

MULTISPECIES FISH PASSAGE BEHAVIOUR IN A VERTICAL SLOT FISHWAY ON
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ABSTRACT

A shift from target species to ecosystem restoration has generated interest in developing fishways that are capable of passing entire fish communities. Although a number of multispecies fishways now exist in North America, evaluations of these fishways are lacking. We used a passive integrated transponder antenna array to quantify passage success and passage duration of fish using a vertical slot fishway (85 m in length, 2.65 m elevation rise, 12 regular pools and 2 turning basins) at a low head dam on the Richelieu River in Quebec, Canada. Fourteen of the 18 tagged species re-ascended the fishway, and passage efficiency was highly variable among species (range 25%–100%); however, it was >50% for five of the species well represented in this study ($n > 10$) (Atlantic salmon, channel catfish, smallmouth bass, walleye and white sucker). Passage duration was likewise highly variable both among and within species (e.g. 1.0–452.9 h for smallmouth bass, 2.4–237.5 h for shorthead redhorse). Although this fishway design was not uniformly successful in passing fish of all species, this study does reveal the species that have problems with ascent and provides an estimate on the time spent in the fishway that is an important component of passage delay. Such information could be used to inform future design refinements to facilitate passage of the entire assemblage with minimal delay. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS: fishway; migration; connectivity; fish community

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INTRODUCTION

Dams associated with hydropower production or water management can serve as barriers to fish migration (Lucas and Baras, 2001), reducing watershed connectivity and resulting in changes to fish community structure and system productivity (Sheer and Steel, 2006). Despite this knowledge, the construction of dams continues to increase throughout the world to match the growing needs of water users (Rosenberg *et al.*, 2000). Fish passage facilities, collectively referred to as 'fishways', are progressively being viewed as a solution to overcome migration obstacles for fish, where suitable habitats exist beyond the barrier (Clay, 1995; Katopodis, 2005; Roscoe and Hinch, 2010).

Much of the current knowledge on fishway design and success stems from the myriad of research conducted on high priority species, particularly salmonids (Roscoe and Hinch, 2010; Katopodis and Williams, 2011). In some cases, transfer

of salmonid fishway designs to non-salmonid waters has resulted in poor success (Mallen-Cooper and Brand, 2007), with changes in design often proving to be a more suitable alternative for some species (e.g. Stuart and Mallen-Cooper, 1999). However, few fishways have been subject to the necessary biological evaluations to determine if they are indeed successful in passing target fish (Bunt *et al.*, 2011). When evaluations are conducted, they often focus on simply documenting the species that are captured in a fishway trap at the top of the fishway rather than evaluating passage efficiency (Roscoe and Hinch, 2010; Bunt *et al.*, 2011). In some instances, the failure of fishways is a result of poor entrance location (e.g. too far downstream), which, depending on construction, may be difficult to correct, or inadequate attraction that can potentially be improved by altering attraction flows (Clay, 1995; Lucas and Baras, 2001; Katopodis, 2005; Katopodis and Williams, 2011). Modifications right at the fishway entrance may provide fish passage improvements (e.g. Bunt, 2001). In other cases, fish are able to locate the fishway; however, they are unwilling or unable to ascend the structure (e.g. Moser *et al.*, 2002). Appreciating fish behaviour and devising suitable fishway designs is a key ingredient for effective passage (Williams *et al.*, 2011).

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The few fishways that have been studied from a biological perspective tend to focus on one or two key sportfish and fail to examine the broader fish community, particularly in North America. Roscoe and Hinch (2010) reported that only 4% of published North American fishway studies examined the entire fish community, compared with the broader taxonomic scopes of fishway studies conducted in Europe (38%), South America and Australia (94% combined). Despite this broader scope in other regions, fishways reported to successfully pass entire fish communities remain uncommon (Mallen-Cooper and Brand, 2007), with failure often attributed to the diversity in behaviours, morphology, physiological capacity and swimming ability of the different species using these structures. Given the need to broaden the scope of riverine restoration efforts (Poudevigne *et al.*, 2002) and that 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). The potential for hydropower expansion or upgrading of existing facilities in river systems throughout North America (Kosnik, 2010) further highlights the need to provide science to support future fishway design.

We conducted a field study at a vertical slot fishway on the Richelieu River in Quebec to determine the behaviour of fish utilizing this multispecies fishway. Specifically, we were interested in determining passage efficiency and passage duration among species at this site, to determine if this fishway design could serve as a model for warm water community passage.

