Behaviour and energetics of sturgeon fishway passage

By

Jason D. Thiem

A thesis submitted to the Faculty of Graduate and Postdoctoral Affairs in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Biology

Carleton University
Ottawa, Ontario

Abstract

Global reliance on water resource development has resulted in the disconnection of key migratory pathways for numerous fish species, leading to population declines. Fishways represent one solution for reinstating connectivity, although their biological effectiveness often remains unknown and the mechanisms contributing to successful passage for most species is poorly understood. This thesis applied an interdisciplinary approach to investigate fishway passage by lake sturgeon. Identification of key spawning habitats downstream of a dam equipped with a fishway revealed that attraction and passage efficiency of the fishway unlikely limit reproductive success in this population of lake sturgeon; nevertheless, lake sturgeon still locate and pass the fishway annually. Overall fishway passage efficiency was 36% and successful passage was unrelated to adult sturgeon size or water temperatures. Successful passage events were highly variable in duration, and turning basins within the fishway considerably delayed passage and increased failure rates, leading to speculation that variability in energy use resulting from path selection may be a possible mechanism for delayed or failed passage. New methods were developed for the field quantification of sturgeon swimming activity and energy use using animal-borne accelerometers. Calibrations demonstrated the utility of accelerometers as a direct measure of volitional swimming speed and identified that sturgeon are capable of swimming at speeds in excess of those previously observed. Field application identified that sturgeon rarely used high speed swimming to traverse the fishway and that energy use was not predictive of successful passage, although successful individuals exhibited a higher cost of transport. Successful fishway passage resulted in an energetic cost equivalent to individuals travelling 2.1–13.3 km in a lentic system. Other

endogenous (i.e. internal state, navigational ability) or exogenous (i.e. fine scale hydraulics) factors possibly influence passage success, although these remain unknown and represent an area for future research on sturgeon and numerous other species. Fishways remain a promising solution for maintaining connectivity in fragmented systems and this thesis serves as a useful model for gaining insight into fishway effectiveness for a single species. It also highlights the challenges and necessary knowledge required to ensure optimal habitats are available to all species.

Acknowledgements

Completing this thesis (and not only surviving, but immensely enjoying my time in Canada) wouldn't have been possible without the support and friendship of a lot of people. My supervisor, Steve Cooke, was extremely supportive right from our first meeting in New Zealand prior to my move to Canada. Throughout my PhD his enthusiasm for fish and research has been an inspiration, and he has provided me with endless opportunities well beyond my expectations that I will always appreciate. Jeff Dawson co-supervised me and I'm grateful for his patience with my never-ending questions and for giving me his time to continually bounce ideas around with him. Pierre Dumont and Daniel Hatin from the Ministère des Ressources naturelles et de la Faune provided a huge amount of resources for this project in terms of their time, staff and equipment which made the project possible. Steve Perry and Chris Katopodis served on my committee and provided valuable support and guidance throughout my PhD. The entire Cooke Lab, past and present, were a continual source of friendship and helped to make me feel a part of one of the best workplaces I could imagine. The friendships I formed here also played a significant part in my time outside of work, providing a welcome distraction, whether it was simply sitting in a pub watching hockey, going camping, fishing or hunting, or inviting me to their family home during holidays as mine was so far away.

I am extremely appreciative of the large number of people that contributed to this thesis via field assistance, technical assistance or collaboration including: Florent Archambault, Jeffrey Beardsall, Tom Binder, Jake Brownscombe, André Brunelle, Nich Burnett, Ted Castro-Santos, Keith Clarke, Andy Danylchuk, Sylvain Desloges, Adrian

Gleiss, Nicolas Guillerault, Lee Gutowsky, Alex Haro, Caleb Hasler, Charles Hatry, Mike Jutting, Jean Larochelle, Mélissa Larochelle, Jean Leclerc, Guillaume Lemieux, Robert Lennox, Adam Marriner, Eduardo Martins, Jacquie Matsumoto, Gord McDonald, Brent McDougall, Juan Molina, Karen Murchie, Guy Noël, John Norieka, Graham Raby, Travis Raison, Karen Smokorowski, Keith Stamplecoskie, Lauren Stoot, Mark Taylor, Glen Van Der Kraak, Lucie Veilleux, Stephen Walk, Rory Wilson, Sam Wilson and David Zhu. Project funding was provided by a NSERC HydroNet Strategic Network Grant. Equipment support was provided by the Canada Foundation for Innovation, the Ontario Research Fund and the NSERC RTI program. I was supported by a President's graduate scholarship from Carleton University.

Numerous family and friends in Australia and Canada have provided support and encouragement throughout this endeavor. In particular, Brendan Ebner put me on the research path and provided me with the opportunities that eventually led to me undertaking this PhD for which I'm extremely grateful. My parents Annette and David and my sister Bec have been nothing short of amazing in their support and encouragement throughout everything in my life and are a constant source of inspiration to me – I hope I've made you proud.

Lastly I'd like to thank my wife Sally. You gave up 4 years of your life to share this crazy adventure with me – I wouldn't have made it through without you! Thanks for always believing in me and giving me the confidence in myself to go through with this, you've been amazing.

Co-authorship

Chapter 2: Biology of lake sturgeon (*Acipenser fulvescens*) spawning below a dam on the Richelieu River, Quebec: behaviour, egg deposition and endocrinology.

Thiem JD, Hatin D, Dumont P, Van Der Kraak G, Cooke SJ (2013). Canadian Journal of Zoology 91:175–186

This paper was conceived by Thiem, Hatin, Dumont and Cooke. Thiem collected data with significant contributions from Hatin and Dumont. Van Der Kraak ran laboratory blood samples. Thiem analysed data and wrote the paper. All co-authors reviewed the paper.

Chapter 3: Behaviour and passage success of upriver-migrating lake sturgeon (*Acipenser fulvescens*) in a vertical slot fishway on the Richelieu River, Quebec.

Thiem JD, Binder TR, Dawson JW, Dumont P, Hatin D, Katopodis C, Zhu DZ, Cooke SJ (2011) Endangered Species Research 15:1–11

This paper was conceived by Thiem, Binder, Hatin, Dumont and Cooke. Thiem collected data with significant contributions from Binder, Hatin and Dumont. Thiem analysed data and wrote the paper. All co-authors reviewed the paper.

Chapter 4: Accelerometer-derived activity correlates with volitional swimming speed in lake sturgeon.

Thiem JD, Dawson JW, Gleiss AC, Martins EG, Haro A, Castro-Santos T, Danylchuk AJ, Wilson RP, Cooke SJ. Submitting to Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology.

This paper was conceived by Thiem and Cooke. Thiem collected data with significant contributions from Haro, Castro-Santos, Danylchuk and Wilson. Thiem analysed data with assistance from Dawson, Gleiss and Martins. Thiem wrote the paper and all co-authors reviewed the paper.

Chapter 5: Swimming activity and energetic costs of adult lake sturgeon during fishway passage.

Thiem JD, Dawson JW, Hatin D, Danylchuk AJ, Dumont P, Gleiss AC, Wilson RP, Cooke SJ. Submitting to Journal of Experimental Biology.

This paper was conceived by Thiem and Cooke. Thiem collected data with significant contributions from Hatin and Danylchuk. Thiem analysed data and wrote the paper and all co-authors reviewed the paper.

Table of Contents

List of Tables

List of Figures

Chapter 1. General Introduction

Migration biology

The movement of animals is a fundamental characteristic of life that determines individual fate and fitness, and is governed by a combination of internal state, environmental factors, and capacity for both navigation and motion (Nathan et al. 2008). Migration represents a particular type of movement that is both persistent and directional, occurs over a larger spatial scale than everyday movements and often results in the inhibition of responses to stimuli that would typically halt everyday movements (Dingle 1996). Migratory movements can be driven by increased opportunities for feeding and/or reproduction, or alternatively may be driven by predation pressure (Fryxell and Sinclair 1988). While migrations are undertaken to maximise fitness at the individual level, they can directly affect population persistence, ecological function and integrity and are thus an integral component of the life history of an organism. Numerous, and often emotive, examples of vertebrate migrations exist. Notable examples include migrations undertaken by large herbivores such as caribou (*Rangifer tarandus*) in North America and wildebeest (*Connochaetes taurinus*) in Africa, the southbound fall migration and northbound return migrations in spring of numerous northern hemisphere birds, and the return migration of adult Pacific salmon (*Oncorhynchus* spp.) from the ocean to their natal freshwater streams.

Although the direct benefits of migration to an individual or population are often clear, there are also numerous indirect benefits to ecosystems. For example, the migration of large herbivores supports the long-term stability of ecosystems by preventing vegetation collapse that would otherwise occur through continual cropping (Fryxell and

Sinclair 1988). Some fish migrations benefit unionid mussels, which form dense beds in rivers and play an important role in filtering nutrients, as their glochidia larvae parasitise fish and ‘hitchhike’ to reach upstream locations (Schwalb et al. 2011). The migration of Pacific salmon is one of the most well known examples of indirect ecosystem benefits. Each year along the west coast of North America the return migration of semelparous Pacific salmon to streams results in the transfer of large quantities of marine-derived phosphorous, nitrogen and carbon to watersheds (Gresh et al. 2000; Naiman et al 2002). These nutrients support juvenile salmon as they grow in otherwise oligotrophic lakes, provide a reliable food source for scavengers including bears and increase the production and diversity of riparian plant communities (Naiman et al. 2002).

Given the spatial scale of animal migrations can be vast, in some cases thousands of kilometres, it is unsurprising that migration is often energetically demanding. Indeed Dingle (1996) defines the reallocation of energy to specifically support movement as a key attribute in characterising migratory behaviour. Energy is often referred to as the currency of life as it fuels biological processes at all levels. Energetic resources are taken from the environment by organisms and allocated to fitness-enhancing processes including survival, growth and reproduction (Brown et al. 2004). Throughout everyday life these processes typically form a balanced equation whereby total energy intake is proportioned to the maintenance functions of metabolism (standard metabolism, costs of activity and specific dynamic action) and waste losses (excretion of soluble wastes and egestion of indigestible wastes), with any remaining energy allocated to a gain (somatic growth and gonad growth) (Kitchell 1983). For particularly demanding activities such as long distance migrations where the fuel used to complete the activity (in addition to maintaining other functions) exceeds intake, then an energetic loss may occur. This loss may be further exacerbated by a reduction or absence of feeding during migration.

In fish, longer riverine migrations have been linked with a higher density of somatic energy to fuel migration, and a more fusiform body shape and fewer eggs to aid in swimming efficiency within a single species (e.g. sockeye salmon *Oncorhynchus nerka*; Crossin et al. 2004). Longer migrations also favour a larger body size among species (e.g. migratory distance increases with body size in sturgeon *Acipenser* spp.; Auer 1996*a*) as optimum speed scales with size and thus with higher speeds individuals can travel longer distances with relatively less energy expenditure (Dingle 1996). Reproductive strategy also influences the allocation of energy to migration. For semelparous species (i.e. only reproduce once in their lifetime and subsequently die) all available energetic resources are allocated to fuelling their migration and maximising reproductive output. In iteroparous species (i.e. reproduction occurs multiple times throughout their life), energy is reserved to maintain regular function and reproductive output is typically smaller for any given reproductive episode. Further, the energy remaining to individuals following completion of migrations can directly affect fitness as the actual reproductive events following migration can be energetically demanding. Brett (1995) identified that the activity metabolism on spawning grounds for sockeye salmon increased by 14% for females and 59% for males in comparison to activity metabolism associated with migration, and was primarily attributed to repeated bursts of digging in female salmon and aggressive territorial defence in male salmon.

Given that migrations are energetically taxing, cost optimisation strategies are frequently observed where very specific movement paths are selected that minimise energy expenditure (i.e. are fuelled aerobically via slower locomotion). For example, Standen et al. (2002) observed active path selection by migrating Pacific salmon that minimised swimming through areas of high water velocity or turbulence. This strategy increases migration time although results in a decreased frequency of swimming at burst speeds which result in the rapid depletion of energy stores via anaerobic metabolism. Moreover, if anaerobic pathways are utilised, an oxygen debt occurs which further constrains locomotory activity until the debt has been repaid (Beamish 1978).

Anthropogenic interruptions to migrations

Many animal migrations of the size and scale historically observed may be a relic of days gone by, with anthropogenic impacts such as climate change, habitat loss, overexploitation and physical obstacles to migration the primary causes of declines in numerous migratory species (Wilcove and Wikelski 2008). Climate change has been implicated in mistimed migrations that can ultimately result in population declines through increased mortality indirectly (e.g. reduced feeding opportunities for birds; Both et al. 2006) or directly (e.g. increased water temperatures have a direct physiological impact on fish; Martins et al. 2011). Habitat loss in both terrestrial and aquatic ecosystems is consistently linked with population declines in numerous animal groups worldwide, although is typically considered to have a smaller effect on migratory species in comparison to resident species (e.g. Bender et al. 1998). Overharvest of many of the world's marine fisheries resources represents one of the best known examples of overexploitation (e.g. Pauly et al. 1998; Baum et al. 2003; Myers and Worm 2003), and the scale of migrations of numerous marine species mean that localised harvest can have broader consequences. Physical obstacles such as roads prevent migration either through avoidance (caribou; Dyer et al. 2002), direct mortality (amphibians and reptiles; Fahrig et al. 1995) or simply pose an insurmountable obstacle (fish; Warren and Pardew 1998).

In riverine systems connectivity is critical to the functioning of key ecosystem processes, including the movement of individuals, materials, nutrients and energy (Vannote et al. 1980; Wiens 2002). The construction of dams on rivers has resulted in fragmentation of riverine habitats throughout the world, with estimates in excess of 45 000 large dams primarily for hydropower and flood control, and 800 000 small dams (Dynesius and Nilsson 1994; Rosenberg et al. 2000; Nilsson et al. 2005). The resulting disconnection of key migratory pathways, while only one symptom of water resource development, has directly resulted in population declines in numerous migratory fish species (Lucas et al. 2001). Dams not only form insurmountable barriers that block both upstream and downstream migration, but can also result directly in mortality including from migrating fish passing over dams, pressure changes or blade strikes when fish pass through hydropower turbines or impingement on diversion screens (Lucas et al. 2001).

Fish passage

As barriers to migration have the potential to influence entire ecosystems, there is a need to provide access to optimal habitats for all species that reside within a watershed (Agostinho et al. 2002). Given the negative ecological impacts of riverine impoundment, the soundest ecological solution may be to simply remove barriers (Cowx and Welcomme 1998). Indeed dam removal is becoming increasingly common in some places (e.g. US Atlantic coast; Brown et al. 2013); however a general worldwide reliance on dams for flood control, irrigation, potable water and hydropower means that in many cases alternatives to removal are required. Consequently, numerous types of devices are used to facilitate passage of migratory fish past barriers, and when adult fish are migrating upstream to reach spawning areas these can be broadly classified into two types of passes; fish locks or elevators, and fishways. Locks and elevators typically lift fish over an obstruction. Fishways require fish to swim upstream under their own volition and locomotory ability. Fishways can be defined as a water passage around or through an obstruction, and are designed to dissipate the energy in the water to enable fish to ascend without undue stress (Clay 1995). Successful implementation of fishways requires a thorough knowledge of the life history of a species, knowledge of the behavioural attraction to the entrance of the fishway, and detailed knowledge of swimming performance (Lucas et al. 2001).

Laboratory swimming trials in enclosed flumes represent the most common method used to determine the swimming ability (i.e. sustained, prolonged or burst swimming speeds) of a species, which are then related to the length and water velocity of a particular fishway design to predict successful passage (e.g. Peake et al. 1997). Sustained swimming occurs at low water velocities and represents a speed that can be maintained for more than 200 min and is fuelled purely from aerobic metabolism (Beamish 1978). Prolonged swimming represents a transition from aerobic to anaerobic metabolism and results in fatigue, is typically maintainable for between 20 sec and 200 min, and the period of time a speed can be maintained decreases with increasing water velocity (Beamish 1978). Burst swimming is fuelled exclusively by anaerobic metabolism, lasts for less than 20 sec and results in rapid depletion of energy stores (Beamish 1978).

Within a fishway the water velocity should be less than the maximum attainable speed for a target species and size class, and the distance required for successful passage can be calculated from the endurance of an individual at a given swimming speed (Peake et al. 1997). Engineers attempt to incorporate biological design criteria related to swimming ability of fish into fishway design but the information generated in laboratory swimming trials may fail to represent the real capabilities of fish (e.g. Peake 2004). Further, as knowledge of fishway design and success has historically stemmed from the myriad of research conducted on high priority species such as salmonids that have generally evolved for long distance migrations and high speed swimming (Roscoe and Hinch 2010), transfer of this knowledge to non-salmonid waters has often met with poor success (e.g. Mallen-Cooper and Brand 2007). These deficiencies in knowledge have been further exacerbated by a general lack of appropriate effectiveness monitoring to inform future designs for non-salmonids (Bunt et al. 2012; Hatry et al. 2013).

Electronic tagging and tracking

The allocation of time individuals assign to different behaviours across the landscape affects individual survival and fitness, and can ultimately affect population dynamics (Morales et al. 2010). In fish, the quantification of behaviour is often difficult to measure by direct observation given that movements such as migrations can occur over vast spatial scales. Further, the habitats occupied by fish in freshwater often preclude direct observation as a result of high turbidity, extreme depth, complex habitats, high water velocities or ice cover (Cooke et al. 2013). Thus electronic tagging and tracking represents a particularly effective method for studying the spatial behaviour of fish in freshwater (Lucas and Baras 2000; Cooke et al. 2013). An additional advantage of electronic tagging is that it enables repeat observations to be made of the same individual through time, often remotely so as not to affect individual behaviour. These repeat observations offer numerous advantages including being able to determine the spatial extent of movements from the same individual and enabling an understanding of the role abiotic and biotic factors have on movement and behaviour at the individual level. First applied to fish in the 1950's, the use and applications of electronic tagging and tracking have significantly progressed over the past few decades, resulting in rapid advancement of our understanding of fish behaviour and migration (Lucas and Baras 2000). Electronic tags can be broadly classified into passive tags that contain no internal battery and when energised transmit an individual-specific code, telemetry tags that rely on a battery and actively transmit either a unique code or operate on a unique frequency to enable active or passive tracking of individuals, and data logging tags that record information onboard and require retrieval and subsequent downloading. The incorporation of sensors into transmitting or data logging tags, broadly termed biotelemetry, can further enable measurement of the physiology, behaviour or energetics of individuals through time and in their natural environment (Cooke et al. 2004).

The use of electronic tagging has greatly improved our understanding of species-specific migrations as well as fishway performance. For example, the benchmark for evaluating fishway effectiveness and performance is generally recognised to include measures of attraction efficiency and passage efficiency (Bunt et al. 2012, Cooke and

Hinch 2013). Attraction efficiency refers to the proportion of tagged individuals released during a study that are subsequently located at the fishway entrance, and passage efficiency is defined as the proportion of attracted individuals successfully passed. Both of these measures can technically be achieved through more traditional mark-recapture methods following the placement of a unique external (non-electronic) mark on each individual, although requires subsequent recapture. More commonly, electronic tagging is used as it requires only a single capture event (with 'repeat' captures resulting from tag detection) and fishway performance measures can be monitored remotely, thus without the requirement of recapture. Further, electronic tagging also enables the quantification of behaviour in and around a fishway, as well as calculation of fishway passage duration and passage delays, and location-specific failure rates. The development of relatively inexpensive automated Passive Integrated Transponder (PIT) antenna arrays to detect fish fitted with small passive tags was pioneered by Castro-Santos et al. (1996) and now represents the most common method for fishway evaluation and calculation of the above performance measures.

In some instances biotelemetry tags have also been used to determine activity-specific behaviours and swimming speeds of fish at fishways (e.g. electromyogram radio telemetry: Gowans et al. 2003; Pon et al. 2009), although fishway assessments incorporating individual behaviour, physiology or energetics are typically uncommon (Hasler et al. 2009; Roscoe and Hinch 2010). Recent advances in archival data loggers that measure dynamic acceleration due to animal movement (e.g. Wilson et al. 2008) show promise for the field determination of activity-specific behaviours in fish. Strong relationships between accelerometer derived activity metrics and energy use have been demonstrated for a wide range of aquatic and terrestrial animals (*see* Halsey et al. 2011), however, as yet their application remains untested in fishways.

Sturgeon as a model group

Sturgeon are a long-lived organism of the Acipenseridae family that comprise 27 living species spanning the temperate zones of Europe, Asia and North America (Bemis and Kynard 1997). Sturgeon were an important food source historically, although overexploitation and habitat modification has placed the majority of species under threat of extinction throughout their broad geographic range (Rochard et al. 1990; Birstein 1993). As adults, sturgeon species occupy a variety of different habitats including large rivers and freshwater lakes, estuaries and shallow offshore environments (Rochard et al. 1990; Bemis and Kynard 1997; Figure 1.1). Despite their variability in habitat occupation, all species share a number of common life history strategies; spawning always takes place in freshwater typically in large rivers and locations of higher water velocity, sexual maturity is late (i.e. age at first spawning is 20–25 years for female and 15–20 years for male lake sturgeon (*Acipenser fulvescens*); Bruch and Binkowski 2002) and all species are iteroparous although spawning does not occur annually (Bemis and Kynard 1997). In an eight year study monitoring the same individuals through time, Forsythe et al. (2012*a*) identified that lake sturgeon females spawned on average every 3.7 years and males every 2.3 years, and that the timing of spawning and spawning site were repeatable among individuals. Pre-spawning migrations are typical for sturgeon and can be classified into anadromy (i.e. spend most of their lives at sea or in estuaries, but migrate to freshwater to spawn) or potamodromy (i.e. migrate entirely within freshwater)

(Figure 1.1). While the spatial extent of spawning migrations can vary among species and is strongly correlated with the size of adults (Auer 1996*a*), it is this life stage and the associated synchronised movement among individuals that historically made sturgeon particularly susceptible to overharvest.

More recently, dams that block the passage of migratory pathways of sturgeon are recognised as a key threat to all species and limit population recovery (Rochard et al. 1990). Despite this, there is a paucity of information on fishway passage by sturgeon, with a single study on the Columbia River documenting low fishway passage success for white sturgeon (*Acipenser transmontanus*) (Parsley et al. 2007). Guidelines for the provision of appropriate passage based on traditional approaches of laboratory-derived swimming models to inform fishway design criteria remain untested in the field (Peake et al. 1997); although there is increasing evidence of poor transferability between laboratory-derived swimming and successful passage for other species (e.g. Peake 2004).

One explanation for the apparent lack of fishway passage by sturgeon relates to their swimming ability. They represent an evolutionally basal group of fishes—the presence of fused fin rays means they have limited ability to manipulate their fins, and locomotion is primarily derived from body undulations and associated movements of median and paired fins (Breder 1926; Wilga and Lauder 1999; Liao and Lauder 2000). Sturgeon exhibit a number of morphological limitations including a comparatively high drag resulting from body form and external scutes, as well as low thrust resulting from their heterocercal tail (Webb 1986). Sturgeon also have a relatively limited capacity for high speed burst swimming as well as a comparatively poor aerobic capacity (Peake et al. 1997). Taken together this information suggests that sturgeon may not have the capacity for the high speed swimming required to pass a fishway as it may be too energetically demanding. It is worthwhile noting however, that the limitations imposed by the physical size of adult sturgeon frequently preclude use of swim tunnels to measure swimming ability. McElroy et al. (2012) recently provided field data to demonstrate energetic optimisation in pallid sturgeon (*Scaphirhynchus albus*) that actively selected migration pathways through sections of river with the lowest water velocities, presumably in response to their poor swimming ability. However as Peake et al. (1997) emphasise, the physical size of mature sturgeon can result in high absolute swimming speeds and the physical size of fishways needed to accommodate large numbers of migrating adults may be a limiting factor. Indeed, Parsley et al. (2007) noted that one fishway on the Columbia River was limiting upstream passage of adult white sturgeon simply due to the small size of the vertical slots and the comparatively large size of adults present.

The lack of information regarding what constitutes a successful fishway is not unique to sturgeon. Indeed, recent syntheses of published fishway evaluations are universal in their call for more effectiveness monitoring to optimise existing designs as the literature is sparse for most species (Roscoe and Hinch 2010; Bunt et al. 2012; Noonan et al. 2012; Cooke and Hinch 2013; Hatry et al. 2013). Further, when effectiveness monitoring does occur, passage rates are frequently low although a mechanistic understanding of the causes are rarely explored (Roscoe and Hinch 2010; Cooke and Hinch 2013).

Goals

The purpose of this thesis is to gain insight into the reproductive biology and behavioural ecology of a locally abundant lake sturgeon (*Acipenser fulvescens*) population. Specifically, this population of lake sturgeon is known to pass upstream via a fishway during the reproductive period each year and subsequently represents one of the few known examples of successful fishway passage worldwide by any sturgeon species. Given global concerns for this imperiled group of animals, including their susceptibility to fragmentation following water resource development primarily through the obstruction of key migratory routes on large rivers, undertaking this thesis provides a unique opportunity to investigate the mechanisms that lead to successful fishway passage. As Canada's reliance on water resource development increases, primarily via hydropower to meet growing energy demands, there is strong support for this project at both a provincial and federal level as successful fish passage in general, including sturgeon passage, is rare. As such, I undertook this thesis with an overall objective of utilising aspects of pure science to answer an applied topic.

This thesis is organised into four manuscript chapters (2–5). As the identification and protection of essential habitats represents a crucial step in the effective management and recovery of sturgeon populations, in Chapter 2 I used a combination of mark-recapture, non-lethal blood sampling, radio telemetry and egg collection to characterise the spawning population of lake sturgeon in the Richelieu River. Given anecdotal evidence of downstream spawning behaviour in addition to fishway passage by lake sturgeon, presumably to an upstream spawning area, I was specifically interested in determining whether fishway attraction and passage limit reproductive success in this system. In Chapter 3 I used an approach whereby lake sturgeon were introduced into the fishway and allowed to volitionally ascend, as quantitative data on sturgeon use of fishways, including measures of passage efficiency, are severely lacking. Specifically, I predicted that passage success and maximum upstream location would increase with increasing fish size and water temperature, given that swimming performance increases with both. In addition I examined passage behaviour among successful and unsuccessful individuals, predicting that multiple attempts resulting in larger distances moved would be indicative of passage failure as a result of hyperactivity and subsequent fatigue. I also predicted that passage duration through different fishway basins would vary as result of differences in fishway structure and subsequent hydraulics, as previous literature has identified that higher velocities are more likely to stimulate upstream movements and that lower velocities (i.e. turning basins) may be a necessary provision to facilitate rest and recovery in exhausted sturgeon. In Chapter 4 I used a captive group of lake sturgeon to develop methods for the calculation of energy expenditure associated with volitional swimming. Measures of the swimming performance of sturgeon are typically difficult to obtain in swim tunnels given their large size and ability to hold station under high water velocities. Based on previous literature I predicted that use of an open channel flume would provide more field-relevant swimming speed values for lake sturgeon. A large open channel flume was used to generate paired measures of swimming speeds of lake sturgeon with simultaneous animal-borne accelerometer-derived metrics of activity, to provide a valid technique for field quantification of swimming speed and indirect measures of energy expenditure. The goal of Chapter 5 was to determine the energetic cost of passage exhibited by sturgeon in the fishway using the methods developed in

Chapter 4. Given a poor capacity for high speed swimming in sturgeon it was hypothesised that fishway passage is energetically demanding. I predicted that inter-individual differences in path selection reflected by differences in energy use would explain the variation in passage success previously observed, and tested the utility of energy use as the sole predictor of successful fishway passage. I also examined location-specific energy use given the delayed passage and increased failure rates observed in turning basins in Chapter 3. In Chapter 6 I discuss the findings of my research in the context of the migratory behaviour of sturgeon, fishway passage and hydropower development, providing recommendations for future research priorities.

Study area

The majority of the data collection during this thesis (Chapters 2, 3 and 5) was undertaken on the Richelieu River in southwestern Quebec, Canada. The Richelieu River begins in New York and Vermont, USA, and after travelling through Lake Champlain exits into the St Lawrence River near Sorel, northeast of Montreal. The river is 124 km long and has a mean annual discharge of 362 $m^3 s^{-1}$. The St Ours dam is located 18 km upstream of the confluence between the Richelieu and St Lawrence rivers and comprises a 180 m wide, 3.4 m high structure divided into a series of five submersible gates (each 30 m wide, and the fishway) (Figure 1.2, 1.3a). The main function of the dam is to maintain a stable water level upstream for navigation purposes, with boat traffic able to pass the dam via a canal comprising of a series of locks adjacent to the dam. The dam and canal were originally constructed in 1849, and from this time until 1969 fish passage was possible either over the dam or through a fishway. Construction of a new dam in 1969 effectively prevented upstream fish passage, and subsequently in 2001 the Vianney-Legendre vertical slot fishway was constructed on the western shoreline to provide access to an additional ~50 km of unimpounded river upstream of the dam. The fishway was constructed to provide upstream access for key migratory species including copper redhorse (*Moxostoma hubbsi*), lake sturgeon (Figure 1.3c), American shad (*Alosa sapidissima*) and American eel (*Anguilla rostrata*). The total number of fish ascending the fishway each year is unknown, although a fish trap is used at the upstream end of the fishway during May and June each year and indicates that the fishway successfully passes at least 36 species currently (Desrochers 2009). The fishway is an ~85 m long concrete structure with a floor height rise of 2.65 m and includes large entrance and exit basins on small slopes (floor height rise of 0.1 and 0.15 m, respectively) (Figure 1.3b; *also see* Figure 3.2). The rest of fishway is divided into 12 uniform rectangular basins (3.5 × 3.0 m) connected by two resting/turning basins with horizontal floors and curved walls (2.75 m radius). The uniform basins have successive floor drops of 0.15 m for a total rise of 2.4 m and are each separated by a 0.6 m wide vertical slot (2.3–4.0 m height range). The fishway discharge is approximately 1 $m^3 s^{-1}$ with a capacity for an additional 6.5 $m^3 s^{-1}$ attraction flow near the entrance basin via a pass-through chamber beneath the fishway. Maximum water velocities of 1.72 $m s^{-1}$ occur through the vertical slots.

Figures

Figure 1.1 Examples of potamodromy and anadromy typically exhibited by sturgeon. In potamodromy juvenile and adult sturgeon (e.g. lake sturgeon) spend their entire lifecycle in freshwater, typically foraging in lakes and large rivers, with spawning taking after an upstream riverine migration followed by a return to foraging areas. In anadromy juvenile and adult sturgeon (e.g. Atlantic sturgeon *Acipenser oxyrinchus*) forage in the estuary and ocean environments, with an upstream riverine migration similarly preceding spawning followed by a return to downstream foraging areas. (*Adapted from* Bemis and Kynard 1997)

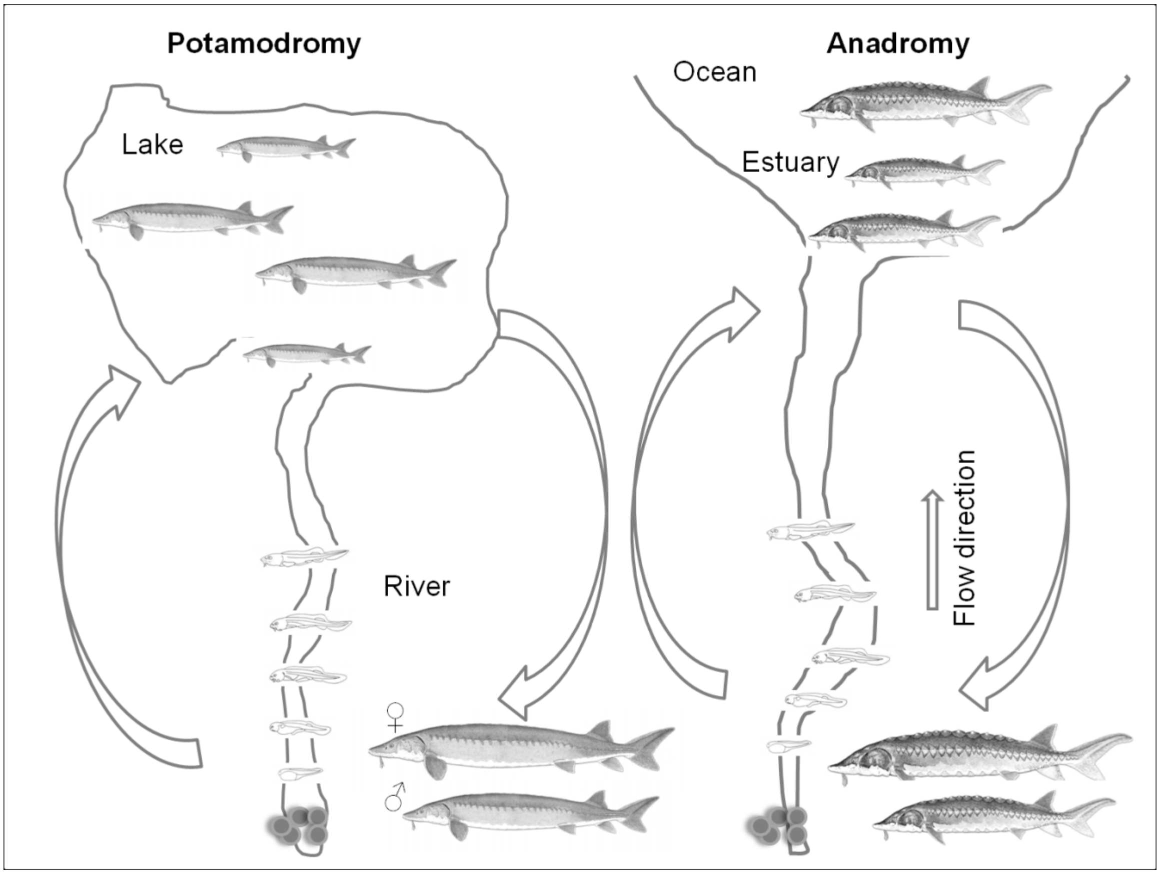


Figure 1.2 Location of the Vianney-Legendre fishway and the St Ours dam on the Richelieu River in southwestern Quebec, Canada.

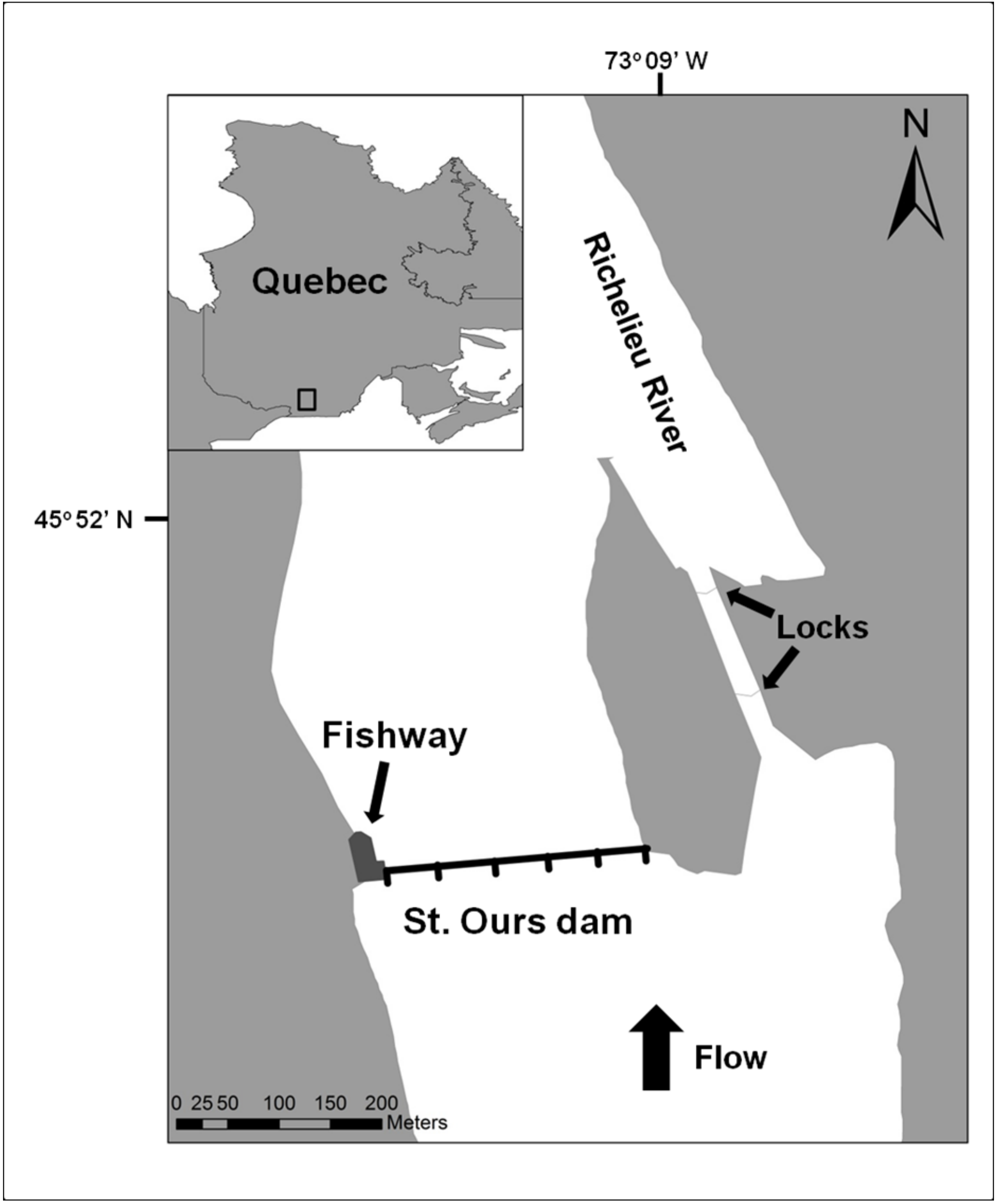
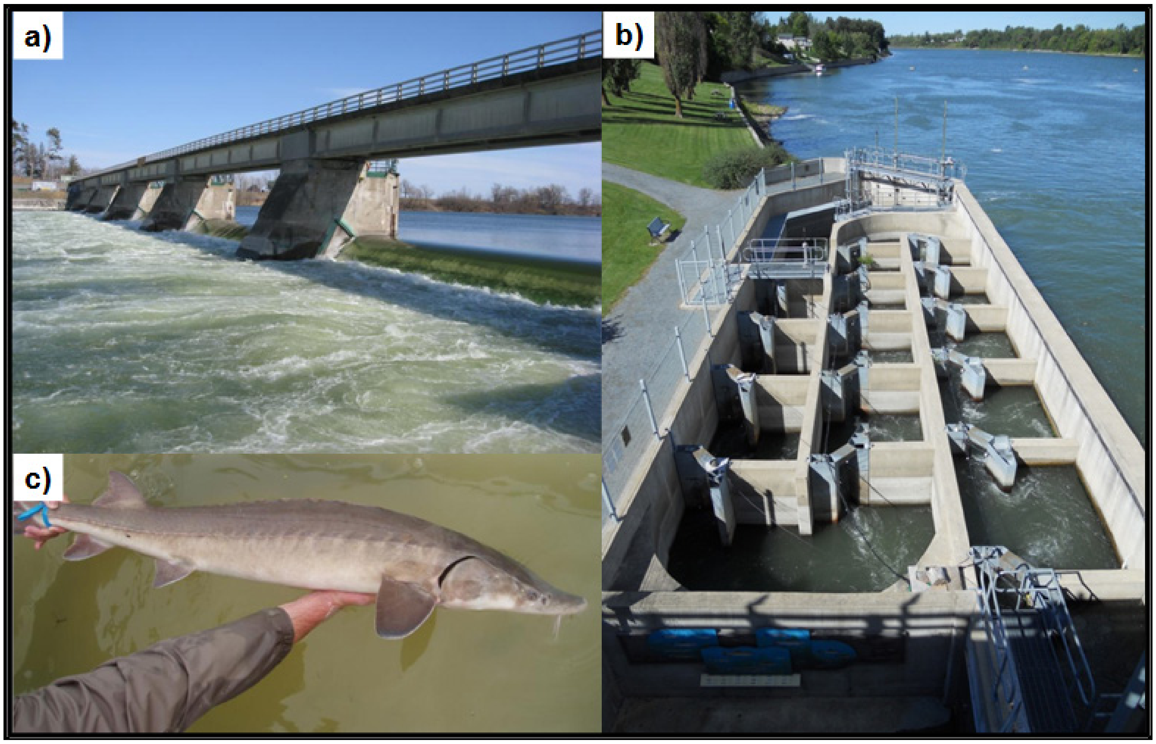


Figure 1.3 a) The St Ours dam on the Richelieu River, which forms an impassable obstacle to upstream migrating fish, b) a top view of the Vianney-Legendre vertical slot fishway facing downstream, which was installed in 2001 to facilitate upstream passage for numerous migratory fish species including lake sturgeon and, c) a small adult (~ 950 mm) lake sturgeon captured immediately downstream of the St Ours dam.



