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Attraction and Passage Efficiency of White Suckers and Smallmouth Bass by Two Denil Fishways

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Abstract.—We compared two Denil fishways, located on the west (low velocity, 10% slope) and east (high velocity, 20% slope) sides of the Mannheim weir, Grand River, Ontario, for use by upstream-migrating white suckers *Catostomus commersoni* and smallmouth bass *Micropterus dolomieu*. Mark–recapture and radiotelemetry were used to assess attraction and fish passage. Movement of 85 radio-tagged fish was monitored continuously during spring and early summer of 1995 and 1996. Attraction and passage efficiencies of white suckers at the west fishway were approximately 50%, and 55%, respectively. Attraction efficiency of white suckers at the east fishway was approximately 59%, and passage efficiency was 38%. The attraction and passage efficiencies of smallmouth bass at the west fishway were approximately 82% and 36%, respectively. At the east fishway, attraction efficiency of smallmouth bass was approximately 55%, and passage efficiency was 33%. There was an exponential decline in the numbers of both species that used each fishway relative to water velocity. The maximum water velocity used by white suckers was 0.96 m/s and that used by smallmouth bass was 0.99 m/s. Distracting flows near the west fishway appeared to affect attraction. Both fishways passed equal numbers of smallmouth bass per year, and smallmouth bass that used the east fishway were significantly larger than individuals that used the west fishway. In contrast, more than twice as many white suckers used the west fishway, and these fish were significantly larger than those that used the east fishway. Differences in passage were related to burst and critical swimming speeds and the use of velocity refugia within the fishways.

Fishways allow upstream-migrating fish to bypass natural and artificial river barriers (Beach 1984; Clay 1995). Biologically oriented fishway research has focused on anadromous fishes, such as salmonids and clupeids. As a result, fishways do not usually include design features that are relevant to the behavior and swimming performance of freshwater fish (Lucas and Frear 1997). This information is vital if fishways designed to accommodate freshwater species are to be successful.

Dams and other river barriers increasingly compromise fish movements in temperate and tropical streams and rivers. Many families of warmwater fishes including centrarchids, catostomids, esocids, percids, cyprinids and ictalurids migrate up streams and rivers, especially during spawning periods (Raney and Webster 1942; Schultz 1955; Rawson 1957). Some members of these families are known to use fishways (Nelson 1983; Derksen 1988; Langhurst and Schoenike 1990; Harris and Mallen-Cooper 1994; Lucas and Frear 1997). Fishway use varies, however, according to fishway design, water velocities within the fishways, water temperature, time of day, fish size, and swimming ability (Fernet 1984; Schwalme et al. 1985; Derksen 1988; Pavlov 1989; Katopodis et al. 1991). Passage efficiency of a limited number of coolwater, coldwater, and warmwater fishes has been investigated using mark–recapture (Linlokken 1993) and videography (Dexter and Ledet 1996; Haro and Kynard 1997). Radiotelemetry has not been used to track individual movements and behavior of nonsalmonid fishes in fishways to determine attraction and passage efficiency.

The objectives of this study were to describe conditions during fishway use and to quantify attraction efficiency and passage efficiency of white suckers *Catostomus commersoni* and smallmouth

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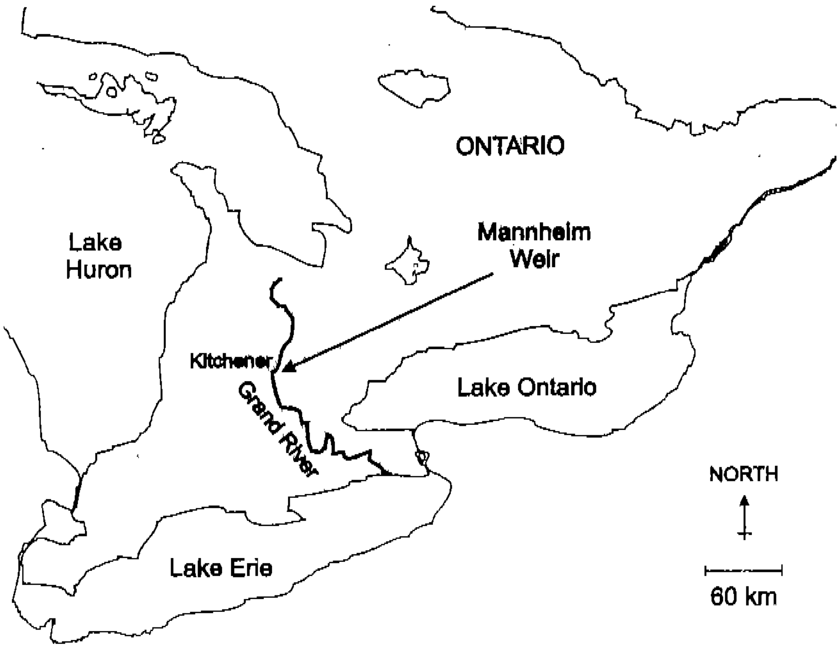