METHODS

Study site

This study was undertaken 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 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 has a mean annual discharge of $362 \text{ m}^3 \text{ s}^{-1}$. 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), with its main function to maintain a stable water level upstream for navigation and water intake purposes. The fishway was constructed on the left bank of the dam in 2001 to provide upstream access for key migratory species including lake sturgeon (*Acipenser fulvescens*), copper redhorse (*Moxostoma hubbsi*), river redhorse (*Moxostoma carinatum*), American shad (*Alosa sapidissima*) and American eel (*Anguilla*

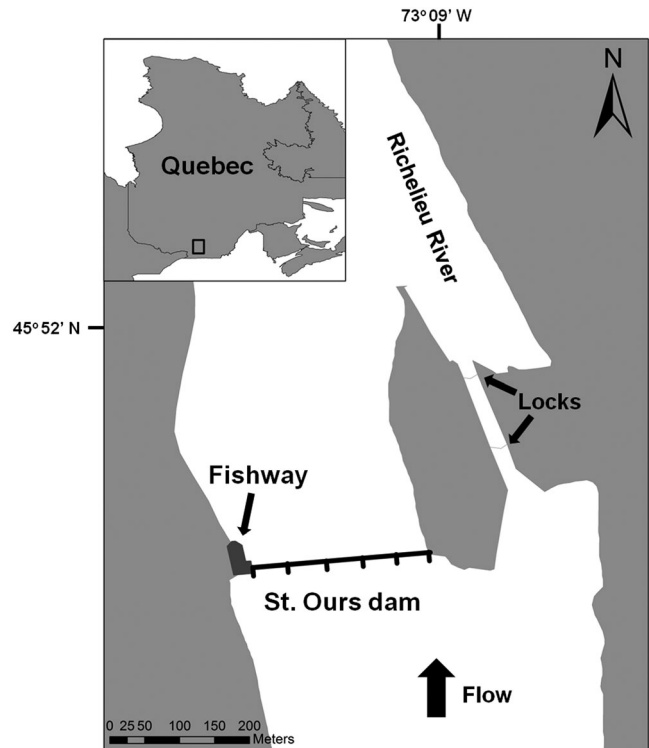


Figure 1. Location of the Vianney-Legendre vertical slot fishway on the Richelieu River, Quebec

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). The rest of fishway is divided into 12 uniform rectangular basins ($3.5 \times 3.0 \text{ m}$) connected by two resting/turning basins with horizontal floors and curved walls (2.75 m radius; Figure 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). The fishway discharge is approximately $1 \text{ m}^3 \text{ s}^{-1}$, with a capacity for an additional $6.5 \text{ m}^3 \text{ s}^{-1}$ attraction flow near the entrance basin via a pass-through chamber beneath the fishway. Further details of the fishway are provided by Thiem *et al.* (2011). Water velocity measurements collected in the centre of each vertical slot during the study period (model 2000 Marsh-McBirney flo-mate; Marsh McBirney Inc., Frederick, MD, USA) indicated that average velocity approached the theoretical velocity of 1.72 m s^{-1} (calculated using the equation $(2g \Delta h)^{1/2}$, where Δh is the water surface drop and assumed to be the same as the

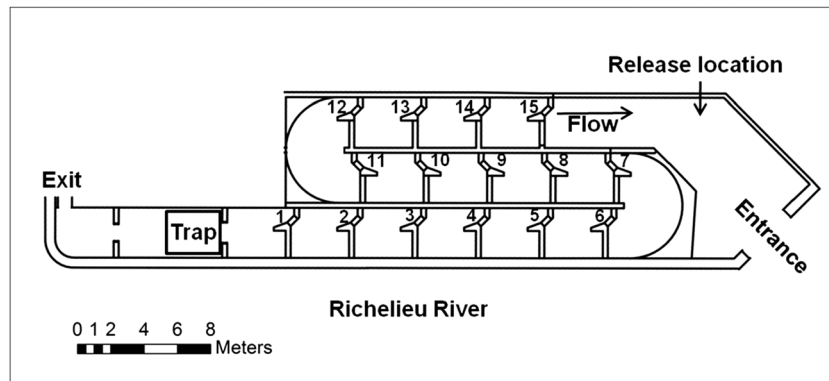


Figure 2. Schematic of the Vianney-Legendre fishway, with numbers indicating PIT antenna locations used to determine movement, behaviour and passage success

successive floor drop (0.15 m) and g is gravitational acceleration (9.81 m s^{-2}) and were 1.63 ± 0.01 , 1.68 ± 0.01 and $1.68 \pm 0.02 \text{ m s}^{-1}$ at 0.2, 0.6 and 0.8 of total depth, respectively, pooled among slots.

Experimental design

A passive integrated transponder (PIT) array consisting of 15 complete pass-through antennas [beginning at antenna 15 downstream and ending at antenna 1 upstream (Figure 2)] was installed within the fishway during a dewatering period in early May. PIT systems offer a number of advantages over other conventional tagging technologies to monitor fish movement in fishways, including low cost thus facilitating increased sample sizes (see Castro-Santos *et al.*, 1996). Methods and equipment were identical to those used by Thiem *et al.* (2011) with the exception that an antenna on the fishway exit gate was not monitored in this study because of the presence of a fish trap limiting passage. Each antenna was connected to a remote tuner box (Oregon RFID, Portland, OR, USA), each of which were connected in groups of three or four via twin-axial cable to a multiplexer unit (Oregon RFID). Antennas were manually tuned during operational water levels to maximize detection range ($\sim 0.5 \text{ m}$) and performance. Multiplexers were programmed to scan at high speed sequentially through all antennas and upon positive detection stored a unique tag identification number, antenna number and provided date and time stamps that were downloaded to a personal computer twice weekly.

