



Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design

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(Received 15 November 1996, Accepted 30 April 1997)

Swimming ability of wild brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, anadromous Atlantic salmon *Salmo salar*, and landlocked Atlantic salmon was examined using fixed and increasing velocity tests. Although brook trout and salmon parr were collected from the same site, brook trout were found generally in slow-moving pools whereas salmon were more common in faster riffle areas. Salmon parr could hold station indefinitely in currents in which brook trout could only maintain themselves briefly. Therefore, selection of fast-water areas by salmon parr may impose a velocity barrier to sympatric juvenile brook trout, reducing competition between the species. Performance comparisons also indicate that anadromous Atlantic salmon possess slightly greater sustained ability than landlocked salmon, possibly due to altered selective pressure associated with their different life histories. Finally, fishways and culverts in Newfoundland can now be designed using models generated from performance data collected from native salmonid species.

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Key words: swimming performance; salmonids; habitat selection; fishways.

INTRODUCTION

Competition among fish can be reduced if sympatric species are able to dominate different microhabitats (Hearn, 1987). In rivers where juvenile Atlantic salmon *Salmo salar* L., brown trout *S. trutta* L., and brook trout, *Salvelinus fontinalis* Mitchill coexist, salmon tend to inhabit shallow, fast moving riffle sections while trout frequent deeper pools and undercut banks (Gibson, 1966; Heggenes & Saltveit, 1990). While species separation can be maintained by territorial behaviour (Gibson, 1978, Arnold *et al.* (1991) suggested that areas of strong current preferred by salmon parr may represent a velocity barrier to other species if they are less able swimmers. Thus, swimming capacity may be important in separating, and therefore reducing competition between, sympatric juvenile Atlantic salmon and brook trout; however, this hypothesis has not yet been examined quantitatively.

Another strategy that can reduce competition among fish, particularly for food, is migration (McKeown, 1984). Anadromous Atlantic salmon migrate to the ocean to feed and grow, and then return to rivers to reproduce. In contrast, landlocked Atlantic salmon do not migrate to the sea. Juveniles often inhabit

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small nursery streams, while older fish tend to move into larger rivers and lakes. Thus, it may be that selection for swimming ability has relaxed in these populations, as shown similarly for salinity tolerance in some Newfoundland landlocked salmon populations (Burton & Idler, 1984; Birt & Green, 1993). Reduced swimming performance of landlocked sockeye salmon *Oncorhynchus nerka* (Walbaum) and three-spined stickleback *Gasterosteus aculeatus* L., has been reported (Taylor & McPhail, 1986; Taylor & Foote, 1991); however, comparisons involving Atlantic salmon have not yet been made.

Swimming behaviour of fish can fall into one of three general categories: sustained, prolonged, or burst. Sustained swimming occurs at relatively slow speeds and utilizes primarily red muscle fibres which are fuelled by energy derived from aerobic metabolism (Beamish, 1978). This allows fish to maintain sustained swimming velocities for long periods (at least 200 min) without fatiguing (Beamish, 1978). Burst swimming involves white muscle fibres which utilize energy from anaerobic processes to attain relatively high speeds for <15–20 s (Beamish, 1978). Prolonged swimming covers a spectrum of velocities between sustained and burst, using both red (aerobic) and white (anaerobic) muscle.

The present study used fixed and increasing velocity tests to examine sustained, prolonged, and burst performance of wild juvenile anadromous Atlantic salmon, brook trout, brown trout, and landlocked Atlantic salmon, with respect to body length and ambient water temperature. The first objective was to compare performance of sympatric anadromous salmon parr and brook trout, to determine if current speed is important in segregating the two species. Secondly, performance of anadromous Atlantic salmon was compared to that of landlocked Atlantic salmon to determine if the populations have diverged with respect to swimming ability. The third objective was to derive models that describe the swimming ability of each species so that fishways and culverts in Newfoundland can be designed to optimize fish access to habitat upstream from man-made and natural obstructions.

MATERIALS AND METHODS

During summer (June to October) 1995, 109 anadromous Atlantic salmon parr (4.8–13.1 cm fork length (FL)), 374 stream resident brook trout (6.2–40.5 cm FL) and 117 landlocked salmon (9.1–23.7 cm (FL)) were collected from the Indian River watershed in north central Newfoundland, Canada, using dip and fyke nets. A further 115 migrating Atlantic salmon smolts (12.4–21.1 cm FL) were collected from a counting fence in the Indian River during June, c. 40 km upstream from the estuary. These fish were obtained daily, as required, and moved <1 km to the Department of Fisheries and Oceans (DFO) Indian River Research Station where experiments took place.

In addition, 308 brown trout (5.1–26.0 cm FL) were obtained from the South Brook and Virginia rivers, on the Waterford and Rennies watersheds, St John's, using an electrofisher. Preliminary testing, involving swimming performance tests and X-rays, indicated that our electrofishing equipment and technique did not cause spinal injury or affect swimming ability of the test fish. Brown trout were collected from late September to mid-November 1995, and transported 2–15 km to the DFO, White Hills, Newfoundland station where experiments took place. Brown trout were held in 2000-l aerated holding tanks, constantly supplied with fresh water at a rate of approximately 0.51 s^{-1} . One hundred and sixty-six of the 308 brown trout were tested (within 48 h of collection)

at ambient water temperatures ($6.0 \pm 0.5^\circ \text{C}$), while the rest were tested at $12.0 \pm 0.5^\circ \text{C}$. The warmer temperature was achieved by heating water gradually ($0.5^\circ \text{C day}^{-1}$) with electric heaters. Brown trout were allowed to acclimate to the higher temperature for 3 weeks prior to experiments.