FIGURE 1.—The location of the Mannheim weir on the Grand River, near Kitchener, Ontario. Approximately 6,700 km² are drained into Lake Erie by the Grand River watershed.

bass *Micropterus dolomieu* downstream from a recently constructed weir equipped with two Denil fishways. We chose to study white suckers and smallmouth bass because they are morphologically distinct and differ in swimming ability. The primary null hypotheses for each species were (1) east fishway attraction efficiency equals west fishway attraction efficiency, and (2) east fishway passage efficiency equals west fishway passage efficiency. We also measured the critical swimming speeds of adult smallmouth bass and used similar data for white suckers from the literature to help explain successful passage relative to hydraulic conditions within the two fishways.

Methods

Study area.—This study was conducted at the Mannheim weir on the Grand River, near Kitchener, Ontario. The Grand River is a mid-order stream that flows 297 km from its source in Dundalk, Ontario, to the eastern basin of Lake Erie (Smith 1994). The Mannheim weir is located approximately midway along the river (Figure 1) and creates an impoundment for the extraction of regional drinking water. Mean depth downstream from the weir is approximately 0.5 m, mean annual discharge is approximately 33 m^3/s, and primary substrates consist of cobble and broken rock (Bunt et al. 1998). The construction of the 2.2-m high weir and fishways was completed in 1990. Characteristic of Denil fishways, those at the Mannheim weir use baffles to turn the flow of water back on itself to reduce the velocity of a primary flow, through which fish must swim. Prior to 1990, fish movements were not restricted at this site.

To allow upstream passage of fish, a 27-m Denil fishway that doubled back on itself twice was constructed from reinforced concrete along the west bank of the river (Figure 2). Each of three parallel flumes (slope 10%) were fitted with metal baffles spaced approximately 25 cm apart. On the east bank of the river, a much simpler and less expensive Denil fishway was constructed. It consisted of a single 11-m reinforced concrete flume with baffles along a 20% slope (Figure 2). All flumes were 0.6 m wide and 2.15 m deep and were completely covered with removable steel plates.

Telemetry.—Digitally coded radio tags (1.9 g in water; 10.6 mm × 28 mm × 7 mm; 2.5-s pulse rates) were externally attached to 32 white suckers and 53 smallmouth bass exceeding 300 mm total length. External tagging was chosen because most fish were ready to spawn and therefore considered unfit for surgical implantation without the risk of affecting normal behavior. We tagged equal proportions of males and females of each species. The

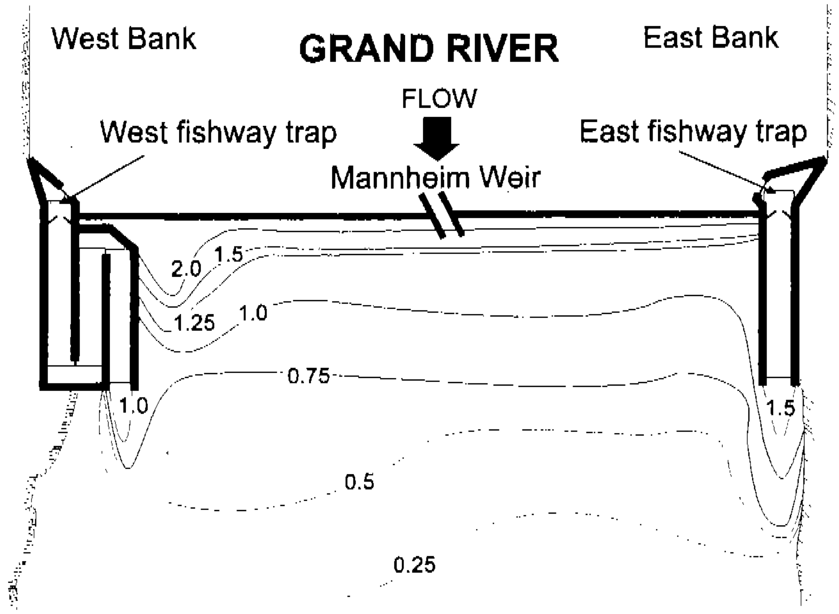

FIGURE 2.—Schematic of the fishways (not to scale) and the region immediately downstream from the Mannheim weir. Shaded areas in the fishways indicate the reception zones monitored by the underwater telemetry antennas. Relative velocity isopleths indicate surface water velocities (m/s) downstream from the weir, as measured with a Sigma PVM velocity meter.

ratio between tag weight and fish weight was less than 2%, as recommended by Winter (1983). After a brief recovery period, each transmitter was tested and fish were released at randomly chosen sites, approximately 150 m downstream from the weir.

