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The wetted ramp as a useful tool to service smaller-bodied finfishes at low-head acquatic barriers

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The Wetted Ramp as a Useful Tool for Passing Smaller-Bodied Finfishes over Low-Head Aquatic Barriers

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Abstract

This study examined the effects of finfish length and behavior on passage success on the wetted ramp, a proposed passage device for finfishes at low-head aquatic barriers. There were two hypotheses: there is a size effect to passage success because larger fish have relatively less propulsive surface area in partial submersion, and fish respond to changes in ramp angle of inclination during a passage attempt. Creek chub (*Semotilus atromaculatus*) and white sucker (*Catostomus commersonii*) were observed, using a high speed camera, as they attempted to scale the wetted ramp. Smaller fish traveled farther and were also able to accelerate on the ramp despite entering at lower velocities. Larger fish had relatively greater head and tail amplitudes and greater body bending during strokes, suggesting the use of a less efficient swimming mode. Finfish as a group did not respond behaviorally to a change in ramp angle of inclination. The wetted ramp appears to be a size selective passage device, suggesting its use at low-head obstructions to service smaller-bodied finfishes.

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Introduction

Altering the connectivity of rivers and streams can have far-reaching effects on aquatic ecosystems and the organisms that live there (Bednarek 2001; Fahrig 2003; Rosco and Hinch 2010; McKay et al. 2013; Baker 2014). Anthropogenic changes, such as damming, are often responsible for many negative ecosystem level consequences and even local extinctions in some cases (Nehlson et al. 1991; Rosco and Hinch 2010; McKay et al. 2013). It is therefore important from a conservation standpoint that we have a full understanding of how these anthropogenic obstructions effect aquatic biota. Anadromous and catadromous fishes, for example, make annual spawning migrations between freshwater river systems and the ocean. Blocking these migration routes without careful consideration for how we are to mitigate damages to these fish populations would be a poor management decision (Nehlson et al. 1991; Fahrig 2003). Unfortunately, many of the dams and barriers in place today were built long before society had an understanding of the ecological impacts their construction might have.

River and stream connectivity has long been an issue facing fisheries management (Denil 1909). In the United States alone, nearly 2.5 million dams obstruct the movement of fishes and other aquatic organisms (Pohl 2003). While dam construction in the United States has all but stopped, developing parts of the world continue to build dams for hydroelectric and irrigation purposes (Tu et al. 2011). As the number of dams and barriers worldwide continues to rise, issues of river and stream connectivity will only grow more pressing. Where feasible, dam removal is a promising option for river restoration, but it can be expensive and time consuming (Bednarek 2001; Pohl 2003; Roni et al. 2008). To mitigate the effects barriers have on fish populations, fishways (fish-passes or fish-ladders) have been installed in many river systems to guide and assist fish in navigating around these obstructions (Castro-Santos et al. 2009; McKay et al. 2013).

A fishway is a device designed to facilitate the movement of fishes, usually migratory species, around waterfalls, dams, and other in-river barriers (Clay 1995). Many fishways are built with a particular species swimming ability in mind, so they can be highly variable in design (Clay 1995). On the west coast of the United States, where salmonid migration is of high economic importance, numerous pool-and-weir style fish passes catering to the strong jumping ability of salmonids have been built (Nehlson et al. 1991; Clay 1995; Calles and Greenburg 2005). However, the swimming abilities of many other ecologically important species and fishways designed with those swimming abilities in mind have not been as well studied.

One of the primary criticisms of fishways designed for salmonids, such as the pool-and-weir, is that they cater only to strong swimming and jumping species (Mallen-Cooper 1999; Roscoe and Hinch 2010). Other migratory fishes, fishes moving within a river system, and even other aquatic organisms such as amphibians may be restricted from using these types of fishways because they lack the physical ability to successfully complete the fish pass (Richter et al. 1997; Mallen-Cooper 1999; Cushman 2006; Tocker et al. 2010; Gustafsson et al. 2013). As a result, these fishes and other aquatic organisms may suffer from habitat and population connectivity issues even though a fishway is present. To address this need, researchers have begun studying the swimming abilities of other fishes and designing fishways for larger groups of aquatic biota (Eberstaller et al. 1998; Mallen-Cooper 1999; Calles and Greenberg 2005; Baker 2014).

Before the first salmon fishways were designed and constructed, studies first sought to better understand the swimming abilities of these fish (Collins 1952). In similar fashion, recent years have seen a tremendous upswing in studies to better quantify and analyze the swimming ability of numerous other fishes (Lin et al. 2008; Tu et al. 2011; Tierney 2011; Baker 2014). Smaller-bodied fishes, which are often weaker swimmers (Bainbridge 1958), have often been overlooked in fish passage studies because larger species, and larger individuals within a species, garner more attention. Many amphidromous fishes, or species that migrate from fresh to saltwater or vice versa outside of the breeding season, migrate at sizes of 2–10cm (Baker 2014). These smaller-bodied fishes lack the physical swimming ability of larger fish and are especially disadvantaged in pool-and-weir, vertical-slot, and similar fishways that require strong swimming and jumping ability. As a result, researchers have looked for alternative passage methods for these smaller-bodied fishes (Baker and Boubée 2006; Doehring et al. 2011; Baker 2014).

Nature-like fishways are designed to replicate natural rivers or streams and, by doing so, promote an aquatic environment as if no barrier existed (Parasiewicz et al. 1998; Calles and Greenberg 2005; Gustafsson et al. 2013). The idea is that by reproducing the environmental conditions and qualities of the original river or stream, all aquatic organisms present before the barrier was built should be able to use the fishway (Calles and Greenberg 2005; Gustafsson et al. 2013). However, due to the gentle slope required in most nature-like fishways to reproduce similar hydrological conditions, space can be a limiting factor. This makes nature-like fishways unusable at some installations, and thus efforts have continued to design more applicable fish passes (Mallen-Cooper 1999; Baker 2014).

A simple wetted ramp has been proposed as an effective method to pass small-bodied fishes over low-head barriers (Figure 1) (Yasuda et al. 2004; Baker and Boubée 2006; Baker 2014). The wetted ramp serves as a passage device by offering a shallow inclined plane that fish can swim up, providing another option for fish unable to jump a low-head barrier. Although large dams are of continued concern, low-head barriers, such as culverts and weirs, make up the majority of in-river obstructions in the United States (Bednark 2001; Pohl 2003).To some extent, the wetted ramp is a cousin of the nature-like fishway in that it provides a shallow slope for fish to swim up, thus making it more useable by smaller-bodied fishes. The major difference, however, is that it works over much smaller spatial distances. A simple wetted ramp can be installed at a low-head barrier for a much less than it would cost to design and construct a nature-like fishway.

Studies have suggested the use of baffles and other substrate-altering additions to wetted ramps to increase the passage efficiency of small, often climbing, fishes (Baker and Boubée 2006; MacDonald and Davies 2007; Doehring et al. 2012; Baker 2014). Climbing species rely on unique morphological adaptations, such as modified pelvic fins, rather than strong swimming ability, to navigate the edges of waterfalls and other barriers (Baker 2014). By increasing the roughness of the ramp, water velocity will slow slightly and smaller climbing species may be able to find additional purchase. Many variables can be manipulated and differ from ramp to ramp (material used, substrate, shape, etc.), and these variables all likely contribute to passage success, but setting the appropriate ramp angle of inclination and ramp length is a task required of all ramps used for fish passage (Baker 2014). Ramp angle of inclination has been shown to be most important for climbing species while both ramp length and angle of inclination have been shown important for passage success of non-climbing species (Baker 2014). In the Great Lakes region, a smooth wetted ramp has been proposed as a way to move finfishes over low-head sea lamprey barriers (Sherburne and Reinhardt 2016; Reinhardt, personal communication).

The smooth wetted ramp used in this study differs from the baffled design primarily in that it lacks any sort of substrate roughening elements for water velocity reduction or climbing. Instead, scaling the smooth wetted ramp requires a short bout of burst swimming. This is similar to many other fishways that challenge fishes with multiple bouts of burst swimming followed by resting areas in low-velocity refuges. The wetted ramp differs from these other designs because it reduces the number of burst swimming sections to one. In the Great Lakes region, where invasive sea lamprey (*Petromyzon marinus*) make annual spawning runs up rivers, the smooth wetted ramp has been proposed as a selective fishway that will pass non-target finfishes, or true fish, over sea lamprey barriers (Sherburne and Reinhardt 2016). The single session of burst swimming required to scale a smooth wetted ramp has been shown to be enough to separate migrating lamprey from migrating finfishes (Reinhardt 2009).

The Wetted Ramp as a Selective Sea Lamprey Barrier

In the Great Lakes region, low-head dams are often used as barriers for sea lamprey migration (Smith and Tibbles 1980). The sea lamprey (*Petromyzon marinus*) is a jawless fish native to the Atlantic Ocean. Instead of a jaw, they have a suction cup like mouth with rows of inward facing conical teeth used to latch onto their host. Once attached, lampreys use their toothy tongue to scrape and rasp a hole in the host from which they can then consume the hosts' blood and other bodily fluids (Smith and Tibbles 1980). When the Welland Canal was completed in the 1930s, it connected the once isolated upper Great Lakes with Lake Ontario. This allowed sea lampreys and other aquatic organisms once blocked by Niagara Falls access to the four upper Great Lakes (Smith and Tibbles 1980). By the late 1940s/ early 1950s, sea lampreys were successfully established in all five Great Lake ecosystems. Shortly thereafter, the multimillion dollar lake trout (*Salvelinus namaycush*) fishery collapsed (Smith and Tibbles 1980). In an effort to control lamprey populations, mechanical weirs were installed in rivers along Lake Huron to block migrating lamprey and prevent them from reaching spawning habitat.

Sea lampreys are anadromous, meaning they spend their adult life at sea, or in a large lake, but migrate upriver to spawn (Richardson et al. 2010). After depositing their eggs in a silty freshwater river bed most adults then die. Larval lamprey, or ammocoetes, will then hatch and spend 4–6 years filter feeding before migrating downriver. The parasitic stage, or the hematophagous stage, only begins when the lampreys have reached the ocean or large lake (Silva et al. 2013). Adult sea lampreys will then spend the next year or two parasitizing other fish before metamorphosing again and migrating upriver to breed and die (Richardson et al. 2010). Due to the vastness of the Great Lakes and the effort it would take to attempt to control lamprey populations while they are actively parasitizing fish; efforts focus largely on controlling populations during spawning runs when the sea lampreys congregate in rivers (Smith and Tibbles 1980).

There are two primary methods for controlling lamprey populations. The first emphasizes the use of barriers to prevent adult migratory stage lamprey from successfully reaching spawning habitat. The mechanized weirs and low-head dams installed in the 1950s and after stressed this method. Unfortunately, these barriers also stop the movement of other non-target fish species. This includes migratory species from the Great Lakes such as Lake Sturgeon (*Acipenser fulvescens*) as well as potamodromous species moving within river systems (Mclaughlin et al. 2007). In the 1960s, it became clear that the mechanized weirs and low-head dams installed to block migrating lamprey were having adverse effects on native fish populations, so an alternative method was developed (McDonald et al. 2007).

