Field-based measurements of oxygen uptake and swimming performance with adult Pacific salmon using a mobile respirometer swim tunnel


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Novel field measurements of critical swimming speed (U_{crit}) and oxygen uptake (M_{O2}) in three species of adult Pacific salmon Oncorhynchus spp. up to 3.5 kg in body mass were made using two newly designed, mobile Brett-type swim tunnel respirometers sited at a number of field locations in British Columbia, Canada. Measurements of U_{crit}, which ranged from 1.68 to 2.17 body lengths s^{-1}, and maximum M_{O2}, which ranged from 8.74 to 12.63 mg O2 kg^{-1} min^{-1} depending on the species and field location, were judged to be of similar quality when compared with available data for laboratory-based studies. Therefore high quality respirometry studies were possible in the field using adult wild swimming salmonids. In addition, the recovery of wild adult Pacific salmon from the exhaustive U_{crit} swim test was sufficiently rapid that swimming performance could be repeated with <1 h of recovery time between the termination of the initial swim test and the start of the second test. Moreover, this repeat swimming performance was possible without routine M_{O2} being reestablished. This result suggests that wild adult salmon are capable of carrying a moderate excess post-exercise oxygen consumption without adversely affecting U_{crit}, maximum M_{O2} or swimming economy. Such capabilities may be extremely important for timely migratory passages when salmonids face repetitive hydraulic challenges on their upstream migration.

Key words: field respirometry; critical swimming speed; repeat swimming; recovery; Oncorhynchus.

INTRODUCTION

Swimming performance and studies of energy consumption have held the interest of fish researchers since the pioneer work of Brett and co-workers began over 40 years ago (Brett, 1965, 1971; Beamish, 1978). The majority of studies have focused on immature cultured fishes in a laboratory setting, and information on the swimming energetics of adult wild salmon species is limited. Some studies have transported wild adult salmonids to a laboratory for study (Jones et al., 1974; Farrell
but very few have performed tests in the field, where fishes can be tested at ambient temperature and photoperiod and in natal water (Jones et al., 1974; Farrell et al., 2001). For example, Williams et al. (1986) inserted swimming flumes into a modified streambed to assess swimming performance of pink salmon Oncorhynchus gorbuscha (Walbaum). Similarly, Farrell et al. (2001) submersed a swimming flume in the ocean to measure swimming capabilities of sockeye salmon Oncorhynchus nerka (Walbaum) following commercial capture by gillnet.

In contrast to the studies of swimming performance, field-based respirometry, wherein oxygen uptake ($M_{O_2}$) during swimming is assessed, is presently lacking for adult migratory salmonids. Respirometry experiments are limited either to wild adult salmonids after they have been transported long distances to laboratories (Jones et al., 1974; Williams et al., 1986; Randall et al., 1987; Farrell et al., 1998; Jain et al., 1998) or to adult fishes that were hatchery-reared (Kiceniuk & Jones, 1977). Field-based physiological radiotelemetry on adult salmonids has provided information on patterns of energy usage and swimming behaviour by monitoring skeletal muscle contractions associated with swimming (Hinch & Rand, 1998; Rand & Hinch, 1998). These measures, however, have not been calibrated against comparable field-based respirometry studies.

The paucity of data on the swimming energetics for adult migratory salmonids is clearly a handicap for fisheries managers who make annual predictions of migration success for salmonid stocks returning to natal streams. In this regard, a particular problem for migration is the annual fluctuation in both river water velocity and water temperature. For example, in the Fraser River, British Columbia, extremes of either high temperature or water velocity in recent years have contributed to incomplete or delayed fish passage through difficult stretches of the river (Macdonald et al., 2000). Thus, field evaluations of adult salmonid swimming performance could find application in defining hydraulic barriers and temperature thresholds for migration, as well as defining any differences that might exist in the aerobic capacities among different salmonid stocks and species. Furthermore, models of energy use of migrating salmonids that rely on physiological telemetry and extrapolations from laboratory respirometry studies (Rand & Hinch, 1998) could benefit from calibration with field-based measurements of $M_{O_2}$.

The present study used a newly developed large, robust Brett-type respirometer swim tunnel that permitted field-based measurements of swimming performance and $M_{O_2}$ with adult Pacific salmon Oncorhynchus sp. Because the swim tunnel was mobile, it was possible to: perform the measurements at various geographical locations without transporting the fish large distances, use different species [sockeye, pink and coho salmon Oncorhynchus kisutch (Walbaum)], and use natal river water at ambient temperature for the tests. The objective of the study was three-fold. The first objective was to show that field-based measurements of $M_{O_2}$ during critical swimming speed ($U_{crit}$) tests could be comparable to more controlled laboratory measurements. The second objective was to compare swimming energetics among three species of salmon from different locations of the same watershed. Species differences certainly exist in swimming performance among juvenile salmonids (Brett, 1971), but the consequence of these differences in $M_{O_2}$ in adult salmonids has not been thoroughly considered. The third objective was to test the hypothesis that wild fishes rapidly recover their ability to swim following
a $U_{crit}$ test. Rapid recovery may be extremely important for timely migratory passages when salmonids face repetitive hydraulic challenges on their upstream migration. This aspect of adult wild salmonid physiology, however, has not been studied from the perspective of whether they can repeat their swimming performance with as little as a 45 min recovery period following exhaustion, as has been shown in laboratory experiments (Jain et al., 1997; Farrell et al., 1998).