Upstream migrating fish were sourced from a trap (beginning 31 May 2010), located at the upstream end of the fishway (Figure 2), which was raised twice daily (~ 0900 and 1500 h). The rectangular trap was 2 m wide by 2.15 m high with an entrance width of 0.28 m and is constructed of galvanized steel with a shade mesh floor to prevent damage to fish during the raising process and has a horizontal bar

spacing creating a vertical gap of 42 mm, biasing capture towards larger species and individuals. Prior to raising the trap, a gate with the same bar spacing was lowered temporarily to prevent passage during sorting and tagging. Species were tagged as encountered over 11 days, except for locally abundant species (river redhorse; shorthead redhorse, *Moxostoma macrolepidotum*; channel catfish, *Ictalurus punctatus*; mooneye, *Hiodon tergisus*; and silver redhorse, *Moxostoma anisurum*), where tags were held in reserve to boost sample sizes of less frequently encountered species. Total length (TL) of captured individuals was measured to the nearest mm, and each individual had a uniquely coded PIT tag ($23 \times 3.85 \text{ mm HDX}$; Texas Instruments, Dallas, TX, USA) implanted into the peritoneal cavity. Each fish was placed ventral side up in a v-shaped cradle, and following a small incision ($< 5 \text{ mm}$), a PIT tag was inserted using a 6-gauge plunger (Baras *et al.*, 1999), with no anaesthetics or sutures used. The entire handling process took $< 1 \text{ min}$, and care was taken to minimize air exposure. Following tagging, individuals were immediately transferred to a flow-through net pen located in the fishway entrance basin and allowed 1–2 h to recover from handling prior to release. Re-ascension of the fishway was volitional, with fish able to leave the fishway and ascend at a later time or not at all. This technique of fish capture at the top of fishways and subsequent evaluation of re-ascension has been successfully used in the past to assess fishway use by other species (e.g. Bunt *et al.*, 1999; Pon *et al.*, 2009). Tagging was completed by 10 June 2010, and the fishway was monitored from 31 May to 30 June 2010, inclusive.

Water quality values were recorded daily during the study (YSI model 556; YSI Incorporated, Yellow Springs, OH, USA) and were as follows: conductivity, $165.00 \pm 3.55 \mu\text{S cm}^{-1}$; pH, 6.52 ± 0.08 ; and dissolved oxygen, $8.91 \pm 0.06 \text{ mg L}^{-1}$. Hourly water temperature was recorded within the fishway (DS1921Z iButton; Maxim Integrated Products, Sunnyvale, CA, USA) and was $18.99 \pm 0.05^\circ\text{C}$ (range, 16.75°C – 21.38°C).

Data analysis

We defined successful passage as the first detection of an individual on the most upstream antenna (antenna 1). As the fish trap was operated intermittently following tagging 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. Antenna locations were converted to distance metrics, beginning at the most downstream antenna encountered (antenna 15, 0 m) and ending at the most upstream antenna, immediately downstream of the trap (antenna 1, 56.2 m) (Figure 2). Maximum distance of ascent was plotted for each species and was determined using the proportional loss of individuals (i.e. failure to ascend past this point) at antenna locations compared with the total number of individuals attempting to re-ascend. Passage duration was calculated for successful passage events of each individual as the time taken between the first detection in the fishway (antenna 15) and the first detection on antenna 1. Occasional missed detections on antenna 15 resulted in an inability to calculate passage duration for some individuals, despite successful passage occurring. Entrance delay was determined as the time elapsed from release until first entrance into the fishway. Diel patterns of fishway use were determined for each species by plotting the pooled proportion of PIT records by hour of the day for the entire study period. Passage efficiency was calculated as the proportion of successful fishway passage events compared with the number of fish attempting to pass (Bunt *et al.*, 1999). Reproductive status at the time of the study was assigned to all species based on known spawning windows from available literature (e.g. Scott and Crossman, 1973; Mongeau *et al.*, 1992) (Table I); however, the sexual maturation level of individuals was not identified in the field. The fate of individuals not re-entering the fishway during the study period was unknown. Differences in the mean length of fish entering the fishway and not succeeding were compared with those succeeding, using independent sample *t* tests or equivalent nonparametric Wilcoxon rank sum test, where $n \geq 10$ individuals. Nonparametric Spearman rank correlations were used to test for relationships between fish length and passage duration, where $n \geq 10$ individuals. One-way analysis of variance tests were used to determine if significant differences occurred among species for both passage duration (log transformed) and entrance delay (log transformed), where $n \geq 10$ individuals. Tukey's honestly significant difference tests were used to ascertain homogeneous groups following significant results. Where appropriate, data were first tested for the assumptions of normality and homogeneity of variance following the methods outlined by Grafen and Hails (2002). All statistical analyses were deemed significant at $p < 0.05$ and conducted using JMP statistical software (version 8.0; SAS Institute Inc., Cary,

NC, USA). All data are presented as mean \pm standard error unless otherwise stated.

RESULTS

Eighteen species comprising 492 individuals were tagged and released (Table I). Attempts to re-ascend the fishway were made by individuals of 14 species. Among the six species in low abundance ($n \leq 3$ tagged) in the catch, lake sturgeon, brown bullhead (*Ameiurus nebulosus*), quillback (*Carpoides cyprinus*) and longnose gar (*Lepisosteus osseus*) did not attempt to re-ascend and presumably left the fishway entrance, whereas all freshwater drum (*Aplodinotus grunniens*) and common carp (*Cyprinus carpio*) attempted to re-ascend the fishway. Among fish species well represented in the catch, attempts to re-ascend were proportionally low for mooneye and the four redhorse species (Table I) and proportionally high (>50%) for the seven remaining species. Sauger (*Sander canadensis*) presented the highest proportion (15 of 16) of re-attempts.