Swimming performance was measured using Blazka-type swimming flumes (Beamish, 1978) having volumes of 6, 40 and 120 l. All flumes were calibrated using pitot tubes and flow was rectilinear in profile. To ensure that fish were not being tested at non-ambient temperatures, water was drawn from the home stream (in the case of Atlantic salmon and brook trout) which ran through the Indian River Research Station property. The water was circulated through the swim chambers at $c. 20 \text{ l min}^{-1}$. Maximum cross-sectional area of all fish was $<10\%$ of the flume in which they were tested, eliminating the need to adjust for blocking effect (Smit *et al.*, 1971). Each fish was placed in a swim chamber and acclimated to a velocity corresponding to approximately 2 body lengths per second (bl s^{-1}) for 2 h. Following acclimation, fixed velocity trials were conducted by increasing water velocity to a particular test speed and recording time to fatigue. By conducting fixed velocity trials over a range of test speeds, sustained, prolonged, and burst activity could be identified. Initial trials were conducted at low speeds, while subsequent trials involved increasingly higher test velocities until maximum speeds were reached. Fish were not tested at speeds which they could not maintain for more than 1 s. Anadromous Atlantic salmon parr and smolts were tested at speeds ranging from 0.53 to 0.90 m s^{-1} and 0.99 to 1.95 m s^{-1} respectively. Brook trout and brown trout were tested at velocities ranging from 0.29 to 1.45 m s^{-1} and 0.50 to 1.79 m s^{-1} respectively. Landlocked Atlantic salmon were tested at speeds ranging from 1.01 to 1.74 m s^{-1} . Experiments were terminated if fish maintained a given speed for more than 200 min.

Increasing velocity trials were conducted using the protocol described by Beamish (1978) and calculated using the formula described by Brett (1964) as follows:

$$S = V + (t\Delta t^{-1}) \Delta v,$$

where S is swimming speed (m s^{-1}), Δt is the time interval (min), Δv is the velocity increment (m s^{-1}), t is time elapsed at final velocity (min), and V is the highest velocity maintained for the prescribed Δt (m s^{-1}). As fish passage through fishways and culverts often occurs over a short period, time intervals of 2, 5 and 10 min were used instead of the traditional 30- or 60-min intervals used in critical swimming speed determinations (Brett, 1964). As such, results of our increasing velocity tests should not be taken to represent critical swimming speed. They are a measure of prolonged swimming capacity (Beamish, 1978) and simply indicate swimming speeds that can be maintained for 2, 5 or 10 min, depending on the time interval used. Velocity increments corresponding to $c. 0.3 \text{ bl s}^{-1}$ were used. Small deviations from this value were considered not to have affected the results since velocity increments between one-fourth and one-ninth of the final value do not affect the outcome of the tests (Jones, 1971; Beamish, 1978).

Electric shocking was not used in this study to force fish to swim; however, they were stimulated occasionally using short, sharp fluctuations in velocity followed by an immediate return to the test velocity. In all cases, fish were considered fatigued when they failed to leave the downstream screen despite several attempts to stimulate them. In most cases, onset of fatigue was obvious. After experiments, fork length and mass were measured. To minimize possible stress and/or damage to the experimental animals, all fish were captured, tested, and released within 48 h, except for brown trout tested at 12°C (these fish were held to allow acclimation to the warmer temperature).

The relationship between speed maintained, fish length, water temperature, and endurance was estimated using multiple regression (Steel & Torrie, 1960) as follows:

$$S = a_0 + a_1X + a_2Y + a_3Z + e$$

where S is speed (m s^{-1}), X is fork length (cm), Y is water temperature ($^\circ \text{C}$), Z is time (min), and e is a normally distributed error term with mean 0 and variance σ^2 . P values <0.05 indicated statistical significance.

RESULTS

Models derived from fixed velocity trials conducted on each species are given in Table I. Sustained models estimate speeds that fish can maintain indefinitely, while prolonged/burst models estimate speeds that result in fatigue after a given period of time. Models derived from increasing velocity test data for each species are given in Table II.

In general, anadromous Atlantic salmon parr did not swim, but remained close to the bottom of the flume, using their pectoral and anal fins to hold themselves in the current. Thus, swimming ability of parr will be referred to as holding ability. If a parr was able to hold itself against a particular water speed, generally it could do so indefinitely. If not, typically fatigue occurred following less than 5 min of intermittent swimming and holding. Thus, data from fixed velocity tests fell into two general groups: one in which fish were stopped after holding position for 200 min, and one in which fatigue occurred within a short time. Atlantic salmon parr did, however, swim during fixed velocity trials where water speed was increased, from acclimation, to a high speed that could be maintained only for a few seconds. As such, probably these high velocities can be taken to represent burst swimming ability of anadromous Atlantic salmon parr.