Movement of radio-tagged smallmouth bass and white suckers was determined using an array of seven stationary submerged antennas near the weir and within the fishways. One antenna was positioned within each of the three flumes of the west fishway and another was positioned midway within the east fishway. One antenna was also positioned at the entrance of each fishway, and the final antenna was positioned between the fishway entrances to record back and forth movement. All seven antennas were scanned every 7.5 ms for telemetry signals. A receiver and digital spectrum processor (SRX 400 and DSP 500., respectively, of Lotek Engineering Limited) equipped with fast multiple antenna switching capabilities were used to determine transmitter locations relative to the focal point of the nearest antenna. Pulse-code discrimination was used to identify valid signals. Signal-strength calibrations allowed us to accurately determine the distance between transmitters and receiving antennas to within 0.3 m. The signal reception areas at the weir were verified regularly by manually shifting reference radio tags throughout the zones monitored by the antenna array. Reception cell radii varied between 3 and 4 m, depending on water depth (usually <1 m) and conductivity (range 450–550 μS/cm). Visual observations of radio-tagged fish were often possible and were used to corroborate telemetry data.

Our goal was to describe fishway use among a group of smallmouth bass and white suckers that had a propensity to enter and use the fishways but faced variable flow conditions. We recognized that an evaluation of fishway passage efficiency of free swimming fish is a complicated and difficult task. Tagged fish may react negatively in high-velocity flows, or radio-tagged fish may react variably such that some fish may repeatedly enter a fishway and exit again downstream. For this study, such behavior was considered to be partial or unsuccessful fishway use. Complete or successful fishway use consisted of trapping or detection of radio-tagged fish within the fishway trap. Attraction efficiency was calculated as the ratio between the number of individuals that were detected at each fishway entrance and the number that were released downstream. Passage efficiency was determined from the ratio of successful to overall attempts to use a fishway. We created control groups by anchor-tagging a large number of both species and comparing their recapture patterns with radio-tagged fish. We were not able to collect all fish for anchor-tagging and radio attachment from the fishway traps. Therefore, by angling we captured 11 smallmouth bass near the fishway entrances and statistically compared their use of the fishways with smallmouth bass that were caught in the fishway traps. If no differences were detected between the number of angled versus trapped smallmouth bass that used the fishways, data for smallmouth bass were pooled.

Mark–recapture and data analysis.—Fish that successfully ascended each of the two fishways were trapped just before the upstream exit in fishway traps that consisted of aluminum blocking screens (mesh size 1.5 cm) and removable aluminum funnels made from 2-cm wire mesh (Figure 2). Installation and monitoring of fishway traps began in mid-April before any fish were observed near the weir. Water temperatures were recorded each time fishway traps were checked and at midday using a hand-held thermometer at the west fishway entrance. The Grand River is well mixed, and there is no difference in water temperature on either side of the weir. When the water temperature was warm enough, white suckers were trapped in the fishways and smallmouth bass were either trapped in the fishways or angled near the fishway entrances. These fish were either radio-tagged, or externally marked (Floy FD-94 anchor tag), and released at randomly chosen release sites, downstream. Fishway traps were checked and cleared daily between 0900 and 1400 hours and between 1600 and 0200 hours. All trapped fish were removed from the fishway traps with a dipnet, enumerated, and measured for total length (TL, mm). Most were tagged and released downstream. In all situations, fish that returned to either fishway trap more than once were released upstream from the weir. The mean total lengths of white suckers and smallmouth bass, including recaptured fish collected from the fishway traps but excluding juveniles (<200 mm for both species [Scott and Crossman 1973]), were compared with one-way analysis of variance (ANOVA). Numbers of anchor-tagged and radio-tagged fish that were subsequently recaptured in the fishway traps were compared with chi-square contingency analysis. Radio-tagged smallmouth bass and white suckers that were recaptured or detected in the fishway traps were considered to have made a successful attempt at using a fishway. Attempts to use a fishway occurred when radio-tagged fish were detected more than 2 m inside either fishway entrance. Attraction and passage efficiencies of both species were compared at each fishway using 2 × 2 contingency analysis for proportions with corrections for continuity, and the power of the performed test was determined according to the methods in Zar (1984). All statistical tests were considered significant at an alpha level of 0.05, and all means are reported ±1 SE.