Chapter 2. Biology of lake sturgeon (*Acipenser fulvescens*) spawning below a dam on the Richelieu River, Quebec: behaviour, egg deposition and endocrinology

Abstract

Knowledge of the reproductive biology of wild sturgeon populations is critical to ensure the survival of this group of animals. We combined gill netting surveys, non-lethal blood sampling, radio telemetry and egg collection to examine the reproductive biology of lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) at a suspected spawning ground below a dam on the Richelieu River, Quebec. Lake sturgeon were present at the beginning of sampling in early May, and spawning took place from 26 May – 5 June when water temperature averaged 13.4 ± 0.1 ^{o}C (range 11.5–15.5 ^{o}C). Daily spawning population estimates ranged from 285–1282 individuals and the sex ratio of spawners was estimated at 2.1 males per female. The presence of radio tagged individuals on the spawning grounds peaked from 20–28 May, corresponding with known spawning bouts. Residence time of spawners on the spawning ground ranged from 1–27 days (median = 5 days) and there were no differences in residence time between sexes. Non-lethal blood sampling enabled the quantification of steroid levels to determine the spawning population sex ratio, and steroid levels were highest before spawning was known to occur and decreased concurrently with, and after, known spawning events.

Introduction

Sturgeons represent one of the most threatened group of fishes in the world, with 18 of the 27 recognised species of Acipenseriformes listed as Endangered or Critically Endangered (IUCN 2010). Due to their life-history characteristics including slow growth and late age at maturity, sturgeon are particularly sensitive to low levels of exploitation and habitat degradation (Rochard et al. 1990; Bemis and Kynard 1997). Given the propensity of all species to spawn in freshwater rivers, river fragmentation resulting in the loss of critical spawning habitat places limits on the recovery of many populations already decimated through overharvest (Rochard et al. 1990). Knowledge of the reproductive biology of wild populations of sturgeon is therefore critical to ensure the perpetuation of this group of animals (Haxton 2006).

Lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) are the most widely distributed of the five *Acipenser* spp. occurring in North America (Peterson et al. 2007). Similar to most sturgeons, lake sturgeon have undergone severe population declines across their range (Scott and Crossman 1973; Peterson et al. 2007). In Canada, the Committee on the Status of Endangered Wildlife (COSEWIC) has listed lake sturgeon populations as being of special concern, threatened or endangered depending on the population status in designatable units (COSEWIC 2002). Lake sturgeon are potamodromous and generally undertake spawning migrations over a distance of 10’s to 100’s of kilometres (Auer 1996*a*). Typically, the construction of dams on large rivers is considered as a threatening process for sturgeon as barriers limit access to historic upstream spawning and nursery areas and isolate populations (Jager et al. 2001), although lake sturgeon will spawn below dams where suitable habitat exists (e.g. LaHaye et al.

1992; Auer 1996*b*; Bruch and Binkowski 2002; Haxton 2006). The creation of artificial spawning grounds or expansion of existing spawning grounds holds promise for the recovery of the species where suitable spawning grounds are not naturally available (LaHaye et al. 1992; Johnson et al. 2006; Dumont et al. 2011).

To date, there have been several studies of lake sturgeon reproductive biology in riverine systems (e.g. LaHaye et al. 1992; Bruch and Binkowski 2002; Dumont et al. 2011). Lake sturgeon typically migrate to spawning grounds in May and June, soon after ice-off (Scott and Crossman 1973). As spawning is periodical (every 2 years for males and 3–5 years for females; Bruch and Binkowski 2002), migrations are not undertaken by all individuals each year (Rusak and Mosindy 1997). Spawning grounds are generally located near rapids, in shallow water with moderate to high water velocities (0.25–0.85 m depth and 0.4–1.39 m s^{-1} in the L'Assomption River, Quebec, Canada) over coarse gravel or cobble substrate (LaHaye et al. 1992; Auer 1996*b*). Spawning has been observed over a wide range of water temperatures (8.8–21.1 ^{o}C), although generally occurs at water temperatures of 11.5–16 ^{o}C (Bruch and Binkowski 2002). Males typically arrive first at spawning grounds and actively search for ovulating females, with spawning activity mainly occurring for 2–4 days at each site (Bruch and Binkowski 2002). Pre-spawn males are frequently differentiated by the expulsion of gametes, however as this is rarely observed in females, pre-spawn peaks and post-spawn declines in steroids from non-lethal blood samples can be used to differentiate among sexes (McKinley et al. 1998). Females are typically serviced by multiple males and eggs are broadcast over preferred substrate (Bruch and Binkowski 2002). The demersal, adhesive eggs attach to substrate and hatch after 5–8 days (Scott and Crossman 1973). Several studies have independently monitored egg deposition, behaviour (e.g. arrival at spawning grounds, residency, spawning behaviours, post-spawning behaviour) and endocrine status. Combining these approaches to collectively define lake sturgeon reproductive biology enables the use of multiple lines of evidence to identify and characterise critical spawning habitat and assess key spawning population characteristics. For example, relying solely on fish behaviour and presence/absence of mature adults fails to provide direct evidence of spawning without information on gamete deposition and/or the reproductive state of sturgeon. The identification and protection of essential habitats represents a crucial step in the effective management and recovery of lake sturgeon populations.

The objective of this study was to characterise the reproductive biology of lake sturgeon downstream of the St Ours dam on the Richelieu River in Quebec, Canada. Specifically, we were interested in determining the location of the spawning ground and quantifying key habitats as well as determining the timing of spawning, and the abundance, composition and residency of spawners. This study site which is downstream from a dam equipped with a fishway that is known to pass lake sturgeon to access upstream spawning habitat (Chapter 3) enabled a further goal which was to determine if lake sturgeon are able to find and use suitable spawning sites downstream of the dam.

Methods

Study site

This study was conducted on the Richelieu River, immediately downstream of the St Ours dam in southwestern Quebec, Canada (45°51'48"N, 73°08'60"W; Figure 2.1). The Richelieu River originates in Vermont and New York, USA and, after exiting Lake

Champlain, empties into the St Lawrence River near the town of Sorel, Quebec, Canada. The river is 124 km long and its average annual discharge is 362 $m^3 s^{-1}$. The St Ours dam is located 18 km upstream of the confluence between the Richelieu and St Lawrence rivers and comprises a 180 m wide, 3.4 m high structure divided into a series of five submersible gates (each 30 m wide and a fishway) that are typically open for a short period (2–4 weeks) during the spring flood and then closed from the 3rd week of May onwards. A vertical slot fishway provides access to an additional ~50 km of unimpounded river upstream of the dam and a large set of rapids offering suitable spawning habitat. This study was conducted in an unusually high discharge year in comparison with the historical average daily discharge (Figure 2.2a), resulting in open dam gates for almost the entire duration of the study to prevent upstream flooding and causing the fishway to be inoperable for most of the study period.

Capture, tagging and tracking

Lake sturgeon were captured between 4 May and 3 June 2011 downstream of the St Ours dam in the Richelieu River using monofilament gill nets (three 10 m long panels with stretched mesh 20.3, 25.4 and 30.5 cm). Gill nets were set for 24 hours, perpendicular to the shore and downstream of the dam and locks, in a deep hole located away from the main river current with low water velocity (Figure 2. 1). This site was chosen based on extensive gill netting surveys conducted during the same period in 2010 for the collection of adults for a separate study (Chapter 3), with sampling at other nearby locations resulting in low or zero catch rates. The same capture method is used by government agencies during the spring period for routine lake sturgeon monitoring and the fish are robust to the stress associated with capture (Baker et al. 2008).

Following capture, sturgeon were immediately transferred to a holding tank and measured (total length (TL) mm) and weighed (kg). All sturgeon were tagged with a uniquely coded PIT tag (23 × 3.85 mm HDX, Texas Instruments, Dallas, Texas, USA). Each fish was placed ventral side up in a v-shaped cradle, and following a small incision (<5 mm), a PIT tag was inserted approximately 10 cm anterior of the vent and slightly off centre of the ventral midline using a 6-gauge plunger (Baras et al. 1999) and surgical wounds were sealed with cyanoacrylate. No anaesthetics or sutures were used and the entire handling process took <1 min, with care taken to minimize air exposure.

Radio telemetry was used to monitor lake sturgeon movement onto and away from the spawning grounds. A subset of all captured sturgeon (*n* = 51) and representing approximate length (1287 ± 18 mm TL, range 955–1620 mm) and weights (13.6 ± 0.7 kg, range 5.1–29.9 kg) of the total catch were fitted with coded external radio tags (149 MHz, 30 × 8 mm, 8 g weight in air, burst rate 2 sec, 90 day battery life, Sigma Eight Inc., Newmarket, Ontario, Canada) at the base of the dorsal fin (Hatin 1999; Hatin et al. 2002). All individuals were tagged between 6–18 May 2011 which encompassed the period prior to detection of any spawning events, and were released immediately following tagging near the point of capture (Figure 2. 1), with release locations alternating between both river banks each day. Sturgeon were tracked between 7 May and 30 June 2011 using four fixed radio telemetry receivers (SRX 600, Lotek Inc., Newmarket, Ontario, Canada) combined with three- or five-element yagi antennas. A total of 15 antennas were installed to determine residence time of radio tagged lake sturgeon on and around the spawning grounds and monitor movements in close proximity (~50 m) of the dam as well as radio tagged sturgeon attraction to, and entrance into the nearby fishway, and potential upstream passage through the fishway. Five antennas monitored each of the five dam gates, three antennas monitored attraction to and entrance into the fishway, two antennas faced upstream of the dam to monitor possible upstream passage and two antennas monitored approximately 200 m of shoreline on the east and west riverbank. Three antennas were positioned on the west bank of the river approximately 200 m downstream of the dam facing into the river channel to monitor the suspected spawning site based on previous identification of suitable lake sturgeon spawning substrate in this location (Dumont et al. 1997).

To determine the sex ratio of the spawning population of lake sturgeon we obtained blood samples from the caudal vasculature of all captured sturgeon using 3 ml Vacutainers (Becton Dickinson, Mississauga, Ontario, Canada) and 3.8 cm long, 21 gauge needles. Blood vials were immediately placed into a water-ice slurry for <1 hr prior to centrifuging at 10000 × g (Compact II Centrifuge; Clay Adams). Plasma was aliquoted into vials and frozen in liquid nitrogen prior to transferring samples to a -80°C freezer. The plasma content of the circulating steroids 17β-estradiol, 11-ketotestosterone and testosterone were determined for a subset of individuals (*n*=152) to determine sex ratios of the spawning population and to examine temporal trends in steroid levels in response to spawning events. The samples used were representative of the size range of individuals captured in the study, encompassed the entire capture period and included 48 radio tagged individuals. Steroid levels were determined by radioimmunoassay following the methods described by Van Der Kraak et al. (1984, 1990) and Wade and Van Der

Kraak (1991). The lowest quantifiable concentrations were 0.1 ng mL^{-1} of plasma for 17β-estradiol, 1.25 ng mL^{-1} for testosterone and 5 ng mL^{-1} for 11-ketotestosterone. The difference in the detection limits for the three steroids reflects the manner in which the samples were diluted for analysis. Sex was assigned to individuals based on the expulsion of gametes at the time of capture (*n*=52, comprising 51 ♂and 1 ♀) or based on the solved classification functions provided by Webb et al. (2002) for white sturgeon (*Acipenser transmontanus* Richardson, 1836) and previously applied to lake sturgeon (Craig et al. 2009; Shaw et al. 2012):

$-1.6727 + 2.3678(\log_{10}T) - -3.5783(\log_{10}E)$ for females, and

$-5.2972 + 5.2524 (\log_{10}T) – 7.5539(\log_{10}E)$ for males,

with paired values of 17β-estradiol (E2) and testosterone (T) from individuals substituted and the highest value of the two equations used to predict sex. Four known males were misclassified as females by this method, however as the sex of >92% of known individuals was correctly identified by this method it was deemed appropriate. Steroid levels were plotted separately for males and females to determine if steroid levels exhibited temporal trends. Pre-spawning, spawning and post-spawning periods were defined by the back calculation of the embryonic age of eggs (Table 2. 1) and retrospectively assigned to individual samples based on the timing of adult capture coinciding with these periods. Steroid levels were not determined more than once for any individual, and do not provide direct evidence of spawning as we were unable to validate that spawning was undertaken by the individuals for which steroid levels were measured.

Egg collection

The location and timing of lake sturgeon spawning was studied using 68 artificial egg collection mats deployed in a grid sampling design. The design comprised 17 rows with four mats in each row deployed and anchored in the area presenting suitable substrate and water velocity conditions for lake sturgeon reproduction between 12 May and 13 June 2011 (Figure 2. 1). Egg mats were checked every 2–6 days (median = 4 days), which is shorter than the expected incubation period (e.g. ~9 days from fertilisation to complete hatching at 15 ^{o}C; Wang et al. 1985) at the water temperatures observed in this study. Egg collection mats were modified from McCabe and Beckman (1990) and comprised carpets of latex-coated synthetic animal hair wrapped around a concrete block. Location, depth and bottom water velocity (Gurley Price water velocity meter, Gurley Precision Instruments, Troy, New York, USA) were determined at each mat lift. The mean of each of these variables over the study period was used to describe the physical location and habitat for each egg collection mat. Dominant substrate was obtained for the location of each egg collection mat by first digitising an existing habitat classification map of the study site consisting of 158 substrate point locations (Dumont et al. 1997) in ArcMap (ESRI, Redlands, USA). Universal Kriging (Oliver and Webster 1990) was subsequently conducted on the digitised data using the Geostatistical Analyst tool in ArcMap to interpolate dominant substrate at each egg mat location. Hourly water temperature was recorded in the river at the benthos for the duration of the study

(DS1921Z iButton, Maxim Integrated Products, San Jose, California, USA) and 15-min discharge data was obtained from a nearby gauging station (<http://www.wateroffice.ec.gc.ca/index_e.html> accessed 7th Sept 2011. Station: 02OJ007).

Each egg collection mat was inspected to find the adhesive sturgeon eggs prior to cleaning with a high pressure hose and re-deployment at the same location. Eggs were identified to species (other species eggs collected included: American shad (*Alosa sapidissima* Wilson, 1811) (*n*=7 eggs at 7 locations), mooneye (*Hiodon tergisus* Lesueur, 1818) (*n*=12 eggs at 11 locations) and *Catostomus* spp. (n=55 eggs at 27 locations)), counted and preserved in 5% formaldehyde for later embryonic staging in the laboratory. Embryonic stage of each lake sturgeon egg was determined according to Dettlaff et al. (1981). The approximate time of fertilisation of lake sturgeon eggs was calculated using the exponential equation provided by Wang et al. (1985) for lake sturgeon:

$$Y = ae^{bT}$$

where Y refers to Y-hours after fertilisation, T refers to temperature and a and b refer to the coefficient and slope combinations provided by the authors (*see* Table 2. 2 of Wang et al. 1985) for embryonic developmental stages 14, 22, 29, 35, 36, 40 and 44 (as per Dettlaff et al. 1981). Time of fertilisation was interpolated for each embryonic stage identified in the laboratory using the new equation resulting from the original solved equation of Wang et al. (1985) which included mean hourly water temperature for the duration of each egg mat soak time at the study site (Table 2. 1).

Data analysis

Estimates of the spawning population abundance were determined using the Seber-Jolly method to account for multiple census dates and an open population (i.e. immigration/emigration). Estimates were obtained for different census dates using the package 'FSA' (version 0.3-4, Ogle 2013) in R (version 2.14.2, R Development Core Team 2012). Estimates were deemed reliable on census dates when the total number of recaptures equalled or exceeded three, or the total number of individuals released on a census date and recaptured at a later date equalled or exceeded three (Ricker 1975) resulting in six daily estimates from 23 sampling occasions. On one of these included census dates the standard error of the estimate was not calculated due to zero recaptures on that date, although abundance was estimated as eight individuals tagged on that date were recaptured at a later date. Analysis of Covariance (ANCOVA) was used to determine if (log transformed) egg abundance (i.e. the total number of eggs collected at a site) covaried with water velocity and differed among substrate types whilst controlling for water velocity. Post-hoc tests were performed using a Bonferroni correction (Field 2009). Telemetry data were filtered to remove the first 24 hrs of data for each individual to allow for the resumption of normal behaviour following handling. Data were also filtered by fish ID and corresponding frequency channel to remove any erroneous records and data was only retained if there was at least one positive detection within 15 minutes of another (effectively three full scan cycles) to eliminate the possibility of false detections. As 98% of detections from radio tagged individuals were from antennas monitoring the spawning site, and no evidence of upstream passage or fishway entry was observed, analysis of radio telemetry data focussed entirely on presence in and around the spawning site using pooled data from four antennas connected to a single receiver (Figure 1) where detection range of pooled antennas encompassed the entire spawning ground. A residency index was calculated for each individual as the number of days present at the site divided by the number of days monitored (O'Toole et al. 2011). An independent samples t-test was used to compare differences in residence time between sexes. Where appropriate, data were first tested for the assumptions of normality and homogeneity of variance following the methods outlined by Grafen and Hails (2002) and were transformed and re-evaluated if they did not meet these assumptions. Additionally, the assumption of homogeneity of regression slopes was tested according to the methods outlined by Field (2009) for the ANCOVA. All statistical analyses were deemed significant at $P < 0.05$ and conducted using SPSS version 18 (SPSS Inc., Chicago, Illinois, USA). All data are presented as mean ± SE unless otherwise stated.

Results

We captured 334 lake sturgeon from 4 May and 3 June 2011 ($n = 306$ individuals, 1213 ± 8 mm TL (range 862–1653 mm); 10.9 ± 0.3 kg (range 2.6–30.0 kg), Figure 2. 3a) including 28 recaptures resulting in daily spawning population estimates (SE) of 349 (NA), 704 (582), 1202 (1087), 746 (658), 361 (384) and 285 (332) individuals corresponding to 10, 11, 12, 13, 16 and 17 May 2011, respectively. The subset of individuals (n= 152) used in the analysis of circulating steroid levels indicated the sex ratio of the spawning population was 2.1:1 male to female lake sturgeon, respectively. Mean length and weight were respectively 1308 ± 24 mm (range: 954–1653 mm) and

14.8 ± 0.9 kg (range: 4.0–30.0 kg) for females and 1203 ± 12 mm (range: 888–1538 mm) and 10.2 ± 0.4 kg (range: 3.5–22.2 kg) for males (Figure 2. 3b). Females were differentiated by higher levels of 17β-estradiol (2.20 ± 0.22 ng mL^{-1} plasma for females and 0.40 ± 0.03 ng mL^{-1} plasma for males). Differences were largely absent between females and males in terms of testosterone (15.2 ± 2.1 ng mL^{-1} plasma for females and 21.1 ± 2.2 ng mL^{-1} plasma for males) or 11-ketotestosterone levels (17.7 ± 1.8 ng mL^{-1} plasma for females and 21.0 ± 1.5 ng mL^{-1} plasma for males). Levels of all three steroids decreased for both sexes over time when data was separated into pre-, during and post-spawning periods based on embryonic age (Figure 2. 4). These data suggest that steroid levels are highest before spawning was known to occur, decrease concurrently with known spawning events, and further drop after spawning was finished.

At the beginning of the gillnetting operation on 3 May 2011, lake sturgeon were already present in low abundance downstream of the dam, but CPUE peaked rapidly and was highest on the 12 May 2011 (Figure 2. 2b). During the spawning period, a total of 155 lake sturgeon eggs (136 viable eggs and 19 non-viable eggs) were collected at 46 egg mat stations. Spawning was first detected on 30 May, and subsequently on 2 and 6 June. Relative abundance of eggs was highest on 30 May (0.36 eggs mat^{-1} day-^{1}; Table 2. 1, Figure 2. 2b) and declined by 2 June (0.18 eggs mat^{-1} day-^{1}) and 6 June (0.10 eggs mat^{-1} day-^{1}). The embryonic stage of eggs ranged from 6–19 on 30 May, 2–31 on 2 June and 1–30 on 6 June (Table 2. 1). Back calculation of embryonic age indicated that fertilisation occurred 19–68 hrs prior to collection on 30 May, 11–163 hrs prior to collection on 2 June and 10–146 hrs prior to 6 June (Table 2. 1), indicating spawning events took place between 26 May and 5 June 2011 when water temperature averaged 13.4 ± 0.1 ^{o}C (range 11.5–15.5 ^{o}C).

Abundance of viable lake sturgeon eggs ranged from 1–14 among stations, with viable eggs not collected from 23 sampling locations, or 34% of the 68 locations sampled (Figure 2. 5). Viable eggs were collected from water depths of 6.05 ± 0.14 m (4.24–7.78 m range) and water velocities of 0.93 ± 0.02 m s^{-1} (range 0.52–1.27 m s^{-1}). Lake sturgeon eggs were found mainly at near substrate water velocities from 0.76–1.00 m s^{-1} (Figure 2. 6a) and dominated by fine and coarse gravel substrates (80%; Figure 2. 6b). Abundance of lake sturgeon eggs at sampling locations was significantly related to the covariate water velocity ($F_{[1, 64]} = 4.852$, $P = 0.031$) and was also significantly different among substrate types after controlling for the effect of water velocity ($F_{[2, 64]} = 3.484$, $P = 0.037$). Post-hoc comparisons identified significantly higher abundances of lake sturgeon eggs at locations comprising coarse gravel compared to sand, with no significant differences at locations comprising fine gravel with either sand or coarse gravel substrates.

Of the 51 sturgeon equipped with radio tags, 32 were confirmed as male, 18 as female and the sex of one individual was unknown. Eight individuals (representing 15.7% of the tagged samples, 5♂ and 3♀) were never re-located on the fixed radio telemetry station. Of the remaining 43 individuals (27♂, 15♀ and one unknown sex) that were re-located, none were documented approaching or entering the fishway and subsequently no upstream passage past the dam via the fishway was documented. Ten individuals (5♂, 4♀ and 1 unknown sex) were recorded approaching the dam on a combined total of 13 occasions, and although passage over the flooded dam gates was possible during all occasions, no upstream passage was observed. Presence at the spawning site ranged from 1–27 days (median = 5 days) (Figure 2. 7). There were no differences in the residency index (proportion of days present to days tagged) when comparing between males (median 0.11, range 0.02–0.43) and females (median 0.09, range 0.04–0.23) over the study period (log transformed, independent samples t-test: $t_{[40]} = 0.490$, $P = 0.627$). Residency at the spawning ground peaked from 20–28 May, with 22–42% of radio tagged individuals present during this period (Figure 2. 8), coinciding with immediate pre-spawning and early spawning events, water temperatures of 9.9–13.2 ^{o}C and river discharges of 1284–1560 $m^3 s^{-1}$.

Discussion

Lake sturgeon spawned in late May and early June in the Richelieu River downstream of the St Ours dam, and at water temperatures consistent with previous studies of this species that promotes optimal survival of eggs and larvae (Wang et al. 1985; LaHaye et al. 1992; Bruch and Binkowski 2002; Caswell et al. 2004; Dumont et al. 2011). The technique developed by Wang et al. (1985) for estimating the duration of early embryonic development in controlled conditions provided a useful method for estimating the actual timing of spawning in the current study, although field application of the technique necessitates the over simplification of variable water temperatures. Survival of eggs to larvae was not quantified in the current study, and year-class strength in this region is predominantly a function of June water temperatures and discharge (Nilo et al. 1997; Dumont et al. 2011).

Lake sturgeon likely form a homogeneous phenotypic and genotypic stock in a section of the St Lawrence River spanning over 350 km, from Beauharnois Dam at the head of Lac Saint-Louis, to the brackish waters downstream of Quebec City including the lower reaches of its tributaries (Fortin et al. 1993; Guénette et al. 1993). After a long period of decline, evidence of a spawning area used by lake sturgeon, which was disused for a long period or previously did not exist (P Dumont, Unpublished data), is promising (Mailhot et al. 2011). The capture of large numbers of running ripe adults over a three year period (2010–2012; Chapter 3; J Thiem, Unpublished data) during the expected spawning window for the species, and of a size range typical for that observed on other spawning grounds (e.g. Des Prairies River; Dumont et al. 2011), indicates that use of this spawning site is not an anomaly. The first indication of lake sturgeon spawning activity downstream of the St Ours dam occurred on 1 June 2005 when ~100 sturgeon eggs were observed in the stomach contents of an American shad captured downstream of the fishway entrance (P. Bilodeau and H. Massé, MRNF, Unpublished data).

Using multiple lines of evidence, we confirmed the location of a lake sturgeon spawning ground in the current study. The location of the spawning ground, directly below a dam, is not surprising given that numerous lake sturgeon spawning grounds are located immediately downstream of impassable obstacles, and these obstacles frequently provide the necessary habitat requirements conducive to spawning and egg survival including coarse substrate and/or high water velocities (LaHaye et al. 1992; Auer 1996*b*; Bruch and Binkowski 2002; Haxton 2006; Dumont et al. 2011). Although the barrier in the current study is fitted with a fishway used by lake sturgeon (*see* Chapter 3), no observations were made of passage past the dam during the study period or through the fishway by any of the radio tagged individuals in this study. Suitable sturgeon spawning habitat exists ~50 km upstream of the dam at another set of rapids, and presumably the mature individuals known to use the fishway during spawning periods access these grounds (Dumont et al. 1997). It should be noted that the current study was conducted during atypical high flood conditions for the site, and during this study the fishway was largely inoperable.

Analysis of plasma levels of circulating steroids provided an appropriate method for sexing lake sturgeon in the current study. Although other non-destructive methods exist for sexing and/or staging adult sturgeon including ultrasound (Colombo et al. 2004), endoscopes (Kynard and Kieffer 2002) and observation of the urogenital opening (Vecsei et al. 2003), the lack of universal acceptance of a single method is indicative that each method is not without its shortcomings. One possible limitation of the current study, and most others involving the sampling of wild fish, is that the stress associated with capture and sampling may affect circulating steroid levels (reviewed in Fuzzen et al. 2011). However, based on known sex of individuals in the current study (predominantly males), the equations provided by Webb et al. (2002) for white sturgeon resulted in >92% accuracy for differentiation of sex of lake sturgeon. This result is largely similar to the findings of Webb et al. (2002) where the technique resulted in the correct sex classification 79% of the time for males and 85% of the time for females. Whilst both vitellogenin (Vtg) protein, a female-specific egg-yolk precursor, and calcium (Ca^{2+}) have also been used to differentiate sex in sturgeons (e.g. Webb et al. 2002; Craig et al. 2009), ratios of testosterone and estradiol are reliable predictors of sex (Ceapa et al. 2002).

Circulating steroids followed a temporal trend of decreasing levels over time for both males and females in the current study, based on the collection of fertilised eggs on the spawning mats and back calculated egg fertilisation times. Although sample sizes were small for during and, particularly, post-spawn categories, depressed levels of steroids either upon final maturation or post reproduction were expected based on previous study of lake sturgeon (McKinley et al. 1998) and other sturgeon species (Barannikova et al. 2004). In a study of lake sturgeon steroids spanning May–October, McKinley et al. (1998) observed a significant decrease in testosterone and 11-ketotestosterone (although not estradiol) in males and a significant decrease in all three steroids in females, corresponding to immediate pre- and post-spawning periods confirmed by gonadosomatic indices. The temporal trends identified in this study do not provide direct evidence of spawning as we were unable to validate that spawning occurred for the individuals for which steroid levels were measured. However the results do follow the temporal trend we expected if some or all of these individuals undertook spawning. In the absence of fertilised eggs this information would have provided an additional line of evidence to indicate the possibility of spawning.

Male and female lake sturgeon present at the site when netting began in early May did not demonstrate any differences in residency at the spawning ground and were present for a median period of 5 days (max. 27 days) following telemetry tagging. This result suggests that the daily abundance estimates for the site likely underestimated the total number of sturgeon in the area during the study period given individuals tagged at the start of sampling were unlikely to be present at the end of the study. Whilst initiation of migration can occur as early as ice-off, or prior to this, arrival at spawning grounds doesn’t typically occur until two weeks prior to the first spawning event and is primarily modulated by water temperature, discharge and the lunar cycle (Bruch and Binkowski 2002; Forsythe et al. 2012*b*). Sturgeon were present from at least the beginning of May (22 days prior to spawning) until the end of June in the current study, although spawning was only detected over a 10 day period. This spawning duration is in the range identified by Bruch and Binkowski (2002) from data collected over a 16 year period (range 2–14 days). Dumont et al. (2011) also identified spawning occurred over a 9–19 day range in the Des Prairies River from 5 years of monitoring, although spawning peaked for 2–6 days. The breeding strategy of lake sturgeon maximises genetic diversity through polygamy, and the opportunities for males to breed multiple times within a single season can maximise opportunities which otherwise do not occur every season as inter-spawning intervals are typically 2 years for males and 4 years for females (Bruch and Binkowski 2002; Forsythe et al. 2012*a*). This difference in the length of the gonad maturation cycle and the fact that males mature at an earlier age than females (age of sexual maturation is 18–20 years for males and 26 years for females (Scott and Crossman 1973)) explain why, in this study and many others (Bruch and Binkowski 2002; Dumont et al. 2011), the number of males present on the spawning grounds generally exceeds the number of females.

Lake sturgeon exhibited a preference to spawning over coarser substrates in the current study, once water velocity was controlled for. Despite evidence that successful spawning does not always transfer to successful recruitment, as sturgeon are known to repeatedly spawn in unsuitable habitat (Paragamian 2012), the results of the current study indicate that suitable spawning habitat is both available and being utilised at this site.

Coarser substrates than those currently sampled do exist at this site, although safety issues precluded sampling for eggs closer to the dam where larger substrate sizes and higher water velocities than those sampled predominate. This could potentially explain the low abundance of eggs collected in the current study in comparison to the relatively large numbers of mature adults that were present. Alternatively adult spawning effort could be highly localised, and the surface area of egg collection stations represents a small proportion of the available river at this site and may not be indicative of reproductive intensity (Paragamian 2012). Further, actual locations of spawning bouts can shift from year to year depending upon river height and discharge (Dumont et al. 2011).

Restoring connectivity of riverine systems that have been fragmented by dams is often viewed as a critical step towards rebuilding sturgeon populations and preventing extinction (Auer 1996*a*). The current study and numerous others have identified that lake sturgeon will spawn below water control structures if suitable habitat exists (e.g. LaHaye et al. 1992). However, as spawning does not always transfer to successful recruitment (e.g. Paragamian 2012), this result should be viewed with caution and is not universally transferable. Dam construction often results in the loss of large spawning areas by blocking upstream fish passage and altering spawning ground characteristics in the lower and upper reaches of these new barriers (Haxton and Findlay 2008). In the lower St Lawrence River, considering the location of the major spawning grounds in the upstream portion of the system, the downstream larval drift to the lower reaches and the size distribution observed among sub-adults and adults in the river, which suggests a downstream-upstream colonization from juvenile to adult stages, Mailhot et al. (2011)

considered that preventing additional fragmentation of this 350 km stretch of fluvial habitat is an important protective measure in order to prevent permanent disruption of the life cycle of the lake sturgeon population. The current study also highlights the challenges of studying passage without also knowing about presence of spawning sites downstream (*see* Pelicice and Agostinho 2008).

Tables

Table 2.1 Embryonic stage and age of lake sturgeon eggs collected at a spawning site on the Richelieu River, Quebec. Values are presented as mean ± SE and range.

Capture date	Water temperature (°C)	Number of viable eggs (total n)	CPUE (eggs/mat/day^{-1})	Embryonic stage	Embryonic age (hrs)*
30 May[a]	12.19 ± 0.05	46 (57)	0.36	14 ± 2.28	42.09 ± 1.79
				6–19	18.70–65.55
30 May[b]	11.84 ± 0.03	30 (34)	–	14 ± 2.15	42.62 ± 2.28
				7–19	21.06–67.76
2 June	14.21 ± 0.11	35 (37)	0.18	18 ± 3.05	69.77 ± 9.12
				2–31	11.46–162.84
6 June	14.38 ± 0.05	25 (27)	0.10	24 ± 2.31	93.66 ± 6.76
				1–30	10.38–145.68

*Determined from the equation of Wang et al. (1985) for lake sturgeon embryonic development using the substituted water temperature values from this study.

[a] Corresponding values are calculated based on egg mats deployed from 25–30 May.

[b] Corresponding values are calculated based on egg mats deployed from 27–30 May.

Figures

Figure 2.1 Location of the St Ours dam on the Richelieu River, Quebec, showing egg collection stations (s*n*), gill net locations and the location of the radio telemetry monitoring station used to determine residence of radio tagged lake sturgeon. Approximate detection ranges of antennas are indicated by ellipses. Note additional telemetry stations monitored for movement in and around the dam and fishway, although did not detect any upstream passage and minimal activity near the dam and are not represented here.

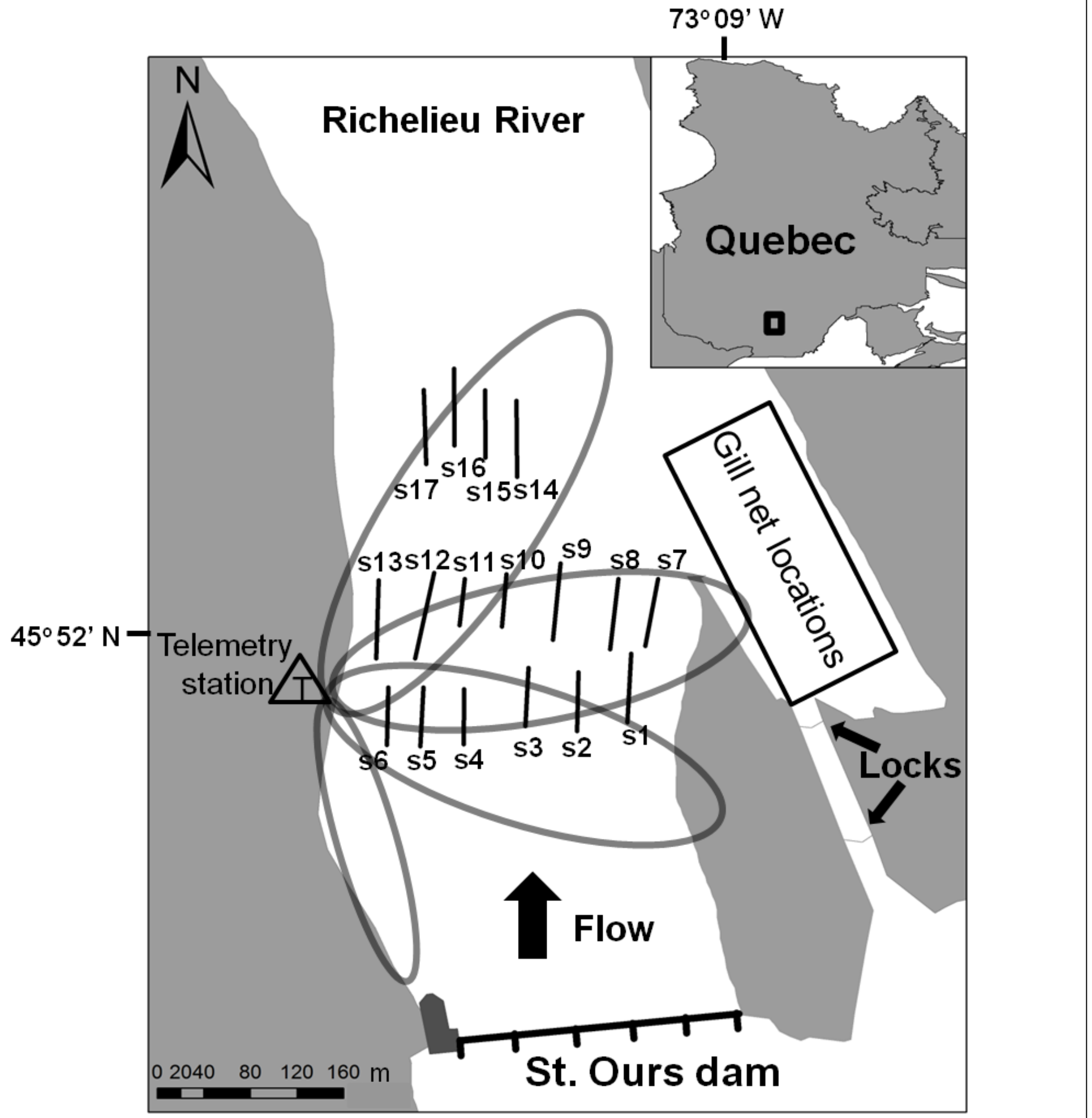


Figure 2.2 a) Water temperature (°C) (—) and daily discharge (m^3 s^{-1}) (—) in the Richelieu River for the study period as well as historical daily discharge (m^3 s^{-1}) (- -) over the period of record (1937–2011) and, b) catch per unit effort (CPUE) of lake sturgeon (□ number of sturgeon per net night^{-1}) and of lake sturgeon eggs (■ number of eggs per egg mat night^{-1} × 10). Grey shading indicates estimated spawning. * refers to periods where no netting for lake sturgeon was undertaken and does not represent zero CPUE. Zero CPUE of lake sturgeon eggs occurred on 17–20 May, 24–25 May, 27 May, 9 June and 13 June 2011.