Anadromous Atlantic salmon smolts did not exhibit the holding behaviour of parr but swam actively in the water column. Smolts were able to maintain relatively low speeds for indefinite periods; however, at higher speeds most fish fatigued quickly as described for parr. Swimming behaviour and general morphology of landlocked Atlantic salmon were intermediate between those of anadromous salmon parr and smolts. Smolt-sized landlocked salmon (12–20 cm FL) were not silver and visible parr markings were evident on some fish. Landlocked salmon also tended to swim actively, although a few of the smaller fish occasionally held position in the swim chamber as described for anadromous salmon parr. Landlocked salmon also tended to swim either indefinitely or for a short time. Brook and brown trout, of all sizes, swam actively in the current and, unlike salmon, fatigue times up to 150 min were recorded.

The relationship between sustainable swimming/holding speed (as determined from fixed velocity tests), fork length and water temperature varied significantly among test species (ANCOVA, $P < 0.05$). Sustained ability of brook trout was significantly lower than that of all other species examined (Tukey's multiple comparison test). In addition, sustained swimming performance of landlocked Atlantic salmon was significantly lower than that of anadromous Atlantic salmon smolts (Tukey's multiple comparison test).

The relationship between prolonged/burst swimming/holding speed (as determined from fixed velocity tests), fork length, water temperature, and swimming/holding time also varied significantly among test species (ANCOVA, $P < 0.05$). Performance of brook trout was again significantly lower than that of all other species; however, no other significant differences were found (Tukey's multiple comparison test).

The relationship between prolonged swimming/holding ability (as determined from increasing velocity tests), fork length, water temperature, and time interval (i.e. swimming/holding time) varied significantly among test species (ANCOVA,

TABLE I. Models that estimate the swimming (or holding) speed (S ; m s^{-1}) that a fish of given fork length (X ; cm) at a given temperature (Y ; $^{\circ}\text{C}$) can maintain for a prescribed (log transformed) time period (Z ; min) as follows: $\hat{S} = a_0 + a_1X + a_2Y + a_3Z$

Species Model	Adjusted r^2	d.f.	a_0 , Intercept	a_1 , Length (range)	a_2 , Temperature (range)	a_3 , Log time (range)
Anadromous S. salar smolts						
Prolonged and burst	0.51	61	0.850	0.040 (13.7–21.1)	— (14.0–18.5)	– 0.284 (0.05–14.58)
Sustained	N/A	13 ^a	1.135 ^b	— (13.0–17.8)	— (14.0–17.5)	Indefinite
Anadromous S. salar parr						
Prolonged and burst	0.35	37	0.547	0.025 (5.5–14.7)	— (9.5–20.0)	— (0.11–21.6)
Sustained	0.62	16	0.361	0.035 (5.7–13.4)	— (12.5–19.0)	Indefinite
Landlocked S. salar						
Prolonged and burst	0.54	33	0.813	0.040 (10.0–21.8)	— (3.5–17.5)	– 0.347 (0.03–18.1)
Sustained	N/A	12 ^a	0.981 ^b	— (12.1–19.1)	— (12.0–15.0)	Indefinite
Brook trout						
Prolonged and burst	0.76	211	– 0.039	0.051 (6.3–25.9)	0.015 (14.0–20.0)	– 0.135 (0.03–154.4)
Sustained	0.81	42	– 0.402	0.038 (6.2–26.8)	0.030 (14.0–20.0)	Indefinite
Brown trout						
Prolonged and burst	0.66	138	0.305	0.061 (5.1–26.0)	— (5.5–12.5)	– 0.174 (0.01–110.0)
Sustained	0.88	27	0.000	0.048 (5.6–23.6)	0.020 (5.5–12.5)	Indefinite

Values of length, temperature and time should fall within the ranges specified.
—, indicates that the coefficient was not significant ($P > 0.05$) and was not included in the model. Insufficient data were collected to allow regression analysis for sustained swimming performance of anadromous Atlantic salmon smolts and landlocked salmon.
^aRepresents the number of individuals tested.
^bRepresented mean speed (m s^{-1}) that could be maintained indefinitely.

TABLE II. Models that estimate the swimming (or holding) speed (S ; m s^{-1}) that a fish of given fork length (X ; cm) at a given temperature (Y ; $^{\circ}\text{C}$) can maintain for a prescribed time period (Z ; min) as follows: $S=a_0+a_1X+a_2Y+a_3Z$

Species	Adjusted r^2	d.f.	a_0 , Intercept	a_1 , Length (range)	a_2 , Temperature (range)	a_3 , Time (range)
Anadromous <i>S. salar</i> smolts	0.23	42	0.252	0.063 (12.4–18.0)	— (12.8–16.3)	— (2–10)
Anadromous <i>S. salar</i> parr	0.43	52	0.135	0.031 (4.8–12.4)	0.018 (12.3–20.5)	— (2–10)
Landlocked <i>S. salar</i>	0.55	78	0.516	0.043 (9.1–23.7)	— (11.0–20.5)	— (2–10)
Brook trout	0.83	120	0.151	0.045 (7.1–40.5)	— (12.7–20.0)	–0.011 (2–10)
Brown trout	0.78	140	0.113	0.048 (5.2–26.0)	0.023 (5.5–12.5)	–0.011 (2–10)

Values of length, temperature and time should fall within the ranges specified.
—, Indicates that the coefficient was not significant ($P>0.05$) and was not included in the model.

