THESIS

JUMPING AND SWIMMING PERFORMANCE OF BURBOT AND WHITE SUCKER: IMPLICATIONS FOR BARRIER DESIGN

Submitted by

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ABSTRACT

JUMPING AND SWIMMING PERFORMANCE OF BURBOT AND WHITE SUCKER: IMPLICATIONS FOR BARRIER DESIGN

Chapter 1- Illegally introduced burbot (*Lota lota*) populations have spread throughout the Green River drainage (GRD) of the upper Colorado River Basin in Wyoming and Utah, USA where they are having adverse effects on native and sport fisheries. We analyzed existing data to evaluate the status of burbot in southwestern Wyoming. Burbot appear to have been illegally introduced into Big Sandy Reservoir in the early- to mid-1990's, based on capture of burbot in 2003 that included one 16 year old fish and several between 7 and 12 years of age. Burbot began expanding throughout the Green River Drainage in the early 2000s and, with the assistance of a secondary introduction into Fontenelle Reservoir, have successfully invaded most portions of the GRD upstream of the Flaming Gorge Dam. Only one burbot has been captured downstream of Flaming Gorge Reservoir, but this detection indicates potential for downstream establishment in the future. Burbot are difficult to sample, especially in large rivers, so we recommend sampling techniques to monitor the expansion of burbot in lotic and lentic habitats of the upper Colorado River Basin as well as highlight research opportunities associated with this invasion.

Chapter 2 -Burbot (*Lota lota* L.) and white suckers (*Catostomus commersonii* L.) are managed as invasive species in the upper Colorado River Basin and physical barriers to their upstream dispersal could be important tools for preventing their spread. A three-tiered lab-based experimental approach was used to define design parameters for both species utilizing a hybrid barrier that combines a vertical drop with a downstream velocity segment. The first tier of the study measured fish jumping ability over a range of waterfall height × plunge pool depth

treatments to refine waterfall design parameters. Jumping attempt and waterfall exploration data were collected in each trial to allow a novel approach for examining the behavior associated with individual motivation to ascend the barrier, and to confirm that all height × depth treatments were challenged. The second tier of the study used constant acceleration trials (CATs) to define the length-specific burst transition (B_t) from aerobic (high-endurance; sustained) to anaerobic (rapid-fatigue; burst) swimming. Finally, the third tier of the study used fixed velocity trials at velocities > B_t to collect anaerobic endurance data that were used to solve Peake's equation to identify velocity × barrier length combinations that prevented upstream passage. To account for peak-performing individuals, upper 99% prediction intervals were used to determine design criteria that would prevent passage of fish of the total length (TL) in their system of interest. Minimum waterfall heights > 85% and 100% of the TL of the largest white sucker and burbot, respectively, in the system were found to prevent passage. Coupling these heights with plunge pools <40% and 30% of white sucker and burbot TL increases the difficulty these species have ascending the fall. The CATs indicated that velocity barriers that deliver minimum velocities of 4.0 and 3.2 times the TL of the largest white sucker and burbot, respectively, in the system will ensure anaerobic swimming and thus fatigue fish prior to leaping attempts. A variety of velocity barrier length × velocity design parameters are defined for each species to prevent passage based on the FVTs and Peake's equation analysis.

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PREFACE

This thesis consists of two chapters. The first is titled "Invasion of Illegally Introduced Burbot in the Upper Colorado River Basin, USA" and was published in the Journal of Applied Ichthyology in September of 2011 (Gardunio, E. I, C. A. Myrick, R. A. Ridenour, R. M. Keith and C. J. Amadio. 2011. Invasion of illegally introduced burbot in the upper Colorado River Basin, USA. Journal of Applied Ichthyology 27:36-42.). Eric Gardunio was the researcher primarily responsible for the synthesis of the data and writing of this manuscript. This chapter represents an overview of the invasion of burbot in the Green River Drainage of Wyoming that was the impetus for the research conducted on creating barrier design criteria for burbot and white sucker. The second chapter is "A Three-phase Approach to Designing Fish Barriers for Burbot and White Sucker Based on Laboratory Flume and Waterfall Experiments" and comprises the majority of research conducted by Eric Gardunio in pursuance of a Masters of Science from the Department of Fish, Wildlife and Conservation Biology at Colorado State University.

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CHAPTER 1: INVASION OF ILLEGALLY INTRODUCED BURBOT IN THE UPPER COLORADO RIVER BASIN, USA*

INTRODUCTION

Freshwater ecosystems are among our most highly invaded ecosystems (Moyle, 1999), having been colonized by a host of fishes, invertebrates, and plants (Dudgeon et al., 2006). Introduced, invasive fishes are considered to be a primary factor contributing to declines or extirpations of native fish fauna globally and are a leading cause of biotic homogenization (Rahel, 2002; Helfman, 2007). A species must be introduced, become established, spread and have an impact on its introduced system to be considered invasive (Kolar and Lodge, 2002). Species introductions are occurring widely and a recent example is that of the burbot (*Lota lota*) in the upper Colorado River Basin (UCRB). Burbot are an aggressive species that fit the criteria to be considered an invader and are likely impacting native and sport fisheries in the UCRB.

The Colorado River has a relatively high level of aquatic endemism, with four federally endangered species in the upper basin: the bonytail (*Gila elegans*), Colorado pikeminnow (*Ptychocheilus lucius*), humpback chub (*G. cypha*), and razorback sucker (*Xyrauchen texanus*) (Johnson et al., 2008). Additionally, the UCRB also has native populations of bluehead sucker (*Catostomus discobolus*), flannelmouth sucker (*C. latipinnis*), and roundtail chub (*G. robusta*) that are currently classified as declining or threatened throughout their native distributions (Bezzerides and Bestgen, 2002; Compton et al., 2008). Previous research has shown that native fishes of the UCRB have been impacted through habitat alterations associated with dams and by adverse interactions (competition, predation and hybridization) with invasive fish species (Tyus and Saunders, 2000; Bezzerides and Bestgen, 2002; Whitledge et al., 2007; Johnson et al., 2008).

In Wyoming, burbot were native to the Tongue, Big Horn and Wind River drainages (Miller

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1970), but were extirpated from the Tongue River drainage by the 1990s (Fig. 1.1; Krueger and Hubert, 1997). Burbot fisheries were regarded by Wyoming residents as “outstanding winter attractions” and a valuable winter food source through the 1960s, but have since declined in popularity due to declining burbot populations (Bjorn, 1939; Krueger and Hubert, 1997). The status of burbot also varies throughout their range both within and outside of Wyoming. Many populations are extirpated or declining. This is due to angler exploitation, habitat fragmentation and alterations to thermal and flow regimes associated with dams (Krueger and Hubert, 1997; Paragamian and Wakkinen, 2008; Stapanian et al., 2010). Currently the burbot is considered a “Species of Greatest Conservation Need” throughout its’ native range in Wyoming (WGFD, 2005; WGFD, 2010).

While burbot have received global attention due to their conservation need, they are receiving increased attention in Wyoming and Utah because of their invasive nature in the Green River drainage (GRD). The primary objective of this paper is to describe the ongoing invasion of the GRD by burbot through a qualitative evaluation of capture and diet data collected by the Wyoming Game and Fish Department (WGFD) and the Utah Division of Wildlife Resources (UDWR). We further discuss the actions being implemented to mitigate invasion, potential pathways for burbot introduction into the UCRB downstream of Flaming Gorge Reservoir (FGR), possible sampling strategies for efficiently monitoring burbot in the UCRB, and future research opportunities.

Study Area

The Green River originates in the Wind River and Wyoming mountain ranges in southwestern Wyoming and flows south to where it meets the Colorado River in Canyonlands National Park, UT (Fig. 1.2). The upper Green River is joined by the New Fork River before flowing into Fontenelle Reservoir. Downstream of Fontenelle Reservoir, the Big Sandy River flows into the Green River from the northeast. The Big Sandy River is impounded by Big Sandy Dam 94 km upstream from its confluence with the Green River. Downstream of this confluence, near the town of Green River, Wyoming, Bitter Creek enters the Green River from the east. A diversion removes water from the Green River to fill Jim Bridger Pond. The Green River then enters Flaming Gorge Reservoir on the Wyoming-Utah border. Flaming

Gorge Reservoir is broken into three management areas, the upstream Inflow area, the middle Open Hills area, and the downstream Canyon area. Downstream of FGR, the Green River flows through the northeast corner of Utah, into the northwest corner of Colorado, where it is joined by the Yampa River before turning back into Utah where it enters the Colorado River.

METHODS

Most of the data for this review were obtained from the sampling records and internal reports of the WGFD. Additional data were obtained from the UDWR. Reported data are from WGFD except where noted parenthetically.

Reservoir netting data were standardized to catch per unit effort (CPUE; fish hr^{-1}) by net type (gill, trap, or trammel) to allow gross comparisons of burbot capture rates over spatial and temporal scales. Trammel netting events in Fontenelle and FGR represent yearly standardized sampling events which are conducted at the same locations, and times of year to allow for yearly comparisons of capture rates. Nets were set along the substrate and left overnight in stationary sets. Trammel nets were 48.8 by 1.83 m, with panels constructed of multifilament thread with mesh sizes of 2.54 and 25.4 cm mesh for the inner and outer panels, respectively. Graduated mesh experimental nets with eight 7.62-m panels (mesh sizes: 1.91, 2.54, 3.18, 3.81, 4.45, 5.08, 5.72 and 6.35 cm square) constructed of monofilament were used in FGR. Gill nets used in Fontenelle and Big Sandy reservoirs were random mesh with eight 6.1-m panels (mesh sizes: 1.91, 2.54, 3.18, 3.81, 4.45, 5.08, 5.72 and 6.35 cm square). Trap nets consisted of 1.22 by 6.1 m lead lines, attached to a 1.22 by 1.83 m rectangular mouth, with a 3.81-m trap with three, 0.91-m diameter fiberglass hoops.

The number of fish captured, total length (TL) range (mm), sampling effort, and sampling locations were compiled and ordered by date. Catch rate (CPUE) was not calculated for river sampling due to high variability in the methods, timing, and sampling effort, that likely resulted in large differences in efficiency. For sampling that occurred in rivers, number of burbot captured, TL range, distance of sampling event (m), sampling type, and sampling location data were compiled (when available) and ordered by sampling date. Each sampling location was assigned an abbreviation that included a river acronym (BC = Bitter Creek, BSR = Big Sandy River, GR = Green River, NFR = New Fork River) and a number that increases with time of collection (i.e., GR1 is the first time burbot were sampled in the Green River, and GR5 is the fifth). The time between sampling events in each drainage varies. Maps were created using vector data from the U. S. Geological Survey National Hydrography Dataset and were distilled using ArcGIS Version 9.3.1.

Diet data were collected from stomachs removed from burbot captured during 2009 trammel netting efforts in Fontenelle (n = 50) and Flaming Gorge (n = 150) reservoirs, and from e-fishing removal efforts conducted on the Big Sandy River in 2009 (n = 661; BSR 6). Whole stomachs were removed in the field immediately following burbot capture, and opened to identify contents. Diet items were categorized as zooplankton, aquatic invertebrates, or crayfish, and fish remains were identified to species when possible. In the event that the fish remains were not explicitly identifiable by biologists, they were recorded as 'unidentified fish'. Contents of stomachs were not quantified by mass. Diet data are reported as the percentage of burbot stomachs examined containing a particular prey item.

RESULTS

Expansion

Rapid burbot invasion was documented in the lotic and lentic habitats of the GRD upstream of Flaming Gorge Dam between 2001 and 2010. Several angler accounts of catching burbot in Big Sandy Reservoir were reported prior to 2001. In 2001, burbot were first documented by WGFD in the GRD in the Big Sandy River 57 km downstream of Big Sandy Reservoir (Table 1.1; BSR1; Gill et al., 2004). In December 2003, burbot were captured by the WGFD in Big Sandy Reservoir by ice-fishing (Table 1.2). Sagittal otoliths were collected from angled burbot and age determination indicated they varied in age from 4 to 16 years. From Big Sandy Reservoir, burbot have been documented 86 km upstream in the Big Sandy River and downstream throughout the Green River. In 2009 (BSR6) and 2010 (BSR7), 661 and 526 burbot, respectively, were removed from a contiguous 85 km reach of the Big Sandy River upstream of Big Sandy Reservoir. Burbot were sampled in the Green River between the Fontenelle Reservoir Dam and FGR in 2003 during salvage operations in a 0.04 ha dewatered reach of river near the town of Green River, Wyoming (GR1). Additionally, in 2004, a single burbot was captured by an angler directly downstream of Fontenelle Dam (GR2). A single burbot was also recovered in Jim Bridger Pond in 2004 during a rotenone treatment; burbot were subsequently detected in 2007 and 2008.

Burbot were first captured in Fontenelle Reservoir in 2005 during spring gill netting. Autumn trammel netting initiated in 2006 to monitor burbot numbers in Fontenelle Reservoir indicated a rapid increase in burbot CPUE from 0.12 to 0.93 fish hr^{-1} between 2006 and 2008, followed by a slight increase since 2008 (Fig. 1.3). From Fontenelle Reservoir, burbot were able to move upstream into the upper New Fork and Green rivers where low numbers were captured in 2006 (NFR1) and 2007 (GR6), respectively. In 2009, 50 burbot were captured in the Green River 9 km upstream of Fontenelle Reservoir.

In the spring of 2006, burbot were first detected in FGR, in the upstream Inflow area during spring gill netting. An autumn trammel netting survey was initiated in Flaming Gorge in 2006 to monitor burbot population status. In 2006, burbot were captured in both the Inflow and Open Hills areas. Catch rates (CPUE) increased from 0.77 to 1.99 fish hr^{-1}, and 0.63 to 1.66 fish hr^{-1}in the Inflow and Open Hills areas, respectively. Catch rates plateaued in 2007 and then declined by 2010 in the Inflow and Open Hills areas. Burbot were first detected in the downstream Canyon section during a trammel netting survey in 2009.

Occurrence of burbot downstream of FGR was documented on July 28, 2010, when UDWR captured a burbot 141 km downstream of the dam while conducting night raft electrofishing. This is the only confirmed capture below FGR at the time of writing.

Diet

Fish remains were present in 18.6 % of the burbot stomachs collected during the removal efforts in Big Sandy River (BSR6; WGFD, unpublished data). Among the contents were Catostomidae remains, including bluehead sucker. Diet data collected in Fontenelle Reservoir showed that nearly 30% of burbot stomachs examined contained crayfish. Similarly, in FGR, diet data indicated that crayfish were present in 75% of the stomachs. In addition to crayfish, Utah chub (*G. atraria*), and non-endemic smallmouth bass (*Micropterus dolomieu*) and kokanee (*Oncorhynchus nerka*) remains were also observed in burbot diets from Flaming Gorge.

DISCUSSION

As a result of illegal introductions into Big Sandy and Fontenelle reservoirs, burbot have become successfully established throughout the GRD. They are present at least 340 km, 325 km and 290 km upstream of Flaming Gorge Dam in the Big Sandy (BSR4), New Fork (NFR1) and Green rivers (GR6), respectively. The burbot sampled in Jim Bridger Pond are likely transiting the diversion pipe from the Green River and highlight the capability of water diversions to facilitate invasions. The burbot population in Fontenelle Reservoir stabilized in 2007 based on trammel net monitoring data. The populations of burbot in the Inflow and Open Hills areas of FGR increased through 2007, but have declined in recent years, likely due to angling pressure. However, the spread of burbot into the Canyon section of FGR is concerning because it will increase the likelihood of spread to downstream portions of the UCRB. Burbot establishment has not been documented in the Green River downstream of FGR, but the presence of a single fish downstream of the reservoir in 2010 (GR10) indicates that this is likely.

The rapid invasion of burbot in the GRD is surprising given their declining populations in many portions of their native distribution, including those in eastern Wyoming (Krueger and Hubert, 1997; Stapanian et al., 2010). Mechanisms leading to this rapid invasion have yet to be identified, however, altered thermal regimes resulting from impoundment may be facilitating burbot persistence. A southern population of burbot in the Missouri River, MT was shown to increase in abundance due to decreased water temperatures associated with dam construction (Horton and Strainer, 2008). This suggests that burbot may be able to establish populations much further south than their current distribution, as the UCRB contains several dams that could serve as thermal refugia. Additionally, cold winter water temperatures in the UCRB may provide a window for range expansion, in concert with spawning migrations. Further examination of the mechanisms leading to this invasion, as well as the potential limitations to downstream expansion in the UCRB should be explored.

Clear evidence of an impact from burbot on fish communities in the GRD is lacking. This stems from the recent nature of the invasion and a lack of studies focused on quantifying impact. The frequent consumption of crayfish by burbot in Fontenelle and FGR coincides with an observed decline in crayfish abundance. Burbot have been shown to exert significant predation pressure on crayfish (Paragamian, 2009). In addition to crayfish predation, burbot do consume a variety of fishes (McPhail and Paragamian, 2000; Hensler et al., 2008). Managers are concerned that burbot will alter food web interactions in FGR thereby decreasing its quality as a sport fishery. Stable isotope analysis of the FGR food web indicated that 85% of the energy used for burbot growth is derived from crayfish or other benthic invertebrates (Luecke and Mears, 2009). Observed declines in angler catch rates for smallmouth bass are thought to result from direct predation on juveniles by burbot, or from interspecific competition for crayfish. Managers of FGR are also concerned that predation by burbot may lead to kokanee population declines, leading to a negative impact on the trophy lake trout (*Salvelinus namaycush*) population. In the Great Lakes, interspecific competition between burbot and lake trout is suspected (Stapanian et al., 2006), suggesting that a similar situation may arise in FGR.

Managers are also concerned that burbot may be exerting predation pressure on native fishes of the Green and Big Sandy rivers based on native fish remains in burbot from the Big Sandy River, and because Cyprinidae and Catostomidae are known burbot prey items (McPhail and Paragamian, 2000). Although population impacts have not been clearly demonstrated in the GRD from burbot, predation from other nonnative piscivores has negatively impacted native fish populations in the UCRB (Quist et al., 2006; Whitledge et al., 2007; Johnson et al., 2008). Further investigations into the potential effects of burbot predation on native fish communities are warranted.

Fisheries managers in the GRD are limited in the actions available to reduce the spread and population size of burbot. In the Big Sandy River, removal efforts are ongoing and have been responsible for the removal of high numbers of burbot. These efforts did not result in a decline in burbot numbers between 2009 (BSR6) and 2010 (BSR7), however, fewer adult fish were sampled in 2010 than 2009. Mechanical removal efforts are often limited because of high costs, but are commonly necessary to control invasive species (Simberloff, 2003; Johnson et al., 2009).

Overfishing is thought to be cause for decline of burbot populations in their native distribution in Wyoming (Hubert et al. 2008). Angler harvest may represent an inexpensive alternative to controlling invasive fish. The Wyoming Game and Fish Department conducted a public education campaign, issuing press releases and conducting seminars outlining angling strategies to successfully target burbot. This was done in conjunction with a regulation change allowing unlimited harvest of burbot throughout the GRD and a mandatory kill regulation in Utah. These efforts have resulted in high public use of Flaming Gorge and Fontenelle reservoirs as evidenced by a yearly burbot ice fishing tournament that had 485 anglers who removed 4,012 burbot over seven evenings of fishing in 2011. The use of anglers as a control tool in the GRD offers an opportunity to evaluate the viability this option of invasive species. A potential drawback could be increasing the number of dedicated burbot anglers who may introduce them elsewhere. Monitoring angler attitudes toward burbot could allow insight into changing angler interest in burbot fisheries, and into whether anglers will target burbot in their native range if robust populations are restored.

Further illegal introductions of burbot are likely given their appeal as a sport and food fish (Krueger and Hubert, 1997). Illegal introduction of sport fish by anglers is a global fisheries management issue, leading to the diversion of valuable agency resources into mitigation programs (Johnson et al., 2009). Within the UCRB, illegally introduced non-native species are contributing to the decline of native fishes. Control of non-natives is costing the endangered fish recovery program U.S. \$1 million y^{-1} in control efforts in the UCRB (Johnson et al., 2009). The proximity of a robust burbot population in FGR provides a source for future illegal introductions into the UCRB. A search of two popular Colorado-based fishing forum sites (ColoradoFisherman.com and FishExplorer.com) conducted on January 3, 2011 returned two posts that voiced a desire to have burbot as a sport fish in Colorado reservoirs and one that proposed illegal introduction into Jefferson Lake, Colorado. With this kind of sentiment, it seems that continued illegal introductions are not only possible, but likely.

Downstream escapement from FGR into the Green River is another pathway that may allow burbot expansion into the UCRB. As of this writing, burbot have not attained high numbers in the downstream Canyon section of FGR. If the southern population size does increase, the likelihood of burbot passage through the dam will increase. Despite multiple causes of mortality when passing through dams, downstream survival is well documented, particularly for juvenile fish (Coutant and Whitney, 2000).

The spread of burbot within the GRD appears to have demonstrated a lag phase typical of many invasions and should be viewed with caution by managers downstream of FGR (Sakai et al., 2001; Crooks, 2005). Observed lag times may not be representative of true population densities over time, but rather may be the result of low detection probability associated with sampling for an unknown, novel species (Crooks, 2005). Age data collected from Big Sandy Reservoir in 2003 suggest that burbot were present in the early 1990s. It was not until 2001 that burbot were first detected and large numbers were not observed until the mid-2000s when burbot had spread through much of the GRD. The rapid expansion observed from 2003-2007 in the GRD should be a warning to fisheries managers downstream of FGR. Low detection probability likely delayed the initial detection of burbot and led to an underestimation of their distribution and population density during the expansion phase of the invasion. The single burbot sampled downstream of Flaming Gorge in 2010 (GR10) may be part of a larger population that is not being efficiently sampled.

Early detection is extremely important for managers to effectively remove invasive species (Simberloff, 2003). Once a species becomes established, the likelihood of removal decreases while costs increase (Simberloff, 2003). Having a thorough monitoring program outside of the current distribution of burbot will allow managers to detect their presence early and begin control efforts when necessary. Potential control methods include angler harvest, mechanical removal, targeting spawning aggregations and installing barriers to upstream habitats in lotic systems. Each of these methods will have benefits and drawbacks (Table 1.3), making quantitative evaluation of their relative value critical.

