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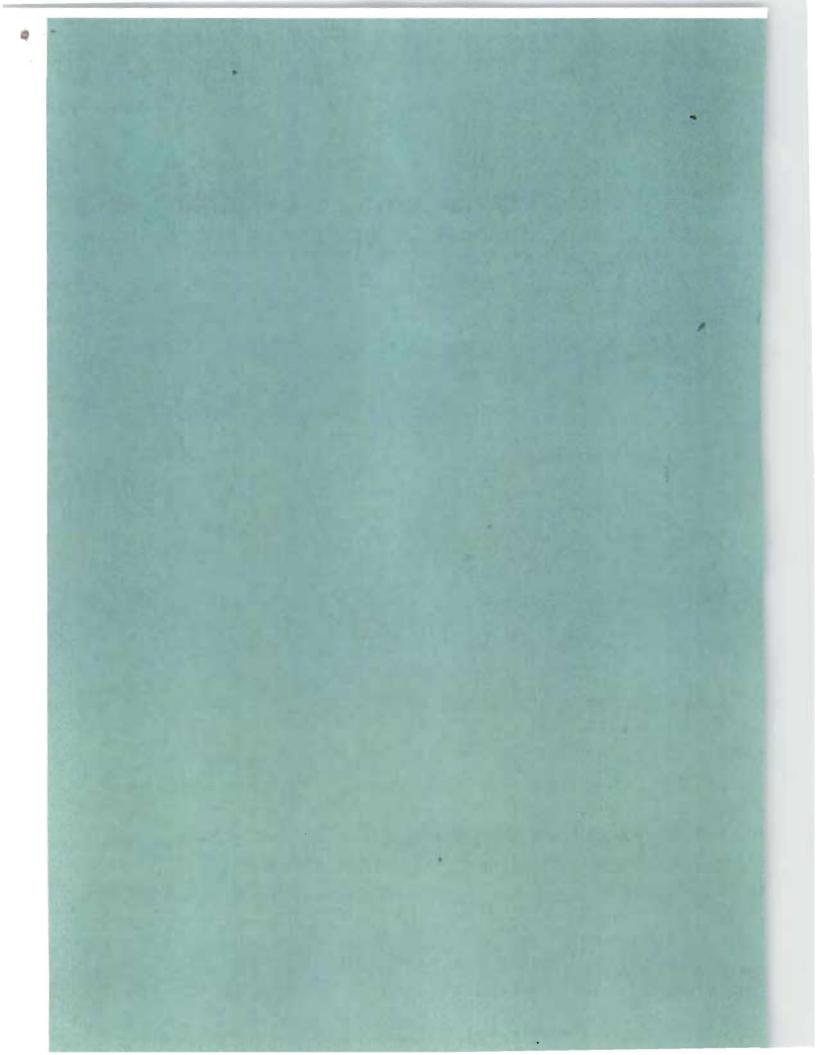
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Swimming Performance of Post Spawning Adult (Kelts) and Juvenile (Smolts) Atlantic Salmon, Salmo salar

by

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ABSTRACT

Booth, R.K., E.B. Bombardier, R.S. McKinley, D.A. Scruton, and R.F. Goosney. 1997. Swimming Performance of Post Spawning Adult (Kelts) and Juvenile (Smolts) Atlantic Salmon, Salmo salar. Can. Manuscr. Rep. Fish. Aquat. Sci. No. 2406: v + 18 p.