The second method emphasizes the use of lampricides and other chemicals to target lamprey during their filter-feeding juvenile stage. Large areas of lamprey spawning habitat are treated each year with lampricides, and although this method is effective, it is not ideal

(Mclaughlin et al. 2007). Due to the rising cost of lampricide production and the unknown effects it could be having on non-target species, particularly amphibian populations, the Great Lakes Fishery Commission (GLFC) released a statement in 1992 with a goal to reduce reliance on lampricides and improve and/or develop alternate control methods (McDonald et al. 2007; Mclaughlin et al. 2007). Milestone three of the GLFC sea lamprey management plan released in 2001 stated their goal to reduce reliance on lampricides by up to 50% by the end of the decade (Mclaughlin et al. 2007). More efficient and more selective trap designs would need to be developed as well as more reliable ways to pass non-target species over lamprey barriers. As a result, there has been a tremendous upswing in research aimed at addressing this need (Reinhardt 2009; D’Aguir 2010; Bunt et al. 2012; Mclean 2014; Sherburne and Reinhardt 2016).

The smooth wetted ramp has been proposed as an effective way to allow finfish to pass over low-head dams and weirs while still blocking the movement of lampreys (Reinhardt 2009; Sherburne and Reinhardt 2016). The ramp relies on the difference in swimming ability due to different swimming styles to sort fishes. The swimming methods employed by finfishes, such as the carangiform and sub-carangiform methods, allow more powerful burst swimming than the anguilliform method used by lamprey (Beamish 1978; Viedler 1993). It has been suggested that most sea lampreys are unable to scale short ramps that exceeded half of their total length at 30° to 45° because they are not adept climbers, nor are they capable of sustained, strong burst swimming (Viedler 1993; Reinhardt 2009). In contrast, preliminary studies suggest that finfish are able to scale wetted ramps that most lampreys cannot, possibly due to their stronger burst swimming ability (Reinhardt, personal communication). Ideally, a wetted ramp would be used at low-head sea lamprey barriers in the Great Lakes region to pass non-target finfish while the barrier continues to prevent lamprey migration upstream.

Unfortunately, the wetted ramp has suffered from low passage success in field tests. Passage efficiency, measured as the percent of individuals that pass the wetted ramp out of the total number of individuals that approach it, has been lower than expected based on lab results (Reinhardt, unpublished data). Finfish attempting to scale a 15°, 1.5m long wetted ramp at a lamprey barrier in the Brule River, Wisconsin, appeared to be largely unable to do so, with 2% finfish completion in 2014 and 14% finfish completion in 2015 (Reinhardt, unpublished data). If the wetted ramp is to become a useful tool for lamprey management, we must better understand the variables that determine passage success for finfishes. In the following sections, I will address two variables, in particular: swimming mechanics and fish behavior.

Section 1: Swimming mechanics

As the wetted ramp represents a physical challenge, the swimming ability of finfishes is important when determining passage success. The swimming ability of fishes has been studied in depth in the literature, largely to aid in the design and construction of fish passes (Bainbridge 1958; Webb 1971; Wardle 1975; and many others). However, the wetted ramp represents a unique challenge in that it requires fish to swim up an incline through a shallow film of water. How this unique environment affects the swimming ability of fishes is not fully understood. The effect of fish size on swimming ability has been well studied in fully submerged environments (Bainbridge 1958; Webb 1976; Viedler 1993; Ojanguren and Braña 2003), but it has never been studied for fish swimming in thin films of water, or in thin films of water at an incline. In this study, I address this knowledge gap.

Preliminary analysis suggested that there may be a size effect to passage success on the smooth wetted ramp, with smaller individuals doing better than larger fish (Reinhardt, unpublished data). This is the opposite of what one might expect, as larger fish have been shown to be stronger swimmers capable of reaching higher velocities and so better suited for burst swimming (Bainbridge 1958; Webb 1971; Wardle 1975; Ojanguren and Braña 2003). Larger fish have greater muscle mass and propulsive surface area, allowing for greater maximum swimming velocities (Webb 1971; Wiehs 1973; Vielder 1993). As such, it would be reasonable to expect larger fish to have greater success, measured in distance traveled on the wetted ramp, than smaller fish. The wetted ramp represents a burst swimming challenge, so individuals capable of higher burst swimming speeds should be at an advantage. However, based on preliminary video analysis, this does not seem to be the case (Reinhardt, unpublished data). This size dependent swimming ability in a partial film of water has never been reported or quantified.

Acceleration, unlike maximum swimming speed, is relatively unaffected by body size for fully submerged fish (Webb 1976). Larger individuals have more muscle mass and propulsive surface area, but this is counterbalanced by the increase in overall mass needed to be moved and surface drag with the water (Webb 1976). Larger fish are able to achieve higher swimming velocities because they accelerate longer than smaller individuals, even though the two groups accelerate at approximately the same rate (Webb 1976). The wetted ramp may not offer enough time for larger fish to gain enough speed for their additional muscle mass and propulsive surface area to be an advantage. In one study, the largest fish accelerated 30% longer than the smallest individuals (Webb 1976). Thus, the wetted ramp may select against larger individuals because it does not offer enough space and time for bigger fish to build up velocity. This is likely not the only factor working against larger fish though. The same size advantage that gives larger fish an edge in fully submerged environments may be a liability in a shallow film of water. Relatively less of a large fishes' propulsive surfaces are submerged at any given time in a shallow film of water, and larger fish must also move more mass.

In this study, I test to see if there is a size effect on passage success on the wetted ramp, with smaller individuals having more success than larger individuals. I hypothesize that size will affect passage success on the wetted ramp because there is a relationship between increasing fish size and relative submerged propulsive surface area in shallow films of water. I predict that larger fish will enter with higher initial velocities but will be unable to accelerate and so will achieve less total distance traveled than smaller individuals.

Section 2: Fish Behavior

A well-designed fishway that caters to the physical abilities of its target species will fail if fish lack the motivation to attempt and complete the pass (Williams et al. 2012). Understanding motivation and behavior has often been overlooked in fish passage studies, with researchers choosing to focus on the swimming ability of their target species instead. Recent publications, however, have begun to address this literature gap and explore how motivation and fish behavior affect passage success (Williams et al. 2012). Although this is a start, we are far from fully grasping how fish make decisions about fish passes. A better understanding of fish behavior is paramount to optimizing passage success.

It is well-understood that fish orient themselves into the strongest water flow while migrating to avoid unsuitable tributaries and other dead ends (Bunt et al. 2012). This rheotaxis has been used successfully to increase fish guidance and attempt rates at numerous fishways (Arnekleiv and Kraabøl 1996; Nestler et al. 2008; Bunt et al. 2012). Before discussing this further, it will be useful to define a few key concepts. Attraction rate is simply how efficiently a given fishway draws fish towards its entrance, or the number of individuals near the fishway entrance out of the total number of individuals swimming upriver (Bunt et al. 2012). Attempt rate, then, is the number of individuals that try out of the total number of individuals attracted to the pass, or the number of fish that begin the fishway out of the total number of fish at the entrance (Castro-Santos 2004). Attraction rate and attempt rate are therefore similar in that they both work before fish enter the fishway. If attraction rate is low, a high attempt rate will mean less in terms of number of fish passed while the same is true for the inverse scenario. Passage efficiency is defined as the number of individuals that complete a fishway out of the total number of fish attracted to its entrance (Bunt et al. 2012). Although passage efficiency may not be directly related to attraction rate and attempt rate, in that a high number of attempts may not necessarily mean a large number of successes, the three concepts have often been considered related (Arnekleiv and Kraabøl 1996; Nestler et al. 2008; Bunt et al. 2012). Improving attraction rate before the fishway and improving attempt rate should improve passage success on/in a fishway.

It has been suggested that proper attraction flow is one of the greatest determinants of passage success because proper attraction leads to high attempt rates, and higher attempt rates lead to greater passage success simply because more fish are trying (Castro-Santos 2004). Attraction flow, in this sense, works to motivate fish *before* they are on/in the fishway by coercing hesitant or unsure individuals to swim in a particular direction (Arnekleiv and Kraabøl 1996; Nestler et al. 2008; Bunt et al. 2012). Attraction flows have been mostly used in fish passage studies to motivate fish to swim in a particular direction in-river and help them find the fishway entrance. To my knowledge, however, there are no studies that have looked at motivating fish *during* passage attempts through fishways.

While there are numerous studies that have observed fish in passes, they have focused almost solely on the physical ability of fishes and how this may determine success, or distance traveled through a fishway (Baker 2014; Makrakis et al. 2011; Fernandez[A] et al. 2007; Fernandez[B] et al. 2007; Kahler et al. 1998; etc.) In motivational studies, the focus tends to be on improving attraction and attempt rates rather than improving attempt quality. A high-quality attempt in which a fish exerts optimal effort to complete the pass would be much more valuable than multiple attempts in which the fish tries half-heartedly. Improving attempt rates is an important goal in improving passage success but so is improving the quality of each attempt. By increasing the effort each fish puts into each attempt in addition to increasing the attempt rate, we may be able to significantly improve the number of fish making it through fishways. In this study, I look at how fish respond to changes in on-ramp characteristics *during* a passage attempt over a fish pass.

It is not yet understood how changes during a passage attempt will affect fish motivation, behavior, and ultimately passage success. Fish, like other organisms, constantly perceive their environment and make decisions about how to act based on the information they receive (Williams et al. 2012). By adjusting the physical characteristics of fishways, we should be able to adjust the environment fish perceive. In this study, I manipulate the physical characteristics of the wetted ramp to see how fish respond. If fish fail to respond to changes in on-ramp characteristics during an attempt, this may suggest that future efforts in improving motivation be focused elsewhere. Instead, efforts in improving motivation could be focused on pre-attempt behavior to increase passage attempts and passage success (Castro-Santos 2004). However, if fish do respond to changes in on-ramp characteristics, design improvements to the wetted ramp could result in improved motivation and passage success.

In this study, I look at how on-ramp changes during an attempt, specifically a change in angle of inclination, affect fish behavior. Fish, like other organisms, use their inner ear to maintain balance and determine their spatial orientation (Popper et al. 2005). Therefore, a fish would likely perceive changes in on-ramp angle of inclination. If fish adjust their behavior in response to a change in angle of inclination, we may be able to manipulate the physical structure of the ramp to improve motivation. Rather than relying on straight ramps with continuous angles of inclination, a curved/bent ramp or some mix of different angles may be more effective at passing fish. Steeper sections of ramp might have greater water velocity, but they will also represent a more difficult challenge; while shallower sections might be easier to swim up, but will offer less motivational cues in the form of discharge rate (Ohlberger 2007; Bunt et al. 2012; Williams et al. 2012). To my knowledge, how fish respond to these different signals in a short time frame has never been investigated.