Selecting appropriate sampling methods will be critical in monitoring burbot. Trammel nets are a highly efficient means of sampling burbot in lentic habitats. A comparison of gear types conducted on Boysen Reservoir and Torrey Lake, Wyoming, found that trammel nets had on average six and 20 times higher capture rates for adult burbot than did hoop nets and cod traps, respectively (WGFD, unpublished data). In lotic systems, burbot have been sampled using electrofishing, cod and hoop nets and slat traps (Paragamian, 2000; Horton and Strainer, 2008). In the Missouri River, Montana, no significant difference was observed in the capture rates of burbot between the three netting methods (Horton and Strainer, 2008). Given the effectiveness of trammel nets in lentic systems, exploring their use for burbot in rivers may be worthwhile. The sampling used to monitor burbot presence, absence, or population size should be conducted at times and in locations that maximize the likelihood of burbot detection. Burbot prefer habitat with rock substrates where they use interstitial spaces for cover during the day, moving to foraging habitats during nocturnal feeding periods (Ryder and Pesendorfer, 1992; Fischer et al., 2001; Dixon and Vokoun, 2009). Sampling at night near preferred habitats should increase detection probability for burbot. The robust burbot population in the GRD offers an opportunity to evaluate the comparative utility of differing sampling strategies.

The rapid invasion of burbot in the UCRB has created a necessity for further research to provide fisheries managers in the UCRB with relevant information to base management decisions. Of primary importance is monitoring for burbot in both the invaded area and below FGR. Conducting research on optimal sampling techniques will allow increased efficiency in monitoring. It will also be important to evaluate the relative effectiveness of differing control strategies within the UCRB. Quantifying the impacts that burbot are having on GRD fish communities will be useful for determining the necessity of control efforts. Studying the angler response to burbot fisheries in the GRD will give insight into the effectiveness of angling as a control agent, and into how the public may react to management strategies in both the invaded and native burbot distributions. Finally, evaluating the mechanisms allowing burbot invasion in the GRD may offer insights into conservation strategies in their native distribution. This invasion offers a suite of potential research opportunities of value to the management of this invasion, the study of invasion biology, and the conservation of native burbot populations.

TABLES AND FIGURES

Table 1.1: Burbot *Lota lota* numbers (n), location abbreviation (Loc.; Matching locations displayed in Fig. 2), total length range (TL; mm), sampling distance (m), and gear type for sampling events occurring between 2001 and 2010 in lotic portions of the Green River drainage. All sampling events were conducted during the day unless otherwise noted.

Year	Date	Loc.	n	TL (mm)	Distance (m)	Gear type
2001	May	BSR1	2	juvenile	-	Backpack e-fishing
2003	19-Aug	BSR2	3	230-472	200	Shore mounted e-fishing
2005	-	BSR3	1	572	200	Backpack e-fishing
2008	Sept	BSR4	4	384-607	200	Backpack e-fishing
2009	Apr 27-July 7	BSR5	36		-	Weir
2009	Jul 8-Sept 23	BSR6	661	152-762	85300	Barge e-fishing
2010	Jul-Sept	BSR7	526	51-508	85300	Barge e-fishing
2003	Aug	GR1	3	305-558	-	Dip netting
2004	-	GR2	1	609	-	Angling
2006	Apr	GR3	1	351	6800	Raft e-fishing (night)
2006	Apr 7-11	GR4	6	196-549	7200	Raft e-fishing (night)
2007	6-Apr-10	GR5	5	317-465	7000	Raft e-fishing (night)
2007	Oct 8-10	GR6	1	462	4990	Raft e-fishing (night)
2009	Apr 30, July 28	GR7	43	-	-	Dip netting
2009	May 9, 10, 14,	GR8	5	-	-	Boat e-fishing
2009	21-Sep	GR9	50	147-508	5960	Raft e-fishing (night)
2010	28-Jul	GR10	1	535	-	Raft e-fishing
2006	Sept 11, 13, 14	NFR1	1	495	6760	Raft e-fishing (night)
2009	Apr 9-July 2	BC1	21	152-483	-	Weir

Table 1.2: Burbot *Lota lota* numbers (n), location, total length range (TL; mm), catch per unit effort (CPUE; fish net^{-1} hr^{-1}) and gear type for sampling events occurring between 2003 and 2009 in lentic portions of the Green River drainage, Wyoming. All netting was conducted at night using stationary sets. Hook and line sampling was conducted through the ice by WGFD personnel.

Year	Date	Location	n	TL (mm)	CPUE	Gear
2003	10-Dec	Big Sandy Res.	16	-	-	Hook and line
2004	May	Big Sandy Res.	4	211-635	0.05	Gill net
2004	29-Sep	Jim Bridger Pond	1	Juvenile	-	Rotenone
2007	9-Oct	Jim Bridger Pond	1	508	0.01	Trap net
2008	29-Sep	Jim Bridger Pond	8	157-185	0.06	Trap net
2005	11-Oct	Fontenelle Res.	2	391-406	0.02	Gill net
2006	25-Oct	Fontenelle Res.	15	386-605	0.12	Trammel net
2007	1-Nov	Fontenelle Res.	16	574-714	0.27	Trammel net
2008	27-Oct	Fontenelle Res	52	348-805	0.93	Trammel net
2009	9-Nov	Fontenelle Res	50	340-790	0.98	Trammel net
2010	5-Nov	Fontenelle Res	60	358-826	1.03	Trammel net
2006	2-May	Flaming Gorge Res (Inflow)	26	234-457	0.35	Gill net
2006	6-Nov	Flaming Gorge Res (Inflow)	46	267-602	0.77	Trammel net
2007	2-May	Flaming Gorge Res (Inflow)	66	290-597	1.22	Trammel net
2007	7-Nov	Flaming Gorge Res (Inflow)	104	318-686	1.99	Trammel net
2008	6-Nov	Flaming Gorge Res (Inflow)	78	323-721	1.63	Trammel net
2009	2-Nov	Flaming Gorge Res (Inflow)	97	295-749	1.77	Trammel net
2010	2-Nov	Flaming Gorge Res (Inflow)	67	305-747	1.2	Trammel net
2006	7-Nov	Flaming Gorge Res (Open Hills)	34	297-536	0.63	Trammel net
2007	8-Nov	Flaming Gorge Res (Open Hills)	86	333-696	1.66	Trammel net
2008	6-Nov	Flaming Gorge Res (Open Hills)	56	315-742	1.45	Trammel net
2009	3-Nov	Flaming Gorge Res (Open Hills)	78	320-734	1.3	Trammel net
2010	3-Nov	Flaming Gorge Res (Open Hills)	56	315-790	0.93	Trammel net
2009	4-Nov	Flaming Gorge Res (Canyon)	6	478-711	0.1	Trammel net
2010	Nov	Flaming Gorge Res (Canyon)	-	-	0.07	Trammel net

Table 1.3: Advantages and disadvantages of options for controlling invasive burbot *Lota lota* in the Upper Colorado River Basin.

Method	Advantages	Disadvantages
Angler Harvest	Inexpensive. Can facilitate angler support of control efforts.	Can lead to increased recognition of burbot as a sport fish leading to further illegal introductions or resistance to control efforts. If successful, anglers may not favor lowsupport burbot numbers.
Mechanical Removal	Allows focused removal of burbot by managers.	Expensive and time-consuming. Potential for by-catch of non-target species.
Target Spawning Aggregations	Burbot highly concentrated during winter spawning events.	Harsh winter conditions (e.g., ice cover) limit access.
Fish Barriers	Protect upstream, non-invaded habitats from invasion.	Prevents movement of native species. Costly to implement and maintain. Can be navigation hazards. Difficult to identify suitable locations.

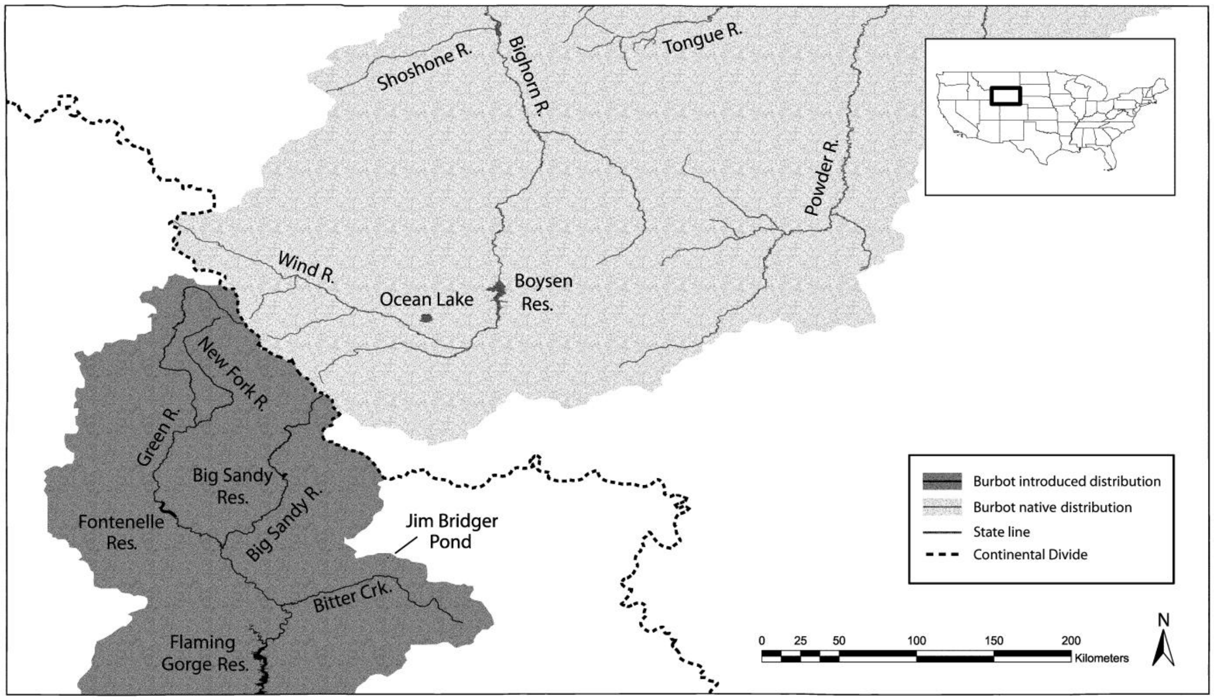

Figure 1.1: Native and introduced distributions of burbot (*Lota lota*) in Wyoming, USA as of November 2010.

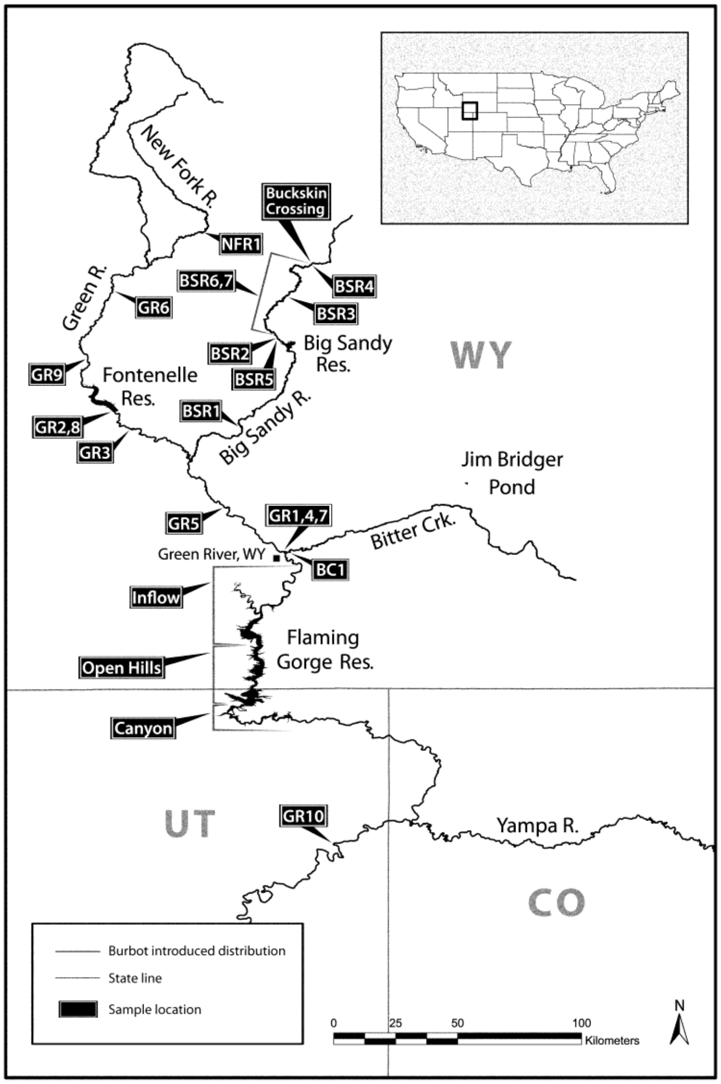

Figure 1.2: Invaded distribution of burbot within the Green River drainage of Wyoming, Colorado and Utah, USA as of November 2010. Locations associated with sampling events that captured burbot between 2001 and 2010 are displayed along with regional landmarks. Acronyms stand for rivers (BC = Bitter Creek, BSR = Big Sandy River, GR = Green River, NFR = New Fork River) and the number increases with time of collection (i.e., GR1 is the first time burbot were sampled in the Green River, and GR5 is the fifth).

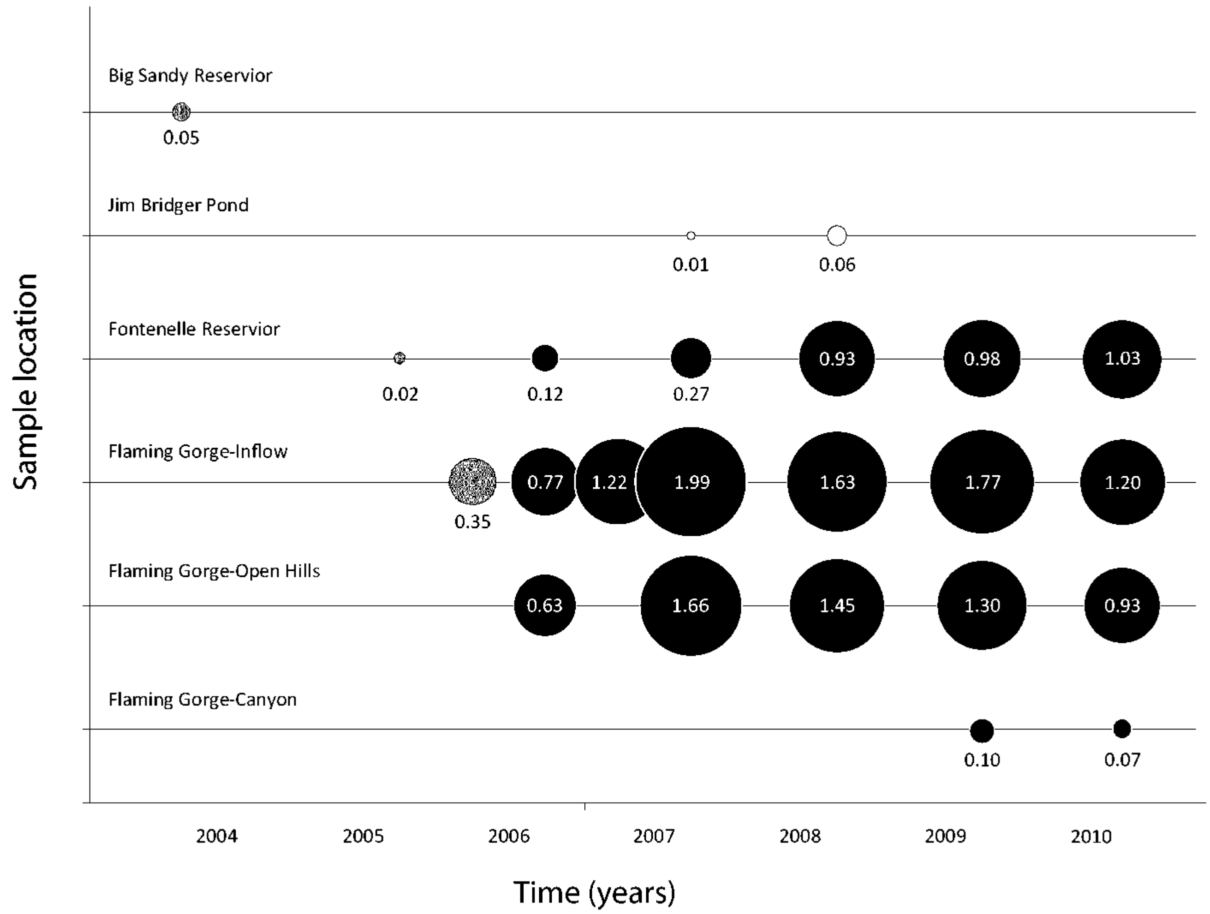

Figure 1.3: Catch per unit effort (CPUE; fish hr^{-1}) data for burbot captured in the Green River drainage by gill net (grey circles), trap net (white circles) or trammel net (black circles) between 2004 and 2010.

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CHAPTER 2: A THREE-PHASE APPROACH TO DESIGNING FISH BARRIERS FOR BURBOT AND WHITE SUCKER BASED ON LABORATORY FLUME AND WATERFALL EXPERIMENTS

INTRODUCTION

Burbot (*Lota lota*) and white suckers (*Catostomus commersonii*) are managed as invasive species in the upper Colorado River Basin (UCRB) due to their negative interactions with both native and sport fishes (Quist et al. 2009; Gardunio et al. 2011; Lepak et al. 2012). Predation by burbot are altering food webs in popular sport-fishing reservoirs, and are reducing native bluehead sucker (*Catostomus discobolus)* and flannelmouth sucker (*Catostomus latipinnis)* populations in the Green River Drainage. Establishment downstream of Flaming Gorge Reservoir would likely cause declines in endemic populations of endangered species in the UCRB including the Colorado pikeminnow (*Ptychochelius lucius*), bonytail (*Gila elegans*), humpback chub (*Gila cypha*) and razorback sucker (*Xyrauchen texanus*) (Gardunio et al. 2011). White suckers impact native bluehead and flannelmouth suckers through hybridization and competition, often resulting in reduced populations of genetically pure native suckers (Compton et al. 2008; McDonald et al. 2008). Extinction through hybridization is a conservation concern, particularly when rare native species are confronted with dense populations of species capable of hybridization (Rhymer and Simberloff 1996). In addition to the hybridization concerns, throughout North America, white suckers exhibit diet overlap with salmonid species, causing niche shifts, resulting in decreased growth, survival and yield of salmonid sportfish (see Lepak et al. 2012 for full review).

Burbot and white suckers often exhibit migratory life history strategies (Paragamian 2000; Wakefield and Beckman 2005; Paragamian and Wakkinen 2008; Doherty et al. 2010) requiring habitat connectivity to sustain persistence (Schlosser and Angermeier 1995). Disrupting this connectivity can reduce the ability of these species to move between habitats, resulting in negative impacts to their populations. While this would be viewed as undesirable to conservation efforts, it could be a useful tool in the management of non-native populations of these species. In-stream barriers to migration offer one tool for disrupting this connectivity, and can be used to prevent the invasion of habitats or can be incorporated into reclamation projects for restoring invaded waters.

Vertical drop barriers are commonly used to prevent upstream migrations of undesirable fishes (Thompson and Rahel 1998; Kondratieff and Myrick 2005; Kondratieff and Myrick 2006) These barriers are effective at preventing passage provided they incorporate dimensions that exceed the jumping capabilities of the target species and that they are impermeable to fish passage through interstitial spaces (Kondratieff and Myrick 2006; Thompson and Rahel 1998). Studies of the leaping capacity of undesirable fishes are desirable of elucidating effective design criteria for vertical drop barriers; however, few studies on the leaping capabilities of invasive species with the focus of barrier design have been conducted. In general, combinations of higher waterfalls, and shallower plunge pools have been shown to limit passage (Holthe et al. 2005; Kondratieff and Myrick 2006; Ficke et al. 2011). By measuring the jumping abilities of both native and nonnative fishes at a range of waterfall design parameters, species-selective vertical barriers may be feasible provided the species of interest exhibit sufficiently different jumping performances (Holthe et al. 2005). Species-selectivity, however, is of secondary importance to creating a barrier that effectively blocks all individuals of the target species.

Combining high velocity downstream ramps with the barrier attributes of vertical drop structures may result in a design that offers greater redundancy against barrier failure (Figure 2.1). Rivers are dynamic systems that may cause either structural barrier failure or temporal periods of reduced effectiveness due to stochastic flow events, and design redundancy will allow a broader range of durability and barrier function. This redundancy also provides increased assurance that peak performing individual fish will not pass if each component exceeds the expected physiological capability of the target species. Additionally, river morphology may result in design constraints where either a vertical drop or a high velocity ramp is more feasible to implement. For example, in a low gradient river, a longer velocity barrier may be easier to implement because the slope of the river precludes the ability to design a vertical drop structure of an appropriate height to prevent passage. Conversely, in a high gradient stream, a vertical drop barrier may be more desirable.

An effective velocity barrier would require that the splash pad and tailrace section downstream of the waterfall maintain water velocities that force fish moving upstream to utilize burst swimming resulting in the fatigue of their anaerobic, white (fast glycolytic) muscles (Moyle and Cech 2004). However, successfully employing this approach requires data on the burst swimming capability of the target species. Traditional estimates of maximum aerobic swimming capacity were calculated using the U_{crit} methodology developed by Brett (1964). More recently, flume and open channel swimming trials using increasing water velocities have produced more physiologically relevant and less biased estimates of the velocities whereupon fish transition from using their aerobic swimming muscles (red, or slow-oxidative muscles) to their anaerobic musculature, termed the burst transition (B_t) (Drucker 1996; Reidy et al. 2000; Peake and Farrell 2004; Peake 2008; Marras et al. 2010). These studies use a constantly accelerating current to cause fish to switch to anaerobic swimming gaits when B_t is reached.

Constant acceleration trials are useful for defining the gait transition velocity, however, they underestimate the maximal speed and time that a fish can swim because the fish are being fatigued during the acceleration. Fixed-velocity flume trials are often used to develop less-biased estimates of maximum swimming speed and endurance at given flume velocities (Jones et al. 1974; Peake et al. 1997; Ficke et al. 2011). Regressions relating trial velocity to endurance can be used with Peake's equation to estimate the required length and velocity combinations of a velocity ramp that would prevent passage of undesirable species (Peake et al. 1997).

This study used a three-phase experimental approach to define the vertical leaping capabilities, anaerobic gait transition and anaerobic endurance of burbot and white suckers in order to develop fish barrier design guidelines for these species. The jumping potion of the study used repeated trials on individual burbot and white suckers in two large modified Kondratieff Flume-type artificial waterfalls (Kondratieff and Myrick 2005) to determine waterfall height × plunge pool depth combinations that prevented successful ascent while accounting for individual behavioral responses to the experimental conditions of the study. To define the burst transition (B_t) from aerobic to anaerobic swimming, flume-based constant acceleration trials were conducted for both species. Fixed-velocity flume trials were then used to measure endurance at velocities greater than the B_t in order to estimate barrier length × velocity combinations that would prevent passage using P

eake's equation (Peake et al. 1997).

