REGULATED RIVERS: RESEARCH & MANAGEMENT
Regul. Rivers: Res. Mgmt. **14:** *41-51 (1998)*

MEASUREMENT OF BURST SWIMMING PERFORMANCE IN WILD ATLANTIC SALMON (*SALMO SALAR* L.) USING DIGITAL TELEMETRY

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ABSTRACT

Swimming performance of wild Atlantic salmon (*Salmo salar* L.) was investigated in an experimental flume using coded radio signals. To calculate swimming speed, distance moved and time elapsed were measured with a digital spectrum processor using near real-time spectrum analysis. This device was designed to be used in a coprocessing arrangement with a receiver, thereby providing pulse position code discrimination, verification and continuous data storage. Radio-tagged adults (48.3 to 54.8 cm long) voluntarily swam against water velocities, ranging from 1.32 to 2.85 m s^-1, in an 18 m long flume at a mean water temperature of 10.1 ± 1.6°C. At water velocities of 1.32–1.55 m s^-1, individuals successfully ascended the flume at swimming speeds of 1.61–2.55 m s^-1, or 3.30-4.79 body lengths per second (1 s^-1), respectively. At high water velocities ranging from 1.92 to 2.85 m s^-1, individual swimming speeds increased from 2.55 to 3.60 m s^-1, or 4.94-7.27 1 s^-1, respectively. However, above a threshold value of 1.92 m s^-1, individuals traversed shorter distances and were unable to ascend the flume. The highest swimming speed observed was 4.13 m s^-1, or 8.35 1 s^-1. The results of this study indicate that in addition to its applicability in the determination of burst swimming speeds, digital telemetry could prove a useful tool in the design and evaluation of future fishways and culvert installations. ©1998 John Wiley & Sons, Ltd.

KEY WORDS: burst swimming; *Salmo salar;* water velocity; digital telemetry

INTRODUCTION

Dams have been widely constructed on waterways to provide a stable water supply, to control floods and, to provide hydroelectric power. Some of these dams have constructed fishways intended to provide safe passage for fishes. High flow rates are often associated with fishway entrances, and for a fish to progress through a fishway it must be able to swim at velocities greater than the opposing water currents. Generally, successful passage requires a high swimming speed. However, few studies have assessed burst swimming capabilities in salmonids in relation to fishway design.

Swimming of fish can be classified into three major categories: sustained, prolonged and burst swimming speeds. Sustained swimming occurs at relatively low water velocities and represents speeds that can be maintained for longer than 200 min (Beamish, 1978). It uses energy derived exclusively from aerobic processes. Prolonged swimming covers a spectrum of speeds between' burst and sustained and is often categorized by steady swimming interspersed with periods of vigorous effort. The highest speeds of which fish are capable are classified as burst swimming. In fish, as in all vertebrates, the highest levels of exercise performance are achieved anaerobically (Jones, 1982). These high speeds can be maintained only for brief periods (less than 20 s), and are terminated by the exhaustion of extracellular energy supplies or by accumulation of waste products.

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CCC 0886-9375/98/010041-11$17.50

Received 15 December 1996
Accepted 15 July 1997

The capacity for high speed swimming for short periods of time is important for the survival of many fish species. Acceleration involved in fast-starts from rest, high speed manoeuvres or speed changes from one steady speed to another is an integral part of swimming. The former two propulsive patterns involve high rates of acceleration and are important in prey capture, escape from predators (Hunter, 1972) and in the successful negotiation of such obstacles as waterfalls and fish ladders (Katopodis, 1994). A few species like salmon use high speed bursts to swim up or leap otherwise impassable water falls, allowing the fish to migrate upstream to reach spawning grounds. In addition, biologists have suggested that by alternating periods of fast swimming and gliding fish can greatly reduce energy expenditure (Weihs, 1974; Videler and Weihs, 1982). Thus, fast bursts of swimming are vital components of a fish's locomotory repertoire and are of high ecological importance.