This study was conducted to investigate the swimming capabilities of juvenile (smolts) and post spawning adult (kelts) Atlantic salmon (Salmo salar) to develop biological criteria for use in the design of downstream fish passage facilities. Studies were conducted using wild fish collected from the Exploits River, central Newfoundland. Swimming performance trials were conducted on site using Blazka-type swim speed chambers (35 and 70 litre capacity) and ambient river water. A total of 34 kelt and 121 smolt were tested between temperatures of 5 to 9°C and 7 to 18°C. respectively. Critical swimming velocity of kelts was dependent on body size and was approximated by a velocity twice the body length (0.97 to 1.20 m³s⁻¹). Conversely, the critical swimming velocity of smolts (0.70 to 1.12 m³s⁻¹) was related to water temperature but unaffected by body size. The sustained swimming speed of kelts was $0.5 \text{ m}^3\text{s}^{-1}$ (approx. 1 body length per second, bl·s⁻¹), burst activity commenced at 0.8 m³s⁻¹ (approx. 1.4 bl·s⁻¹), and fish could no longer swim above 1.4 m³s⁻¹ (approx. 2.2 bl·s⁻¹). The sustained swimming speed of smolts was also 0.5 m³s⁻¹ (approx. 2.6 bl·s⁻¹) and unrelated to temperature. Prolonged swimming was between 0.5 and 0.9 m³s⁻¹ (2.5 and 4.5 bl s⁻¹, respectively) at both 7 and 12°C and burst activity commenced at 1.0 m³s⁻¹ (5 bl·s⁻¹). At 17^oC, prolonged swimming was maintained as high as 1.3 m³s⁻¹ (8 bl·s⁻¹) and burst activity did not occur until speeds of $1.7 \text{ m}^3 \text{s}^{-1}$ (10 bl·s⁻¹). The study indicates that smolts possess higher critical, sustained and burst capabilities (expressed per body length) than kelts at similar water temperatures. However, when expressed independent of length, both smolt and kelt swimming capabilities were similar. Consequently, it will be possible to design a fish passage facility using a single range of water velocities suitable for both life stages.

RESUMÉ

Booth, R.K., E.B. Bombardier, R.S. McKinley, D.A. Scruton, and R.F. Goosney. 1997. Swimming Performance of Post Spawning Adult (Kelts) and Juvenile (Smolts) Atlantic Salmon, Salmo salar. Can. Manuscr. Rep. Fish. Aquat. Sci. No. 2406: v + 18 p.

Notre étude avait pour but d'examiner la capacité natatoire de saumons atlantiques (*Salmo salar*) juvéniles (smolts) et ayant frayé (charognards), en vue d'établir des critères biologiques utiles à la conception des passes à poissons en dévalaison. Nous avons employé pour cette étude des poissons sauvages capturés dans la rivière des Exploits, dans le centre de Terre-Neuve. Les essais de performance natatoire ont été menés sur place avec des chambres de mesure de la vitesse de nage de type Blazka (capacité de 35 et 70 litres) et avec l'eau de la rivière. Au total, 34 charognards et 121 smolts ont été soumis aux essais, respectivement à des températures de 5 à 9°C et de 7 à 18°C. La vitesse critique de nage des charognards dépendait de la taille corporelle et se rapproachait d'une vitesse correspondant à deux fois la longueur corporelle (0,97 à 1,20 m³s⁻¹). Par contre, la vitesse critique de nage des smolts (0,70 à 1,12 m³s⁻¹) était en rapport avec la

température de l'eau mais non affectée par la taille corporelle. La vitesse soutenue de nage des charognards était de 0,5 m³s⁻¹ (environ 1 longueur corporelle par seconde, lc·s⁻¹), l'effort de pointe commençait à 0.8 m³s⁻¹ (environ 1,4 lc·s⁻¹) et les poissons étaient dans l'incapacité denager audessus de 1,4 m³s⁻¹ (environ, 2,2 lc·s⁻¹). La vitesse soutenue de nage des smolts était aussi de 0,5 m³s⁻¹ (environ 2,6 lc·s⁻¹), et n'était pas liée à la température. L'effort de nage prolongé se situait entre, 0,5 et 0.9 m³s⁻¹ (2,5 et 4,5 lc·s⁻¹ respectivement), à 7 et à 12°C, et l'effort de pointe commençait à 1,0 m³s⁻¹ (5 lc·s⁻¹). À 17°C, l'effort prolongé de nage se maintenait jusqu'à 1,3 m³s⁻¹ (8 lc·s⁻¹), et l'effort de pointe ne commençait qu'à des vitesses de 1,7 m³s⁻¹ (10 lc·s⁻¹). L'étude indique que les smolts possèdent, à température comparable, des capacités supérieures à celles des charognards pour l'effort critique, soutenu et de pointe (exprimés en longueur corporelle). Toutefois, si on ne tient pas compte de la longueur, les capacités de nage des smolts et des charognards étaient similaires. Il sera donc possible de concevoir une passe à poissons qui présente une seule plage de vitesse convenant aux deux stades biologiques.

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1.0 INTRODUCTION

The Atlantic salmon (*Salmo salar*) is one of Canada's most economically important fish species. Unfortunately, by the late 1980's the number of Atlantic salmon returning to spawn in Canadian rivers was declining. In order to help rebuild Atlantic salmon populations, federal and provincial governments have closed most commercial scale fisheries and imposed strict regulations on the recreational fisheries for Atlantic salmon (Pearse, 1988). Intensive re-stocking and habitat restoration programs have also been implemented in many Atlantic salmon rivers across Canada. In addition, regulations have been implemented requiring that all indigenous migratory fish species be able to pass dam and weir structures constructed on Canadian rivers.