Fishway conditions.—Denil fishway water depths, discharge, velocities, and water surface profiles are interdependent and relationships between them have been developed through hydraulic model studies (Katopodis and Rajaratnam 1983; Rajaratnam and Katopodis 1984). Several extensive laboratory investigations with scale and prototype models of Denil fishways have been conducted (Rajaratnam and Katopodis 1984; Katopodis et al. 1997). In these studies, two model scales (1:6 and 1:3) were examined and compared with a prototype scale (1:1) for the standard Denil design, similar to those at the Mannheim weir. The similarity of the results from the three scales was demonstrated, and the three data sets fit the same curve. Results were also confirmed in a field study (Rajaratnam et al. 1992), which proved the reliability of these relationships and the use of depth measurements to estimate fishway discharges and velocities. In addition, concordance between estimated velocities and actual velocities at the Mannheim weir was verified with direct measurements of water velocity within the fishways with a Sigma PVM ultrasonic velocity meter. Water depths were therefore measured directly at the Mannheim weir and used to calculate velocities in the two fishways.

Water depths downstream from each fishway trap were recorded to produce a flow profile and to estimate water velocities from a velocity-rating curve. The minimum velocities yielded by the rating curves were 0.24 and 0.33 m/s for the west and east fishways, respectively. Using a calibrated rod, we measured the vertical distance (nearest cm) to the water surface at a series of fixed points along the fishway. Water depths for the various measurement locations were calculated by subtracting these field measurements from the previously measured vertical distance to the baffle crests. Turbulence at the surface of the primary flow compromises true estimates of velocity (Katopodis and Rajaratnam 1983). Calculations of maximum water velocity that any fish would experience during fishway use were therefore derived for a region corresponding to 0.8 × water depth.

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Swimming abilities.—We determined the critical swimming speeds (U crit) for Grand River smallmouth bass that were similar in size to fish chosen for radio-tagging. Critical swimming speed is a measure of prolonged swimming and represents the maximum velocity a fish can maintain for a prescribed period of time (Brett 1964). Fish were held without food for 48 h prior to experimentation. All swimming speed experiments were conducted in ambient river water using a modified 70-L Blazka-Fry respirometer. Fish were acclimated to the respirometer for 24 h at water velocities that approximated 0.5 body lengths (BL)/s. Critical swimming speeds (m/s) were determined using 10 min increments between constant step-wise velocity increases of approximately 1–1.5 BL/s according to the procedures of Brett (1964). Velocities were corrected (Smit et al. 1971) for blocking effects caused by the flow of water around the bodies of large fish within the swim tube. The water temperature for all trials ranged between 15°C and 20°C, and all fish were acclimated to natural light: dark cycles to minimize the effects of photoperiod and temperature on centrarchid swimming performance (Kolok 1991). Relationships between U crit and total length were determined using regression analysis. Information of swimming ability of white suckers was derived from the available literature (Jones et al. 1974).

Results

Hydraulic Conditions in Fishways

The mean water velocity in the west fishway (0.89 ± 0.02 m/s, range <0.24–1.57 m/s, $N = 207$) was significantly less than the water velocity in the east fishway (0.99 ± 0.03 m/s, range <0.33–2.05 m/s, $N = 162$, $P < 0.001$), except during rare occasions when large amounts of debris accumulated on the east fishway blocking screen. Variable accumulations of debris on upstream blocking screens altered water depths so that a range of water velocities was available in both fishways throughout the study period. Velocities in the fishways varied on a daily basis as debris accumulated and was cleared from the blocking screens. Variations in flow and velocity were most pronounced after mid-June, when macrophytes became established upstream. Velocities were greatest after fishway traps and blocking screens were cleaned. Velocities were lowest after large amounts of debris had accumulated on blocking screens after storms. Maximum fishway use occurred at intermediate velocities when some debris had accumulated on the blocking screens.

White Suckers

White suckers were first observed at the fishway entrances and began to use both fishways on 3 May 1995 after which, midday water temperatures were consistently above 9°C. Maximum passage occurred on 3 May 1995 when 92 white suckers were captured in the west fishway trap. The last recorded passage was on 15 July 1995 when two white suckers were caught in the east fishway and the water temperature was 23°C. In 1996, white suckers began to use the west fishway on 6 May, after which water temperatures were consistently above 8°C. Maximum passage at the west fishway occurred on 17 May when 101 white suckers passed upstream and the water temperature was 11°C. White suckers began to use the east fishway on 9 May 1996 when the water temperature was consistently above 10°C. Maximum passage at the east fishway occurred on 11 May 1996 when 76 white suckers used the fishway and the water temperature was 10°C. The last recorded passage of white suckers at the west and east fishways was on 9 July (18°C) and 15 July (21°C), respectively. White suckers were caught most frequently in the fishway traps from 3 May to 12 May 1995 and 6 May to 18 May 1996. Aggregations of white suckers were observed near the weir and fish often appeared to follow one another.