White suckers (*Catostomus commersoni*) comprised the greatest number of successful re-ascensions. Passage efficiency was >50% for five well-represented species including white sucker, channel catfish, smallmouth bass (*Micropterus dolomieu*), Atlantic salmon (*Salmo salar*) and walleye (*Sander vitreus*) and two fish species captured in low numbers, freshwater drum and common carp. Passage efficiency was 100% among Atlantic salmon (Table I and Figure 3). There were no significant differences in the size of fish that failed to re-ascend and those that succeeded for the four species for which there were adequate data to enable such analyses (longnose sucker (*Catostomus catostomus*): $t = -0.483$, $p = 0.632$; white sucker: $t = -0.037$, $p = 0.970$; channel catfish: $z = 1.331$, $p = 0.183$; shorthead redhorse: $z = 0.178$, $p = 0.859$). The locations of failure within the fishway were species specific and followed no discernable trend (Figure 3). A number of species exhibited failure throughout the fishway including white sucker (Figure 3c) and sauger (Figure 3l). Failure generally occurred in the downstream part of the fishway for smallmouth bass (Figure 3g), river redhorse (Figure 3i) and shorthead redhorse (Figure 3j). Conversely, failure was greatest in the upstream portion of the fishway for channel catfish (Figure 3f).

Time from release until first entrance into the fishway (entrance delay) was significantly different among the eight species for which there were adequate data to enable such analyses ($F_{7, 178} = 13.608$, $p < 0.001$) (Table I). Entrance delay was shortest for river redhorse, white sucker and longnose sucker; intermediate for silver redhorse, smallmouth bass and shorthead redhorse; and longest for channel catfish and sauger (Table I). Passage duration was highly variable both among and within species (Table I). For example, passage

Table I. Composition of fish species PIT tagged and released into the Vianney-Legendre fishway

Family	Species	TL (mm)	Number captured	Number tagged	Number attempted	Number passed*	Passage efficiency (%)	Entrance delay (h)**	Passage duration (h)**
Acipenseridae	<i>Acipenser fulvescens</i>	914–1180	2	2	0	0			
	Lake sturgeon ^r								
Catostomidae	<i>Carpoides cyprinus</i>	431	1	1	0	0			
	Quillback ^r								
	<i>Catostomus catostomus</i>	390.6 ± 3.3	76	56	39	19	48.7	16.8 ± 6.7	27.5 ± 12.7
	Longnose sucker ⁿ	332–440						0.1–218.9 (38) ^{ab}	1.3–164.6 (16)
	<i>Catostomus commersoni</i>	378.2 ± 8.2	67	40	33	25	75.8	9.8 ± 3.6	30.1 ± 15.9
	White sucker ⁿ	270–463						0.1–98.7 (32) ^{ab}	0.8–240.3 (15)
	<i>Moxostoma anisurum</i>	432.4 ± 12.4	182	42	10	3	30.0	74.1 ± 49.0	2.6 ± 1.3
	Silver redhorse ^r	220–598						0.0–447.9 (10) ^b	1.0–5.2 (3)
	<i>Moxostoma carinatum</i>	559.7 ± 8.7	228	87	26	8	30.8	14.2 ± 9.4	5.6 ± 1.1
	River redhorse ^r	312–679						0.0–218.6 (26) ^a	1.0–11.4 (8)
	<i>Moxostoma macrolepidotum</i>	360.3 ± 6.3	344	74	22	10	45.5	15.3 ± 8.1	81.2 ± 38.1
	Shorthead redhorse ^r	255–540						0.9–182.6 (22) ^{b,c}	2.4–237.5 (6)
	<i>Moxostoma valenciennesi</i>	538.7 ± 16.6	20	16	4	1	25.0	118.1 ± 75.8	
	Greater redhorse ^r	389–644						0.2–320.5 (4)	
Cyprinidae	<i>Cyprinus carpio</i>	660–735	2	2	2	2	100	0.2–426.7 (2)	1.4–2.4 (2)
	Common carp ^r								
Centrarchidae	<i>Micropterus dolomieu</i>	390.1 ± 16.4	18	14	11	7	63.6	36.3 ± 11.9	79.2 ± 74.8
	Smallmouth bass ^r	297–504						0.2–117.7 (10) ^{b,c}	1.0–452.9 (6)
Hiodontidae	<i>Hiodon tergisus</i>	305.1 ± 4.0	190	46	5	2	40.0	35.5 ± 35.5	25.6 (1)
	Mooneye ^r	250–377						0.0–106.6 (3)	
Ictaluridae	<i>Ancistrus nebulosus</i>	253–269	2	2	0	0			
	Brown bullhead ^r								
	<i>Ictalurus punctatus</i>	432.9 ± 15.2	313	66	36	19	52.8	163.9 ± 32.1	55.5 ± 31.8
	Channel catfish ^r	306–751						0.0–541.1 (36) ^c	1.7–413.5 (13)
Lepisosteidae	<i>Lepisosteus osseus</i>	778	1	1	0	0			
	Longnose gar ^r								
Percidae	<i>Sander canadensis</i>	373.4 ± 5.8	31	16	15	6	40.0	72.6 ± 22.7	157.5 ± 108.5
	Sauger ⁿ	330–428						4.5–232.0 (13) ^c	28.4–373.1 (3)
	<i>Sander vitreus</i>	399.6 ± 19.8	12	11	7	4	57.1	65.0 ± 36.2	484.1 (1)
	Walleye ⁿ	301–522						4.5–234.0 (7)	
Salmonidae	<i>Salmo salar</i>	511.5 ± 5.9	16	13	8	8	100	27.2 ± 5.3	8.8 ± 8.1
	Atlantic salmon ⁿ	485–543						0.1–49.2 (8)	0.4–25.1 (3)
Sciaenidae	<i>Aplodinotus grunniens</i>	613.7 ± 69.3	4	3	3	2	66.7	55.1 ± 41.0	21.6–147.8 (2)
	Freshwater drum ^r	501–740						0.3–135.4 (3)	