There are several biological and environmental constraints on fish swimming which deserve consideration. In a laboratory study on burst swimming, Bainbridge (1958) supported the view that fish up to 1 m in length should be able to swim up to 10 times their own body length for a short time of about 1 s (1 s ^-1), beyond which swimming speed would decrease exponentially. Recent studies suggest variability in burst swimming among species and for some, the relative performance maximum of 10 1 s^-1 is a conservative measure (Webb and Corolla, 1981; Wardle and He, 1988). Furthermore, the maximum speed that fish can achieve is influenced by fish size (Webb, 1975) and body form (Webb 1978; Taylor and McPhail, 1985). Anaerobic metabolism at burst activity levels is relatively independent of water temperatures (Webb, 1978), however, recent studies indicate that temperature acclimation can affect muscle properties (Johnston *et al.,* 1990; Beddow *et al.,* 1995). Therefore, biological factors such as size and species, as well as environmental factors, may affect burst swimming performance.

The main objective of this research project was to assess high speed swimming performance in migrating anadromous Atlantic salmon *(Salmo salar* L.) in an experimental passage structure. In particular this study focused on the influence of flume velocity on the burst swimming speeds of this species during its spawning migration.

MATERIALS AND METHODS

Experimental flume

The study was conducted in an experimental stream flume constructed at the Noel Paul's Brook Research Facility in central Newfoundland, Canada (approximately 49°N latitude, 57°W longitude). The flume consisted of an upstream head pond (upper pool, area *6* m²) created in the existing sluiceway of the

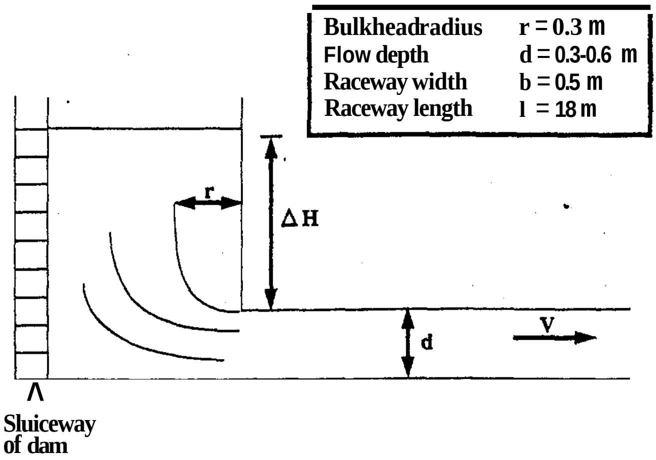


Figure 1. Flow from Noel Paul's Brook enters the upper pool and compresses through the upstream end of the flume. A stop log section in the first sluiceway of the dam controls head elevation (5*H*) and subsequent water velocities (V) downstream

Table I, DSP_500 and SRX_400 specifications

General	
Size (cm)	22.0 x 20.4 x 8.8
Weight (kg)	2.5
Operating voltage range (V)	12 (DC)
Operating current (A)	1.5
Operating temperature range ("C)	−30 to +50°C (LCD: −20°C)
Electrical	
Detection bandwidth (kHz)	25 discrete frequencies in 20 kHz steps
Detection sensitivity (dBm)	−115
Dynamic range (dB)	< 100
Dynamic gain control range (dB)	90
Memory	
Program memory (K)	128
Data memory (K)	512
Controls and I/O	
Interface	50 ohms BNC input for RFRS-232 (9-pin male) serial communication port and antenna switch control port
Controls	2 external power sockets, 2 RS-232 ports, LCD display, BNC (50 ohm) antenna jack, 16 key weatherproof keypad

dam and a downstream pond (lower pool, area 17 m^2) constructed in Noel Paul's Brook (Figure 1). Between these two pools was a wooden flume which measured 18 m long by 0.50 m wide and 0.61 m deep. Water was diverted from the river into the flume through a vertical sluice gate located on the dam. The discharge into the upper pool was controlled by varying the number of stop-logs in the first sluiceway of the dam. In addition, two gates in the stop-log section were regulated to adjust and stabilize the water level in the head pond. The fish exit (water entrance) was modified to reduce turbulence, remove standing waves from the water surface and develop as laminar a flow as possible. This was accomplished by constructing a straight section on the top and two sides of the flume entrance. Test fish were held in the lower pool while experiments were being conducted. The flume had a slope of 2% and where it entered the upper pool its bottom was flush with the floor of the upper pool.

Radio telemetry equipment

Radio telemetry equipment was used to monitor the movements of fish in the flume (Lotek Eng. Ltd, Newmarket, Ontario). Radio transmitters were cylindrical, 5 cm in length and 1 cm in diameter, weighed 8.6 g in air, had a 24 cm insulated trailing antennae and were tapered to a 0.5 cm diameter at one end. Transmitters were encapsulated in waterproof epoxy resin and activated by a magnetic reed switch. Transmitters were uniquely coded and were designed to broadcast at frequency intervals of 20 kHz within an operating band of 149.54–149.74 MHz with a battery life of 15 days. The receiving system was programmed to record coded signals from each fish at 1.25 s intervals.