White suckers were periodically within the vicinity of the weir (within 20 m) for 12 ± 2 d. During this period 50% (95% CI = 33–67%) and 59% (95% CI = 42–76%) of radio-tagged white suckers were attracted to the west and east fishways, respectively. The attraction efficiency of white suckers at both fishways was not significantly different ($Z = 0.78$, $P > 0.5$). Radio-tagged white suckers were detected near the weir and fishway entrances within 1 d of release (mean 0.75 ± 0.25 d). Twenty-two fish approached the weir, and 45% were first detected in the high velocity zone upstream from the west fishway entrance (Figure 2). Highly variable exploratory movements (Figure 3a) as well as long periods with no movement near the weir and fishways were common.

Approximately half of all radio-tagged white suckers that entered the west fishway ($N = 11$) swam to the exit. Passage efficiency of white suckers by the west fishway was estimated to be 55% (95% CI = 25–84%). There were eight attempts to use the east fishway, where passage efficiency of white suckers was estimated at 38% (95% CI = 4–71%). Passage efficiency at each fishway did not differ statistically ($Z = 0.17$, $P > 0.5$). Over

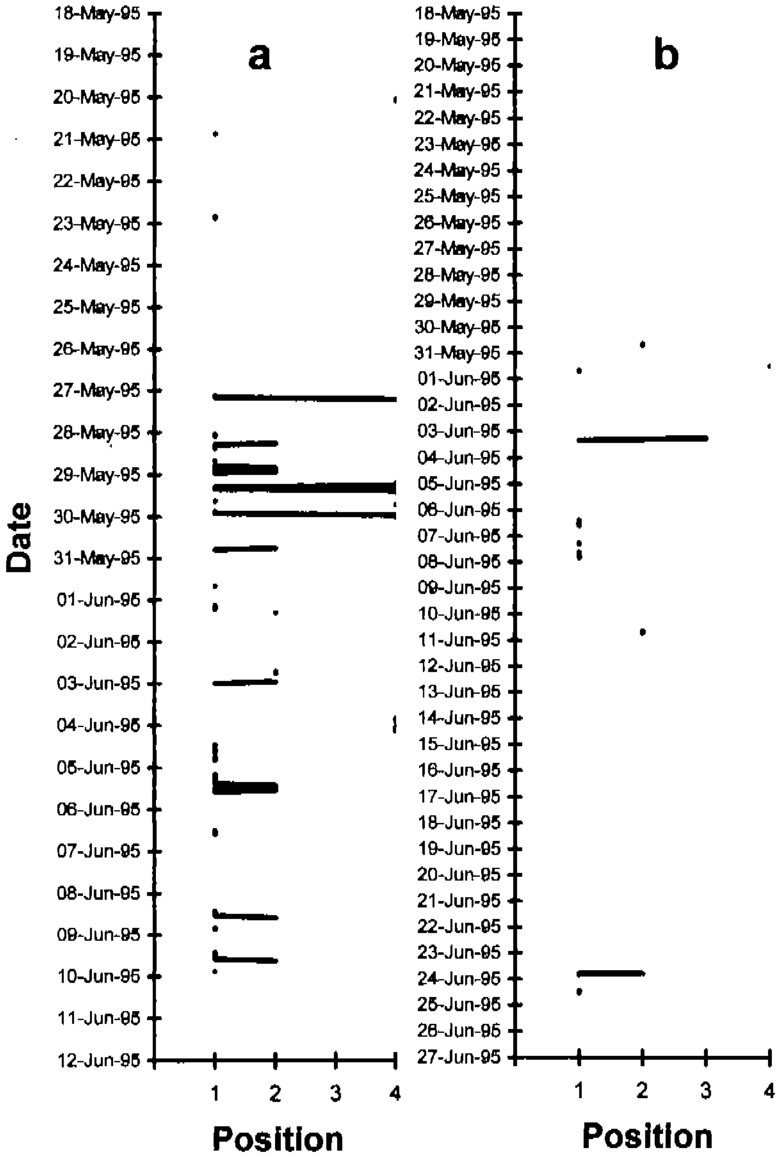

FIGURE 3.—Examples of back and forth movements by (**a**) white suckers and (**b**) smallmouth bass immediately downstream from the weir during the spring of 1995. Positions along the abscissa are as follows: 1 = west fishway entrance, 2 = high-velocity area in spillway, 3 = region between fishway entrances, and 4 = east fishway entrance.