*Determined as the number of individuals reaching the most upstream antenna. This value does not necessarily indicate passage success.

**Numbers in parentheses are the number of individuals for which entrance delay and passage duration could be determined.

^{r,n}Classification of reproductive status during the time of study (r = reproductive, n = non-reproductive).^{a,b,c}Homogenous subsets based on Tukey's honestly significant difference *post hoc* test.

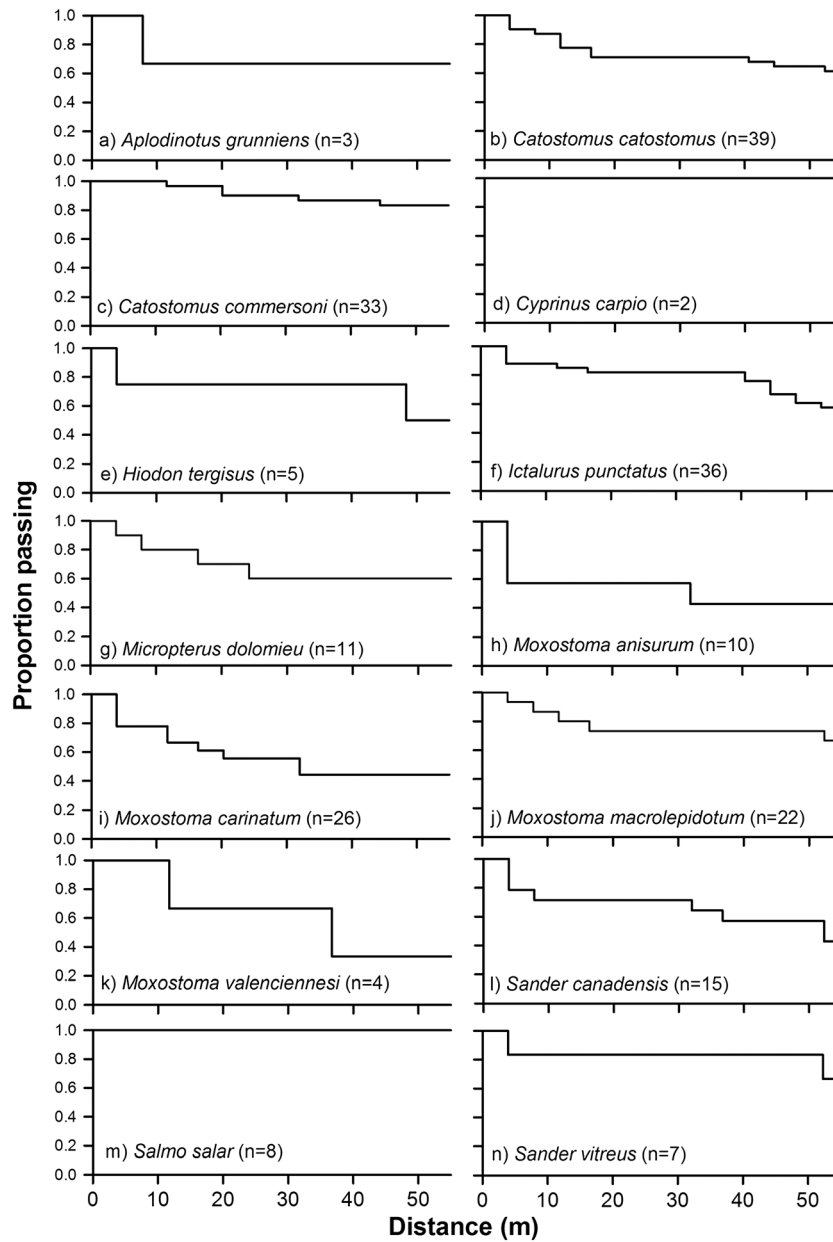


Figure 3. Proportional maximum upstream distance achieved by 14 species attempting to pass the Vianney-Legendre vertical slot fishway. Note individuals from four tagged species made no attempt to re-enter or pass the fishway following tagging and release (Table I) and are excluded