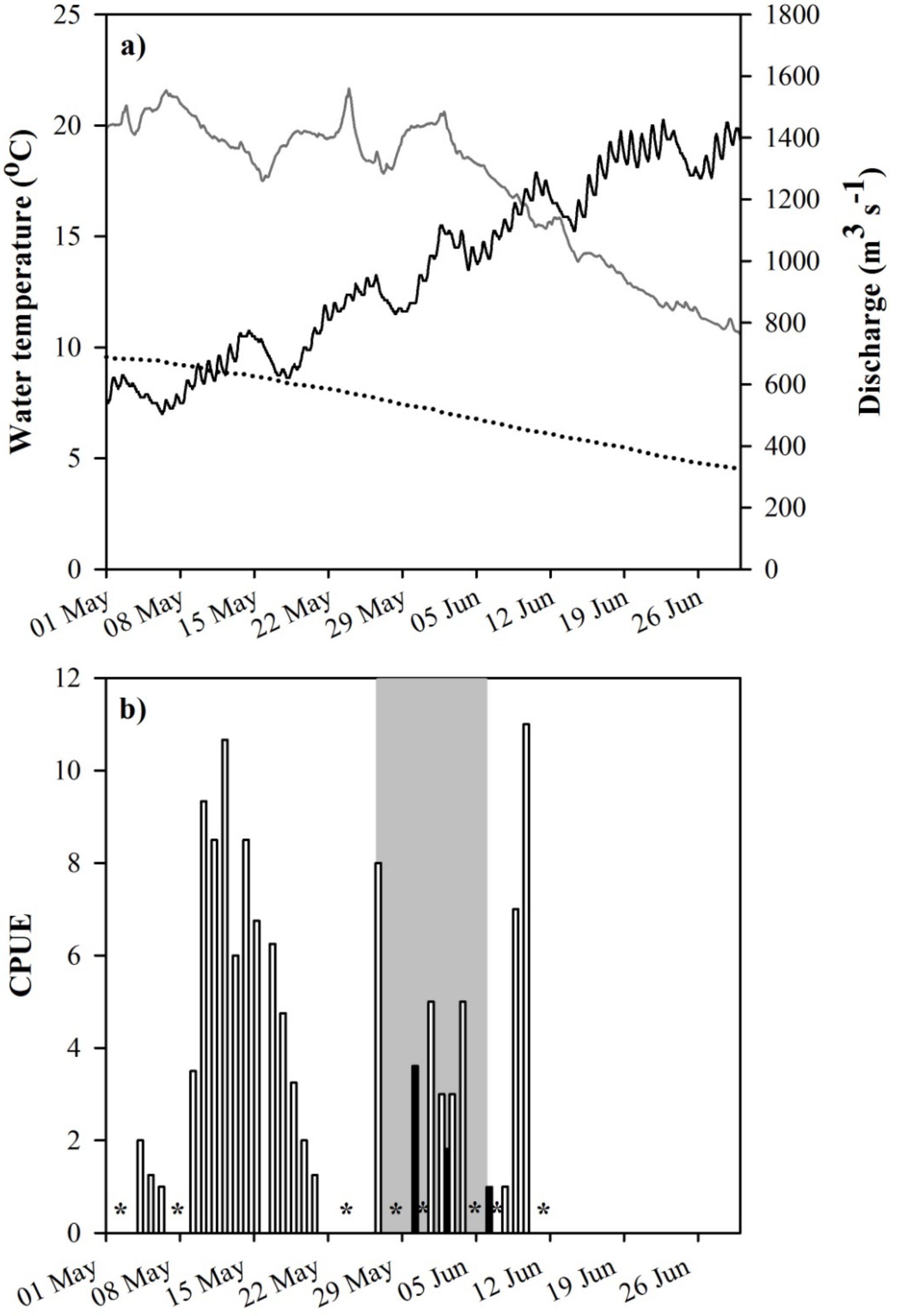


Figure 2.3 Length frequency distribution of lake sturgeon captured downstream of the St Ours dam on the Richelieu River, Quebec for a) the total number of number captured (n=306) and, b) males (white bars, n=103) and females (black bars, n= 49), where sex was determined via concentrations of circulating plasma steroids.

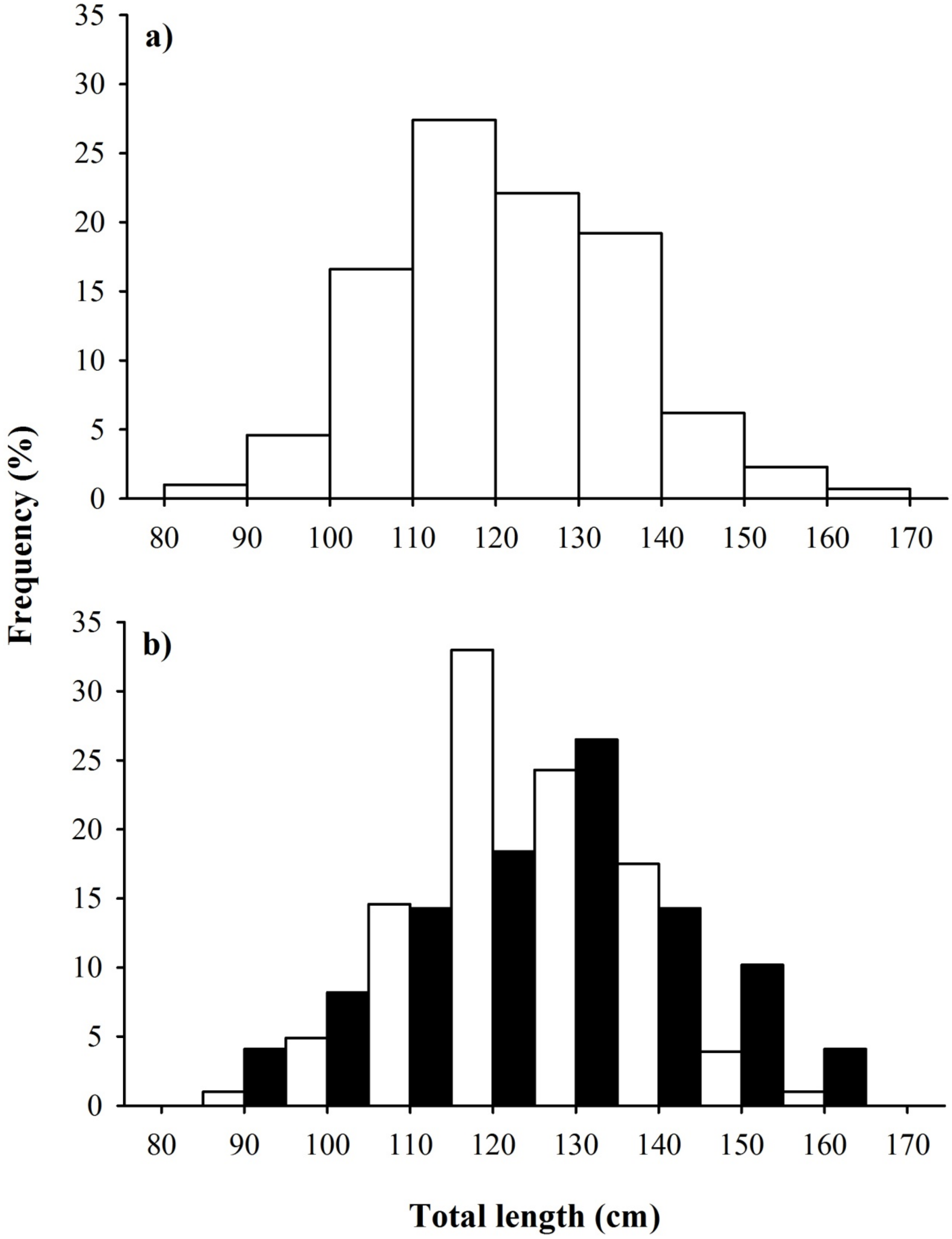


Figure 2.4 Circulating plasma steroid levels 17β-estradiol (black), testosterone (white) and 11-ketotestosterone (grey) for a) male and b) female lake sturgeon. Pre-spawning, spawning and post-spawning periods were defined by the back calculation of the embryonic age of eggs (see Table 2. 1) and retrospectively assigned to individual samples based on the timing of adult capture coinciding with these periods. Data are represented as mean ± SE. Note the log y-axis scales.

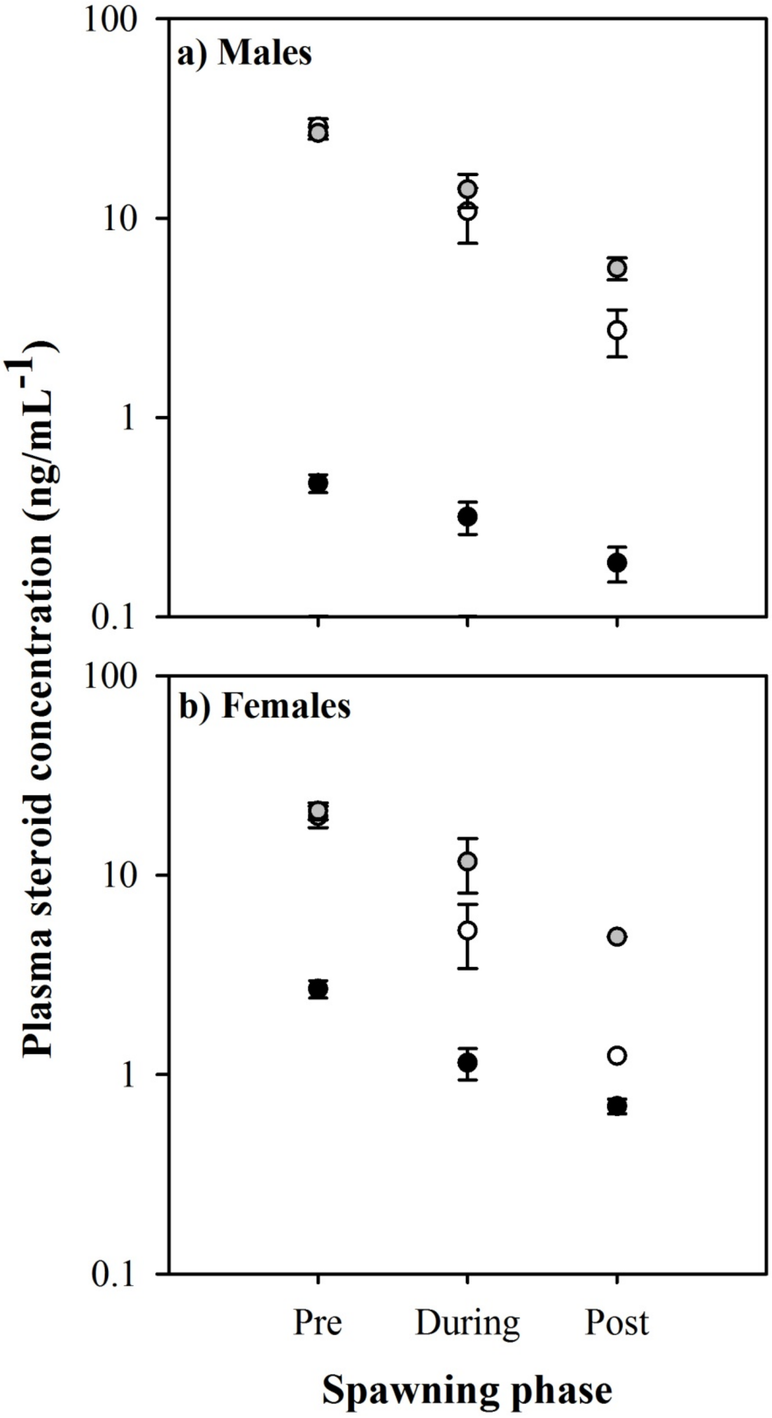


Figure 2.5 Location of lake sturgeon egg collection stations, with circles indicating the total number of viable eggs collected at each location and shading indicating dominant substrate.

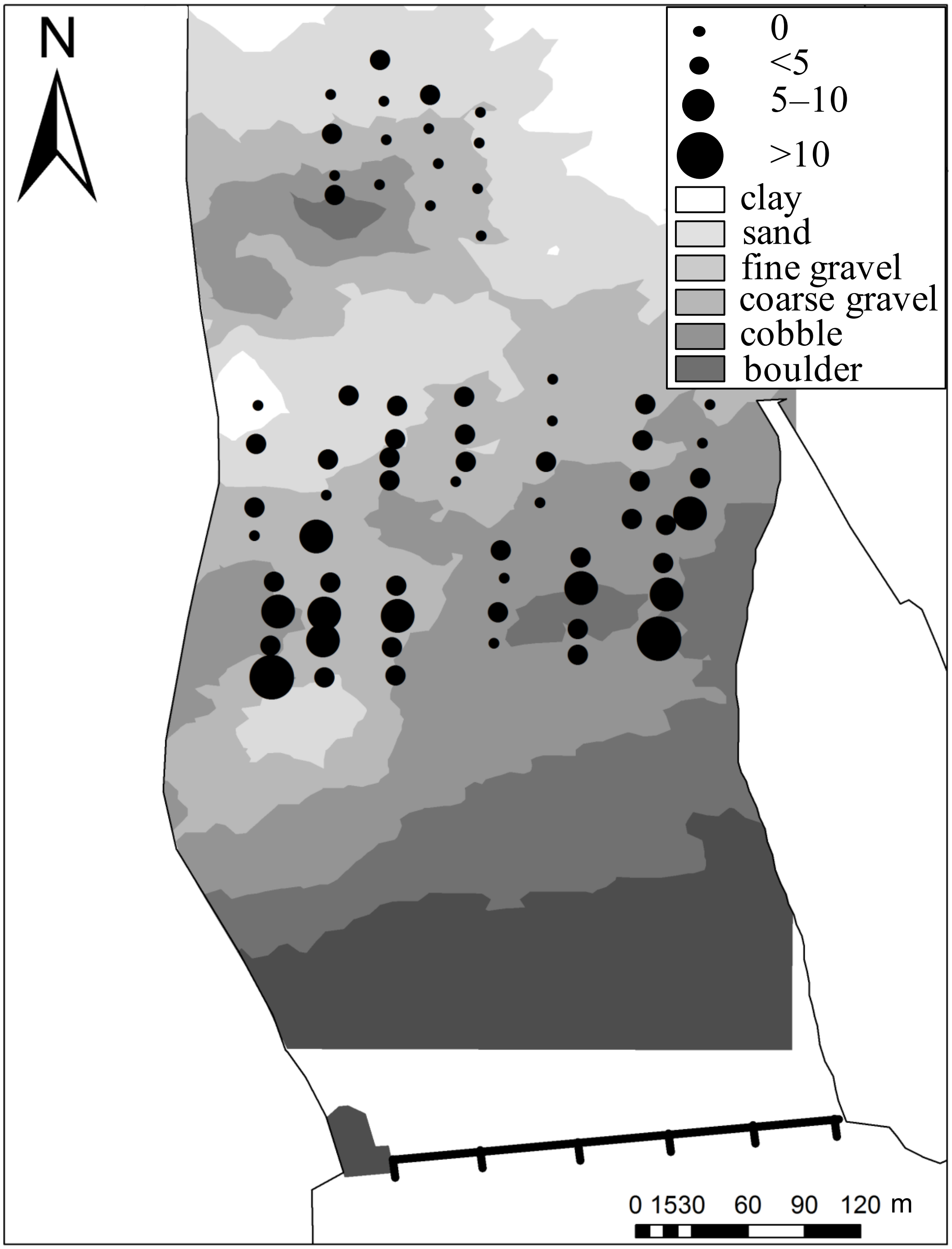


Figure 2.6 Frequency of a) bottom water velocities (m s^{-1}) and b) dominant substrate types from locations where lake sturgeon eggs were collected.

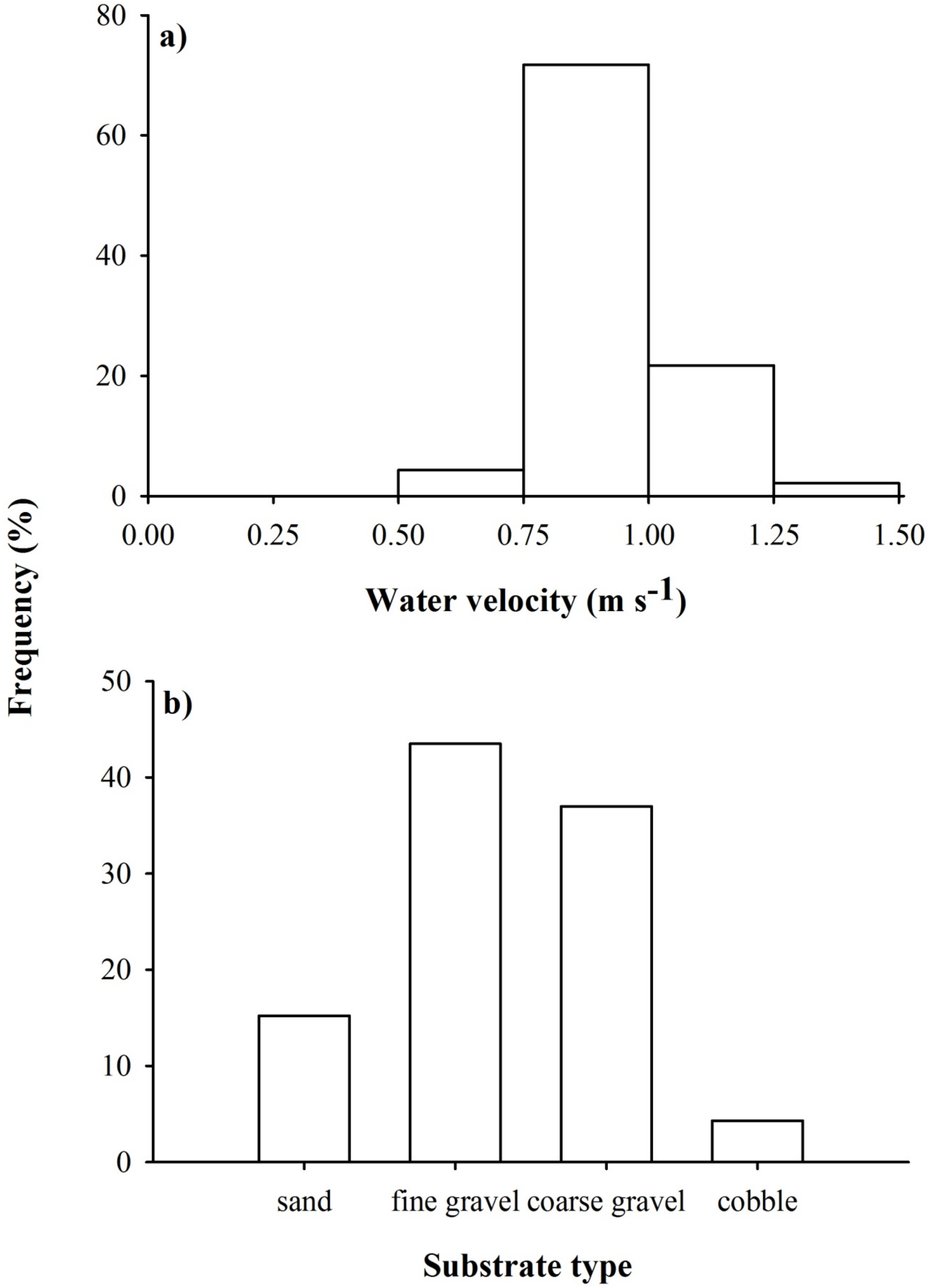


Figure 2.7 Frequency of the number of days radio tagged lake sturgeon were detected in proximity to a spawning site on the Richelieu River, Quebec. Note: data from individuals never detected (n=8) are not included.

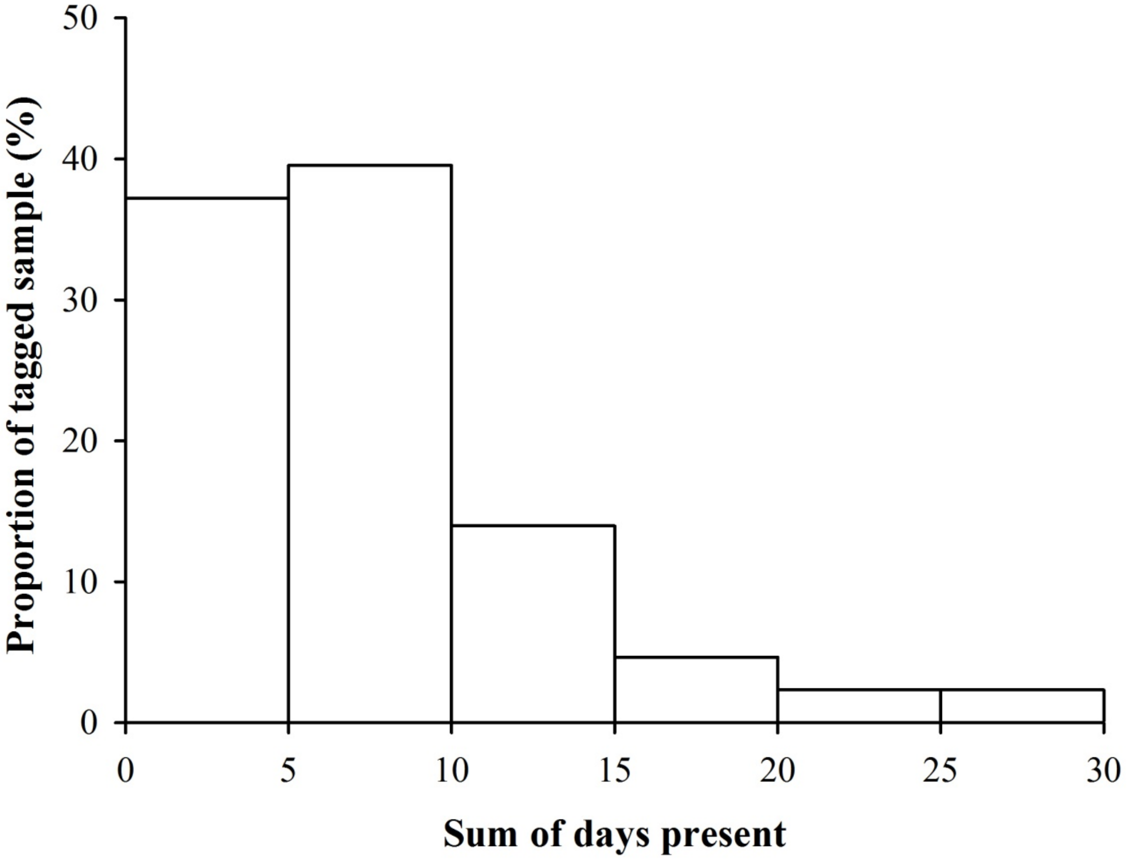
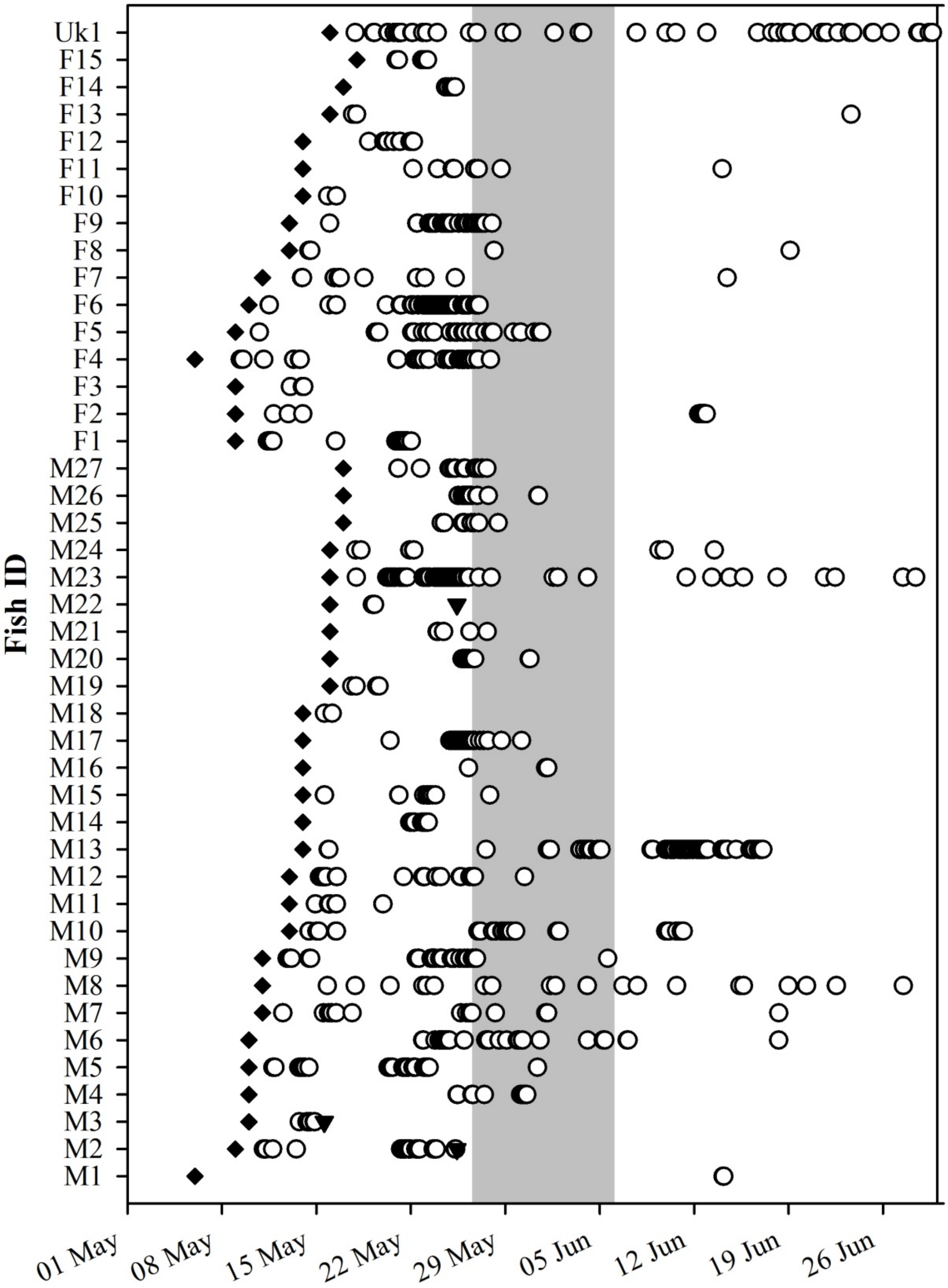


Figure 2.8 Presence of individual radio tagged lake sturgeon (M=male, F=female, Uk=unknown sex) presence at a spawning ground (○), with tagging dates (♦) and tag loss (▼) also indicated. Grey shading denotes the estimated spawning period based on back calculated embryonic age (see Table 2. 1). Note individuals radio tagged but never redetected (n=8) are excluded.



Chapter 3. Behaviour and passage success of upriver-migrating lake sturgeon (*Acipenser fulvescens*) in a vertical slot fishway on the Richelieu River, Quebec

Abstract

Spawning migrations of sturgeon have been affected by the construction of dams which create barriers to migration and have contributed to their imperilment. Although devices have been installed to facilitate the upstream passage of fish at barriers, they have been generally unsuccessful and not designed for sturgeon. We examined fine scale movements of adult lake sturgeon (*Acipenser fulvescens*) during passage through a vertical slot fishway located on the Richelieu River in Quebec, Canada, to determine passage success, passage duration and inter-individual differences in fishway use. Migratory lake sturgeon (n=107, range 939–1625 mm total length [TL]) were captured immediately downstream of the fishway, tagged with passive integrated transponder (PIT) tags and released into the fishway entrance basin over a period of two weeks (water temperature 11–20^{o}C). An array of 16 PIT antennas acted as gates to enable quantification of movements within the fishway. Volitional entry into the fishway occurred for most individuals (82.2%), 32 individuals successfully ascended the entire fishway and overall passage efficiency was 36.4%. Sturgeon exhibited an ability to traverse the fishway quickly (minimum duration of 1.2 hrs upon entry into the fishway), however, the duration of successful passage events was variable (6.2–75.4 hrs following release). Neither passage duration nor maximum distance of ascent was correlated with TL or water temperature. Passage behaviour was variable, in some cases resulting in

cumulative upstream movements three times in excess of fishway length. Passage durations through the two turning basins were disproportionately longer compared with other basins, however, the activity of individuals within these and other locations remain unknown and represent an important knowledge gap. Collectively, data from this study contributes to understanding how fishways can be used to facilitate the upstream passage of imperilled sturgeon at dams.

Introduction

The construction of dams on large rivers, primarily for hydropower and flood control, has resulted in fragmentation of riverine habitats throughout the world, with estimates in excess of 45 000 large dams (Nilsson et al. 2005). This disconnection has resulted in a loss of key migratory pathways for numerous fish species, often reflected by population declines (e.g. Sheer and Steel 2006) or genetic isolation (e.g. Jager et al. 2001). Artificial barriers to movement, therefore, are regarded as a threat to many fish populations worldwide (e.g. Rochard et al. 1990), with the construction and subsequent evaluation of fish passage facilities, collectively referred to as "fishways", representing a growing field of research (Katopodis 2005; Roscoe and Hinch 2010).

Despite this, fishways commonly prevent or delay passage for many species (Roscoe and Hinch 2010). In some instances, passage failure can result from poor attraction which can potentially be improved by altering attraction flows and/or modifying the entrance to the fish passage facility (e.g. Bunt 2001; Laine et al. 2002). In other cases, fish are able to locate a fishway, but are unable or unwilling to ascend the device (Katopodis 2005). Passage failure can be a result of inappropriate behavioural decisions (e.g. Hinch and Bratty 2000), physiological condition (e.g. Pon et al. 2009) or swimming capacity (e.g. Peake et al. 1997). In many cases the mechanistic causes of failure remain unknown.

Frequently, fishway design and operation targets just a few species and the needs of other species may not be met (Katopodis 2005; Mallen-Cooper and Brand 2007; Parsley et al. 2007). Unsuccessful fishway passage remains a particular concern for sturgeons, as passage is rare (Parsley et al. 2007) and limits population recovery for numerous species (Rochard et al. 1990). Sturgeons are long-lived organisms of the Acipenseridae family that comprise 27 living species spanning the temperate zones of Europe, Asia and North America (Bemis and Kynard 1997). Historically an important food source, exploitation and habitat modification have placed the majority of species under threat of extinction throughout their broad geographic range (Rochard et al. 1990; Birstein 1993). Sturgeons exhibit a variety of life history strategies throughout their distribution, with adults of some species remaining at sea for much of their life, whilst others are confined solely to freshwater (Rochard et al. 1990; Bemis and Kynard 1997). All species share a common strategy, migrating up predominantly large rivers to spawn (Bemis and Kynard 1997). Subsequently, barriers that block the passage of migratory pathways are recognised as a key threat to all sturgeon species and have been implicated in their global imperilment (Rochard et al. 1990). This is of particular concern because sturgeons represent one of the world's most threatened groups of animals, with 16 species currently listed as Critically Endangered and two species as Endangered (IUCN 2010).

Quantitative information on sturgeon use of fishways in the field is limited to a single peer-reviewed study (Parsley et al. 2007), with the majority of information derived from either laboratory simulations of fishways (Cheong et al. 2006; Webber et al. 2007) or extrapolated from swimming performance in a flume (Peake et al. 1997). While sturgeons have been documented entering fishways designed for other species, a large proportion of fish are either unwilling or unable to ascend, and thus, successful upstream passage is rarely documented (Parsely et al. 2007). Successful negotiation of simulated fishways in flumes by sturgeon suggests the number of attempts and passage speed increase with decreased turbulence and increased velocity, however, passage efficiency in flumes can still be relatively poor (Cheong et al. 2006). Further, sturgeon exhibit different behavioural responses during passage, bursting through high velocity areas and resting in low velocity areas (Webber et al. 2007), presumably in response to their quick fatigue times (Peake et al. 1997). Captive sturgeons also respond to high flows in flumes by stationing themselves on the benthos (e.g. Adams et al. 2003), a presumed energy conserving behaviour that has also been documented in the field in response to hydro peaking flows (Geist et al. 2005). As sturgeon swimming performance increases at higher water temperatures and for larger individuals, successful fishway passage by sturgeon is expected increase with larger size and higher water temperatures for a given combination of hydraulic conditions, assuming that swimming performance limits passage success (Peake et al. 1997). To date this has not been examined within fishways in a field setting, nor has any behavioural information including attempt rate or passage duration of upstream migrating sturgeon been quantified.

We used locally abundant lake sturgeon (*Acipenser fulvescens*) as a model species to identify the frequency of different behaviours exhibited during fishway ascension at a vertical slot fishway in Quebec, Canada. Nationally, the Committee on the Status of Endangered Wildlife in Canada has listed lake sturgeon populations as of special concern, threatened or endangered depending on the population (COSEWIC 2002). Given the annual spawning migrations of this species, a barrier-free 250–300 km combined river and lake range has been suggested as a minimum distance to support self-sustaining lake sturgeon populations (Auer 1996*a*). The installation of fishways is currently used as a remedial management tool when a barrier blocks access to upstream spawning locations and cannot be removed; however success is rarely known. For this study we aimed to compare passage duration and behavioural differences between successful and unsuccessful migrant lake sturgeon at a vertical slot fishway, and identify any areas of difficult passage. We tested multiple hypotheses, the first of which was that passage success and maximum upstream location are related to fish size and water temperature, predicting that both success and upstream location will increase in response to both variables as swimming performance is a function of both size and temperature. The second hypothesis was that successful and unsuccessful sturgeon would exhibit behavioural differences during fishway passage, predicting that passage failure would likely increase with an increasing number of attempts due to fatigue. The third hypothesis was that passage duration is not uniform throughout the fishway given the hydraulic differences among turning and regular basins, predicting that the slower water velocities in turning basins would increase passage duration as they provide both an opportunity for rest and reduced hydraulic cues. Data from this study have the potential to be used to enhance fish passage success for lake sturgeon and other con-familials throughout their range.

Methods

Study site

This study was conducted at the Vianney-Legendre Fishway, a vertical slot fishway located on the Richelieu River adjacent to the St. Ours dam in south western Quebec, Canada (Figure 3. 1). The Richelieu River originates in Vermont and New York, USA and, after exiting Lake Champlain, empties into the St. Lawrence River near the town of Sorel, Quebec, Canada. The river is 124 km long and its average annual discharge is 362 $m^3 s^{-1}$. The St. Ours dam is located 18 km upstream of the confluence between the Richelieu and St. Lawrence rivers and comprises a 180 m wide, 3.4 m high structure divided into a series of five submersible gates (each 30 m wide, plus the fishway). Its main function is to maintain a stable water level upstream for navigation purposes. The fishway was constructed on the West bank of the dam in 2001 to provide upstream access for key migratory species including lake sturgeon, copper redhorse (*Moxostoma hubbsi*), river redhorse (*M. carinatum*), American shad (*Alosa sapidissima*) and American eel (*Anguilla rostrata*). The total number of fish ascending the fishway is not known; however, monitoring since 2001 during May–June each year indicates the fishway passes more than 35 species of fish. Between 5 and 52 lake sturgeon use the fishway each year to access upstream spawning areas (P. Dumont, Unpublished data).

The fishway is an 85 m long concrete structure which rises 2.65 m and includes large entrance and exit basins on small slopes. The rest of fishway is divided into 12 uniform rectangular basins (3.5 × 3.0 m) connected by two resting/turning basins with horizontal floors and curved walls (2.75 m radius; Figure 3. 2). The uniform basins have successive floor drops of 0.15 m for a total rise of 2.4 m and are each separated by a 0.6 m wide vertical slot (2.3–4.0 m height range). This vertical slot width, $b_0 = 0.6$ m, and uniform basin size ($5.8b_0 \times 5b_0$) is smaller compared to standard designs of $10b_0$ length by $8b_0$ width (Rajaratnam et al. 1992) and results in a relatively larger velocity variation between the basins and a different velocity pattern inside each basin (*see* Liu et al. 2006). Originally rock and cobble substrate was placed throughout the bottom of the fishway. This substrate has since redistributed and has predominantly accumulated in the turning basins. Migrating fish are required to swim a minimum of 14.8 m through the entrance basin and an additional 70.5 m after encountering the first vertical slot in order to successfully pass. The fishway passes approximately 1 $m^3 s^{-1}$ of water, with a capacity for an additional 6.5 $m^3 s^{-1}$ attraction flow near the entrance basin via a pass through chamber beneath the fishway. However, attraction flow was not used in this study given that fish were introduced into the first basin and the focus of the study was not on attraction efficiency (the proportion of released individuals attracted to the fishway [Bunt et al. 1999]). An estimate of the velocity at the vertical slot can be made using a water surface drop being the same as the successive floor drop ($\Delta h = 0.15$ m), which results in a predicted velocity of $(2g \Delta h)^{1/2}$ or 1.72 m s^{-1}, where g is gravitational acceleration (9.81 m s^{-1}). During the study water velocity measurements were collected at 20, 60 and 80% of total depth at each vertical slot (Marsh-McBirney flow mate, model 2000, Frederick USA). Velocity approached predicted values at upstream locations (e.g. 1.65 ± 0.02 m s^{-1} averaged across all depths at the most upstream vertical slot; Figure 3. 2); however, velocity was considerably lower at extreme downstream locations (e.g. 1.11 ± 0.02 m s^{-1} averaged across all depths at the most downstream vertical slot; Figure 3. 2) due to elevated tailwater associated with blocking the fishway entrance (see *experimental design*). Overall average water velocity for all vertical slots and depths was 1.40 ± 0.01 m s^{-1}. We were unable to manipulate flows within the fishway due to its fixed slope. Attempts to vary vertical slot water velocities by manipulating the (upstream) exit gate height were limited due to the placement of an antenna at the exit gate; subsequently flow was not used as a covariate in any analysis.