**MATERIALS AND METHODS**

The experiments were performed during the normal spawning migrations of Pacific salmon during the summer or autumn of three consecutive years (1998, 1999 and 2000). Only swimming performance was assessed in the first year, and respirometry was added for the second and third years. The oxygen measurement method was improved in the third year by using a portable oxygen meter with an analogue output, which was placed outside, rather than inside, the swim tunnel in a re-circulating water loop. Also, two similar designs of swim tunnel were used, one larger than the other to accommodate bigger fishes. Fish transportation prior to experimentation was minimized because the swim tunnels were mobile and could be located at remote field locations that were often only accessible by gravel roads. The majority of experiments were conducted in the field at or near the site of capture and at ambient river temperature using natal water. In some cases, the power requirements of the swim tunnel necessitated that it was assembled a short distance from the sampling location, requiring transport of fishes over a short distance to the test location. For comparison, some fishes were transported longer distances by road to Simon Fraser University (SFU) or by ship to Bamfield Marine Station (BMS). When transported by road, fishes were placed into a 3301 insulated transport tank containing oxygenated water that was chilled with blocks of ice. A dilute Marinil anaesthetic (0.02 mg l$^{-1}$ metomidate hydrochloride, Syndel International Inc., Vancouver, B.C., Canada) was added to the water to calm the fishes during transportation. The largest swim tunnel accommodated Pacific salmon up to 3.5 kg in body mass and therefore was considerably larger than the transportable respirometer produced by Bargard et al. (1989), which accommodated a maximum fish mass of only 1.2 kg. The first design utilized a 20.3 cm internal diameter (ID) swimming chamber and was used to test sockeye salmon in 1998 and 1999. The second design had a swim chamber ID of 25.4 cm and was used to test pink salmon in 1999, and coho salmon and sockeye salmon in 2000.

**MOBILE SWIM TUNNEL DESIGNS**

The main design features of both swim tunnels are presented below (see also: http://www.sfu.ca/biology/faculty/farrell/swimtunnel/swimtunnel.html). The smaller swim tunnel was a 2151 Brett-type respirometer, modelled after the design used by Gehrke et al. (1990). It consisted of a 124.3 cm Plexiglas swim chamber with a removable lid (19 x 67 cm), a PVC expansion chamber and three additional PVC sections. The swim chamber was delineated upstream by a stainless steel mesh (0.75 cm$^2$) and downstream by a shocking grid that consisted of seven horizontal, graphite electrodes (0.5 cm diameter) c. 1.5 cm apart. A variable voltage (2–10 V; 0.4–2.0 W), watertight transformer was used to supply a d.c. current to the graphite electrodes in an alternating pattern. The upright section of the PVC tube from the impellor contained four cross-shaped PVC flowstraightening vanes to promote a rectilinear water flow in the swim chamber (Beamish, 1978). Plastic collars on either side of the swim chamber supported the swim chamber and expansion sections. The entire swim tunnel was assembled with stainless steel and aluminium fittings. When assembled, the swim tunnel was c. 8 m long and 2.5 m high and careful attention was taken to assure that the swim tunnel was balanced and level. Water flow was driven by a 29 cm diameter fibreglass centrifugal impellor pump that was coupled to a 7.5 hp, 208 V, 3-phase, 1200-rpm motor and controlled by a Siemens Midimaster Vector frequency drive (PLAD, Coquitlam, B.C., Canada). The control unit was operated manually.
by varying the frequency of the motor. When in operation, the controller assembly and swim tunnel were protected by tarpaulins to minimize unnecessary weathering.

The swim tunnel was placed on a single-axle 1000 kg boat trailer, reinforced with a 7 cm galvanized steel frame. The controller, pump and motor were mounted to an aluminium base plate that was attached to the trailer and could be relocated directly over the rear axle of the trailer during transport by means of a track mounted on to the trailer and 9 cm ball bearing wheels on the base plate. The control unit was removed from the motor-pump assembly during transportation. By using a fibreglass impellor, PVC tubing, galvanized steel framework, and stainless steel and aluminium fittings, it was possible to routinely use sea water in the swim tunnel. The swim tunnel could be moved in one trip using a full-size ‘three-quarter tonne pick-up’ truck. Complete assembly required two people and took c. 4 h.

To permit the testing of larger fishes, a second and larger swim tunnel was used (volume = 471.2 l). The swim chamber was longer (185.5 cm) and had a larger opening (20.5 × 78.5 cm). The expansion chamber was also larger (maximum ID = 30 cm). All remaining PVC pieces were 25.4 cm in ID except for the PVC sections to and from the impellor (20.3 and 15.2 cm, respectively). The remainder of the design, including the motor, impellor, controller and trailer, was similar to that described above. When assembled the trailer was c. 7 m long and 2.7 m high.

RESPIROMETER FLOW CALIBRATION

Water velocity within the swim chamber was regularly calibrated (Fig. 1) with a Valeport impellor-type flow-probe (Valeport Marine Scientific Ltd, Dartmouth, U.K.), connected to a digital read-out unit (m s⁻¹) (Science Technical Workshop, SFU). The flow-probe was

![Fig. 1. Examples of the water velocity calibration x impellor frequency for the (a) small and (b) large swim tunnels. The variation in flow across the diameter of the swim chamber was minor as shown by the measurements of water velocity at different heights across the width of the swim chamber (as indicated by the position numbers: •, 1; ○, 2; ▲, 3; ▼, 4; ■, 5) at both the front (c) and rear (d) of the large swim tunnel.](image-url)
held in the swim chamber with a bracket made from 1 cm PVC tubing. At the highest motor frequency, water velocity could reach 264 cm s⁻¹ in the small swim tunnel and 200 cm s⁻¹ in the large swim tunnel, but these velocities were never reached by any of the fish tested. Examples of the calibration curves for the small and large swim tunnels and over the range of water velocities that were used to test fish are shown in Fig. 1(a), (b). The water velocity at the front of the swim chamber in the large swim tunnel was between 0.5 and 4% greater than the other positions [Fig. 1(c)], with the greatest variation being observed at the lowest water velocity (5 cm s⁻¹). The rear section of the large swim tunnel had similar characteristics [Fig. 1(d)].