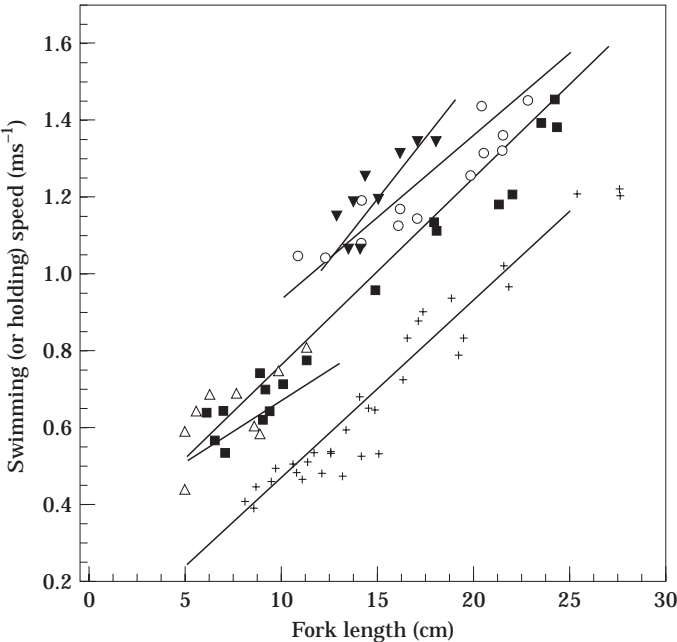


FIG. 1. Data and regression lines from increasing velocity tests performed on brook trout (+), brown trout (■), landlocked Atlantic salmon (○), anadromous Atlantic salmon parr (△) and anadromous salmon smolts (▼). Line position for each species was calculated using models from Table II. A temperature value of 12.5 $^{\circ}\text{C}$ was used in regressions for salmon parr and brown trout.

$P<0.05$; Fig. 1). Performance was not significantly different between brown trout and landlocked Atlantic salmon, or between brown trout and anadromous Atlantic salmon parr (Tukey's multiple comparison test). Prolonged swimming/

holding ability was, however, significantly different in all other species comparisons (Tukey's multiple comparison test).

DISCUSSION

Hatchery rearing can alter wild-type morphology, behaviour and swimming ability of fish (Kazakov & Kozlov, 1985; Duthie, 1987; Fleming *et al.*, 1994). Therefore, wild stock should be used in collecting performance data, particularly if it may be used to set appropriate flow speeds in fishways and culverts, or discharge rates from hydroelectric facilities. Although tests were performed on a large number of fish (117–374 individuals per species), correlations between swimming performance, body length and water temperature were weaker than expected, especially for Atlantic salmon. This may have resulted from the relatively narrow range of fatigue times observed for this species compared to that of trout. All salmon that fatigued did so in under 24 min, whereas brook and brown trout often swam in excess of 100 min before stopping. Also, the wild origin of the fish may have resulted in more variance than would be expected from domestic stock, as reported by Jones *et al.* (1974).

According to popular theories of fish locomotion, a particular swimming speed either can be maintained indefinitely (sustained swimming) or it will result in fatigue (prolonged and burst swimming). As swimming speed decreases within the prolonged envelope, time to fatigue increases and approaches a value of approximately 200 min (Beamish, 1978). If speed is further reduced, a shift to sustained swimming occurs. Thus, on a typical endurance curve (Fig. 2), the point of inflection between sustained and prolonged modes corresponds to a fatigue time of exactly 200 min. In spite of this, our results indicate that, for juvenile Atlantic salmon, this inflection occurs at a value of 15–20, rather than 200 min (Fig. 2). Deviations from the 200-min rule have also been observed in other species. Bernatchez & Dodson (1985) reported that lake whitefish *Coregonus clupeaformis* (Mitchill) and cisco *C. artedii* Lesueur did not fatigue if they were able to swim longer than 75 and 30 min respectively. Therefore, the idea that sustained swimming occurs at speeds maintainable for more than 200 min may hold for most species; however, juvenile Atlantic salmon, lake whitefish, and cisco appear to be exceptions to that rule.

Atlantic salmon parr and juvenile brook trout were collected from the same river stretches. The theory of competitive exclusion would suggest that these fish, having similar food intake requirements, would need to separate along some axis of the niche. Suggested candidates for this axis include substrate (Rimmer *et al.*, 1983) and cover characteristics (McCrimmon, 1954), as well as water depth (Egglisshaw & Shackley, 1985); however, separation along these axes would be maintained primarily through interactive segregation, or separation produced by competition-related behavioural interactions (Nilsson, 1967). Water velocity has also been suggested as the primary factor that separates salmon parr from other species (DeGraaf & Bain, 1986; Morantz *et al.*, 1987; Arnold *et al.*, 1991). In this case, separation would also be maintained by selective segregation, a term that implies that evolved morphological differences exist between sympatric species, which allow one to dominate a particular microhabitat to the relative exclusion of the other.