69% of total white sucker passage occurred at the west fishway (Table 1). These white suckers were significantly larger than white suckers that used the east fishway ($F = 25.75$, df = 1328, $P < 0.001$; Table 1). Approximately 27% of white suckers caught in the west fishway used velocities less than 0.24 m/s. Similarly, approximately 70% of white suckers used the east fishway when water velocities were less than 0.33 m/s. Numbers of white suckers using each fishway declined exponentially relative to water velocity. The maximum water velocities used by white suckers was 0.96 m/s. White suckers were located near both fishways at night, but twice as many attempts to use either fishway occurred during daylight hours (Table 2).

Smallmouth Bass

Smallmouth bass began to use both fishways on 9 May 1995 when the water temperature was consistently above 10°C. Maximum passage at both

TABLE 1.—Mean total length (±SE) of smallmouth bass and white suckers caught in the fishway traps between May and July 1995 and 1996. Numbers of anchor-tagged and radio-tagged fish and subsequent recaptures from the fishway traps are shown. For each species, total lengths (TLs) were significantly different ($P < 0.05$) between fishways, numbers of fish caught were similar for smallmouth bass but significantly different ($P < 0.05$) for white suckers.

Species	West fishway		East fishway		Number of fish		Number of recaptures (%)	
	TL (mm)	N	TL (mm)	N	Anchor-tagged	Radio-tagged	Anchor tag	Radio tag
Smallmouth bass	326.8 ± 6.3	37	348.8 ± 7.2	48	51	53	3 (5.9)	2 (3.8)
White suckers	321.9 ± 2.2	919	302.3 ± 3.2	410	818	32	42 (5.1)	1 (3.1)

fishways occurred on 5 June 1995, when eight smallmouth bass were caught in each fishway trap and the water temperature was 16°C. The last recorded passage of smallmouth bass in 1995 was on 27 June (water temperature = 20°C) and 17 June (18°C) for the west and east fishway, respectively. In 1996, smallmouth bass began using the east fishway on 18 May (14°C). Maximum passage occurred on 18 May, when nine smallmouth bass used the east fishway. Passage at the west fishway began on 20 May (16°C). The last recorded passage for smallmouth bass in the west and east fishways was on 14 July and 15 July, respectively, when the water temperature was 21°C. Most smallmouth bass were captured in the fishway traps from 15 May to 5 June 1995 and 18 May to 13 June 1996. Frequent freshets and abnormally cool June temperatures interrupted smallmouth bass migrations in 1996. Tagged and untagged smallmouth bass were often observed in the high- velocity zone near the west fishway entrance (Figure 2). Smallmouth bass were first detected near the weir and fishway entrances 3.0 ± 0.5 d after release. There was no difference in time to detection or in attempts to use the fishways among trapped and angled fish, so data for smallmouth bass were pooled.

TABLE 2.—Tracking summary, diel use of the fishways, and patterns of use by white suckers and smallmouth bass.

Variable	White suckers	Smallmouth bass
***N* (%) tracked near the fishways**		
1995	12 (67)	22 (76)
1996	11 (79)	17 (68)
Attempts to use fishway[a]		
Nocturnal, west fishway	3	2
Daytime, west fishway	8	10
Nocturnal, east fishway	2	1
Daytime, east fishway	6	2
Times spent (min)		
In pool 1, west fishway	1–20	2–80
In pool 2, west fishway	5–176	3–1140
For full ascent, west fishway	12–85	43–1240
For full ascent, east fishway	4–6	1
Overall[b] and successful attempts to use fishway		
Overall, west fishway	11	11
Successful, west fishway	6	4
Overall, east fishway	8	3
Successful, east fishway	3	1
Passage (P) and attraction (A) efficiency (%) and 95% confidence interval		
A, west fishway	50 (33–67)	82 (69–95)
P, west fishway	55 (25–84)	36 (8–65)
A, east fishway	59 (42–76)	55 (38–72)
P, east fishway	38 (4–71)	33 (1–87)

[a] Nocturnal attempts were between 2000 and 0600 hours.
[b] Overall attempts may not equal the sum of nocturnal and daytime attempts because some fish waited overnight in resting pools of the west fishway.