duration for smallmouth bass ranged from 1.0 to 452.9 h and that for shorthead redhorse ranged from 2.4 to 237.5 h. The shortest passage duration occurred for an Atlantic salmon (0.4 h). On average, passage duration was shortest for common carp, silver redhorse, river redhorse and Atlantic salmon. No significant difference occurred in passage duration among the three species of fish (white sucker, longnose sucker, channel catfish) for which there were adequate data to enable such analyses ($F_{2, 41} = 0.148$, $p = 0.863$). Within species, no

significant correlations occurred between passage duration and the size (TL) of fish for the three species for which there were adequate data to enable such analyses (longnose sucker: $r_s = -0.026$, $p = 0.924$; white sucker: $r_s = 0.061$, $p = 0.830$; channel catfish: $r_s = -0.366$, $p = 0.218$).

Diel use of the fishway varied among species, although it followed some clear patterns (Figure 4). Use of the fishway by both freshwater drum (Figure 4a) and channel catfish (Figure 4f) was primarily nocturnal. Sauger (Figure 4l) and

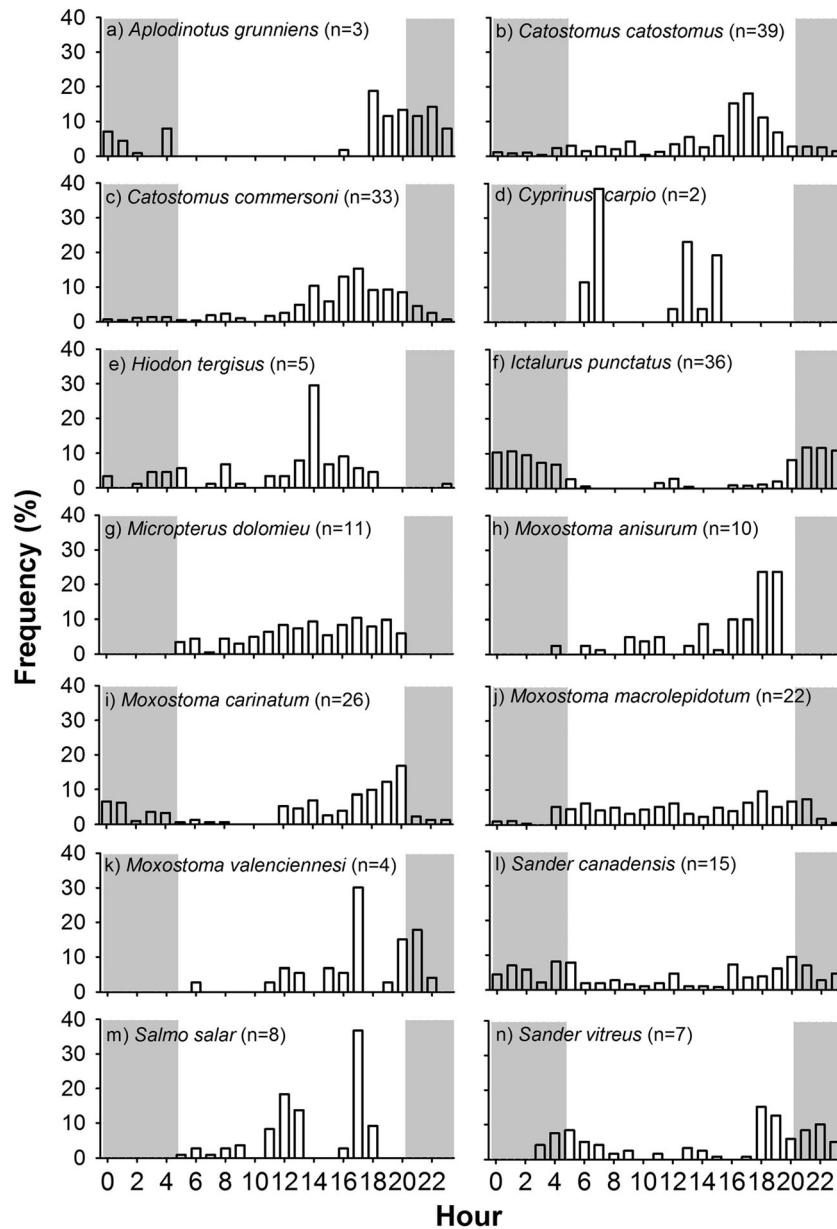


Figure 4. Frequency of PIT records differentiated by time of day for 14 species attempting to re-ascend the Vianney-Legendre vertical slot fishway. Grey bars indicate approximate night periods based on local sunrise and sunset times

walleye (Figure 4n) exhibited a trend towards crepuscular use of the fishway, whereas common carp (Figure 4d), smallmouth bass (Figure 4g) and Atlantic salmon (Figure 4m) use of the fishway was exclusively diurnal. Shorthead redhorse used the fishway predominantly during diurnal periods, and longnose sucker, white sucker, mooneye, silver redhorse, river redhorse and greater redhorse (*Moxostoma valenciennesi*) (Figure 4b, c, e, h, i and k, respectively) were predominantly diurnal with noticeable peaks in the afternoon or early evening.