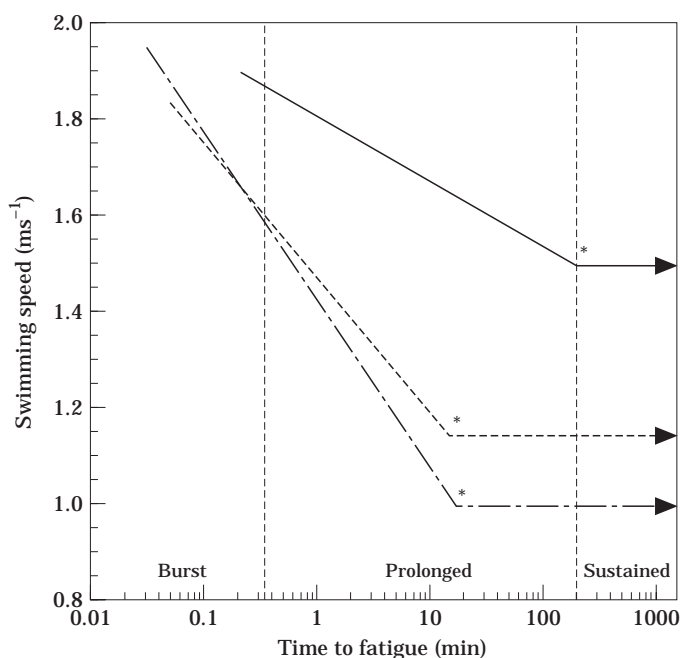


FIG. 2. A comparison of sustained, prolonged, and burst swimming capabilities of anadromous Atlantic salmon smolts (---) and landlocked Atlantic salmon (----). Horizontal lines with arrows indicate mean sustainable speeds, taken from Table 1, for anadromous (mean length: 15.2 cm) and landlocked salmon (mean length: 15.4 cm) respectively. Line positions were calculated for 15.2- and 15.4-cm anadromous and landlocked fish, using prolonged/burst models given in Table 1. Lines extend from the lowest swimming time recorded to the highest. Dotted lines indicate where one swimming mode should transition to another according to Beamish (1978). *Indicates where the transition from sustained to prolonged swimming modes actually occurred. A typical endurance curve (—) is shown also.

The present results suggest that selective segregation may, indeed, be most important in reducing competition between sympatric Atlantic salmon parr and juvenile brook trout. With their relatively low buoyancy and large pectoral fins (Hearn, 1987), parr can hold indefinitely in current speeds that exceed the sustained swimming ability of trout, even when trout are significantly larger (Fig. 3). For example, in this study a 13.0-cm brook trout could swim indefinitely in water speeds up to 0.54 m s^{-1} ; however, a 6.0-cm salmon parr could anchor itself indefinitely in flows up to 0.57 m s^{-1} . For similarly sized fish, sustained holding performance of parr eclipsed not only the sustained swimming ability of the trout, but much of its prolonged ability (Fig. 4). A 10.0-cm parr could hold 0.72 m s^{-1} indefinitely, while a 10.0-cm trout could maintain this speed for less than 1 min.

Field observations appear to validate the present finding that 6.0 to 13.0 cm Atlantic salmon parr can inhabit, and prefer, water moving up to 0.57 and 0.82 m s^{-1} , respectively. Symons & Heland (1978) reported that the highest densities of Atlantic salmon parr, in the Miramichi River, occurred where water velocities averaged 0.50 – 0.65 m s^{-1} . In addition, Gibson (1966) observed significantly more brook trout than salmon in pools where water velocity averaged 0.30 m s^{-1} , similar numbers of both species in 0.52 m s^{-1} riffles, and

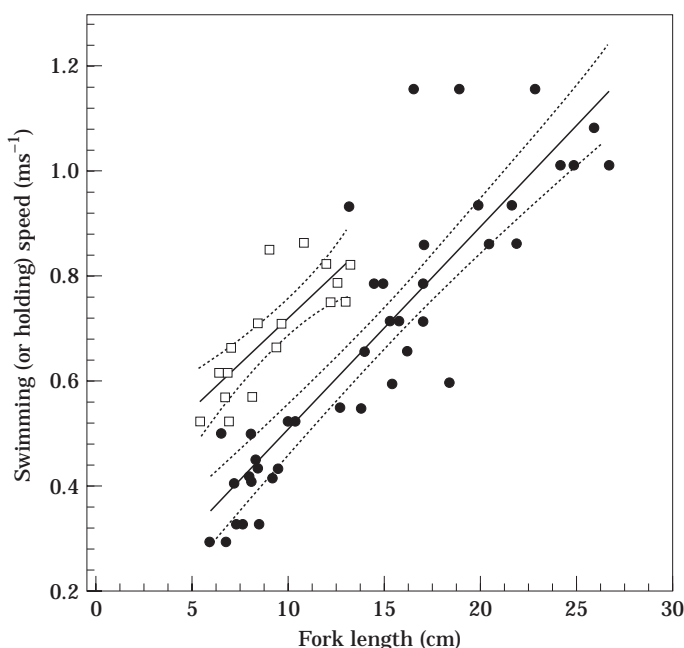


FIG. 3. A comparison of the sustained holding ability of Atlantic salmon parr (\square) and the sustained swimming ability of brook trout (\bullet). Dotted lines indicate 95% confidence limits.

significantly more salmon than brook trout in riffles where velocity averaged 0.89 m s^{-1} . Finally, Gibson (1981) reported that brook trout compete more successfully with Atlantic salmon in pools than in faster-moving water.