Preliminary video analysis from a ramp installed on the Brule River, Wisconsin, provided by the USFWS, of finfish attempting to scale a wetted ramp suggests that many finfish have the physical ability to scale the ramp, but fail due to lack of motivation (Reinhardt, unpublished data). In this study, I look at whether or not finfish notice changes in on-ramp angle of inclination and respond accordingly. Fish perceive changes in spatial orientation because they have an inner ear, so they should respond to a change in angle of inclination with a change in behavior. I predict that a steeper angle of inclination will result in a greater tail beat frequency as fish compensate for the more difficult task by exerting more effort.

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Methods

Study Location and Experimental Set-up

Experiments were carried out at the Saline Fisheries Research Station in Saline, MI. Fish were collected bi-weekly from the Koch Warner Drain and the Saline River, located on research station property, using electrofishing equipment and seines. Individuals were housed on site in re-circulating tanks. Creek Chub (*Semotilus atromaculatus*) and White Sucker (*Catostomus commersonii*) were selected because of their abundance and size range. Chub size ranged from 10.5 cm to 24 cm while suckers ranged from 10 cm to 25 cm total length.

To test whether fish respond to on-ramp changes in angle of inclination, two different ramps were used. The first was a control with a constant angle of inclination. The second ramp had the same initial angle of inclination as the control, but the angle of inclination increased by 6° after 33 cm. The ramp specifications will be discussed in further detail below. During each trial, fish were housed in a small, covered trough, measuring 30 cm depth x 40 cm x 40 cm, or about 48000 cm^3. Fish were allowed to freely attempt to swim up the ramp, and other than flow attraction, no other motivational cues were used. A JAI 5000MCC high speed camera and infrared lights were mounted above the runs and attempts were recorded at 90 FPS using the JAI Camera Control Software. Photo-electric eyes placed at the start of each ramp were used to trigger recordings, and recordings lasted for 8 seconds. Due to system limitations, there was a 30–60 second delay between recordings as the system saved an attempt and was re-primed to record the next. Water was drawn directly from the Koch Warner Drain, but to increase flow, a recirculating pump system was also used.

Ramp Specifications

The ramps were made by bending 0.635 cm acrylic plastic. The control ramp measured 1 m x .3 m (L x W) and the bent ramp measured 0.8 m x 0.3 m (Figure 1). Maximum measurable distance traveled on the control ramp was 65 cm and maximum measureable distance traveled on the bent ramp was 70 cm due to limitations on camera positioning. Both ramps were positioned so that they started with an initial angle of inclination of 8.4°. The control ramp had a continuous angle of inclination of 8.4° throughout while the bent ramps' angle of inclination increased to 14.4° after 33 cm. The control ramp had a total rise of 15 cm while the bent ramp had a rise of 16 cm. Solid black lines were drawn across each ramp in 10 cm increments to measure distance traveled. The ramps were positioned such that the first 5 centimeters of ramp were below the water line in the fish run when water flow was turned off to help guide fish to the ramp entrance.

Flow Characteristics

Maximum achievable discharge on both ramps was found to be approximately 2 liter/second. Average water depth on the bent ramp at the 70 cm mark was about 0.8 cm and gradually decreased to an average depth of about 0.4 cm at the 10 cm mark. Average water depth on the control ramp at the 80 cm mark was about 0.8 cm and gradually decreased to an average of 0.4 cm at the 10 cm mark. Water depths were not measured beyond the 70 and 80 cm mark respectively because the ramps extended beyond the cameras field of view. Depth was measured by affixing a bolt to the surface of the ramp while water was turned on and then measuring the displacement of a nut attached to the bolt after the bolt was twisted so that it no longer was in contact with the water, made observable from ripples. To determine water velocity, an object was timed as it floated down each ramp. Water velocity on the bent ramp increased from an average of 81.32 cm/s between the 70–60 cm segment to an average of 164.87 cm/s in the last 10 cm of the ramp. Water velocity on the control ramp increased from an average of 119.08 cm/s in the 70–60 cm segment to 147.65 cm/s in the last 10 cm of the ramp. Water velocities were not measured in segments beyond 70 cm because they were out of the cameras' field of view. Water temperature varied from 15°C to 25°C throughout the summer, but the effect of water temperature was not studied.

Trials

Trials were conducted June–August 2015. Three naïve fish were introduced each night to each ramp, for a total of six naïve fish used each night. Due to poor performance in consecutive nights, each fish only ever saw one ramp and was then released upriver behind a dam to avoid recapture. Although the two parallel runs were identical, they were separate so fish introduced to one ramp would never see the other. To identify individuals during post trial video analysis, three fish of differing sizes were used (small, medium, and large). Fish species' were determined, and each individual's total length was recorded before each trial. These lengths were used to identify individual fish by comparing the fishes recorded length with the 10 cm increments drawn onto each ramp. Trials were conducted from dusk until approximately 1am, or whenever the attempt rate began to decline markedly. An attempt began when a fish reached 10 cm onto the ramp, and triggered the camera to record for 8 seconds. After an attempt, the video file was manually saved and the system was re-primed to record another attempt.

Data Analysis

Video files were analyzed using ImageJ, a free digitizing software. Data were extracted from the video files by recording the following: distance each fish traveled up the ramp, fish size (for identification and analysis purposes), tail beat frequency before and after the inflection, on ramp curvature, frames between each 10cm increment, and snout and tail amplitudes. Curvature, a measure of stroke wavelength, was defined as the straight-line distance from snout to tail when a fish curves its body during a stroke divided by the total length of the fish. A larger curvature, therefore, represents a fish with minimal bending during its strokes while a small curvature represents an individual with smaller wavelengths and greater body bending. For this study, curvature was measured when the fish was in the “s” shape, and because curvature is independent of size, it is a useful measurement to compare fish of differing sizes. Snout and tail amplitude were defined as the total lateral distance moved in one direction, plus the total lateral distance moved in the opposite direction during a swim stroke by the respective body part. A fish moving its snout or tail from side to side to further extremes would thus have greater amplitude for the respective measure. Statistical analysis was done using Systat software.

Simple linear regressions were used to compare chub length and average snout distance traveled up the control ramp for all attempts as well as chub length and average snout distance traveled up the bent ramp for all attempts. Fish length and distance traveled were also compared for suckers in the same fashion. Maximum distance measurements were not used because the ramp is finite, and maximum distances would be truncated and non-representative for many individuals. Additional linear regressions were used to regress fish length on average initial velocity and maximum initial velocity on both the control and the bent ramps combined. Initial velocities were determined by counting the frames it took each fish to travel the first 10 cm past the photo-electric eye. A general linear model was used to test if there was a significant ramp effect on the relationship between fish length and initial velocity.

The on-ramp acceleration of each fish was assessed in two ways, average acceleration and "best performance" acceleration. Average acceleration was defined as the average acceleration for a fish as it ascended the ramp through all of its attempts. If a fish had fewer than three attempts, average acceleration was not calculated. "Best performance" acceleration was defined as the acceleration of the attempt in which the fish reached its highest point on the ramp, or if it reached the same height in multiple attempts, the attempt in which it reached the highest point in the fewest number of frames. To assess acceleration, the velocity between each 10 centimeter increment was determined by counting the number of frames it took a fish to travel the given distance. Acceleration was then the difference in velocity between each successive 10 cm segment. Simple linear regressions comparing fish length and average acceleration as well as fish length and best performance acceleration were done for both the control ramp and the bent ramp.

To assess the effect of fish length on on-ramp behavior, a linear regression was used to relate chub length to on-ramp curvature. If larger fish behave differently on ramp than smaller individuals, we would expect to see a relationship between fish length and on-ramp curvature. On-ramp curvature was only measured for attempts on the control ramp to avoid the additional variable the change in angle of inclination would introduce on the bent ramp. Only the best performance attempt for each fish was measured. Suckers were excluded from this analysis due to their limited population size.

To test whether or not fish noticed a change in on-ramp angle of inclination, average, maximum, and minimum tail beat frequency were determined before and after the inflection point for both ramps. To do this, tail beat frequency was measured for the last 10 cm before the inflection point (from about the 23 cm mark to the 33 cm mark). Tail beat frequency after the inflection point was measured for the first 10 cm or until the entire fish had cleared the inflection point. This was to allow fish time to experience the change in angle of inclination and have the opportunity to respond. For measurements on the control ramp, the "inflection point" was set at 33 cm to correspond with the bent ramp. A diagram of the ramp arrangements has been included for reference (Figure 1).

Comparisons were made for average, maximum, and minimum tail beat frequencies before the inflection point between both ramps; and for average, maximum, and minimum tail beat frequencies after the inflection point between both ramps. Average tail beat frequency was defined as the average frequency over all attempts for all fish. Maximum tail beat frequency was calculated by averaging the maximum recorded tail beat frequency for each fish at each location (before the inflection and after the inflection). Minimum tail beat frequency was calculated in the same fashion. For analysis, a Hoteling's t-test was used to compare average, maximum, and minimum tail beat frequencies at each point between each ramp.

Results

Each night, attempts began approximately 30 minutes after lights out. This was not always the case, though, and varied from night to night. Sometimes fish began attempting within the first 15 minutes, and other times fish failed to attempt within the first hour. There seemed to be a trend with "fresher fish," or fish captured that day, being more active than fish that had been in the holding tank for a longer period of time. Most nights the rate of attempts was highest earlier in the evening, and tapered off slowly as the night continued. This is possibly due to a loss in fish motivation as fish attempted and realized the ramps did not lead anywhere, but could also be due to fish fatigue. As with time to first attempt, fresher fish seemed to attempt more often than fish that had been in holding longer.

Chubs on the control ramp had an attempt rate of about 80% and a passage efficiency of about 40%, while suckers on the control ramp had an attempt rate of about 67% and a passage efficiency of around 33%. Chubs on the bent ramp had an attempt rate of about 80% and a passage efficiency of about 30%, while suckers on the bent ramp had an attempt rate of about 68% and a passage efficiency of about 9%. Combined, the control ramp had an attempt rate of about 74% and a passage efficiency of about 37% while the bent ramp had an attempt rate of about 76% and a passage efficiency of about 24%. It should be noted that an attempt was considered successful on the control ramp if a fish reached the 65 cm mark and successful on the bent ramp if a fish reached the 70 cm mark due to camera positioning limitations.

Effect of Fish Length on Distance Traveled

For the control ramp, there was a strong negative relationship between fish length and average snout distance traveled for both chubs and suckers ($p=0.001$, $N=36$; and $p=0.011$, $N=16$, respectively) (Figure 2). For chubs, mean distance traveled decreased at a rate of approximately 2.5 cm/cm increase in fish length. For suckers, mean distanced traveled decreased at a rate of approximately 3 cm/cm increase in fish length. For the bent ramp, there was also a strong negative relationship between fish length and mean snout distance traveled for both chubs and suckers (p=0.002, N=37; and p=0.008, N=15, respectively) (Figure 3). As chub length increased, mean distance traveled decreased at a rate of approximately 2.1 cm/cm increase in fish length. For suckers, mean distance traveled decreased at a rate of approximately 4 cm/cm increase in fish length.