METHODS

Fish Collection and Maintenance

The study was conducted using wild-caught white suckers and burbot. White suckers were collected via backpack electrofishing from the Poudre River in Fort Collins, CO and the Big Thompson River in Loveland, CO. Care was taken to avoid injuring white suckers during collection. Burbot were collected from Flaming Gorge Reservoir, WY using either trammel nets in the spring and fall or by hook and line sampling with barbless hooks during the late fall and winter months. Care was taken to avoid collecting burbot from depths exceeding 10 m to avoid problems with decompression (Neufeld and Spence 2004). Individuals of both species were observed to verify that they were not injured during collection prior to trials.

All fish were transported to the Colorado State University Foothills Fisheries Laboratory (FFL) in a hauling tank containing oxygenated water (near-saturation levels) from the collection location. Dissolved ammonia levels were controlled in longer trips with AmQuel Plus (Kordon, LLC). During warm periods, ice was added to the tanks, to cool the water and reduce hauling stress (Carmichael and Tomasso 2001).

Fish were held in four insulated and covered 1550-L circular polyethylene tanks receiving 10-15 L min^{-1} of air-saturated water from spray bars located above the tanks. When fish arrived at the FFL, holding tank temperatures were adjusted to the transport tank temperature ± 2°C prior to transferring fish. Water temperatures were then adjusted at a rate of 2°C · d^{-1} to the desired test temperatures. Test temperatures for the jumping trials for white suckers were 14°C and 22°C; burbot were tested at 13°C and 6°C. The 14°C white sucker, and 13°C burbot temperatures were selected because they were near the center of the thermal tolerance range of the species (range: 11-22°C for white suckers and 11-16°C for burbot) (Beitinger and Bennett 2000; Paakkonen and Marjomaki 2000; Hoffman and Fischer 2002). The 22°C white sucker treatment was used after I observed increased performance at higher temperatures in pilot swimming trials. The 6°C temperature used for burbot was an attempt to trigger more leaping attempts after preliminary trials showed few of those; burbot have pre-spawn migratory life history of burbot at relatively low temperatures (Paragamian and Wakkinen 2008). For swimming trials, white suckers swam at 5°C and burbot swam at 20°C in addition to the jumping trial temperatures for each species. Fish were allowed to acclimate to these temperatures for at least five days prior to the initiation of trials. Although this acclimation period was shorter than what is generally used (Lyytikäinen et al. 1997), it was deemed desirable after observed declines in performance in pilot trials, particularly in the case of white suckers when held in the lab for longer periods. White suckers and burbot were fed daily to satiation with bloodworms (San Francisco Bay Brand) and frozen silversides (*Menidia menidia;* San Francisco Bay Brand), respectively.

Jumping Trials

Prior to jumping trials, fish were anesthetized (80 mg $\cdot$ L^{-1} MS-222) and given individual visual implant elastomer (VIE) marks. Elastomer was injected in the tissue on the left and right ventral surfaces of the dentary in unique color combinations as described by Ficke and Myrick (2011). Fish were allowed to recover in oxygen-saturated water before being returned to their holding tanks, where they were held for at least 5 days prior to being used in jumping trials.

Trials were conducted in two large modified Kondratieff Flume-type artificial waterfalls (Kondratieff and Myrick 2005) using a 75 L$\cdot$ min^{-1} recirculating flow (Figure 2.2). The Kondratieff waterfalls were housed in a 315 cm (l) × 132 cm (w) × 124 cm (d) custom-made aluminum tank. Cinderblocks were used to raise the lip of the waterfall apparatus 130 cm above the bottom of the flume. A vertically adjustable aluminum floor allowed alterations of the plunge pool depth. A 48-cm (w) × 86-cm (l) three-sided box made of perforated Coroplast™ (Coroplast, Inc. Vanceburg, KY) of one of two heights (155 or 94 cm, depending on total height of the plunge pool depth × waterfall height combinations being tested) was placed on this adjustable floor. Pilot trials demonstrated that these secondary boxes increased the number of attempts fish made to ascend the fall.

Water was pumped (75 L · min^{-1}) from the bottom of the aluminum tank through twin 5-cm diameter high-pressure flexible pipes into the baffle section of the upstream chamber of the waterfall apparatus. This allowed a constant 2.5 cm critical depth flowing over the lip of the fall. Water temperatures within each apparatus were maintained at test temperatures ± 2°C by an Aqua Logic Delta Star chiller (Model AE7).

All individual fish were tested at each of 15 waterfall height (H; 100, 250, 400, 550 and 700 mm) × plunge-pool depth (D; 200, 400 and 600 mm) treatments. Prior studies of jumping performance only used each individual fish or group of fish for one height × depth combination (see Brandt et al. 2005; Kondratieff et al. 2006; Ficke et al. 2011). This study used repeated measures on individual fish to evaluate the effects of the experimental design on individual performance over repeated trials. The order of treatment combinations was randomized for each fish, and two fish were chosen at random each day (one fish per fall). Once the treatment waterfall height × plunge pool depth was determined and set, the fish were placed into the Coroplast boxes. Fish jumping attempts were recorded at 30 frames per second with a Unibrain Fire-i digital video camera mounted 1 m above each fall. The cameras were controlled by the SecuritySpy video monitoring program (Myrick 2009). Red lights were placed above the fall and plunge pool to illuminate the apparatus at night and allow filming, while preventing alteration of the fishes behavior (Anthony and Hawkins 1983), by allowing them to maintain a natural photoperiod.

For each trial, fish were allowed 20 h to ascend the waterfall. Following this 20-h period, fish were removed from the waterfalls, weighed, measured, and returned to the holding tanks. New fish were loaded each evening, and individual fish were never used on consecutive nights to allow at least a one-day recovery period between trials.

The repeated trials were physically demanding on both species of fish, and fish occasionally sustained damage to their dermal layer from contacting the sidewalls of the plunge pool during attempts. To encourage healing from such injuries, fish were held for one hour following each trial in a 100-L recovery tank containing oxygen-saturated water and treated with Stress Coat (Mars Fishcare North America, Inc.). Despite these precautions, two white suckers (one each at 14 and 22°C) and three burbot (one at 6°C and two at 13°C) were euthanized because of secondary infections during the study. Data from videos that showed compromised ability were not used in analyses.

Digital videos of all jumping trials were manually reviewed using Apple Quicktime Player 7 to allow behavioral observations and to ensure that fish attempted to pass all height × depth treatment combinations. Three types of behavior were described for both species: explorations, attempts and successes. Explorations (E) were defined as instances where fish slowly extended their heads above the water at the base of the fall. This behavior typically corresponded with periods of increased activity when attempts were likely to happen. Attempts (A) were defined as an upward acceleration of fish at the base of the fall coupled with rapid tail beats. Successes (S) were recorded when fish jumped into the upper chamber of the fall. No further data (explorations, attempts or successes) were recorded for a given trial following a successful ascent, even if the fish returned to the lower pool. The time of each attempt or exploration was recorded, along with whether it was successful. Fish total length (TL; mm), number of previous trials (P_t), number of previous successful trials (P_s), condition (C; relative weight [Wr]), and treatment temperature (T; °C) were recorded for each trial (Table 2.1).

Statistical Analyses – Jumping

Separate Generalized Linear Models (GLMs) were fit with explorations, attempts and successes as response variables for each species using the GLM function in R. A Poisson logit link function was used for the exploration and attempt models, and overdispersion was tested with the “dispersiontest” function in R. A binomial logit link function was used for the success models. For the exploration models, height (H), depth (D), total length (TL), relative weight (C), temperature (T; °C), number of previous trials (P_t) and number of previously successful trials (P_s) were used as predictor variables. For the attempt model, the same predictors were used with the addition explorations (E) to determine if explorations were predictors of attempts. Similarly, the success models were the same as above except they included both explorations and attempts as predictors.

Models were selected with the MuMin package in R using Burnham and Anderson's (2002) guidelines. For each response variable (explorations, attempts or successes) models were fit using all possible combinations of predictor variables. Each model was then assigned an AICc score and relative model weight prior to being ranked by ΔAICc (see Appendix A and B for top 20 AICc models and their weights). For the exploration and attempt models, an averaged parameter estimate for all predictor variables were created based on the cumulative weight that each predictor obtained across all weighted models. This approach allowed maintenance of the information obtained from all predictors, and permitted a comparison of relative predictor importance based on the cumulative model weights.

An alternate approach for model selection was used for the success models because I wanted to maintain conservative parameter estimates for a predictive model of probability of successful waterfall ascent. The model-averaged parameter estimates with relatively high (>0.5) cumulative weights were maintained while other parameters were dropped from the model. The remaining parameters were set to realistic levels that would maximize probability of success to create a predictive model of probability of success over the H and TL values within the range tested (white sucker parameters: H=100-700mm, TL=300-500mm, E=0 (minimum), P_t=0 (minimum), A= 3 (mean)). Instead of using the mean response, 95% and 99%-prediction intervals were calculated to identify conservative design parameters that account for the strongest leapers in the fish population tested.

Swimming Trials

Two types of swimming trials were conducted: constant acceleration trials (CAT) and fixed velocity trials (FVT). All swimming trials were conducted in a Loligo Model 185 swim flume with automated velocity control provided by Auto-Resp software (Loligo Systems) running on a desktop PC. Water flowed into the flume at 110 L · min^{-1}; temperature was regulated by recirculating 8 L · min^{-1} through a chiller (Aqua Logic Delta Star model AE3). The swimming chamber of the flume was 25 cm (w) × 25 cm (d) × 100 cm (l), which provided a large enough cross-sectional area that the cross-sectional area of the fish were always < 10% of the chamber cross-sectional area.

Following pilot swimming trials with burbot, a 2.5-cm thick section of plastic honeycomb material was attached to the downstream screen of the chamber. Both burbot and white suckers avoided touching this material with their caudal fins, and thus did not require the use of additional stimuli to prevent fish from resting on the rear screen. The forward 36 cm and 15 cm of the swimming chamber were covered on the top and side, respectively, with 2-mm thick black Cloroplast. These opaque covers encouraged fish to occupy positions near the front of the swim chamber. Burbot are nocturnal and swam better during low light periods in pilot studies, so all burbot trials were conducted at night with the use of diffuse red illumination (Anthony and Hawkins 1983) for video recording purposes. Digital video of each trial was recorded using the same digital video camera system described in the jumping trials.

For all swimming trials, individual fish were selected from the holding tank and gently placed into the swimming chamber, minimizing the duration of air exposure. No individual fish were used for both the swimming and jumping trials. The velocity was set to 25 $cm \cdot s^{-1}$ for 1 h to allow the fish to recover metabolically from handling. Following this recovery period, water velocities were automatically increased in accordance to the specific trial protocol (constant acceleration or fixed-velocity; see below for specifics). Video recording began at the start of the experimental period. At the end of the trial, fish were euthanized (MS-222, 250 $mg \cdot L^{-1}$). Following euthanasia, fish were weighed to the nearest g and measured to the nearest mm for TL.

Constant Acceleration Trials

Constant acceleration trials were conducted at three temperatures each across the range of tolerable temperatures for burbot and white suckers (Table 2.2). Water velocities in the CATs were increased from 25 $cm \cdot s^{-1}$ at a constant rate of 10 $cm \cdot s^{-1} \cdot min^{-1}$. CAT trials were concluded once a velocity was reached that resulted in fish impinging upon the rear screen of the swimming chamber, and not resuming regular swimming after a sudden (< 5 s) reversal of flow direction. Analyses of CAT videos identified the size-specific velocities at which fish transitioned between swimming gaits. The transition from a steady, aerobic swimming gait to an unsteady, burst-and-glide gait characterized by fast tail undulations was used to identify $B_{t.}$

Fixed Velocity Trials

To obtain an estimate of anaerobic endurance, and maximal burst swimming velocity, pilot fixed velocity trials were conducted at a range of high velocities for fish of both species over a range of size classes and at all test temperatures. The velocity ranges between B_t to the maximal, size-specific swimming velocities obtained from these pilot trials were used as an approximation for the scope for anaerobic swimming capability. Full-scale FVT measurements were then taken across this range to determine fish endurance time at anaerobic swimming velocities.

For the FVTs, three burbot were swum at each of five anaerobic test velocities (Tables 2.3 and 2.4). Because there was a strong TL-specific relationship in B_t for white suckers, they were stratified into three size groups where three fish were swum at each of five different velocity treatments. Burbot were not stratified by length because the size range of burbot available was smaller than for white suckers and because there was less length-dependence in performance.

At the start of each fixed velocity trial, the water velocity was increased to a "preparatory" level 10 $cm \cdot s^{-1}$ below B_t for a given size class. This increase in velocity helped the overall performance of the fish, as it seemed to initiate a focused swimming behavior with little resting above B_t. The "preparatory" velocity was maintained for <10 s, and then the velocity was increased to the trial velocity. The trial continued until the fish became impinged on the rear screen of the swim flume. Fish were processed as in the CAT experiments, and the swimming videos were reviewed to determine how long the fish swam at the test velocity before impingement. The time at impingement was termed the failure time (F_t).

Statistical Analyses – Swimming

For CATs, linear regression models were fit with B_t as the response variable. Total length (TL), days the fish was in the lab (D_l), the difference in temperature between the holding tank and the swim flume (T_{diff}), T, and C were used as predictor variables. For each response variable, models were fit using all possible combinations of predictor variables. Each model was assigned a relative model weight and

AICc score, and a final model was created using averaged parameter estimates based on relative covariate weights (Burnham and Anderson 2002; see Appendices C and D for top 20 AICc models and their weights).

For FVTs, a linear regression model was fit for each species with $\log(F_t)$ as the response variable. The log transformation was necessary to ensure that the model met the assumptions of homogeneity of variance and linearity necessary for linear regression. Total length (TL), condition (C), temperature (T), temperature difference (T_{diff}), and trial velocity (V; $cm \cdot s^{-1}$) were used as predictor variables.

Similar to the success model from the jumping analysis, a conservative approach for model selection was used for the FVT data. Models using all possible combinations of predictor variables were fit and ranked by AICc (see Appendix E for top 20 AICc models and their weights). A final model containing model-averaged parameter estimates was generated. For the final model, only parameters whose estimates had high cumulative model-averaged weights (> 0.5) were retained. A range of total length and velocity values encompassing the range of values tested was used to generate 95% and 99%-prediction intervals with all other predictors set to conservative values (white sucker parameters: V=50-170 cm/s, TL= 100-400 mm; burbot parameters: V= 100-160 cm/s, TL= 300-570 mm, T=6°C (minimum)). This prediction interval was then used to produce conservative endurance (F_v) predictions based upon total length and velocity.

Velocity Barrier Development

The conservative F_t predictions were then used with Peake's equation (Peake et al. 1997) to estimate the required velocity of a barrier of a given length necessary to prevent passage as follows:

$$V_f = V_s - d/F_v$$

where V_f is the required velocity in the velocity barrier, d is the distance a fish can ascend the barrier, and F_v is the endurance or time until impingement calculated from the FVTs. The V_s parameter represents the velocity that the fish is swimming relative to the water velocity and is equivalent to the velocity treatments of the FVTs. The required barrier velocity (V_f) and d are unknown in this equation, so realistic values for both parameters were specified. By substituting several values of d into Peake's equation, curves were developed to describe the minimum V_f based on the collected data of a fish swimming at V_s where the difference between V_f and V_s is equivalent to the positive ground speed that a fish attains as it ascends a velocity barrier.

RESULTS

Jumping Trials

The number of explorations and attempts decreased for white suckers at 22°C and in treatments with greater depths and heights (Figure 2.3). Despite this difference, the number of successes between temperature treatments was similar, with white suckers only succeeding at heights of 100 and 250 mm across all depth treatments. Similarly, the number of explorations and attempts decreased at 6°C compared to 13°C and at deeper plunge pool depths and waterfall heights for burbot (Figure 2.4). However, the number of successes was the same at each temperature with burbot successfully ascending 100-mm waterfalls from all plunge pool depths. White suckers were more likely to explore, attempt and succeed in the afternoon until dusk (Figure 2.5) while burbot jumping activity peaked during the night (Figure 2.6).

For both species all predictor variables were included in the final AICc averaged models for number of explorations and attempts because these models are descriptive in nature (Table 2.5). For both white suckers and burbot the cumulative predictor weights for H and D had strong negative effects on number of explorations and attempts. Condition had a weak positive effect on number of explorations, but a strong positive effect on number of attempts for both species. Temperature was also a strong predictor of attempts and successes, but had opposite effects for each species. Burbot activity increased with T while white sucker activity decreased. For white suckers TL was a strong predictor with larger fish making more explorations and fewer attempts. For burbot TL was only a strong predictor of attempts, with larger burbot having fewer attempts than smaller burbot. For both species, number of previous trials had a strong negative effect on explorations and a strong positive effect on attempts. Similarly, number of previously successful trials had a strong negative effect on the number of explorations for both species. For white suckers it also had a strong negative effect on attempts, while for burbot it was not a strong predictor of attempts. The number of explorations in a trial had a strong positive relationship to the number of attempts.

The low numbers of successes in the burbot trials caused extreme variance in the success model. This precluded quantitative predictions of barrier height requirements to prevent passage, although the parameter estimates and associated averaged model weights are still presented (Table 2.6). For the final white sucker success model, only the parameters with strong cumulative weights were retained. Waterfall height, total length, number of explorations, and previous trials all had strong negative effects on the probability of success for white suckers. Additionally, there was a strong positive effect of attempts on success as expected. The other parameters, including number of previous successes, condition, temperature and depth were dropped. The included parameters were set to conservative values, and height and total length were varied across the range of values tested to generate a predictive table that can be used to determine waterfall heights to prevent passage of white suckers of specific maximum TL (see Appendix F for predictive table).

Swimming Trials

Burst transition (B_t) in the CATs occurred at higher velocities for larger individuals, however, on a per-body-length basis, the transition occurred at higher velocities for white suckers (Figures 2.7 and 2.8). Additionally, smaller fish were more capable on a per-body–length basis than larger fish. This difference was more apparent in white suckers than burbot, and resulted in the length stratification for velocity treatments described above for the FVTs.

All predictor variables were included in the final AICc averaged models for B_t for each species because these models were descriptive in nature (Table 2.7). Total length was a strong, positive predictor of B_t for both species.   Temperature had a strong positive effect on white sucker swimming performance across all CAT models, and a strong negative effect for burbot.   The number of days in the lab was a relatively strong predictor across all models, having a negative effect on white sucker B_t, and a positive effect for burbot B_t. For burbot, condition was a strong positive predictor of B_t. For both species T_{diff} was a poor predictor.

In the FVTs, both species had lower endurance times at higher velocities (Figure 2.9). For white suckers, there was high variability in failure time at velocities under 90 cm· s^{-1}across all temperature treatments. For burbot, this trend was evident at velocities under 130 cm· s^{-1}in the 6° and 14°C treatments, although the variability was less than that observed for white suckers.

Trial velocity was the strongest predictor for both species in the AICc averaged FVT models (Table 2.8). Individual total length was also a strong positive predictor for both species. For burbot, temperature had a strong negative effect on failure time. For the final predictive model, all variables with low cumulative weights were dropped. These variables included temperature difference and condition for both species in addition to temperature for white suckers.

Peake's equation was used with 95 and 99%-prediction intervals from each FVT response model to generate curves designating required design velocities to prevent passage of the largest individuals tested from each species for velocity barriers of a given length (Figures 2.10 and 2.11). A cumulative table was also created to allow determinations of barrier length and velocity requirements to prevent passage of burbot or white suckers of a given TL (see Appendices G and H for predictive table).

DISCUSSION

This study used a three-phase approach to develop design guidelines for hybrid vertical-velocity barriers to restrict the upstream movements of burbot and white suckers. The three-phase approach used quantitative measurements of fish jumping ability, constant acceleration swimming performance, and fixed velocity swimming endurance to generate the 99%-prediction intervals that are the backbone of the design guidelines. As discussed below, white sucker performance tended to exceed that of the burbot, particularly with respect to jumping heights and maximum swimming endurance, so, in general, barriers designed to prevent the movement of white suckers should also prevent the movement of burbot, provided that size-related differences are accounted for.

Jumping - Design Recommendations

This study on fish jumping was the first to record quantitative data on individual explorations, attempts and successes, and one of few studies of fish jumping capability (but see: Brandt et al. 2005; Holthe et al. 2005; Kondratieff and Myrick 2005; Lauritzen et al. 2005; Kondratieff and Myrick 2006; Ficke et al. 2011). Collecting data from individual trials allowed this study to accurately describe the waterfall heights that prevent passage of white suckers of a given size by statistically accounting for the effects of the experimental conditions on individual performance. Additionally, quantifying attempts allowed confirmation of the assumption that fish attempted to negotiate all waterfall heights lending an increased level of confidence to the minimum waterfall height recommendations that would be absent from success-only data as presented in Kondratieff and Myrick (2006).

White suckers were stronger leapers than burbot, but were not particularly successful at higher falls when compared to other species only ascending fall heights of up to 250-mm. The shortest white sucker to ascend the 250-mm high drop was a 292-mm long individual; this is equivalent to a leap of 85.6% of its TL, substantially lower than the 290-470% total length (L_t) leaps reported for brook trout, brassy minnows, and common shiner by Kondratieff and Myrick (2006) and Ficke et al. (2011). The predictive table generated from these data provides clear design criteria to prevent passage of white suckers within the size range tested in this study (see Appendix F for predictive table). This table allows managers to determine the probability of success for white suckers of various sizes with a level of confidence up to 99%. Using the total length of the largest white sucker expected in the system will allow robust design to all individuals in the population, particularly if designs exceed these 99% recommendations to the extent practically feasible.

The low rate of success for burbot was encouraging from a barrier design standpoint indicating that burbot are not strong leapers, despite the fact that it precluded the development of a quantitative predictive model of success. Burbot only successfully ascended 100-mm vertical drops, and the shortest fish that ascended this fall height was 392 mm long; thus this fish ascended a drop that was 25.5% of its total length. Although burbot were never observed leaving the water completely, they did perform a "tail-walking" behavior wherein they moved rapidly across the surface of the water with a substantial proportion of their body protruding vertically from the water, propelling themselves across the surface on their caudal fin and lateral portion of their body. No successful ascents were observed as a result of this behavior, although several individuals were able to get their heads over the lip of the fall at heights up to 400-mm. In these situations, it appeared that burbot lacked the leverage to pull the remainder of their bodies over the lip of the fall. In a natural situation where the critical depth of the water flowing over the lip of the fall exceeds the experimental conditions of this study (critical depth=2.54 cm) burbot may gain sufficient leverage to ascend the fall if their head gets over the lip. Given these observations, a conservative fall height for burbot would be one that is higher than the maximum total length of burbot in the fishery of interest. This would greatly exceed the highest length-specific height where burbot successfully ascended the fall in this study and should be very robust to prevent passage. For burbot, future studies using focused data collection on waterfall heights < 300 mm may result in greater number of successes allowing a more quantitative description of burbot leaping.