**BAMFIELD MARINE STATION – SOCKEYE SALMON**

Thirty adult Alberni Inlet sockeye salmon were captured in June 1998, using a purse seine near Chup Point (Barkley Sound, B.C.) during a test fishery by Fisheries and Oceans Canada. Individual fish were transferred by dipnet into the vessel’s hold and transported to BMS (Fig. 2) within 2 h. Previously, this procedure had been successfully used to transport Alberni Inlet sockeye salmon over considerably longer distances (Farrell *et al.*, 1998).

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**FIG. 2.** Map of British Columbia, Canada to illustrate the locations of fish sampling and testing, and the major hydrodynamic challenges (*) faced by long-distance migrating Fraser River salmonids.
Fish were held at BMS in two 4000l covered outdoor tanks supplied with aerated sea water at ambient temperature (mean ± s.e. = 11.8 ± 0.4°C). To manage fungal infections, two separate chloramine-T (Syndel Laboratories, Vancouver, B.C., Canada) treatments were employed on the second and third days post-capture. These treatments consisted of immersion in a static, aerated water-bath containing 8–10 mg l⁻¹ of chloramine (added pre-dissolved). The same procedure had been used previously for Alberni Inlet sockeye (Farrell et al., 1998). Experiments were conducted on six healthy fish that remained after 2 weeks of holding (mass, 1.88 ± 0.19 kg and fork length, $L_F$, 55.3 ± 1.8 cm; mean ± s.e.).

PACIFICA PAPERS, PORT ALBERNI – SOCKEYE SALMON

Pacifica Papers (PP), Port Alberni, B.C. (Fig. 2) supplied space and electrical power to operate the swim tunnel near to the entrance of the Somass River, through which sockeye salmon migrate to reach Great Central Lake. Groups of sockeye salmon (three to five adult fish) were removed from a metal fence (brailer) located at the Great Central Lake fish ladder during July to September 1998. Fish were transported in <2.5 mins to the PP site where they were held for no more than 3 days in a 1200l holding tank supplied with ambient fresh water pumped from the Somass River. During experimentation in 1998, the Somass River water temperature averaged 20.8 ± 0.4°C and fish were prone to fungal infections if the skin was abraded. Experiments were conducted on eight sockeye salmon that had no fungal infection (mass, 2.27 ± 0.17 kg and $L_F$, 60.3 ± 1.5 cm).

ROBERTSON CREEK FISH HATCHERY – SOCKEYE SALMON

Robertson Creek Hatchery (RCH), located 25 km from Port Alberni, B.C. (Fig. 2), provided easy on-site fish capture and maintenance during the autumn of 1998. Fish were removed from a brailer and held in a covered 6000l tank for up to 2 weeks. The hatchery fresh water (12.9 ± 0.2°C) was produced by mixing cold water from the bottom of Great Central Lake with warmer stream water. Experiments were conducted on eight healthy sockeye salmon (mass, 2.23 ± 0.19 kg and $L_F$, 61.5 ± 2.1 cm). These fish were nearing spawning condition.

SETON HYDROELECTRIC DAM – PINK SALMON

In October 1999, the swim tunnel was assembled at the B.C. Hydro's Seton (STN) Dam site (Fig. 2) near Lillooet, B.C. Pink salmon were dip-netted on-site at the top of a fish ladder and immediately placed into the swim tunnel and allowed to habituate overnight. Water (11.3 ± 0.8°C) was pumped from above the dam site into the tunnel. Experiments were conducted on seven healthy pink salmon (mass, 1.61 ± 0.28 kg and $L_F$, 52.7 ± 2.5 cm). The fish were released after the experiments. These fish were ripe and within days of spawning.

SIMON FRASER UNIVERSITY – SOCKEYE SALMON

Sockeye salmon were captured with a beach seine from the Weaver River (WVR) (Fig. 2) in September 2000 and transported a short distance to SFU. The water was chilled with blocks of ice and oxygenated during transportation, which lasted c. 1.5 h. Fish were held in 1000l holding tanks for at least 3 days before testing commenced. De-chlorinated municipal water (15.0 ± 0.4°C) was pumped from holding tanks into the swim tunnel. Once placed in the swim tunnels, fish were permitted to habituate overnight before the swim tests. Experiments were conducted on seven healthy sockeye salmon (mass, 2.64 ± 0.70 kg and $L_F$, 60.8 ± 4.2 cm). After the initial trial, five of the fish were sequentially transferred to the second swim tunnel where they were each allowed to recover and habituate for 48 h to examine the effect of a longer habituation time on routine $M_O^2$.  

CHEHALIS RIVER FISH HATCHERY – COHO SALMON

In October 2000, the swim tunnel was assembled at Chehalis River Fish Hatchery (CHE) (Fig. 2) near Harrison Lake, B.C. Fish were captured with a knotless cotton net and were held in fishways until they were placed into the swim tunnel where they were allowed to habituate overnight. Hatchery water (9-8 ± 0-2°C) was pumped from the fishway into the tunnel. Experiments were conducted on seven healthy coho salmon (mass, 2-13 ± 0-29 kg and $L_F$, 56-3 ± 1-9 cm).