Experimental design

A passive integrated transponder (PIT) array consisting of 16 antennas (beginning at antenna 16 downstream and ending at antenna 1 upstream [see Figure 3. 2]) was installed within the fishway during a dewatering period in early May. This method is suited for use within fishways as fish are required to swim through known locations, and has previously been used with high success (*see* Castro-Santos et al. 1996 for an overview). Complete pass-through antennas were attached to the upstream facing side of each vertical slot baffle (n = 15) and consisted of 12 gauge stranded electrical wire fixed in place at each corner to create a rectangular shape of 0.65 m width and varying height (2.2–3.2 m) depending upon vertical slot dimensions. An additional pass through antenna was installed on the upstream exit gate. A minimum distance of 5 cm was maintained between antennas and concrete walls/metal baffles to maximise detection efficiency. Each antenna was connected to a remote tuner box (Oregon RFID, Portland USA), each of which were connected in groups of four via twin-axial cable to a multiplexor unit (Oregon RFID). Antennas were manually tuned during operational water levels to maximise detection range (~0.5 m) and performance. Multiplexors were programmed to sequentially scan at high speed through all four antenna channels and upon positive detection store a unique tag identification number, antenna number and date and time stamp. Detection efficiency of individual antennas during the study was 86.2 ± 2.4% (range 68.8–97.5%) and was calculated as the number of antennas individuals were known to have encountered compared with the number of antennas on which individuals were detected (Castro-Santos et al. 1996).

Lake sturgeon (n = 107, mean ± SE total length (TL) and weight: 1213 ± 14 mm and 10.4 ± 0.4 kg, respectively) were captured (11–25 May 2010) in the first 700 m downstream of the fishway using 20.3, 25.4 and 30.5 cm (stretched mesh) gillnets, which were checked twice daily at 09:00 and 15:00 hrs. The same method is used by government agencies during the spring period for routine lake sturgeon monitoring and the fish are robust to the stress associated with capture (Baker et al. 2008). Captured sturgeon were immediately transferred to on-site holding facilities and measured, weighed and tagged with a uniquely coded PIT tag (32 × 3.85 mm HDX, Texas Instruments, Dallas USA) which was intra-muscularly implanted into the abdominal wall. Tags were inserted using a 6 gauge needle and surgical wounds were sealed with cyanoacrylate. The entire handling process took less than 2 min and care was taken to minimise air exposure. Anaesthetics were not used. We also attempted to assign sex to each individual based on the expulsion of gametes; however, we were only successful in determining the sex of 28 individuals comprising 27 males and one female all of which were in pre-spawn condition.

Sturgeon were held indoors immediately adjacent to the fishway in 2250 L flow through hatchery tanks (with water pumped directly from the river replaced at a rate of c. 50 L min^{-1}) at a density of no more than 20 kg per 1000 L^{-1} for 1–3 days prior to release. There was no mortality associated with capture, handling or holding and fish were not fed during holding. Sturgeon were released (13–26 May 2010, 12:00–19:00 hrs) in five groups (Trial 1–5; Table 3. 1) into the entrance basin of the fishway to minimise holding times and to provide potential for passage over a range of water temperatures. There was no significant difference detected in TL among release groups (one way ANOVA: $F_{4, 102} = 0.854$, $p = 0.494$). Prior to release, a block net was added to the entrance (downstream) gate to ensure fishway exit only occurred upon successful passage. Sturgeon were allowed 40–86 hrs to volitionally enter and pass the fishway, after which the entrance gate was lowered and the remaining sturgeon were flushed from the fishway through a slow dewatering process. One trial was shortened (40 hrs) due to an operational problem with the fishway. Water quality values were recorded daily during the study (YSI model 556 water quality meter, Yellow Springs, Ohio, USA) and were: conductivity 135.33 ± 1.98 µS cm^{-1}, pH 6.69 ± 0.11 and dissolved oxygen 10.78 ± 0.33 mg L^{-1}. In addition, hourly water temperature was recorded in the fishway at the downstream entrance basin at 1 m depth (DS1921Z iButton, Maxim integrated products, Sunnyvale, USA).

Data analysis

Antenna locations were converted to distance metrics beginning at the first antenna (antenna 16, 0 m) and ending at the fishway exit (antenna 1, 70.5 m), enabling calculation of minimum distances moved throughout the fishway for each sturgeon, as well as the maximum upstream distance of ascent. As only 16 fish (of the 107) were detected by the most downstream antenna and could not be confirmed to have actually entered the fishway (a minimum of two antennas are required to determine direction), and three fish (of the 107) were not detected by any antennas, all subsequent analyses were conducted on the remaining 88 sturgeon. Sturgeon movements through the fishway were reconstructed over time and individuals were grouped into behavioural categories based on evidence of single or multiple attempts at passage. A passage attempt was defined as any movement into the fishway (to at least the second antenna [antenna 15] encountered) and terminated upon either successful passage or return to the downstream staging area.

Passage efficiency was calculated as the proportion of successful fishway passage events compared to the number of fish attempting to pass, both for each trial and overall. Size (TL) was compared across the whole sample, between successful and unsuccessful individuals, using an independent samples t-test. Log-rank survival analysis was used to test whether the maximum distance of ascent achieved by individuals differed between trials, given data censoring precludes ordinary least squares techniques (Hosmer and Lemeshow 1999), and was then plotted for the entire study using a Kaplan-Meier survival estimate. Pearson product moment correlations (or non-parametric Spearman rank equivalents) were used to determine relationships between either water temperature or TL and passage speed and maximum upstream distance. Mean water temperature for each trial was used in the analysis given that within trial variation was minimal (Table 3. 1). Lag was determined as the time elapsed from release until first entrance into the fishway. A Wilcoxon rank sum test was used to determine whether fish entering the fishway earlier (shorter lag) were more likely to succeed and a Spearman rank correlation was used to determine the relationship between lag and maximum distance of ascent. All statistical analyses were deemed significant at $p < 0.05$ and conducted using JMP statistical software (version 8.0, SAS Institute, Cary, North Carolina, USA). All data were first examined for normality and/or homogeneity of variance where appropriate, transformed (log) and reassessed if it did not meet these assumptions, and analysed using non-parametric equivalents where necessary. All data is presented as means ± SE, unless otherwise stated.

Results

Attempts to pass the fishway were made by 82.2% (88 of 107) of sturgeon in this study. The remaining individuals either made no attempt to enter the fishway (2.8%, n = 3) or were only recorded on the most downstream antenna (15%, n = 16). Given the detection range (~0.5 m) of the equipment used, we were unable to distinguish between fish entering the fishway and those simply probing the entrance (in some cases on multiple occasions). Successful fishway ascension occurred for 29.9% (n = 32) of sturgeon released into the fishway and overall passage efficiency (the proportion of sturgeon entering the fishway [n = 88] compared to the proportion succeeding [n = 32]) was 36.4% (range 27.3–47.4% among trials; Table 3. 1). We found no difference between TL of sturgeon successfully passing the fishway (1232 ± 25 mm; n = 32) and those entering but failing to pass (1203 ± 19 mm; n = 56; independent samples t-test, t = 0.921, $p = 0.360$). There was also no difference between TL of sturgeon failing to enter the fishway (1209 ± 34 mm; n=19) and those successfully passing (independent samples t-test, t = -0.547, $p = 0.587$).

Passage behaviours exhibited by sturgeon were broadly grouped into single attempts (represented by both failure [Figure 3. 3a] and success [Figure 3. 3c]) and multiple attempts (represented by both failure [Figure 3. 3b] and success [Figure 3. 3d]). Sturgeon exhibiting a single attempt and failing characteristically moved short distances upstream (cumulative upstream distance, 14.3 ± 4.3 m) in comparison to multiple attempt failures (70.1 ± 7.4 m; Table 3. 2). Sturgeon requiring multiple attempts to pass the fishway before succeeding swam an average of 49.1 m farther upstream (136.1 ± 12.9 m) in comparison to individuals which passed the fishway on their first attempt (87.0 ± 4.8 m; Table 3. 2). The maximum upstream location of the fishway reached by sturgeon did not differ between trials (Log-Rank survival analysis: $\chi^2 = 1.119$, df = 4, $p = 0.891$), nor was it correlated with TL (Spearman correlation: $r_s = 0.059$, $p = 0.588$) or water temperature (Spearman correlation: $r_s = -0.052$, $p = 0.632$). Passage failure was most likely to occur in the downstream half of the fishway (52.3%), with failure uncommon (11.4%) beyond this point (Figure 3. 3). Fourteen individuals (15.9%) reached, but failed to pass the first turning basin (11.7 m into the fishway; Figure 3. 4), representing the location with the single greatest loss.

Although fishway passage occurred all day long, it was primarily undertaken during crepuscular or nocturnal periods (Figure 3. 5). Successful individuals required between 6.19 and 75.38 hrs (median 27.38 hrs) to pass the fishway following release. Upon initiation of a successful attempt, passage duration ranged between 1.16 and 30.75 hrs (median 3.17 hrs). Passage duration (log transformed) was not significantly correlated with TL, either from release (Pearson product moment correlation: $r_p = -0.266$, $p = 0.228$) or from initiation of a successful attempt (Pearson product moment correlation: $r_p = -0.059$, $p = 0.798$). Passage duration was not significantly correlated with water temperature, either from release (Spearman correlation: $r_s = -0.388$, $p = 0.074$) or from initiation of a successful attempt (Spearman correlation: $r_s = 0.160$, $p = 0.489$). No motivational differences were evident between successful and unsuccessful passage events. Time from release until first entrance into the fishway (lag) ranged from 0.03–30.28 hrs (median 2.66 hrs) and was not significantly different between successful or unsuccessful individuals (Wilcoxon Rank Sum test: $z = -0.358$, $p = 0.721$) or correlated with maximum distance of ascent (Spearman correlation: $r_s = -0.094$, $p = 0.547$).

Passage duration through different basins within the fishway was not uniform. Sturgeon took longer to pass through turning basins (13–12 and 8–7) than through other basins during both unsuccessful (Figure 3. 6a) and successful passage events (Figure 3. 6b). In addition, sturgeon took longer to pass from basin 2–1 (last vertical slot to the exit; Figure 3. 2) in comparison to other basins (turning basins notwithstanding; Figure 3. 6b) during successful passage; however it should be noted that this distance is three times greater than turning basins and 3.6 times greater than through remaining basins.

Discussion

Globally, sturgeon passage through fishways is poorly understood, despite acknowledgement that barriers to migration are a concern for all species (e.g. Rochard et al. 1990). In this study, we documented a passage efficiency of lake sturgeon in the Vianney-Legendre fishway of 36.4%. This is comparable with the only other passage efficiency estimate that we located in a peer reviewed study. Parsley et al. (2007) reported a passage estimate of 41.2% (seven of 17 sturgeon that entered the fishway, passed) for white sturgeon (*Acipenser transmontanus*) at two fishways on The Dalles Dam on the Columbia River which were designed for Pacific salmon. Parsley's et al. (2007) study more likely represents a true estimate of fishway success given sturgeon were attracted to and volitionally entered fishways over a two year period. In our study fish were captured downstream and introduced into the fishway to enable an experimental evaluation of passage success. Capture stress and potential differences in motivation could have led to low passage success while confining fish to the fishway could have led to elevated success. Direct comparisons are also cautioned, given that the fishways on

The Dalles Dam are >500 m in length and are pool and weir type with submerged orifices, as opposed to the 70 m long, vertical slot fishway used in the current study. Given greater fishway length, a similar study design and fishway conditions, we would expect passage efficiency may be significantly lower than the estimate generated using this experimental approach.

The current study design enabled identification of finer scale passage behaviour than previously reported in most fishway studies. Specifically, we identified that passage failure most commonly occurred in the lower (downstream) portion of the fishway and also that the first turning basin presented an obstacle to passage for 14 of the 88 sturgeon that entered the fishway. The usefulness of turning or resting pools in fishways have been questioned for other species (e.g. walleye *Sander vitreus*, Bunt et al. 2000; bony herring *Nematalosa erebi*, silver perch *Bidyanus bidyanus* and golden perch *Macquaria ambigua*, White et al. 2011). Turning basins were incorporated into the Vianney-Legendre fishway to create a more compact design, enabling the fishway entrance to be located near to the barrier in a site where surveys prior to the fishway design indicated higher fish densities. Despite a number of studies examining white sturgeon negotiation of obstacles in flumes (Cheong et al. 2006; Webber et al. 2007), no information currently exists with which to compare these findings.

Successful and unsuccessful attempts by sturgeon were delayed through turns during fishway passage. Given the first turning basin is encountered 11.7 m into the fishway, the second 20.3 m after the first and a mean water velocity (through vertical slots) of 1.4 m s^{-1}, it is reasonable to conclude that turning basins are used for resting, particularly given that Peake et al. (1997) estimated that a comparable length of fishway is passable by 120 cm lake sturgeon at 1.4 m s^{-1} prior to fatigue. Indeed, Webber et al. (2007) recommend provision of low velocity (0.51–0.68 m s^{-1}) resting areas be incorporated into fishways designed for sturgeon, given white sturgeon used these to recover following bursts through high velocity (up to 2.52 m s^{-1}) regions in a flume. A trade-off exists, however, in the provision of low velocity refuges in fishways. For example, both Cheong et al. (2006) and Webber et al. (2007) found white sturgeon more likely to attempt upstream passage when exposed to faster flume velocities. It may be that the creation of flow refuges in turning basins deters fishway passage by some sturgeon due to a lack of motivational cues. Flow refuging and presumably energy conservation is achievable by sturgeon in high velocity areas through benthic station holding (e.g. Adams et al. 2003; Geist et al. 2005) and so resting pools may not be a necessary provision in sturgeon fishways.

Lake sturgeon often moved greater cumulative upstream distances than the length of the fishway in the current study, primarily due to multiple attempts at passage resulting in both success and failure. Multiple attempts have also been observed for numerous other species during passage ascension (e.g. Bunt et al. 1999; Castro-Santos 2004), suggesting this behaviour should be considered when matching fishway design with laboratory swimming capacity (e.g. Peake et al. 1997). However, in some instances swimming performance estimates (e.g. critical swim speed) can have no direct relevance beyond the laboratory (Beamish 1978). For example, Peake (2004) found laboratory swimming performance a poor indicator of successful passage in smallmouth bass (*Micropterus dolomieu*), as field success was high among all water velocities tested and independent of fish length and water temperature. Similarly, we found no relationship between water temperature or fish length and passage speed, passage success or maximum upstream distance, despite previous work identifying that both of these are important factors influencing lake sturgeon swimming performance in the laboratory (Peake et al. 1997). It may be that for fish to be successful during passage events and maximise their potential, behavioural choices resulting in a switch to the optimal gait when faced with variable hydraulic conditions are required (Castro-Santos 2005). However, Castro-Santos (2005) identified that only three of six species studied (note – sturgeon were not studied) used an optimal swim mode when traversing a velocity barrier, with the behavioural choices of others resulting in a failure to maximise distance ascended.

Navigational choices that affect time to exhaustion may also explain the inter-individual variation in successful fishway passage exhibited by sturgeon in the current study. For example, Hinch and Bratty (2000) found some sockeye salmon (*Oncorhynchus nerka*) exhibited hyperactivity which resulted in passage failure while others probably chose a less difficult route, resulting in reduced energy expenditure and ultimately successful passage. Certainly swimming in higher turbulence, but at the same velocity, can be more energetically costly and subsequently decrease endurance (Enders et al. 2005). However a trade-off can occur, where the more turbulent environment may also represent the shortest route, thus minimising migration time when chosen (e.g. Standen et al. 2002). Spatial variation in water velocity, resulting in multiple paths of differing hydraulic conditions being available for fish to move through, certainly exists within vertical slot fishways. For example Wu et al. (1999) observed that in vertical slot fishways, even for fishways with slopes of 5% or less when flow patterns are relatively simpler than steeper slopes, the direction and magnitude of water velocity within basins are spatially variable. Path selection as it relates to hydraulic conditions within fishways (i.e. turbulent kinetic energy, Reynold's shear stress; Silva et al. 2011) represents a logical next step to identify favourable hydraulic conditions conducive to sturgeon passage. Further, activity levels of sturgeon during fishway ascension were not assessed in the current study. Use of techniques including acceleration sensors on biologging or biotelemetry devices or visualization using video or acoustic cameras represent an important next step in identification of activity (and subsequent energy use) at different locations within fishways and may distinguish successful and unsuccessful individuals. Such an approach would also enable one to generate more direct relationships between fine-scale hydraulic conditions and fish behaviour.

Endogenous factors relating to differences in energy stores, stress or motivation (i.e. endocrine/maturation state) also represent potential explanations for inter-individual variability in passage success, although these factors were not tested in the current study. Stress is unlikely to explain individual differences in behaviour given that all sturgeon were subjected to the same treatment, and previous work by Baker et al. (2008) indicates that both the holding duration (1–3 days) and time allowed for fishway ascension (2–3 days) are sufficient to allow for recovery from any adverse responses to either handling, capture or tagging techniques for this species at comparable water temperatures. Gross somatic energy density has previously been found to correlate with maximum distance travelled during upstream migrations of Chinook salmon (*Oncorhynchus tshawytscha*) (Hasler et al. 2009), although its use to differentiate fishway passage success remains untested. It is possible that motivational differences may explain variation in fishway success among sturgeon and the measurement of sex steroid levels (e.g. McKinley et al. 1998) to assess this represents a logical next step. Interestingly, Kynard et al. (in press) used odour of pre-spawning females in an attempt to encourage passage through a flume from reluctant male shortnose sturgeons (*Acipenser brevirostrum*), although no measureable effect on passage success was observed.

Restoring connectivity of riverine systems that have been fragmented by dams is a critical step towards rebuilding sturgeon populations and preventing extinction (Auer 1996*a*; Jager 2006). Although fishways are regarded as a potential strategy for mitigating the installation of barriers, a range of studies have documented that their efficiency can be highly variable (Roscoe and Hinch 2010). Given that adult sturgeon tend to migrate upstream to spawn, and that there are few examples of successful fishways for sturgeon, we focused our efforts on a promising vertical slot fishway in Quebec. Using an experimental approach where adult lake sturgeon were released into the bottom pool of the fishway, we were able to generate an estimate of passage success as well as to identify detailed behaviours within the fishway. Of particular concern was the fact that we identified that sturgeon had difficulties passing through turning basins. Such knowledge will be useful in identifying potential means of improving passage of sturgeon in existing and future fishways. If sturgeon populations in rivers with migration barriers are to recover, provisions for effective fish passage are critical. Additional work is needed to identify the biotic, environmental and hydraulic characteristics that influence both attraction and passage efficiency for sturgeon as well as other riverine fish species that are susceptible to habitat fragmentation by dams.

Tables

Table 3.1 Summary information for PIT tagged lake sturgeon released into the Vianney-Legendre vertical slot fishway. TL: total length

Trial	Date	n	TL (mm)	Water temperature (^{o}C)	Trial duration (hrs)	Number successfully passed	Passage efficiency (%)
1	13–16 May 2010	22	1033–1505	11.9 ± 0.3	72	4	36.4
2	16–18 May 2010	34	984–1558	12.2 ± 0.1	40	11	36.7
3	19–22 May 2010	21	990–1625	14.5 ± 0.1	72	9	47.4
4	22–26 May 2010	19	939–1375	17.1 ± 0.1	86	5	29.4
5	26–29 May 2010	11	982–1445	19.8 ± 0.0	72	3	27.3

Table 3.2 Behavioural characteristics exhibited by lake sturgeon during upstream passage through a vertical slot fishway.

	Cumulative upstream distance moved (m)					
	No attempt	**Probe**	**Unsuccessful Passage**		**Successful passage**	
			Single attempt	**Multiple attempts**	**Single attempt**	**Multiple attempts**
Mean			14.3	70.1	87.0	136.1
SE			4.3	7.4	4.8	12.9
Range			3.9–43.7	11.7–194.3	70.5–139.2	74.4–222.7
n	3	16	10	46	16	16

Figures

Figure 3.1 Location of the Vianney-Legendre vertical slot fishway on the Richelieu River, Quebec.

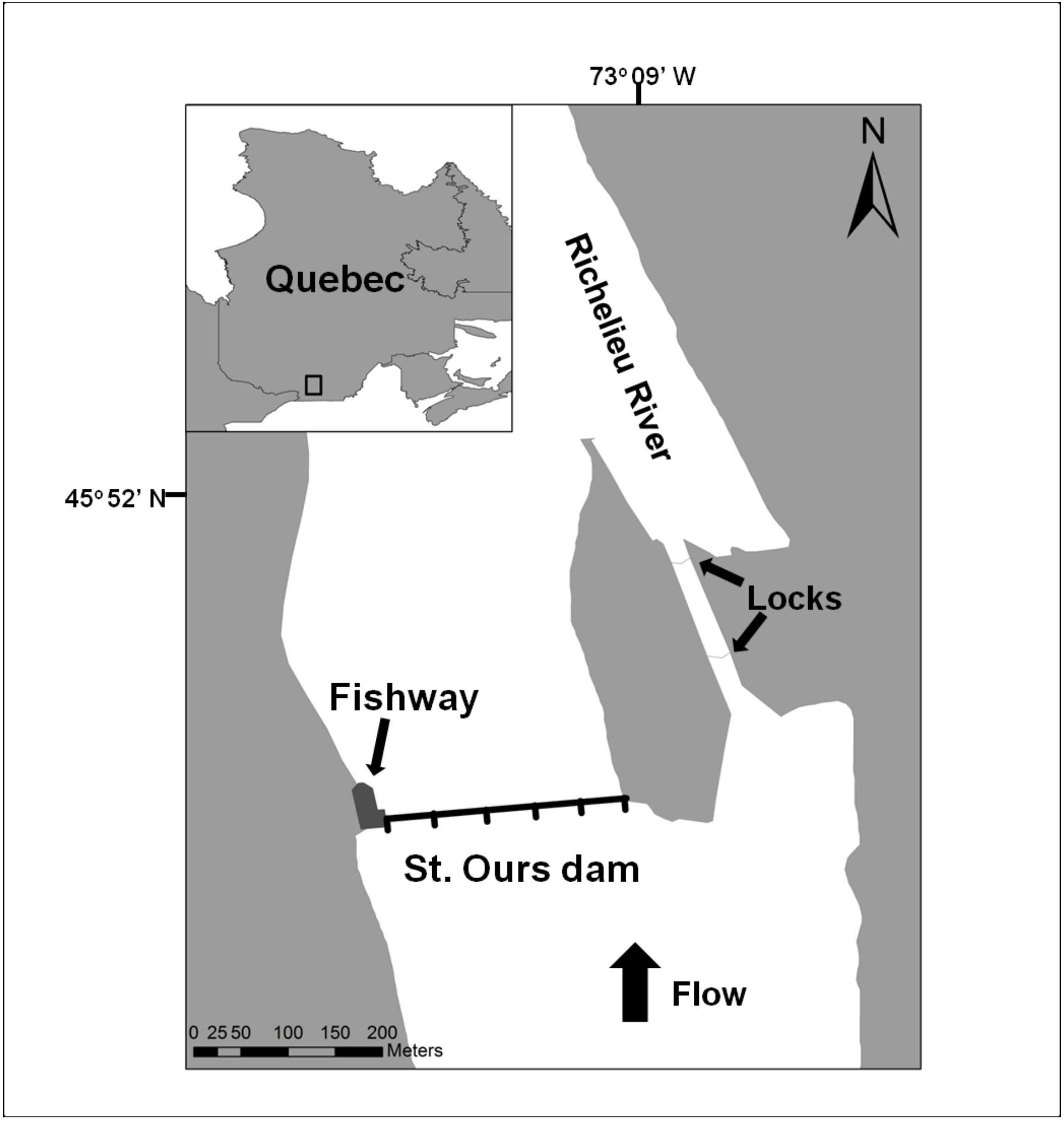


Figure 3.2 Schematic of the Vianney-Legendre fishway, with numbers indicating PIT antenna locations used to determine sturgeon movement, behaviour and passage success.

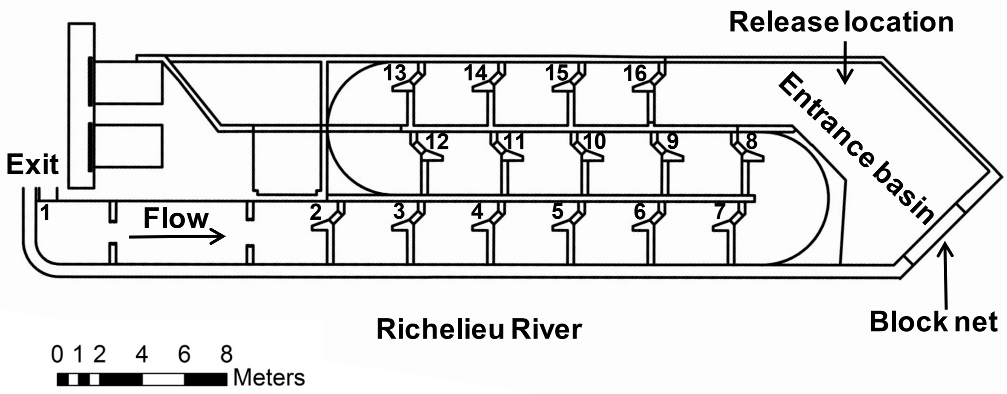


Figure 3.3 Examples of individual movements exhibited by lake sturgeon during passage through a vertical slot fishway representing: a) a single attempt and failure (1207 mm TL, 12.2°C), b) multiple attempts and failure (1218 mm TL, 19.8°C), c) a single attempt and pass (1266 mm TL, 19.8°C) and, d) multiple attempts and pass (1312 mm TL, 19.8°C). Entrance into the fishway occurs at distance 0 m and fishway exit occurs at distance 70.5 m. Note different x-axis scales.

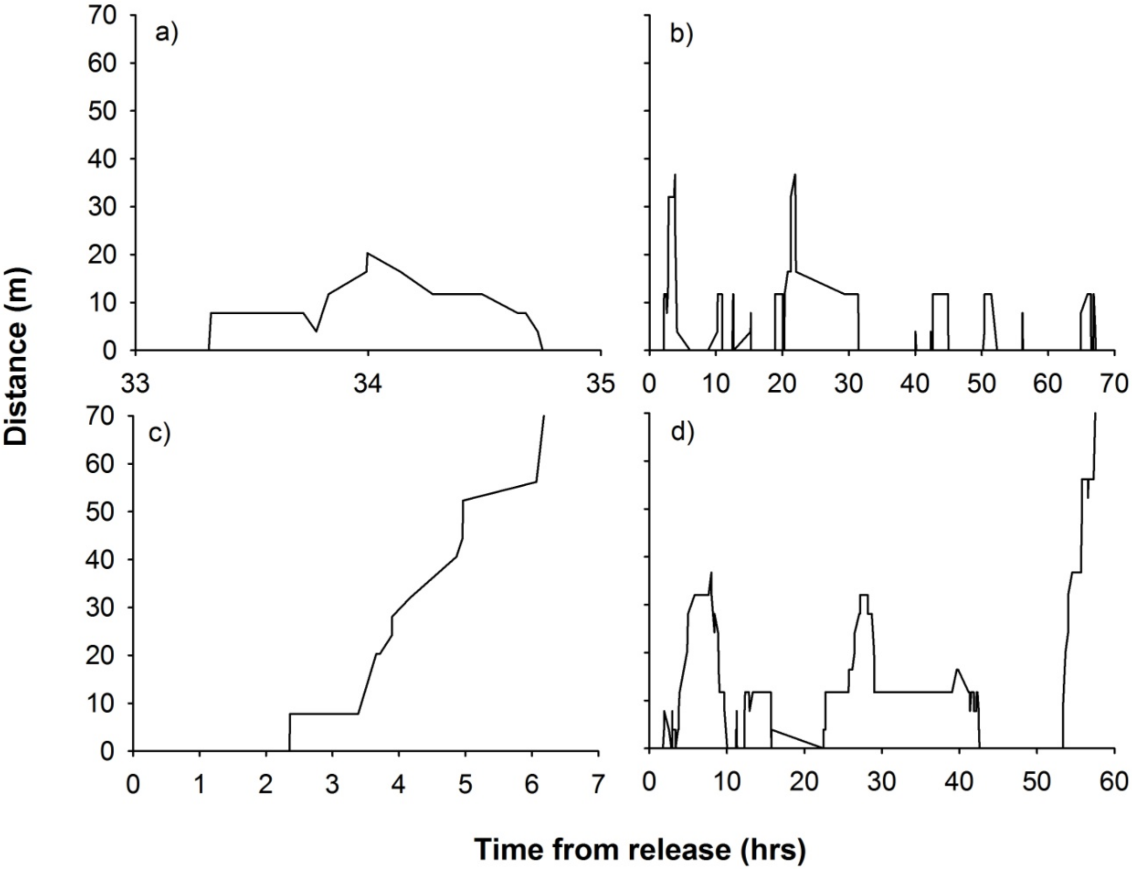


Figure 3.4 Maximum upstream distance achieved by lake sturgeon attempting to pass the Vianney-Legendre vertical slot fishway determined using Kaplan-Meier survival analysis (n = 88).

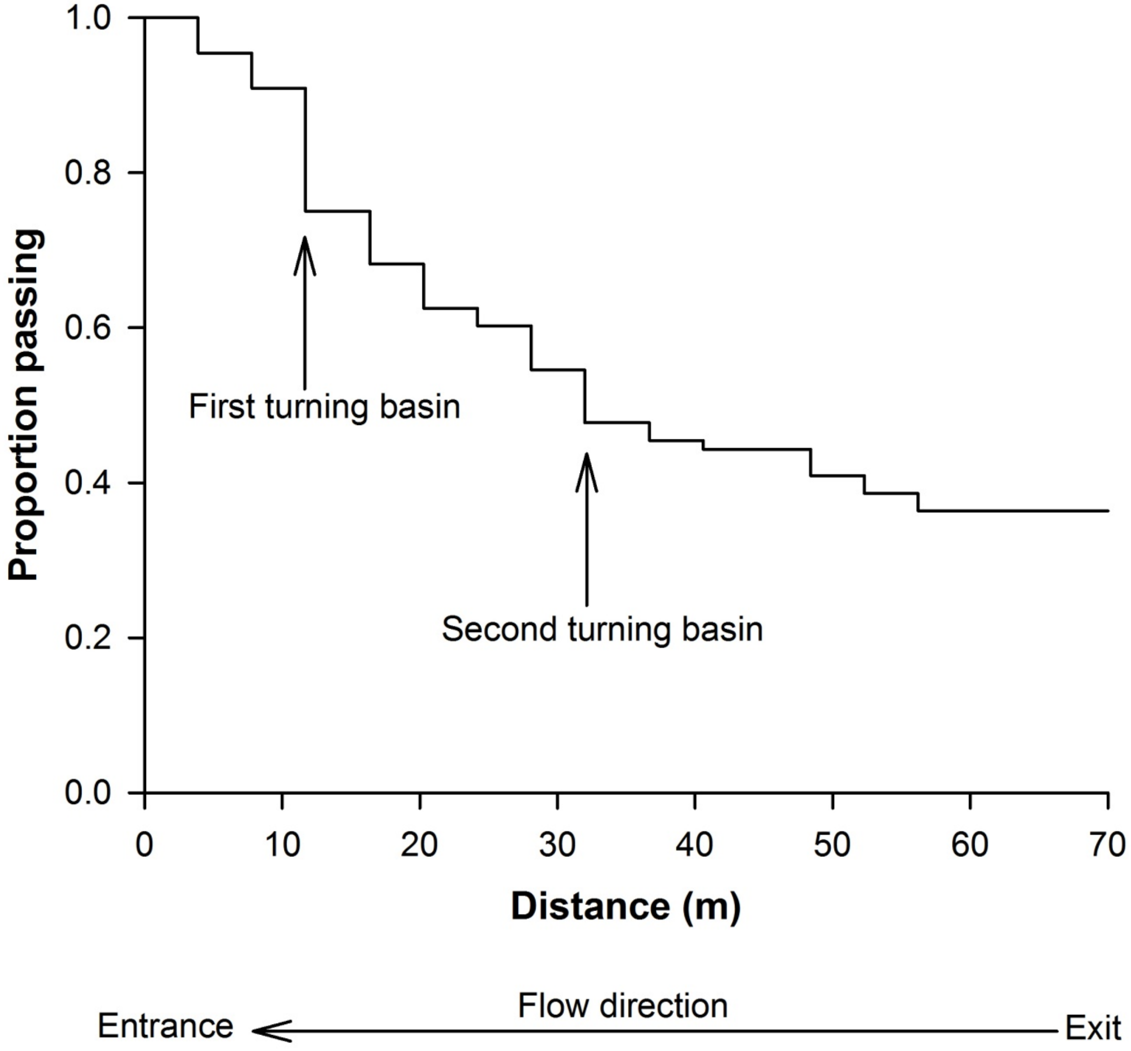


Figure 3.5 Frequency of PIT records differentiated by time of day from tagged lake sturgeon using the Vianney-Legendre vertical slot fishway. Grey bars indicate night periods based on local sunrise and sunset times.

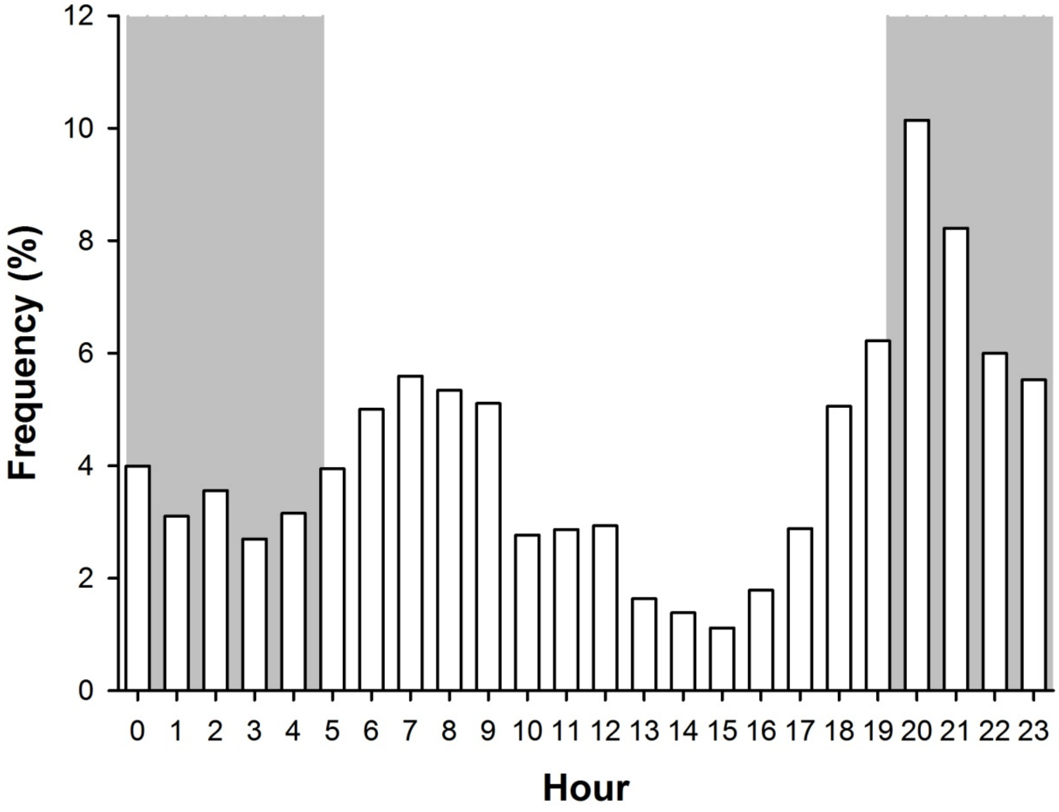
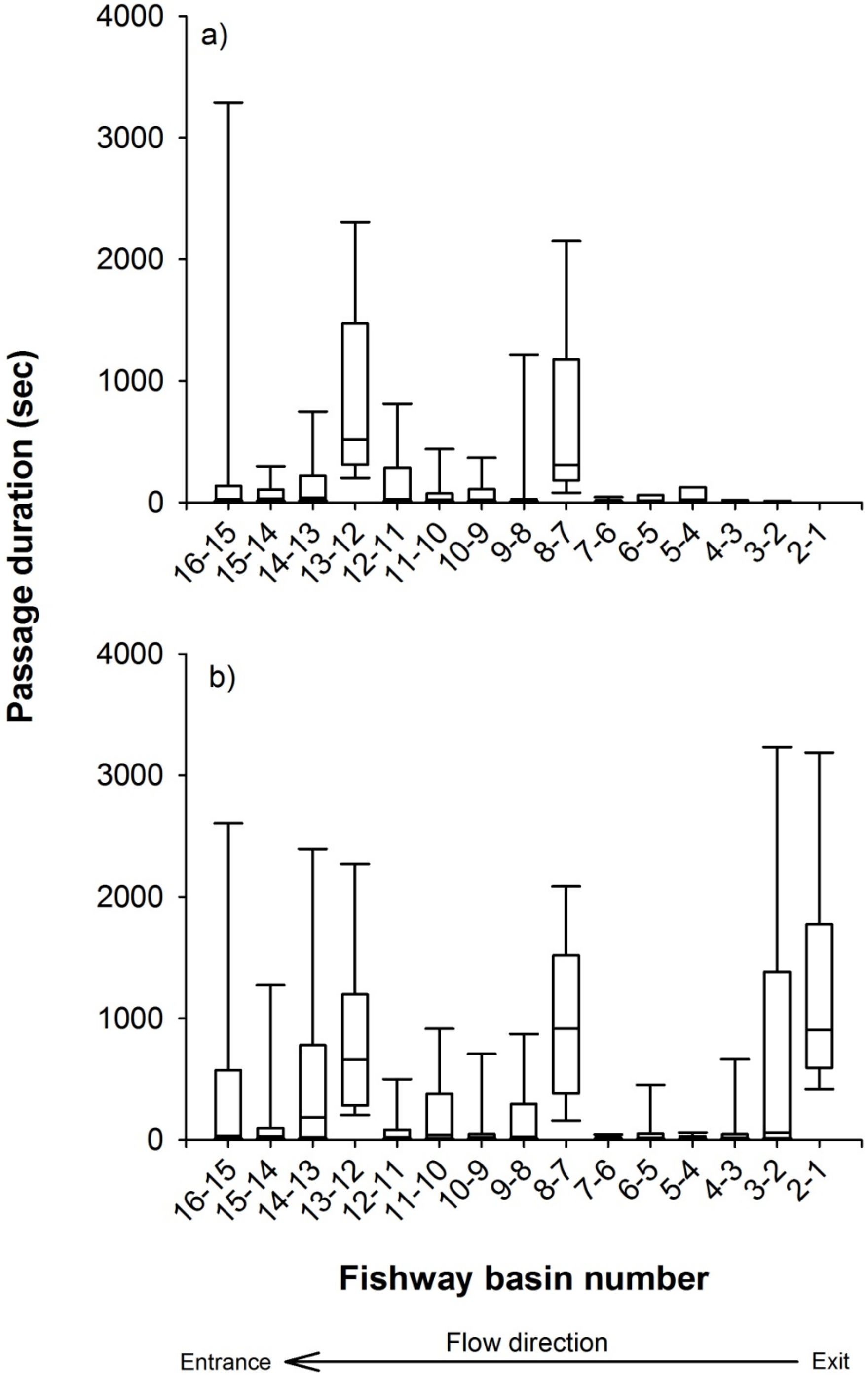


Figure 3.6 Duration of passage through different locations during upstream movement by lake sturgeon through a vertical slot fishway for: a) unsuccessful individuals (n = 56) and, b) successful individuals (n = 32). Boxes represent 25th and 75th percentiles with the median enclosed within, and whiskers represent 10th and 90th percentiles. Numbers on the x-axis refer to passage duration between consecutive antenna locations (see Figure 3. 2). Note 13–12 and 8–7 are turning basins and the distance from 2–1 (14.25 m) is much greater than between regular basins (3.9 m).