<u>Effect of Fish Length on Initial Velocity</u>

Initial velocity was measured as the number of frames needed to travel the first 10 cm after the photo-electric eye triggered a recording, or from the 10 cm mark to the 20 cm mark. A general linear model used to test if there was an effect of ramp type on the relationship between chub length and velocity yielded no significant effect, so initial velocity data from both ramps were combined. A strong positive relationship between chub length and mean initial velocity as well as between chub length and maximum initial velocity was found (p=0.0065, N=45, and p=0.0003, N=48, respectively) (Figure 4). As chub length increased, mean initial velocity across both ramps also increased. Mean initial velocity increased at a rate of approximately 1.6 cm/s per cm increase in chub length while maximum initial velocity increased at a rate of approximately 4.2 cm/s per cm increase in fish length. The mean initial velocity for the 10 cm chubs was about 50cm/s, while the 25 cm chubs had a mean initial velocity of around 70 0cm/s. The maximum initial velocity for 10 cm chubs was around 60 cm/s, while the maximum initial velocity for the 25 cm chubs was around 120 cm/s.

The effect of fish size on initial velocity for suckers was measured the same way it was for chubs. Again, a general linear model used to test if there was an effect of ramp type on the relationship between sucker length and velocity yielded no significant effect, so initial velocity data from both ramps were combined. There did not appear to be any effect of fish length on average or maximum initial velocity for suckers (Figure 5). There was a slight negative relationship between sucker length and mean initial velocity as well as between sucker length and maximum initial velocity, but neither of these were significant ($p=0.1447$, $N=23$; and $p=0.5620$, $N=23$, respectively). Mean initial velocity decreased at a rate of approximately -2.5 cm/s per cm increase while maximum initial velocity decreased at a rate of approximately -1.7 cm/s per cm increase in fish length.

Effect of Fish Length on On-Ramp Acceleration

On-ramp acceleration was the difference in velocity between each successive 10 cm segment. There was a strong negative relationship with increasing chub length and mean on-ramp acceleration on the bent ramp ($p=0.001$, $N=19$) (Figure 6). Fish larger than approximately 15 cm were unable to accelerate as they ascended. On-ramp acceleration decreased at a rate of around -2.5cm /s/s per centimeter increase in chub length. There was also a strong negative relationship between chub length and best performance acceleration on the bent ramp ($p=0.001$, $N=23$). Again, fish larger than approximately 15 cm appeared to be unable to accelerate. On-ramp acceleration decreased at a rate of around -3 cm/s/s per centimeter increase in chub length (Figure 7). Although there was a slight negative relationship between sucker length and mean on-ramp acceleration on the bent ramp, as well as between sucker length and best performance acceleration on the bent ramp, neither relationship was significant (p=0.950, N=7 (Figure 6) and p=0.830, N=10 (Figure 7), respectively).

On the control ramp, neither chubs nor suckers showed a significant relationship between fish length and mean acceleration, although both suggested negative relationships (p=0.105, N=12 and p=0.625, N=7, respectively) (Figure 8). However, there was a strong negative relationship between chub length and best performance acceleration on the control ramp (p=0.001, N=21) (Figure 9). Chubs larger than approximately 16 cm appeared to be unable to accelerate on-ramp as they ascended, and on-ramp acceleration decreased at a rate of around -2.5 cm/s/s per centimeter increase in chub length. Suckers also showed a negative relationship between fish length and best performance on-ramp acceleration, but this relationship was not significant (p=0.851, N=10) (Figure 9).

Effect of Fish Length on On-Ramp Behavior

On-ramp curvature was used as a metric for on-ramp behavior. More erratic, exaggerated snout and tail movements would result in a smaller curvature. There was a significant relationship between curvature and fish length (p=0.012, N=30) for chubs on the control ramp (Figure 10). As chub length increased, curvature decreased. There was also a significant positive relationship between curvature and distance traveled for chubs (p<.001, N=30) (Figure 11). As curvature increased, distance traveled also increased. A significant positive relationship was also seen between relative head amplitude and fish length, and between relative tail amplitude and fish length ((p<0.001, N=30) and (p=0.05, N=30)) (Figure 12). As fish length increased, both relative tail amplitude and relative head amplitude increased.

Effect of a Change in Angle of Inclination on On-Ramp Behavior

Tail beat frequency was used to assess fish behavior in response to a change in angle of inclination during a passage attempt. There was no significant effect of change in angle of inclination on tail beat frequency for either chubs or suckers for any of the comparisons in the Hoteling's t-test (Tables 1 and 2). For chubs, the closest comparison to significance was between maximum tail beat frequencies after the inflection point. Chubs on the control ramp averaged 34.6±5.5 hz after the inflection point while chubs on the bent ramp averaged 38.7±8.9 hz ($p=.2987$). For suckers, the closest comparison to significance was also between maximum tail beat frequencies after the inflection point. Suckers on the control ramp averaged 30.9±5.8 hz after the inflection while suckers on the bent ramp averaged 34.4±7.1 hz ($p=.3313$).

Discussion

The wetted ramp appeared to be a size-selective passage device, with smaller finfish having more success than larger individuals (Figures 2 and 3). Although larger chubs entered at a higher initial velocity (Figure 4), most were unable to accelerate on the ramp (Figures 6, 7, and 9). Smaller chubs entered at lower initial velocities, but their ability to accelerate on-ramp allowed them to reach greater distances. Larger fish may be at a disadvantage because they have greater muscle mass to move upward and also have relatively less submerged propulsive surface area.

There may have also been a size-dependent behavioral difference in swimming style on the wetted ramp. Larger fish tended to use more exaggerated, less controlled, body undulations on the wetted ramp resulting in smaller curvatures (Figure 10) and greater relative head and tail amplitudes (Figure 12). There was also a strong relationship between body curvature and distance traveled, suggesting that swimming styles with larger curvatures, and thus more controlled body undulations, may be more efficient on ramp (Figure 11). Lastly, finfish as a group do not appear to respond to an increase in angle of inclination (Tables 1 and 2), as this study did not see any significant differences in tail beat frequencies at the population level. I further discuss the swimming mechanics of chubs (*Semotilus atromaculatus*) and suckers (*Catostomus commersonii*) on the wetted ramp.

Section 1: Swimming Mechanics

Creek Chub (Semotilus atromaculatus). As hypothesized, there was a strong inverse relationship between chub length and distance traveled on the wetted ramp (Figures 2 and 3). As fish length increased, distance traveled significantly decreased, suggesting that larger fish have a harder time going up the ramp and are possibly at a disadvantage. This is consistent with what Reinhardt (unpublished data) found in field trials, but is contrary to what would be expected based on studies of fish engaged in submerged swimming. Those studies suggest that larger fish should be at an advantage because they have greater muscle mass and relatively more propulsive surface area, better equipping them for burst swimming challenges (Webb 1971; Wardle 1975). However this does not appear to be the case on the wetted ramp.

On both ramps combined, larger chubs entered at higher mean and maximum initial velocities than smaller individuals (Figure 4). In a fully submerged environment, such as the holding tank before each ramp, larger fish are able to use their greater muscle mass and greater relative propulsive surface area to generate more thrust (Bainbridge 1958; Wardle 1975). However, this increased velocity at the beginning of each ramp does not appear to translate into on-ramp success, measured in distance traveled (Figure 2). Smaller chubs entered at lower average and maximum velocities (Figure 4) but were able to achieve greater distances on the wetted ramps (Figures 2 and 3). This suggests that initial velocity is a poor predictor of passage success for chubs in this size range on wetted ramps or inclines at these specifications; a 1m ramp with a 8.4° incline. For a shorter ramp, initial velocity may be a better predictor of passage success as the time for deceleration may be much shorter, but it was not the case here.

If initial velocity is a poor predictor of passage success, on-ramp acceleration may be more important. These results suggest that smaller chubs are able to accelerate on-ramp while most larger individuals are unable (Figures 6, 7, and 9). For both mean acceleration and best performance acceleration on the bent ramp, chubs showed a significant negative relationship between increasing fish length and on-ramp acceleration (Figures 6 and 7). On the control ramp, chubs again showed a significant negative relationship between fish length and best performance on-ramp acceleration (Figure 9), but there was no significant relationship between mean acceleration and fish length (Figure 8). In all three significant cases, chubs above approximately 15 cm were unable to accelerate as they ascended the ramp (Figures 6, 7, and 8). This suggests that smaller fish may have more success, measured in distance traveled, because they are able to accelerate on the ramp.

For chubs on the control ramp, mean acceleration was not significantly related to fish length (Figure 8). It is likely that this is a result of low sample size, as average acceleration was only calculated if a fish attempted at least three times and achieved a great enough distance in each attempt to measure velocity over three points. However, it should be mentioned that there could be a biological explanation for this observation. The control and bent ramps were identical in every aspect except for the change in angle of inclination 33cm into the ramp. In order for an attempt to be included in the mean acceleration measurement, a fish had to make it to the 43cm mark or higher (to obtain three velocity measurements). This minimum distance of 10cm of increased angle of inclination on the bent ramp could have affected fish behavior and/or swimming mechanics. Perhaps there is a relationship between angle of inclination and the effect fish length has on acceleration.

White Sucker (Catostomus commersonii). Like chubs, white suckers showed a significant negative relationship between fish length and distance traveled on both the bent ramp and the control ramp (Figures 2 and 3). As fish length increased, distance traveled significantly decreased. This suggests that the relationship between fish length and distance traveled on the wetted ramp is consistent across multiple species. Despite expectations, larger suckers appear to be unable to use their larger muscle mass and greater relative propulsive surface area to achieve greater distance on the wetted ramp (Figures 2 and 3) (Webb 1971; Wardle 1975). Instead, smaller fish appear to have the advantage.

However, unlike chubs, there was no significant relationship between sucker length and mean and maximum initial velocities (Figure 5). Whether this is a result of the smaller size range and smaller sample size in suckers, or an actual biological difference between species, is not clear. In addition, there was no significant relationship between sucker length and on-ramp acceleration (Figures 6, 7, 8, and 9). Although all acceleration and size relationships were negative, none were significant. While these non-significant relationships could be experimental artifacts, a biological explanation for these observations may exist. The swimming ability of different species can be markedly different (Bainbridge 1958; Tierney 2011; Fu et al. 2013; Baker 2014; Sherburne and Reinhardt 2016), so it is possible that the relationship between fish size and on-ramp acceleration is different in suckers than it is in chubs. However, both species have fusiform, or trout-like, body shapes, and all suckers used in the study were of similar size to the chubs used. Instead it is more likely that if there is a biological explanation for the differences observed between chubs and suckers, it is something behavioral (Williams et al. 2012).