EXPERIMENTAL PROTOCOLS

Immediately prior to testing, a knotless-nylon net (Redden Net, Vancouver, B.C., Canada) was used to remove the fish from the holding area and place it in an anaesthetic solution [0.2 mg l$^{-1}$ MS222 in either sea water or buffered (0.2 mg l$^{-1}$ NaHCO$_3$) fresh water]. The fish was only lightly anaesthetized to permit measurements of body mass, recovery following the initial factor was applied for blocking effects of 10$^{20}$ U swimming performance tests:

Many fishes simply rested on the bottom of the swim chamber for the duration but did not necessitate swimming, although some fishes would swim intermittently. The fish was habituated to the swim tunnel at a water velocity of 0 and maximum depth and width (measured to the nearest mm) before it was placed in the water asb as do not h i sp e r f o r m an c e .

Approximately 45 min after introducing the fish into the swim tunnel, the fish performed a conditioning swim test (Jain et al., 1997) during which water velocity was increased in 0-15 BL s$^{-1}$ increments every 2 min until the fish was unwilling to swim any faster. Following the conditioning swim, the water velocity was returned to 0-45 BL s$^{-1}$. After an overnight recovery, measurements of $M_{O_2}$ and $U_{crit}$ began at between 0800 and 1000 hours (i.e. 14–16 h after the conditioning swim). Each fish was tested using a ramp-$U_{crit}$ protocol previously described by Jain et al. (1997, 1998). The fish was ramped up to 50–70% of the maximum speed achieved in the previous day’s conditioning swim using velocity increments of 0-15 BL s$^{-1}$ every 5 min. Subsequently, water velocity was increased in increments of 0-15 BL s$^{-1}$ every 20 min until the fish stopped swimming. The swim test was terminated when the fish failed to move off the rear grid after 20 s. The initial $U_{crit}$ ($U_{crit1}$) was based on this performance. $U_{crit}$ values were calculated as in Brett (1965):

$$U_{crit} = U_{f} + t_{i}(t_{f}U_{f})^{-1},$$

where $U_{f}$ is the water velocity of the last fully completed increment, $t_{i}$ is the time spent on the last water velocity increment, $t_{f}$ is the time period for each completed water velocity increment (20 min) and $U_{i}$ is the water velocity increment ($0-15$ BL s$^{-1}$). $U_{crit}$ values were corrected where necessary for solid blocking effects as outlined by Bell & Terhune (1970). A streamline shape factor was used in the correction equation:

$$U_{crit corrected} = U_{crit} \left\{ 1 + \frac{L_T}{2F_{W-D}} \left[ \frac{0.0625 \pi (W+D)^2}{A} \right]^{1.5} \right\},$$

where $L_T$ is the total length of the fish, $W$ is maximum fish width, $D$ is the maximum fish depth and $A$ is the cross-sectional area of the swim chamber. A $U_{crit}$ correction factor was applied for blocking effects of 10–20%. To test the ability of the fish to recover following the initial $U_{crit}$ test, a second ramp-$U_{crit}$ protocol ($U_{crit2}$) was performed after allowing the fish to recover for 45 min at 0-45 BL s$^{-1}$. This water velocity permitted, but did not necessitate swimming, although some fishes would swim intermittently. Many fishes simply rested on the bottom of the swim chamber for the duration of the recovery period. A recovery ratio ($RR$) expressed the ratio of the two swimming performance tests: $U_{crit2}$/$U_{crit1}$. Thus, when $RR$ is equal to unity, the $U_{crit}$ performance in both swim tests was identical. Throughout the course of the test,
water temperature in the swim tunnel did not fluctuate >0.5°C. At the end of the experiment, the fish was removed from the swim tunnel, anaesthetized and killed by a blow to the head.

MEASUREMENT OF OXYGEN UPTAKE

Oxygen uptake (mg O₂ kg⁻¹ min⁻¹) was measured for pink salmon (STN), coho salmon (CHE) and one sockeye salmon stock (WVR) only during the second and third field seasons. In the second field season for the STN study, an OxyGuard Mark III oxygen electrode (resolution = 0.1 mg O₂ l⁻¹; Point Four Systems, Port Moody, B.C., Canada) was inserted inside the swim tunnel to measure changes in water oxygen concentration. The head of the oxygen electrode was held c. 1 cm recessed and perpendicular to the water flow in the swim tunnel by a rubber O-ringed coupling upstream of the expansion chamber. Within its recessed cavity and without a fish in the swim chamber, the OxyGuard output signal did not vary throughout the working water velocity range of 5–200 cm s⁻¹. Because the oxygen probe quickly registered localized oxygen depletion when either there was no water flow or it was recessed too deeply, and measurements were erratic when the head of the probe was advanced into a high water flow, close attention had to be given to the probe placement. To avoid these concerns and to automate the measurement, a Mark IV OxyGuard probe, which had an analogue output for data acquisition (resolution = 0.01 mg O₂ l⁻¹), was housed outside the swim tunnel in a 600 ml flow-through cylindrical housing (c. 11 cm in diameter and 8 cm deep) that was supplied with water from the swim tunnel at a rate of 30 ml s⁻¹ using a Masterflex peristaltic pump and was used for the studies at SFU and CHE. The oxygen probes were air-calibrated and compensated for salinity and temperature.