There are numerous types of by-pass systems in operation but, typically, fish are passed upstream using fishways and/or elevators and passed downstream using sluices or louvre and screen systems. Fishways are constructed such that the movement of water is slowed by baffles (i.e. Denil or vertical slot design) or by a series of pools (i.e. pool and weir design). In contrast, louver and screens divert a portion of the water and fish away from high water areas or water intake systems. While both fishways and screen and louver systems are used extensively in Canada, there is limited information on their effectiveness and their impact on the well being of the fish using them.

The design criteria used in the construction of fish pass systems has typically been derived from studies on the swimming performance of fish. A large number of these studies, however, initially focused on economically important species such as the Pacific salmonids. In Atlantic Canada, fish bypass systems have been designed for other species (e.g. Atlantic salmon) and criteria used to set water velocities and depths were often obtained from studies of Pacific salmon. This extrapolation of swim performance data between species may be inadequate due to the influences of body morphology, age, genetics, physiological status and environmental factors on the swimming abilities of fish. For example, when juvenile Atlantic salmon develop from parr to smolts, the physiological changes associated with smoltification have been shown to reduce swimming performance of fish (Giorgi *et al.*, 1988). Smolts also experience greater metabolic disturbances when exposed to a period of continuous swimming and show higher post exercise mortality than parr (Giorgi *et al.*, 1988; Virtanan and Forsman, 1987). Additionally, adult salmon typically swim at considerably higher water velocities than smolts, but smolts posses greater overall swimming capabilities when expressed in terms of body size. Consequently, the design of fish passage structures should not only consider the targeted species, but also the specific life history stage and size of the individuals which the system intends to pass.

Fish passage systems designed to direct downstream migrating salmon around water intakes have typically focused on the passage of juvenile individuals. However, many adult Atlantic salmon survive following spawning and make a return migration to the sea as spent fish (referred to as kelts). These individuals represent an important component of the population and often return as larger repeat spawners but are typically overlooked in the design of many fish passage systems. This may be due, in part, to a failure to consider the swimming characteristics of these individuals in the design of fish passage systems and the reliance on data from Pacific salmon which do not posses a post spawning population.

The swimming capabilities of fish are typically determined using critical swimming speed and endurance tests (Beamish, 1978). These tests are useful because they indicate the range in swimming capability of fish (i.e. sustained, prolonged and burst). Burst activity represents the upper limit of swimming potential of fish and is usually of short duration (i.e. less than 20 seconds by definition). In contrast, sustained and prolonged activity can be maintained from several minutes to several hours. Critical swim trials are useful in determining the maximum velocity fish can achieve over a specific period. Together these tests provide useful data in the development of criteria for fish passage structures.

There are no studies describing the critical swimming speed and swimming endurance of Atlantic salmon kelts and few studies reporting swim speed information for wild Atlantic salmon smolts. Consequently it is generally unknown whether existing fish passage structures are effective in safely passing these life history stages. Consequently, the purpose of the present study was to

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investigate the swimming capabilities of the downstream migrating life stages of Atlantic salmon including both juveniles (smolts) and post spawning adults (kelts). This study was intended to develop a set of biological criteria on swimming capability for use in the design of downstream fish passage facilities.

2.0 MATERIALS AND METHODS

2.1 Animals

Wild adult Atlantic salmon kelts (*mean fork length*: 55.50 cm) and smolts (*mean fork length*: 17.50 cm) were collected from a smolt bypass system located at the Abitibi-Price hydroelectric generating station located on the Exploits River in Bishop Falls Newfoundland, Canada (49°N, 57°W). Collection of experimental fish coincided with the peak downstream migration period of smolts and kelts (May 1st to June 30th, 1996) and at seasonal water temperatures (5-18°C). Salmon were not held during experimentation and all individuals were collected and tested on a daily basis. Experiments were also conducted on site to eliminate the effects of transportation stress. Typically swim trials are performed on individuals which have undergone a period of food deprivation to ensure that all individuals are in a post-absorptive state. In the wild, Atlantic salmon feed at will (excepting upstream migrating adults), and thus their swimming performance will be reflective of their nutritional status. On this basis we did not attempt to feed or starve individuals in this study.