While it appears that anadromous Atlantic salmon parr have adapted the ability to utilize fast-water habitat in order to reduce interspecies competition, it is also possible that the ability was evolved in an attempt to maximize energy available for growth. Parr are generally ambush feeders, holding to the bottom and then darting into the flow to capture drifting food (Godin & Rangeley, 1989). In contrast, brook trout tend to swim actively and feed in the water column (Keenleyside, 1962). If a salmon parr can conserve energy by holding to the bottom, rather than swimming in the current, more energy is available for growth. In this case, fast moving water would be preferred as it often contains more drifting food than occurs in slow pools (Grant & Noakes, 1987). Whether the current holding ability of Atlantic salmon parr was first evolved to conserve energy or to reduce competition is difficult to argue either way; however, it is apparent that both benefits are realized.

Brown trout were remarkably strong swimmers, with only anadromous Atlantic salmon smolts possessing significantly greater ability. It must be stressed, however, that brown trout were collected from a watershed different from that of the other species and probably were exposed to different selective pressures. Nevertheless, our results indicate that swimming ability might aid in separating sympatric brook and brown trout. However, studies of the interactions of brown and brook trout report conflicting findings. Fausch & White (1981) found that adult brown trout excluded sympatric brook trout from profitable stream sites (which were generally associated with faster-moving

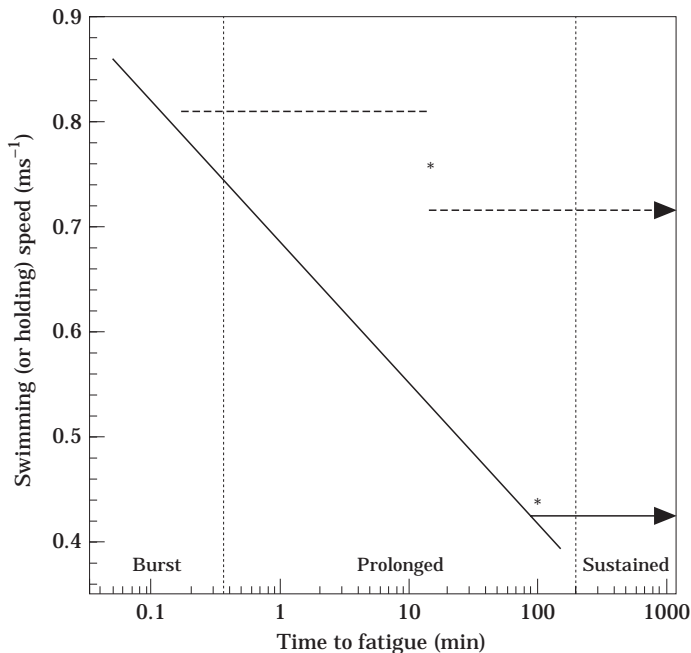


FIG. 4. A comparison of sustained and prolonged holding abilities and burst swimming capability of 10-cm anadromous Atlantic salmon parr (---) and sustained, prolonged, and burst swimming abilities of 10-cm brook trout (—). Line positions were calculated for both species using prolonged/burst models given in Table I and extend from the lowest swimming time recorded to the highest. Horizontal lines with arrows represent maximum sustainable speed of salmon parr and trout, as calculated from sustained models in Table I. Note that time to fatigue at (or below) these speeds would be indefinite. Temperature used in trout regressions was 15°C. Dotted lines indicate where one swimming mode should transition to another according to Beamish (1978). *Indicates where the transition from sustained to prolonged modes actually occurred.

water), while Fausch & White (1986) reported the opposite for juvenile brook and brown trout. In both cases, however, the dominated species moved into the faster water when released from competition. This suggests that segregation is probably maintained primarily by aggressive behaviour independent of swimming ability.

It is also likely that brown trout, from the present study, would have been capable of competing directly with the anadromous Atlantic salmon parr population. Despite this, there is general agreement among studies that brown trout are displaced by juvenile salmon (Fausch & White, 1986; Heggenes & Saltveit, 1990; Thomas, 1962), indicating that swimming/holding ability may not be important in separating these species.

Landlocked Atlantic salmon possessed similar prolonged and burst swimming abilities to those of anadromous salmon smolts (Fig. 2). This finding is corroborated by the fact that prolonged swimming ability (as determined by increasing velocity tests) was not significantly different between landlocked and anadromous salmon smolts. In contrast, mean sustainable swimming speeds of landlocked salmon were 15 cm s^{-1} (1 bl s^{-1}) less than those of anadromous smolts of similar size (Fig. 2). Interestingly, Taylor & Foote (1991) reported that sustained performance of landlocked sockeye salmon (kokanee) was also