Dissolved oxygen concentration was monitored continuously throughout the experiments. To measure \( \dot{M}O_2 \), the water flow to the tunnel was stopped, trapped air bubbles were released through a valve at the highest point of the respirometer and elapsed time was measured while oxygen concentration decreased by 0.3–1.0 mg O₂. At higher velocities, this change could take as little as 5 min, whereas up to 20 min could be needed to measure routine \( \dot{M}O_2 \). Routine \( \dot{M}O_2 \) values were determined in the morning after overnight recovery and immediately prior to the swim tests. For the WVR sockeye salmon and CHE coho salmon, additional \( \dot{M}O_2 \) measurements were made towards the end of every other 20 min velocity increment. The \( \dot{M}O_2 \) at \( U_{crit} \) was designated maximum \( \dot{M}O_2 \) (\( \dot{M}O_{2max} \)). For STN pink salmon, however, \( \dot{M}O_2 \) was not measured during the swim test and \( \dot{M}O_{2max} \) was based on a 2 min measurement made immediately after the fish stopped swimming. \( \dot{M}O_2 \) was re-measured immediately prior to the second swim test for all three species and the same measurements described above were repeated for the second swim test. When \( \dot{M}O_2 \) was not being measured, water flow to the swim tunnel was restored and dissolved oxygen concentration never fell below 69% saturation during the experiments. \( \dot{M}O_2 \) was calculated as: \( (\text{Oxygen concentration})(\text{swim tunnel water volume})(\text{fish mass})(\text{time}) \)⁻¹, where oxygen concentration was measured in mg O₂ l⁻¹; swim tunnel water volume was equal to total volume of the swim tunnel (215 or 471 l) minus the fish’s volume (assuming 1 kg = 1 l); time was in min. The swim tunnel was thoroughly flushed after each experiment and regularly bleached between experiments. Background oxygen consumption was assessed on a bi-weekly basis at all test locations. Because no change in water oxygen concentration was ever detected during a 20 min recording period without a fish in the swim tunnel, background oxygen consumption was assumed to be negligible.

DATA ANALYSIS AND STATISTICAL ANALYSIS

Factorial aerobic scope was calculated from \( \dot{M}O_{2max} \) routine \( \dot{M}O_2 \)⁻¹. Swimming economy for both swim tests was calculated at \( U_{crit} \) from \( \dot{M}O_{2max} U_{crit} \)⁻¹. Statistical comparisons were performed with \( t \)-tests or ANOVA using \( P < 0.05 \) as the level of statistical significance. Mean values are presented with the S.E.M. Fitting regressions to the data were accomplished iteratively, beginning with simple power functions and increasing in complexity until the curve closely represented the trend alluded to by the data.
Regressions were initially chosen on the basis of the $r^2$ value. In instances where differences in $r^2$ values became negligible, extrapolation of curves and adherence to physiological relationships were used to discern the better fit.

RESULTS

PERFORMANCE OF SWIM TUNNEL

Calibration of both swim tunnels generated reliable relationships between the water velocity and the impellor frequency, even though the entire assembly was dismantled, moved over long distances on rough roadways and reassembled several times. Examples of the water velocity calibrations in the swim chamber are presented in Fig.1. Consistently, there was a near linear relationship between the impellor frequency and water velocity over the range used to swim fishes. In addition, the variation in water velocity across the diameter of the swim chamber was not large. In the small swim tunnel, water velocity was measured centrally, as well as 3 cm above and 3 cm below this point; the variation was rarely >2%, except at the very lowest water velocity used in the calibration. Similar results were found for the larger swim tunnel, where water velocity was calibrated at both the front [Fig.1(c)] and rear [Fig.1(d)] positions of the swim chamber and at c. 4 cm increments across the diameter.

SWIMMING PERFORMANCE

Sockeye salmon

Individual sockeye salmon tested at BMS, PP and RCH had $U_{\text{crit 1}}$ values ranging from 1.59 to 2.59 BL s$^{-1}$ (Table I). There were no significant differences among mean $U_{\text{crit 1}}$ values for the three locations. No attempt was made to control differences among locations such as water quality (sea water at BMS and fresh water at PP and RCH), water temperature, which ranged from 11.8$^\circ$C at BMS to 20.8$^\circ$C at PP, and sexual maturation, which increased as fish migrated from BMS to RCH. Because there were no significant differences between $U_{\text{crit 1}}$ and $U_{\text{crit 2}}$ values ($P > 0.05$, all contrasts), the average $RR$ was not significantly different from 1.0, which ranged from 0.86 to 1.13 for individual fish (Table I). Therefore, the 45 min recovery period between the completion of the first swim test and the start of the second swim test provided sufficient recovery time for the fish to perform a second $U_{\text{crit 1}}$ test at the same level of performance as in the first test.

Individual WVR sockeye salmon had $U_{\text{crit 1}}$ values ranging from 1.52 to 2.13 BL s$^{-1}$ (Table I). Routine $Mo_2$ was $2.97 \pm 0.23$ mg O$_2$ kg$^{-1}$ min$^{-1}$ (Table II). For the fish that were retested after a 48 h habituation period, routine $Mo_2$ was significantly lower ($1.72 \pm 0.17$ mg O$_2$ kg$^{-1}$ min$^{-1}$; $P < 0.05$). The increase in $Mo_2$ that accompanied incremental increases in swimming velocity is illustrated in Fig.3. $Mo_{2,\text{max}}$ was $12.28 \pm 0.75$ mg O$_2$ kg$^{-1}$ min$^{-1}$ for the initial swim and represented a factorial aerobic scope of 4.1. $Mo_{2,\text{max}}$ and $U_{\text{crit 1}}$ were unchanged for the second swim and the average $RR$ was not significantly different from 1.0 (individual $RR$ values ranged from 0.94 to 1.10), even though $Mo_2$ measured immediately prior to the second swim test was 40% greater ($4.15 \pm 0.43$ mg O$_2$ kg$^{-1}$ min$^{-1}$; $P < 0.05$) than the routine $Mo_2$ (Table II).
### TABLE I. Swimming performance of adult Pacific salmon species measured at various field locations with a portable swim tunnel. The initial and second critical swimming speeds ($U_{crit1}$ and $U_{crit2}$) are reported for individual fish along with the recovery ratio ($RR; U_{crit2} / U_{crit1}$)