The Swimming Mechanics of Fusiform Finfish on the Wetted Ramp. My results show that smaller fish traveled farther on the wetted ramp (Figures 2 and 3). A larger body size may actually be a disadvantage in a situation where the body is only partially submerged. Bigger fish have more mass, and increased mass requires more thrust to move up an incline (Bainbridge 1958). These data also suggest that initial velocity is a poor predictor of passage success, whereas on-ramp acceleration may be more important (Figures 4–9). Fish of varying sizes tend to accelerate at approximately the same rate in submerged environments (Webb 1976). Larger fish have more muscle mass and propulsive surface area than smaller individuals, but this advantage is counterbalanced by the added effects of drag during acceleration (Webb 1976). Larger fish are able to achieve greater swimming velocities in submerged environments because they accelerate longer than small individuals; however, this may not be possible on the wetted ramp. Fish on the wetted ramp may never reach maximum possible burst swimming velocity because the force of gravity and water pressure are constantly pulling them back as they swim upward. Numerous studies have shown that fish mass increases exponentially with increasing fish length (Beckman 1948; Cren 1951; Webb 1976; Moutopoulos and Stergiou 2002; Froese 2006; etc.) (Figure 13), because volume increases exponentially with linear increases in surface area (Froese 2006). Thus, larger fish have no advantage in being able to accelerate longer on the wetted ramp, but have exponentially greater mass to move upward.

In addition to their greater mass, relatively less of larger fish's propulsive surfaces are submerged on the wetted ramp because it is a shallow film of water. Imagine a two-dimensional rectangular shaped species of fish, with a 3:1 aspect ratio in length vs. height; a 10 cm long fish would be 3.33 cm tall. Likewise, a 25 cm fish would be 8.33 cm tall. If you assume all surface area is used for propulsion, the smaller individual would have 66.6 cm^2 of available propulsive surface area (front and back) in a fully submerged environment while the larger individual would have 416.5 cm^2 available. However, if you reduce the water depth to 0.5 cm, the smaller individual is left with 10cm^2 of propulsive surface area while the larger individual is reduced to 25 cm^2. The smaller individual retains 15% of its available propulsive surface area while the larger fish retains only 6%. This may be an oversimplification of the relationship between size and propulsive forces, but less relative submerged surface area likely contributes to the lack of success larger fish have on the wetted ramp.

Thrust is generated by the propagation of propulsive waves down the body of the fish towards the caudal fin (Webb 1971). As the propulsive wave moves laterally down the fish, momentum is generated by the backwards force of the adjacent water, so acceleration is likely a function of water depth and submerged propulsive surface area (Webb 1971). Therefore, thrust is intimately related to water depth, as fully submerged fins will have more water adjacent and thus more backwards force with which to generate thrust. The shallow film of water on the wetted ramp, combined with the necessity to move a greater mass (Bainbridge 1958; Wardle 1975; Froese 2006), likely contribute to the increased difficulty large fish have in scaling the ramp.

These results together suggest that the wetted ramp is a size-selective passage device. Most larger individuals lacking the necessary submerged surface area and having greater mass were unable to accelerate on-ramp and so were unable to achieve the same level of success, measured in distance traveled, as smaller individuals, despite entering at higher velocities. It should be noted that the observed relationship between fish length and distance traveled on the wetted ramp may only apply for finfishes in this size range. It has been shown that larger fish have more success on a similar wetted ramp (Doehring 2012), but the fish used in that study were much smaller than those used in this one. Fish less than 10cm likely experience difficulty on wetted ramps because they lack sufficient muscle mass and propulsive surface area to generate the necessary thrust to travel upward. It seems that there is an ideal size range for passage success. There may also be a size-dependent behavioral component to passage success on the wetted ramp, and that will be explored in the next section.

Section 2: Finfish Behavior on the Wetted Ramp

Size Dependent-Behavior on the wetted ramp. Curvature is a length-independent measurement comparing the bent length of a fish, or the distance from snout to tail during a stroke, to the total fish length. Larger curvatures suggest controlled, short body undulations while small curvatures suggest the opposite (Figure 14). For chubs on the control ramp, there was a strong negative relationship between fish length and on-ramp curvature, suggesting that larger fish bend their body more on the ramp than do smaller individuals (Figure 10). There was also a strong positive correlation between increasing curvature and distance traveled on the control ramp (Figure 11). As curvature increases, distance traveled also increases, suggesting that greater curvatures during swim strokes may lead to greater distance on the wetted ramp. This implies that there may be an optimal swimming style to achieve success; short, controlled body movements may produce more success.

In addition to a size effect on curvature, there was also a significant positive relationship between fish length and both head and tail amplitude (Figure 12). As fish length increased, relative head and relative tail amplitude also significantly increased. This suggests that larger fish are using more erratic, less controlled swimming methods on the wetted ramp. Short controlled movements may be more efficient on-ramp and may explain why smaller fish have more success. A fish using large exaggerated, body undulations on the wetted ramp may have less success because it is exposing itself to additional water drag (Hertel 1966). When a fish swims against a current, it must overcome the drag pulling it in the opposite direction. Fast swimming fishes, such as fusiforms, use streamlined body shapes to reduce this drag (Hertel 1966), but when a fish bends its body in excess against the flow of water, this drag will increase. Larger fish displaying smaller curvatures are therefore using a less efficient swimming style.

Whether this use of a less efficient swimming style is a result of poor on ramp performance, or a cause of poor on-ramp performance, remains to be determined. Larger fish may be pre-disposed to use more exaggerated body undulations in shallow films of water because less of their relative surface area is submerged. Without the presence of adjacent water with which to push off and generate thrust, more erratic undulations could result. Conversely, larger fish could resort to more erratic body undulations because they are experiencing more difficulty on the wetted ramp for reasons discussed earlier. Perhaps a large fish abandons short, controlled movements for more erratic undulations in a last-ditch attempt to make it over the barrier as it senses that it is decelerating.

Future studies should address whether there is a relationship between ramp angle of inclination and the effect fish length has on acceleration. Steeper ramps of the same length used in this study may have a greater size effect, because more thrust will be required to move a greater mass up a steeper incline. We should also look to see if the size and behavioral relationships observed in chubs are consistent across other species. It is possible that other fishes behave differently in a partial film of water, and/or in a partial film of water at an incline. It would also be worthwhile to examine whether larger fish are predisposed to use more exaggerated body undulations in shallow films of water, or whether larger fish resort to more erratic body undulations because they are experiencing more difficulty. A better understanding of these questions could guide future fish passage studies and fish passage design. In the final section, I discuss how finfish respond to changes in on-ramp angle of inclination.

Change in Finfish Behavior During Passage Attempt. A change in ramp angle of inclination appeared to have no effect on on-ramp behavior for either chubs or suckers as a group. There were no significant differences between tail beat frequency after the inflection point on the control ramp and tail beat frequency after the inflection point on the bent ramp (Tables 1 and 2). Instead, it appeared as though fish beat their tail in the same fashion on both ramps regardless of a change in angle of inclination.

It is possible that the wetted ramp used in this study was simply not long enough for fish to make, and act on, a motivational decision during an attempt. The average attempt lasted less than five seconds, and this could be too short for fish to sense changes, make decisions, and act on them (Williams et al. 2012) In addition, the change in angle of inclination was not immediate. As outlined in the methods, the experimental ramp increased its angle of inclination after 33 cm. This further truncated the length of time in which the fish is to make a decision about how hard to try after experiencing an increase in angle of inclination (Williams et al. 2012). Fish may sense the change in angle of inclination but fail to react simply because they do not have enough time to do so on the wetted ramp. This may not apply to all fishways though, as a typical fishway requires multiple bouts of burst swimming and this may offer more time for fish to respond to changes.

The level of behavioral variation between fish and between attempts by the same fish was quite large, as demonstrated by the large standard deviations in each mean, maximum, and minimum tail beat frequency measurement (Tables 1 and 2). Many interacting variables may affect fish behavior on the wetted ramp. Discharge rate (Arnekleiv and Kraabøl 1996; Bunt et al. 2012)), diel variation, sexual maturity, water temperature (Fernandez[A] et al. 2007; Fernandez[B] et al. 2007), and even a species' own odor (Paglianti et al. 2006), among other variables, have all been suggested as important motivational direction cues in fishes. Fish on the wetted ramp may notice a change in angle of inclination but fail to respond in a measureable way due to interference from numerous other interacting signals. Many of the aforementioned variables likely do not change during a single passage attempt, but water temperature and diel variation, for example, may have influenced fish differently at different times of the night and this could account for some of the variation between attempts for the same fish (Fernandez[A] et al. 2007; Fernandez[B] et al. 2007). There may have also been an effect of fatigue, both motivational and physical, over multiple attempts by the same individual (Katapodis and Gervais 2012). Future studies should seek to assess fish on an individual basis, as each individual may have noticed and responded to the change in angle of inclination in a different way, but this would be lost in a population level assessment. By looking at individual fish, we may be able to see a behavioral response to changes in on-ramp characteristics.

However, if fish do not assess their status and react as they travel up the wetted ramp, perhaps it makes the most sense to focus our efforts on improving attraction and attempt rates (Clay 1995; Castro-Santos 2004; Bunt et al. 2012; Williams et al. 2012). By improving attraction and attempt rates, we should be able to increase the number of fish successfully using passage devices. It should be stressed that a high attraction and attempt rate does not necessarily equal a high completion rate. Although there should be a higher gross number of fish that complete a pass if more fish try, that does not mean a higher completion rate (Bunt et al. 2012). Future studies will need to better determine the relationship between attraction, attempt, and completion rates for each fish passage device as it will vary for each.

For the wetted ramp, we should try using longer ramps with greater distances for fish to make and act on motivational decisions. The ramps used in this study may have been too short, but a longer ramp may offer more opportunity for fish to respond. We should also seek to better separate and identify the many interacting variables that impact fish behavior on the wetted ramp. By better identifying each variable, we may be able to better manipulate them and thereby manipulate fish behavior and motivation. Future studies could also try different ramp arrangements. A ramp bent in the opposite direction of the bent ramp used in this study, going from a steep section to a shallow ramp section, for example, could result in unique and interesting data as fish experience the different environments in the opposite order. Expounding on this idea, perhaps it would be possible to create a "step-like" ramp, with multiple shallow and steep sections to manipulate perception and motivation. Again, it is important to stress the importance of the ramp being a selective passage device in the Great Lakes region as it must block lamprey while still passing finfishes. Further study and experimentation may find a better ramp design to meet these needs.

Conclusion

My results suggest that the wetted ramp could be a useful passage device for otherwise underserviced small-bodied fishes (Baker 2014; Forty et al. 2016). Although a single ramp would only be useful at a low-head barrier such as a culvert, multiple ramps could be used in succession to navigate around larger, more obstructive, barriers. In this way, the data presented here could be seen as a model for larger projects. These results also offer insight into the mechanics of swimming under partial submersion, where fish must move through shallow films of water. This could be applicable to the design and construction of a multitude of fish passes, including other wetted ramps and shallow-water culverts (Goerig et al. 2016). Understanding fish behavior on passage devices such as the wetted ramp is an important goal if we seek to improve passage efficiency.

Different fishes have been shown to behave differently on wetted ramps (Baker 2014), so continued study will be needed to assess all species of interest. There is likely no single solution for all species, as behavior and swimming mechanics vary from species to species (Baker 2014; Sherburne and Reinhardt 2016). Although my data showed no significant difference in finfish behavior in response to a change in angle of inclination, future studies should test to see if a longer ramp with longer trials shows any difference. It is likely that fish will respond to changes during passage attempts, and continued study may find ways to improve motivation and passage success.