During the study, 82% (95% CI = 69−95%) of smallmouth bass were attracted to the west fishway, and 55% (95% CI = 38−72%) were attracted to the east fishway. The attraction efficiency of smallmouth bass by each fishway was not significantly different ($Z = 1.82$, $0.1 < P < 0.05$, power = 0.43). As with white suckers, exploratory movements were common (Figure 3b) and lasted for 16 ± 2 d for fish that did not successfully pass upstream from the weir. The number of attempts to use the fishways during the day exceeded nocturnal use by a factor of five (Table 2).

Passage efficiency of smallmouth bass at the west fishway was estimated to be 36% (95% CI = 8−65%). Only three radio-tagged smallmouth bass entered the east fishway, and one swam upstream to the exit. Therefore, east fishway passage efficiency of smallmouth bass was roughly estimated to be 33% (95% CI = 0−87%). Passage efficiency of smallmouth bass at the west fishway did not appear to differ from passage efficiency at the east fishway ($Z = 0.08$, $P > 0.5$). Eighty-five untagged and tagged smallmouth bass were recovered from the fishway traps, and 48 (56%) were caught in the east fishway (Table 1). Equal numbers of smallmouth bass used each fishway ($\chi^2 = 1.42$, $P < 0.25$), and equal proportions of radio-tagged and anchor-tagged smallmouth bass were recaptured in the fishway traps (Table 1). More than 71% of smallmouth bass used the west fishway when water velocities were less than 0.24 m/s. At the east fishway a similar pattern emerged: 60% of smallmouth bass used water velocities less than 0.33 m/s. Numbers of smallmouth bass using each fishway declined exponentially relative to water velocity. The maximum water velocities used by smallmouth bass in the west and east fishway were 0.72 and 0.99 m/s, respectively. Smallmouth bass that used the east fishway were significantly larger than smallmouth bass that used the west fishway (F = 4.93, df = 84, P = 0.03; Table 1).

Critical Swimming Speeds

The range of critical swimming speeds recorded for smallmouth bass 262–378 mm TL was 0.50–1.18 m/s. There was a highly significant positive relationship between critical swimming speed and total length of fish tested ($N = 11$, $r = 0.43$, $P < 0.001$). The relationship was best described as U crit = $0.009534 \times TL^{0.7626}$.

Discussion

Studying fishway use and effectiveness from a biological perspective is a notoriously difficult challenge (Beach 1984), and this study was no exception. Various misfortunes confronted us during this project. For example, antennas were temporarily severed twice from debris accumulation during storms, which may have resulted in undetected attempts at the east fishway. We were unable to collect sufficient numbers of fish that were potentially naive of the weir, and this may have affected our estimates of attraction and passage. Learning among fish has not been proven to exist, and we therefore feel that these effects were negligible. Our observations suggest that some fish migrate upstream to barriers. Others find habitat that suits them downstream from river barriers and may never interact with the barriers. Clearly, some fish within a spatially distinct area will naturally relocate in the springtime while others will not. It is therefore impossible to know, a priori, which individuals have a propensity for physical displacement. Even if fish for this study had been collected from areas away from the weir, there would be no evidence they had not interacted with the fishways or the weir prior to this work. As such, it is extremely difficult to gauge the importance of fishways with random samples of fish collected downstream from river barriers. Other problems that we encountered while comparing the Mannheim fishways included the high velocity region upstream from the west fishway that distracted some fish during the study. Also, the modest degree of complete fishway use by radio-tagged fish was insufficient for the application of powerful statistical analyses. It is likely, based on limited numbers of white suckers and smallmouth bass that used each fishway annually, that an economically excessive number of fish would have to be tagged to yield statistically adequate data. Nonetheless, this was the first biological assessment and evaluation of fishway use by warmwater species and some intriguing patterns emerged.

A complete assessment of fishway performance should address entrance attraction efficiency, difficulty or physical output associated with upstream passage, and finally, passage efficiency. Simple observation or mark–recapture experiments at existing fishways (e.g., Fernet 1984; Schwalme et al. 1985; Monk et al. 1989; Dexter and Ledet 1996) have not effectively provided information that relates overall attempts to successful attempts, the timing of fishway use, and other factors necessary for a clear understanding of fishway efficiency. One recent study used two receiver check-points or gate-keepers, spaced 50 m apart to monitor the movements and ascent of barbel *Barbus barbus* over a flow-gauging weir in England (Lucas and Frear 1997). However, until now, no studies have used radiotelemetry to continuously monitor the detailed behavior of warmwater fish in fishways. Although the literature contains numerous quantitative and anecdotal reports of anadromous fish passage, we are not aware of any study relating the success and failures of individual attempts to use fishways by warmwater fish.