2.2 Swimming chambers and experimental design

Swimming performance trials were conducted using Blazka-type swim speed chambers (Figure 1). This type of swim speed chamber is characterised by a tube within a tube design which permits water to be circulated within a smaller area compared to Brett-type tunnel swim speed chambers. Ambient, untreated river water was supplied to the chamber via an external pump. Water velocity within the chamber is rheostatically controlled and maximum water velocity can be attained within 2 seconds.

Two swim chambers were used and chosen based on the fork length (FL) and girth (GT) of the fish. Smolts (FL = 15-25 cm; GT = 12-16 cm) were tested in a 35 litre chamber and kelts (FL = 48-62 cm; GT = 16-24 cm) were tested in a 70 litre chamber. The maximum cross-sectional area of salmon used in swim trials was less than 10% of the swimming flume area, eliminating the need to adjust for the influence of the body of fish on water flow within the chamber (Smit *et al.*, 1971).

Critical swimming performance and swimming endurance tests were conducted for both kelts and smolts. These tests were conducted between 5 and 9°C for kelts and between 7 and 18°C for smolts. In total, 8 kelts and 36 smolts were used to determine critical swimming velocity and 26 kelts and 85 smolts for endurance tests.

2.3 Measurement of critical swimming velocity

Critical swim trials were performed by swimming each of six individuals over a range of increasing water velocities. Prior to testing, all salmon were acclimated to the swim chamber for 6 hours at a swimming velocity of 1 body length per second (bl·s⁻¹). Following this acclimation period the water velocity was increased in a stepwise progression until the fish fatigued. Critical swimming speeds (U_{crit}) were calculated using the equation of Brett (1964):

$$U_{\text{crit}} = \mathbf{V} + (\mathbf{t}_i / \mathbf{t}_{ii})\mathbf{u}_i$$

where: V is the highest velocity maintained for the prescribed period (cm s⁻¹), t_i is the time elapsed at final velocity (min.), t_i is the time increment (min.) and u_i is the velocity increment (cm·s⁻¹). In the present study a ten minute time interval was used. This interval was considered more relevant to fishway design (i.e. passage time) than the more commonly used 30 or 60 minute intervals.

2.4 Measurement of swimming endurance

Endurance tests were performed by swimming individual fish at a single water velocity until

fatigue. Individuals were examined at each of the following velocities: *kelts*: 0.5, 0.8, 1.1 and 1.4 m·s⁻¹; *smolts*: 0.5, 0.9, 1.3, 1.7 and 2.0 m¹s . Endurance tests were initiated following 2 hours of acclimation. Kelts were acclimated at 0.5 body lengths per second and smolts at 1 body length per second. Measurement of swimming endurance depends on an accurate and consistent recognition of fish fatigue. The procedure used to determine metabolic fatigue involved stimulating individuals to continue swimming using rapid changes in water velocity. In all cases, fish were considered fatigued when they failed to leave the downstream screen despite repeated attempts to stimulate them by raising and lowering the water velocity.

Sustained, prolonged and burst activity are important components of swimming performance of fish (Beamish, 1978). Sustained swimming was determined in this study as the swimming velocity which individuals could maintain for 200 minutes. At speeds above the sustained swimming speeds fish enter prolonged activity. The definition of prolonged swimming used in this study was the ranges of velocities which fish could maintain swimming for a minimum of 1 minute and up to 200 minutes. The final phase of endurance of a fish is its burst activity. Burst activity was identified as the swimming velocity which fish could maintain for less than 1 minute.

2.5 Statistical analyses

All values are represented as means ± 1 standard error. Linear regression analyses were used to correlate swimming speed with body size for kelts and temperature for smolts.

3.0 RESULTS

The majority of kelts were captured and tested between May 10^{th} and May 28^{th} , 1996 when water temperatures ranged between 5 and 9°C. Kelts were not available after this period and, therefore, critical and endurance tests on kelts were only conducted during their peak migratory period and at ambient temperatures. Smolts were available on a continuous basis between May and July, but peaked during the period June 2^{nd} to 26^{th} , 1996 when water temperatures were between 7 and 18° C. Critical and endurance tests on smolts occurred at these temperatures. The mean fork length of kelts used in this study was 55.50 ± 3.18 cm while the mean fork length of smolts was 17.50 ± 0.92 cm.