Chapter 4. Accelerometer-derived activity correlates with volitional swimming speed in lake sturgeon

Abstract

Quantifying fine-scale locomotor behaviour and estimating energy costs associated with different activities is challenging for free-swimming fish. Biologging and biotelemetry tools can help address this problem. We used an open channel flume to generate volitional swimming speed (U_s) estimates of cultured lake sturgeon (*Acipenser fulvescens*) and paired the estimates with simultaneously recorded accelerometer-derived metrics of activity obtained from three types of data storage tags attached to individual fish. We tested whether activity metrics (tailbeat frequency (TBF), tailbeat acceleration amplitude (TBAA) and overall dynamic body acceleration (ODBA)) were indicative of total swimming effort, and thus accurately measure the rate of work. Volitional U_s of sturgeon ranged from 0.48–2.70 m s^{-1} or 0.51–3.18 body lengths s^{-1}. Models including U_s and sturgeon total length best described TBF ($R^2 = 0.96$). The relationship between TBAA and U_s was best described through the inclusion of tag type (n=3 tag types, $R^2 = 0.87$), and ODBA was best described by U_s and the inclusion of tag type ($R^2 = 0.92$). All accelerometer-derived metrics of activity increased linearly with U_s, with TBF increasing 2.30 Hz for every 1 m s^{-1} increase in U_s and TBAA and ODBA increasing 0.98 *g* and 1.68 *g* for every 1 m s^{-1} increase in U_s, respectively. These results demonstrate that data storage tags provide an indirect measure of energy expenditure in free-swimming sturgeon.

Introduction

Allocation of an organism's time and energy to different behaviours can influence survival and fitness, and ultimately influence population dynamics (Morales et al. 2010). As such, the rate at which animals expend energy is a key component to understanding how they interact with their surrounding environment. Activity, primarily derived through locomotion, represents the principal energy cost in addition to basic metabolism, with field metabolic rates typically three times that of basic metabolism (Alexander 1999). Biotelemetry and biologging tools show promise for the field measurement of key variables including activity and specific energy metabolism in aquatic animals (Cooke et al. 2004; Castro-Santos and Haro 2006), but can often be inaccurate, imprecise, or unreliable (Geist et al. 2002; Enders et al. 2008). Accelerometers, which provide a measure of individual locomotory activity, are increasingly being used in aquatic environments (e.g. using telemetry; Lowe et al. 1998; O'Toole et al. 2010; Murchie et al. 2011; and biologgers; Watanabe et al. 2012; Brownscombe et al. 2013). Laboratory calibrations indicate strong correlations between accelerometer-derived metrics of activity and both swimming speed (U_S) and oxygen consumption (MO_2) for a range of aquatic taxa (e.g. elasmobranchs: Gleiss et al. 2010; cephalopods: Payne et al. 2011; fish: Clark et al. 2010; Wilson et al. 2013). When paired with field deployments, these calibrations have also enabled quantification of energy use in the wild for the same range of taxa (Payne et al. 2011; Semmens et al. 2013; Wilson et al. 2013).

Interest in the comparative swimming ability of aquatic taxa, in terms of energetics, speed, and endurance, has resulted in the widespread use of swim tunnels where individuals are forced to swim against known water velocities to maintain position (Beamish 1978; Hammer 1995). Swim tunnels are also used in the calibration of accelerometer data with U_s and/or MO_2. However, practical limitations exist based on the size of study animals and corresponding test facilities. For example, Lowe (1996) demonstrated reduced tailbeat amplitude (TBA), and corresponding stride length, associated with the restricted swimming of scalloped hammerhead sharks (*Sphyrna lewini*) in a swim tunnel in comparison to free-swimming. In a later study on the same species, Gleiss et al. (2010) demonstrated that the biologged acceleration values from exercised sharks in a swim tunnel did not adequately represent the range of speeds (and corresponding acceleration values) observed in free-swimming individuals. Swim tunnel experiments are typically restricted to smaller species or juveniles in large animals, and it is sometimes necessary to conduct *in situ* calibrations in the field for larger animals and/or borrow established relationships from other species (e.g. Semmens et al. 2013). There is also increasing evidence that the relationships developed from forced swimming experiments may not be directly transferable to free-swimming animals. For example, Peake (2004) identified that swimming performance measures from a swim tunnel were a poor predictor of passage ascent when smallmouth bass (*Micropterus dolomieu*) were faced with a velocity challenge, and advised caution in transferring laboratory data to field applications. The use of open channel flumes, of an appropriate size so as not to restrict TBA and that rely on volitional U_s and behaviours hold promise for the determination of more field relevant U_s and corresponding acceleration-derived metrics (e.g. Castro-Santos 2005; Castro-Santos et al. 2013).

Sturgeon are long-lived organisms of the Acipenseridae family that occur in large rivers spanning the temperate zones of Asia, Europe and North America, and often represent the largest animals in a freshwater fauna (Bemis and Kynard 1997). They represent an evolutionally basal group of fishes—presence of fused fin rays means they have limited ability to manipulate their fins, and locomotion is primarily driven by body undulations and associated movements of median and paired fins (Breder 1926; Wilga and Lauder 1999; Liao and Lauder 2000). Sturgeon exhibit a number of morphological limitations including a comparatively high drag resulting from body form and external scutes, as well as low thrust resulting from their heterocercal tail (Webb 1986). Combined with a relatively limited capacity for high speed swimming resulting from a poor aerobic capacity (Peake et al. 1997), these factors collectively contribute to the reduced swimming capacity of sturgeon in comparison with similarly sized salmonids. These and other observations have led to the widespread perception of sturgeon as relatively poor swimmers. However sturgeon often spawn in the moderate to high velocity regions of large rivers (e.g. Chapter 2) preceded in many cases by large-scale migrations (Auer 1996*a*) that may sometimes include passage through natural rapids (e.g. Welsh and McLeod 2010). Laboratory studies indicate that sturgeon are capable of short periods of energetically demanding burst swimming when traversing high velocity regions, followed by utilisation of low velocity regions for recovery (Webber et al. 2007; Cocherell et al. 2011). In some instances benthic station holding is used in high velocity regions as an energy conservation strategy (e.g. Adams et al. 2003; Geist et al. 2005). Alternatively, individuals may actively seek a path of least resistance (e.g. McElroy et al. 2012). In either case, some measure of the rate of work is required via the monitoring of individual activity to estimate and better understand energy expenditure and its role in limiting movement and distribution.

Before using accelerometers to determine the rate at which animals expend energy, it is necessary to validate relationships on a species-specific basis. Doing so enables researchers to apply such devices to free-ranging animals to quantify behaviour and estimate energy expenditure in the field. The objectives of this study were to measure a range of sturgeon U_s and to determine whether accelerometer-derived metrics (tailbeat frequency (TBF), tailbeat acceleration amplitude (TBAA) and overall dynamic body acceleration (ODBA)) accurately measure the rate of work (U_s), and thus energy expenditure. Volitional swimming was used as it more likely represents the range of U_s attained by free-swimming animals. We used a widely distributed North American sturgeon species, lake sturgeon (*Acipenser fulvescens*). This species is of particular interest given its local abundance, existing literature regarding swimming performance and associated MO_2, and the postulation that the poor swimming capacity of sturgeon in general elicits a variety of behavioural responses to high velocities including short bursts of high U_s and/or benthic station holding.

Methods

Trial protocol

An open channel outdoor flume was used to develop relationships between volitional U_s and accelerometer-derived activity metrics in lake sturgeon. The flume was located at the U. S. Geological Survey S. O. Conte Anadromous Fish Research Laboratory fish passage complex, Turners Falls, Massachusetts and was 1 m wide × 1 m deep × 20 m in length with zero slope. The apparatus was the same as that described by Castro-Santos et al. (2013). Ambient river water was supplied to the flume from an adjacent hydroelectric power canal fed by the Connecticut River. Water entered the flume through a 76.2 cm diameter pipe, regulated with a 61.0 cm butterfly valve, into a head tank control structure. Water from the head tank entered the test flume and flow was regulated with a submerged vertical lift gate. Water exited the flume into a large, low velocity downstream staging area (3.6 m long × 4.9 m wide × 1.45 m deep) mounted off-center from the flume channel, and with a floor 12 cm below the floor of the flume. Water was discharged from this staging area via three outlets, and the water depth in the staging area was regulated using stoplogs (wooden boards positioned in slots at each outlet). Depth and velocity of flow within the flume were regulated using a combination of valve opening, head tank depth, head gate height, and staging area depth. Screens were placed just upstream of the stoplogs. This arrangement kept fish from being swept downstream and helped to prevent them from becoming impinged on screens by distributing discharge over the full depth of the staging area.

Two trials consisting of a slow, medium and fast water velocity treatment were conducted, and water velocities were largely repeatable among trials (Table 4. 1). Detailed velocity measurements were made every 2 m throughout the flume for each combination of trial and treatment, although only measurements taken in the centre of the flume length are reported (Table 4. 1) as they were representative for all locations. Cross-sections were spaced 0.2 of flume width and every 0.25 of total depth for medium and fast treatments, and 0.3 of total depth for slow treatments, with water velocity measured using a two-directional electromagnetic velocity meter (model 523, Marsh-McBirney, Loveland USA). An automated passive integrated transponder (PIT) system was used to record the position of fish swimming up the length of the flume (*see* Castro-Santos et al. 1996, 2013). Ten PIT antennas were mounted along the length of the flume at 2.0 m intervals (from 0.5 to 18.5 m) and a control computer logged tag detection data (tag code, date, time to the nearest 0.1 s, and antenna location) from PIT readers at a rate of 10 Hz.

Captive lake sturgeon were used for swimming trials and these were Wolf River, WI, stock obtained in 1993 as cultured 2-yr juveniles and thereafter housed at the SO Conte Anadromous Fish Research Center (US Geological Survey, Biological Resources Division). All sturgeon had previously been fitted with PIT tags (32 × 3.85 mm half duplex tags, Texas Instruments, Dallas USA) via intracoelomic implantation, for individual identification. Prior to tagging, individuals were measured and weighed and subsequently immobilized for the tagging procedure using electrical narcosis (30 VDC impressed voltage; Henyey et al. 2002). Each sturgeon was fitted with a tri-axial accelerometer data storage tag mounted externally at the base of the dorsal fin (Figure 4. 1). Accelerometers were attached by passing a single piece of 18 gauge stainless steel wire through a hole at each end of the tag, or affixing wire to the tag temporarily with electrical tape. The wire was passed through a neoprene pad to prevent abrasion and then through two hypodermic needles passed through the dorsal musculature of the fish. Following removal of the needles an additional neoprene pad was added followed by a 5 mm thick plastic backing plate with pre-drilled holes. Tags were secured by creating two separate 90^{o} bends in each end of the wire to lock it onto the outside of the backing plate.

Three types of tri-axial accelerometer data storage tags were used in this study to maximise sample sizes and enabled us to evaluate the strengths and weaknesses of different designs to inform future studies by our team. Tags are hereafter referred to as tag type 1 (model G6a, 40 mm × 28 mm × 16.3 mm, 7.3 g in air, CEFAS Technology LTD, Suffolk UK), type 2 (model X6-2, 52 mm × 28 mm × 8 mm, 20 g in air, Gulf Coast Data Concepts, Waveland USA) and type 3 (daily diary, 120 mm × 25 mm, 63 g in air; Wilson et al. 2008), respectively. Tags were programmed to record acceleration in units of gravity (*g*), equivalent to 9.8 m s^{-2}, in separate X, Y and Z planes (measurement range: ±2 *g*) at user defined intervals of 20 Hz (tag types 1 and 3) or 25 Hz (tag type 2). Device output was calibrated by rotating the device through known angles to real *g* (Gleiss et al. 2010). Accelerometers were attached on 26 September 2011 (n=7) and on 26 October 2011 (n=15). Immediately following tag attachment, lake sturgeon were released into the flume staging area where they were able to volitionally ascend the flume from a low velocity staging area over ~20 hours at each of the three water velocity treatments, over a 3 day period. Trial 1 began at the medium velocity treatment (1.00 m s^{-1}), followed by slow (0.48 m s^{-1}) and then fast (1.36 m s^{-1}) treatments. Trial 2 began at the slow velocity treatment (0.48 m s^{-1}), followed by fast (1.38 m s^{-1}) and then medium (0.99 m s^{-1}) treatments. Following cessation of trials sturgeon were recaptured, external tag packages removed to enable downloading of data, and the time difference between individual accelerometers and the independent PIT system noted for later time synchronisation. Water temperatures for trials one and two were 20.05 ± 0.03 ^{o}C and 10.39 ± 0.07 ^{o}C, respectively.

Data analysis

Accelerometer output was divided into static and dynamic acceleration components using a weighted smoothing interval of 1.5 s (Shepard et al. 2008), where the static component represents the gravitational acceleration acting on the tag and the dynamic component is a function of device movement imparted via muscular contraction (Gleiss et al. 2011). Smoothed acceleration values in each axis were subtracted from raw acceleration to yield the dynamic component (Figure 4. 2a). Three activity metrics were derived from dynamic acceleration: ODBA (*g*) (Figure 4. 2b), TBF (Hz) and TBAA (*g*) (Figure 4. 2c). Overall dynamic body acceleration represents a single integrated measure of body motion in all three spatial dimensions, and instantaneous (20 Hz) ODBA values were obtained by summing the absolute values of dynamic acceleration in all three axes (Wilson et al. 1996; Gleiss et al. 2011). Tailbeat frequency and TBAA were derived from the dynamic acceleration component of the sway (Z) axis, and represent dynamic motion through body and caudal fin oscillations. Use of the term amplitude does not refer directly to TBA, but rather to the amplitude of the signal derived from the accelerometer through motion of the body and caudal fin during swimming (Whitney et al. 2010). An acceleration spectrogram was first created using continuous wavelet transformation with the Mortlet wavelet function in the Ethographer extension (Sakamoto et al. 2009; http://bre.soc.i.kyoto-u.ac.jp/bls/index.php?Ethographer) in Igor Pro (version 6.0, WaveMetrics Inc., Lake Oswego, OR, USA). The peak tracer option in Ethographer was subsequently used to determine the dominant frequency and amplitude of the fitted wavelet, resulting in TBF and TBAA values for every second of sway acceleration. Manual validation of TBF was performed on a subset of data and confirmed the accuracy of the peak tracer method.

Initial attempts to pair instantaneous U_s estimates with corresponding accelerometer derived metrics (TBF, TBAA and ODBA) failed due to slight time offsets between the PIT system and some accelerometers. Subsequently a single U_s estimate was generated for each individual at a nominal velocity, if volitional ascent occurred, and the first full ascent of the flume (typically this was the first attempt) was used in this calculation and paired with mean corresponding TBF, TBAA and ODBA values over the flume ascent. Given the use of 32 mm PIT tags in this study (resulting in a larger detection range than smaller PIT tags; Burnett et al. 2013) and the narrower antenna spacing than previously used (e.g. 2.5 m combined with 32 mm tags; Castro-Santos 2004; Haro et al. 2004), continuous detection of an individual occurred on the PIT system resulting in simultaneous records at adjacent antennas. An adjacent averaging smoothing algorithm was subsequently applied to the dataset to provide continuous spatial positioning within the flume (e.g. Figure 4. 2d). Data were removed past antenna 9 (16.5 m) due to increased turbulence beyond this location. The time difference between first record of a full flume ascent and the time corresponding to the maximum upstream distance (antenna 9) was used in the calculation of groundspeed (U_g). Groundspeed (m s^{-1}) was determined by the difference between the adjacent averaged minimum distance (flume entry) and the first record of maximum distance, divided by the corresponding period of time. Swimming speed (U_s; m s^{-1}) was calculated by adding the measured water velocity for a given treatment to the U_g.

Given that multiple data points were collected for some individuals (maximum of three when an individual ascended the flume at each velocity treatment) potentially violating the assumption of independence for the statistical treatments, linear mixed models were initially identified as the appropriate approach to examine the relationships between sturgeon acceleration response variables (ODBA, TBF or TBAA) and predictors

(U_s, total length and tag type). To assess the need for a mixed modelling approach, full models (i.e. all predictors) including random intercept, random slope or random intercept and slope combinations were compared, using the Akaike Information Criterion (AIC), with a model having the same predictors but no random effects (Zuur et al. 2009). This comparison was done using package *nlme* (Pinhero et al. 2012) in R (version 2.14.2; R Development Core Team 2012) and revealed that the use of a LME model did not result in improved model fit. Subsequently, models without random effects (i.e. ordinary multiple regression) were used for all further analyses.

A number of alternative models were fitted, always including U_s *a priori*. Models included swimming speed alone or combinations of total length and tag type as predictors, with n=4 competing models for each combination of an accelerometer-derived metric and swimming speed. Model selection and multimodel inference were carried out using AIC adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002) using package *AICcmodavg* (Mazerolle 2012). According to this criterion, the model with the lowest AIC_c value is the most parsimonious one describing the data and models with a Δ_i (representing the difference in AIC_c scores relative to the top model) of <2, 4–7 and >10 are regarded as having substantial, considerably less and essentially no support from the data, respectively (Burnham and Anderson 2002). The AIC_c weight (w_i) of the models was also determined and represents the probability of a given model in the set being the most parsimonious one to describe the data (Burnham and Anderson 2002). To account for model selection uncertainty, model-averaged estimates and unconditional 95% confidence intervals were computed using the scaled w_i of the models included in a 95% confidence set (cumulative weight) for the best model (Burnham and Anderson 2002). In addition, the relative importance of variables total length and tag type were computed from the entire candidate set using the sum of Akaike weights across all models in the set where they occurred (Burnham and Anderson 2002). For graphical representation of the model-averaged estimates, total length was held at its average value (904 mm TL) and tag type 1 was used in the prediction as it was represented by the largest sample size (n=11 ascents compared to n=8 and n=7 ascents for tag types 2 and 3, respectively).

The relationship between MO_2 and U_s developed by McKinley and Power (1992) for lake sturgeon swimming at 10 ^{o}C was substituted into the model-averaged estimates derived from this study. This was done to simulate the energetic expenditure associated with lake sturgeon swimming at the speeds observed in this study, and to develop new predictive relationships between acceleration response variables and MO_2 at U_s likely to be achieved in the wild. It is important to note that while similarly sized individuals were used in the McKinley and Power (1992) study, their relationship only holds true for a narrower range of U_s (0.30–0.80 m s^{-1}), likely a consequence of non-volitional swimming and the physical confinement of individuals. As such, the relationships presented here represent a theoretical extrapolation beyond these U_s and require a number of assumptions. The major assumptions are that the data are transferable to this study, and if they are, that MO_2 scales linearly with U_s throughout the range of U_s observed and that purely aerobic respiration is occurring. In addition, we recognise that there are errors associated with both this study and that of McKinley and Power (1992), although only the error associated with data generated for this study is available (represented by 95% confidence intervals).

Results

Lake sturgeon volitionally entered and ascended the flume during both trials and at all water velocity treatments. Tag failure (tag type 3 only) occurred on six occasions for unknown reasons, resulting in loss of data for an entire trial, or missing data for a water velocity treatment. In addition some individuals did not ascend the flume during any treatment (n=3), although more frequently individuals ascended during one treatment and not others. Final sample size consisted of 26 ascents paired with acceleration data, comprising 16 individuals (Table 4. 1). Total length ranged from 810–980 mm (mean ± SE: 904 ± 12 mm TL). Volitional U_s ranged from 0.48–2.70 m s^{-1} or 0.51–3.18 body lengths s^{-1}. Mean accelerometer-derived activity metrics ranged from 0.06–3.96 *g* for ODBA, 0.43–5.79 Hz for TBF and 0.04–2.45 *g* for TBAA.

The most parsimonious model for describing the relationship between TBF and U_s included TL, although there was substantial support for the effect of U_s alone, and considerably less support for the inclusion of tag type alone or total length and tag type (Table 4. 2). Total length was a more important variable relative to tag type, being 9.3 times more supported (relative importance 0.65 compared to 0.07 for tag type; Table 4. 2). The most parsimonious model for describing the relationship between TBAA and U_s included tag type (Table 4. 2). There was considerably less support for the inclusion of both TL and tag type in the model (Table 4. 2). Tag type was 5.8 times more supported than TL, indicating it was a more important variable (relative importance 0.98 compared to 0.17 for TL; Table 4. 2). Inclusion of U_s and tag type resulted in the most parsimonious model for ODBA, although there was also substantial support for inclusion U_s alone (Table 4. 2). There was considerably less support for the inclusion of TL alone, or TL and tag type together (Table 4. 2). Tag type was a more important variable than TL, with a relative importance of 0.56 compared to 0.25, indicating tag type was 2.2 times more supported (Table 4. 2). Overall, models including TBF as a response variable had the best fit in comparison to TBAA and ODBA (Figure 4. 3a, c, and e; Table 4. 2). All accelerometer-derived activity metrics positively increased with increasing U_s (Figure 4. 3a, c, and e; Table 4. 3). Tail beat frequency increased by 2.30 Hz for every 1 m s^{-1} increase in U_s, whereas TBAA and ODBA increased at a ratio of 0.98 *g* and 1.68 *g*, respectively, for every 1 m s^{-1} increase in U_s (Table 4. 3). Individuals with a larger TL had a higher TBF, although this increase was small (Table 4. 3). Reduced TBAA and ODBA were associated with use of tag type 3 in comparison to tag type 1 (Table 4. 3).

Theoretical MO_2 for a lake sturgeon swimming in 10 ^{o}C water and at the U_s observed in this study would range between 95.8 and 337.8 mg O_2 kg^{-1} h^{-1}, assuming a linear relationship. In reality, MO_2 values above 128.8 mg O_2 kg^{-1} h^{-1}, corresponding to model-averaged values of 1.52 Hz (95% CI: 1.36–1.68) for TBF, 0.55 *g* (95% CI: 0.37–0.73) for TBAA and 0.56 *g* (95% CI: 0.31–0.81) for ODBA (Figure 4. 3b, d, and f respectively), and represent an extrapolation beyond the limits of the data.

Discussion

We identified that all three accelerometer-derived metrics of activity used in this study were accurately related to U_s by linear relationships, and thus have provided a useful tool for the field measurement of activity in lake sturgeon. Further, use of an open channel flume to obtain volitional swimming speeds enabled a wider range of speeds than would be expected from use of a swim tunnel, and more likely represents the range of U_s

attained by free-swimming lake sturgeon. When using confined swim tunnels, it is notoriously difficult to generate U_s data for sturgeon as they frequently exhibit station holding when forced to swim at high water velocities; a behavioural strategy that enables them to occupy high velocity areas while minimising energy expenditure (Adams et al. 2003; Geist et al. 2005). Subsequently, techniques including prodding (Peake et al. 1997; Adams et al. 2003) or training (McKinley and Power 1992; Geist et al. 2005) are often necessary to induce swimming. Interestingly, the U_s observed in this study are well above the upper limits of those previously identified for this species (maximum 1.80 m s^{-1}; Peake et al. 1997). This particular result is consistent with recent findings for other species when large flumes are used to generate volitional U_s (Tudorache et al. 2007; 2010; Castro-Santos et al. 2013). Using a swim tunnel to generate endurance-fatigue curves for lake sturgeon, Peake et al. (1997) predicted that a 1200 mm lake sturgeon swimming at 14 ^{o}C could cover a distance of only ~13 m prior to fatigue at the upper water velocity treatment used in this study (1.38 m s^{-1}). They also noted that maximum distance decreased with decreasing fish length and increasing water temperature. This represents an underestimate based on the findings of the current study. Others have noted high U_s is achievable by sturgeon which is unsurprising given their large size can equate to relatively high absolute U_s. For example, Webber et al. (2007) found that larger (1350–1980 mm) white sturgeon (*Acipenser transmontanus*) were able to achieve positive U_g over short distances against high water velocities (2.54 m s^{-1}), although the distances that could be achieved at these speeds and U_s remain unknown.

Oxygen consumption was not directly quantified in this study, but rather extrapolated from a previous study of similarly sized lake sturgeon and assumed to increase linearly within the range of swimming speeds observed. Given the swimming speeds observed in this study (0.48–2.70 m s^{-1}) are greater than those used to develop the initial U_s– MO_2 relationship (0.30–0.80 m s^{-1}; McKinley and Power 1992), the extrapolations presented here should be interpreted with caution. It is possible that the study of McKinley and Power (1992) represents an overestimate of MO_2 for free-swimming lake sturgeon, as reductions in stride length and increases in tailbeat frequency for the same U_s have been observed for other taxa during confined swimming in comparison to free-swimming (Lowe 1996). Further, MO_2 may not necessarily increase linearly with U_s for all species, or across such a broad range of U_s. Swimming speed in teleosts more typically increases with the logarithm of MO_2, and at higher swimming speeds energetic demands transition from being met by aerobic respiration to being met anaerobically (Beamish 1978; Jayne and Lauder 1994). Thus the extrapolations presented here are more likely an underestimate of MO_2. There was also evidence of variability in accelerometer metrics during flume ascent which is presumably indicative of burst-and-coast swimming behaviour (*see* Figure 4. 2), although the frequency of this behaviour was not quantified and this variability was not incorporated into models. Burst-and-coast swimming can be energetically advantageous as it prolongs exhaustion (Weihs 1974; Videler and Weihs 1982; Tudorache et al. 2007). However burst-and-coast swimming at moderate and high speeds can involve recruitment of anaerobic white muscle fibres (Jayne and Lauder 1994), resulting in glycogen depletion and lactate accumulation (Peake and Farrell 2004). Incorporating finer temporal information on U_s and accelerometer derived metrics demonstrates promise to elucidate gait transitions. Although until new U_s–MO_2 relationships are established, across a broad range of field relevant U_s, the activity-specific costs of these behaviours remain theoretical. Further, the limitations imposed by the physical size of some animals, including for adults of many members of the Acipenseridae, and the resulting difficulties of constructing large swim tunnels/respirometers, indicate that extrapolation (this study) or borrowing from similar species (e.g. Semmens et al. 2013) is currently necessary.

The predictive relationships between U_s and acceleration developed in this study are largely reflective of steady swimming by lake sturgeon in a low turbulence environment. Others have suggested that ODBA would be a better predictor than TBF of unsteady swimming behaviours, such as those comprising frequent turns and bursting and coasting, as ODBA is more indicative of total work output (Gleiss et al. 2010; 2011). Turbulence is known to increase the energetic costs of swimming, although this increase has only been quantified in a few cases (e.g. Enders et al. 2003). Under some circumstances fish are able to capitalise on turbulent flows and reduce the energetic costs of swimming, although this largely depends on vorticity structure (e.g. Liao et al. 2003) and appears more the exception than the rule.

We identified evidence for an effect of tag type on the derivation of TBAA, and to a lesser extent ODBA, although there was considerably less support for an effect on TBF. One possible explanation for the variability observed may be related to the effect of water temperature on swimming kinematics (e.g. Webb 1978). The study design applied here does not enable disentangling among temperature and tag type effects, as each tag type was only used at a single water temperature. It appears most likely that the differences observed among tag types are related to tag orientation rather than tag type, although we do not discount possible temperature effects. For example, the alignment of the axes of the logger with respect to a tagged individual changes the measured acceleration within each axis based on simple trigonometry. Thus the values derived from a single axis such as the amplitude of the signal (i.e. TBAA), or the sum of values derived from multiple axes (i.e. ODBA), would be expected to differ based on orientation. This is the reasoning behind the proposition of Gleiss et al. (2011) for using the vectorial component of dynamic body acceleration, rather than the sum. More recently, Qasem et al. (2012) demonstrated no significant improvement when using the vectorial component in comparison to previously used ODBA as a proxy for MO_2. Unsurprisingly, the frequency of a signal (i.e. TBF) remains unaffected by tag orientation. Given that tag orientation was uniform for any given tag type with respect to attachment location and orientation, it appears that use of tag type 3 did not result in the optimal orientation to maximise ODBA and TBAA values, thus accounting for the differences observed.

This study is in agreement with the growing body of evidence supporting animal-borne accelerometers as a useful tool for the derivation of activity and energy expenditure across a broad range of aquatic and terrestrial taxa (Halsey et al. 2011). Further, this type of data can be used in the determination of landscape-dependent energy expenditure and the subsequent construction of energy landscapes (Wilson et al. 2012). While the relationships between unsteady swimming and accelerometer-derived metrics of activity remain unknown, and represent and important knowledge gap, we demonstrated the utility of accelerometers as a direct measure of volitional U_s in sturgeon. Extension of this relationship to estimate the energy expenditure of wild sturgeon in the context of measuring routine activity, or potentially energetically demanding activities such as migrations holds promise, although a lack of published data on U_s–MO_2 requires a number of assumptions and highlights the need for further work.

Tables

Table 4.1 Trial information including the number of lake sturgeon used, the number of individuals ascending the flume at least once (the number with useable data, given tag failure, is indicated in parentheses), and hydraulic characteristics for each trial. Velocity and depth data were taken from the centre of the flume, with cross-sectional velocity data pooled among depths and flume width locations. Note the same individuals were exposed to all water velocities in Trial 1, and similarly in Trial 2, although individuals from Trial 1 were not used in Trial 2.

Trial	N	N ascending	Water velocity (m s^{-1})	Depth (m)
1a	7	5 (1)	0.48 ± 0.00	0.23
1b	7	6 (4)	1.00 ± 0.01	0.40
1c	7	6 (2)	1.36 ± 0.01	0.41
2a	15	7 (6)	0.48 ± 0.00	0.27
2b	15	5 (4)	0.99 ± 0.00	0.40
2c	15	10 (9)	1.38 ± 0.01	0.40

Table 4.2 Multiple regression models describing lake sturgeon swimming activity metrics (tailbeat frequency (TBF), tailbeat acceleration amplitude (TBAA) and overall dynamic body acceleration (ODBA)) derived from data storage accelerometer tags in relation to swimming speed (Speed), total length (TL) and tag type (Tag). Candidate models are ranked based on Akaike weight (w_i), equivalent to relative importance of the model. AICc = Akaike's information criterion corrected for small sample size; Δ_i = difference in AICc scores relative to the top model; K = number of estimable parameters; Adj. R^2 = coefficient of determination.

Response	**Model**	**AIC$_c$**	**Δ_i**	**w_i**	**K**	**Adj. R^2**
TBF	$X_{\text{Speed}} + X_{\text{TL}}$	16.31	0.00	0.62	4	0.96
	X_{Speed}	17.63	1.32	0.32	3	0.96
	$X_{\text{Speed}} + X_{Tag}$	22.01	5.70	0.04	5	0.96
	$X_{\text{Speed}} + X_{\text{TL}} + X_{\text{Tag}}$	22.70	6.38	0.03	6	0.96
TBAA	$X_{\text{Speed}} + X_{\text{Tag}}$	11.84	0.00	0.83	5	0.87
	$X_{\text{Speed}} + X_{\text{TL}} + X_{\text{Tag}}$	15.25	3.41	0.15	6	0.86
	$X_{\text{Speed}} + X_{\text{TL}}$	19.46	7.62	0.02	4	0.81
	X_{Speed}	21.80	9.96	0.01	3	0.78
ODBA	$X_{\text{Speed}} + X_{\text{Tag}}$	25.16	0.00	0.47	5	0.92
	X_{Speed}	26.15	0.99	0.28	3	0.90
	$X_{\text{Speed}} + X_{\text{TL}}$	27.32	2.16	0.16	4	0.90
	$X_{\text{Speed}} + X_{\text{TL}} + X_{\text{Tag}}$	28.46	3.30	0.09	6	0.91

Table 4.3 Model-averaged parameter estimates and 95% confidence intervals (CIs) explaining lake sturgeon swimming activity (tailbeat frequency (TBF), tailbeat acceleration amplitude (TBAA) and, overall dynamic body acceleration (ODBA)) in relation to swimming speed (Speed), total length (TL) and tag type (Tag). Values were computed using the scaled AICc weight (w_i) of the models included in a 95% confidence set (cumulative weight) for the best model. Bold text indicates parameter estimates with CIs not overlapping zero. Note: Tag types 2 and 3 are compared to tag type 1, which is the reference level.

Variable	**Parameter**				
	Intercept	X_{Speed}	X_{TL}	$X_{\mathrm{Tag\ 2}}$	$X_{\mathrm{Tag\ 3}}$
TBF					
Parameter estimate	-1.3755	**2.2953**	**0.0019**	0.0229	0.1673
Lower 95% CI	-3.5177	2.1176	0.0000	-0.2622	-0.1289
Upper 95% CI	0.7667	2.4730	0.0038	0.3081	0.4647
TBAA					
Parameter estimate	-0.1966	**0.9800**	-0.0001	-0.1340	**-0.5278**
Lower 95% CI	-0.9857	0.8258	-0.0023	-0.3712	-0.7845
Upper 95% CI	0.5925	1.1343	0.0021	0.1032	-0.2711
ODBA					
Parameter estimate	-0.5728	**1.6758**	-0.0008	-0.1092	**-0.4178**
Lower 95% CI	-2.0653	1.4687	-0.0039	-0.4159	-0.7511
Upper 95% CI	0.9196	1.8829	0.0023	0.1974	-0.0846

Figures

Figure 4.1 Location of an accelerometer (tag type 1) mounted at the base of the dorsal fin on a lake sturgeon.

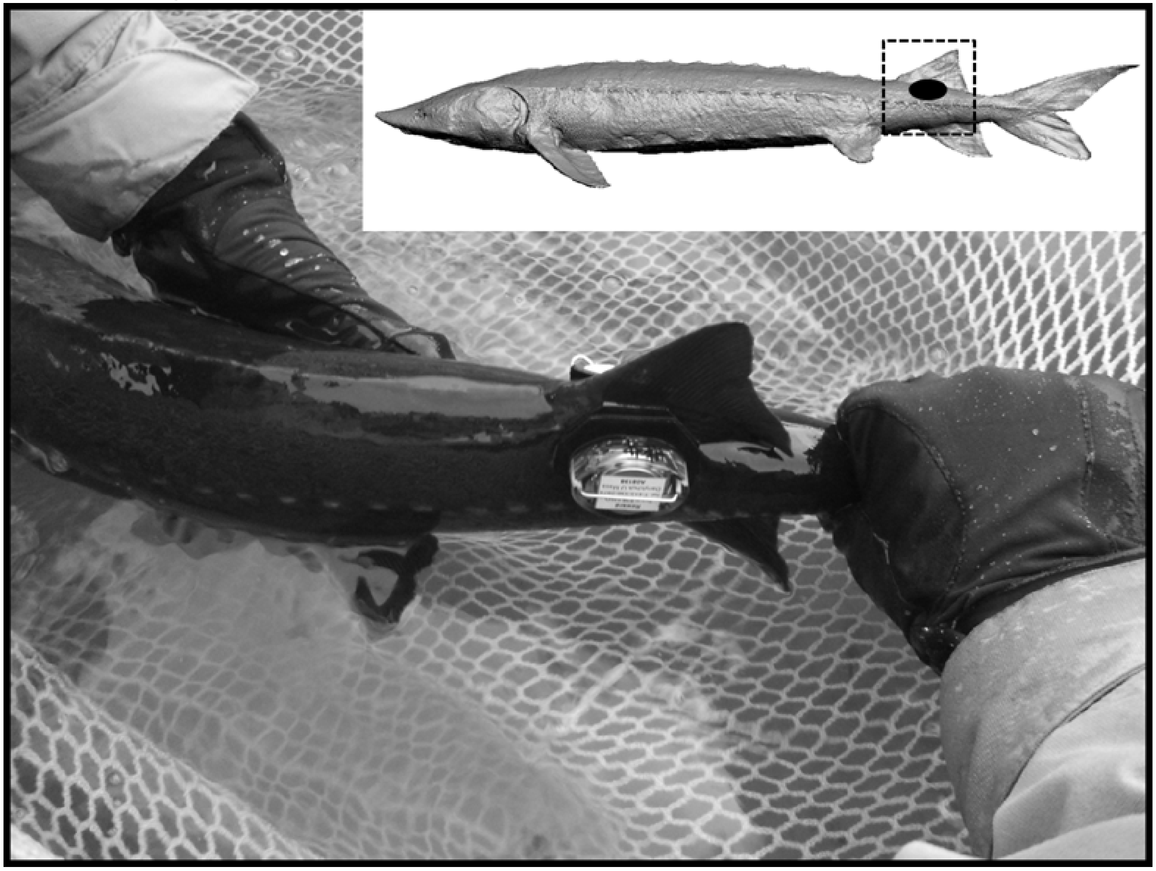


Figure 4.2 Acceleration profile of a lake sturgeon (950 mm TL) during ascension of a 18 m open channel flume swimming against 1.38 m s^{-1} water velocity, represented by a) the dynamic component of acceleration (expressed in g) presented for separate X (light grey), Y (dark grey) and Z (black) axes, with a +4 g and -4 g added to X and Z axes respectively for graphical purposes only; b) overall dynamic body acceleration (derived from the absolute sum of dynamic acceleration in all three axes); c) tailbeat frequency (solid line) and tailbeat acceleration amplitude (dashed line), derived from Z axis (sway) dynamic acceleration, and; d) spatial location within the flume, expressed as distance from flume entry (0 m), with location determined using a passive integrated transponder antennas spaced every 2 m.