Transmitted signals were detected by seven fixed antennae connected to a receiver and digital spectrum processor (models SRX_400 and DSP_500). The digital spectrum processor (DSP) is a receiver/coprocessor capable of providing frequency discrimination using near real-time spectrum analysis (Table I). The DSP was optimized to detect many frequencies simultaneously and transfer information concerning pulse arrival times, antenna position and frequencies to the receiver, which performed code discrimination, code error correction and data storage. In addition, the receiving system was equipped with multiple antennae switching capability which determined the location of a transmitter relative to the seven antennae (Figure 2). This was achieved via pulse position code discrimination, in which each radio transmission is assigned a unique coded time signature. Antennae were simultaneously scanned every 7.5 ms. The underwater antennae array was placed at equally spaced intervals along the bottom of the flume (0, 2.53, 5.06, 7.59, 10.12, 12.65, 15.18 m). Calibration of the signal strength permitted determination of the distance between transmitter and antennae, thereby eliminating non-quantitative visual monitoring. This procedure involved mapping individual antenna reception areas and areas of cell connection zones down the length of the flume prior to experimentation. The DSP continually recorded events in real time, provided measurements of transmitter position and thereby monitored fish passage through the flume.

Fish

Wild adult Atlantic salmon (*n* = 18, 1.16 ± 0.18 kg, fork length = 51.2 ± 2.3 cm, girth = 23.1 ± 1.4 cm: mean ± S.D.) were collected from fishway traps located on the Exploits River watershed during late August 1995 (mean temperature: 15°C, range: 14-16°C). The Exploits River is the longest river and largest watershed in insular Newfoundland. The river is 267 km long and has a drainage area of 1 1272 km^2. Fish were transported to an incubation facility at Noel Paul's Brook, a large tributary of the middle Exploits. Chemical analyses of water samples from the collection and experimental sites were similar (median pH = 6.5, average conductivites ranged from 20 to 30 ***uS*** cm^-1 and total hardness = 7.7 mg 1^-1 ± 1.1; mean ± S.D.). Individuals were retained in large rectangular outdoor pens which measured 8 m long and 12 m wide. Depth in the enclosures ranged from 0.6 to 1 m. The bottom was composed of gravel substrate similar to that of the river bed and overhead cover was provided. These pens were positioned in a 100 m long channel parallel to the river. Water from the river was diverted through the raceway by upstream intake valves and flowed through it at approximately 40 cm s^-1. All animals were allowed to recover from transport for 7 days prior to swim speed trials in the flume.

All salmon were removed from their holding pen 24 h prior to surgery and placed in a separate pen to recover from the stress of capture. Prior to transmitter implantation, fish were quickly immobilized by immersion in an aerated and buffered solution of MS-222 (tricaine methanesulfonate, 60 mg 1^-1, pH 7.0). Anaesthetized fish were placed ventral side up in a non-abrasive V-shaped surgical table with their heads submerged in freshwater. The individual's head and trunk was kept moist by a cover of pre-soaked towelling. Implantation involved inserting the tapered end of the tag into the urogenital papilla, and gently pushing it anteriorly into the body cavity of the fish (Peake er *al.*, 1996). The transmitter's antenna was allowed to trail externally from the oviduct and the implantation procedure averaged one minute. When size and volume of transmitter were compared with that of the fish (tag ratio was less than 1%), it was considered that stress following insertion was negligible (Solomon and Storeton-West, 1983; Heggberget *et al.*, 1988).