3.1 Critical swimming velocities of kelts and smolts

The critical swimming velocity (U_{crit}) of kelts appeared to be dependent on its body size. Figure 2 shows that an increase in fish length from 48 to 62 cm resulted in an increase in the critical swimming velocity from 0.97 m·s⁻¹ to 1.20 m·s⁻¹. The relationship between body size and critical swimming velocity of kelts is described by equation 1.

$$U_{crit} = 0.0182$$
 (fork length) + 0.0901, $R^2 = 0.84$ equation 1

The critical swimming velocity of kelts can be approximated by a water velocity equal to twice the fork length of fish per second.

The critical swimming velocity of smolts ranged from $0.70 \pm 0.19 \text{ m} \cdot \text{s}^{-1}$ at water temperatures between 5 and 9°C to 1.12 m·s at water temperatures between 16 and 18 C (Fig. 3). The relationship between critical swimming velocity and temperature is described by equation 2.

$$U_{crit} = 0.0317$$
 (temperature) + 0.4857, $R^2 = 0.75$ equation 2

The mean fork length of smolts was 17.5 ± 0.92 cm but ranged between 15 and 25cm. There was no effect of body size on swimming critical swimming velocity of smolts tested at temperatures between 5 and 9°C (R² = 0.026) or 14 to 18°C (R² = 0.019).

3.2 Endurance swimming

The sustained, prolonged and burst swimming activities of kelts are shown in Figure 4. The sustained swimming velocity of kelts was $0.5 \text{ m} \text{s}^{-1}$ or approximately 1 body length per second. Burst activity commenced when fish were forced to swim at velocities greater than $0.8 \text{ m} \cdot \text{s}^{-1}$ (approx. 1.4 body lengths) and kelts could no longer swim at water velocities in excess of 1.4 m sec⁻¹ (approx. 2.2 body lengths). A definite period of prolonged performance was absent in kelts tested in this study.

The sustained swimming velocities of smolts was also found to be 0.5 m·s⁻¹ (approx. 2.6 body lengths) and independent of temperature (Fig. 5). In contrast, the prolonged swimming of Atlantic salmon smolts was highly dependent on temperature. At both 7 and 12°C prolonged swimming occurred between 0.5 and 0.9 m·s⁻¹ (2.5 and 4.5 body lengths) and burst activity commenced at water velocities in excess of 1.0 m·s⁻¹ (5.0 body lengths). However, at 17°C smolts maintained prolonged activity at speeds as high as 1.3 m·s⁻¹ (approx. 8 body lengths) and burst activity did not occur until water velocities approached 1.7 m·s⁻¹ (10 body lengths).

4.0 DISCUSSION

Numerous fish species undertake upstream and downstream migrations when they are feeding, rearing, and on route to spawning and over-wintering habitats. For many species, upstream and downstream migrations occur during specific periods of their life history and are essential for survival. The presence of dams and industrial developments on many salmon rivers have been shown to adversely affect the upstream and downstream movements of fish and may be important determinants in the well-being of many migrating fish stocks (Giorgi *et al.*, 1988; Notes for Guidance on the Provision of Fish Passes and Screens for the Safe Passage of Salmon, 1995).

The design and construction of fish passage systems has largely been approached from a engineering perspective. Water hydraulics, material selection and fishway design have traditionally been the most important factors in the construction of fish passes. However, knowledge of the swimming capabilities of indigenous fish species is also an important component in the design of these structures, particularly on rivers which possess numerous genera and species of fish. It has been shown that considerable variability exists in the swimming capabilities of closely related species as well as different sexes and ages of the same species. Moreover, body size, water temperature, and time of year have all been shown to significantly influence the swimming performance of fish (Brett, 1964; Bernatchez and Dodson, 1985; Taylor and Foote, 1991; Webb, 1978). Failure to understand the variability in the swimming capabilities among targeted genera and species, and between individuals of the same species could, therefore, result in the inability of some individuals to effectively utilize the passage system. This may result in the inability of some fish to reach spawning habitats, expend more energy for passage and reduce available energy for reproduction and increase turbine related mortalities among downstream migrants.