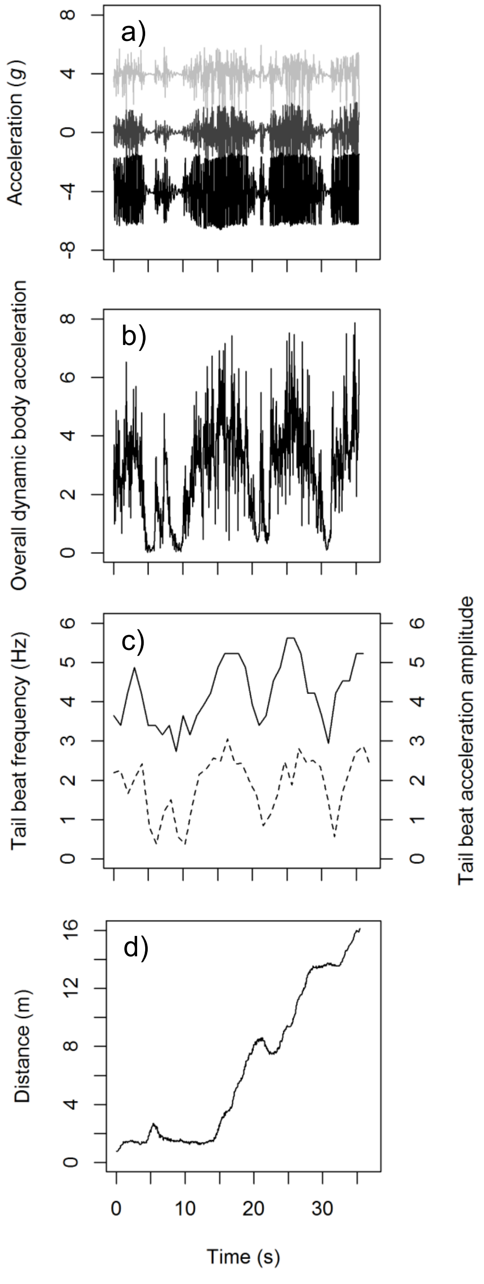
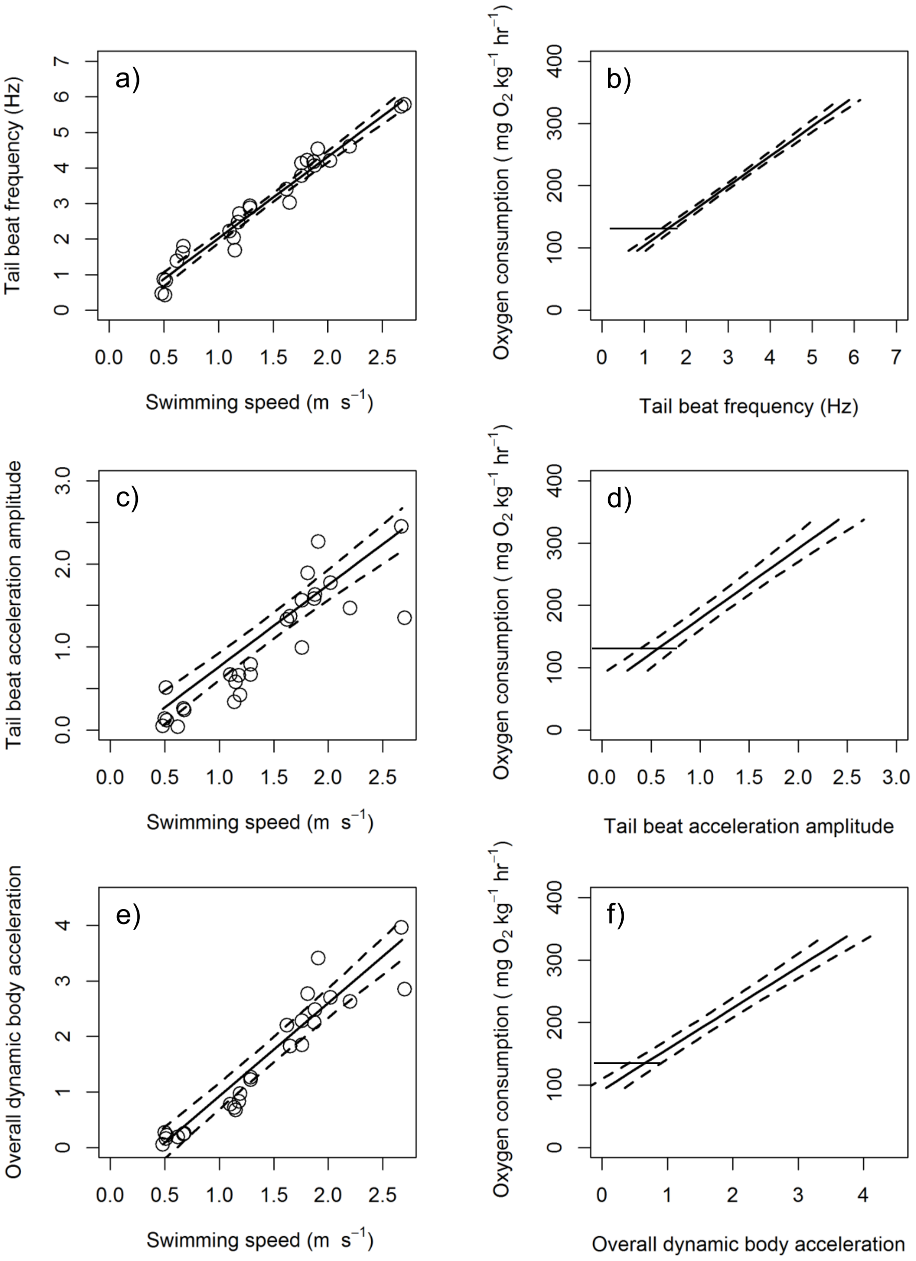


Figure 4.3 Model-averaged estimates of swimming speed (U_s) of lake sturgeon in relation to: a) tailbeat frequency, c) tailbeat acceleration amplitude, and e) overall dynamic body acceleration. Corresponding oxygen consumption values in relation to model-averaged estimates are presented for: b) tailbeat frequency, d) tailbeat acceleration amplitude, and f) overall dynamic body acceleration and were calculated using established relationships from McKinley and Power (1992) (under the horizontal bar) for the same species, and extrapolated (above the horizontal bar) to this study assuming a linear relationship. Solid lines indicate the estimate and dashed lines indicate lower and upper 95% confidence intervals. Raw data is indicated by open circles. For graphical purposes only, total length was held at its average value and tag type 1 was used (see Methods).



Chapter 5. Swimming activity and energetic costs of adult lake sturgeon during fishway passage

Abstract

Fish migrations through riverine systems can be energetically demanding and the presence of fishways to facilitate upstream passage past anthropogenic barriers can add an additional energetic cost that may directly affect fitness. We quantified the energetic expenditure of adult lake sturgeon (*Acipenser fulvescens*) swimming through a vertical slot fishway (2.65m elevation rise, 12 regular pools and 2 turning basins) installed to facilitate upstream passage past a low head dam. Specifically we used triaxial accelerometers to estimate location-specific swimming activity of sturgeon in a field setting, to determine whether individual behaviour or path selection, resulting in differences in cumulative energy use, explain fishway passage success. Most individuals attempted to pass the fishway (n=30/44; 68%), although successful passage only occurred for a subset of those attempting (n=7/30; 23%). High speed swimming was rarely observed during upstream passage through fishway basins, and was of short duration. Two turning basins delayed passage, subsequently resulting in a higher energetic cost. The rate at which energy was expended did not differ among successful and unsuccessful individuals, although successful sturgeon exhibited higher costs of transport per unit distance (13.51 *vs.*7.83 J kg^{-1} m^{-1}). The energy expenditure metrics including total energy used, rate of energy use and cost of transport were not predictive of successful fishway passage, leading us to conclude that other endogenous or exogenous factors influence passage success. In a practical application of field measurements of energy expenditure,

we demonstrate that fishway passage through a structure designed to facilitate migration does result in an energetic loss for lake sturgeon (883–5540 J kg^{-1}), equivalent to individuals travelling 2.1–13.3 km in a lentic system.

Introduction

The rate at which animals expend energy is a key component to understanding how they interact with their surrounding environment (McNabb 2002). The allocation of time and energy to different behaviours across the landscape affects individual survival and fitness (Morales et al. 2010; Wilson et al. 2012). In fish, locomotor activity can account for a considerable portion of an energy budget (Boisclair and Leggett 1989). Thus energetic cost optimisation through the evolution of morphological (e.g. body form and fin shape), physiological (e.g. muscular efficiency) or behavioural (e.g. schooling) traits is often observed (Weihs and Webb 1983). In lotic systems, and where positive rheotaxis occurs, drag and water velocity typically govern energetic expenditure. Position can be maintained and energy expenditure minimised through behavioural strategies including benthic station holding by some species at high water velocities (Webb et al. 1996) or simply occupation of less demanding microhabitats (McLaughlin and Noakes 1998). However, behaviours including migrations that require a net directional upstream movement can be energetically demanding (Lucas et al. 2001).

The energy expended by fish during upstream spawning migrations can result in a net loss for species that cease feeding (Brett 1995). Further, where challenging hydraulic conditions are encountered, individuals are often required to make behavioural adjustments that affect energetic expenditure and ultimately fitness. For example, migrating sockeye salmon (*Oncorhynchus nerka*) that selected paths resulting in slow swimming speeds were more likely to successfully pass through a challenging river reach (Hinch and Bratty 2000). In comparison, individuals that exhibited hyper-activity via inappropriate path selection, resulting in depletion of energy stores, subsequently failed to pass the same reach (Hinch and Bratty 2000). McElroy et al. (2012) demonstrated that pallid sturgeon (*Scaphirhynchus albus*) exhibited energetic optimisation by selecting migration pathways through sections of a river with the lowest water velocities. A trade-off often exists, however, between time and energy during migrations. Standen et al. (2002) observed that sockeye and pink salmon (*O. gorbuscha*) adopted one of two strategies; they either swam slowly and took more time searching for lower velocity areas, thus increasing passage time (cost optimisation strategy), or swam quickly through higher velocity areas (time optimisation strategy). The time optimisation strategy is clearly beneficial if energy is not a limiting factor and the timing of arrival at spawning grounds governs fitness. As energy is not replenished, the cost optimisation strategy may be preferable for poor swimmers or through particularly demanding areas. A third possibility is that the total energy used to traverse a given location may be similar between the two strategies, as low energy use over a longer period of time may amount to the same total energetic cost as high energy use over a short period of time. In this example the advantage would be with the individual adopting the time optimisation strategy.

To add further complexity, many key migratory pathways have been blocked by anthropogenic barriers (Lucas et al. 2001). Fishways are increasingly being installed at these barriers and represent one solution to facilitate upstream passage of migrating fish, requiring volitional entry and passage through the structure via an individual’s locomotor ability (Clay 1995). To be effective, fishways must allow for the upstream passage of fishes with minimal energy expenditure to reduce potential fitness consequences (Castro-Santos and Haro 2010). As such, considerable effort has been devoted to linking species-specific swimming ability with fishway design (e.g. Peake et al. 1997). However, fishways that are uniformly successful at passing all individuals or species are rare (Bunt et al. 2012), and individuals that are successful may still exhibit delayed mortality (Roscoe et al. 2011). Recent evidence suggests that laboratory derived data from forced swimming trials is not indicative of volitional performance (Castro-Santos et al. 2013; Peake 2004). Further, fishways often represent dynamically turbulent environments (Tarrade et al. 2008), and increases in turbulence generally increase the cost of locomotion (Enders et al. 2003) and decrease fishway efficiency (Silva et al. 2011). Individual differences in path selection can also result in a higher cost of passage for some individuals (Khan 2006), and although this may explain differential success, it typically remains unknown.

Sturgeon represent a group of animals for which barriers to migration often limit access to upstream spawning areas and subsequently threaten population persistence (Rochard et al. 1990). Sturgeon have a relatively limited capacity for high speed swimming, resulting from an increased profile drag (Webb 1986) and a poor aerobic capacity (Peake et al. 1997). Considerable attention has been devoted to facilitating upstream passage of sturgeon at fishways via laboratory derived swimming models (Peake et al. 1997), observations of captive sturgeon ascending experimental fishways (Cheong et al. 2006; Cocherell et al. 2011; Kynard et al. 2011; Webber et al. 2007) and field observations of passage behaviour including quantification of fishway efficiency (Parsley et al. 2007; Chapter 3). Given their poor swimming ability, it is possible that fishways impose a particularly high energetic cost to migrating sturgeon, and that energetic expenditure may explain differences in passage success.

We examined the energetic costs of upstream passage through a vertical slot fishway by lake sturgeon (*Acipenser fulvescens*), a locally abundant species endemic to North America that undertake comparatively short distance spawning migrations that are typically less than 200 km (Auer 1996*a*). By using a combined tagging approach to determine both spatial location and indirect measures of energy expenditure, we provide an example application of fundamental science to inform an applied issue. Specifically we were interested in determining whether: 1) ground speed, swimming speed or energy use differ among locations within the fishway, 2) energetic costs differ among successful and unsuccessful individuals, and 3) the probability of successful passage is a function of energy expenditure.

Methods

Study site

This study was conducted at the Vianney-Legendre Fishway, a vertical slot fishway located on the Richelieu River adjacent to the St. Ours dam (45°51'48"N, 73°08'60"W) in southwestern Quebec, Canada. The fishway was installed in 2001 to facilitate upstream passage for migrating fish past a low level dam (3.4 m height), and is an 85 m long concrete structure with an elevation rise of 2.65 m that includes large entrance and exit basins on small slopes. The remainder of the fishway is divided into 12 uniform rectangular basins (3.5 × 3.0 m) connected by two resting/turning basins with horizontal floors and curved walls (2.75 m radius; Figure 5. 1) that potentially provide low velocity resting areas for upstream migrating fish during passage. The uniform basins have successive floor drops of 0.15 m for a total rise of 2.4 m and are each separated by a 0.6 m wide vertical slot (2.3–4.0 m height range). The fishway passes approximately 1 m^3 s^{-1} of water, with a capacity for an additional 6.5 m^3 s^{-1} attraction flow near the entrance basin via a pass through chamber beneath the fishway, although attraction flow was not used in this study. Maximum water velocities of 1.72 m s^{-1} occur at the vertical slots. A more detailed description of the fishway and the Richelieu River is provided in Chapter 3 and Thiem et al. (2013).

Capture and tagging

Lake sturgeon (n=44, 1222 ± 21 mm total length (TL) (939–1555 mm TL range) and 10.56 ± 0.68 kg (4.40–24.61 kg range)) were captured between 18 April and 4 May 2012 downstream of the St. Ours dam using monofilament gill nets. The methods and capture locations were identical to those previously used, and lake sturgeon congregate at this location prior to spawning at this site or passing upstream via the fishway to spawn (Chapter 2, Chapter 3). Captured sturgeon were immediately transferred to on-site indoor holding facilities adjacent to the fishway and held in 2250 l flow-through hatchery tanks (with water pumped directly from the river replaced at a rate of ca. 50 l min^{-1}) at a density of no more than 20 kg per 1000 l for 1–3 d prior to release to ensure adequate sample sizes. There was no mortality associated with capture, handling or holding, and fish were not fed during holding. Immediately prior to release sturgeon were measured, weighed and had a uniquely coded PIT tag (32 mm × 3.85 mm HDX; Texas Instruments, Dallas, Texas, USA) inserted into the coelomic cavity using the methods described in Chapter 3. Each sturgeon was also fitted with an external package at the base of the dorsal fin (Chapter 4) comprising a tri-axial accelerometer data storage tag (model G6a, 40 mm × 28 mm × 16.3 mm, 7.3 g in air, CEFAS Technology LTD, Suffolk UK) and a coded radio tag to facilitate accelerometer retrieval (149 MHz, 30mm× 8 mm, 8 g mass in air, burst rate 2 s, 90 day battery life; Sigma Eight Inc., Newmarket, Ontario, Canada). Total package weight was 32 g and never exceeded 0.8% of total fish mass. No anaesthetics or sutures were used and the entire handling process took <5 min, with care taken to minimize air exposure. Accelerometers were programmed to record acceleration in units of gravity (*g*), equivalent to 9.8 m s^{-2}, in separate X (surge), Y (heave) and Z (sway) planes (measurement range: ±2 *g*) at user defined intervals of 20 Hz, where total acceleration comprised the sum of both static (due to gravity) and dynamic (due to animal movement) components. Device output was calibrated by rotating the device through known angles to real *g* (Gleiss et al. 2010).

A passive integrated transponder (PIT) array consisting of 15 complete pass-through antennas (beginning at antenna 15 downstream (0 m) and ending at antenna 1 upstream (56.2 m); Figure 5. 1) was installed within the fishway during a dewatering period in early April 2012. The antenna array was identical to that described by Thiem et al. (2013). A multiplexer allowed the antennas to be scanned sequentially at high speed (i.e. each antenna was scanned 2.5 times per second) and upon positive detection stored a unique tag identification number, antenna number and the date and time of detection to the nearest second. Detection efficiency of the system was 97 ± 1.5% for 32 mm tags, based on a separate study undertaken at this site (Burnett et al. 2013). Sturgeon were released into the entrance basin of the fishway immediately following tag attachment and in three separate groups to minimise the number of sturgeon in the fishway at any time whilst maintaining adequate sample sizes. Trials ran for 72 h (Trial 1 (n=15): 20–23 April, average water temperature 9.2 ± 0.1 ^{o}C; Trial 2 (n=14): 27–30 April, average water temperature 7.8 ± 0.0 ^{o}C; Trial 3 (n=15): 4–7 May 2012, average water temperature 10.4 ± 0.1 ^{o}C), and sturgeon were able to volitionally enter the fishway from the entrance basin, and pass to the upstream section of the fishway. Sturgeon were prevented from exiting the fishway by a block net that was added to the entrance (downstream) gate and a fish trap operating upstream of antenna 1 (Figure 5. 1). Following cessation of each trial, a slow dewatering of the fishway enabled recapture of sturgeon, removal of external tag packages and release at the point of capture.

Data analysis

Sturgeon movements through the fishway over time were reconstructed by converting antenna locations to distance metrics beginning at the first antenna (antenna 15, 0 m) and ending at the most upstream vertical slot (antenna 1, 56.2 m) (Figure 5. 1; Thiem et al. 2013). This enabled calculation of movement metrics for each individual including minimum cumulative distance moved throughout the fishway, maximum distance of ascent and cumulative upstream distance moved (Chapter 3). As 14 fish were either not detected within the fishway (n=4), or not beyond the most downstream antenna (n=10) (and could not be confirmed to have actually entered the fishway; a minimum of two antennas are required to determine direction), all subsequent analyses were conducted on the remaining 30 sturgeon. A passage attempt was defined as any movement into the fishway (to at least the second antenna encountered; antenna 14) and terminated upon either successful passage or return to the downstream staging area.

Successful passage was defined as the first detection of an individual on the most upstream antenna (antenna 1), which was located one basin downstream of a fish trap. As the trap was present to prevent complete passage of individuals (and subsequent loss of tags), and aversion to fish traps at fishways has been documented by others (e.g. Stuart et al., 2008), we felt this removed any potential bias the trap may have had on behaviour.

Accelerometer output for each tag was time calibrated with the PIT antenna system. Static and dynamic acceleration components were separated using a weighted smoothing interval of 1.5 s (Shepard et al. 2008) in Igor Pro (version 6.0, WaveMetrics Inc., Lake Oswego, Oregon, USA) (Figure 5. 2a). Absolute values of dynamic acceleration from each acceleration axis were summed to yield instantaneous Overall Dynamic Body Acceleration (ODBA; Wilson et al. 2006). We used ODBA as it represents a single integrated measure of body motion in all three spatial dimensions and is generally considered more indicative of total work output than tail beat frequency during unsteady swimming behaviours such as those comprising frequent turns or bursting and coasting (Gleiss et al. 2010; Gleiss et al. 2011).

To determine location specific behaviour among lake sturgeon during upstream passage, each individual was assigned a location (basin) each second during upstream movements. Upstream movements were categorised as any upstream directional movement determined from records on sequential antennas. When this occurred, a location was assigned based on the time of the last detection of the downstream antenna and the time of the first detection on the upstream antenna. Groundspeed during upstream movements through basins was determined by the time difference between the two antennas divided by the minimum distance travelled (3.9 m for regular basins and 4.7 m for turning basins), although the actual distance travelled is unknown. A corresponding median swimming speed (m s^{-1}) estimate was also allocated for upstream passage through each basin, derived from the median ODBA value during ascent based on an ODBA-swimming speed relationship previously identified for this species (Chapter 4):

$$Swimming\ speed\ = \frac{0.6907 + ODBA}{1.6802} \quad (1),$$

Median ODBA values always fell within the range of those previously used for ODBA-swimming speed calibrations for this species (Chapter 4). An estimate of the total energetic cost to pass upstream through any given basin was also calculated and expressed as the cost of transport (COT; J kg^{-1} m^{-1}). One second swimming speed values were first derived from ODBA (as above), and values outside of the previously calibrated ODBA range of 0.06–3.96 *g* (Chapter 4), corresponding to swimming speeds of 0.45–2.77 m s^{-1}, were conservatively allocated a value of 0 m s^{-1} (when <0.45 m s^{-1}) or 2.77 (when >2.77 m s^{-1}). Swimming speeds were subsequently converted to an oxygen consumption rate (mg kg^{-1} hr^{-1}) using the equation from McKinley and Power (1992) for a lake sturgeon swimming at 10°C (which represents the approximate water temperatures observed during this study), where swimming speed was first converted to cm s^{-1}:

$$Oxygen\ consumption = 43 + 1.1(swimming\ speed) \quad (2),$$

Total metabolic rates (TMR) were determined by multiplying oxygen consumption by an oxycalorific coefficient of 13.598 J/ mg^{-1} O_2 (Brett and Groves 1979). Cost of transport (J kg^{-1} m^{-1}) through a fishway basin was determined as:

$$COT = \frac{\sum TMR - \sum SMR}{distance} \quad (3),$$

Where SMR represents the standard metabolic rate (43 mg O_2 kg^{-1} hr^{-1} or 584.71 J kg^{-1} h^{-1} for a lake sturgeon swimming at 10°C extrapolated to 0 cm s^{-1} swimming speed; McKinley and Power 1992) and distance is the minimum distance required for a fish to travel through a basin (3.9 or 4.7 m). As these COT estimates assume purely aerobic respiration during passage through fishway basins (where location is defined above), an estimate of the proportion of time each individual exceeded its critical swimming speed (U_{crit}) was also determined, as U_{crit} is widely recognised in laboratory experiments as a transitional phase from the use of purely aerobic red muscle fibres to the recruitment of anaerobic, white muscle fibres that result in muscle fatigue and an oxygen debt (Beamish 1978; Burgetz et al. 1998). We calculated the proportion of time individuals spent exceeding U_{crit} during their entire time within the fishway, as well as the continuous duration (bout length) for which U_{crit} and 80% of U_{crit} was exceeded when traversing fishway basins. We determined U_{crit} from the equation provided by Peake (2005) encompassing three species of sturgeon (including lake sturgeon), where:

$$U_{crit} = 21.05 + 0.84 \times FL \quad (4),$$

where U_{crit} is in cm s^{-1}, and fork length (FL) is in cm. Total length (TL) of sturgeon was first converted to fork length by rearranging the equation provided by Fortin et al. (1996) for St Lawrence lake sturgeon to be as follows (and where FL and TL are in mm):

$$FL = \frac{TL - 35.97}{1.06} \qquad (5),$$

To determine location specific differences in groundspeed, swimming speed and COT among fishway locations (basins) we used a linear mixed effects (LME) model selection approach (Zuur et al. 2009) using the package *nlme* (Pinhero et al. 2012) in R (version 2.14.2, R Development Core Team 2012). Initially fishway basins (n=14) were grouped into five fishway sections (Figure 5. 1; Table 5. 2). We included covariates fishway section, total length, average hourly water temperature (collected from within the fishway; DS1921Z iButton, Maxim Integrated, San Jose, California, USA) and a binary pass/fail response depending upon whether an attempt resulted in successful or unsuccessful passage. Initially a full model including all covariates was fitted using generalised least squares (GLS) and compared with a LME model that included a random intercept term of attempt number nested within fish ID. In all cases inclusion of a random intercept significantly improved model fit and we proceeded with model selection using LME. A variance structure to account for heterogeneity of variance among fishway sections for models of groundspeed and swimming speed improved model fit and residual spread; although a log transformation was required for the COT model. Temporal auto-correlation of residuals was assessed visually (Zuur et al. 2009). The optimal fixed structure of models was assessed using likelihood ratio tests applied to models fitted using maximum likelihood (ML) estimation based on sequential removal of covariates. Final models were subsequently refitted using restricted maximum likelihood estimation (REML). Post-hoc tests for differences among fishway sections were conducted using a Bonferroni correction in the package *multcomp* (Hothorn et al. 2013). For graphical purposes, predictions of groundspeed, swimming speed and COT along with corresponding confidence intervals were computed using *AICcmodavg* (Mazerolle, 2012), with covariates held at their average value where applicable.

To determine overall differences in the rate of energy use and the cost of transport among successful and unsuccessful individuals we calculated total energy use by lake sturgeon during fishway passage. Total energy use (J kg^{-1}) was calculated using eqn. 1, 2, and 3, and represents a cumulative value for each second a sturgeon was within the fishway, regardless of location (Figure 5. 1b). The rate of energy use (J kg^{-1} h^{-1}) was determined as the total estimated energy used divided by the duration of time (hours) in the fishway. Total COT (J kg^{-1} m^{-1}) was calculated as per eqn. 3, where distance was the total distance moved within the fishway. Differences in the rate of energy use and total COT were compared among successful and unsuccessful individuals using unequal variances t-tests performed on ranked data due to non-normality (Ruxton 2006). Linear regressions were used to describe relationships between energy use and time in the fishway, maximum upstream location, cumulative upstream distance moved and total distance moved. Passage success or failure was modelled as a binary response variable with total energy use, rate of energy use and COT using logistic regression, to determine if any of these three variables alone could adequately predict the probability of passage success.

Results

Thirty lake sturgeon made at least one attempt to pass the fishway, and seven fish successfully passed resulting in a passage efficiency estimate of 23%. Individuals typically made multiple attempts to pass the fishway (up to 22 attempts; Table 5. 1), with successful passage requiring 2–16 attempts. The amount of time sturgeon spent in the fishway ranged from 0.03–12.26 hours, and individuals successfully passing the fishway occupied the fishway for 1.45–7.89 hours (Table 5. 1). Sturgeon most frequently swam at speeds less than 0.75 m s^{-1} during passage through fishway basins (Figure 5. 3). Critical swimming speed for an average sized sturgeon in this study was 1.17 m s^{-1}, and ranged from 0.96–1.41 m s^{-1} for minimum and maximum sized individuals, respectively. Sturgeon rarely (1.55 ± 0.36% of the time) exceeded their respective U_{crit} whilst within the fishway (Table 5. 1; Figure 5. 3). Where U_{crit} was exceeded during passage through basins, bout lengths were typically of short duration (<3 s) for both total U_{crit} and 80% of U_{crit} (Figure 5. 4).

Groundspeeds of lake sturgeon were higher through regular basins in comparison to turning basins during upstream passage (Table 5. 2). Groundspeed was best described through the inclusion of the covariate water temperature and the fixed factor pass/fail (Table 5. 3). Groundspeeds positively covaried with water temperature and were slower during successful passage attempts (Table 5. 3). In addition, sturgeon exhibited significantly higher groundspeeds when passing upstream through regular basins in comparison to turning basins (Table 5. 2; Figure 5. 5a). Median swimming speeds during upstream passage were higher in regular basins in comparison to turning basins (Table 5.

2; Figure 5. 5b). The final model included water temperature, which covaried positively with swimming speed (Table 5. 3). Swimming speed was significantly higher in section 5 than other sections, and also significantly higher in section 3 than all other sections (except section 5) (Table 5. 2). Sturgeon swimming speed was significantly higher in section 1 compared to section 2, although sections 1 and 4 were similar, as were sections 2 and 4 (Table 5. 2). The final model describing the COT for sturgeon through different fishway sections did not include other covariates (Table 5. 3). Energetic costs for sturgeon to move upstream were significantly higher through turning basins (sections 2 and 4) in comparison to regular basins (sections 1, 3 and 5) (Table 5. 2; Figure 5. 5c). Passing upstream through turning basins in section 2 and 4, lake sturgeon used a median of 11.03 and 10.78 J kg^{-1} m^{-1}, respectively, in comparison to 1.90, 2.53 and 1.84 J kg^{-1} m^{-1}, respectively for sections 1, 3 and 5 (Table 5. 2).

Total energy used by lake sturgeon whilst in the fishway ranged from 33–7330 J kg^{-1} for unsuccessful individuals and 883–5540 J kg^{-1} for successful individuals (Table 5. 1). The rate of energy use did not significantly differ between unsuccessful (median (range): 706.3 J kg^{-1} h^{-1} (490.2–1266.7)) and successful individuals (702.2 J kg^{-1} h^{-1} (585.8–727.4)) over the total time they spent in the fishway ($t_{16.781} = 0.847$, $P = 0.409$). Unsuccessful lake sturgeon typically moved shorter total distances within the fishway (54.6 m (7.8–289)) in comparison to successful sturgeon (121.8 m (104.6–443.2)). The COT for unsuccessful sturgeon whilst in the fishway was significantly lower (7.83 J kg^{-1} m^{-1} (2.12–60.64)) than for successful sturgeon (13.51 J kg^{-1} m^{-1} (7.97–30.87)) ($t_{15.915} = -2.145$, $P = 0.048$). Cumulative upstream distances moved were shorter for unsuccessful sturgeon (27.3 m (3.9–144.5)) in comparison to successful sturgeon (89.0 m (80.4–

245.8)). There was a strong linear relationship between the time sturgeon spent in the fishway and the amount of energy used (Figure 5. 6a) for both successful (*Energy* = -24.4 + 677.2(*Time*), $r^2 = 0.95$) and unsuccessful fish (*Energy* = 51.0 + 614.7(*Time*), $r^2 = 0.99$). A weak linear relationship existed between the total energy used by individuals within the fishway and the maximum upstream location (*Energy* = 207.1 + 58.8(*Distance*), $r^2 = 0.39$; Figure 5. 6b). Energy use increased at differing rates for unsuccessful and successful sturgeon in response to upstream distance moved (unsuccessful: *Energy* = -78.2 + 29.8(*Distance*), $r^2 = 0.60$; successful: *Energy* = 822.1 + 16.9(*Distance*), $r^2 = 0.58$; Figure 5. 6c) and total distance moved (unsuccessful: *Energy* = --78.2 + 14.9(*Distance*), $r^2 = 0.60$; successful: *Energy* = 1305.9 + 8.4(*Distance*), $r^2 = 0.59$; Figure 5. 6d), although there was limited overlap of data as successful sturgeon typically moved greater distances upstream and greater total distances. Total energy use, the rate of energy use and COT were not predictive of successful passage by sturgeon (Table 5. 4).

Discussion

This study found a small proportion of lake sturgeon attempting to pass the fishway were successful. Total energy expenditure and the rate of energy expenditure did not differ between successful and unsuccessful lake sturgeon, although COT estimates indicate that successful sturgeon typically expended more energy per unit distance than unsuccessful sturgeon. There was little evidence of cost optimisation exhibited by successful sturgeon, rather the data presented here supports a time optimising strategy which was linearly related to energy optimisation. This is most likely explained by the physical size of individuals in comparison to the fishway dimensions. Although vertical slot fishways have spatially and temporally heterogeneous hydraulics within basins, any possible cost optimisation strategy may be precluded as all individuals are required to pass through the highest velocities, which occur at the vertical slots, in order to travel upstream. Further, there was considerable variability among successful individuals in terms of the total energy used, and this was likewise linked to passage duration and corresponding distance travelled. Variability in passage behaviour by lake sturgeon was similarly observed at this site in Chapter 3.

Energy expenditure metrics were not predictive of successful fishway passage by lake sturgeon. Other factors most likely influence passage success including individual motivation or navigational ability. The approach used in this study of downstream capture and subsequent release into the fishway provides an artificial measure of passage efficiency (Cooke and Hinch 2013), as volitional entry into the fishway (attraction) did not occur. Further, one spawning site occurs downstream of the fishway (Chapter 2) and thus differentiation between individuals motivated to pass upstream of the dam or spawn downstream remains unknown. Nonetheless, while energy expenditure metrics (total energy used, rate of energy use and COT) were not predictive of successful passage through the fishway, passage did result in an energetic loss (883–5540 J kg^{-1}) that was largely determined by passage duration. Roscoe et al. (2011) demonstrate that for sockeye salmon, passage success does not necessarily transfer directly to reproductive success. The authors identified evidence of delayed post-passage consequences including *en route* mortality or a reduced competitive ability at spawning grounds. Similarly, Caudill et al. (2007) identified that delayed dam passage was indicative of reproductive failure in Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*), with one possible mechanism being premature depletion of energy stores.

The post-passage reproductive success of lake sturgeon in the current study was not evaluated, and the delayed consequences of energy expenditure resulting from fishway passage remain unknown. However, given lake sturgeon typically undertake comparatively short distance migrations (Auer 1996*a*) and thus may allocate less energy to migrations in comparison to longer distance migrants (e.g. Crossin et al. 2004), it is possible any additional energy expenditure could influence migratory or reproductive success. To place the results of this study in the context of migration in general for this species, we compared the total energy used by successful lake sturgeon during fishway passage with the equivalent energy used and corresponding distance travelled for sturgeon swimming at a range of speeds (0.25–1.50 m s^{-1}). For simplicity we assumed that this movement occurred in a lentic system, which is typical habitat for this species throughout much of the year (Scott and Crossman 1973). The energy expended by successful lake sturgeon in the current study to swim an estimated 104–443 m through the fishway is equivalent to individuals travelling 2.1–13.3 km in a lentic system (Figure 5. 7). Thus while energy expenditure may not be predictive of, or indeed limit successful passage in lake sturgeon, the evidence presented here suggests that the energy expended during fishway passage may have unintended consequences on individual fitness.

Swimming speeds and corresponding groundspeeds were slower when sturgeon were moving upstream through turning basins in the current study, and the corresponding cost of transport through these sections was higher in comparison to regular basins. Previous studies have identified that the presence of turning basins increases passage failure and delays passage (Bunt et al. 2000; White et al. 2011), including for this species (Chapter 3). While the provision of low velocity resting areas for sturgeon, such as turning basins, has been recommend by others (Webber et al. 2007), we identified that anaerobic swimming was of short duration during passage through basins. Further, the proportion of time spent swimming anaerobically typically represented a small proportion of the total time spent swimming in the fishway and most likely occurred during passage through vertical slots where velocities are highest. Similarly, Alexandre et al. (2013) identified that high speed swimming by Iberian barbell (*Luciobarbus bocagei*) typically occurred only through passage of submerged orifices in a pool-type fishway, and that U_{crit} was rarely exceeded. Hinch and Bratty (2000) found that sockeye salmon exhibiting hyper-activity by exceeding U_{crit} for more than 10 min continuously were more likely to exhibit fallback, although U_{crit} was never exceeded for this length of time in the current study. We do not advocate against low velocity areas, but rather it appears that the heterogeneous nature of hydraulics in the basins of the vertical slot fishway studied here provides an adequate quantity of low velocity refuges. Further, sturgeon are capable of station holding to conserve energy in high velocity areas (Adams et al. 2003; Geist et al. 2005). In terms of a time optimisation strategy, the absence of turning basins would be beneficial as the addition of large low velocity regions appears delay passage presumably due to the absence of high velocity cues.

Lake sturgeon exhibited a range of swimming speeds during fishway passage in this study. This is unsurprising given the range of water velocities likely encountered, although previous data indicates that even when faced with a constant water velocity, swimming speed also varies over short timescales (Chapter 4). In a theoretical simulation of the energetic cost of passage through a fishway by Pacific salmon (*Onchorhynchus* spp.), Khan (2006) assumed a constant swimming speed of 3 m s^{-1} regardless of the velocity encountered. A constant swimming speed represents a simplistic approach as it does not require any gait adjustment by the individual, although results in constant changes in groundspeed based on the velocities encountered. In the current study this would require that the swimming speed of any individual was greater than the highest water velocity (~1.7 m s^{-1} through vertical slots) to maintain an overall positive groundspeed and result in net upstream movement, resulting in U_{crit} being exceeded 100% of the time. Maintaining a constant swimming speed through varying water velocities likely represents a poor strategy, however, as distance in relation to endurance is not optimised (Castro-Santos 2005). We were unable to establish whether lake sturgeon in the current study exhibited a distance optimising strategy, as the actual paths selected and water velocities encountered remain unknown, although adaptation of a random movement path scenario (McElroy et al. 2012) represents a potential solution.