DISCUSSION

We identified use of a vertical slot fishway by 18 species and successful re-ascension by 14 of these species in the current study. Seven species exhibited passage efficiency estimates greater than 50% in this study. Bunt *et al.* (1999) previously reported lower passage efficiency estimates of 38%–55% for white sucker and 33%–38% for smallmouth bass at two Denil fishways, using radiotelemetry methods. Pratt *et al.* (2009) found passage efficiency across 3 years ranged from

36% to 88% for white sucker at one vertical slot fishway and 6% to 9% at another, with modifications to the former accounting for increased passage success. In contrast, Bunt *et al.* (2000) found that radio-tagged walleye were unable to pass a different Denil fishway, despite 17 attempts by five separate individuals, with repeated failure at the first bend encountered. Failure at turning basins did not occur for walleye or other species in the current study, despite evidence of failure at turns for lake sturgeon at this site in a previous study (Thiem *et al.*, 2011). Gowans *et al.* (1999) reported 100% passage efficiency for Atlantic salmon ascending a 310 m pool-and-orifice fishway, and in a later study, Gowans *et al.* (2003) report a passage efficiency of 72% for Atlantic salmon passing a 275-m whole river, pool-and-overfall fishway. Stuart *et al.* (2008) found that passage efficiency was 81% for common carp passing a large vertical slot fishway. Comparative fishway passage efficiency estimates do not exist in the literature for freshwater drum or channel catfish. It should be noted that passage efficiency estimates for most species in this study were still below the 90%–100% values recommended by Lucas and Baras (2001). Bunt *et al.* (2011) recently identified that variation in fishway passage was related to fishway type, slope and elevation change, whereas variation in fish attraction was primarily driven by biological characteristics. The current study design did not enable quantification of fishway attraction efficiency or the number of migrating individuals congregating downstream of the fishway. This information is important and represents a logical next step as <2% of the mean annual discharge passes through the fishway to attract fish to the entrance compared with 5%–10% of the total river discharge suggested by Katopodis and Williams (2011).

We were able to quantify migratory delay in terms of both times to re-enter and re-ascend the fishway in the current study. Delayed re-entry (maximum 22.5 days) and passage (maximum 20 days) occurred for numerous species. Delays have potential fitness consequences, given that passage through fishways is intended to occur at a similar rate to that expected in free-flowing waters, as if the barrier were transparent (Castro-Santos and Haro, 2010). Delays associated with fishway passage have frequently been observed by others for both salmonids (e.g. Laine *et al.*, 2002; Gowans *et al.*, 2003) and non-salmonids (e.g. White *et al.*, 2011). Delayed migrants are thought to use more energy through repeated (unsuccessful) attempts at fishway passage (Hinch and Bratty, 2000). Indeed, Caudill *et al.* (2007) identified that for two species of salmonids, delayed dam passage resulted in failure to reach spawning tributaries. When individuals arrive late at their spawning grounds, they can also miss their spawning window or have a reduced opportunity to maximize their genetic fitness through shorter residency times (Lucas and Baras, 2001; Roscoe *et al.*, 2011). The reproductive fate of individuals used in the current study

remains unknown, however, and this represents an important knowledge gap in this and numerous other fishway studies (Roscoe and Hinch, 2010).

The variability in passage success and duration observed in the current study did not appear related to the differential life history strategies of the species examined. A large proportion of species are obligate riverine migrants, some with spawning windows overlapping with the study period (Table I). However, among the species with the highest passage efficiency, two are early spring (April–May) spawners (walleye and white sucker), two are late spring (June) spawners (smallmouth bass and channel catfish) and one is a fall (October–November) spawner with strong pre-spawning migratory tendencies (Atlantic salmon) (Scott and Crossman, 1973). Pratt *et al.* (2009) attributed differences in attraction and passage efficiency between white sucker and rock bass (*Ambloplites rupestris*) at a fishway to motivation, with comparatively poor passage of the latter species attributed to its facultative migratory tendency. Previous fishway studies have observed overlapping timing of fishway use with shared species from the current study. For example, Schwalm *et al.* (1985) observed longnose and white suckers ascending at a similar time of year to this study, presumably after their peak reproductive period, and Bunt *et al.* (1999) reported June fishway ascension by both white sucker and smallmouth bass. In the current study, smallmouth bass were frequently observed preying upon schools of emerald shiner (*Notropis atherinoides*) within the fishway, potentially explaining the slow passage duration of some individuals of this species. Katopodis *et al.* (1991) suggested that foraging may have contributed to thousands of northern pike (*Esox lucius*) observed waiting 2–3 weeks before using a Denil fishway at Cowan Dam in Saskatchewan, Canada. Some species have been known to reside within fishways for long periods; for example, Parsley *et al.* (2007) observed 6-month residency for a white sturgeon (*Acipenser transmontanus*) within a fishway on the Columbia River. Conversely, large-scale movements may occur for some species outside of reproductive windows and may be associated with explorations or a shift in home range (e.g. Ebner and Thiem, 2009). Baumgartner *et al.* (2010) identified year-round use of three vertical slot fishways on the Murray River, Australia. It may be that use of fishways during ‘off-peak’ (i.e. non-reproductive) periods is important for maintaining the community structure of facultative migrants; however, poor fishway efficiency remains a management concern for obligate migrants during reproductive periods.