The effects of temperature on swimming performance have been reported for numerous species including sockeye salmon (Brett and Glass, 1972); rainbow trout (Webb, 1978), whitefish and cisco (Bernatchez and Dodson, 1985), sturgeon (Peake *et al.*, 1995) and Atlantic salmon (Booth *et al.*, 1995). Typically, swimming performance increases at a rate comparable to the change in water

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temperature up to a point after which time swimming performance decreases. This is largely because fish are poikilotherms and their metabolic rate is determined by their body temperature and hence water (seasonal) temperature. We found the critical swimming speeds and swimming endurance of Atlantic salmon smolts to be highly dependent on temperature. The increase in the critical swimming speeds of smolts in the present study, from 4 bl·s⁻¹ at 7 C to 7.5 bl·s⁻¹ at 17 C, is supported by previous investigations of critical swimming speeds for juvenile Sockeye salmon, which typically range from 2.5 bl·s⁻¹ at 10°C (Taylor and Foote, 1991) to approximately 7 bl·s⁻¹ at 20°C (see equation provided in Brett and Glass, 1972).

In contrast to critical swimming speeds, the sustained activity of smolts is temperature independent (Fig. 5). These results are in contrast to previous studies which found sustained activity of sockeye smolts to be temperature dependent (Brett, 1964). The reasons for differences between our study and that of previous studies are unclear but could be explained by the use of wild smolts in this study versus hatchery reared juveniles which were used in previous studies. Hatchery fish are often acclimated to experimental temperatures for several weeks prior to being tested, whereas wild smolts may be forced to acclimate to a range of temperatures over a very short period of time. Short acclimation periods could, therefore, make wild smolts less sensitive to changes in temperature than hatchery smolts. It is also possible that smoltification may be a determinant in our results. It has been shown that wild salmon undergoing smoltification experience rapid behavioral, morphological and physiological changes which typically result in reduced swimming efficiency (Virtanan and Forsman, 1987). The reduction in swimming performance among wild smolts may, therefore, result in a threshold for swimming ability which is insensitive to temperature. However, to our knowledge, this has not been investigated.

The biochemical processes involved in burst activity are largely independent of temperature (Wardle, 1980), while the contractile properties of the muscles themselves are very much dependent on temperature (Rome *et al.*, 1992). As a result, there has been considerable debate whether the burst activity of fish is temperature dependent or independent. In the present study, smolts were found to enter burst activity at swimming velocities close to 7 bl·s⁻¹ at both 7 and 12°C but when

water temperatures reached 17°C burst activity did not occur until water velocities exceeded 10 bl·s⁻¹ at (Fig. 5). These results strongly suggest that the burst activity of smolts is temperature dependent. It has been suggested that higher burst velocities at warmer temperatures may be related to the reduction in the contraction time of muscle fibres, and consequently higher power output, at warmer temperatures. However, smolts exhibit the same sustained swimming velocities at all three temperatures. As a result, at warmer temperatures there is an increase in the range of prolonged swimming velocities. We found that smolts examined at 17°C exhibited greater prolonged activity than smolts at colder temperatures which was also greater than the prolonged activity of kelts.

During their spawning migration, adult Atlantic salmon suspend feeding and derive all of the energy required for locomotion, sexual maturation and post-spawning survival from stored reserves. Much of the energy required during the early phases of migration come from fats stored in visceral tissues prior to migration. As migration continues, white muscle proteins are mobilized as sources of energy and there is considerable deterioration of the swimming musculature (Ando *et al.*, 1986; Martin *et al.*, 1993). An important consequence of muscle deterioration is the depletion of energy (lipid) reserves, loss of muscle function in both the red and white muscle and reduction in swimming performance. This could explain why kelts in the present study possessed critical swimming speeds close to 1.8 bl·s⁻¹, while those of pre-spawning Atlantic salmon were close to 4 bl·s⁻¹ (Booth *et al.*, 1995). Smolts were found to possess higher sustained, prolonged and burst swimming capabilities than kelts swum at similar temperatures.

Previous studies have reported a relationship between fish length and critical swimming speeds (Brett, 1964). In the present study kelts possessed critical swimming speeds which were size independent. For example, the critical swimming speed of a 48 cm kelt was found to be 1.75 bl·s⁻¹ which was similar to that of a larger 62 cm kelt at 1.80 bl·s⁻¹ (Fig. 2). Unfortunately, the migratory period of kelts occurs over a narrow range of temperatures and insufficient individuals were available to investigate the effects of temperature on the swimming performance of this life history stage.