The most surprising behavioral finding in this study was the negative relationship between total length and probability of success for white suckers. Larger fish should be more capable of leaping the fall than smaller fish (Holthe et al. 2005), however, shallow plunge pools have been shown to reduce jumping success (Kondratieff and Myrick 2005; Kondratieff and Myrick 2006;)**.** When tested in the 200-mm depth treatment, both species often made jumping attempts while lying on their side on the bottom of the pool, aggressively undulating their body as if burst swimming, apparently trying to become oriented vertically to attempt to leap the fall. This suggests that the shallow plunge pools were problematic, especially for larger fish. Despite this observation, plunge pool depth was not a strong predictor; however, the strong predictive capability of total length in the model may have masked the effect of depth if larger individuals had more difficulty at the 200-mm depth treatment. Testing of an interaction term between depth and total length was not pursued to avoid *post hoc* bias. Nevertheless, the negative effect of depth on success is well documented (Kondratieff and Myrick 2005; Kondratieff and Myrick 2006), and the shallowest plunge pool depths possible should be utilized in barrier design.

Combining the waterfall height and plunge pool depth recommendations for each species allows broad recommendations for barrier design. In the case of white suckers, the 99% prediction interval for probability of success can be used to select waterfall heights driven by the total length of the largest white sucker expected in the system (See Appendix F for predictive table). For white suckers larger than those tested (>502 mm TL), the highest fall ascended was 85.6% of the total length of the individual ascending the fall, so falls exceeding this percentage of the TL of the largest individual in the system should be sufficient to prevent passage, particularly when coupled with the plunge pool depth and velocity recommendations described in this study. Similarly, for burbot the highest total length specific height leaped was 25.5%, however, a vertical drop that exceeds 100% of the total length of the largest burbot expected in the system is recommended due to the tail-walking behavior observed. For both species, larger individuals at the 200-mm depth treatment struggled to leap. The 200-mm plunge pool translated to a depth of 28.7% total length of the largest burbot tested (696 mm) and 39.8% TL of the largest white sucker (502 mm), and plunge-pools shallower than these percentages of the total length of the smallest individuals of interest are recommended. When possible, higher falls and shallower plunge pools than the minimums defined should be constructed.

Jumping – Behavioral Observations

The approach of reviewing the videos from each jumping trial was useful for collecting more refined data associated with the motivations of these species to jump. Accounting for such motivations allowed statistical control of the behavioral changes associated with a lab study and helped account for variability associated with the experimental design that can be useful for guiding future research.

For both species, the negative effect of barrier height on explorations and attempts suggests that both species conserved energy by remaining relatively inactive when faced with waterfalls that exceeded their jumping capabilities. Fish passage structures have been shown to require hydraulic conditions that encourage fish to attempt passage in order to be successful (Bunt et al. 2012; Williams et al. 2012). The behavioral avoidance of attempting to pass vertical barriers that exceed the leaping capabilities of a target species could stem from similar cues, and likely allows for more energetically efficient movement between habitats. Collecting data on attempts and explorations allowed an evaluation of these behaviors and provided reassurance that all H treatments were attempted by the species of interest. Additionally, the reduced number of attempts at higher H treatments would assist in barrier effectiveness, as it should limit the number of times a functioning barrier is challenged in a natural setting.

The negative relationship of depth to numbers of explorations and attempts suggests that fish were more motivated to move when in shallow plunge pools as opposed to deeper pools that may have been perceived as refugia (Labbe and Fausch 2000). This may represent a behavioral adaptation to being exposed to predation or desiccation (Schlosser 1988), starvation, or suffocation in shallow water situations (Davey et al. 2006). In drought situations with declining water depth fish have been shown to instinctually move toward areas of deeper water refugia (Gagen et al. 1998; Huntingford et al. 1999), and a similar mechanism may have been increasing the number of attempts in the low-depth treatments.

The effect of condition on explorations and attempts was positive suggesting behavioral reductions in activity by both species in response to reduced condition. Anaerobic swimming capacity declines with declining condition (Lowery and Somero 1990; Martinez et al. 2003), which suggests that the ability of fish to use burst swimming to leap a barrier may be reduced at lower condition levels. The behavioral effects of reduced body condition on fish activity suggest that fish may reduce activity to maintain energy reserves during times of physiological stress or low food availability (Sogard and Olla 1996). This study suggests that for both burbot and white suckers activity (attempts and explorations) decreased with decreasing condition in order to maintain energy reserves, however, condition was not a strong predictor of success suggesting that reduced condition did not reduce leaping ability. Future studies should attempt to maximize condition to obtain greater numbers of jumping attempts, keeping in mind that doing so may produce results that do not directly apply to wild fish populations that do not have the same high levels of condition.

The levels of burbot and white sucker activity (explorations and attempts) were strongly influenced by water temperature, though not necessarily in the manner predicted. Perhaps more importantly, however, was the fact that temperature did *not* affect the outcome of the attempts, as both species were equally successful at jumping at all tested temperatures. The positive and negative effect of temperature on burbot and white sucker activity, respectively, is likely a result of the temperature treatments they were exposed to. Burbot undergo migrations to spawn in the winter months (Paragamian 2000; Paragamian and Wakkinen 2008), so the 6°C treatment was selected to take advantage of this greater drive to migrate by using pre-spawn burbot to generate more jumping attempts. However, given that more ascent attempts were made at 13°C than at 6°C, it appears that this was unsuccessful. The 13°C treatment was closer to the optimal metabolic temperature for burbot (Paakkonen and Marjomaki 2000; Hoffman and Fischer 2002)**.**

A similar result was seen in white suckers, wherein more attempts occurred near their optimal temperature of 15°C (Beitinger and Bennett 2000) than at 22°C. Despite the temperature-related differences in attempts, both species were equally successful across temperature treatments. This suggests that the physiological effect of temperature on jumping capacity is negligible for these species despite the significant effects on behavioral activity. Ficke et al. 2011 found that temperature did not affect the success of common shiners (*Luxilus cornutus*) but did find that Arkansas darters (*Etheostoma cragini*) and brassy minnows (*Hybognathus hankinsoni*) were more successful at higher temperatures. Future studies should consider using treatment temperatures near the metabolic optimum of the study species to maximize attempts along with higher treatment temperatures to evaluate the effects of temperature on jumping success.

The number of previous trials and successes reduced the propensity of both species to explore the fall but was correlated with an increase in the number of attempts. This suggests that there may have been a training effect similar to that observed in fish swimming studies (Hammond and Hickman 1966; Farlinger and Beamish 1978) whereby fish became accustomed to the fall and began focusing more energy on attempting to ascend the fall in subsequent trials.

In general, fish that explored the fall more were more likely to make attempts, however, in the case of white suckers, individuals with higher numbers of explorations were less likely to successfully ascend the fall, so greater exploration on an individual basis did not automatically translate into greater passage success. For white suckers explorations, attempts and successes were more likely to occur from mid-day until dark, while burbot were more active in the night. Similarly, Reebs et al. (1995) found that wild juvenile white suckers were more active near noon with decreased activity after dark suggesting a diurnal activity strategy that is counter to the nocturnal life-history suggested by Campbell (1971), Emery (1973) and Kavaliers (1980). The differential findings for white suckers suggest that they may have a plastic diel life history dependent on the ecology of the habitat they are in. Conversely, burbot are known to be nocturnal (Ryder and Pesendorfer 1992; Fischer et al. 2001; Dixon and Vokoun 2009), and this study supports that finding.

Swimming – Design Recommendations

The use of both CAT and FVT experiments in this study allowed a robust description of the both the TL-specific velocities that fish begin swimming anaerobically ($V>B_t$) as well as their endurance across their anaerobic swimming velocities. This allowed a multi-tiered description of the swimming capacity of these fishes at barrier design velocities that cause rapid fatigue.

Forcing fish to swim anaerobically prior to attempting to ascend a waterfall should reduce their probability of success and will allow the construction of shorter vertical barriers to prevent passage. In this study, burbot appear to be less capable aerobic swimmers than white suckers, transitioning to anaerobic swimming modes at lower velocities (1.1-2.3 BL/s for burbot and 1.4-5.8 BL/s for white suckers; Figures 2.7 and 2.8). Using these TL-specific velocity ranges as minimum design velocities will ensure that fish are fatigued prior to leaping the fall, however, they do not elucidate endurance at those velocities.

Endurance trials conducted at fixed velocities in swimming flumes have long been used to determine physiological performance of fishes and to create design criteria for fish passage structures (Brett 1964; Jones et al. 1974; Beamish, 1978; Bestgen et al. 2010). The equation developed by Peake et al. (1997) using endurance data from fixed velocity swimming trials was initially used to determine the maximum distance that lake sturgeon (*Acipenser fulvescens*) could ascend fishways operating at variable velocities. These same methods can be adopted to specify design minima for velocity-based fish barriers, and may be more useful for barrier design because they designate a minimal design velocity based on a theoretical optimal positive groundspeed.

The endurance capacity found in our study for white suckers exceeds that found in early work conducted by Jones et al. (1974) who measured endurance in closed swim flumes. The Jones et al. (1974) study used critical velocity to determine the ability of fish of a given size to pass a 100-m velocity barrier, but did not evaluate their anaerobic endurance, thus helping to explain the ability of white suckers to overcome higher velocities tested in the FVT trials conducted in the current study. Ficke et al. (2012) conducted a similar critical swimming trial on white suckers tagged with passive integrated transponders, and found critical swimming speeds averaged 2.1 to 2.5 BL/s for untagged control fish which is substantially lower than the 3-6 BL/s gait transitions observed for white suckers in the current study. Critical swimming speeds offer a strong method for comparing control and treatment groups as was done by Ficke et al. (2012), but likely offers biased estimations of the actual transition from aerobic to anaerobic metabolism when compared to behaviorally-determined transitions obtained from CAT trials.

Open channel, volitional swimming studies have been shown to obtain higher estimations of fish endurance due to the elimination of forced swimming and confined swim chambers which limit natural burst and glide swimming behaviors. Two open channel volitional studies of white suckers have been performed that demonstrated higher endurance than the estimations obtained from the FVT trials in the current study. Haro et al. (2004) found that white suckers could swim up to 18 meters against velocities of 150 cm/s and Peake (2008) found that over 62% of the white suckers attempting 50 m long ramps successfully ascended against velocities of 120 cm/s. Similarly, Vokoun and Watrous (2009) report endurance in excess of what I observed in the FVT trials in an open channel experiment conducted on burbot. Their results indicated burbot could ascend a 15-m long channel against 105 cm/s velocity. An important distinction between flume based studies and open channel studies of endurance is that velocity control is higher and much more precise in flume based studies. Fish will aggressively seek out velocity refuges, and open channel experiments do have such refugia near the corners of the open channels, where the velocities that the fish are overcoming may be substantially less than the experimental objectives that could bias endurance estimates high. Open channel experiments are useful, however in that they are closer approximations of what fish may encounter in a natural setting. The potential for underestimation of endurance from flume based FVTs underscores the value of the dual approach suggested for barrier construction as well as the desirability for barrier designs that exceed estimated endurance findings.

The FVT data did underscore the relationships between velocity and total length as related to swimming endurance for both species, and when used with Peake's equation, were instrumental in the development of the predictive tables identifying combinations of barrier length and velocity that should prevent upstream passage of both species. Peake's equation artificially designates differential positive ground speeds (the difference between V_f and V_s) and can be adapted to then create curves whose peak represents the positive groundspeed where a fish can reach a given distance (*d*) most efficiently (Peake et al. 1997). In the predictive tables generated in Appendix G and H the bold values represent these peaks, or the worst-case scenarios, and are the optimal *minimum* design velocities to prevent passage of a fish of the designated TL in a velocity barrier of the specified *d*. For fish length × barrier length combinations that do not include a bolded value, the "worst-case-scenario" positive ground speed velocity is not included within the values tested, and design of a barrier of the given length and velocity is not recommended.

As with the jumping study, the predictive models generated from the FVTs are only valid for fish within the total lengths tested. However, the inverse relationship between TL and relative B_t can be used to make conservative estimates of design velocities that force fish larger than those tested to use velocities above their B_t. White suckers > 200 mm transitioned to burst swimming at velocities < 4 BL/s, while burbot of all sizes transitioned at velocities < 2.3 BL/s. Multiplying these transition velocities by the length of the largest fish in the system should ensure anaerobic swimming for all fish in the system, given the negative relationship observed between TL and length-specific B_t. For example if a 100-cm TL burbot were expected to be the largest in the system of interest, a velocity of 230 cm/s should force anaerobic swimming and rapid fatigue regardless of barrier length. The predictive tables presented in Appendix G and H can be used to identify conservative estimates of minimum design velocity for barriers of a given length. For example, a 50-cm burbot would not be able to ascend a 10-m long barrier with a current velocity of 67.7 cm/s or 1.35 BL/s. Applying this BL/s velocity to a 100-cm TL burbot would predict that a 10-m long barrier with a velocity of 135 cm/s would prevent passage based on the conservative assumption that larger fish are less efficient swimmers than smaller fish. Again, when possible, designing barriers that exceed these guidelines will add assurance against passage.

Swimming – Behavioral Observations

The constant acceleration methodology used in this study allowed a clear, velocity-based definition of B_t. These types of experiments have recently emerged as a way of collecting physiologically relevant estimates of gait changes (Drucker 1996; Reidy et al. 2000; Peake and Farrell 2004; Peake 2008; Marras et al. 2010) such as the B_t from aerobic to anaerobic swimming that are more accurate than the U_{crit} methodology classically used (Brett 1964). These new CAT studies rely on observing behavioral changes in gait to gain insight into swimming behavior at different velocities for species that physiologically alternate gait. The burst-and-glide or unsteady swimming behavior, coupled with higher frequency tail beats as used to define B_t in this study has been previously documented during anaerobic swimming when fast-twitch white muscle fibers are recruited (Coughlin and Rome 1996; Marras et al. 2010). White muscles are fueled through glycolytic metabolic processes, and lack the endurance of red muscles (Moyle and Cech 2004; Rome 2005). This lack of endurance and change between muscle fiber utilization is what allows the visual identification of changed swimming gait at B_t that is based on direct physiological observations, and makes barrier designs that force fish to swim anaerobically desirable.

Following the CATs with the FVTs provided an opportunity to evaluate the ability of CATs to accurately describe the shift from aerobic to anaerobic swimming. There was a negative relationship for both species between fish length and B_t for both species where larger fish were less capable than smaller fish on a per-body-length basis. In addition to this length-specific difference in performance, there was less variability in the time to failure data collected from the FVTs for burbot as compared to white suckers. For both species this variability was concentrated around velocities approaching B_t (less than 130 cm/s and 90 cm/s for burbot and white suckers, respectively), suggesting that the B_t estimate from the CATs may have been too low. The average B_t was used to define the lower bound of the FVT velocity treatments, and variability among individuals at lower velocity FVT treatments may be a result of individual variability in performance around the velocity at mean B_t which would result in large differences in failure time between individuals swimming aerobically versus anaerobically. Defining FVT treatments based on the upper 99% bound of B_t (rather than the mean) may offer a more conservative estimate of the switch to anaerobic endurance. Constant acceleration trials are likely to underestimate the upper bounds of swimming capability due to fatigue endured during the acceleration process. This fatiguing effect may also bias the estimation of B_t, depending on the effect of acceleration rate on aerobic endurance at velocities $< B_t$ and further investigations on the effect of various acceleration rates on B_t may offer insight into determining experimental acceleration rates that minimize bias.

Recently, the applicability of flume-based endurance trials have been questioned because of behavioral alterations associated with forced swimming in an enclosed area that prevents fish from swimming at an optimal positive ground speed (Peake and Farrell 2006; Peake 2008). Open-channel trials have been shown to offer a less biased means of determining endurance (Haro et al. 2004), but require large flumes and flow capabilities that are unavailable for many researchers. The methodology used in this study may offer a viable alternative for designing velocity barriers that, at a minimum, exceed the anaerobic transition velocity determined from the CATs. Coupling this design parameter with waterfall heights that exceed the jumping capabilities of the target species creates robust barrier designs that should fatigue fish prior to their leaping attempts. In the event that the fish reach the base of the vertical drop, this design presents unfavorable hydraulic conditions at the base of the fall to leap from, despite any bias associated with flume-based endurance trials. In the future, however, performing controlled field studies using mobile waterfall or fishway designs may help reduce lab- and flume-based bias, by allowing researchers to use open-channel designs to challenge fish under natural conditions.

Barrier Implementation Considerations

While it would be theoretically possible to create vertical barriers that completely exclude all upstream fish movements, or velocity barriers that achieve the same function, the information in this study suggests that an even more effective design is a combined velocity and vertical barrier. Such a barrier would use the downstream high-velocity portion to reduce the likelihood of fish even reaching the vertical portion, and, should they do so, would present such unfavorable conditions to initiate a vertical leap that a successful ascent of the waterfall portion would be highly unlikely. Mechanistically, the swimming data collected in this study indicates that the anaerobic energy reserves necessary for sprint swimming would be depleted upon arrival at the base of the fall. Anaerobic sprint swimming is what fish use to leap, and depletion of these reserves will decrease leaping performance, and the ability of fish to make multiple attempts to ascend the fall.

This has been demonstrated in a natural setting where Adams et al. (2000) found that upstream movements of invasive brook trout (*Salvelinus fontinalis*) were inhibited in steep (versus gradual) stream sections containing nearly vertical natural falls. High-gradient streams may force potential invaders to expend a more effort to getting to the base of a vertical fall when compared to lower gradient streams and create more turbulent hydrodynamics at the base of falls producing unfavorable leaping conditions resulting in a decreased leaping ability, and thus probability of success, when attempting to ascend a fall. In high gradient systems, the natural resistance to upstream colonization may reduce the necessity for some redundancy.

Like high gradient streams, culverts and in-stream diversion structures negatively impact fish populations by inadvertently acting as fish barriers due to the presence of sections of high water velocities that extend for a greater distance than fish can swim anaerobically, resulting in passage failure (Warren and Pardew 1998; Gibson et al. 2005; Feurich et al. 2012). Perched culverts with high-velocity currents that require fish to both jump and swim for successful passage are particularly known to reduce passage efficiency because of the combinations of waterfall height, water column depth, and current velocity within the culvert (Makrakis et al. 2012; Mariano et al. 2012). Using these types of design combinations in intentional fish barriers should be beneficial to preventing passage, provided that they operate at the specified design minima over a temporal range of conditions.

In addition to the physiological constraints that a dual-mode barrier would present to fish, this design offers some assurance against issues associated with lab-based trials. Despite cares taken to maintain the health of the fish in this study, holding them in the lab prior to trials likely had an effect on their performance in the trials. In the case of the jumping study, these effects may have limited the number of attempts as well as the individual performance in those attempts. Also, the measured success was relative to the conditions in our falls. Only depth and height were varied in this study, and the morphology of the downstream pool may have altered the probability of success when related to a natural system. Similarly, flume based studies have been shown to underestimate endurance due to behavioral responses associated with forced swimming and with being confined to relatively small swimming chambers that limit energetic efficiency (Peake and Farrell 2006). The redundancy proposed in this study allows for conservative barrier design despite any bias associated with a lab study. Lab studies are however valuable due to their ability to closely control experimental conditions. Future study designs should work to create these types of controlled experimental conditions in a more natural setting to limit lab-related bias.

Kondratieff and Myrick (2005) outlined the importance of considering the natural variability of hydrological conditions in the stream system of interest prior to designing and installing a fish barrier. The minimum design constraints recommended in this study should be met across the range of flow conditions present in a system. Manning's open channel flow equation (see Chow 1959) can be solved across all expected flow conditions to determine the design slope required to maintain the recommended minimum velocities to prevent passage across the temporal scale of interest. Similarly, the variety of flow conditions should be considered to maintain waterfall height and depth requirements across changing water depth conditions, particularly in the pool downstream of the velocity ramp. Increasing flows will likely shorten the length of the barrier and height of the fall while increasing the depth of the plunge pool.

Considerations of the stochastic nature of rivers pertaining to the frequency of high magnitude, low occurrence events are essential for barrier longevity and function. The dual-mode design proposed here should provide some flexibility to address this stochasticity, and will allow increased robustness to passage in extreme conditions where one portion of the barrier may maintain function while the other is being overwhelmed. In order to maintain design specifications and long-term barrier durability, finding barrier locations with favorable geomorphology is desirable. Desirable morphologies include areas that have higher gradient that will allow both the vertical and velocity components to be constructed. Barrier longevity will be maximized in areas containing stable bed conditions to anchor the structure to. Designs should account for proper sediment conveyance and take care to avoid hydrological conditions that may lead to channel instability through processes such as head-cutting.

The design of robust barriers is ideal for preventing passage of invasive species, but may have adverse effects on native fishes by interrupting habitat connectivity. Placement of fish barriers should maintain both suitable habitat quality for native species to effectively carry out their life history requirements and spatial quantity to allow persistence in the face of demographic and environmental stochasticity over a relevant temporal scale (Kruse et al. 2001; Harig and Fausch 2002; Novinger and Rahel 2003). Maintaining minimum stream lengths that meet these life history requirements is critical to the persistence of populations of native species being protected by barriers. In situations where factors other than dispersal capabilities limit the upstream extent of invasions, barriers may be unnecessary, and could negatively impact desirable native fishes by bisecting movement corridors (Adams et al. 2000). Fine-scale studies using movement data or genetic techniques to elucidate the importance of habitat connectivity for the metapopulation persistence of native fishes are recommended to compare the relative effectiveness of potential barrier locations prior to instillation (see Muhlfeld et al. 2012).

In addition to the usefulness of this research for barrier design, the specifications can be used to design fish passage structures, or alter existing fish barriers to allow passage of these species in their native ranges. Particularly, the estimates of maximal aerobic velocity determined in the CAT trials will be useful. Applying these velocities as the upper design limit for fishways will allow fish to maintain aerobic swimming, with its greater endurance, and should therefore increase passage probability. Similarly, the jumping data could be used as maximum design parameters for perched culverts and other vertical barriers. As when designing barriers, care should be taken to acknowledge that these are maximal values. Taking a conservative approach towards implementing passage structures, in addition to taking into account the length-specific effects on performance is desirable to maximize passage probability.

The design recommendations from this study should offer managers clear minimal design criteria to install velocity based and vertical drop barriers. In situations where financial resources and stream channel morphology are favorable, designs should exceed the recommendations from this study for added redundancy against passage of individual fish of unexpected ability. In addition to the usefulness of this study from a barrier design standpoint, these recommendations can also be used as maximal values for fish passage structures designed to benefit burbot and white suckers in their native ranges.