<table>
<thead>
<tr>
<th></th>
<th>Sex</th>
<th>$U_{crit1}$ (BL s$^{-1}$)</th>
<th>$U_{crit2}$ (BL s$^{-1}$)</th>
<th>$U_{crit1}$ (cm s$^{-1}$)</th>
<th>$U_{crit2}$ (cm s$^{-1}$)</th>
<th>$RR$</th>
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<td>118.8</td>
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<td>2.55</td>
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</table>

Cohosalmon

Individual CHE coho salmon had $U_{crit}$ values ranging from 1.41 to 1.94 BL s$^{-1}$ (Table I). Routine $M_o_2$ was 2.91 ± 0.25 mg O$_2$ kg$^{-1}$ min$^{-1}$ (Table II). The increase in $M_o_2$ that accompanied incremental increases in swimming velocity is illustrated in Fig. 3. $M_o_{2max}$ was 8.74 ± 0.25 mg O$_2$ kg$^{-1}$ min$^{-1}$ for the initial swim, the lowest among the fish groups. The low factorial aerobic scope of 3.0 corresponded to the lowest $U_{crit}$ value among all the fish groups tested. Routine $M_o_2$ was restored prior to the second swim test. $M_o_{2max}$ and $U_{crit}$ were unchanged for the second swim and $RR$ was 1.00 (Tables I and II).

Pink salmon

Individual STN pink salmon had $U_{crit}$ values ranging from 1.63 to 3.15 BL s$^{-1}$. Routine $M_o_2$ was 4.25 ± 0.69 mg O$_2$ kg$^{-1}$ min$^{-1}$ and was the highest measured among the various fish groups (Table II). $M_o_{2max}$ was 12.63 ± 0.44 mg O$_2$ kg$^{-1}$ min$^{-1}$ for the initial swim and so the low factorial aerobic scope of 3.0 reflected the high routine $M_o_2$. STN pink salmon swam almost 20% faster on the second swim since $RR$ averaged 1.17. Nevertheless, $M_o_{2max}$ was unchanged for the second swim (Table II) and $M_o_2$ measured prior to the second swim test was c. 60% greater ($P < 0.05$) than routine $M_o_2$.

SWIMMING ECONOMY AT $U_{CRIT}$

Swimming economy at $U_{crit}$ varied by 2.7-fold among individual fish and species (Table II). Swimming economy, however, was much more repeatable for a given individual because values for the first and second swims never varied by >30%, with only one exception (Table II). $U_{crit}$ swimming for CHE coho salmon was c. 25% more economical (0.13–0.14 mg O$_2$ kg$^{-1}$ m$^{-1}$) compared with either STN pink salmon or WVR sockeye salmon (0.18–0.19 mg O$_2$ kg$^{-1}$ m$^{-1}$) (Table II). Swimming economy and ambient water temperature are compared in Fig. 4. A lower water temperature could have accounted for the better swimming economy.
TABLE II. Oxygen uptake ($M_o2$) measurements of adult Pacific salmon species measured at various field locations with a portable swim tunnel that were taken concurrently with the swimming performance shown in Table I. Swimming economy at critical swimming speed ($U_{crit}$) was calculated from $M_o2 U_{crit}^{-1}$. The values appearing in the parentheses for routine $M_o2$ of Weaver River (WVR) sockeye salmon are second measurements made after a 48 h habituation period.

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F, female; M, male.
FIG. 3. Individual oxygen uptake values as a function of swimming velocity for (a) Chehalis (CHE) coho salmon (●, CHE-01; ○, CHE-02; ▼, CHE-03; ▼, CHE-04; ■, CHE-05; □, CHE-06; ●, CHE-07) and (b) Weaver (WVR) sockeye salmon (●, WVR-01; ○, WVR-02; ▼, WVR-03; ▼, WVR-04; ■, WVR-05; □, WVR-07; ●, WVR-09) and (c) the mean ± s.e.m. oxygen uptake values for ○, CHE coho and ●, WVR sockeye salmon. The lines were fitted by: CHE coho, $y = 2.93 + 7.02 [1 + e^{-(x-5.65)}]^{-1}$, $r^2 = 0.988$; WVR sockeye, $y = 2.98 + 14.15 [1 + e^{-(x-4.68)}]^{-1}$, $r^2 = 0.990$. 

in CHE coho salmon, but CHE coho salmon also had lower $U_{\text{crit}}$ and $M_o^{2\text{max}}$ values compared with STN pink salmon and WVR sockeye salmon. Clearly, the difference in water temperature between STN pink salmon and WVR sockeye salmon did not result in any appreciable differences in swimming economy or $M_o^{2\text{max}}$.

**DISCUSSION**

Measurements of $M_o$ and $U_{\text{crit}}$ were generated in the present study using three species of adult Pacific salmon at a number of geographical locations in British Columbia. Many of these measurements were novel in that they were performed under field conditions using a mobile swim tunnel. The $U_{\text{crit}}$ and $M_o$ data for sockeye salmon obtained here are consistent with the only comprehensive, laboratory-based study of the swimming energetics that has been performed with any adult salmon species (Brett & Glass, 1973). $U_{\text{crit}}$ values of 2.2–2.4 BL s$^{-1}$ for adult sockeye at 15°C (Brett & Glass, 1973) are consistent with those reported in the present study for sockeye salmon. Similarly, the corresponding $M_o^{2\text{max}}$ of 12 mg O$_2$ kg$^{-1}$ min$^{-1}$ (Brett & Glass, 1973) is identical to that reported here for sockeye salmon. Consequently, the present results provide strong evidence that reliable respirometry can be performed on wild adult salmonids in field locations using a mobile swim tunnel. Thus, by foregoing long transportation times and retaining ambient water quality and temperature when performing field-based measurements, it may be possible to reliably replicate swimming performance and
energetics of wild fishes in situ, and this may be especially valuable for fishes that are too fragile for transportation.