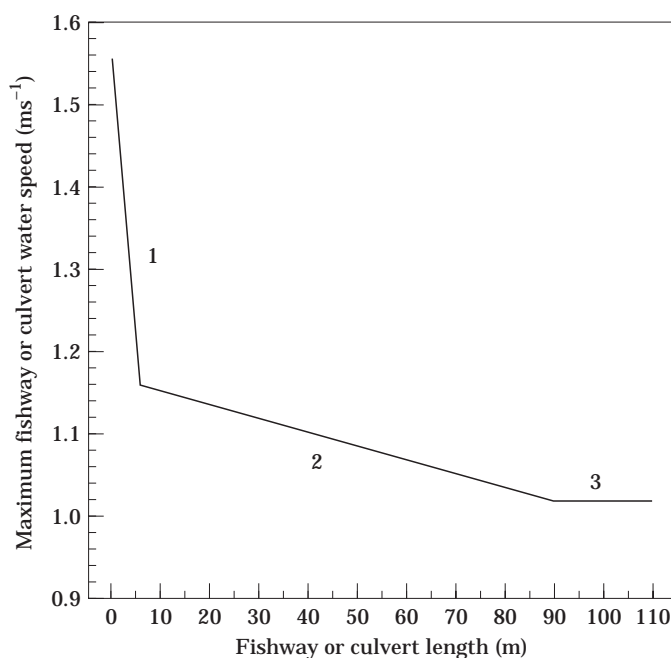


FIG. 5. Fishway or culvert design characteristics that would allow passage of a 25-cm brook trout swimming in 16° C water. Methods for determining line positions are given in the text.

1 bl s⁻¹ lower than that of anadromous sockeye. The authors suggested that relaxed selection for sustained swimming ability and the less fusiform shape of the kokanee may have resulted in the difference. Mean condition factor of juvenile landlocked Atlantic salmon, in the present study, was significantly greater than that of anadromous salmon smolts. Therefore, observed differences in sustained swimming ability of landlocked and anadromous salmonids may not be site or species specific, but related to differences inherent to body form and migratory behaviour.

Finally, as rivers are increasingly altered by roads and hydroelectric facilities, fishways and culverts must be installed to allow volitional movement of juvenile and adult fish. If passage of juvenile fish is not facilitated, they may congregate below obstructions in large numbers, increasing their susceptibility to predation. Jones *et al.* (1974) used data from increasing velocity tests to estimate fishway and culvert water velocities that would allow passage of several species from the Mackenzie River (species used in the present study were not tested). Since Jones *et al.* (1974) only used 10-min time intervals in their swim tests, the analysis is based on the assumption that fish will always require a 10-min period to ascend the culvert. Models derived from our 2, 5 and 10 min increasing velocity (Table II) and fixed velocity data (Table I) allow for more flexibility in the analysis.

For example, a manager might want to design a culvert that will pass all brook trout (in 16–20° C water) 25 cm in length or longer. The analysis could be completed as shown in Fig. 5. Line 1 estimates distances that the trout would cover if the fish used burst swimming to ascend a relatively short culvert. It is derived from the prolonged/burst model (Table I) using a length value of 25 cm,

a temperature value of 16° C, and a time value of 15 s. The model estimates that the trout can maintain a speed of 1.56 m s⁻¹ for the 15-s burst. Thus, if the water speed in the culvert is moving at 1.56 m s⁻¹ the fish will make no headway. If the water speed is 1.16 m s⁻¹ the trout will be able to move about 6 m (1.56 m s⁻¹ - 1.16 m s⁻¹ × 15 s) before fatiguing. Line 2 estimates distances that the trout could cover if it used prolonged swimming to ascend a somewhat longer culvert. In this case, the manager could decide to allow for a transit time ranging from 2 to 10 min. In the example, a 10-min ascent time was chosen. Using the brook trout model in Table II, the 25-cm trout could maintain a speed of 1.17 m s⁻¹ for 10 min. If the water speed in the culvert was set at 1.16 m s⁻¹, the trout would only move about 6 m. If the water speed were set at 1.02 m s⁻¹ the trout could swim about 90 m. Water speed in the culvert would never have to be set lower than 1.02 m s⁻¹ (line 3), since this represents a sustainable speed for the 25-cm brook trout as determined from the sustained model in Table I. Although this analysis may not be useful in the case of downstream migrating Atlantic salmon smolts, the approach can be used for any species in this study provided the length, temperature, and time values used fall within the ranges tested.

We thank the staff at the Indian River DFO Research Station, the Alma Aquaculture Station, and P. Rose and C. Kelly for technical assistance; and M. Power and B. Dempson for critical review of the manuscript. Funding for the study was provided by a grant from the Department of Fisheries and Oceans and from the Natural Sciences and Engineering Research Council of Canada to RSM.

References

- Arnold, G. P., Webb, P. W. & Holford, B. H. (1991). The role of the pectoral fins in station-holding of Atlantic salmon parr (*Salmo salar* L.). *Journal of Experimental Biology* **156**, 625–629.
- Beamish, F. W. H. (1978). Swimming Capacity. In *Fish Physiology*, Vol. 7 (Hoar, W. S. & Randall, D. J., eds), pp. 101–187. New York: Academic Press.
- Bernatchez, L. & Dodson, J. J. (1985). Influence of temperature and current speed on the swimming capacity of lake whitefish (*Coregonus clupeaformis*) and cisco (*C. artedii*). *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 1522–1529.
- Birt, T. P. & Green, J. M. (1993). Acclimation to seawater of dwarf non-anadromous Atlantic salmon (*Salmo salar*). *Canadian Journal of Zoology* **71**, 1912–1916.
- Brett, J. R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *Journal of the Fisheries Research Board of Canada* **2**, 1183–1226.
- Burton, M. P. & Idler, D. R. (1984). Can Newfoundland landlocked salmon (*Salmo salar*) adapt to seawater? *Journal of Fish Biology* **24**, 59–64.
- DeGraaf, D. A. & Bain, L. H. (1986). Habitat use by and preferences of juvenile Atlantic salmon in two Newfoundland rivers. *Transactions of the American Fisheries Society* **115**, 671–681.
- Duthie, G. G. (1987). Observations of poor swimming performance among hatchery reared rainbow trout (*Salmo gairdneri*). *Environmental Biology of Fishes* **18**, 309–311.
- Egglishaw, H. J. & Shackley, P. E. (1985). Factors governing the production of juvenile Atlantic salmon in Scottish streams. *Journal of Fish Biology* **27**, 27–33.
- Fausch, K. D. & White, R. J. (1981). Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1220–1227.