As mentioned previously, the design of fish passage systems requires knowledge of the

swimming capabilities of the species which the system intends to pass. In the present study we have shown that downstream migrating smolts and kelts possessed very different critical, sustained, prolonged and burst swimming capabilities. However, much of this discussion has focused on swimming speeds relative to body size. While expression of swimming speeds as body lengths has important biological considerations, it offers little information about water velocities suitable for fishway design. For example, smolts possess critical swimming speeds which are 4-6 body lengths faster than those of kelts. However, kelts are much larger than smolts and, when swimming speeds are expressed independently of fish length, we found that the critical swimming speeds were also similar when expressed independently of fish length. For example, the sustained swimming speeds were also similar when expressed independently of fish length. For example, the sustained swimming speeds of both smolts and kelts were found to be 0.5 ms^{-1} , and were independent of temperature (Fig. 4 and 5). In contrast, kelts enter burst swimming at lower water velocities than smolts ($1.4 \text{ m}\cdot\text{s}^{-1}$ vs. $2.0 \text{ m}\cdot\text{s}^{-1}$).

Our study reports biologically relevant data on the swimming capabilities wild Atlantic salmon smolts and kelts. This data indicates that smolts possess higher critical, sustained and burst capabilities than kelts at similar temperatures. Our data also shows, however, that fish size is important in applying biological data to fishway design. For example, swimming performance expressed independently of body size indicates that the swimming capabilities of both kelts and smolts lie within the same range of water velocities. Consequently, it is possible to design a bypass system using a single range of water velocities which is suitable for the passage of both smolts and kelts.

6.0 ACKNOWLEDGEMENTS

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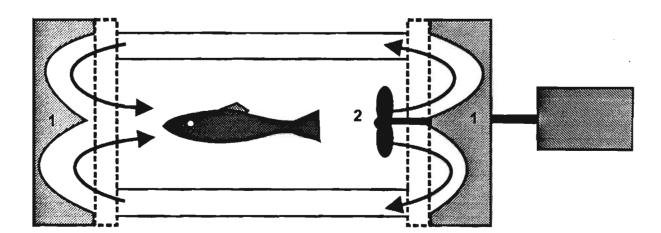
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Figure 1. Schematic representation of the Blaska swim speed chamber used to measure the swimming capabilities of Atlantic salmon smolts and kelts.

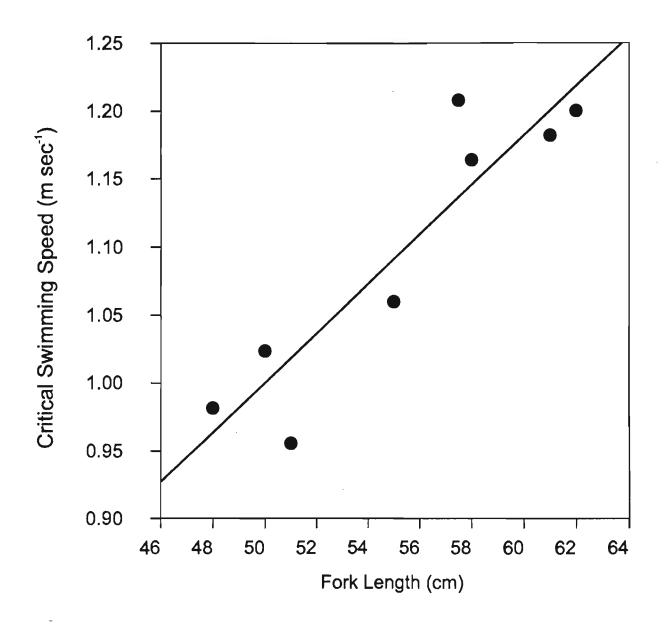


Figure 2. Critical swimming speed (U_{crit}) of Atlantic salmon kelts in relation to body size (fork length). The equation of the relationship is $U_{crit} = 0.0182$ fork length + 0.0991, $R^2=0.84$. Trials were conducted at 7°C.