The wetted ramp offers a promising solution for passing smaller bodied fishes that would otherwise be underserviced at larger installations, or in areas that would limit construction of other passage devices (Baker 2014; Forty et al. 2016). In the Great Lakes region, the wetted ramp could serve as both a passage device and a barrier; a passage device for finfish capable of the necessary burst swimming to pass and a barrier for migrating invasive sea lamprey (*Petromyzon marinus*). With continued study, the wetted ramp could become an integral tool for passing finfish over low-head barriers and help maintain or even increase river and stream connectivity in our continually developing world.

Figures

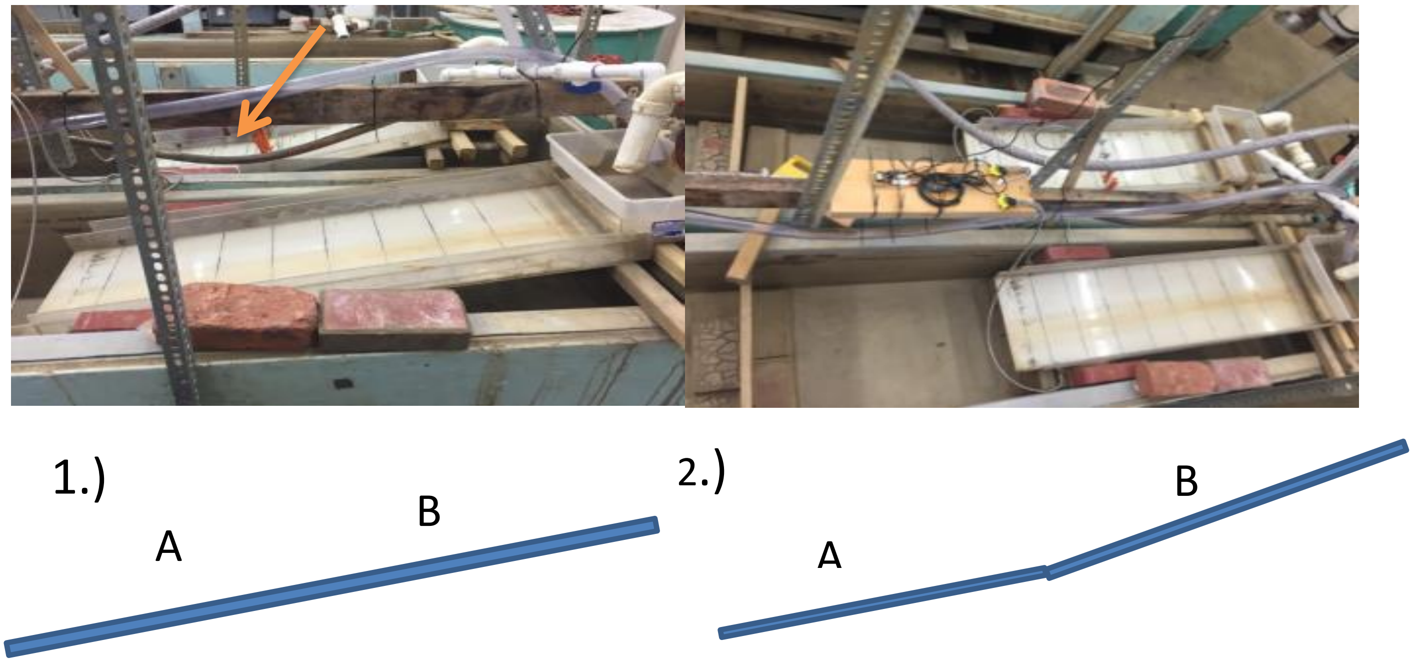

Figure 1. Arrangement of the wetted ramps. The Orange arrow is pointing at the inflection point on the bent ramp. Ramp "1" represents the control whereas ramp "2" represents the bent ramp (note: the angle shown is not to scale). Tail Beat Frequency comparisons are made between points "A" and "B."

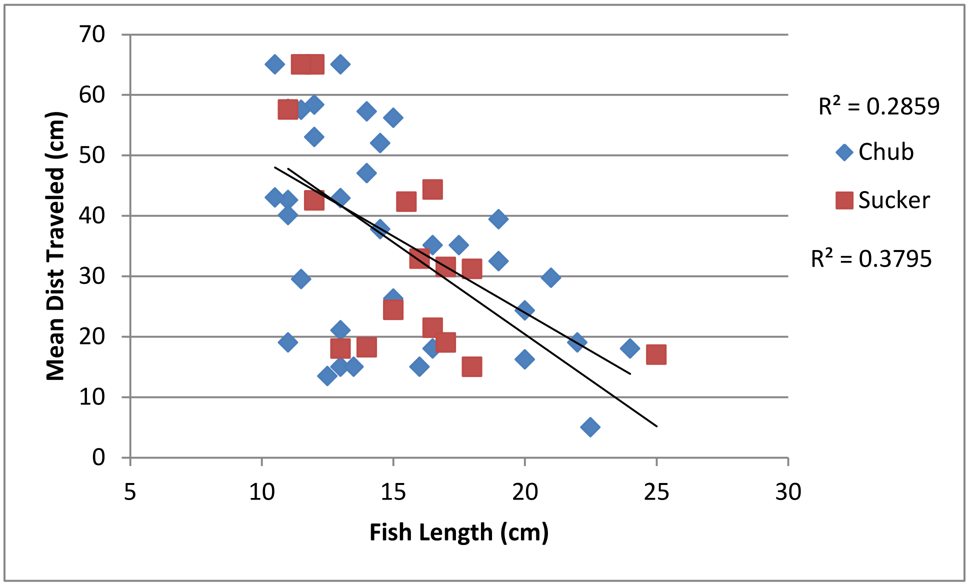

Figure 2. The effect of fish length on average snout distance traveled on the control ramp for suckers and chubs. There is a strong significant negative relationship between fish length and mean snout distance traveled on the control ramp for chubs (p=.001, N=36). There is also a significant negative relationship with fish length and mean snout distance traveled for suckers (p=.011, N=16).

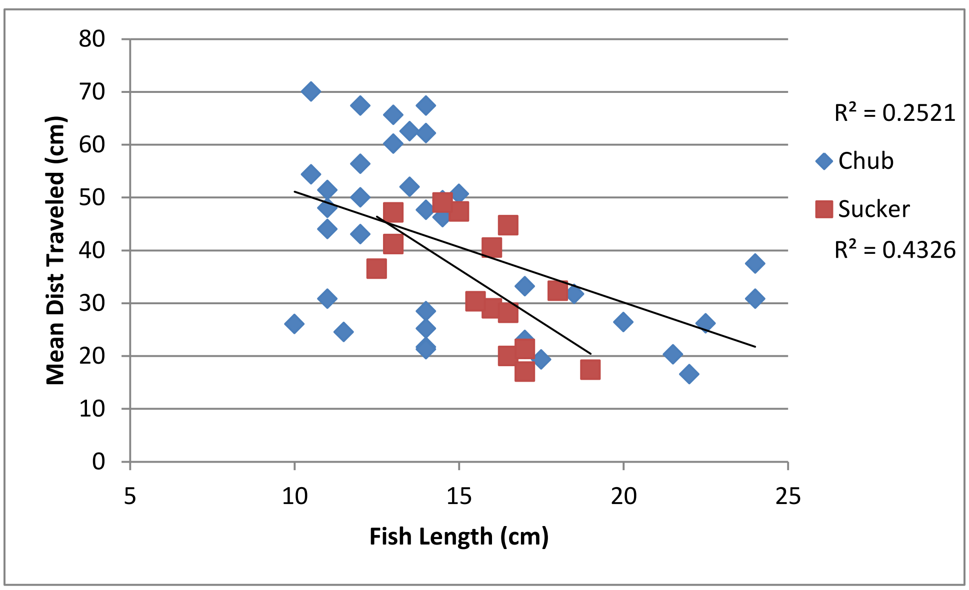

Figure 3. The effect of fish length on average snout distance traveled on the bent ramp for suckers and chubs. There is a strong significant negative relationship between fish length and mean snout distance traveled for chubs (p=.002, N=37). There is also a significant negative relationship between fish length and mean snout distance traveled for suckers (p=.008, N=15).

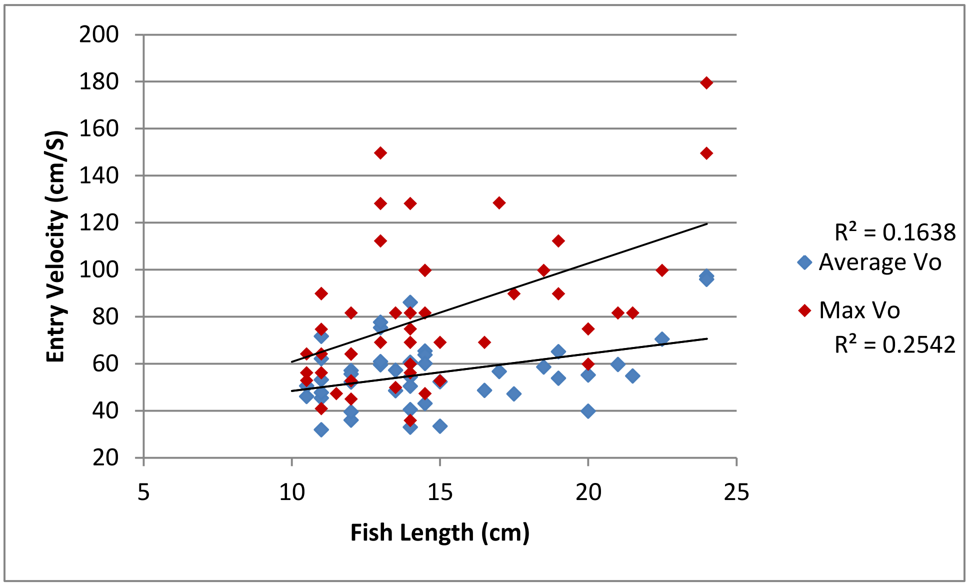

Figure 4. The effect of fish length on initial velocity for chubs on both ramps combined. There is a strong significant positive relationship with chub length and mean initial velocity (p=.0065, N=45). There is also a strong significant positive relationship with chub length and maximum initial velocity (p=.0003, N=48).

