	1079.503	19.4201	0.00002	0.0001	14	1051.2408	3269.359
{s(season)p(fixed)T(winter)}	1079.844	19.7614	0.00001	0	6	1067.792	3320.833
{s(winter)p(fixed*season)T(S*season)}	1079.851	19.7682	0.00001	0	19	1041.3753	3238.677
{s(season)p(fixed)T(season)}	1080.009	19.9259	0.00001	0	7	1065.939	3315.07
{s(season)p(fixed*season)T(winter)}	1080.079	19.9962	0.00001	0	9	1061.967	3302.717
{s(season)p(fixed*season)T(season)}	1080.602	20.5196	0.00001	0	11	1058.4379	3291.742
{s(season)p(fixed*season*cov)T(d*S*winter*cov)}	1080.72	20.637	0.00001	0	32	1015.3872	3157.854
{s(winter)p(fixed*season)T(d*season)}	1081.102	21.018	0.00001	0	14	1052.8395	3274.331

Table 5B-1.—continued.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Par	QDeviance	-2log(L)
{s(.)p(fixed*season)T(S*season)}	1081.762	21.6794	0.00001	0	18	1045.3343	3250.99
{s(season)p(fixed*winter)T(winter)}	1081.816	21.7333	0.00001	0	7	1067.7465	3320.692
{s(.)p(fixed*season)T(S*winter)}	1081.852	21.7694	0.00001	0	13	1055.6251	3282.994
{s(season)p(fixed*winter)T(season)}	1082.147	22.0642	0	0	9	1064.035	3309.149
{s(season)p(fixed)T(d*S*season)}	1085.067	24.9841	0	0	21	1042.4878	3242.137
{s(season)p(fixed)T(d*S*season)}	1085.067	24.9841	0	0	21	1042.4878	3242.137
{s(winter)p(fixed*season)T(season)}	1087.823	27.7403	0	0	10	1067.6861	3320.504
{s(season)p(fixed)T(d*season)}	1089.014	28.931	0	0	13	1062.7867	3305.267
{s(winter)p(fixed*season)T(winter)}	1089.07	28.9868	0	0	8	1072.98	3336.968
{s(.)p(fixed*season)T(season)}	1089.588	29.5054	0	0	9	1071.4761	3332.291
{s(winter)p(fixed)T(d*S*winter)}	1090.099	30.0162	0	0	14	1061.8369	3302.313
{s(winter)p(fixed)T(d*S*season)}	1091.165	31.0826	0	0	20	1050.6394	3267.488
{s(.)p(fixed*season)T(winter)}	1091.297	31.2146	0	0	7	1077.2277	3350.178
{s(winter)p(fixed*winter)T(d*S*winter)}	1091.776	31.6928	0	0	15	1061.4759	3301.19
{s(winter)p(fixed*winter)T(d*S*season)}	1092.871	32.7886	0	0	21	1050.2924	3266.409
{s(winter)p(fixed)T(d*winter)}	1096.009	35.9263	0	0	9	1077.8971	3352.26
{s(season)p(fixed)T(S*season)}	1096.489	36.4063	0	0	16	1064.1492	3309.504
{s(.)p(fixed*winter)T(d*S*winter)}	1097.401	37.3179	0	0	14	1069.1386	3325.021
{s(winter)p(fixed*winter)T(d*winter)}	1097.605	37.5224	0	0	10	1077.4682	3350.926
{s(.)p(fixed*winter)T(d*S*season)}	1097.757	37.6747	0	0	20	1057.2314	3287.99
{s(.)p(fixed*winter)T(d*season)}	1099.859	39.7767	0	0	12	1075.665	3345.318
{s(winter)p(fixed)T(S*winter)}	1100.042	39.9593	0	0	11	1077.8777	3352.2
{s(winter)p(fixed)T(S*season)}	1100.698	40.6149	0	0	16	1068.3578	3322.593
{s(winter)p(fixed*winter)T(S*winter)}	1101.708	41.6257	0	0	12	1077.5141	3351.069
{s(winter)p(fixed)T(d*season)}	1102.43	42.3474	0	0	11	1080.2657	3359.626
{s(.)p(fixed*winter)T(d*winter)}	1102.835	42.7526	0	0	9	1084.7234	3373.49
{s(cov)p(fixed)T(d*S)}	1103.546	43.4629	0	0	10	1083.4087	3369.401
{s(.)p(fixed)T(d*S*winter)}	1103.6	43.5169	0	0	13	1077.3727	3350.629