Catostomids represented the dominant group of fishes in this study, with successful re-ascension observed for six of the seven species tagged (white sucker, longnose sucker, river redhorse, greater redhorse, silver redhorse and short-head redhorse), whereas the single-tagged quillback failed to re-ascend. Copper redhorse also attempt to use the fishway annually, although are generally intercepted for

use in an artificial propagation programme at the site because of their endangered status (Leclerc and Vachon, 2008), and are not tagged in this study. Numerous catostomid species are thought to be particularly susceptible to river fragmentation as they are obligate migrants (Cooke *et al.*, 2005; Reid *et al.*, 2008). Locally abundant catostomids frequently dominate abundance and biomass at fishways within their distribution (e.g. Schwalmé *et al.*, 1985; Bunt *et al.*, 2001; Pratt *et al.*, 2009); however, successful passage is rarely observed for some species. For example, Cooke and Bunt (1999) reported congregations of radio-tagged greater redhorse below a fishway on the Grand River; however, only five fish passed the fishway in a 4-year monitoring period (Bunt *et al.*, 2001). Passage efficiency was relatively high for both longnose and white sucker in the current study; both obligate migrants known to ascend fishways with high success (Schwalmé *et al.*, 1985; Bunt *et al.*, 2001). However, passage efficiency was relatively poor for all four redhorse species tagged in this study, despite their obligate nature and the study being conducted within their reproductive window (Mongeau *et al.*, 1992). A previous study of catostomid use of the Vianney-Legendre fishway in 2005 (Fleury and Desrochers, 2006) identified a combined passage efficiency of 85.9% for six catostomids (comprising copper, greater, river, shorthead and silver redhorse, and white sucker), although 55.6% efficiency for river redhorse ($n = 9$). The study conducted by Fleury and Desrochers (2006) intercepted fish prior to fishway ascension, and it is possible that attempts to re-ascend the fishway in the current study resulted in exhaustion and potentially explain the poor passage efficiency observed; however, the causes of differential fishway success among catostomid species still remain unclear and represent an important knowledge gap.

For all fish species for which it has been well documented, diel fishway use generally followed a pattern similar to what is observed in their natural habitat. For example, channel catfish is a nocturnal species (Scott and Crossman, 1973), and walleye and sauger are crepuscular species (Ali *et al.*, 1977). In contrast, smallmouth bass activity is generally crepuscular (Todd and Rabeni, 1989); however, observations of diurnal feeding on emerald shiner in the fishway may explain diel fishway use. Previous fishway studies have reported afternoon and evening peaks for longnose and white sucker (Schwalmé *et al.*, 1985), primarily daytime ascent by white sucker and smallmouth bass (Bunt *et al.*, 1999) and almost solely diurnal ascent by Atlantic salmon (Gowans *et al.*, 1999), similar to the results of the current study. Interestingly, time of day that fishway entry occurs can also affect passage behaviour. For example, White *et al.* (2011) found that bony herring (*Nematalosa erebi*) entering the fishway during the day passed uninterrupted; however, upon entry in the evening, the same species delayed its passage overnight.

The current study approach of sourcing fish from a trap near the fishway exit and assessing re-ascension introduced a number of biases and limitations in this study. The composition of the fish community using the fishway was underrepresented in this study, both in terms of species diversity and the size range of the species used. For example, this fishway is known to pass at least 18 additional species not reported in this study, many of which either did not enter the fish trap during the study period, were too small to tag (e.g. emerald shiner, Leclerc and Vachon, 2008) if they were captured, or escaped the trap because of its size selective bias towards larger individuals. Indeed, using fine mesh on traps at fishway exits enabled Bunt *et al.* (2001) to collect information on the timing and abundance of numerous small bodied species at two Denil fishways on the Grand River. Modifications to increase trap volume and funnel characteristics (e.g. Pratt *et al.*, 2006; Pratt *et al.*, 2009) also represent viable options to reduce escapement. Capture of fish in traps at fishway exits does not enable quantification of passage efficiency or passage duration; however, trapping (e.g. Baumgartner *et al.*, 2010) or use of underwater video (e.g. Haro and Kynard, 1997) at both the entrance and exit represent viable alternatives. It should also be noted that the use of traps does enable selective passage and is especially useful for the exclusion of invasive species (e.g. sea lampreys *Petromyzon marinus* in the Laurentian Great Lakes; Pratt *et al.*, 2009).

Collectively, this study revealed that the current vertical slot fishway design passes a wide variety of North American species. The study approach supplemented existing trap capture information and identified marked differences among species, in terms of passage efficiency and passage duration, which could not be explained by the facultative or obligate migratory tendencies of many species. This type of information, although often absent (Roscoe and Hinch, 2010; Bunt *et al.*, 2011), is critical to inform future management of aquatic resources as the ecological consequences of failed reproduction, stemming from an inability to reach spawning grounds, can have severe ecosystem consequences. Of particular interest were the numerous delays and low passage efficiency of many catostomids, with the information presented here providing a platform to further elucidate the causes of inter-species and intra-species differences in fishway passage performance and inform future design refinements that could facilitate increased passage with minimal delay.

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