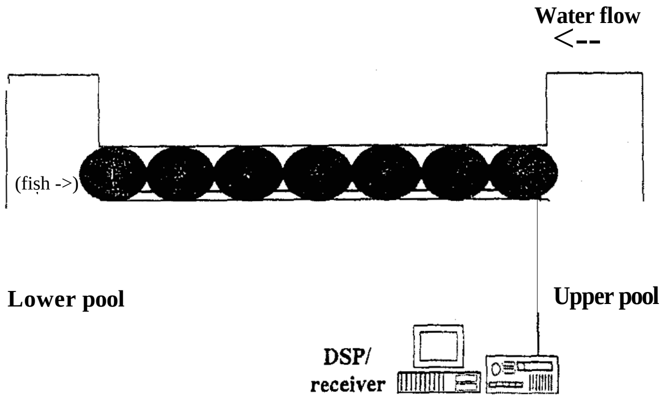


Figure 2. A schematic diagram showing seven fixed antennae stations connected to the receiver/coprocessor system in the experimental flume used for this study. As fish traversed the flume, signals were transmitted and received by the antennae, and information regarding pulse arrival times, antenna position and frequency were processed by the DSP. The receiver performed code discrimination, verification and data storage

After a short recovery in freshwater, fish were introduced into the lower pool of the experimental flume in the stream. They were allowed a 24 h acclimation period at which point the gate to the flume entrance was opened and the head elevation in the upper pool was randomly raised to one of three water velocities (subgroups). Water velocities used were 1.55, 1.92 and 2.55 ± 0.05 m s^-1. A total of 18 wild adult salmon were used. From these, three subgroups of six fish each were equipped with internal transmitters. The number of fish that successfully negotiatied the flume depended on the volitional swimming of individuals as there was no attempt to force fish to swim. Wildlife problems complicated one of our swimming trials and technical interruptions for two other fish were a result of power/recording failures. These three fish were subsequently removed from our analyses. After 72 h, tracking data from the digital spectrum processor were downloaded to a computer via a RS232 serial communication port. Tags were removed from individuals, cleaned, sterilized with alcohol and reused. Fish were then measured for fork length, girth and wet-weight and transferred to separate holding enclosures, grouped by treatment (water velocity) and observed for abnormal behaviour and mortalities for 14 days post-recovery.

Hydraulics

Our approach to quantify flow characteristics in the experimental structure was to use the head pond elevation upstream of the flume. The hydraulics would be described by rating curves and equations relating upstream head pond elevations with the discharge through the flume at a constant slope. Upstream head elevation was fairly stable and was continually monitored during swimming tests. Exceptions to this were noted on two occasions in which rapidly changing weather conditions altered both the water level in the brook and the lower pool. Water velocities and depths were measured at 16 transects equally spaced along the flume's length and at the centre and sides of each transect. Velocity measurements were taken with a two-directional electromagnetic current meter (Marsh-McBirney, model 2000) positioned 3 cm above the flume floor, 3 cm below the water surface and at mid-depth. Mid-depth refers to a point at a vertical distance 0.6 times the water depth below the surface. Mean mid-depth measurements at the centre transects were taken to represent the average velocity through the flume. Depth measurements were recorded to the nearest mm at every transect in order to determine flow rates and develop surface profiles in the flume.

Statistical analyses

The effects of varying water velocities on kinematic variables were analysed in a model-1, randomized design, one-way analysis of variance (ANOVA) with individuals as a random factor and three test water velocities. ANOVA tests incorporated contrasts for polynomial trends, specifically, linear and non-linear trends. All values are represented as means ± standard deviation. Statistical analyses were performed in SYSTAT 5.0 and tests were considered significant at an alpha level of 0.05.

RESULTS

The water temperature in the flume during the study period was 10.1 ± 1.6°C. Water surface profiles for flows during fish tests are shown in Figure 3, Small standing waves are evident as flows were near critical (Froude number was estimated at 0.8–1.2.) At the greatest water velocity tested, flow entered the flume as a turbulent jet concentrated around the central areas of the flume. However, within 1 m of the upstream end the flow had become tranquil and the distribution of velocity across the structure was fairly uniform. Several fish were observed swimming up the flume with their bodies submerged in the water column.

Many fish attempted to ascend the flume during late afternoon and early morning periods (46.7%). At the low water velocity (1.55 m s^-1, n= 5) all fish successfully ascended the flume and reached the upper pool (Figure 4A,B). At the high water velocity (2.55 m s^-1, *n* = 4) no fish were capable of successfully