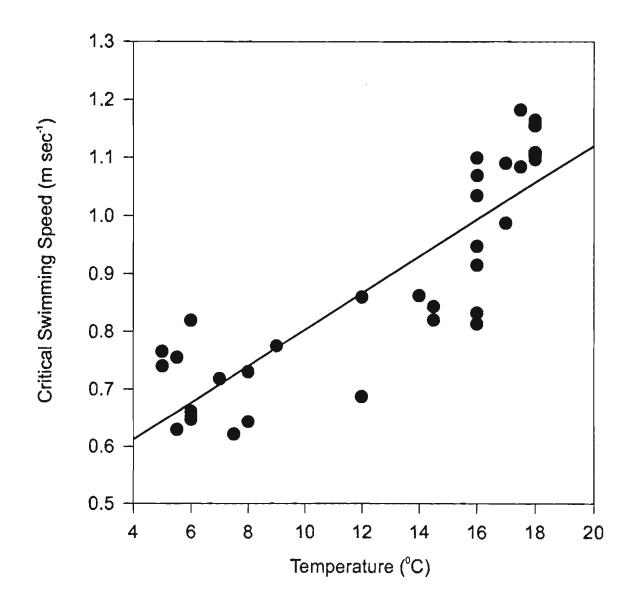


Figure 3. Critical swimming speed (U_{crit}) of Atlantic salmon smolts in relation to temperature. The equation of the regression is: $U_{crit} = 0.031$ temperature + 0.4857, $R^2 = 0.75$. Mean fork length of individuals was 17.5 ± 0.92 cm.

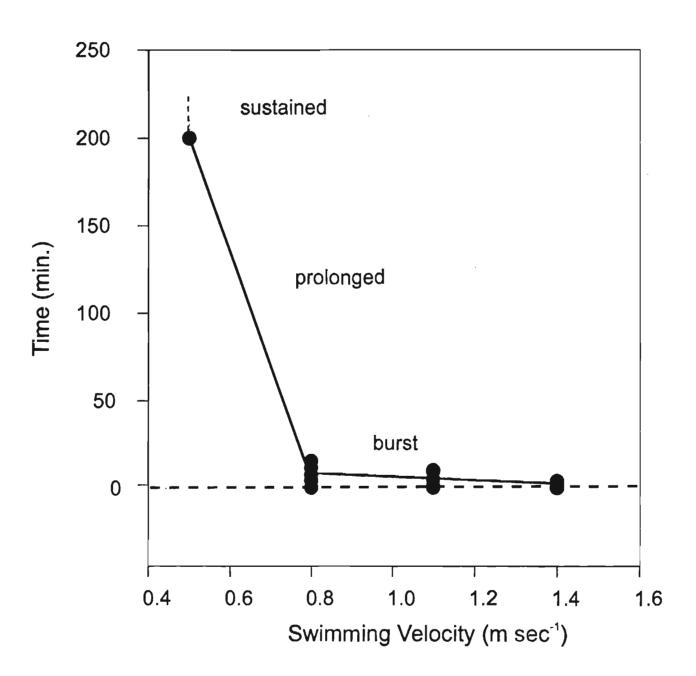


Figure 4. Swimming endurance of Atlantic salmon kelts. Sustained, prolonged and burst swimming ranges are indicated (see text for definition). Trials were conduced at 7°C.

c

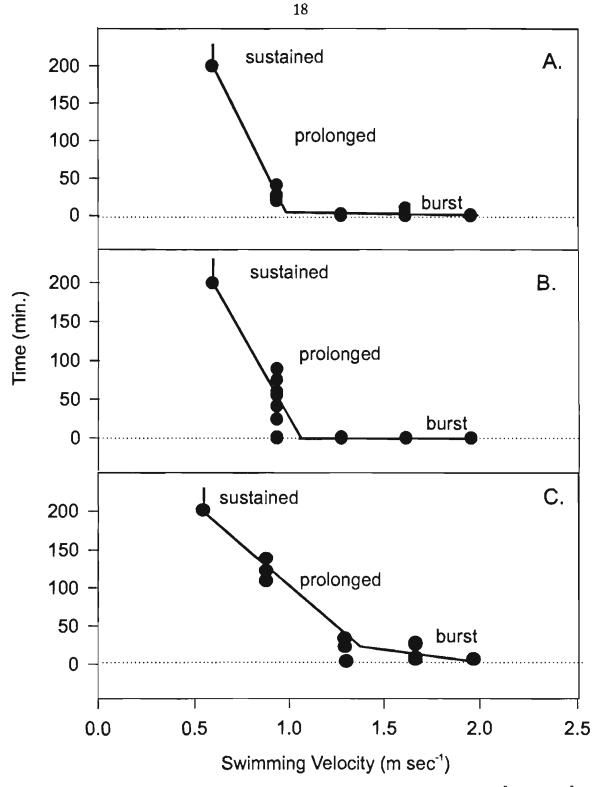


Figure 5. Swimming endurance of Atlantic salmon smolts in relation to (A) 7°C, (B) 14°C, and (C) 17°C. Sustained, prolonged and burst swimming ranges are indicated (see text for definition).