The behavioral and physiological impacts of river barriers on white suckers and smallmouth bass are largely unknown. It appears that upstream movements of both species are interrupted and delayed at dams despite the presence or absence of fishways. In a recently published report, Kanehl et al. (1997) demonstrated the positive effects of low-head dam removal on smallmouth bass abundance and biomass. Numerous other species experience significant delays passing river barriers. For example, delays of several weeks have been reported among northern pike *Esox lucius* in Canada (Fernet 1984), barbel in England (Lucas and Frear 1997), Atlantic salmon *Salmo salar* in Scotland (Webb 1990), and several percid species in Australia (Harris and Mallen-Cooper 1994). At the Mannheim weir, delays were often indefinite, and most radio-tagged fish did not pass upstream. Delays among salmonid and cyprinid species have been

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attributed to a reluctance to swim at high speeds (Priede and Holliday 1980) or to physical inability to swim at speeds necessary for successful ascent (Lucas and Frear 1997). Regardless of the cause, numerous species of fish have demonstrated a potentially catastrophic tendency to resorb gametes after extensive delays below dams (Shikhshabekov 1971).

In our study, water velocities in both fishways were usually less than maximum prolonged swimming speeds, which were 1.18 m/s for smallmouth bass 378 mm TL and 0.73 m/s for white suckers 370 mm fork length (Jones et al. 1974). Such conditions should have permitted successful fishway use. It is interesting to note that white suckers began using the low-velocity fishway earlier in the season and at lower water temperatures than the high-velocity fishway. At low water temperatures, fish rely heavily on anaerobic white muscle tissue to support intense swimming activity (Rome et al. 1992). Cooler water temperatures reduce aerobic swimming capacity (Jayne and Lauder 1994) such that the onset of burst activity occurs sooner and at lower water velocities. Water temperatures below a species-specific minimum prevent fish from achieving and maintaining swimming speeds necessary to negotiate high water velocities along the lengths of some fishways. Comparisons between swimming performance and passage success in Denil fishways may be further obscured by negative behavioral responses to turbulence, entrained air bubbles, and a high-velocity layer of water at the surface of the flow profile. Beach (1984) suggested that fish must swim at least 30% faster than opposing flows to progress upstream. High water velocities and turbulence in the east fishway may have prohibited successful use by some fish, particularly small smallmouth bass and large white suckers. It should be mentioned that the slope of the east fishway exceeds Clay's (1995) recommended maximum.

The tracking method incorporated in the present study permitted direct measurements of the potential delays associated with locating fishway entrances, time spent in resting pools, and total time of passage. Both white suckers and smallmouth bass rested much longer in the second of the two pools in the west fishway, which may be an indication of fatigue. Visual and videographic observations (senior author's unpublished data) of smallmouth bass migrating through Denil fishways with water velocities in excess of approximately 0.5 m/s indicate that fish positions are greatly influenced by turbulence. Nonbenthic species, such as smallmouth bass, must withstand a great deal of turbulence while negotiating maximum water velocities near the surface of Denil fishway flows. These maximum velocities and the behavioral effects of turbulence on fish passage should be addressed to refine design criteria for Denil fishways.

Fish that were able to fit in the spaces between baffles without injury sometimes passed upstream when high water velocities should have prohibited successful fishway use. This was accomplished by burst swimming upstream from refuge to refuge, as observed among cyprinids in other Denil fishways (Schwalme et al. 1985). Fish that were able to maintain position near the bottom of the flow profile, such as benthic suckers, were able to use the fishways when surface water velocities appeared excessive. The relative importance of burst swimming, position-holding abilities within the boundary layers of flows, prolonged swimming abilities, and injury rates caused by impacts with baffles also require further investigation to maximize passage rates of warmwater species through Denil fishways. Experiments using electromyogram telemetry may help to determine relative physiological costs (McKinley and Power 1992; Demers et al. 1996; Hinch et al. 1996) associated with the use of different fishways under a variety of conditions.

In summary, the relatively simple and inexpensive fishway design on the east side of the Mannheim weir permitted large smallmouth bass as well as small white suckers, a species with lesser swimming abilities, to pass upstream. Water velocities in both fishways were generally within the range of critical swimming speeds of smallmouth bass and white suckers, and equal numbers of smallmouth bass were collected from each of the fishway traps. However, the lower-velocity fishway with resting pools, on the west side of the Mannheim weir permitted more white suckers to pass upstream. The number of white suckers and smallmouth bass that used each fishway declined exponentially as water velocities increased. Maximum velocities used by white suckers and smallmouth bass were 0.96 and 0.99 m/s, respectively. Passage efficiencies of each species at both fishways were low to moderate. Future work should address the physiological and behavioral characteristics of fish that affect passage through fishways.

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