We assumed purely aerobic metabolism of energy stores occurred during swimming by lake sturgeon in this study. There was some evidence to suggest an occasional anaerobic contribution and thus our energy expenditure estimates are likely conservative. We used the proportion of time respective U_{crit} values were exceeded as an approximate indicator of the anaerobic contribution to swimming. Lake sturgeon rarely exceeded U_{crit}, and typically not for extended periods, however anaerobic contributions to swimming and the corresponding energy expended can add substantial errors to energy budgets. Burgetz et al. (1998) identified that an anaerobic contribution to metabolism is required to support swimming at speeds as early as 70% of U_{crit} in rainbow trout (*O.*

mykiss), corresponding to 1.48 body lengths s^{-1}. Using this information, the authors provide values that can be added as an additional anaerobic tax to total energy expenditure. For example, the anaerobic contribution can be as high as 205% of oxygen consumption for 30 min of swimming at 100% of U_{crit} when including the necessary post-swimming recovery phase (i.e. oxygen debt) (Burgetz et al. 1998). Similar values do not occur for lake sturgeon, or any sturgeon species, due in part to problems associated with a lack of volitional high speed swimming in swim tunnels and also the physical size of adults of most species. Subsequently we used previously determined calibrations of swimming speed-ODBA based on volitional swimming of lake sturgeon in a large open channel flume to generate swimming speed values well above those previously determined from forced swimming, and more indicative of field estimates (Chapter 4). As a result, the oxygen consumption-swimming speed relationship was borrowed from a previous study (McKinley and Power 1992) and linearly extrapolated to the speeds observed in our calibration study. This requires a number of assumptions, and probably represents an underestimate of energy expenditure particularly at higher swimming speeds, although represents use of the best available data.

We used animal-borne accelerometer data loggers in this study in an example application of fundamental science to inform an applied issue. The use of animal-borne accelerometers is rapidly increasing, and although applied applications are lagging, recent examples include determination of energy expenditure by fish in aquaculture to inform feed rations and stocking densities (Yasuda et al. 2012) and examination of locomotor impairment following a recreational fishing simulation (Brownscombe et al. 2013). Here we provide evidence of the first use of this technology to inform water resource development and specifically fishway design. While the differences in energy expenditure observed were not typically indicative of fishway passage success in lake sturgeon, we were able to quantify the energetic cost of passage. Considering fishways should be designed so as to minimise energy expenditure (Castro-Santos and Haro 2010), we identified that the absence of turning basins in the current fishway design would reduce passage time and correspondingly reduce energy expenditure. Given lake sturgeon have likely evolved for short distance migrations that are not typically energetically demanding, supported by evidence of a comparatively reduced ability for high speed swimming, the energetic costs quantified here may have potential fitness consequences.

Tables

Table 5.1 Summary information for lake sturgeon (n=30) attempting to pass a vertical slot fishway.

Fish ID	TL (mm)	Weight (kg)	Attempts	Maximum upstream location (basin)	Pass /Fail	Time in fishway (h)	Proportion of time (%) exceeding U_{crit} in fishway	Total swimming energy expenditure in fishway (J kg^{-1})	Rate of energy expenditure (J kg^{-1} h^{-1})
1	1214	8.54	2	2	1	2.86	2.1	2013	703.85
2	1330	14.66	3	13	0	2.49	0.5	1845	740.96
3	1295	12.52	8	2	1	6.25	0.9	3661	585.76
4	1209	10.80	5	14	0	0.58	2.2	418	720.69
5	1124	9.16	1	13	0	0.82	1.7	502	612.20
6	1398	18.03	1	14	0	0.03	6.8	38	1266.67
7	1100	6.50	3	14	0	0.45	1.2	259	575.56
8	1337	16.21	5	12	0	0.41	2.7	322	785.37
9	1379	16.71	2	15	0	1.93	0.1	946	490.16
10	1075	6.50	12	9	0	2.90	1.3	2142	738.62
11	1361	13.63	1	15	0	0.17	0.4	134	788.24
12	1267	9.80	1	15	0	0.08	0.3	50	625.00
13	1072	6.05	5	10	0	7.89	1.1	5544	702.66
14	1386	13.07	6	2	1	1.45	0.8	883	608.97
15	1555	24.61	6	4	0	12.26	0.1	7330	597.88
16	1092	5.93	1	14	0	0.03	8.4	33	1100.00
17	1221	8.76	5	9	0	6.94	0.4	3883	559.51
18	1343	14.56	2	6	0	1.63	0.5	1138	698.16
19	1206	10.43	16	2	1	7.89	0.9	5540	702.15
20	1417	16.23	2	2	1	4.53	0.8	2853	629.80
21	1116	6.84	7	3	0	2.31	2.4	1661	719.05
22	1234	10.52	1	15	0	0.04	2.8	38	950.00
23	1351	16.16	22	13	0	2.28	0.2	1527	669.74
24	1471	19.21	1	15	0	0.10	0.6	75	750.00

25	1144	8.03	1	12	0	0.32	1.5	226	706.25
26	1216	9.91	3	13	0	1.79	0.5	996	556.42
27	1379	13.55	3	2	1	3.59	0.8	2594	722.56
28	1197	9.11	12	2	1	5.58	1.5	4058	727.24
29	975	4.40	2	9	0	2.14	2.0	1222	571.03
30	1099	6.17	2	13	0	0.53	1.6	423	798.11

Table 5.2 Fishway section characteristics and lake sturgeon mean (± SE) groundspeed, swimming speed and median (range) energy use during passage though a single fishway basin located within a section of fishway.

	Fishway section				
	1	2	3	4	5
Fishway basins	16, 15, 14	13	12, 11, 10, 9	8	7, 6, 5, 4, 3
Basin type	regular	turning	regular	turning	regular
Groundspeed (m s^{-1})	0.16 ± 0.01	0.02 ± 0.00	0.15 ± 0.02	0.02 ± 0.00	0.21 ± 0.03
Bonferroni contrasts of groundspeed	A	B	A	B	A
Swimming speed (m s^{-1})	0.59 ± 0.01	0.52 ± 0.01	0.65 ± 0.01	0.55 ± 0.02	0.74 ± 0.03
Bonferroni contrasts of swimming speed	C	D	B	C D	A
COT (J kg^{-1} m^{-1})	1.90 (0.50–52.63)	11.03 (2.47–83.55)	2.53 (0.71–63.81)	10.78 (5.65–27.28)	1.84 (0.88–101.04)
Bonferroni contrasts of energy use	B	A	B	A	B

Table 5.3 Linear mixed effect model coefficient estimates for lake sturgeon passage through five different fishway sections.

Response	Parameter	Value	SE	*df*	*t*	*P*
Groundspeed ($m\ s^{-1}$)	(Intercept)	0.0035	0.0765	267	0.0462	0.9632
	Section 2	-0.1330	0.0089	267	-13.7528	<0.0001
	Section 3	0.0127	0.0184	267	0.6935	0.4886
	Section 4	-0.1149	0.0108	267	-10.6391	<0.0001
	Section 5	0.0689	0.0330	267	2.0848	0.0380
	Temperature	0.0189	0.0080	267	2.3824	0.0179
	Pass-fail: pass	-0.0271	0.0093	110	-2.9073	0.0044
Swimming speed ($m\ s^{-1}$)	(Intercept)	0.3905	0.0665	267	5.8663	<0.0001
	Section 2	-0.0592	0.0104	267	-5.6944	<0.0001
	Section 3	0.0646	0.0123	267	5.2559	<0.0001
	Section 4	-0.0322	0.0226	267	-1.4235	0.1558
	Section 5	0.1641	0.0325	267	5.0553	<0.0001
	Temperature	0.0228	0.0069	267	3.2847	0.0012
COT ($J\ kg^{-1}\ m^{-1}$)	(Intercept)	0.8246	0.0853	268	9.6654	<0.0001
	Section 2	1.5515	0.1653	268	9.3879	<0.0001
	Section 3	0.2721	0.1255	268	2.1683	0.0310
	Section 4	1.5974	0.2972	268	5.3749	<0.0001
	Section 5	0.3432	0.1828	268	1.8775	0.0615

Table 5.4 Parameter estimates for logistic regression models assessing the effect of energy use variables on the probability of (binary) successful fishway passage by lake sturgeon.

	Variable		
	Total energy used (cal kg^{-1})	Rate of energy use (cal kg^{-1} h^{-1})	COT (cal kg^{-1} m^{-1})
Constant: β ± SE	-2.134 ± 0.717	1.090 ± 2.727	-1.493 ± 0.688
P	0.003	0.689	0.030
Variable: β ± SE	0.001	-0.003 ± 0.004	0.020 ± 0.034
P	0.054	0.407	0.554
Odds ratio, 95% CI	1.001, 1.000–1.001	0.997, 0.988–1.003	1.020, 0.947–1.095
Model fit	χ^2 (1) = 4.204, *P* = 0.040	χ^2 (1) = 0.806, *P* = 0.369	χ^2 (1) = 0.338, *P* = 0.561

Figures

Figure 5.1 Schematic of the Vianney-Legendre vertical slot fishway on the Richelieu River in Quebec, Canada. Numbers 1–5 indicate fishway sections and corresponding basins. Distance metrics, corresponding to locations of PIT antennas, indicate the cumulative minimum transit distance between successive fishway basins (beginning at 0 m) and were used in calculations of distance moved and location.

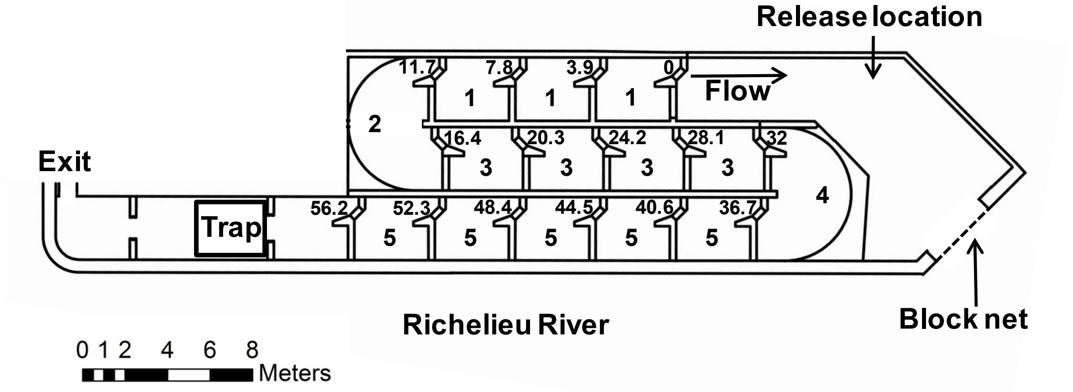


Figure 5.2 Time series passage profile of a lake sturgeon (ID 14; 1386 mm TL, 13.07 kg) ascending a vertical slot fishway, represented by a) the dynamic component of acceleration (presented for separate X (—), Y (—) and Z (—) axes, with a +2 *g* and -2 *g* added to X and Z axes respectively for graphical purposes only; b) swimming speed and cumulative energy use for times when the sturgeon was within the fishway, where swimming speed was derived from the linear relationship between speed and the absolute sum of the dynamic component of all three acceleration axes (overall dynamic body acceleration; ODBA), and; c) approximate spatial location within the fishway, expressed as distance from fishway entry (0 m) until successful passage (56.2 m), with location determined using a passive integrated transponder antennas located on each vertical slot baffle (n=15).

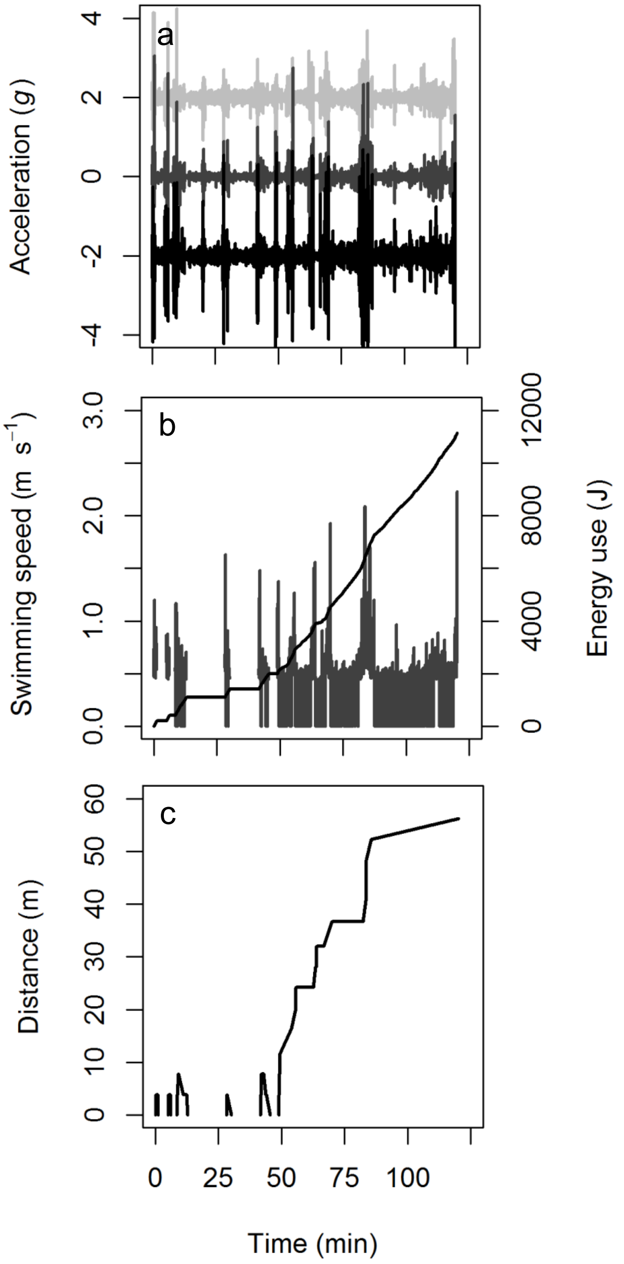


Figure 5.3 Frequency distribution of lake sturgeon (n=30) swimming speeds (m s^{-1}) through pooled basins located in different sections (1–5) of a vertical slot fishway. The black dashed line indicates the critical swimming speed (U_{crit}) of the average sized sturgeon in this study, and grey dashed lines indicate minimum and maximum U_{crit} values for the smallest and largest individuals, respectively.

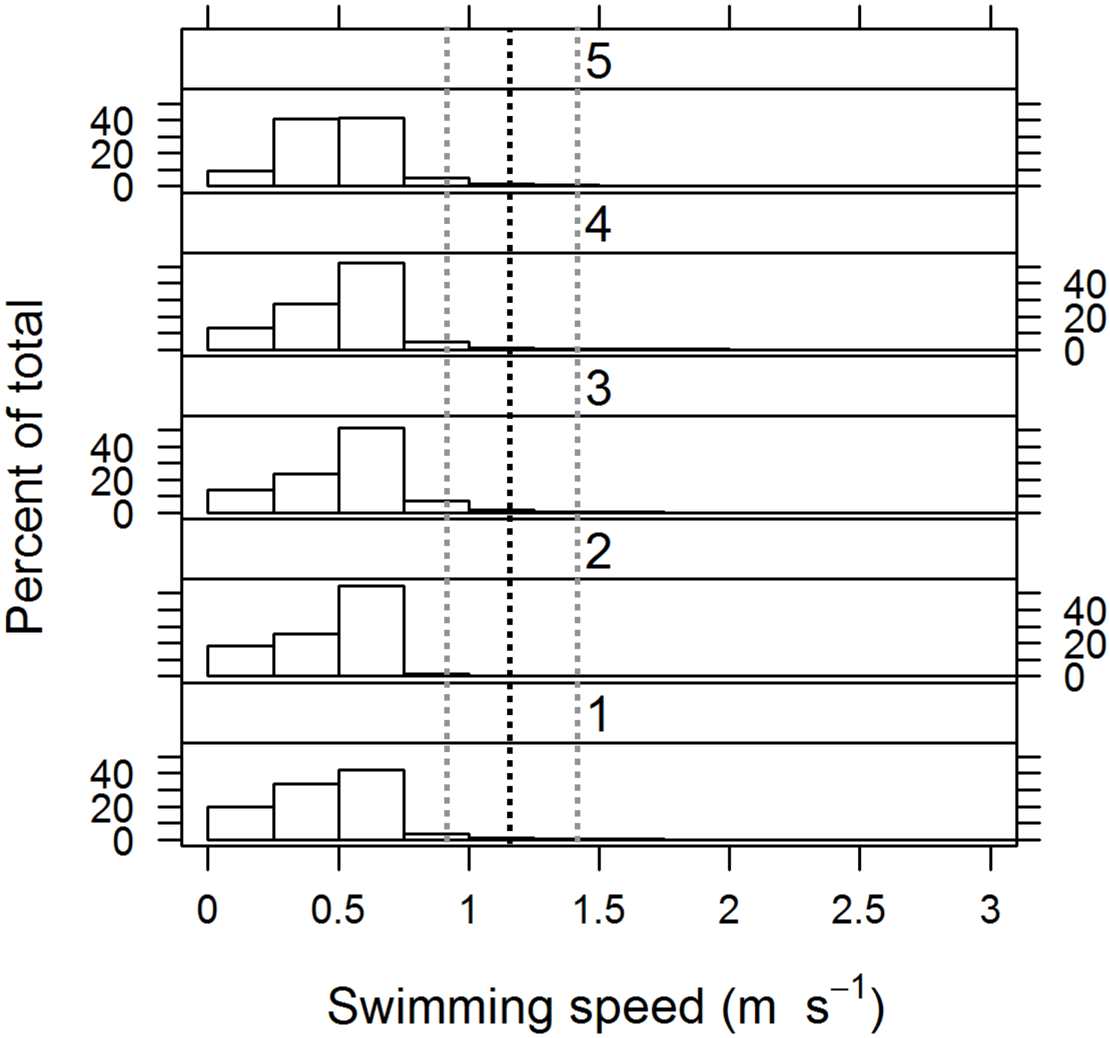


Figure 5.4 Frequency distribution of swimming duration during upstream passage through fishway sections by lake sturgeon, indicating where a) individual critical swimming speed (U_{crit}) was exceeded and, b) 80% of U_{crit} was exceeded.

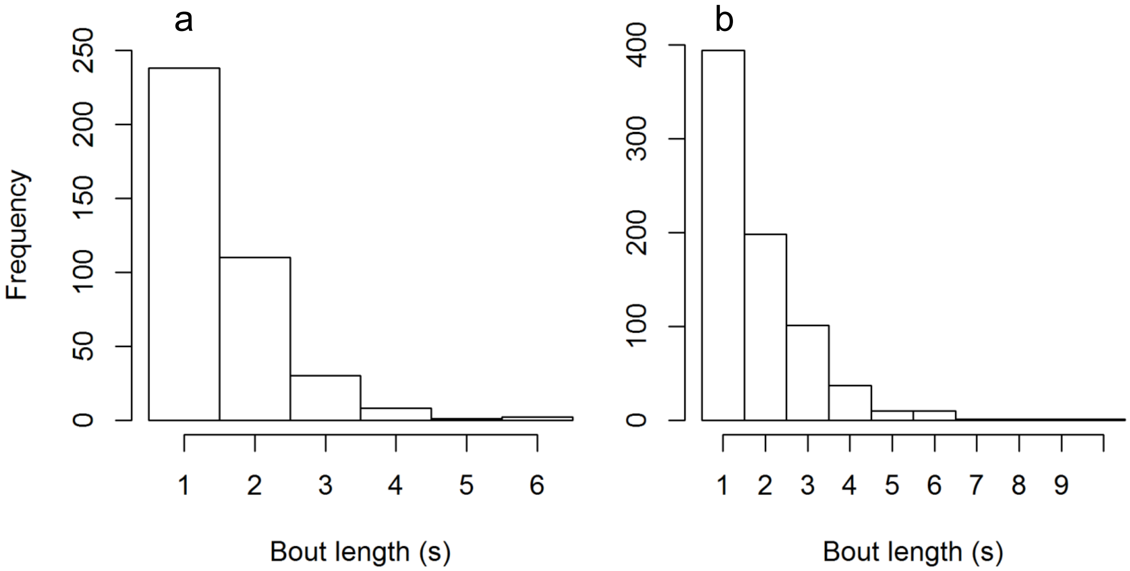


Figure 5.5 Model predictions (± 95% confidence intervals) resulting from linear mixed effects model analysis of lake sturgeon a) groundspeed (where ■ indicates a failed passage attempt, and ■ indicates a successful passage attempt), b) median swimming speed and, c) net cost of transport (COT) during passage through a single fishway basin nested within sections (1–5) of a vertical slot fishway. Water temperature was a significant covariate in models of groundspeed and swimming speed (*see* Table 5. 3), although was held at its average value in model predictions for graphical purposes only.

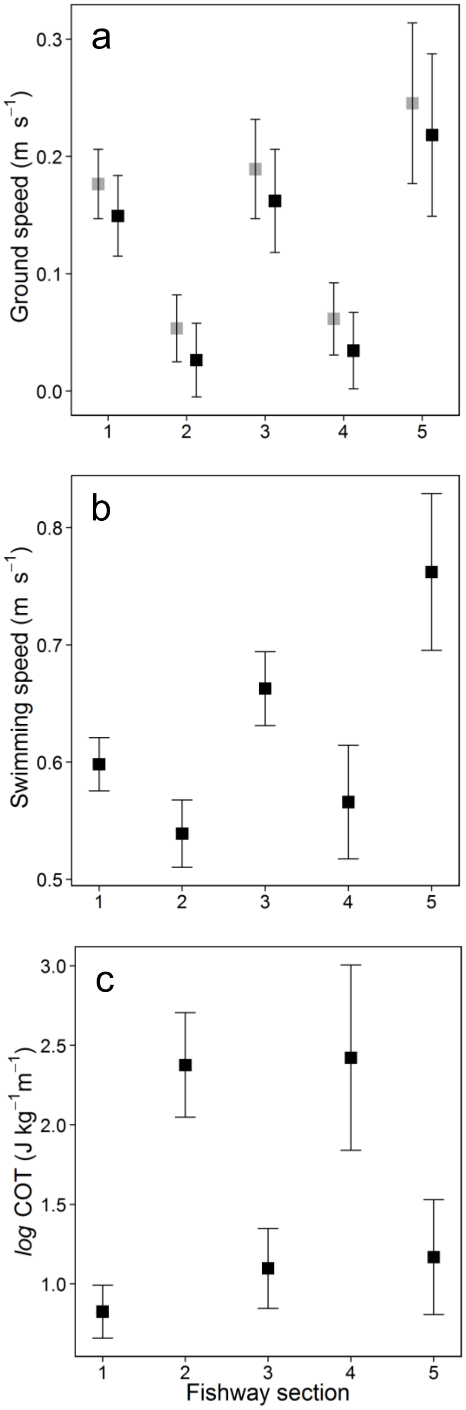


Figure 5.6 Linear relationships between a) total time in the fishway and total energy used for unsuccessful (□,---) and successful individuals (○, ─), b) maximum upstream location and total energy used within the fishway for unsuccessful (□) and successful individuals (○), with ─ indicating the overall best linear fit, c) cumulative upstream distance moved and the corresponding energy used for unsuccessful (□,---) and successful individuals (○, ─), and d) total distance moved and total energy used within the fishway for unsuccessful (□,---) and successful individuals (○, ─).

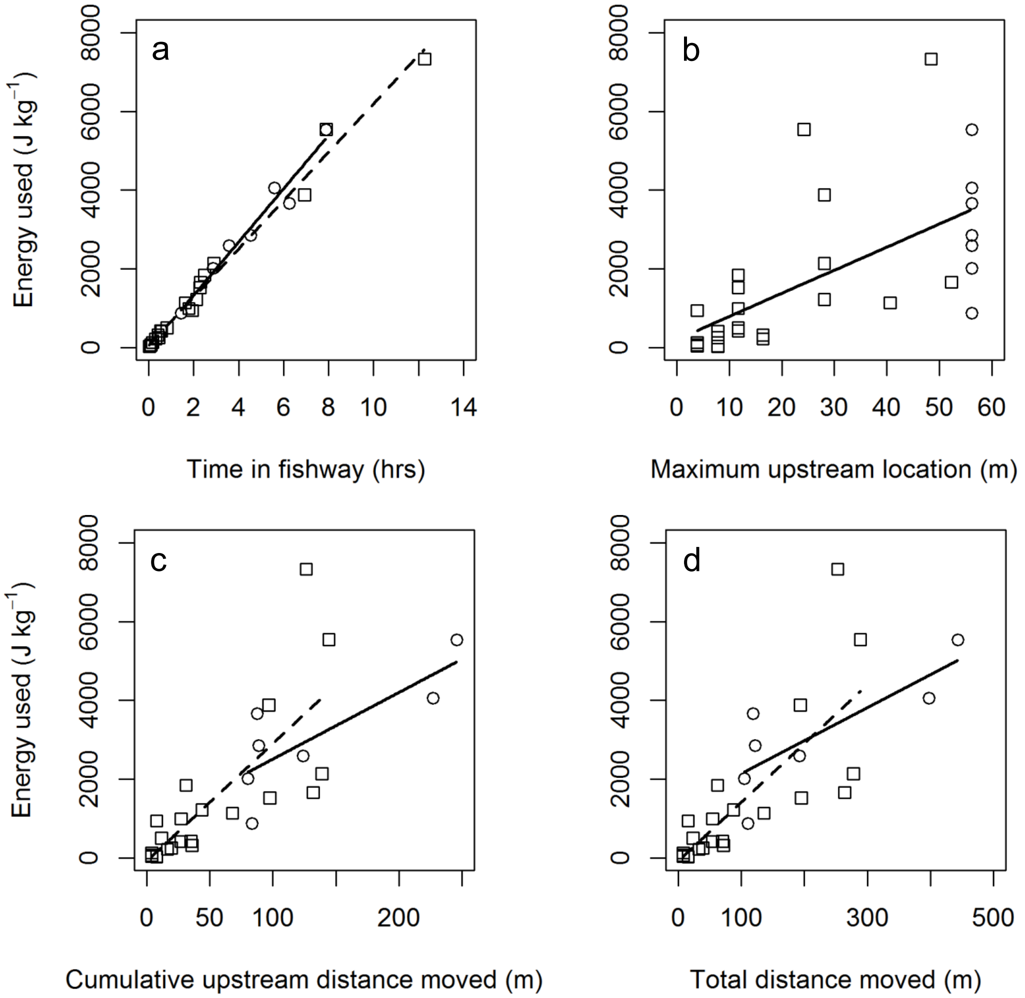
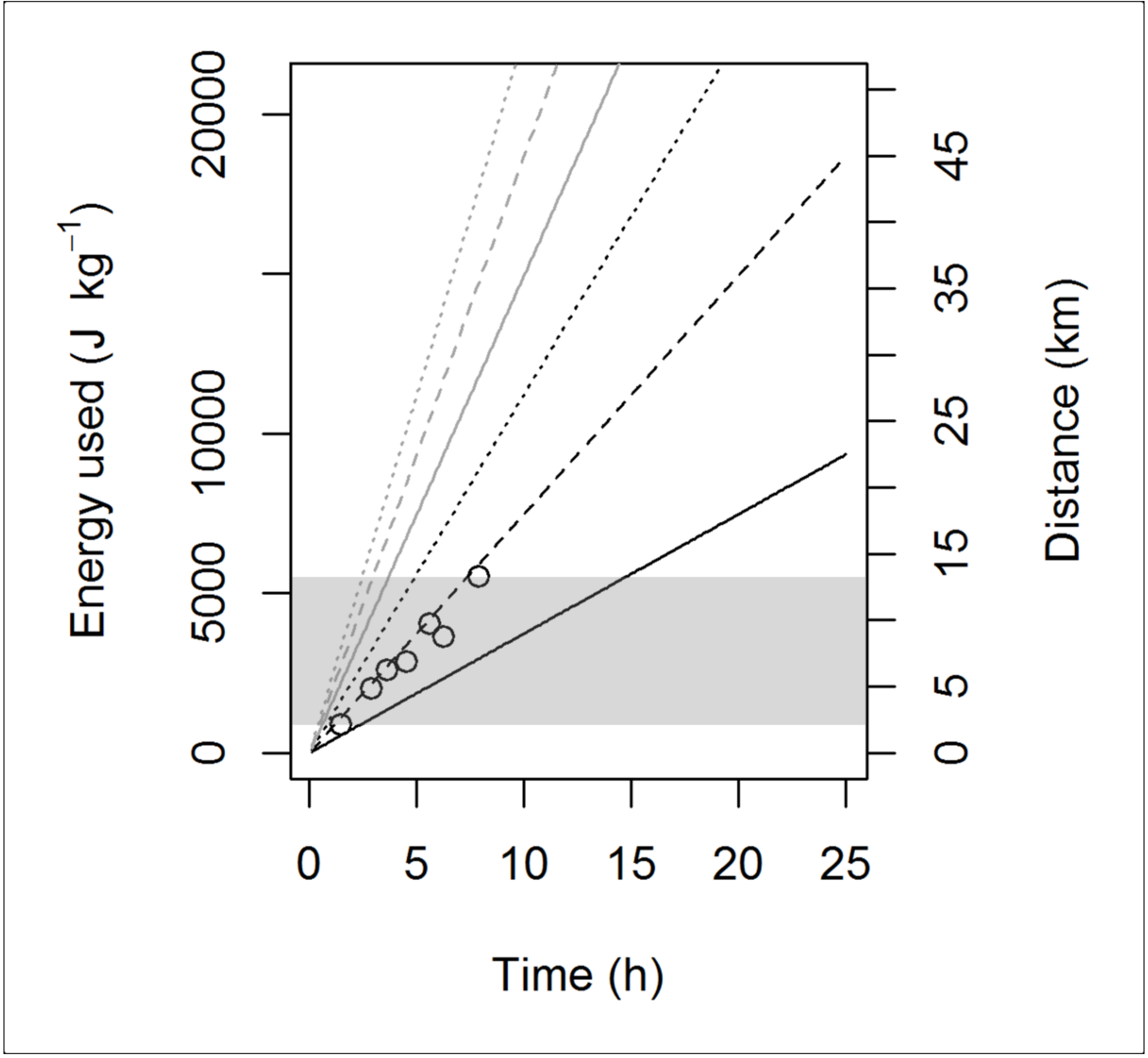


Figure 5.7 Comparison of the energy expenditure and corresponding distance travelled over time for lake sturgeon swimming in lentic water at constant swimming speeds of 0.25 m s^{-1} (—), 0.50 m s^{-1} (---), 0.75 m s^{-1} (···), 1.00 m s^{-1} (—), 1.25 m s^{-1} (---) and 1.50 m s^{-1} (···), with the range of observations from the present study indicated (grey shading) as well as specific values for successful fishway passage (○).



Chapter 6. General discussion and future research directions

Maintaining connectivity within riverine systems is critical to ensure the perpetuation of migratory fish. However, a global reliance on water resource development has resulted in the disconnection of key migratory pathways for numerous fish species, leading to population declines. The broad aim of this thesis was to apply an interdisciplinary approach utilizing aspects of pure and applied science to investigate fishway passage by lake sturgeon in an effort to provide a transferable model for future studies to improve our understanding of fishway use by migratory species. In Chapter 2 I sought to identify key lake sturgeon spawning habitats downstream of a dam equipped with a fishway using multiple lines of evidence, to determine whether attraction and passage efficiency of a fishway limit reproductive success in this population, thus providing a more holistic view of fishway passage in a system-wide context as recommended by Roscoe and Hinch (2010). In Chapter 3 I quantified fishway passage efficiency and examined the location specific behaviour of lake sturgeon within the fishway to elucidate the factors that lead to successful passage, given that only a single fishway field study (i.e. Parsley et al. 2007) exists for any sturgeon species and subsequently our knowledge of sturgeon behaviour and passage within fishways is severely lacking. In Chapter 4 I developed new methods for the field quantification of sturgeon swimming activity and energy use using accelerometers, given that the comparatively poor swimming ability of sturgeon is thought to limit their ability to traverse high velocity areas and complex flows such as those found within fishways (Peake et al. 1997). Chapter 5 demonstrated a field application of the method, enabling quantification of the swimming activity and energy use of successful and unsuccessful passage events. Each chapter built upon previous knowledge of the species and a number of new methods were also either developed or combined for the first time to answer chapter-specific research questions.

The identification of key habitats such as the location of spawning sites is an essential step in the protection and recovery of sturgeon species worldwide (Haxton 2006). In Chapter 2 I applied multiple lines of evidence to confirm spawning and characterize a previously unidentified spawning population of lake sturgeon. Daily estimates of the spawning population indicated a high abundance of lake sturgeon at the site downstream of the dam and fishway. Further, residency of spawners was typically short, spawning took in similar habitats and at comparable temperature to previous studies and levels of circulating steroids coincided with known spawning events. In the absence of fertilized eggs, each of the methods applied in this study (i.e. mark-recapture, radio telemetry, non lethal blood sampling) would have provided an indication of the presence of a spawning site. By combining these methods I was able to not only confirm a new lake sturgeon spawning site but also to provide a methodological framework for future studies to apply in the absence of egg capture. In addition, identification of a lake sturgeon spawning site downstream of the dam and fishway provided key information for interpreting fishway passage. Whilst no upstream passage events were observed from radio tagged individuals, the number of individuals radio tagged (n=51) represents a small proportion of the total number of sturgeon captured, as well as a small proportion of the daily population estimates. Further, the study was conducted during atypical conditions (high water level) resulting in the fishway being inoperable for the majority of the study (and spawning) period. Interestingly, once water levels dropped and the fishway was operable a number of sturgeon were captured in a trap operated at the upstream end of the fishway. Taken together with previous observations of fishway trap capture of lake sturgeon in preceding years during the spawning period (up to 50 individuals) it appears likely that some individuals utilize suitable spawning habitat ~50 km upstream of the dam. Alternatively the presence of sturgeon within the fishway may solely be a result of the high abundance of spawners immediately downstream of the dam, as individuals actively searching for mates or suitable spawning habitats may enter the fishway. Nonetheless, it is clear that the motivation to pass upstream via the fishway may not exist for all individuals. In addition, assuming that the data collected under these atypical conditions are representative for other years then fishway attraction and passage efficiency may not limit reproductive success in the Richelieu River, although this remains unknown and represents an important knowledge gap.

In Chapter 3 I quantified the passage efficiency of the fishway for lake sturgeon. This information represents the minimum requirement for effectiveness monitoring of fishways, although is surprisingly sparse in the literature (Roscoe and Hinch 2010; Bunt et al. 2012; Noonan et al. 2012; Cooke and Hinch 2013; Hatry et al. 2013). The methodology used (i.e. capture downstream and release into the fishway) was somewhat artificial in the quantification of passage efficiency, and also precluded calculation of attraction efficiency which is an important component of assessing fishway performance (Cooke and Hinch 2013). However this study represents only the second field evaluation of a fishway for sturgeon, and the first for this species. Taken together with the results of Chapter 2 it is likely that the motivation to move through the fishway to access upstream spawning areas was not applicable for all individuals. Nonetheless the methodology did enable quantification of passage duration and indentified that passage through turning basins was delayed, and that the first turning basin represented a location of high failure rate. Previous studies have identified that the presence of turning basins in fishways result in passage failure or delays for other species (e.g. Bunt et al. 2000; White et al. 2011), although not for sturgeon. Further, fishway passage requires individuals to ascend under their own locomotor ability, and sturgeon are considered to have a reduced ability for high speed swimming. Given that fishways have highly complex hydraulic conditions including high turbulence and fast water velocities, it appeared likely that the variability in passage success and duration may be a result of differential path selection and subsequent energy use.

The use of a large open channel flume to generate volitional swimming speed estimates for lake sturgeon in Chapter 4 provided new data to indicate that sturgeon are capable of swimming at speeds (and subsequently over distances) in excess of those previously observed in captivity. This result appears consistent with a growing body of literature indicating that traditionally used enclosed swim tunnels inhibit the swimming ability of numerous species, and that the transfer of laboratory derived swimming models to the field may be problematic (e.g. Peake 2004; Tudorache et al. 2007; Castro-Santos et al. 2013). Taken together, these results indicate that previously developed predictive relationships between fishway length and maximum allowable velocities (e.g. Peake et al. 1997 for lake sturgeon) may be conservative. Further, the relationships developed between swimming speed estimates and accelerometer derived metrics of activity indicated the applicability for using animal-borne accelerometers to estimate field-relevant swimming activity in lake sturgeon. By extension the indirect quantification of energy use is also achievable with accelerometers as dynamic movement of the animal-attached device is directly related to muscular contraction, and thus energy expenditure (Gleiss et al. 2011). However, current limitations based on the physical size of sturgeon, their unwillingness to swim in respirometers at field-relevant speeds, as well the problems discussed above with the use of swim tunnels in general required extrapolation of a previously established relationship which is not without its assumptions.

Field application of animal-borne accelerometers attached to sturgeon swimming through the fishway in Chapter 5 identified that sturgeon rarely use high speed swimming to traverse the fishway and that energy use was not predictive of successful passage, although fishway passage does result in individuals incurring a considerable energetic cost. In addition, both slow groundspeeds and swimming speeds through turning basins resulted in a considerably higher energetic cost for sturgeon in comparison to regular fishway basins. Energy use was more closely linked with the cumulative amount of time individuals spent within the fishway rather than any activity specific high energy use behaviour. Delayed passage has been demonstrated to result in reproductive failure for numerous salmonids (Caudill et al. 2007; Roscoe et al. 2011), presumably as a result of depletion of energy stores. The post-passage reproductive success of lake sturgeon was not monitored in this study. Lake sturgeon typically undertake short distance migrations (Auer 1996*a*) and presumably allocate less energy to this behaviour than longer distance migrants (e.g. Crossin et al. 2004). Thus any additional energetic cost may reduce reproductive success.

Collectively this thesis represents a comprehensive body of work that adds to the previously unknown information regarding fishway use by sturgeon. Further, this thesis moved beyond simple effectiveness monitoring and explored the mechanistic basis for failed passage and also incorporated newly acquired knowledge on the presence of a spawning site downstream of the fishway to provide a broader perspective on the factors that lead to successful fishway passage. This type of information is frequently advocated for, although often lacking in the literature (Roscoe and Hinch 2010; Cooke and Hinch 2013).

No causal mechanisms were identified during this thesis that adequately explained the inter-individual variation in fishway passage observed, although clearly individual motivation was a confounding factor given the presence of a large spawning site downstream of the dam and the fishway. Other endogenous (i.e. internal state, navigational ability) or exogenous (i.e. fine scale hydraulics) factors possibly influence passage success, although these remain unknown and represent an area for future research on sturgeon and numerous other species. I placed a strong emphasis on energy use given the previous knowledge of the comparatively poor swimming ability of sturgeon (Peake et al. 1997). I hypothesized that inter-individual differences in path selection would result in differential energy use and subsequently lead to separating successful and unsuccessful individuals, as has been found for other species (e.g. sockeye salmon; Hinch and Bratty 2000). In retrospect this may in part be unsubstantiated given previous models of sturgeon swimming generated through forced swimming in confined tunnels likely underestimate their actual ability based on the findings presented here. Regardless of any predictive relationships, it still appears that fishway passage may indeed be energetically costly for lake sturgeon and this is of concern given that fishways should be designed so as to minimize energy expenditure (Castro-Santos and Haro 2010) and that passage delays can result in direct fitness consequences (Caudill et al. 2007).