Table 2.1: Summary statistics for burbot and white sucker jumping trials conducted in modified artificial Kondratieff-style waterfalls at two treatment test temperatures each including dates of each treatment, individual mean, maximum and minimum total length (mm), relative weight (Wr), temperature (°C), explorations, attempts, total successes and completed trials out of 150 possible per treatment temperature.

Species	Burbot		White Sucker	
Treatment	5°C	12.5°C	14°C	22°C
Dates	1/15/13 - 4/15/13	6/22/11 - 9/13/11	4/12/12 - 7/15/12	8/18/12 - 1/2/13
Total Length	543 (444-683)	538 (405-696)	394 (286-502)	377 (311-494)
Relative Weight	54.4 (40.0-77.9)	59.8 (43.4-76.1)	77.6 (66.1-90.2)	71.2 (53.2-84.1)
Temperature	6.2 (5.3-7.6°C)	12.9 (12.2-13.9°C)	14.6°C (13.6-16.6°C)	21.4°C (18.9-23.2°C)
Explorations	0.7 (0-14)	2.3 (0-27)	5.7 (0-88)	2.6 (0-56)
Attempts	0.6 (0-10)	3.3 (0-48)	4.7 (0-102)	1.0 (0-15)
Total Successes	8	8	20	19
Completed Trials	140	137	148	147

Table 2.2: Summary statistics for burbot and white sucker constant acceleration swimming trials conducted in Loligo Model 185 swim flumes using AutoResp software at three test temperatures. Data on the test period, number of trials conducted, total length (mm), number of days in lab, temperature (°C), absolute value of difference in temperature between holding tank and swim flume at trial initiation and relative weights are provided. Values are individual means, with minimum and maximum values in parentheses).

Burbot			
Treatment	5	12.5	20
Date	3/20/12 – 5/10/12	6/22/12 – 10/24/12	11/9/12 – 11/15/12
Trials (n)	29	33	23
Total Length	390 (279-535)	438 (330-540)	480 (388-568)
Days in Lab	34 (14-65)	15 (7-24)	19 (16-22)
Temperature	5.7 (5.1-6.1	12.9 (12.2-13.7)	19.5 (18.8-20.1)
Δ Temperature	0.4 (0-0.7)	0.4 (0-0.9)	0.4 (0-1.0
Relative Weight	65.4 (51.4-81.8)	64.5 (52.7-78.9)	58.2 (51.5-70.1)
White Sucker			
Treatment	5	14	22
Date	11/18/11 – 12/20/11	10/29/11 – 11/16/11	1/4/12 – 2/2/12
Trials (n)	37	33	37
Total Length	233 (112-461)	210 (112-379)	233 (107-403)
Days in Lab	29 (11-43)	37 (7-51)	24 (14-58)
Temperature	5.3 (4.6-5.9)	14.1 (13.7-14.7)	21.6 (20.7-23.2)
Δ Temperature	0.4 (0-1.4)	0.4 (0-0.9)	0.5 (0-1.3)
Relative Weight	84.3 (65.9-101.5)	82.0 (63.3-110.7)	85.7 (76.7-109.0)

Table 2.3: Summary information for white sucker fixed velocity swimming trials conducted in Loligo Model 185 swim flumes at 5, 14, and 22°C. Reported data include dates of experiments, length classes for which velocity treatments were assigned, velocity treatments (cm/s), number of trials conducted per velocity treatment, total length (mm), relative weight, and absolute value of difference in temperature between holding tank and swim flume at trial initiation. Temperature, TL, W_r, and ΔT values are individual means, with minimum and maximum values in parentheses).

		5°C	
Date		4/3/12 – 5/3/12	
Length Class	≤199	200-299	≥300
Velocities	50, 70, 90, 110, 130	60, 85, 110, 135, 160	70, 95, 120, 145, 170
Number	15	15	15
Temperature	5.2 (4.6-5.6)	5.2 (4.6-5.7)	5.4 (4.7-5.8)
Total Length	148 (112-199)	250 (210-295)	369 (304-418)
Relative Weight	83.2 (71.2-98.1)	86.0 (77.9-99.9)	88.6 (77.0-96.2)
Δ Temp.	0.8 (0.2-1.8)	0.7 (0.1-1.1)	0.6 (0.0-1.7)
		14°C	
Date		5/11/12 – 8/22/12	
Length Class	≤199	200-299	≥300
Velocities	55, 75, 95, 115, 135	80,100, 120, 140, 160	80, 105, 130, 155, 170
Number	15	15	15
Temperature	13.8 (13.3-14.7)	14.3 (13.3-15.2)	13.3 (13.1-13.9)
Total Length	167 (123-197)	249 (207-299)	354 (317-410)
Relative Weight	82.4 (75.7-91.6)	83.8 (75.9-95.4)	84.4 (69.8-96.3)
Δ Temp.	0.3 (0.1-1.1)	0.6 (0.1-1.4)	0.2 (0.0-1.0)
		22°C	
Date		8/22/12 – 10/19/12	
Length Class	≤199	200-299	≥300
Velocities	70, 90,110, 130, 150	80,100, 120, 140, 160	80, 105, 130, 155, 170
Number	26	22	16
Temperature	21.1 (20.0-21.8)	21.3 (20.9-21.8)	21.4 (20.8-21.7)
Total Length	154 (93-199)	257 (201-297)	322 (301-400)
Relative Weight	72.7 (65.6-85.2)	76.2 (65.3-93.4)	80.8 (72.5-89.9)
Δ Temp.	0.6 (0.0-1.2)	0.5 (0.0-1.0)	0.3 (0.0-1.1)

Table 2.4: Summary information for burbot fixed velocity swimming trials conducted in Loligo Model 185 swim flumes at 5, 12.5, and 20°C. Reported data include dates of experiments, length classes for which velocity treatments were assigned, velocity treatments (cm/s), number of trials conducted per velocity treatment, total length (mm), relative weight, and absolute value of difference in temperature between holding tank and swim flume at trial initiation. Temperature, TL, W_r, and ΔT values are individual means, with minimum and maximum values in parentheses).

5°C	
Date	2/5/13 – 2/22/13
Velocities	100, 115, 130, 145, 160
Number	22
Temperature	6.0 (5.8-6.4)
Total Length	434 (312-564)
Relative Weight	54.8 (45.7-70.7)
Δ Temperature	0.7 (0.4-1.0)
12.5°C	
Date	2/28/13 – 3/13/13
Velocities	100, 115, 130, 145,160
Number	23
Temperature	12.0 (10.9-12.5)
Total Length	432 (336-514)
Relative Weight	51.7 (45.2-68.7)
Δ Temperature	0.2 (0-0.8)
20°C	
Date	11/17/12 – 4/18/13
Velocities	100, 115, 130, 145, 160
Number	18
Temperature	19.7 (18.7-20.8)
Total Length	442 (294-574)
Relative Weight	48.8 (40.8-59.5)
Δ Temperature	0.6 (0.1-1.1)

Table 2.5: Model-averaged (AICc) parameter estimates and cumulative predictor weight (parenthesis) for Poisson-distributed generalized linear models of number of explorations and number of attempts for white sucker and burbot jumping trials. Predictor variables include waterfall height (H; mm), plunge-pool depth (D; mm), fish condition (C; Wr), treatment temperature (T; °C), total length (TL), previous trials (P_t), previous successes (P_s), and number of explorations (E).

Exploration									
Species	Intercept	H (mm)	D (mm)	C (Wr)	T (°C)	TL	P_t	P_s	E
White sucker	-3.3970	-0.0019 (1.00)	-0.0019 (1.00)	0.0069 (0.42)	-0.0835 (1.00)	0.0033 (1.00)	-0.0931 (1.00)	-0.1371 (1.00)	-
Burbot	0.4127	-0.0026 (1.00)	-0.0001 (0.41)	0.0023 (0.38)	0.1523 (1.00)	-0.0004 (0.40)	-0.0973 (1.00)	-1.2033 (0.99)	-
Attempt									
White sucker	-3.3910	-0.0017 (1.00)	-0.0010 (1.00)	0.0208 (0.93)	-0.1413 (1.00)	-0.0022 (0.98)	0.0627 (1.00)	-0.4050 (1.00)	0.0323 (1.00)
Burbot	-0.0417	-0.0021 (1.00)	-0.0044 (1.00)	0.0198 (1.00)	0.2249 (1.00)	-0.0022 (0.97)	0.0480 (1.00)	0.0188 (0.26)	0.0949 (1.00)

Table 2.6: Parameter estimates and cumulative predictor weight for binomially distributed generalized linear models of probability of success for white sucker and burbot jumping trials. Predictor variables include waterfall height (H; mm), fish condition (C; W_r), total length (TL), previous trials (P_t), previous successes (P_s), number of attempts (A) and number of explorations (E). Grey cells indicate parameters dropped from predictive model due to low predictive capability.

Species	Intercept	H	TL	E	P_t	A	P_s	C	T	D
White sucker	8.9636	-0.0207 (1.00)	-0.0127 (0.96)	-0.1893 (0.94)	-0.1193 (0.77)	0.0391 (0.58)	0.1407 (0.41)	-0.0012 (0.28)	-0.0071 (0.28)	-0.0001 (0.26)

Table 2.7: Model-averaged (AICc) parameter estimates and cumulative predictor weight (parenthesis) for multiple linear regression models of glide transition (G_t), burst transition (B_t) and impingement velocity (I_v) for constant acceleration trials conducted on burbot and white suckers. Predictor variables include total length (TL; mm), temperature (T; °C), days in lab (D_l), the ΔT between the holding tank and swim chamber (T_{diff}; °C) and condition (C; W_r).

Species	Intercept	TL	T (°C)	D_l	T_{diff} (°C)	C (Wr)
White sucker	32.6034	0.08353 (1.00)	1.0505 (1.00)	-0.0502 (0.50)	0.1993 (0.26)	0.0259 (0.31)
Burbot	41.6612	0.0415 (1.00)	-0.4509 (0.93)	0.0763 (0.70)	0.0982 (0.24)	0.1966 (0.81)

Table 2.8: Model averaged (AICc) parameter estimates and cumulative predictor weight (parenthesis) for multiple logistic regression models of failure time (s) at different velocities for fixed velocity endurance trials (FVTs) for burbot and white suckers. Predictor variables include total length (TL; mm), temperature (T; °C), the absolute difference in temperature between the holding tank and swim chamber (T_{diff}; °C), and condition (C; Wr). Grey cells indicate parameters dropped from predictive model due to low predictive capability.

Species	Intercept	V	TL	T (°C)	T_{diff} (°C)	C (Wr)
White sucker	5.2428	-0.0267 (1.00)	0.0022 (0.96)	0.0016 (0.31)	-0.0756 (0.52)	0.0046 (0.43)
Burbot	5.7824	-0.0317 (1.00)	0.0018 (0.75)	-0.0446 (0.98)	-0.0517 (0.28)	-0.0020 (0.27)

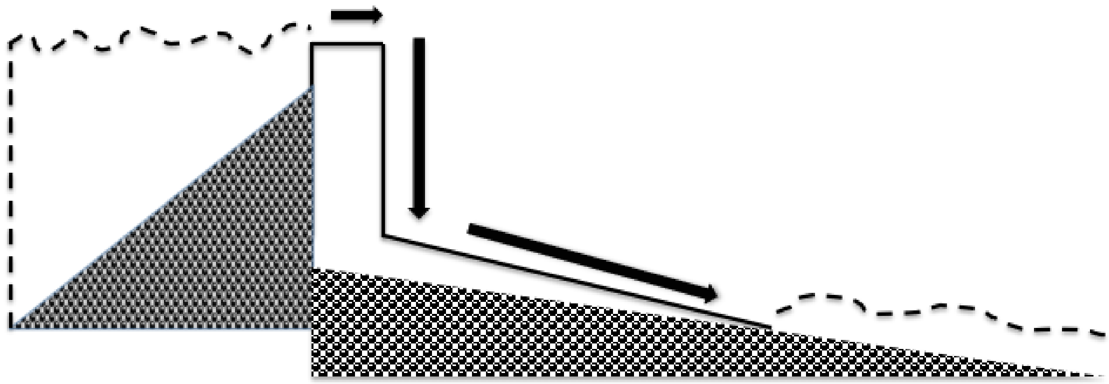

Figure 2.1: Conceptual diagram of vertical drop barrier utilizing a velocity based tail-out section downstream of the vertical drop structure that will require fish to swim anaerobically until they reach the base of the fall, causing fatigue that will further impair the ability of fish to successfully ascend the vertical face of the structure. Dashed lines and arrows indicate water, the white portion indicates the man made barrier, and the shaded section represents the stream substrate.

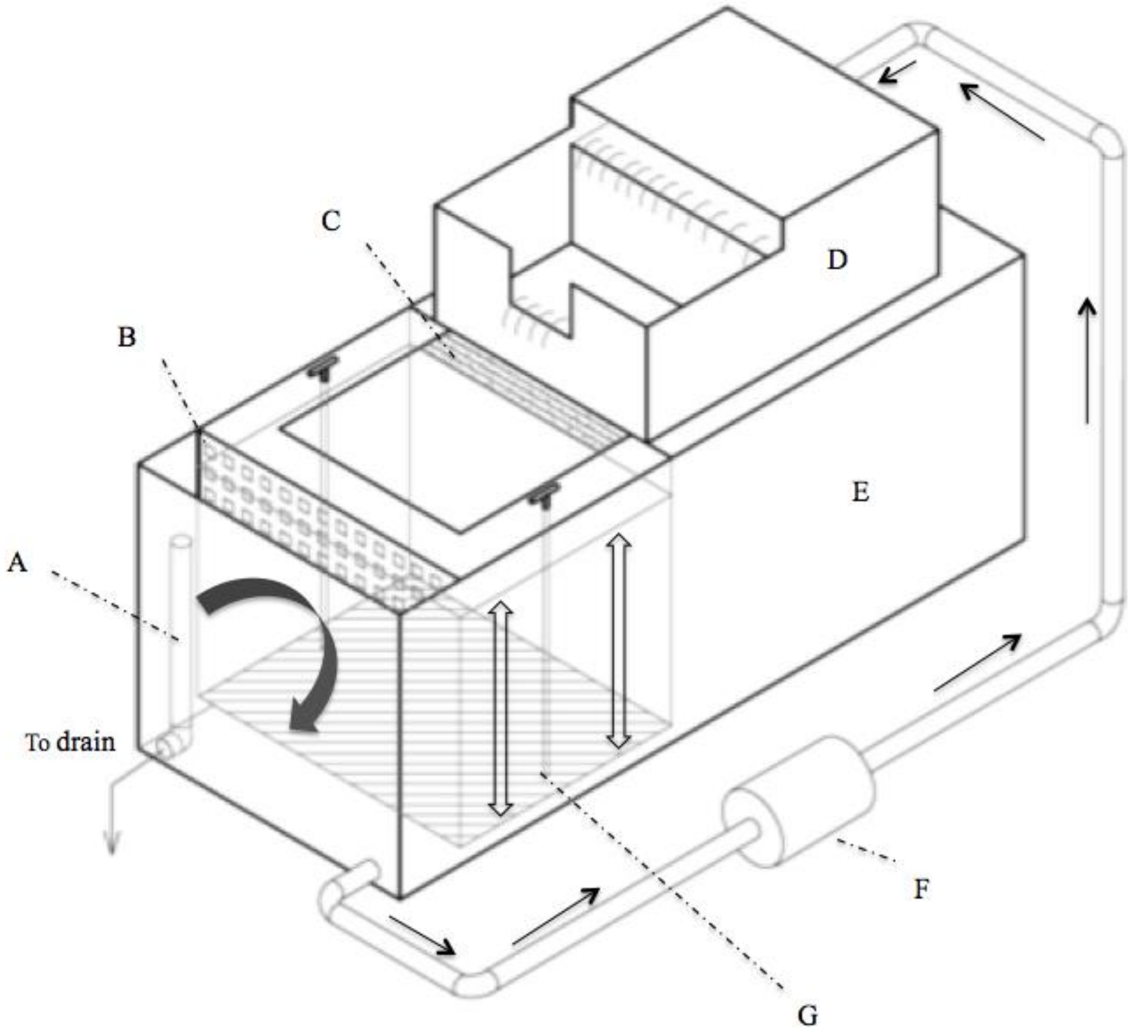

Figure 2.2: Modified Kondratieff Flume-type artificial waterfall used for jumping trials of burbot and white suckers. An adjustable standpipe (A) and adjustable floor section (G) allow alteration of combinations of waterfall height and plunge pool depth below the waterfall up to 1300 mm total. A permeable screen (B) separates the plunge pool area from the drain area. The upper box (D) is held up by cinderblocks so that the lip of the fall is 1300 mm above the floor of the downstream aluminum trough (E). The section where the upper box is supported is separated from the plunge pool area by stacked wood (C) that still allows water flow. Water is pumped from the drain area into the upper box (F).

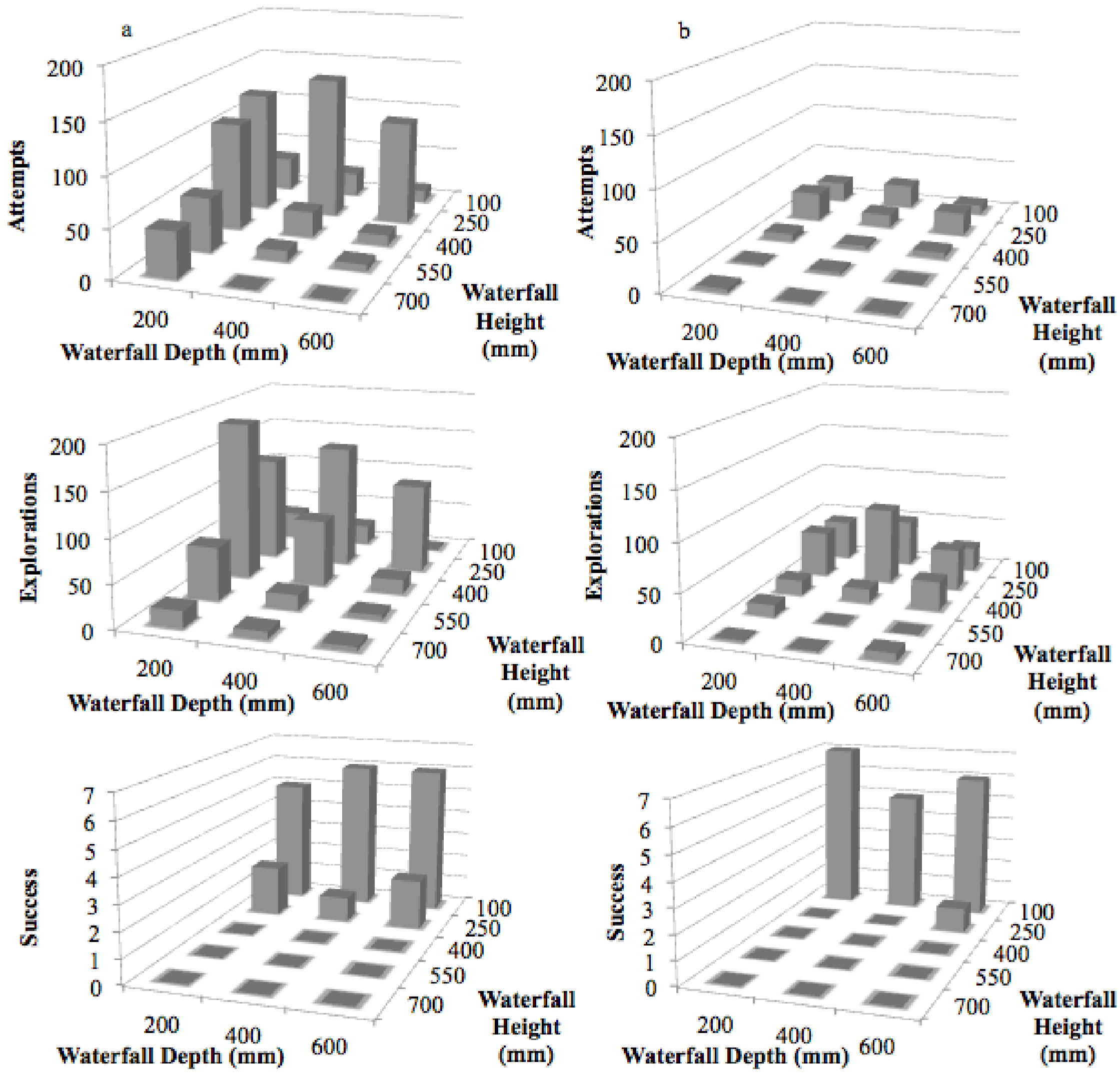

Figure 2.3: Numbers of attempts (top row), explorations (middle row) and successes (bottom row) pooled for ten individual white suckers each at 14°C (left column a) and 22°C (right column b). Each individual was tested at each of 15 waterfall height × plunge pool depth treatments for 20 h.