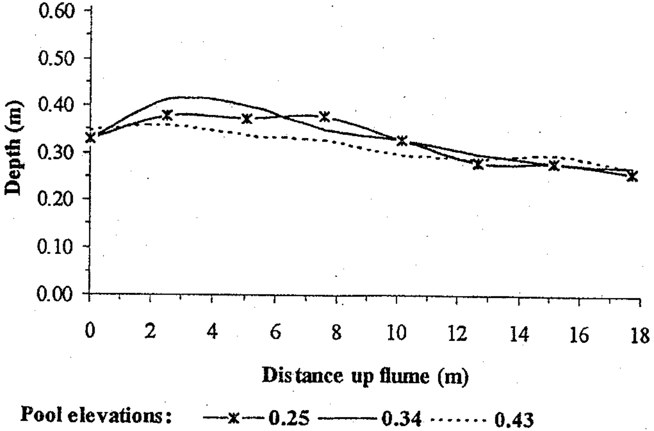


Figure 3. Depth profiles of the flume with corresponding upper pool elevations. Elevations of 0.25, 0.34 and 0.43 represent mean velocities of 1.55, 1.92 and 2.55 m s^{-1}, respectively

ascending (Figure 4C,D). At the moderate velocity (1.92 m s^-1, $n = 6$) the success rate was 33.3% (Figure 5). In addition, the number of unsuccessful passes in front of the flume entrance varied with water velocity and time of day. At high water velocities the number of unsuccessful attempts (1.20 attempts/min) were significantly lower compared with the low and moderate water velocities (2.38 and 2.15 attempts/min, respectively) (p </= 0.05).

Marked differences were noted between the maximum distances attained for each of the three water velocities (Table 11). Distances travelled up the flume significantly declined as water velocity increased (p </=0.05, Figure 6). In addition, mean fish velocity (Figure 7) and acceleration rates, significantly increased with water velocity (p </=0.01). The time spent swimming at each of the low, moderate and high water velocities were 44 ± 17 s, 32 ± 9 and 22 ± 7 s, respectively. Although, the time required for salmon to traverse the experimental fishway decreased with water velocity, this trend was not significant. No significant differences were found between size and condition factor (0.91 ± 0.03) of tested fish versus the kinematic variables listed in Table II. All salmon survived the transmitter attachment and appeared to recover rapidly from the tagging and handling procedures. Mortality during swimming trials and the 14 day post-experimentation period was nil.

DISCUSSION

Behavioural effects from handling and tagging procedures are difficult to estimate (Hawkins *et al.*, 1974). Researchers have shown that the survival, behaviour and egg development in adult salmon fitted with transmitters via oviduct insertion were similar to those of untagged fish (Peake *et al.*, 1996). The ratio of fish mass to transmitter mass, or tag ratio, has been shown to be an important consideration for the biotelemetry researcher, influencing the suitability of external (Greenstreet and Morgan, 1989), internal (Marty and Summerfelt, 1986) and gastric (Summerfelt and Moiser, 1984) attachment procedures. Based on the small size and neglible weight of the transmitters compared with the size of fish, problems associated with reduced swimming capacity (Mellas and Haynes, 1985; Shepherd, 1973) were considered unlikely.

Early studies on high speed swimming qualitatively investigated kinematics (Gero, 1952; Hertel, 1966). Few studies have employed procedures other than laboratory film analysis or accelerometry to study high speed swimming. High speed cinematography has been employed to evaluate specific aspects of fast-starts in relation to predator–prey interactions, and the effects of temperature and body form on escape performance (Webb 1976, 1977). In many of these studies fish were stimulated or shocked to induce movement so performance was likely to be suboptimal. In this study, all fish movements were evaluated under natural conditions and the fish swam voluntarily. Furthermore, since many of the fish tested were active during low visibility hours (46.7%) the use of film was precluded for data collection.

Webb (1975) suggested that, to evaluate fast-start performance properly, data for the duration of the event, mean and maximum accelerations, mean and maximum velocities and the distance covered must all be reported. Maximum distances attained by fish declined as water velocity increased (Figure 6), which suggests a definite distance–velocity barrier resulting in fish fatigue. Beyond moderate water velocities of about 1.92 m s^{-1}, success rates fell significantly. At this water velocity some fish varied their average speed by taking periodic pauses then bursting to maximum speed to complete passage of the flume (Figure 5). These fish may be displaying a burst-and-coast swimming pattern to reduce energy expenditure during high speed swimming (Videler and Weihs, 1982). In addition, individuals made several passes in front of the flume entrance before returning to resting pools in the lower pool. For some, this behaviour continued for hours and even days before an individual attempted to pass through the flume. Delayed salmon passage and excessive energy expended in passage can tax energy reserves (Osborne, 1961), decrease the ability to reach spawning areas and ultimately decrease reproductive success (Geen, 1975).