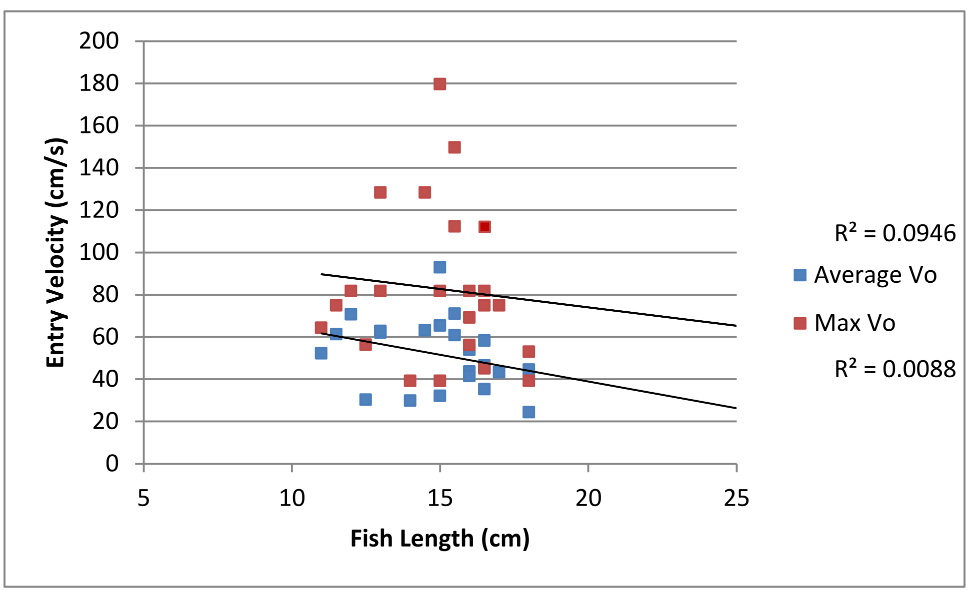

Figure 5. The effect of fish length on initial velocity for suckers on both ramps combined. There is no significant relationship between sucker length and mean initial velocity (p=.1447, N=23). There is also no significant relationship between sucker length and maximum initial velocity (p=.5620, N=23).

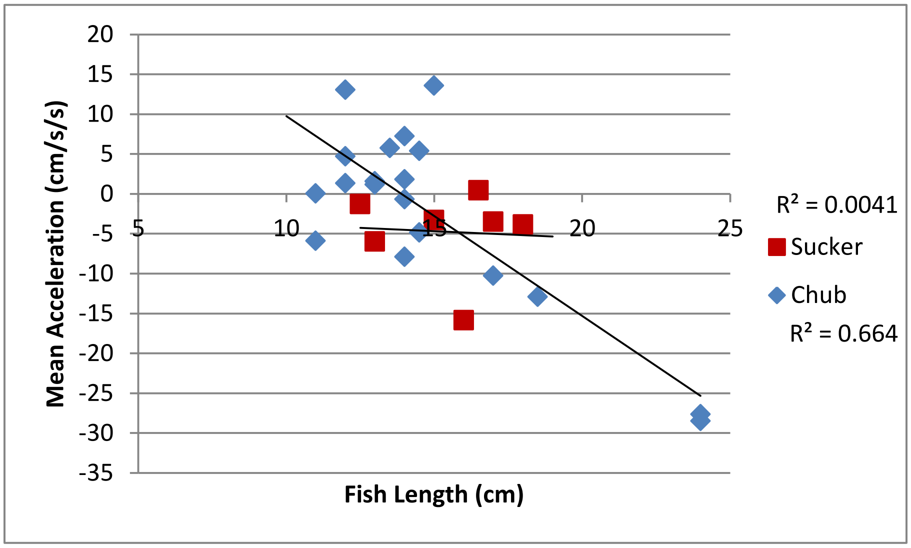

Figure 6. The relationship between fish length and mean acceleration on the bent ramp for chubs and suckers. There is a strong negative relationship between chub length and mean acceleration on the bent ramp (p=.001, N=19). There is a slight negative relationship between sucker length and mean acceleration on the bent ramp, although it is not significant (p=.950, N=7).

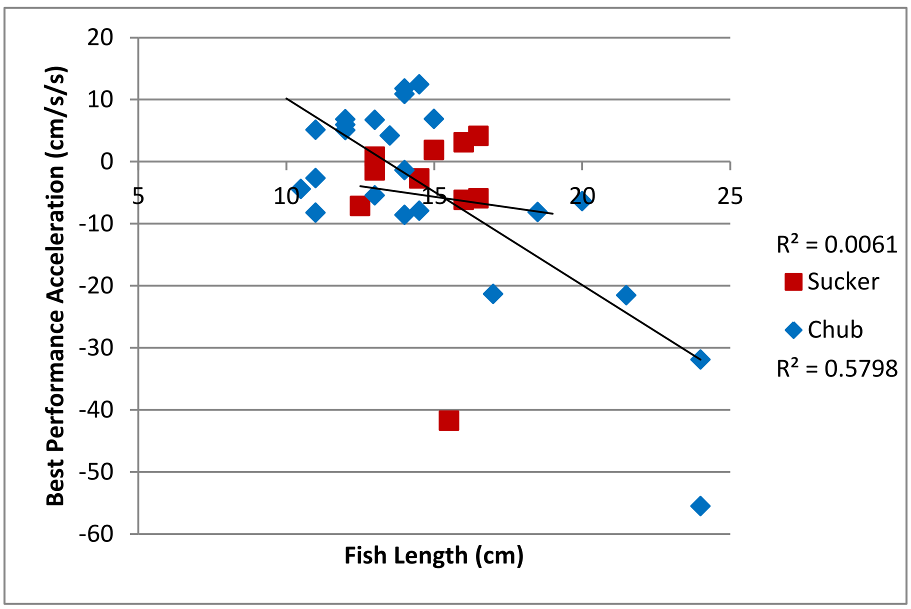

Figure 7. The relationship between fish length and best performance acceleration on the bent ramp for chubs and suckers. There is a strong negative relationship between chub length and best performance acceleration on the bent ramp (p=.001, N=23). There is a slight negative relationship between sucker length and best performance on the bent ramp, but it is not significant (p=.830, N=10).

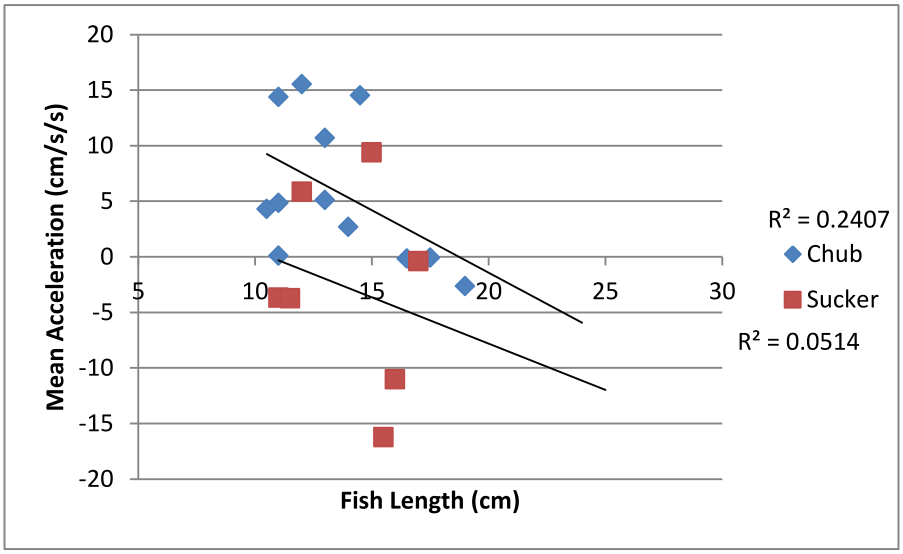

Figure 8. The relationship between fish length and mean acceleration on the control ramp for chubs and suckers. There is a negative relationship with chub length and mean acceleration on the control ramp, but the relationship is not significant (p=.105, N=12). There is a negative relationship with sucker length and average acceleration on the control ramp, but the relationship is not significant (p=.625, N=7).

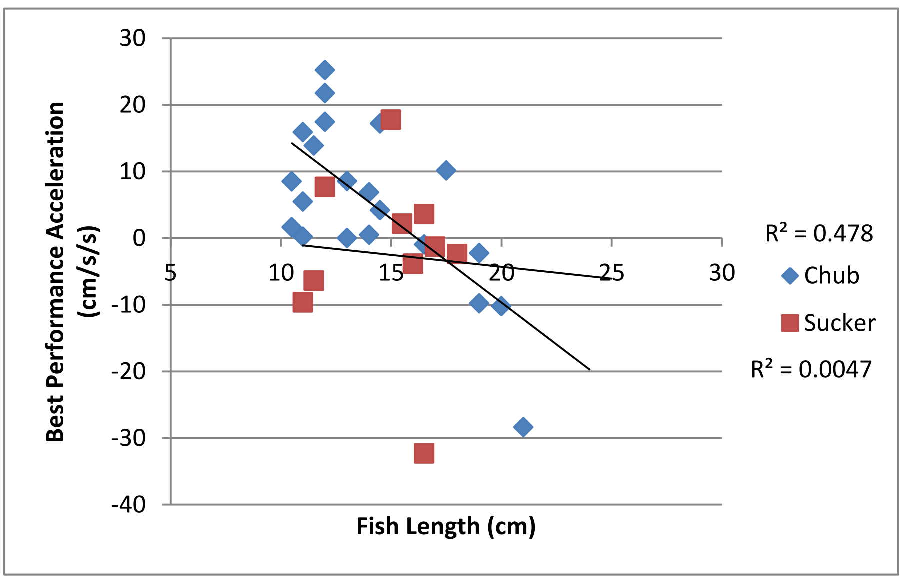

Figure 9. The relationship between fish length and best performance acceleration on the control ramp for chubs and suckers. There is a strong significant negative relationship with chub length and best performance acceleration on the control ramp (p=.001, N=21). There is a slight negative relationship with sucker length and best performance acceleration on the control ramp, but it is not significant (p=.851, N=10).

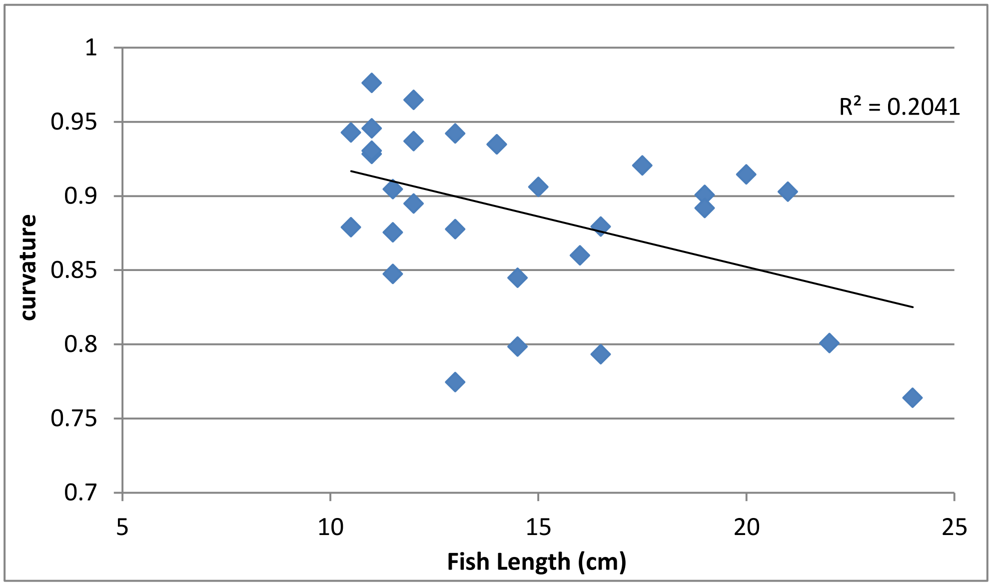

Figure 10. The relationship between fish length and body curvature, or body bending, on a wetted ramp. There is a significant relationship between fish length and body curvature (p=.012, N=30). As fish size increases, curvature of the fish on the ramp decreases.