Table 5B-1.—continued.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Par	QDeviance	-2log(L)
{s(winter)p(fixed*winter)T(d*season)}	1103.751	43.6683	0	0	12	1079.5567	3357.421
{s(.)p(fixed)T(d*S*season)}	1103.99	43.9074	0	0	19	1065.5145	3313.75
{s(.)p(fixed)T(d*S*season)}	1103.99	43.9074	0	0	19	1065.5145	3313.75
{s(cov)p(fixed)T(cov*d*S)}	1105.606	45.5228	0	0	16	1073.2657	3337.856
{s(.)p(fixed)T(d*season)}	1106.229	46.1458	0	0	11	1084.0641	3371.44
{s(cov)p(fixed*cov)T(d*S)}	1107.058	46.9754	0	0	11	1084.8937	3374.019
{s(.)p(fixed*winter)T(S*winter)}	1107.317	47.2344	0	0	11	1085.1527	3374.825
{s(.)p(fixed*winter)T(S*season)}	1107.36	47.2768	0	0	16	1075.0197	3343.311
{s(cov)p(fixed)T(d*S*season)}	1107.388	47.3053	0	0	20	1066.862	3317.941
{s(.)p(fixed)T(d)}	1107.906	47.8234	0	0	5	1097.8688	3414.372
{s(winter)p(fixed)T(season)}	1109.006	48.9231	0	0	7	1094.9362	3405.252
{s(cov)p(fixed*cov)T(cov*d*S)}	1109.062	48.9793	0	0	17	1074.6795	3342.253
{s(.)p(fixed)T(d*winter)}	1109.136	49.0531	0	0	8	1093.0463	3399.374
{s(winter)p(fixed*winter)T(S*season)}	1109.943	49.8599	0	0	16	1077.6028	3351.345
{s(.)p(fixed)T(cov*d)}	1110.461	50.3787	0	0	8	1094.3719	3403.497
{s(winter)p(fixed*winter)T(season)}	1110.63	50.5476	0	0	8	1094.5408	3404.022
{s(winter)p(fixed*winter)T(winter)}	1111.414	51.3313	0	0	6	1099.3619	3419.015
{s(winter)p(fixed*winter)T(winter)}	1111.414	51.3313	0	0	6	1099.3619	3419.015
{s(.)p(fixed)T(cov*S)}	1112.485	52.4027	0	0	11	1090.321	3390.898
{s(.)p(fixed)T(S*winter)}	1113.521	53.4384	0	0	10	1093.3842	3400.425
{s(.)p(fixed)T(S*season)}	1113.592	53.5089	0	0	15	1083.2919	3369.038
{s(cov)p(fixed)T(cov*d)}	1113.62	53.5373	0	0	10	1093.4831	3400.732
{s(.)p(fixed*winter)T(season)}	1115.295	55.2119	0	0	7	1101.225	3424.81
{s(.)p(fixed*winter)T(winter)}	1116.829	56.7461	0	0	5	1106.7915	3442.122
{s(.)p(fixed*winter)T(winter)}	1116.829	56.7461	0	0	5	1106.7915	3442.122
{s(cov)p(fixed)T(cov*S)}	1117.431	57.3479	0	0	12	1093.2362	3399.965
{s(winter)p(fixed)T(winter)}	1119.262	59.1797	0	0	4	1111.2376	3455.949

Table 5B-1.—continued.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Par	QDeviance	-2log(L)
{s(.)p(fixed)T(S)}	1120.13	60.0471	0	0	5	1110.0926	3452.388
{s(.)p(fixed)T(season)}	1121.591	61.5081	0	0	6	1109.5387	3450.665
{s(.)p(fixed)T(winter)}	1123.082	62.9992	0	0	4	1115.0571	3467.828
{s(.)p(fixed)T(.)}	1123.79	63.7071	0	0	3	1117.7749	3476.28
{s(.)p(fixed)T(cov)}	1125.631	65.5481	0	0	5	1115.5936	3469.496
{s(.)p(.)T(.)}	1125.8	65.717	0	0	4	1117.7749	3476.28