- Fausch, K. D. & White, R. J. (1986). Competition among juveniles of coho salmon, brook trout, and brown trout in a laboratory stream, and implications for Great Lakes tributaries. *Transactions of the American Fisheries Society* **115**, 363–381.
- Fleming, I. A., Jonsson, B. & Gross, M. R. (1994). Phenotypic divergence of sea-ranched, farmed, and wild salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 2808–2824.
- Gibson, R. J. (1966). Some factors influencing the distribution of brook trout and young Atlantic salmon. *Journal of the Fisheries Research Board of Canada* **23**, 1977–1980.
- Gibson, R. J. (1978). The behavior of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) with regard to temperature and to water velocity. *Transactions of the American Fisheries Society* **107**, 703–712.
- Gibson, R. J. (1981). Behavioral interactions between coho salmon, Atlantic salmon, brook trout, and steelhead trout at the juvenile fluvial stages. *Canadian Technical Report of Fisheries and Aquatic Sciences* No. **1029**.
- Godin, J. J. & Rangeley, R. W. (1989). Living in the fast lane: effects of cost of locomotion on foraging behavior in juvenile Atlantic salmon. *Animal Behaviour* **37**, 943–954.
- Grant, J. W. A. & Noakes, D. L. G. (1987). Movers and stayers: foraging tactics of young-of-the-year brook char (*Salvelinus fontinalis*). *Journal of Animal Ecology* **56**, 1001–1013.
- Hearn, W. E. (1987). Interspecific competition and habitat segregation among stream-dwelling trout and salmon: a review. *Fisheries* **12**, 24–31.
- Heggenes, J. & Saltveit, S. J. (1990). Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) in a Norwegian river. *Journal of Fish Biology* **36**, 707–720.
- Jones, D. R. (1971). The effect of hypoxia and anaemia on the swimming performance of rainbow trout (*Salmo gairdneri*). *Journal of Experimental Biology* **55**, 541–551.
- Jones, D. R., Kiceniuk, J. W. & Bamford, O. S. (1974). Evaluation of the swimming performance of several fish species from the Mackenzie River. *Journal of the Fisheries Research Board of Canada* **31**, 1641–1647.
- Kazakov, R. V. & Kozlov, V. V. (1985). Quantitative estimation of degree of silvering displayed by Atlantic salmon (*Salmo salar*) juveniles originating from natural populations and from fish-rearing farms. *Aquaculture* **44**, 213–220.
- Keenleyside, M. H. A. (1962). Skin-diving observations of Atlantic salmon and brook trout in the Miramichi river, New Brunswick. *Journal of the Fisheries Research Board of Canada* **19**, 625–634.
- McCrimmon, H. R. (1954). Stream studies on planted Atlantic salmon. *Journal of the Fisheries Research Board of Canada* **11**, 362–403.
- McKeown, B. A. (1984). *Fish Migration*. Portland: Timber Press.
- Morantz, D. L., Sweeney, R. K., Shirvell, C. S. & Longard, D. A. (1987). Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 120–129.
- Nilsson, N. A. (1967). Interactive segregation between fish species. In *The Biological Basis of Freshwater Fish Production* (Gerking, S. D., ed.), pp. 295–313. Oxford: Blackwell Scientific Publications.
- Rimmer, D. M., Paim, U. & Saunders, R. L. (1983). Autumnal habitat shift of juvenile Atlantic salmon (*Salmo salar*) in a small river. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 671–680.
- Smit, H., Amelink-Koutstaal, J. M., Vijverberg, J. & von Voupal-Klein, J. C. (1971). Oxygen consumption and efficiency of swimming in goldfish. *Comparative Biochemistry and Physiology* **39A**, 1–28.
- Steel, R. G. D. & Torrie, J. H. (1960). *Principles and Procedures of Statistics with Special Reference to the Biological Sciences*. New York, N.Y.: McGraw-Hill.
- Symons, P. E. K. & Heland, M. (1978). Stream habitats and behavioral interactions of underyearling and yearling Atlantic salmon. *Journal of the Fisheries Research Board of Canada* **35**, 175–183.

- Taylor, E. B. & Foote, C. J. (1991). Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). *Journal of Fish Biology* **38**, 407–419.
- Taylor, E. B. & McPhail, J. D. (1986). Prolonged and burst swimming in anadromous and freshwater threespine stickleback (*Gasterosteus aculeatus*). *Canadian Journal of Zoology* **64**, 416–420.
- Thomas, J. D. (1962). The food of brown trout and its feeding relationship with the salmon parr (*Salmo salar*) and the eel (*Anguilla anguilla*) in the River Liefy, West Wales. *Journal of Animal Ecology* **31**, 175–206.