An earlier study (Williams et al., 1986) had reported field-based measurements of $U_{\text{crit}}$ for Seton pink salmon that ranged from a high of 3.39 BL s$^{-1}$ for gravid males to 1.73 BL s$^{-1}$ for spawned out females. Given this effect of sexual maturation on swimming performance, $U_{\text{crit}}$ values at the lower end of this range were to be expected for the fully ripe Seton pink salmon that were tested in the present study. Direct comparisons between the two studies, however, are not valid since Williams et al. (1986) measured $U_{\text{crit}}$ at temperatures between 10.5 and 13.6°C, and then adjusted all $U_{\text{crit}}$ values to a common temperature of 15.0°C using an equation that had been validated originally for sockeye salmon. The present study simply reports $U_{\text{crit}}$ for Seton pink salmon at the fish’s ambient temperature of c. 11.3°C. Despite these concerns, there is a remarkably good agreement between measurements of active metabolic rate for both studies with pink salmon [13.8 mg O$_2$ kg$^{-1}$ min$^{-1}$ (Williams et al., 1986) v. 12.63 mg O$_2$ kg$^{-1}$ min$^{-1}$; present study] and sockeye salmon. It should be noted, however, that the pink salmon in the earlier study were transported several hundred kilometres to the BMS for laboratory-based respirometry and they appeared to have lower $U_{\text{crit}}$ values compared with the field-based measurements (there was no individual value >2.5 BL s$^{-1}$, Williams et al., 1986).

A concern at the outset of this study was that the calibration of the swim tunnels would not be reproducible when the swim tunnel was disassembled, transported and reassembled at different locations. Quite to the contrary, the calibration of the water velocity in the swim tunnel proved to be very repeatable and this finding greatly alleviated concerns. In fact, the only problem to arise during more than four seasons of use has been occasional minor breakages of PVC valves during transportation. It was discovered, however, that the controller panel could not withstand travel over a long, unpaved logging road and was removed from the trailer during transport. Both swim tunnels remain in regular use for their intended application.

The second objective of the present investigation was to make comparisons among species. The measurements of $U_{\text{crit}}$, $M_{\text{O}_2\text{max}}$ and swimming economy at $U_{\text{crit}}$ for sockeye salmon and pink salmon are comparable. The $U_{\text{crit}}$, $M_{\text{O}_2\text{max}}$ and swimming economy values for coho salmon, however, were lower than those for pink salmon and sockeye salmon. The lower water temperature for the experiments with CHE coho salmon could have accounted for the difference with sockeye salmon, but perhaps not the difference with pink salmon. A more comprehensive study than the present one will be needed to explore to what extent such differences in swimming performance and energetics relate to factors such as sex, maturation status and species, as well as temperature. Similar to Williams et al. (1986), who noted that both sex and sexual maturation status negatively influenced $U_{\text{crit}}$ for Seton pink salmon (3.39 BL s$^{-1}$ for gravid males v. 2.31 BL s$^{-1}$ for spawned out males and 2.78 BL s$^{-1}$ for gravid females v. 1.73 BL s$^{-1}$ for spawned out females), the present study found that $U_{\text{crit}}$ for sockeye salmon was lower when measured on more mature fish at RCH compared with those of an earlier reproductive state at BMS. Other environmental factors such as differences in salinity and water temperature, however, confound such a comparison. Williams et al. (1986) suggested that at a swimming speed of 1.56 BL s$^{-1}$, male pink salmon had a 15% higher $M_{\text{O}_2}$. 

compared with females (8.25 mg O₂ kg⁻¹ min⁻¹ vs. 7.16 mg O₂ kg⁻¹ min⁻¹). In the present study, no attempt was made to statistically compare males and females, although individual data are presented. Furthermore, given the individual variation observed in the present study, it is unlikely that such small sex-related differences in Mo₂ could be statistically resolved without a considerably larger sample size. Jones et al. (1974) also performed field and laboratory U crit tests on a variety of adult salmonid species. These results showed considerable variability among salmonids species, e.g. Arctic charr Salvelinus alpinus (L.) 2.82 BL s⁻¹, mountain whitefish Prosopium williamsoni (Girard) 1.39 BL s⁻¹, Arctic cisco Coregonus autumnalis (Pallas) 1.90 BL s⁻¹, least cisco Coregonus sardinella Valenciennes 2.03 BL s⁻¹, wild-caught rainbow trout Oncorhynchus mykiss (Walbaum) 2.17 BL s⁻¹ and hatchery-reared rainbow trout 2.78 BL s⁻¹. Nevertheless, the U crit values of all these salmonids fall within a general range of 1.4–2.8 BL s⁻¹, one that is similar to that for Oncorhynchus species.