The physiological and biochemical mechanisms associated with burst-type exercise in fish have been extensively studied (Dobson and Hochachka, 1987; Wood, 1991) but there is considerable variability in

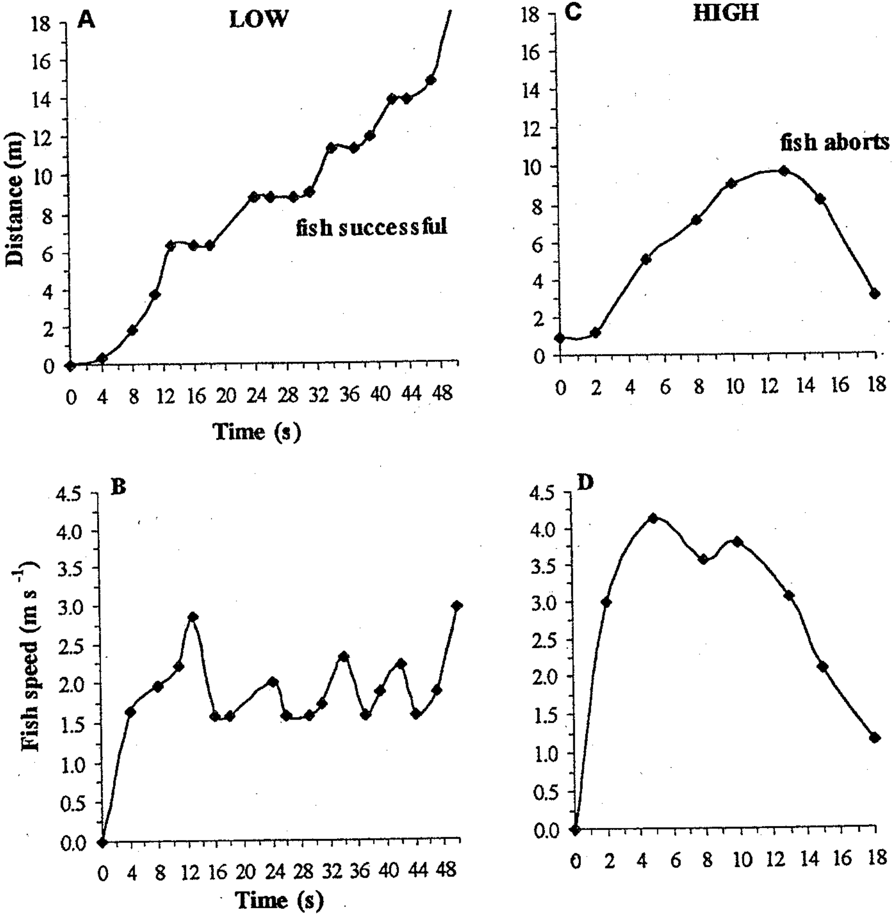
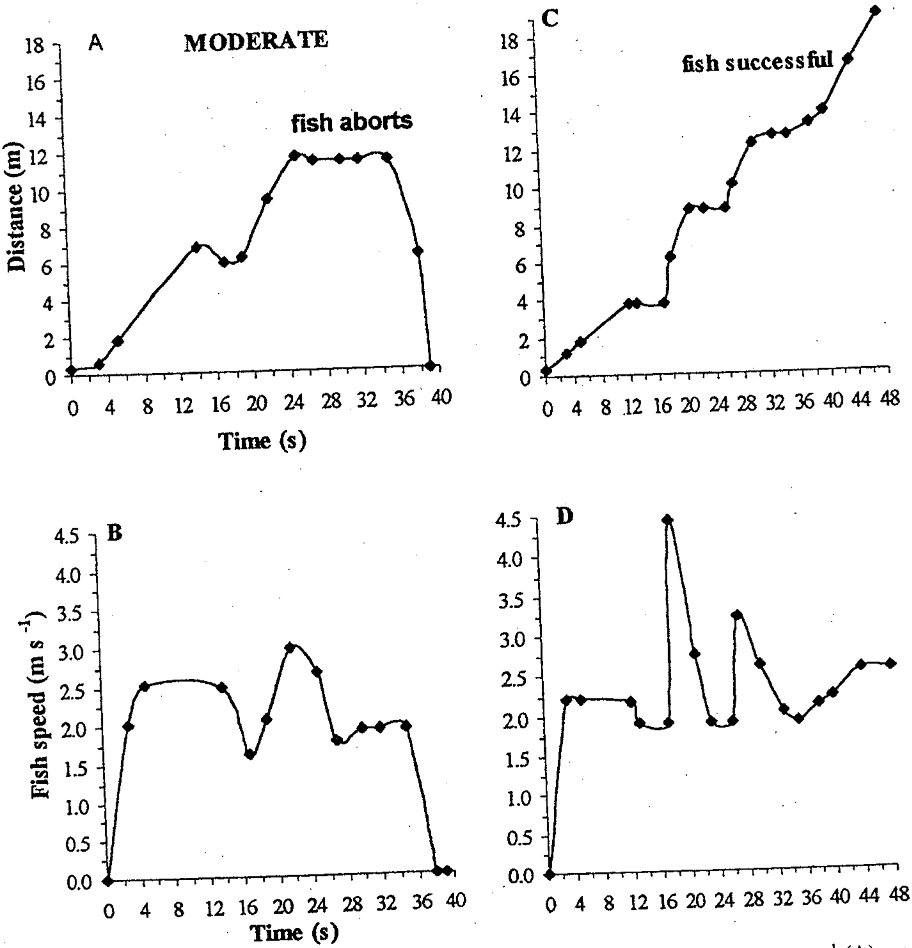