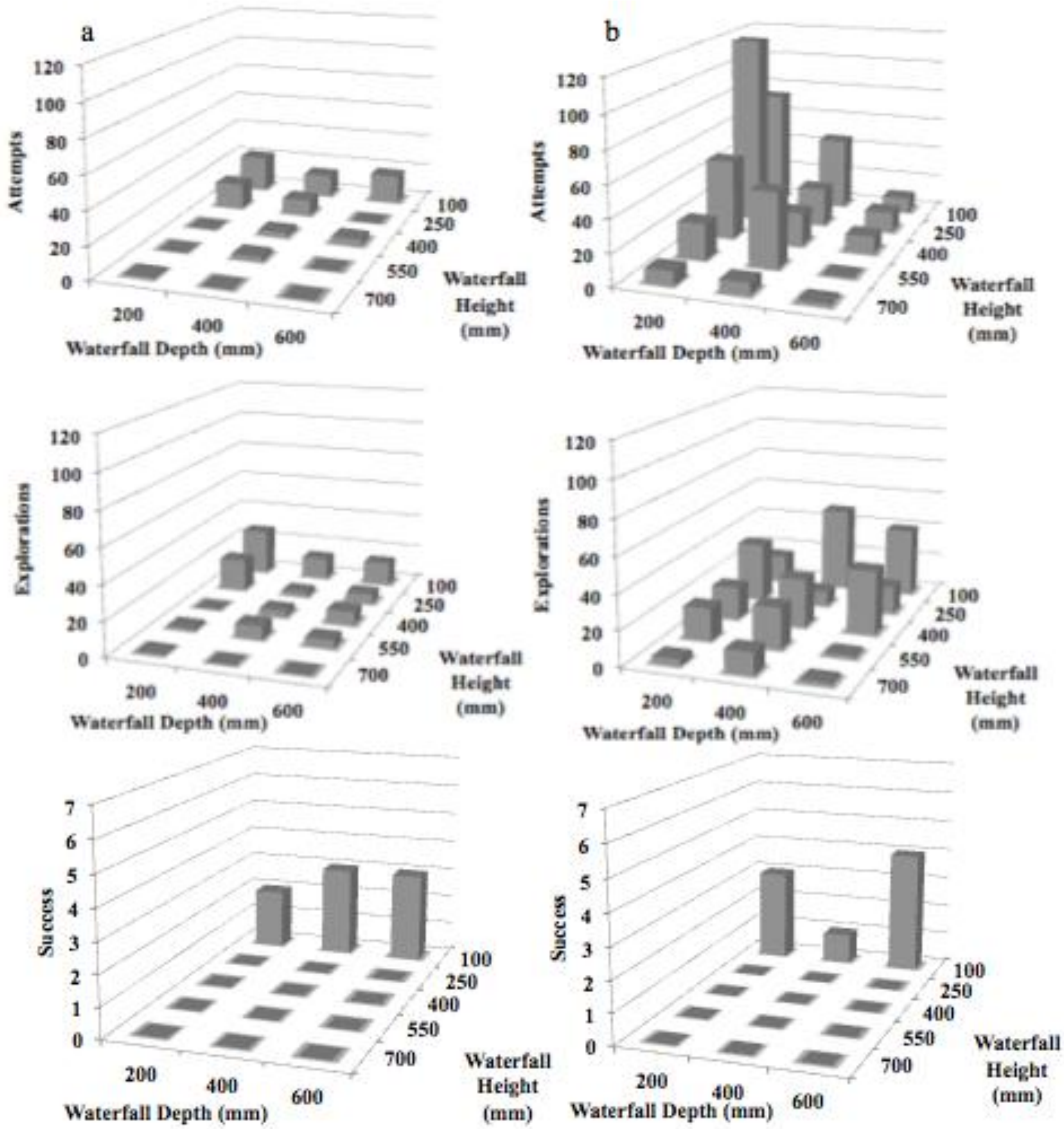

Figure 2.4: Numbers of attempts (top row), explorations (middle row) and successes (bottom row) pooled for ten individual burbot each at 6°C (left column a) and 13°C (right column b). Each individual was tested at each of 15 waterfall height × plunge pool depth treatments for 20 h.

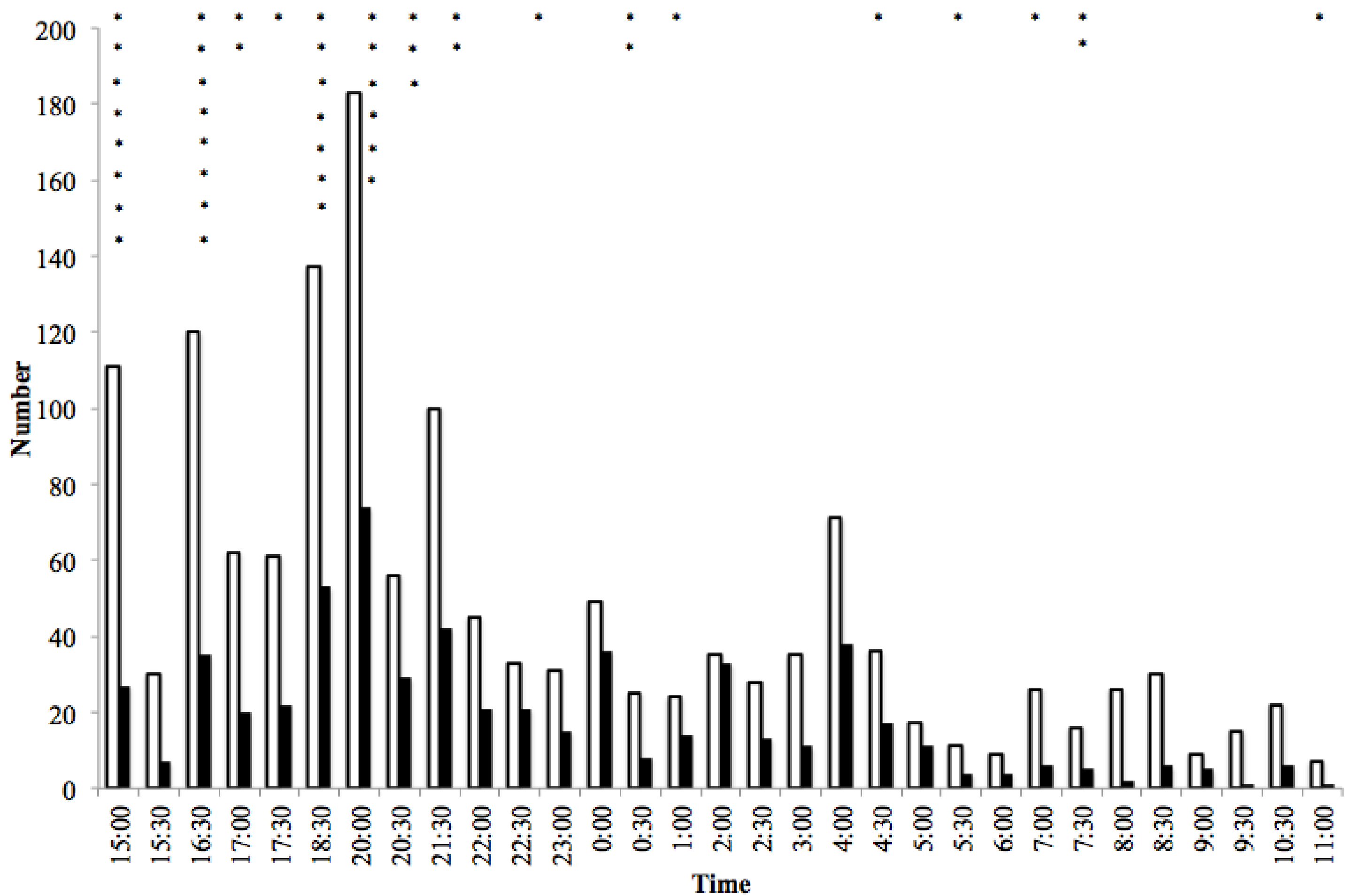

Figure 2.5: Number of explorations (open bars) and attempts (black bars) over time for white suckers pooled across 14°C and 22°C temperature treatments. Asterisks (*) represent successful leaping attempts.

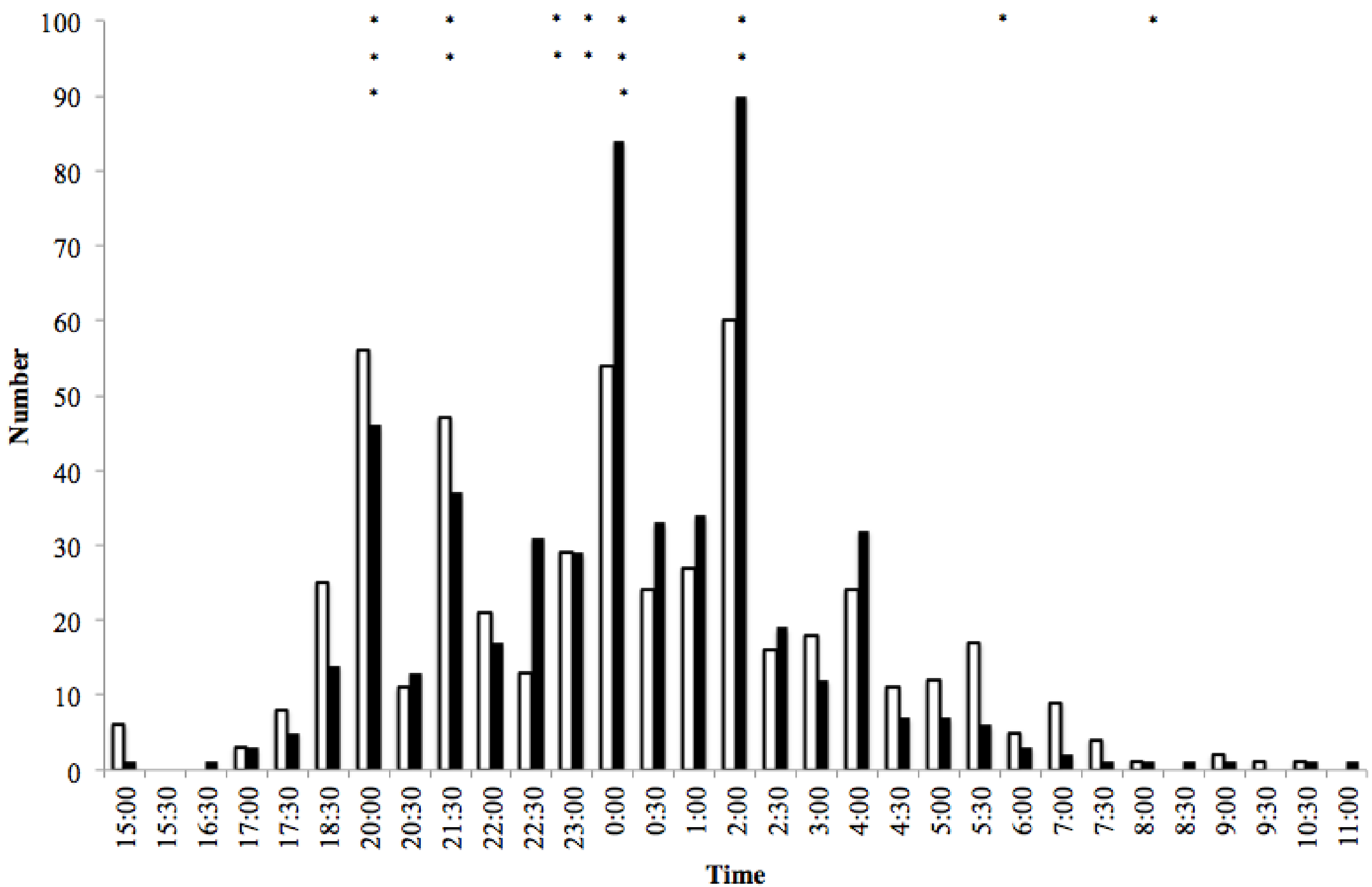

Figure 2.6: Number of explorations (open bars) and attempts (black bars) over time for burbot pooled across 6°C and 20°C temperature treatments. Asterisks (*) represent successful leaping attempts.

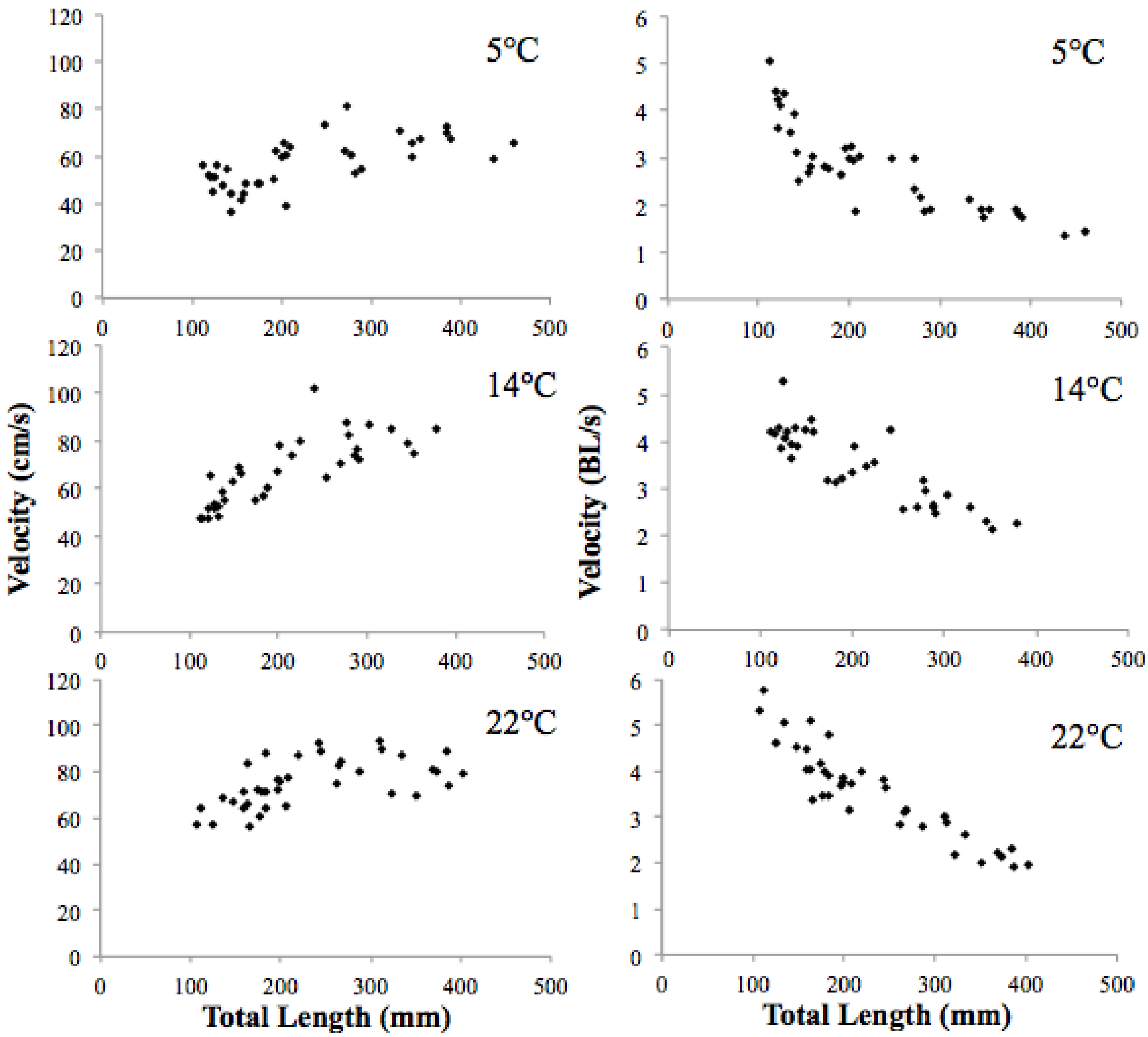

Figure 2.7: Relationship between velocity (cm/s, left panel; body lengths/s, right panel) at gait transition (B_T from aerobic to anaerobic gait) and fish size for white suckers tested in constant acceleration trials (CATs) at 5°, 14°, and 22°C.

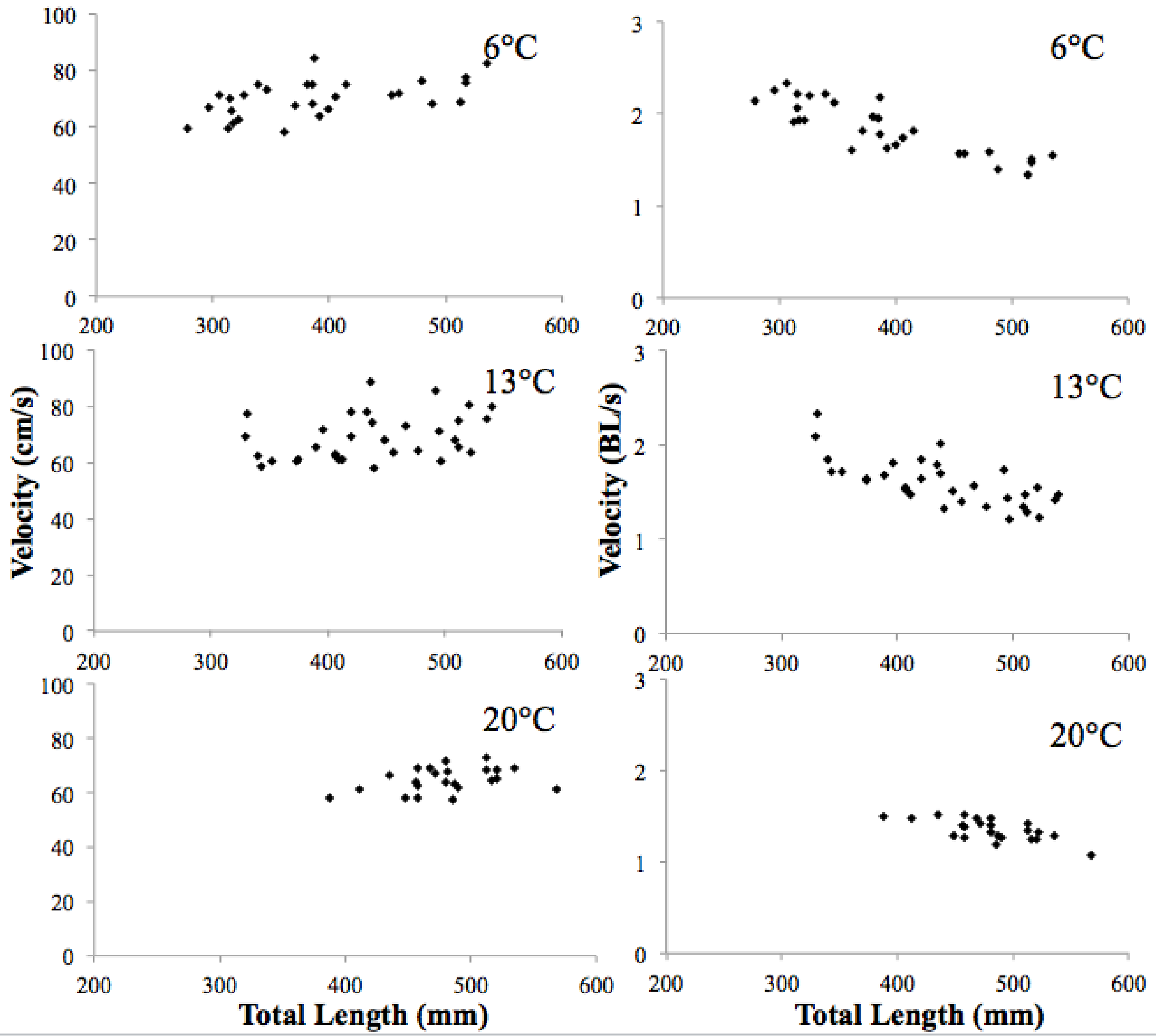

Figure 2.8: Relationship between velocity (cm/s, left panel; body lengths/s, right panel) at gait transition (B_T from aerobic to anaerobic gait) and fish size for burbot tested in constant acceleration trials (CATs) at 6°, 13°, and 20° C.

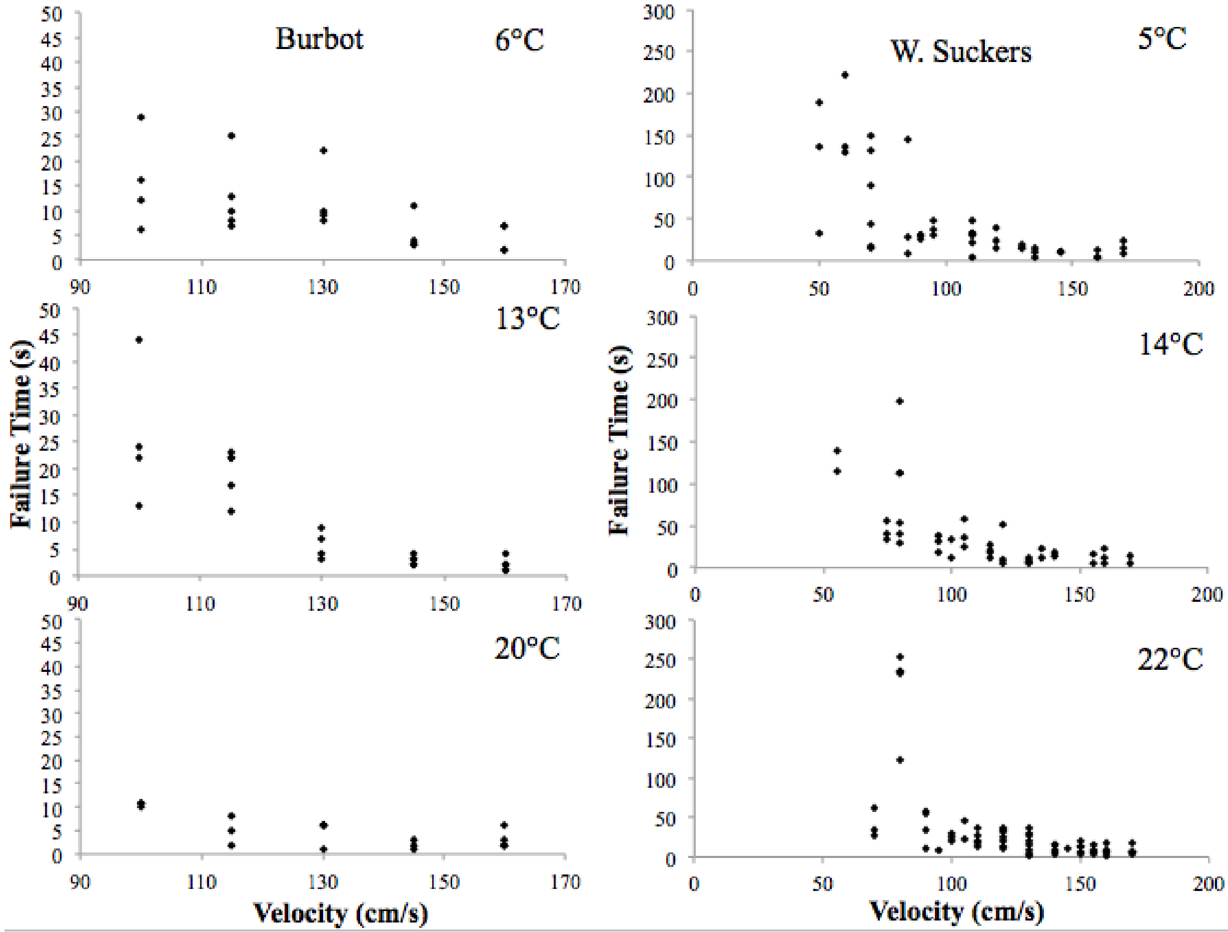

Figure 2.9: Time to failure for burbot (left column) and white suckers (right column) tested at fixed velocities in a swimming flume. Burbot trials were conducted at 6°, 13° and 20°C, while white suckers were run at 5°, 14° and 22°C.