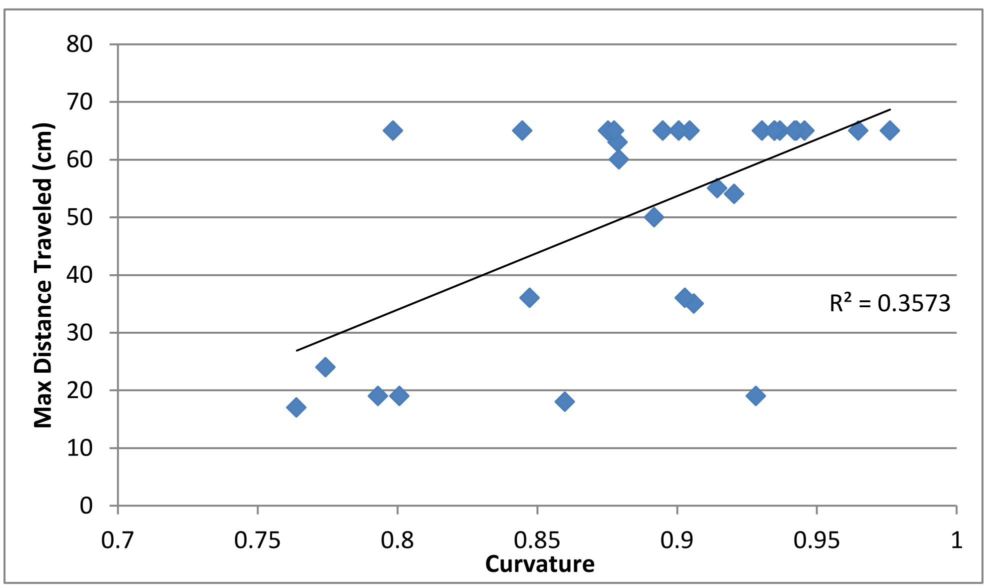

Figure 11. The relationship between body curvature and maximum distance traveled. There is a strong positive relationship between curvature and maximum distance traveled on the wetted ramp (p<.001, N=30). As body curvature increases, mean distance traveled also increases.

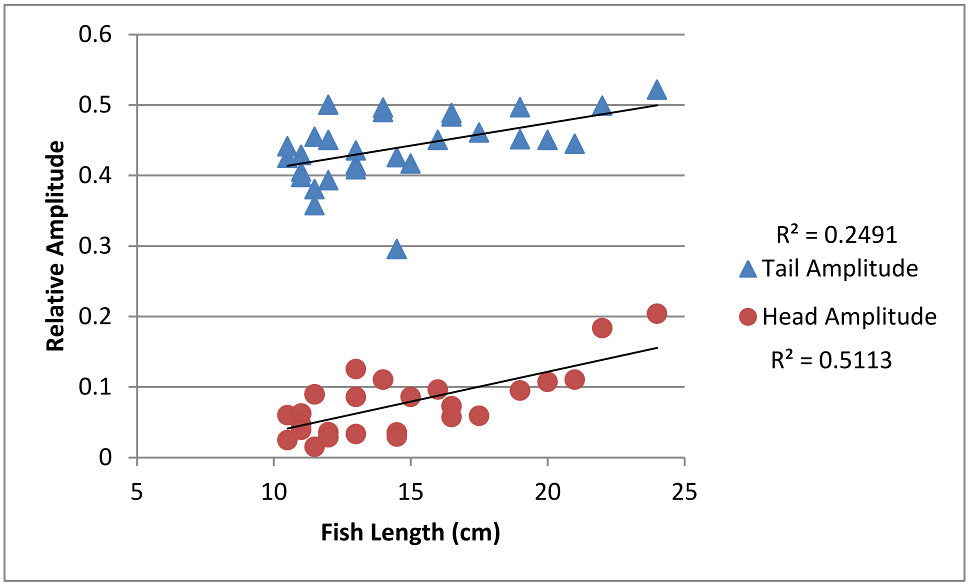

Figure 12. The relationship between chub length and relative head and tail amplitude on the control ramp. There is a strong positive relationship between chub length and relative head amplitude As fish length increases, relative on-ramp head amplitude also increases ($p<.001$, $N=30$).There is a significant positive relationship between chub length and relative tail amplitude. As fish length increases, relative tail amplitude also increases ($p=.05$, $N=30$).

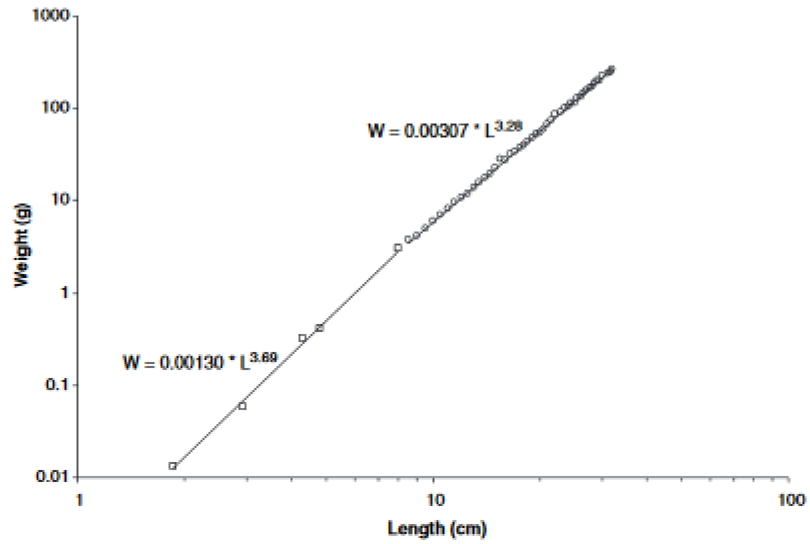

Figure 13.The length-weight relationship for a fusiform fish. A double-logarithmic weight to length relationship for Atlantic Herring (*Clupea harengus*), showing an exponential increase in mass per cm increase in fish length. Adapted from Froese (2006).

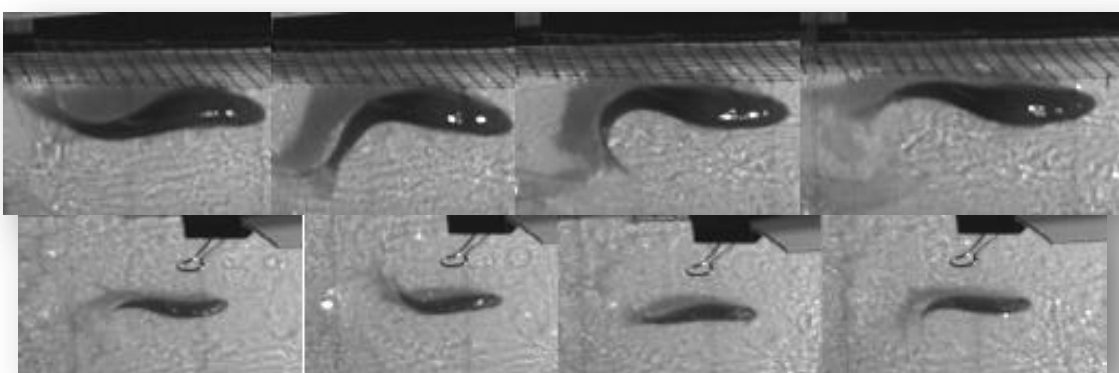

Fig 14. The effect of fish length on body bending, or curvature, during swim strokes. A 20cm chub (top) and a 10.5cm chub (bottom) during an attempt. The larger fish has more exaggerated tail movements, resulting in a smaller curvature.

Tables

Table 1. Tail beat frequencies before and after the inflection point for chubs. There was no significant difference in measured tail beat frequency (TBF) between the control ramp and the bent ramp for any of the comparisons. The closest comparison to significance was between max TBF after the inflection point (p=.2987). Note that Expected Result corresponds to hypothesis predictions.

	TBF on Control Ramp	TBF on Bent Ramp	Expected Result	p-value
Mean TBF before inflection	30.55±3.32hz	30.47±4.01hz	No significant difference	(p= .7703)
Mean TBF after inflection	32.19±4.94hz	33.5±6.4hz	Significant difference	(p=.8250)
Minimum TBF before inflection	28.2±3.9hz	27.1±3.8hz	No significant difference	(p=.3598)
Minimum TBF after inflection	29.9±5.5hz	29.6±6.4hz	Significant difference	(p=.6489)
Maximum TBF before inflection	33.2±4.5hz	34.4±5.8hz	No significant difference	(p=.6795).
Maximum TBF after inflection	34.6±5.5hz	38.7±8.9hz	Significant difference	(p=.2987)

Table 2. Tail beat frequencies before and after the inflection point for suckers. There was no significant difference in tail beat frequency (TBF) between either of the ramps for any of the comparisons. The closest comparison to significance was between max TBF after the inflection point (p=.3313). Note that Expected Result corresponds to hypothesis predictions.

	TBF on Control Ramp	TBF on Bent Ramp	Expected Result	p-value
Mean TBF before inflection	29.5±3.2hz	28.7±4.0hz	No significant difference	(p=.5807)
Mean TBF after inflection	30.1±5.6hz	31.7±5.6hz	Significant difference	(p=.3949)
Minimum TBF before inflection	28.3±3.0hz	27.1±4.0hz	No significant difference	(p= .3796)
Minimum TBF after inflection	28.5±5.1hz	28.0±5.8hz	Significant difference	(p=.9339)
Maximum TBF before inflection	31.6±4.6hz	30.7±5.0hz	No significant difference	(p=.6315)
Maximum TBF after inflection	30.9±5.8hz	34.4±7.1hz	Significant difference	(p=.3313)

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Appendix A: Animal Subject Approval Form

RESEARCH @ EMU

IACUC Determination: **Renewal Approval**

Date: **May 11, 2015**

To: **Ulrich Reinhardt, PhD**
Department of Biology
Eastern Michigan University

Re: **IACUC # 2015-071**

Title: **Refinement of a New Trapping Tool for Migrating Adult Sea Lamprey/Field Comparison of Eel-Ladder-Style and Traditional Sea Lamprey Traps**

Your research project, entitled *Refinement of a New Trapping Tool for Migrating Adult Sea Lamprey/Field Comparison of Eel-Ladder-Style and Traditional Sea Lamprey Traps*, has been approved.

Renewals: This approval is valid for three years and expires on May 11, 2018. You must submit annual progress reports in 2016 and 2017. In 2018, this study will require a de-novo review.

Modifications: All changes must be approved prior to implementation. If you plan to make any minor changes, you must submit a list of these changes and a revised application (with all changes tracked or highlighted) to the IACUC for review.

Good luck in your research. If we can be of further assistance, please contact us at 734-487-3090 or via e-mail at research.compliance@emich.edu. Thank you for your cooperation.

Sincerely,

Sonia Chawla, PhD
Research Compliance Officer
Eastern Michigan University