Figure 4. Movement of individual fish through the flume at (A,B) a low water velocity of 1.55 m s^{-1} and (C,D) at a high water velocity of 2.55 m s^{-1}. Plots correspond to two separate fish


A
MODERATE
fish aborts
Distance (m)
0
2
4
6
8
10
12
14
16
18
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4
8
12
16
20
24
28
32
36
40
Time (s)
C
fish successful
0
2
4
6
8
10
12
14
16
18
0
4
8
12
16
20
24
28
32
36
40
44
48
B
Fish speed (m s $^{-1}$)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
0
4
8
12
16
20
24
28
32
36
40
Time (s)
D
0.0
0.5
1.0
1.5
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48

l (A), and it

Figure 5. One fish's unsuccessful attempt to ascend the flume at a moderate water velocity of 1.92 m s^{-1} (A), and its corresponding high average speed (B). The same fish decreases its average speed, bursting to a maximum speed (D) and successfully ascends (C)

the physiological responses to exhaustive exercise between individual fish. Several factors may contribute to the variability of fish tested during this study. This study examined the swimming speeds of fish collected along their migratory routes at seasonal temperatures. It has been shown, that hormonal factors are closely related to the deterioration of salmon swimming muscle during spawning migration (Ando *et al.*, 1986). During migration, Atlantic salmon experience significant depletions of energy reserves and increases in girth. Extensive gonadal development was evident in several test females, probably contributing to the variance noted. Physical condition, as influenced by age, maturity stage, stress and fatigue, health and probably to some extent the inherent genetic capability for upstream migration, affects passage rates and capability for ascent of the experimental fishway. Thus, additional energetic costs associated with barrier falls, rapids and fishways may result in depletion of a salmon's limited energy reserves.

Thermal history may also lead to changes in muscle recruitment (Rome *et al.*, 1984) and white muscle contractile properties (Johnston *et al.*, 1990; Johnson and Johnston, 1991), suggesting that acute temperature changes and thermal acclimation may significantly influence swimming kinematics. In addition, fish compensate for reduced power output of their muscles at colder temperatures by recruiting more fast fibres, and by swimming at lower maximum speeds (Rome *et al.*, 1990). Investigators have found that the critical swimming speeds of wild salmon were affected by temperatures and were about 1.8 m s^{-1} at similar experimental conditions (Booth *et al.*, 1995). Salmon required to swim at low water temperatures and high velocities may depend heavily on white muscle fibres utilizing anaerobic pathways.