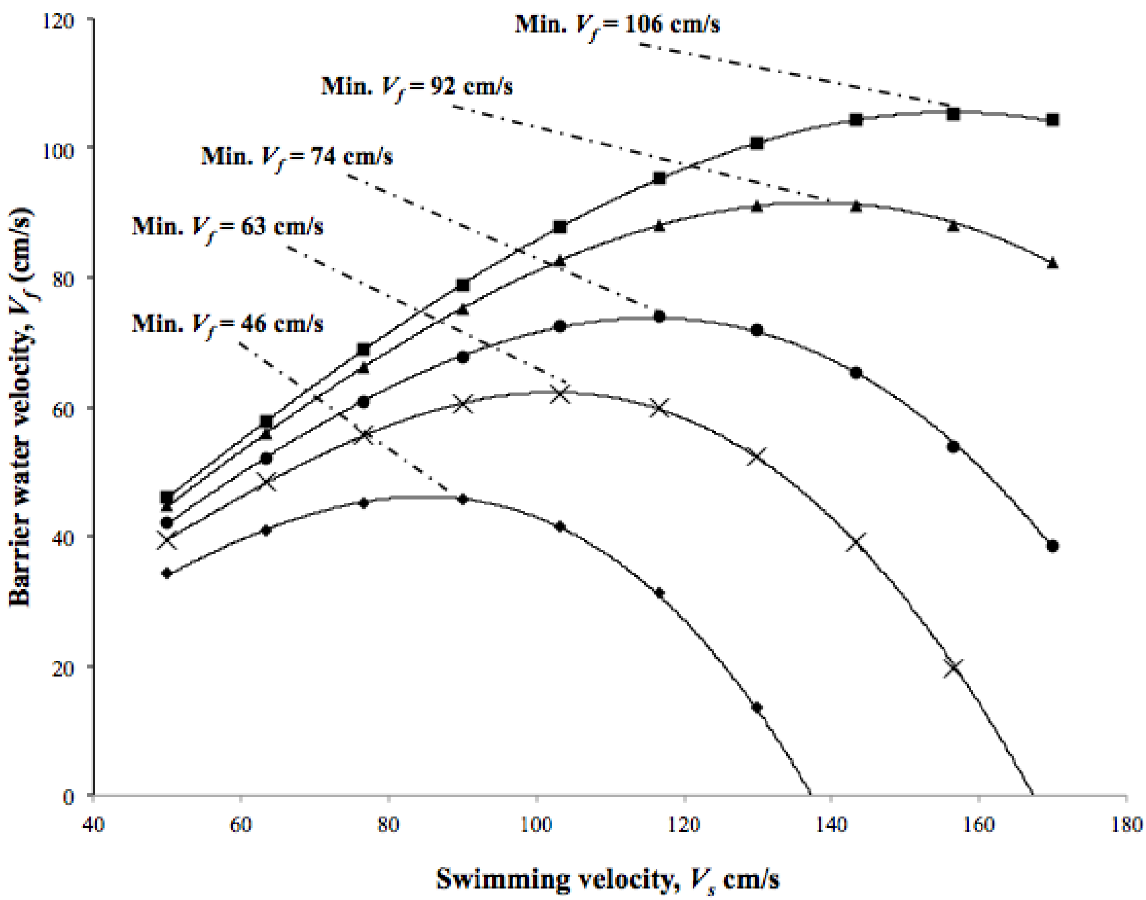

Figure 2.10: Predicted minimum barrier velocities (V_f) necessary to prevent a 400-mm white sucker from successfully ascending velocity barriers of lengths of 7.5 – 30 m. These predictions are based upon plots of fishway water velocity (V_f; cm/s) versus swimming speed (V_s; cm/s) developed using Peake's equation and the upper 99% prediction interval from a regression plot from fixed velocity trials for a 400-mm TL white sucker. Fixed values of V_s were used at barrier lengths (*d*; m) of 7.5 m (□) 10 m (▲), 15 m (●), 20 m(X), and 30 m(◆)).

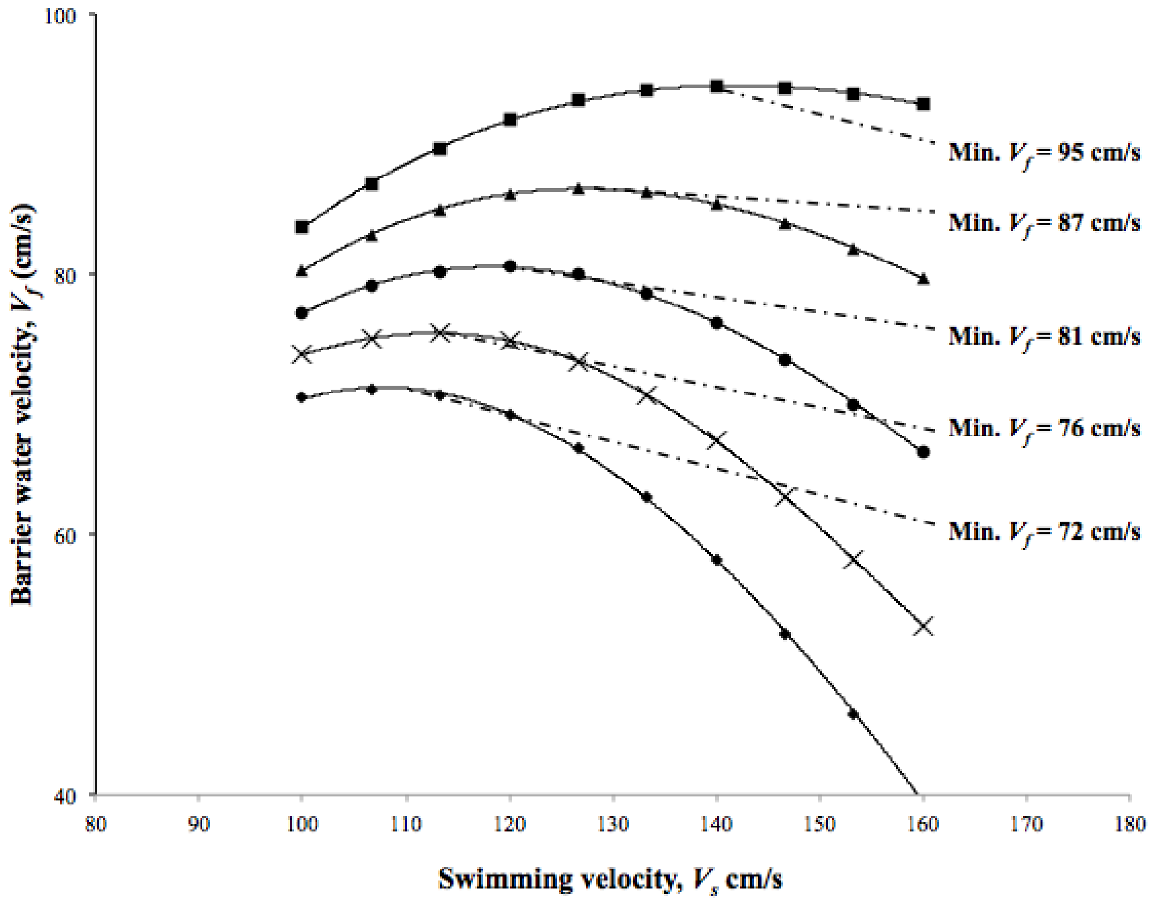

Figure 2.11: Predicted minimum barrier velocities (min V_f) necessary to prevent a 570-mm burbot from successfully ascending a velocity barrier of lengths between 5 and 9 m. Plots of fishway water velocity (V_f; cm/s) versus swimming speed (V_s; cm/s) were developed using Peake's equation and the upper 99% prediction interval from a regression plot from fixed velocity trials for a 570-mm TL burbot. ixed values of V_s were used at barrier lengths (*d*; m) of 5 m (□), 6 m (▲), 7 m (●), 8 m(X), and 9 m(◆).

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APPENDIX A

AIC modeling output (AICc, ΔAICc and cumulative model weight) for top 20 of all possible models (all possible predictor combinations) of explorations, attempts and successes for white sucker jumping experiment. Predictors included plunge pool depth (D; mm), waterfall height (H; mm), explorations (E), attempts (A), number of previous trials (P_t), number of previous successes (P_s), total length of individual (TL; mm), treatment temperature (T; °C) and condition (C, relative weight (W_r). Success model used all predictors, attempt model did not use A, and exploration model did not use A or E.

Explorations				Attempts				Success			
Parameters	AICc	ΔAICc	Wt.	Parameters	AICc	ΔAICc	Wt.	Parameters	AICc	ΔAICc	Wt.
D, H, P_t, P_s, TL, T	3328	0	0.58	D, E, H, P_t, P_s, TL, T, C	1951	0	0.92	A, E, H, P_t, TL	110	0	0.09
D, H, P_t, P_s, TL, T, C	3328	0.7	0.42	D, E, H, P_t, P_s, TL, T	1956	5.3	0.07	A, E, H, P_t, P_s, TL	110	0.1	0.08
D, H, P_t, TL, T	3346	18.2	0	D, E, H, P_t, P_s, T, C	1959	8.5	0.01	E, H, P_t, TL	110	0.7	0.06
D, H, P_t, TL, T, C	3346	18.2	0	D, E, H, P_t, P_s, T	1963	12.2	0	E, H, P_t, P_s, TL	111	1.5	0.04
D, H, P_t, P_s, T	3367	39.7	0	E, H, P_t, P_s, TL, T, C	1966	15.1	0	A, E, H, P_t, P_s, TL	112	2	0.03
D, H, P_t, P_s, T, C	3368	40.5	0	E, H, P_t, P_s, TL, T	1972	20.9	0	A, E, H, P_t, P_s, TL, C	112	2	0.03
D, H, P_t, P_s, TL, C	3406	78.3	0	E, H, P_t, P_s, T, C	1976	24.9	0	A, D, E, H, P_t, TL	112	2	0.03
D, H, P_t, T	3408	80.7	0	E, H, P_t, P_s, T	1980	28.9	0	A, E, H, P_t, TL, T	112	2.1	0.03
D, H, P_t, T, C	3408	80.9	0	D, E, H, P_s, TL, T	1988	37.5	0	A, D, E, H, P_t, P_s, TL	112	2.1	0.03
D, H, P_t, TL, C	3417	89.2	0	D, E, H, P_s, T	1989	38.6	0	A, E, H, P_t, P_s, TL, T	112	2.2	0.03
H, P_t, P_s, TL, T, C	3438	110.8	0	D, E, H, P_s, TL, T, C	1990	39.6	0	E, H, P_t, TL, T	112	2.4	0.03
H, P_t, P_s, TL, T	3439	111	0	D, E, H, P_s, T, C	1991	40.7	0	A, E, H, TL	112	2.4	0.03
D, H, P_s, TL, T, C	3450	122.1	0	E, H, P_s, TL, T	2000	49.4	0	E, H, TL	112	2.7	0.02
D, H, P_t, P_s, TL	3452	124.5	0	E, H, P_s, TL, T, C	2002	51.4	0	D, E, H, P_t, TL	112	2.7	0.02
H, P_t, TL, T, C	3460	132.5	0	E, H, P_s, T	2002	51.6	0	E, H, P_t, TL, C	112	2.7	0.02
H, P_t, TL, T	3461	133.7	0	E, H, P_s, TL, T, C	2004	53.6	0	E, H, P_t, P_s, TL, T	113	3.5	0.02
D, H, P_t, TL	3464	136.3	0	D, E, P_t, P_s, TL, T, C	2031	80.6	0	D, E, H, P_t, P_s, TL	113	3.6	0.01
D, H, P_s, T, C	3468	140.9	0	D, E, P_t, P_s, TL, T	2042	91.8	0	E, H, P_t, P_s, TL, C	113	3.6	0.01
H, P_t, P_s, T, C	3471	143.2	0	D, E, P_t, P_s, T, C	2045	94	0	A, E, H, P_t, TL, T, C	113	3.8	0.01
H, P_t, P_s, T	3475	147.4	0	E, P_t, P_s, TL, T, C	2045	94.4	0	A, D, E, H, P_t, P_s, TL, C	114	4	0.01
…	…	…	…	…	…	…	…	…	…	…	…

APPENDIX B

AIC modeling output (AICc, ΔAICc and cumulative model weight) for top 20 of all possible models (all possible predictor combinations) of explorations, attempts and successes for burbot jumping experiment. Predictors included plunge pool depth (D; mm), waterfall height (H; mm), explorations (E), attempts (A), number of previous trials (P_t), number of previous successes (P_s), total length of individual (TL; mm), treatment temperature (T; °C) and condition (C, relative weight (W_r). Success model used all predictors, attempt model did not use A, and exploration model did not use A or E.

Explorations				Attempts				Success			
Parameters	AICc	ΔAICc	Wt.	Parameters	AICc	ΔAICc	Wt.	Parameters	AICc	ΔAICc	Wt.
H, P_t, P_s, T	1275	0	0.22	D, E, H, P_t, TL, T, C	1331	0	0.72	D, H, P_t, TL, T	12	0	0.04
D, H, P_t, P_s, T	1275	0.7	0.15	D, E, H, P_t, P_s, TL, T, C	1333	2.1	0.25	D, E, H, P_t, TL	12	0	0.04
H, P_t, P_s, TL, T	1276	0.9	0.14	D, E, H, P_t, T, C	1338	7	0.02	D, H, P_t, TL, C	12	0	0.04
H, P_t, P_s, T, C	1276	1	0.14	D, E, H, P_t, P_s, T, C	1340	8.9	0.01	D, H	14	1.4	0.02
D, H, P_t, P_s, TL, T	1276	1.6	0.1	D, E, H, TL, T, C	1347	15.7	0	H	14	1.7	0.01
H, P_t, P_s, TL, T, C	1276	1.8	0.09	D, E, H, P_s, TL, T, C	1349	17.8	0	D, H, P_t	14	2.1	0.01
D, H, P_t, P_s, T, C	1276	1.8	0.09	D, E, H, P_t, TL, T	1351	20	0	D, H, P_t, TL, T, C	14	2.1	0.01
D, H, P_t, P_s, TL, T, C	1277	2.6	0.06	D, E, H, P_t, P_s, TL, T	1352	21.2	0	D, H, P_t, P_s, TL, T	14	2.1	0.01
H, P_t, T	1283	8.7	0	D, E, H, P_t, T	1356	25.1	0	A, D, H, P_t, TL, T	14	2.1	0.01
D, H, P_t, T	1284	8.9	0	D, E, H, P_t, P_s, T	1357	26	0	D, E, H, P_t, TL, T	14	2.1	0.01
H, P_t, TL, T	1284	9.4	0	D, E, H, T, C	1358	26.9	0	D, E, H, P_t, TL, C	14	2.1	0.01
D, H, P_t, TL, T	1284	9.7	0	D, E, H, TL, T	1358	27.3	0	A, D, E, H, P_t, TL	14	2.1	0.01
H, P_t, T, C	1285	10.5	0	D, E, H, P_s, TL, T	1360	28.9	0	D, E, H, P_t, P_s, TL	14	2.1	0.01
D, H, P_t, T, C	1286	10.8	0	D, E, H, P_s, T, C	1360	28.9	0	A, D,H, P_t, TL, C	14	2.1	0.01
H, P_s, TL, T, C	1286	11.2	0	D, E, H, T	1367	35.9	0	D, H, P_t, P_s, TL, C	14	2.1	0.01
D, H, P_s, TL, T, C	1286	11.5	0	D, E, H, P_s, T	1368	37.3	0	D, H, T	14	2.1	0.01
H, P_s, T	1332	57.1	0	D, E, P_t, P_s, TL, T, C	1412	81.4	0	H, T	15	2.4	0.01
D, H, P_s, T	1332	57.5	0	D, E, P_t, TL, T, C	1415	84.1	0	H, P_t	15	2.6	0.01
H, P_s, TL, T	1333	58.7	0	D, E, P_t, P_s, TL, C	1419	88.2	0	D	15	2.7	0.01
…	…	…	…	…	…	…	…	…	…	…	…

APPENDIX C

AIC modeling output (AICc, ΔAICc and cumulative model weight) for top 20 of all possible models (all possible predictor combinations) of holding transition (H_t), burst transition (B_t) and impingement velocity (I_v) for white sucker constant acceleration swimming experiment. Predictors included the absolute value of the difference in temperature between the holding tank and swim flume (T_{diff}; °C), number of days a fish was in the lab prior to the trial (D_l), total length of individual (TL; mm), treatment temperature (T; °C) and condition (C, relative weight (W_r).

Burst Transition (B_t)			
Parameters	AICc	ΔAICc	Weight
D_l, TL, T, C	791.6	0	0.26
TL, T	791.7	0.1	0.24
TL, T, C	793.1	1.6	0.12
D_l, TL, T, C	793.3	1.8	0.11
T_{diff}, D_l, TL, T	793.7	2.1	0.09
T_{diff}, TL, T	793.7	2.1	0.09
$T_{diff,}$ TL, T, C	795.1	3.6	0.04
T_{diff}, D_l, TL, T, C	795.4	3.9	0.04
T_{diff}, D_l, TL	845.6	54	0
D_l, TL	846.4	54.8	0
T_{diff}, D_l, TL, C	847.3	55.7	0
D_l, TL, C	847.9	56.3	0
T, C	847.9	56.3	0
T_{diff}, TL	848.4	56.8	0
T	848.7	57.1	0
D_l, T, C	848.9	57.3	0
TL	848.9	57.4	0
$D_{l,}$ T	849.2	57.6	0
$T_{diff,}$ TL, C	849.5	58	0
TL, C	849.9	58.3	0
…	…	…	…

APPENDIX D

AIC modeling output (AICc, ΔAICc and cumulative model weight) for top 20 of all possible models (all possible predictor combinations) of burst transition (B_t) for burbot constant acceleration swimming experiment. Predictors included the absolute value of the difference in temperature between the holding tank and swim flume (T_{diff}; °C), number of days a fish was in the lab prior to the trial (D_l), total length of individual (TL; mm), treatment temperature (T; °C) and condition (C, relative weight (W_r).

Burst Transition (Bt)			
Parameters	AICc	ΔAICc	Weight
Dl, TL, T, C	552.5	0	0.39
TL, T, C	554.2	1.7	0.17
Tdiff, Dl, TL, T, C	554.9	2.3	0.12
Dl, TL, T	555.6	3.1	0.09
Tdiff, TL, T, C	556.5	3.9	0.06
TL, T	556.5	4	0.05
Dl, TL, C	556.6	4.1	0.05
Tdiff, Dl, TL, T	557.7	5.1	0.03
Tdiff, TL, T	558.8	6.2	0.02
Tdiff, Dl, TL, C	558.8	6.2	0.02
Dl, C	563.4	10.8	0
Dl, T, C	565.2	12.7	0
TL, C	565.3	12.7	0
Tdiff, Dl, C	565.4	12.9	0
Dl, TL	565.8	13.3	0
Tdiff, Dl, TL	567.3	14.7	0
Tdiff, TL, C	567.3	14.8	0
Dl, TL	567.3	14.8	0
T, C	567.8	15.3	0
C	568.9	16.3	0
…	…	…	…

APPENDIX E

AIC modeling output (AICc, ΔAICc and cumulative model weight) for top 20 of all possible models (all possible predictor combinations) of holding transition (H_t), burst transition (B_t) and impingement velocity (I_v) for burbot constant acceleration swimming experiment. Predictors included the absolute value of the difference in temperature between the holding tank and swim flume (T_{diff}; °C), number of days a fish was in the lab prior to the trial (D_l), total length of individual (TL; mm), treatment temperature (T; °C) and condition (C, relative weight (W_r).

White Sucker				Burbot			
Parameters	AICc	ΔAICc	Weight	Parameters	AICc	ΔAICc	Weight
$T_{diff,}$ TL, V	324.8	0	0.23	T, TL, V	119.9	0	0.39
TL, V	325.2	0.3	0.19	T_{diff}, T, TL, V	121.7	1.9	0.15
T_{diff}, TL, V, C	325.7	0.9	0.14	T, TL, V, C	121.8	2	0.14
T, TL, V	326.5	1.7	0.1	T, V	122.1	2.3	0.12
TL, V, C	326.7	1.9	0.09	T_{diff}, T, TL, V, C	123.8	4	0.05
T, TL, V, C	326.7	1.9	0.09	T_{diff}, T, V	123.8	4	0.05
T_{diff}, T, TL, V	327	2.2	0.08	T, V, C	124.1	4.3	0.05
T_{diff}, T, TL, V, C	327.7	2.9	0.05	T_{diff}, T, V, C	126	6.1	0.02
T_{diff}, V, C	330.7	5.8	0.01	TL, V	127.8	7.9	0.01
V, C	332.1	7.3	0.01	V	128.6	8.7	0
T, V, C	332.2	7.4	0.01	TL, V, C	129.9	10.1	0
T_{diff}, T, V, C	332.7	7.9	0	T_{diff}, TL, V	130.1	10.3	0
V	334.2	9.4	0	V, C	130.7	10.8	0
T_{diff}, V	334.3	9.5	0	T_{diff}, V	130.8	11	0
T_{diff}, T, V	335.6	10.7	0	T_{diff}, TL, V, C	132.3	12.5	0
T, V	336.3	11.5	0	T_{diff}, V, C	132.9	13.1	0
TL, C	453.7	128.9	0	T, TL	172	52.2	0
T_{diff}, T	453.8	129	0	T	172	52.2	0
T	453.9	129	0	T, C	172.6	52.7	0
C	454.1	129.3	0	T, TL, C	172.7	52.8	0
…	…	…	…	…	…	…	…

APPENDIX F

Predicted mean, 95 and 99%-confidence intervals for probability of success calculated from AICc averaged GLM model for white suckers of varying lengths. Parameter values of H=100-700mm, TL=300-500mm, E=0 (minimum), P_t=0 (minimum), A= 3 (mean)). were used, and all other parameters were dropped. The bolded values correspond to waterfall heights that should preclude passage of white suckers of a given length with the selected level of confidence.

Total Length (mm)	300			350			400			450			500		
Confidence level	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99
Height (mm)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
100	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
106	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
112	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
118	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
124	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
130	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
136	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
142	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
148	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
155	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
161	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
167	1	1	1	1	1	1	1	1	1	1	1	1	0.99	1	1
173	1	1	1	1	1	1	1	1	1	1	1	1	0.86	1	1
179	1	1	1	1	1	1	1	1	1	1	1	1	0.73	1	1
185	1	1	1	1	1	1	1	1	1	1	1	1	0.61	1	1
191	1	1	1	1	1	1	1	1	1	1	1	1	0.48	1	1
197	1	1	1	1	1	1	1	1	1	0.97	1	1	0.35	1	1
203	1	1	1	1	1	1	1	1	1	0.84	1	1	0.22	1	1
209	1	1	1	1	1	1	1	1	1	0.71	1	1	0.09	1	1
215	1	1	1	1	1	1	1	1	1	0.58	1	1	**0**	1	1

APPENDIX F (cont): White sucker jumping predictions.