A clear management application stemming from this work relates to the presence of turning basins in fishways. The presence of the two turning basins in the Vianney-Legendre fishway provided for a more compact structure, thus enabling the entrance of the fishway to be located closer to the dam face, potentially improving fishway attraction efficiency. Further, turning basins also provided an area of low velocity to facilitate recovery of energy stores during passage and have been advocated for sturgeon by others (e.g. Webber et al. 2007). The results presented here indicate that the absence of turning basins in the vertical slot fishway studied would result in increased passage efficiency as well as facilitating faster passage, resulting in an overall reduction in energy expenditure. The associated implications on fishway attraction efficiency due to having the entrance of the fishway located further from the dam entrance as a result of turning basins not being installed in this or future fishways remains unknown, however, and represents an important knowledge gap.

Fishways remain a promising solution for maintaining connectivity in fragmented systems and this thesis serves as a useful model for gaining insight into fishway effectiveness for a single species. It also highlights the challenges and necessary knowledge required to ensure optimal habitats are available to all species. For example, the knowledge generated on lake sturgeon in this thesis may not be transferable to any or all of the other ~35 fish species that use this fishway annually. Further, this thesis did not explore other options for facilitating upstream passage of sturgeon past barriers including other types of fishways, truck and transport or fish lifts. The significant interest in this research project from provincial and federal government agencies as well as hydropower utilities is indicative of the relevance of this work as well as the growing appreciation that the historical one-size-fits-all strategy is outdated. I am optimistic that the information generated as a result of this thesis is transferable is other locations and species, although it is likely that each case study will present its own set of unique challenges. Indeed even the dam removal movement along the Atlantic and Pacific coasts of the US is not without challenges (*see* Brown et al. 2013) and the benefits of such actions may not be observed for some time to come.

As with any research, a number of knowledge gaps were identified throughout the course of this thesis, that if addressed would broadly enhance our understanding of fish passage if applied to other species, or more specifically to sturgeon. Quantifying the energetics of an entire migration for sturgeon would place the energetic expenditure associated with fishway passage in a broader context. Notable examples of this approach exist for some species of Pacific salmon and American shad. Transferring this approach to sturgeon would first require the development of new swimming speed-oxygen consumption relationships at more field relevant speeds and using new methods considering that appropriate speeds are not achieved using traditional laboratory techniques, although the methods developed in Chapter 4 show promise for the field determination of energy use. Further, during the course of this thesis I was unable to determine the attraction efficiency of this fishway for sturgeon, although I have previously discussed the complications in differentiating among individuals motivated to move upstream when a spawning site exists downstream. The factors contributing to attraction efficiency are generally poorly understood for most species. Development of methods for examining the fine scale interactions between fish and hydraulics would enhance our knowledge of both attraction efficiency and passage efficiency based on path selection, and although the techniques exist (e.g. dual frequency sonar, underwater video) they are often limited to laboratory applications rather than field observations.

References

Adams SR, Adams GL, Parsons GR (2003) Critical swimming speed and behavior of juvenile shovelnose sturgeon and pallid sturgeon. Trans Am Fish Soc 132:392–397

Agostinho AA, Gomes LC, Fernandez DR, Suzuki HI (2002) Efficiency of fish ladders for neotropical ichthyofauna. River Res Appl 18: 299–306

Alexander RM (1999) Energy for animal life. Oxford University Press: Oxford UK

Alexandre CM, Quintella BR, Silva AT, Mateus CS, Romão F, Branco P, Ferreira MT, Almeida PR (2013) Use of electromyogram telemetry to assess the behavior of the Iberian barbel (*Luciobarbus bocagei* Steindachner, 1864) in a pool-type fishway. Ecol Eng 51:191–202

Auer NA (1996*a*) Importance of habitat and migration to sturgeons with emphasis on lake sturgeon. Can J Fish Aquat Sci 53(S1):152–160

Auer NA (1996*b*) Response of spawning lake sturgeons to change in hydroelectric facility operation. Trans Am Fish Soc 125:66–77

Baker DW, Peake SJ, Kieffer JD (2008) The effect of capture, handling, and tagging on haematological variables in wild adult lake sturgeon. N Am J Fish Manage 28:296–300

Barannikova IA, Bayunova LV, Semenkova TB (2004) Serum levels of testosterone, 11-ketotestosterone and oestradiol-17β in three species of sturgeon during gonadal development and final maturation induced by hormonal treatment. J Fish Biol 64:1330–1338

Baras E, Westerloppe L, Melard C, Philippart J-C (1999) Evaluation of implantation procedures for PIT-tagging juvenile Nile tilapia. N Am J Fish Manage 61:246–251

Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA (2003) Collapse and conservation of shark populations in the Northwest Atlantic. Science 299:389–392

Beamish FWH (1978) Swimming capacity. In: Hoar WS, Randall DJ (eds) Fish physiology, Vol. 7. Academic Press Inc., New York. Pp. 101–172.

Bemis W, Kynard B (1997) Sturgeon rivers: an introduction to acipenseriform biogeography and life history. Environ Biol Fishes 48:167–183

Bender DJ, Contreras TA, Fahrig L (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79:517–533

Birstein V (1993) Sturgeon and paddlefishes: threatened fishes in need of conservation. Conserv Biol 7:773–782

Boisclair D, Leggett WC (1989) The importance of activity in bioenergetics models applied to actively foraging fishes. Can J Fish Aquat Sci 46:1859–1867

Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. Nature 441:81–83

Breder CM (1926) The locomotion of fishes. Zoologica 4:159–256

Brett JR (1995) Energetics. In: Groot C, Margolis L, Clarke WC (eds) Physiological Ecology of Pacific Salmon. University of British Columbia Press: Vancouver. Pp. 3–68

Brett JR, Groves TDD (1979) Physiological energetics. In: Hoar WS, Randall DJ, Brett JR (eds) Fish Physiology, Vol. 8. Academic Press Inc., New York. Pp. 279–351.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789

Brown JJ, Limburg KE, Waldman JR, Stephenson K, Glenn EP, Juanes F, Jordaan A (2013) Fish and hydropower on the U.S. Atlantic coast: failed fisheries policies from half-way technologies. Conserv Lett 6:280–286

Brownscombe JW, Thiem JD, Hatry C, Cull F, Haak CR, Danylchuk AJ, Cooke SJ (2013) Recovery bags reduce post-release impairments in locomotory activity and behaviour of bonefish (*Albula* spp.) following exposure to angling-related stressors. J Exp Mar Biol Ecol 440:207–215

Bruch RM, Binkowski FP (2002) Spawning behaviour of lake sturgeon (*Acipenser fulvescens*). J Appl Ichthyol 18:570–579

Bunt CM (2001) Fishway entrance modifications enhance fish attraction. Fish Manag Ecol 8:95–105

Bunt CM, Castro-Santos T, Haro A (2012) Performance of fish passage structures at upstream barriers to migration. River Res Appl 28:457–478

Bunt CM, Cooke SJ, McKinley RS (2000) Assessment of the Dunnville fishway for passage of walleyes from Lake Erie to the Grand River, Ontario. J Gt Lakes Res 26:482–488

Bunt CM, Katopodis C, McKinley RS (1999) Attraction and passage efficiency of white suckers and smallmouth bass by two Denil fishways. N Am J Fish Manage 19:793–803

Burgetz IJ, Rojas-Vargas A, Hinch SG, Randall DJ (1998) Initial recruitment of anaerobic metabolism during sub-maximal swimming in rainbow trout (*Oncorhynchus mykiss*). J Exp Biol 201:2711–2721

Burnett NJ, Stamplecoskie KM, Thiem JD, Cooke SJ (2013) Comparison of detection efficiency among three sizes of half duplex passive integrated transponders using manual tracking and fixed antenna arrays. N Am J Fish Manag 33:7–13

Burnham KP, Anderson DR (2002) Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach. Springer-Verlag: New York, USA

Castro-Santos T (2004) Quantifying the combined effects of attempt rate and swimming capacity on passage through velocity barriers. Can J Fish Aquat Sci 61:1602–1615

Castro-Santos T (2005) Optimal swim speeds for traversing velocity barriers: an analysis of volitional high-speed swimming behavior of migratory fishes. J Exp Biol 208:421–432

Castro-Santos T, Haro A (2006) Biomechanics and fisheries conservation. In: Shadwick RE, Lauder GV (eds), Fish physiology, Vol. 23: fish biomechanics. Academic Press: New York US. Pp. 469–523

Castro-Santos T, Haro A (2010) Fish guidance and passage at barriers. In: Domenci P, Kapoor BG (eds) Fish Locomotion: An Eco-Ethological Perspective. Science Publishers: Enfield, NH. Pp 62–89.

Castro-Santos T, Haro A, Walk S (1996) A passive integrated transponder (PIT) tag system for monitoring fishways. Fish Res 28:253–261

Castro-Santos T, Sanz-Ronda FJ, Ruiz-Legazpi J (2013) Breaking the speed limit — comparative sprinting performance of brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). Can J Fish Aquat Sci 70:280–293

Caswell NM, Peterson DL, Manny BA, Kennedy GW (2004) Spawning by lake sturgeon (*Acipenser fulvescens*) in the Detroit River. J Appl Ichthyol 20:1–6

Caudill CC, Daigle WR, Keefer ML, Boggs CT, Jepson MA, Burke BJ, Zabel RW, Bjornn TC, Peery CA (2007) Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality? Can J Fish Aquat Sci 64:979–995

Ceapa C, Williot P, Le Menn F, Davail-Cuisset B (2002) Plasma sex steroids and vitellogenin levels in stellate sturgeon (*Acipenser stellatus* Pallas) during spawning migration in the Danube River. J Appl Ichthyol 18:391–396

Cheong TS, Kavvas ML, Anderson EK (2006) Evaluation of adult white sturgeon swimming capabilities and applications to fishway design. Environ Biol Fishes 77:197–208

Clark TD, Sandblom E, Hinch SG, Patterson DA, Frappell PB, Farrell AP (2010) Simultaneous biologging of heart rate and acceleration, and their relationships with energy expenditure in free-swimming sockeye salmon (*Oncorhynchus nerka*). J Comp Physiol B 180:673–684

Clay CH (1995) Design of Fishways and Other Fish Facilities, (2nd edn). Lewis Publishers: Boca Raton, FL.

Cocherell DE, Kawabata A, Kratville DW, Cocherell SA, Kaufman RC, Anderson EK, Chen ZQ, Bandeh H, Rotondo MM, Padilla R, Churchwell R, Kavvas ML, Cech Jr JJ (2011) Passage performance and physiological stress response of adult white sturgeon ascending a laboratory fishway. J Appl Ichthyol 27:327–334

Colombo RE, Wills PS, Garvey JE (2004) Use of ultrasound imaging to determine sex of shovelnose sturgeon. N Am J Fish Manage 24:322–326

Cooke SJ, Hinch SG (2013) Improving the reliability of fishway attraction and passage efficiency estimates to inform fishway engineering, science, and practice. Ecol Eng 58:123–132

Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Wolcott TG, Butler PJ (2004) Biotelemetry: a mechanistic approach to ecology. Trends Ecol Evol 19:334–343

Cooke SJ, Midwood JD, Thiem JD, Klimley AP, Lucas MC, Thorstad EB, Eiler J, Holbrook C, Ebner BC (2013) Tracking animals in freshwater with electronic tags: past, present and future. Animal Biotelemetry 1:5

COSEWIC (2002) Committee on the Endangered Status of Wildlife in Canada [online]. Available from http://www.cosewic.gc.ca/eng/sct1/SearchResult_e.cfm?commonName=Lake+sturgeon&scienceName=&Submit=Submit [accessed 14 February 2011].

Cowx IG, Welcomme RL (1998) Rehabilitation of rivers for fish. Fishing News Books Ltd.

Craig JM, Papoulias DM, Thomas MV, Annis ML, Boase J (2009) Sex assignment of lake sturgeon (*Acipenser fulvescens*) based on plasma sex hormone and vitellogenin levels. J Appl Ichthyol 25(Suppl. 2):60–67

Crossin GT, Hinch SG, Farrell AP, Higgs DA, Lotto AG, Oakes JD, Healey MC (2004) Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. J Fish Biol 65:788–810

Desrochers D (2009) Validation de l’efficacité de la passe migratoire Vianney-Legendre au lieu historique national du canal de Saint-Ours – saison 2008. Milieu Inc pour Parcs Canada, Québec, Canada, 47 pp. + 3 annexes.

Dettlaff TA, Ginzburg TA, Shmal'gauzen OI (1981) Development of sturgeon: egg maturation, fertilization, embryonic and prelarval development. Nauka Publishers, Moscow.

Dingle H (1996) Migration: the biology of life on the move. Oxford University Press on Demand.

Dumont P, Amours JD, Thibodeau S, Dubuc N, Verdon R, Garceau S, Bilodeau P, Mailhot Y, Fortin R (2011) Effects of the development of a newly created spawning ground in the Des Prairies River (Quebec, Canada) on the reproductive success of lake sturgeon (*Acipenser fulvescens*). J Appl Ichthyol 27:394–404

Dumont P, J Leclerc, Allard J-D, Paradis S (1997) Libre passage des poissons au barrage de Saint-Ours, rivière Richelieu. Québec, ministère de l'Environnement et de la Faune, Direction régionale de la Montérégie, Service de l'aménagement et de l'exploitation de la faune et Direction des ressources matérielles et des immobilisations, Québec et ministère du Patrimoine canadien (Parcs Canada).

Dyer SJ, O'Neill JP, Wasel SM, Boutin S (2002) Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. Can J Zool 80:839–845

Dynesius M, Nilsson C (1994) Fragmentation and flow regulation of river systems in the northern third of the world. Science 266:753–762

Enders EC, Boisclair D, Roy AG (2003) The effect of turbulence on the cost of swimming for juvenile Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 60:1149–1160

Enders EC, Boisclair D, Roy AG (2005) A model of total swimming costs in turbulent flow for juvenile Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 62:1079–1089

Enders E, Pennell C, Booth R, Scruton D (2008) Energetics related to upstream migration of Atlantic salmon in vertical slot fishways. Canadian Technical Report of Fisheries and Aquatic Sciences 2800.

Fahrig L, Pedlar JH, Pope SE, Taylor PD, Wegner JF (1995) Effect of road traffic on amphibian density. Biol Conserv 73:177–182

Field A (2009) Discovering statistics using SPSS, 3rd edn. SAGE Publications Ltd, Thousand Oaks.

Forsythe PS, Crossman JA, Bello NM, Baker EA, Scribner KT (2012*a*) Individual-based analyses reveal high repeatability in timing and location of reproduction in lake sturgeon (*Acipenser fulvescens*). Can J Fish Aquat Sci 69:60–72

Forsythe PS, Scribner KT, Crossman JA, Ragavendran A, Baker EA, Davis C, Smith KK (2012*b*) Environmental and lunar cues are predictive of the timing of river entry and spawning-site arrival in lake sturgeon *Acipenser fulvescens*. J Fish Biol 81:35–53

Fortin R, Dumont P, Guénette S (1996) Determinants of growth and body condition of lake sturgeon (*Acipenser fulvescens*). Can J Fish Aquat Sci 53:1150–1156

Fortin R, Mongeau J-R, Desjardins G, Dumont P (1993) Movements and biological statistics of lake sturgeon (*Acipenser fulvescens*) populations from the St. Lawrence and Ottawa River system, Quebec. Can J Zool 71:638–650

Fryxell JM, Sinclair ARE (1988) Causes and consequences of migration by large herbivores. Trends Ecol Evol 3:237–241

Fuzzen M, Bernier NJ, Van Der Kraak G (2011) Stress and Reproduction. In: Norris DO, Lopez KH (eds) Hormones and Reproduction in Vertebrates, Vol 1: Fishes. Elsevier, London. Pp.103–117.

Geist DR, Brown RS, Cullinan V, Brink SR, Lepla K, Bates P, Chandler JA (2005) Movement, swimming speed, and oxygen consumption of juvenile white sturgeon in response to changing flow, water temperature, and light level in the Snake River, Idaho. Trans Am Fish Soc 134:803–816

Geist DR, Brown RS, Lepla K, Chandler JA (2002) Practical application of electromyogram radiotelemetry: the suitability of applying laboratory-acquired calibration data to field data. North Am J Fish Manage 22:474–479

Gleiss AC, Dale JJ, Holland KN, Wilson RP (2010) Accelerating estimates of activity-specific metabolic rate in fishes: Testing the applicability of acceleration data-loggers. J Exp Mar Biol Ecol 385:85–91

Gleiss AC, Wilson RP, Shepard ELC (2011) Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. Meth Ecol Evol 2:23–33

Gowans ARD, Armstrong JD, Priede IG, Mckelvey S (2003) Movements of Atlantic salmon migrating upstream through a fish-pass complex in Scotland. Ecol Freshw Fish 12:177–189

Grafen A, Hails R (2002) Modern statistics for the life sciences. Oxford University Press, Oxford, UK.

Gresh T, Lichatowich J, Schoonmaker P (2000) An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries 25:15–21

Guénette S, Fortin R, Rassart E (1993) Mitochondrial DNA variation in lake sturgeon (*Acipenser fulvescens*) from the St. Lawrence River and James Bay drainage basins in Québec, Canada. Can J Fish Aquat Sci 50:659–664

Halsey LG, Shepard ELC, Wilson RP (2011) Assessing the development and application of the accelerometry technique for estimating energy expenditure. Comp Biochem Physiol Part A Mol Integr Physiol 158:305–314

Hammer C (1995) Fatigue and exercise tests with fish. Comp Biochem Physiol Part A: Physiol 112:1–20

Haro A, Castro-Santos T, Noreika J, Odeh M (2004) Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers. Can J Fish Aquat Sci 61:1590–1601

Hasler CT, Pon LB, Roscoe DW, Mossop B, Patterson DA, Hinch SG, Cooke SJ (2009) Expanding the "toolbox" for studying the biological responses of individual fish to hydropower infrastructure and operating strategies. Environ Rev 17:179–197

Hatin D (1999) Déplacements et caractéristiques du stock reproducteur d'esturgeon noir (*Acipenser oxyrinchus*) dans l'estuaire du fleuve Saint-Laurent. M.Sc. thesis, Université du Québec à Montréal, Q.C.

Hatin D, Fortin R, Caron K (2002) Movements and aggregation area of adult Atlantic sturgeon (*Acipenser oxyrinchus*) in the St. Lawrence River estuary, Québec, Canada. J Appl Ichthyol 18:586–594

Hatry C, Binder TR, Thiem JD, Hasler CT, Smokorowski KE, Clark K, Katopodis C, Cooke SJ (2013) The status of fishways in Canada: trends identified using the national CanFishPass database. Rev Fish Biol Fish 23:271–281

Haxton TJ (2006) Characteristics of a lake sturgeon spawning population sampled a half century apart. J Gt Lakes Re. 32:124–130

Haxton TJ, Findlay CS (2008) Variation in lake sturgeon abundance and growth among river reaches in a large regulated river. Can J Fish Aquat Sci 65:646–657

Henyey E, Kynard B, Zhuang P (2002) Use of electrical narcosis to immobilize juvenile shortnose and lake sturgeon for handling. J Appl Ichthyol 18:502–504

Hinch SG, Bratty JM (2000) Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. Trans Am Fish Soc 129:604–612

Hosmer DW, Lemeshow S (1999) Applied survival analysis. Wiley, New York

Hothorn T, Bretz F, Westfall P, Heiberger RM, Schuetzenmeister A (2013) multcomp: simultaneous inference in general parametric models. R package version 1.2-18. http://cran.r-project.org/web/packages/multcomp/index.html

IUCN (2010) IUCN Red List of Threatened Species [online]. Available from www.iucnredlist.org [accessed 9 December 2010].

Jager HI (2006) Chutes and ladders and other games we play with rivers. I. Simulated effects of upstream passage on white sturgeon. Can J Fish Aquat Sci 63:165–175

Jager HI, Chandler JA, Lepla KB, Van Winkle W (2001) A theoretical study of river fragmentation by dams and its effects on white sturgeon populations. Environ Biol Fishes 60:347–361

Jayne BC, Lauder GV (1994) How swimming fish use slow and fast muscle fibers: implications for models of vertebrate muscle recruitment. J Comp Physiol A 175:123–131

Johnson JH, LePan SR, Klindt RM, Schiavone A (2006) Lake sturgeon spawning on artificial habitat in the St Lawrence River. J Appl Ichthyol 22:465–470

Katopodis C (2005) Developing a toolkit for fish passage, ecological flow management and fish habitat works. J Hydraul Res 43(5):451–467

Khan LA (2006) A Three-Dimensional Computational Fluid Dynamics (CFD) Model analysis of free surface hydrodynamics and fish passage energetics in a vertical-slot fishway. North Am J Fish Manage 26:255–267

Kitchell JF (1983) Energetics. In: Webb PW, Weihs D (eds), Fish biomechanics. Praeger: New York USA. Pp. 312–338

Kynard B, Kieffer M (2002) Use of a borescope to determine the sex and egg maturity stage of sturgeons and the effect of borescope use on reproductive structures. J Appl Ichthyol 18:505–508

Kynard B, Pugh D, Parker T (2011) Passage and behaviour of cultured Lake Sturgeon in a prototype side-baffle fish ladder: I. Ladder hydraulics and fish ascent. J Appl Ichthyol 27(Suppl 2):77–88

Kynard B, Pugh D, Parker T (In press) Use of a spiral fish ladder by Connecticut River shortnose sturgeon. In: Life-history and behavior of Connecticut River shortnose sturgeon and other North American sturgeons. American Fisheries Society Monograph, Bethesda.

LaHaye M, Branchaud A, Gendron M, Verdon R, Fortin R (1992) Reproduction, early life history, and characteristics of the spawning grounds of the lake sturgeon (*Acipenser fulvescens*) in Des Prairies and L'Assomption rivers, near Montréal, Quebec. Can J Zool 70:1681–1689

Laine A. Jokivirta T, Katopodis C (2002) Atlantic salmon, *Salmo salar* L., and sea trout, *Salmo trutta* L., passage in a regulated northern river – fishway efficiency, fish entrance and environmental factors. Fish Manag Ecol 9:65–77

Liao J, Beal DN, Lauder GV, Triantafyllou MS (2003) Fish exploiting vortices decrease muscle activity. Science 302:1566–1569

Liao J, Lauder GV (2000) Function of the heterocercal tail in white sturgeon: flow visualization during steady swimming and vertical maneuvering. J Exp Biol 203:3585–3594

Liu M, Rajaratnam N, Zhu DZ (2006) Mean flow and turbulence structure in vertical slot fishways. J Hydraul Eng 132:765–777

Lowe CG (1996) Kinematics and critical swimming speed of juvenile scalloped hammerhead sharks. J Exp Biol 199:2605–2610

Lowe CG, Holland KN, Wolcott TG (1998) A new acoustic tailbeat transmitter for fishes. Fish Res 36:275–283

Lucas MC, Baras E (2000) Methods for studying spatial behaviour of freshwater fishes in the natural environment. Fish Fish 1:283–316

Lucas MC, Baras E, Thom TJ, Duncan A, Slavik O (2001). Migration of Freshwater Fishes. Blackwell Science: Oxford.

Mailhot Y, Dumont P, Vachon N (2011) Management of the lake sturgeon *Acipenser fulvescens* population in the lower St. Lawrence River (Québec, Canada) from the 1910s to the present. J Appl Ichthyol 27:405–410

Mallen-Cooper M, Brand DA (2007) Non-salmonids in a salmonid fishway: what do 50 years of data tell us about past and future fish passage? Fish Manage Ecol 14:319–332

Martins EG, Hinch SG, Patterson DA, Hague MJ, Cooke SJ, Miller KM, Lapointe MF, English KK, Farrell AP (2011) Effects of river temperature and climate warming on stock-specific survival of adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*). Glob Chang Biol 17:99–114

Mazerolle MJ (2012) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 1.26. http://CRAN.R-project.org/package=AICcmodavg.

McCabe GT, Beckman LG (1990) Use of an artificial substrate to collect white sturgeon eggs. Calif Fish Game 76:248–250

McElroy B, DeLonay A, Jacobson R (2012) Optimum swimming pathways of fish spawning migrations in rivers. Ecology 93:29–34

McKinley RS, Power G (1992) Measurement of activity and oxygen consumption for adult lake sturgeon in the wild using radio-transmitted EMG signals. In: Priede IG, Swift SM (eds), Wildlife telemetry: remote monitoring and tracking of animal. Ellis Horwood: West Sussex UK. Pp. 307–318

McKinley S, Van Der Kraak G, Power G (1998) Seasonal migrations and reproductive patterns in the lake sturgeon, *Acipenser fulvescens*, in the vicinity of hydroelectric stations in northern Ontario. Environ Biol Fishes 51:245–256

McLaughlin RL, Noakes DL (1998) Going against the flow: an examination of the propulsive movements made by young brook trout in streams. Can J Fish Aquat Sci 55:853–860

McNab BK (2002) The physiological ecology of vertebrates: a view from energetics. Cornell University Press.

Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT (2010) Building the bridge between animal movement and population dynamics. Philos Trans R Soc Lond B Biol Sci 365:2289–2301

Murchie KJ, Cooke SJ, Danylchuk AJ, Suski CD (2011) Estimates of field activity and metabolic rates of bonefish (*Albula vulpes*) in coastal marine habitats using acoustic tri-axial accelerometer transmitters and intermittent-flow respirometry. J Exp Mar Biol Ecol 396:147–155

Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280–283

Naiman RJ, Bilby RE, Schindler DE, Helfield JM (2002) Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci USA 105:19052–19059

Nilo P, Dumont P, Fortin R (1997) Climatic and hydrological determinants of year-class strength of St. Lawrence River lake sturgeon (*Acipenser fulvescens*). Can J Fish Aquat Sci 54:774–780

Nilsson C, Reidy CA, Dynesius M, Revenga C (2005) Fragmentation and flow regulation of the world's large river systems. Science 308:405–408

Noonan, MJ, Grant JW, Jackson CD (2012) A quantitative assessment of fish passage efficiency. Fish Fish 13:450–464

Ogle DH (2013) FSA: fisheries stock analysis. R package version 0.3-4. Available from http://www.rforge.net/FSA/

Oliver MA, Webster R (1990) Kriging: a method of interpolation for geographical information systems. Int J Geogr Inf Sci 4:313–332

O'Toole AC, Danylchuk AJ, Goldberg TL, Suski CD, Philipp DP, Brooks E, Cooke SJ (2011) Spatial ecology and residency patterns of adult great barracuda (*Sphyraena barracuda*) in coastal waters of The Bahamas. Mar Biol 158:2227–2237

O'Toole AC, Murchie KJ, Pullen C, Hanson KC, Suski CD, Danylchuk AJ, Cooke SJ (2010) Locomotory activity and depth distribution of adult great barracuda (*Sphyraena barracuda*) in Bahamian coastal habitats determined using acceleration and pressure biotelemetry transmitters. Mar Freshw Res 61:1446–1456

Paragamian VL (2012) Kootenai River white sturgeon: synthesis of two decades of research. Endanger Species Res 17:157–167

Parsley MJ, Wright CD, van der Leeuw BK, Kofoot EE, Peery CA, Moser ML (2007) White sturgeon (*Acipenser transmontanus*) passage at the Dalles Dam, Columbia River, USA. J Appl Ichthyol 23:627–635

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing down marine food webs. Science 279:860–863

Payne NL, Gillanders BM, Seymour RS, Webber DM, Snelling EP, Semmens JM (2011) Accelerometry estimates field metabolic rate in giant Australian cuttlefish *Sepia apama* during breeding. J Anim Ecol 80:422–430

Peake S (2004) An evaluation of the use of critical swimming speed for determination of culvert water velocity criteria for smallmouth bass. Trans Am Fish Soc 133:1472–1479

Peake SJ (2005) Swimming and respiration. In: LeBreton GTO, Beamish FWH, McKinley RS (eds) Sturgeons and Paddlefish of North America. Springer: Netherlands. Pp 147–166.

Peake S, Beamish FWH, McKinley RS, Scruton DA, Katopodis C (1997) Relating swimming performance of lake sturgeon, *Acipenser fulvescens*, to fishway design. Can J Fish Aquat Sci 54:1361–1366

Peake SJ, Farrell AP (2004) Locomotory behaviour and post-exercise physiology in relation to swimming speed, gait transition and metabolism in free-swimming smallmouth bass (*Micropterus dolomieu*). J Exp Biol 207:1563–1575

Pelicice FM, Agostinho AA (2008) Fish-passage facilities as ecological traps in large neotropical rivers. Conserv Biol 22(1):180–188

Peterson DL, Vecsei P, Jennings CA (2007) Ecology and biology of the lake sturgeon: a synthesis of current knowledge of a threatened North American *Acipenseridae*. Rev Fish Biol Fisheries 17:59–76

Pinheiro J, Bates D, DebRoy S, Sarkar D, the R Development Core Team (2012) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-106. http://cran.r-project.org/web/packages/nlme/index.html

Pon LB, Hinch SG, Cooke SJ, Patterson DA, Farrell AP (2009) Physiological, energetic and behavioural correlates of successful fishway passage of adult sockeye salmon *Oncorhynchus nerka* in the Seton River, British Columbia. J Fish Biol 74:1323–1336

Qasem L, Cardew A, Wilson A, Griffiths I, Halsey LG, Shepard ELC, Gleiss AC, Wilson RP (2012) Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? PLoS ONE 7(2):e31187

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/.

Rajaratnam N, Katopodis C, Solanki S (1992) New designs for vertical slot fishways. Can J Civil Eng 19:402–414

Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. Bull Fish Res Board Can No. 191.

Rochard E, Castelnaud G, LePage M (1990) Sturgeons (Pisces: Acipenseridae); threats and prospects. J Fish Biol 37(Suppl A):123–132

Roscoe DW, Hinch SG (2010) Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. Fish Fish 11:12–33

Roscoe DW, Hinch SG, Cooke SJ, Patterson DA (2011) Fishway passage and post-passage mortality of up-river migrating sockeye salmon in the Seton River, British Columbia. River Res Appl 27:693–705

Rosenberg DM, McCully P, Pringle CM (2000) Global-scale environmental effects of hydrological alterations: introduction. BioScience 50:746–751

Rusak JA, Mosindy T (1997) Seasonal movements of lake sturgeon in Lake of the Woods and the Rainy River, Ontario. Can J Zool 75:383–395

Ruxton GD (2006) The unequal variance t-test is an underused alternative to Student's t-test and the Mann–Whitney U test. Behav Ecol 17:688–690

Sakamoto KQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, Wanless S (2009) Can ethograms be automatically generated using body acceleration data from free-ranging birds? PLoS ONE 4:e5379

Schwalb AN, Cottenie K, Poos MS, Ackerman JD (2011) Dispersal limitation of unionid mussels and implications for their conservation. Freshw Biol 56:1509–1518

Scott WB, Crossman EJ (1973) Freshwater fishes of Canada. Bull Fish Res Board Can No. 184.

Semmens JM, Payne NL, Huveneers C, Sims DW, Bruce BD (2013) Feeding requirements of white sharks may be higher than originally thought. Sci Rep 3

Shaw SL, Chipps SR, Windels SK, Webb MAH, McLeod DT, Willis DW (2012) Lake sturgeon population attributes and reproductive structure in the Namakan Reservoir, Minnesota and Ontario. J Appl Ichthyol 28:168–175

Sheer MB, Steel EA (2006) Lost watersheds: barriers, aquatic habitat connectivity, and salmon persistence in the Willamette and lower Columbia River basins. Trans Am Fish Soc 135:1654–1669

Shepard ELC, Wilson RP, Halsey LG, Quintana F, Laich AG, Gleiss AC, Liebsch N, Myers AE, Norman B (2008) Derivation of body motion via appropriate smoothing of acceleration data. Aquat Biol 4:235–241

Silva AT, Santos JM, Ferreira MT, Pinheiro AN, Katopodis C (2011) Effects of water velocity and turbulence on the behaviour of Iberian barbell (*Luciobarbus bocagei*, Steindachner 1864) in an experimental pool-type fishway. River Res Applic 27:360–373

Standen EM, Hinch SG, Healey MC, Farrell AP (2002) Energetic costs of migration through the Fraser River Canyon, British Columbia, in adult pink (*Oncorhynchus gorbuscha*) and sockeye (*Oncorhynchus nerka*) salmon as assessed by EMG telemetry. Can J Fish Aquat Sci 59:1809–1818

Stuart IG, Zampatti BP, Baumgartner LJ (2008) Can a low-gradient vertical-slot fishway provide passage for a lowland river fish community? Mar Freshw Res 59:332–346

Tarrade L, Texier A, David L, Larinier M (2008) Topologies and measurements of turbulent flow in vertical slot fishways. Hydrobiologia 609:177–188

Thiem JD, Binder TR, Dumont P, Hatin D, Hatry C, Katopodis C, Stamplecoskie KM, Cooke SJ (2013) Multispecies fish passage behaviour in a vertical slot fishway on the Richelieu River, Quebec, Canada. River Res Appl 29:582–592

Tudorache C, O'Keefe RA, Benfey TJ (2010) Flume length and post-exercise impingement affect anaerobic metabolism in brook charr *Salvelinus fontinalis*. J Fish Biol 76:729–733

Tudorache C, Viaenen P, Blust R, De Boeck G (2007) Longer flumes increase critical swimming speeds by increasing burst and glide swimming duration in carp (*Cyprinus carpio*, L.). J Fish Biol 71:1630–1638

Van Der Kraak G, Donaldson EM, Dye HM (1984) Effects of LH-RH and Des-Gly^{10} (D-Ala^{6})-LH-RH- Ethylamide on plasma sex steroid profiles in adult female coho salmon (*Oncorhynchus kisutch*). Gen Comp Endocrinol 55:36–45

Van Der Kraak G, Rosenblum P, Peter RE (1990) Growth hormone dependent potentiation of gonadotropin stimulated steroid production by ovarian follicles of the goldfish. Gen Comp Endocrinol 79:233–239

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The river continuum concept. Can J Fish Aquat Sci 37:130–137

Vecsei P, Litvak MK, Noakes DLG, Rien T, Hochleithner M (2003) A noninvasive technique for determining sex of live adult North American sturgeons. Environ Biol Fishes 68:333–338

Videler JJ, Weihs D (1982) Energetic advantages of burst-and-coast swimming of fish at high speeds. J Exp Biol 97:169–178

Wade MG, Van Der Kraak G (1991) The control of testicular androgen production in the goldfish: effects of activators of different intracellular signalling pathways. Gen Comp Endocrinol 83:337–344

Wang YL, Binkowski FP, Doroshov SI (1985) Effect of temperature on early development of white and lake sturgeon, *Acipenser transmontanus* and *A. fulvescens*. Environ Biol Fishes 14:43–50

Warren Jr ML, Pardew MG (1998) Road crossings as barriers to small-stream fish movement. Trans Am Fish Soc 127:637–644

Watanabe YY, Lydersen C, Fisk AT, Kovacs KM (2012) The slowest fish: swim speed and tail-beat frequency of Greenland sharks. J Exp Mar Biol Ecol 426–427:5–11

Webb MAH, Feist GW, Foster EP, Schreck CB, Fitzpatrick MS (2002) Potential classification of sex and stage of gonadal maturity of wild white sturgeon using blood plasma indicators. Trans Am Fish Soc 131:132–142

Webb PW (1978) Temperature effects on acceleration of rainbow trout, *Salmo gairdneri*. J Fish Res Board Can 35:1417–1422

Webb PW (1986) Kinematics of lake sturgeon, *Acipenser fulvescens*, at cruising speeds. Can J Zool 64:2137–2141

Webb PW, Gerstner CL, Minton ST (1996) Station-holding by the mottled sculpin, *Cottus bairdi* (Teleostei: Cottidae), and other fishes. Copeia 2:488–493

Webber JD, Chun SN, Maccoll TR, Mirise LT, Kawabata A, Anderson EK, Sung Cheong T, Kavvas L, Mcgee Rotondo M, Hochgraf KL, Churchwell R, Cech Jr JJ (2007) Upstream swimming performance of adult white sturgeon: effects of partial baffles and a ramp. Trans Am Fish Soc 136:402–408

Weihs D (1974) Energetic advantages of burst swimming of fish. J Theor Biol 48:215–229

Weihs D, Webb PW (1983) Optimization of locomotion. In: Webb PW, Weihs D (eds) Fish Biomechanics. Praeger Publishers CBS Educational and Professional Publishing: New York. Pp. 339–371.

Welsh AB, McLeod DT (2010) Detection of natural barriers to movement of lake sturgeon (Acipenser fulvescens) within the Namakan River, Ontario. Can J Zool 88:390–397

White LJ, Harris JH, Keller RJ (2011) Movement of three non-salmonid fish species through a low-gradient vertical-slot fishway. River Res Appl 27:499–510

Whitney NM, Pratt Jr HL, Pratt TC, Carrier JC (2010) Identifying shark mating behaviour using three-dimensional acceleration loggers. Endanger Species Res 10:71–82

Wiens JA (2002) Riverine landscapes: taking landscape ecology into the water. Freshw Biol 47:501–515

Wilcove DS, Wikelski M (2008) Going, going, gone: Is animal migration disappearing? PLoS Biol 6(7):e188

Wilga CD, Lauder GV (1999) Locomotion in sturgeon: function of the pectoral fins. J Exp Biol 202:2413–2432

Wilson RP, Quintana F, Hobson VJ (2012) Construction of energy landscapes can clarify the movement and distribution of foraging animals. Proc R Soc B 279:975–980

Wilson RP, Shepard ELC, Liebsch N (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. Endanger Species Res 4:123–137

Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. J Anim Ecol 75:1081–1090

Wilson SM, Hinch SG, Eliason EJ, Farrell AP, Cooke SJ (2013) Calibrating acoustic acceleration transmitters for estimating energy use by wild adult Pacific salmon. Comp Biochem Physiol Part A Mol Integr Physiol 164:491–498

Wu S, Rajaratnam N, Katopodis C (1999) Structure of flow in vertical slot fishway. J Hydraul Eng 125 (4):351–360

Yasuda T, Komeyama K, Kato K, Mitsunaga Y (2012) Use of acceleration loggers in aquaculture to determine net-cage use and field metabolic rates in red sea bream *Pagrus major*. Fish Sci 78:229–235

Zuur AF, Ieno EL, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer: New York, USA