Table II. Swimming characteristics of Atlantic salmon (*Salmo salar* L.) in the flume

	Mean water velocity ($\mathrm{m\ s^{-1}}$)		
	Low (1.55)	Moderate (1.92)	High (2.55)
Maximum distance (m)	18.706	13.579	10.770*
Mean speed ($\mathrm{m\ s^{-1}}$)	2.019	2.287	3.1681
Maximum speed ($\mathrm{m\ s^{-1}}$)	3.239	3.437	4.060
Mean speed ($1\ \mathrm{s^{-1}}$)	3.831	4.593	6.190*
Maximum speed ($1\ \mathrm{s^{-1}}$)	6.165	6.916	7.906
Mean acceleration ($\mathrm{m\ s^{-2}}$)	1.588	1.965	2.471++
Maximum acceleration ($\mathrm{m\ s^{-2}}$)	2.186	2.793	2.977

Significant differences between values for low, moderate and high-water velocity fish are indicated:* $p \leq 05$ and ++ $p \leq 0.01$
L, body length

Studies have shown that a significant oxygen debt is acquired during exhaustive exercise (Wood, 1991) and this may contribute to delayed mortality. Construction of fishways that avoid high energy expenditure and stress is therefore essential to minimize fish loss.

Ideally, fishways should be able to pass successfully all migratory species inhabiting the river in which they are constructed. Water velocities within fish bypass structures should be less than the maximum attainable speed of all upstream migrating species. To ensure high passage rates for adult salmon within fishways, a water velocity equal to or less than 1.55 $\mathrm{m\ s^{-1}}$ would be ideal. This study revealed a distance–velocity barrier and corresponding low passage success rates by fish traversing at moderate to high water velocities. Thus, to avoid fish fatigue and exhaustive exercise, water velocities within fish bypass structures should be maintained within the prolonged or sustained swimming scope of the species in question. The quantification of burst swimming abilities may aid in optimizing the design of future fishways and culvert installations. Digital telemetry has provided data on kinematics and strategies employed by salmon during high speed swimming which were previously not attainable using conventional mark-and-recapture procedures. Furthermore, digital telemetry can be an important tool in evaluating fishways by providing finer resolution of movements and position of fish within fish bypass structures.

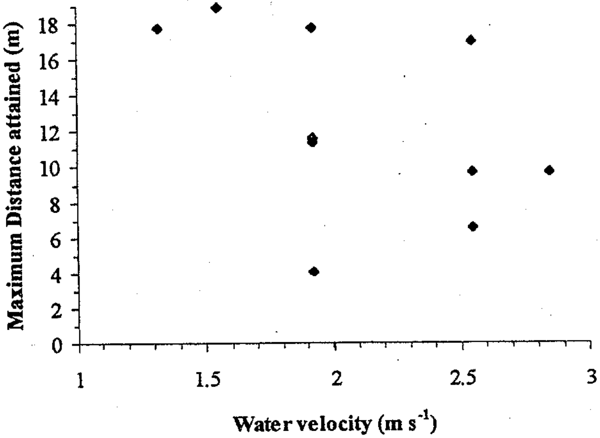

Figure 6. A scatter plot of the maximum distances attained in the flume in relation to increasing water velocity (raw data). As the average water velocity increased, maximum distances traversed by fish signicantly declined (* $p \leq 0.05$). On two occassions, rapid weather changes altered the brook level and corresponding water velocity within the flume. Owing to a heavy rainfall, one fish experienced a swim trial at a water velocity of 2.85 m s^{-1}. Another fish traversed the flume at a lowered water velocity of 1.32 m s^{-1} during a dry and warm day

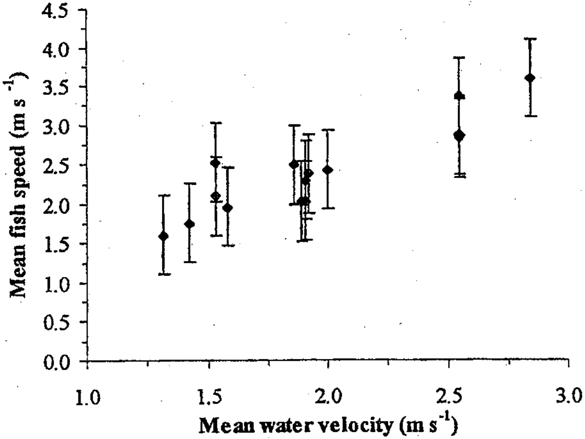

Figure 7. The average fish speed significantly increased with increasing water velocity ($p \leq 0.01$)

ACKNOWLEDGEMENTS

Thanks are extended to J. Mitchell, R. Booth and the DFO Engineering Construction crew for field assistance. We gratefully acknowledge the advice and assistance of Dr T.A. Beddow and Dr G. Power. Financial support was provided by the Habitat Management and Marine Environment, Department of Fisheries and Oceans, St. John's, Newfoundland (to R.S.M.).

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