Total Length (mm)	300			350			400			450			500		
Confidence level	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99
Height (mm)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
221	1	1	1	1	1	1	0.95	1	1	0.45	1	1	**0**	1	1
227	1	1	1	1	1	1	0.82	1	1	0.33	1	1	**0**	1	1
233	1	1	1	1	1	1	0.69	1	1	0.2	1	1	**0**	1	1
239	1	1	1	1	1	1	0.56	1	1	0.07	1	1	**0**	1	1
245	1	1	1	1	1	1	0.43	1	1	**0**	1	1	**0**	1	1
252	1	1	1	1	1	1	0.3	1	1	**0**	1	1	**0**	1	1
258	1	1	1	0.93	1	1	0.17	1	1	**0**	1	1	**0**	1	1
264	1	1	1	0.8	1	1	0.05	1	1	**0**	1	1	**0**	1	1
270	1	1	1	0.67	1	1	**0**	1	1	**0**	1	1	**0**	1	1
276	1	1	1	0.54	1	1	**0**	1	1	**0**	1	1	**0**	1	1
282	1	1	1	0.41	1	1	**0**	1	1	**0**	1	1	**0**	1	1
288	1	1	1	0.28	1	1	**0**	1	1	**0**	1	1	**0**	1	1
294	0.91	1	1	0.15	1	1	**0**	1	1	**0**	1	1	**0**	1	1
300	0.78	1	1	0.02	1	1	**0**	1	1	**0**	1	1	**0**	1	1
306	0.65	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
312	0.52	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
318	0.39	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
324	0.26	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
330	0.13	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
336	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
342	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
348	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
355	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
361	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
367	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
373	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1

APPENDIX F (cont): White sucker jumping predictions.

Total Length (mm)	300			350			400			450			500		
Confidence level	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99
Height (mm)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
379	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
385	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
391	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
397	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
403	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
409	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
415	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
421	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
427	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
433	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
439	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
445	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
452	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
458	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
464	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
470	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
476	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
482	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
488	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
494	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
500	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
506	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
512	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1	**0**	1	1
518	**0**	1	1	**0**	1	1	**0**	1	1	**0**	0.56	1	**0**	0.37	0.21
524	**0**	1	1	**0**	1	1	**0**	0.24	1	**0**	**0**	**0**	**0**	**0**	**0**

APPENDIX F (cont): White sucker jumping predictions.

Total Length (mm)	300			350			400			450			500		
Confidence level	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99
Height (mm)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
530	**0**	1	1	**0**	0.73	1	**0**	**0**	0.83	**0**	**0**	**0**	**0**	**0**	**0**
536	**0**	1	1	**0**	0.38	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
542	**0**	0.92	1	**0**	0.03	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
548	**0**	0.8	1	**0**	**0**	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
555	**0**	0.68	1	**0**	**0**	0.82	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
561	**0**	0.57	1	**0**	**0**	0.4	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
567	**0**	0.45	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
573	**0**	0.34	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
579	**0**	0.22	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
585	**0**	0.11	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
591	**0**	**0**	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
597	**0**	**0**	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
603	**0**	**0**	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
609	**0**	**0**	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
615	**0**	**0**	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
621	**0**	**0**	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
627	**0**	**0**	1	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
633	**0**	**0**	0.99	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
639	**0**	**0**	0.88	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
645	**0**	**0**	0.78	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
652	**0**	**0**	0.67	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
658	**0**	**0**	0.57	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
664	**0**	**0**	0.46	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
670	**0**	**0**	0.36	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**

APPENDIX F (cont): White sucker jumping predictions.

Total Length (mm)	300			350			400			450			500		
Confidence level	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99	mean	0.95	0.99
Height (mm)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
676	**0**	**0**	0.25	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
682	**0**	**0**	0.15	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
688	**0**	**0**	0.05	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
694	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
700	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**

Predicted mean, 95 and 99%-confidence intervals for fish barrier lengths (d; m) and velocities ($V_{f\text{-}x}$; cm/s) that will prevent passage of burbot of a given length (TL; mm) calculated using Peake's equation with data from AICc averaged logistic regression model for failure time in fixed velocity swimming flume trials. Parameter values of V=50-170 cm/s and TL= 100-400 mm were used, and all other parameters were dropped.; burbot parameters: V= 100-160 cm/s, TL= 300-570 mm, T=6°C (minimum)). Bold values represent optimal design criteria to withstand attempts from burbot using an optimal positive groundspeed.

d	TL	V_s	$V_{f\text{-}pred}$	$V_{f\text{-}95}$	$V_{f\text{-}99}$	d	TL	V_s	$V_{f\text{-}pred}$	$V_{f\text{-}95}$	$V_{f\text{-}99}$	d	TL	V_s	$V_{f\text{-}pred}$	$V_{f\text{-}95}$	$V_{f\text{-}99}$	d	TL	V_s	$V_{f\text{-}pred}$	$V_{f\text{-}95}$	$V_{f\text{-}99}$
5	300	100	73.5	77.2	78.2	5	400	100	77.8	80.4	81.1	5	500	100	81.5	83.3	83.8	5	570	100	83.6	85.1	85.6
5	300	107	**73.9**	79.4	80.7	5	400	107	79.2	83	84	5	500	107	83.7	86.5	87.2	5	570	107	86.4	88.7	89.3
5	300	113	72.8	80.8	82.7	5	400	113	**79.4**	85	86.4	5	500	113	**85**	89	90.1	5	570	113	88.3	91.6	92.5
5	300	120	69.8	**81.5**	84.2	5	400	120	78.1	86.3	88.2	5	500	120	84.9	90.9	92.3	5	570	120	**89.1**	93.9	95.1
5	300	127	64.6	**81.5**	85.1	5	400	127	74.8	**86.7**	89.4	5	500	127	83.3	92	94.1	5	570	127	88.4	95.5	97.3
5	300	133	56.6	80.8	85.6	5	400	133	69.2	86.4	90.1	5	500	133	79.7	**92.4**	95.2	5	570	133	86.1	96.4	98.8
5	300	140	45.2	79.5	**85.8**	5	400	140	60.7	85.4	**90.3**	5	500	140	73.7	92	95.8	5	570	140	81.6	**96.6**	99.9
5	300	147	29.4	77.8	85.7	5	400	147	48.6	83.8	90.2	5	500	147	64.7	90.9	**96**	5	570	147	74.4	96.1	100.5
5	300	153	8.3	75.7	85.7	5	400	153	32.1	81.7	89.9	5	500	153	52	89.2	95.9	5	570	153	64	94.9	100.7
5	300	160	-	73.6	85.8	5	400	160	10.1	79.3	89.6	5	500	160	34.7	87.1	95.7	5	570	160	49.5	93.3	**100.8**
7.5	300	100	60.2	**65.8**	67.3	7.5	400	100	66.7	70.6	71.6	7.5	500	100	72.2	74.9	75.7	7.5	570	100	75.5	77.7	78.3
7.5	300	107	57.4	65.7	**67.8**	7.5	400	107	65.5	**71.2**	72.7	7.5	500	107	**72.3**	76.4	77.5	7.5	570	107	**76.3**	79.7	80.6
7.5	300	113	52.5	64.5	67.4	7.5	400	113	62.5	70.9	**73**	7.5	500	113	70.8	**76.9**	78.4	7.5	570	113	75.8	80.7	82
7.5	300	120	44.7	62.3	66.3	7.5	400	120	57.1	69.4	72.3	7.5	500	120	67.4	76.3	**78.5**	7.5	570	120	73.6	**80.9**	**82.7**
7.5	300	127	33.6	59	64.3	7.5	400	127	48.9	66.8	70.8	7.5	500	127	61.7	74.7	77.8	7.5	570	127	69.3	80	82.6
7.5	300	133	18.3	54.6	61.7	7.5	400	133	37.2	63	68.5	7.5	500	133	52.9	71.9	76.1	7.5	570	133	62.4	78	81.6
7.5	300	140	-	49.3	58.6	7.5	400	140	21.1	58.1	65.5	7.5	500	140	40.6	68	73.7	7.5	570	140	52.3	74.9	79.8
7.5	300	147	-	43.3	55.3	7.5	400	147	-	52.4	62	7.5	500	147	23.8	63	70.7	7.5	570	147	38.3	70.8	77.4
7.5	300	153	-	36.9	51.8	7.5	400	153	-	45.8	58.2	7.5	500	153	1.4	57.2	67.2	7.5	570	153	19.3	65.8	74.4
7.5	300	160	-	30.4	48.7	7.5	400	160	-	38.9	54.3	7.5	500	160	-	50.7	63.5	7.5	570	160	-	60	71.1

APPENDIX G (cont): Burbot swimming criteria.

d	TL	V_s	$V_{f\text{-}pred}$	$V_{f\text{-}95}$	$V_{f\text{-}99}$	d	TL	V_s	$V_{f\text{-}pred}$	$V_{f\text{-}95}$	$V_{f\text{-}99}$	d	TL	V_s	$V_{f\text{-}pred}$	$V_{f\text{-}95}$	$V_{f\text{-}99}$	d	TL	V_s	$V_{f\text{-}pred}$	$V_{f\text{-}95}$	$V_{f\text{-}99}$
10	300	100	47	54.4	56.4	10	400	100	55.6	60.8	62.2	10	500	100	62.9	**66.6**	67.6	10	570	100	67.3	70.3	71.1
10	300	107	41	52.1	54.8	10	400	107	51.8	59.4	61.4	10	500	107	60.8	66.3	**67.7**	10	570	107	66.2	**70.6**	**71.9**
10	300	113	32	48.3	52.1	10	400	113	45.5	56.7	59.5	10	500	113	56.6	64.7	66.8	10	570	113	63.3	69.9	71.6
10	300	120	20	43.1	48.4	10	400	120	36.1	52.5	56.4	10	500	120	49.9	61.7	64.7	10	570	120	58.2	67.8	70.3
10	300	127	2.6	36.4	43.6	10	400	127	23	46.8	52.2	10	500	127	40	57.3	61.5	10	570	127	50.2	64.4	67.9
10	300	133	-	28.3	37.9	10	400	133	5.1	39.5	46.9	10	500	133	26.1	51.4	57.1	10	570	133	38.8	59.5	64.3
10	300	140	-	19.1	31.5	10	400	140	-	30.9	40.7	10	500	140	7.5	44	51.7	10	570	140	23.1	53.2	59.8
10	300	147	-	8.9	24.8	10	400	147	-	20.9	33.7	10	500	147	-	35.1	45.4	10	570	147	2.1	45.5	54.3
10	300	153	-	-	18	10	400	153	-	10	26.4	10	500	153	-	25.1	38.5	10	570	153	-	36.6	48.1
10	300	160	-	-	11.5	10	400	160	-	-	19.1	10	500	160	-	14.3	31.3	10	570	160	-	26.7	41.5
13	300	100	34	43	45.5	13	400	100	44.5	51	52.7	13	500	100	53.6	58.2	59.5	13	570	100	59.1	62.8	63.9
13	300	107	25	38.4	41.9	13	400	107	38.1	47.6	50.1	13	500	107	49.3	56.2	58	13	570	107	56.1	61.6	63.1
13	300	113	12	32	36.8	13	400	113	28.5	42.5	46	13	500	113	42.5	52.5	55.1	13	570	113	50.8	59	61.2
13	300	120	-	23.8	30.5	13	400	120	15.2	35.6	40.5	13	500	120	32.4	47.2	50.9	13	570	120	42.7	54.8	57.9
13	300	127	-	13.8	22.8	13	400	127	-	26.8	33.6	13	500	127	18.3	40	45.1	13	570	127	31.1	48.8	53.2
13	300	133	-	2.1	14	13	400	133	-	16.1	25.3	13	500	133	-	30.9	38	13	570	133	15.2	41.1	47.1
13	300	140	-	-	4.4	13	400	140	-	3.6	15.8	13	500	140	-	19.9	29.6	13	570	140	-	31.5	39.7
13	300	147	-	-	-	13	400	147	-	-	5.5	13	500	147	-	7.3	20.1	13	570	147	-	20.2	31.2
13	300	153	-	-	-	13	400	153	-	-	-	13	500	153	-	-	9.8	13	570	153	-	7.4	21.8
13	300	160	-	-	-	13	400	160	-	-	-	13	500	160	-	-	-	13	570	160	-	-	11.9
15	300	100	20	31.6	34.6	15	400	100	33.4	41.2	43.3	15	500	100	44.4	49.9	51.4	15	570	100	50.9	55.4	56.7
15	300	107	8	24.7	28.9	15	400	107	24.4	35.8	38.8	15	500	107	37.9	46.1	48.3	15	570	107	46	52.6	54.4
15	300	113	-	15.8	21.5	15	400	113	11.6	28.4	32.6	15	500	113	28.3	40.4	43.5	15	570	113	38.3	48.2	50.7
15	300	120	-	4.6	12.5	15	400	120	-	18.8	24.6	15	500	120	14.8	32.6	37	15	570	120	27.2	41.8	45.4
15	300	127	-	-	2	15	400	127	-	6.8	15	15	500	127	-	22.7	28.8	15	570	127	12	33.3	38.5
15	300	133	-	-	-	15	400	133	-	-	3.7	15	500	133	-	10.4	18.9	15	570	133	-	22.6	29.8
15	300	140	-	-	-	15	400	140	-	-	-	15	500	140	-	-	7.5	15	570	140	-	9.8	19.6
15	300	147	-	-	-	15	400	147	-	-	-	15	500	147	-	-	-	15	570	147	-	-	8.1
15	300	153	-	-	-	15	400	153	-	-	-	15	500	153	-	-	-	15	570	153	-	-	-
15	300	160	-	-	-	15	400	160	-	-	-	15	500	160	-	-	-	15	570	160	-	-	-

APPENDIX H

Predicted mean, 95 and 99%-confidence intervals for fish barrier lengths (d; m) and velocities ($V_{f\text{-}x}$; cm/s) that will prevent passage of white sucker of a given length (TL; mm) calculated using Peake's equation with data from AICc averaged logistic regression model for failure time in fixed velocity swimming flume trials. Parameter values of V= 100-160 cm/s, TL= 300-570 mm, T=6°C (minimum) were used, and all other parameters were dropped. Bold values represent optimal design criteria to withstand attempts from white suckers using an optimal positive groundspeed.

d	TL	V_s	$V_{f\text{-}pred}$	$V_{f\text{-}95}$	$V_{f\text{-}99}$	d	TL	V_s	$V_{f\text{-}pred}$	$V_{f\text{-}95}$	$V_{f\text{-}99}$	d	TL	V_s	$V_{f\text{-}pred}$	$V_{f\text{-}95}$	$V_{f\text{-}99}$	d	TL	V_s	$V_{f\text{-}pred}$	$V_{f\text{-}95}$	$V_{f\text{-}99}$
5	100	50	44	44	44	5	200	50	45	45	45	5	300	50	46	46	46	5	400	50	47	47	47
5	100	63	54	55	55	5	200	63	56	57	57	5	300	63	58	58	58	5	400	63	59	59	59
5	100	77	64	65	65	5	200	77	67	67	67	5	300	77	69	69	69	5	400	77	70	71	71
5	100	90	72	74	74	5	200	90	76	77	77	5	300	90	79	79	80	5	400	90	81	82	82
5	100	103	77	81	82	5	200	103	83	85	86	5	300	103	87	89	89	5	400	103	91	91	92
5	100	117	**80**	86	88	5	200	117	87	92	93	5	300	117	94	96	97	5	400	117	98	100	101
5	100	130	77	89	92	5	200	130	**88**	96	98	5	300	130	**97**	102	104	5	400	130	104	107	108
5	100	143	68	**91**	95	5	200	143	84	99	102	5	300	143	96	106	108	5	400	143	**106**	113	114
5	100	157	49	90	97	5	200	157	71	**99**	105	5	300	157	89	**108**	112	5	400	157	104	116	119
5	100	170	16	88	99	5	200	170	48	98	106	5	300	170	74	108	114	5	400	170	94	117	122
7.5	100	50	41	41	41	7.5	200	50	43	43	43	7.5	300	50	44	44	44	7.5	400	50	45	46	46
7.5	100	63	50	51	51	7.5	200	63	53	53	53	7.5	300	63	55	55	55	7.5	400	63	57	57	57
7.5	100	77	58	59	59	7.5	200	77	62	62	63	7.5	300	77	65	65	65	7.5	400	77	67	68	68
7.5	100	90	63	65	66	7.5	200	90	69	70	71	7.5	300	90	73	74	74	7.5	400	90	77	77	77
7.5	100	103	**64**	70	71	7.5	200	103	**73**	76	77	7.5	300	103	79	81	82	7.5	400	103	84	85	86
7.5	100	117	61	**71**	73	7.5	200	117	73	79	81	7.5	300	117	**82**	86	87	7.5	400	117	89	92	93
7.5	100	130	51	69	**73**	7.5	200	130	67	**79**	**82**	7.5	300	130	81	**88**	90	7.5	400	130	**91**	96	97
7.5	100	143	30	64	71	7.5	200	143	54	76	81	7.5	300	143	73	87	**91**	7.5	400	143	88	**97**	**100**
7.5	100	157	-	57	68	7.5	200	157	29	70	78	7.5	300	157	56	83	89	7.5	400	157	77	95	**100**
7.5	100	170	-	47	63	7.5	200	170	-13	62	74	7.5	300	170	26	76	86	7.5	400	170	56	90	97

APPENDIX H (cont): White sucker swimming criteria.

d	**TL**	**V_s**	**$V_{f\text{-}pred}$**	**$V_{f\text{-}95}$**	**$V_{f\text{-}99}$**	**d**	**TL**	**V_s**	**$V_{f\text{-}pred}$**	**$V_{f\text{-}95}$**	**$V_{f\text{-}99}$**	**d**	**TL**	**V_s**	**$V_{f\text{-}pred}$**	**$V_{f\text{-}95}$**	**$V_{f\text{-}99}$**	**d**	**TL**	**V_s**	**$V_{f\text{-}pred}$**	**$V_{f\text{-}95}$**	**$V_{f\text{-}99}$**
10	100	50	38	38	38	10	200	50	40	40	41	10	300	50	42	42	42	10	400	50	44	44	44
10	100	63	46	46	47	10	200	63	49	50	50	10	300	63	52	53	53	10	400	63	55	55	55
10	100	77	51	53	54	10	200	77	57	58	58	10	300	77	61	62	62	10	400	77	64	65	65
10	100	90	**54**	57	58	10	200	90	61	63	64	10	300	90	67	69	69	10	400	90	72	73	73
10	100	103	52	**58**	**60**	10	200	103	**62**	**67**	68	10	300	103	**71**	74	74	10	400	103	78	80	80
10	100	117	43	56	59	10	200	117	58	66	**69**	10	300	117	70	**76**	**77**	10	400	117	**80**	84	85
10	100	130	24	49	54	10	200	130	46	62	66	10	300	130	64	74	77	10	400	130	78	**85**	**86**
10	100	143	-	38	47	10	200	143	24	54	61	10	300	143	49	69	73	10	400	143	69	82	85
10	100	157	-	23	38	10	200	157	-	42	52	10	300	157	22	59	67	10	400	157	50	75	81
10	100	170	-	6	28	10	200	170	-	26	42	10	300	170	-	45	58	10	400	170	18	64	73
15	100	50	31	32	32	15	200	50	35	36	36	15	300	50	38	39	39	15	400	50	41	41	41
15	100	63	37	38	38	15	200	63	42	43	43	15	300	63	47	47	47	15	400	63	50	51	51
15	100	77	**39**	**41**	42	15	200	77	47	48	49	15	300	77	53	54	54	15	400	77	58	59	59
15	100	90	36	41	**42**	15	200	90	**47**	**50**	**51**	15	300	90	**56**	58	59	15	400	90	63	64	65
15	100	103	26	36	38	15	200	103	42	48	50	15	300	103	55	**59**	**60**	15	400	103	**65**	**68**	68
15	100	117	6	25	30	15	200	117	29	41	45	15	300	117	47	55	57	15	400	117	62	67	**69**
15	100	130	-	8	17	15	200	130	5	29	34	15	300	130	31	46	50	15	400	130	52	62	65
15	100	143	-	-	-	15	200	143	-	9	19	15	300	143	2	32	38	15	400	143	32	51	56
15	100	157	-	-	-	15	200	157	-	-	0	15	300	157	-	10	22	15	400	157	-	34	43
15	100	170	-	-	-	15	200	170	-	-	-	15	300	170	-	-	1	15	400	170	-	11	25

APPENDIX H (cont): White sucker swimming criteria.

d	TL	V_s	V_{f-pred}	V_{f-95}	V_{f-99}	d	TL	V_s	V_{f-pred}	V_{f-95}	V_{f-99}	d	TL	V_s	V_{f-pred}	V_{f-95}	V_{f-99}	d	TL	V_s	V_{f-pred}	V_{f-95}	V_{f-99}
20	100	50	25	26	26	20	200	50	30	31	31	20	300	50	34	35	35	20	400	50	38	38	38
20	100	63	**28**	**29**	30	20	200	63	35	36	37	20	300	63	41	42	42	20	400	63	46	46	46
20	100	77	26	29	**30**	20	200	77	**37**	**39**	**39**	20	300	77	**45**	46	47	20	400	77	52	52	53
20	100	90	17	24	26	20	200	90	33	37	38	20	300	90	45	**47**	**48**	20	400	90	**54**	**56**	56
20	100	103	-	13	17	20	200	103	21	30	32	20	300	103	39	44	46	20	400	103	52	56	**57**
20	100	117	-	-	1	20	200	117	-	16	21	20	300	117	24	35	38	20	400	117	44	51	52
20	100	130	-	-	-	20	200	130	-	-	2	20	300	130	-	19	24	20	400	130	26	39	43
20	100	143	-	-	-	20	200	143	-	-	-	20	300	143	-	-	4	20	400	143	-	20	27
20	100	157	-	-	-	20	200	157	-	-	-	20	300	157	-	-	-	20	400	157	-	-	4
20	100	170	-	-	-	20	200	170	-	-	-	20	300	170	-	-	-	20	400	170	-	-	-
30	100	50	13	14	14	30	200	50	20	21	22	30	300	50	27	27	27	30	400	50	32	32	32
30	100	63	10	13	13	30	200	63	**21**	**23**	**23**	30	300	63	**30**	31	31	30	400	63	37	38	38
30	100	77	0	6	7	30	200	77	16	20	21	30	300	77	29	**31**	**32**	30	400	77	**39**	**40**	**41**
30	100	90	-	-	-	30	200	90	4	10	12	30	300	90	22	26	27	30	400	90	36	39	40
30	100	103	-	-	-	30	200	103	-	-	-	30	300	103	6	14	17	30	400	103	27	32	33
30	100	117	-	-	-	30	200	117	-	-	-	30	300	117	-	-	-	30	400	117	7	17	20
30	100	130	-	-	-	30	200	130	-	-	-	30	300	130	-	-	-	30	400	130	-	-	-
30	100	143	-	-	-	30	200	143	-	-	-	30	300	143	-	-	-	30	400	143	-	-	-
30	100	157	-	-	-	30	200	157	-	-	-	30	300	157	-	-	-	30	400	157	-	-	-
30	100	170	-	-	-	30	200	170	-	-	-	30	300	170	-	-	-	30	400	170	-	-	-