Telemetry-based energetic models for salmon migration, such as the one developed by Hinch & Rand (1998), rely on three critical pieces of information: the Mo₂ of inactive fish, the telemetered swimming activity of the fish in question, and a reliable calibration between swimming activity and Mo₂. Given the present finding, it appears that such modelling can become more accurate by relying on field-based respirometry for appropriate species and stock when coupled with physiological telemetric study. The energetic models, however, may want to ‘revisit’ the Mo₂ value for inactive fish. Prior to the present study, only standard metabolic rates were available for adult salmonids. For sockeye salmon at 15–19°C, a standard metabolic rate of 1.2 mg O₂ kg⁻¹ min⁻¹ was assigned by extrapolating from the lowest individual Mo₂ values during swimming to a standard metabolic rate (Brett & Glass, 1973). Similarly, for pink salmon at 15°C, a standard metabolic rate of 1.1 mg O₂ kg⁻¹ min⁻¹ was assigned by apparently restricting data analysis to calmer female fish because the authors noted a wide scatter in the data for what the authors describe as ‘more excitable mature’ fish (Williams et al., 1986). The routine Mo₂ values presented here for adult salmon are ×2 to ×3.9 higher than the standard metabolic rates reported earlier (Brett & Glass, 1973; Williams et al., 1986). In fact, the highest routine Mo₂ was for pink salmon and this finding is consistent with the suggestion by Williams et al. (1986) that pink salmon are excitable when placed in a respirometer and the routine Mo₂ for WVR sockeye salmon is comparable with an earlier laboratory-based measurement for Port Alberni sockeye salmon at 20°C (2.1 mg O₂ kg⁻¹ min⁻¹; Farrell et al., 1998). While a difference is expected between standard and routine metabolic rates, a large difference may have ramifications to energetic modelling. In the case of salmonid migration up the Fraser River, the difference may not be too critical in the overall energy budget since Rand & Hinch (1998) suggest that active metabolism is the main contributor to the budget. In energy budgets for non-migrating fishes, however, the standard metabolic rate is a much more important feature (Briggs & Post, 1997).

No attempt was made in the present study to extrapolate data to accurately derive standard metabolic rates for two reasons. First, as shown in Fig 3 and in Williams et al. (1986), individual variability among Mo₂ values can be considerable and therefore extrapolation to a standard metabolic rate has to rely on a sub-sampling of the lowest individual Mo₂ values. Such sub-sampling of data can be done reliably only after repeated individual measurements of routine Mo₂, something
that was not performed in the present study. Second, the validity of extrapolating from swimming data to standard metabolic rate may be questioned on both theoretical and empirical grounds because \( M_o2 \) does not necessarily increase when a salmonid begins to swim [as shown for chinook Salmon *Oncorhynchus tshawytscha* (Walbaum) by Thorarensen et al., 1993; Gallaugher et al., 2001]. Thus, it has been suggested that, with the onset of swimming, the initial increase in oxygen demand of the locomotory muscles can be met by a reallocation of the available oxygen supply in the circulation, and so there is no need to increase \( M_o2 \) during this reallocation process. In support of this idea, gastro-intestinal blood flow decreases linearly with the increase in oxygen consumption during swimming, i.e. blood flow was redistributed away from the gut and made available for the locomotory muscle (Thorarensen et al., 1993). Blood flow redistribution away from the gut to the locomotory muscles during swimming is also reported in earlier studies (Randall & Daxboeck, 1982). Consequently, unless the confounding influence of blood flow redistribution at the onset of swimming is accounted for, standard metabolic rate could be underestimated when derived by extrapolation from active metabolic rates. In fact, the equations presented in Fig.3 for the relationship between active \( M_o2 \) and water velocity for WVR sockeye salmon and CHE coho salmon can be extrapolated to a zero velocity to estimate standard metabolic rate. These estimates of standard metabolic rate (2.98 and 2.93 mg O\(_2\) kg\(^{-1}\) min\(^{-1}\)) turn out to be no different to the measured routine metabolic rates for either species.

Despite the concerns with the use of standard metabolic rate in energetic models and its derivation in fishes, there are issues concerning routine \( M_o2 \). Routine \( M_o2 \) is labile and even in apparently quiescent fishes can show clear diurnal cycles (J.F. Steffensen, pers. comm.). Routine \( M_o2 \) also decreases during habituation to the test equipment (Janz et al., 1991), presumably as the effects of stress and activity wear off. For this reason, routine \( M_o2 \) was re-measured for a small group of sockeye salmon at SFU and a lower routine metabolism was found. The value used for routine (or standard) metabolic rate can have a profound effect on the calculated metabolic scope. Using the data for WVR sockeye salmon as an example, the factorial aerobic scope is 4.1 when the routine \( M_o2 \) after 1 day habituation in the swim tunnel is used, but is only 3.0 when the metabolic rate just before the second swim test is used (note \( U_{crit} \) and \( M_{o2max} \) were identical for the two swim tests). In contrast, factorial aerobic scope is 7.1 when the routine \( M_o2 \) after a 48 h habituation to the swim tunnel is used. Thus, future attempts to measure routine metabolic rate for adult salmonids in the field clearly would benefit from an habituation period that is as long as 48 h. Unfortunately, a longer habituation period may prove to be problematic because adult migrating salmonids have a homing instinct and repeated activity (presumably to escape) often results in cumulative physical damage and acute fungal growth, especially at warmer water temperatures. Clearly, trade-offs will need to be made between habituation time and the health of the test animals.

The third objective was to test the hypothesis that wild fishes can repeat their swim performance without recovering completely from the first exhaustive swim. The reason for this is that most adult Pacific salmon face repetitive swimming challenges during their upstream migration. Consequently, if hydraulic barriers result in exhaustive swimming and the fish has to recover completely before
proceeding, the cumulative delay in migration could be substantial because completely metabolic recovery from exhaustion can take several hours (Milligan, 1996; Kieffer, 2000). Earlier laboratory-based studies with hatchery-raised rainbow trout, as well as with Port Alberni adult sockeye salmon, clearly showed that a 45 min recovery period between swim tests was sufficient for fishes to be able to repeat their swimming performance (and $M_{O_{2}}^{max}$ in the case of sockeye salmon) in a second swim test (Jain et al., 1997, 1998; Farrell et al., 1998). There are two criticisms of these earlier studies. First, $U_{crit}$ was not very high in the sockeye salmon ($<1.5 \, BL \, s^{-1}$), possibly because they had been transported over rather long distances to the laboratory and then tested at a high water temperature. Second, $M_{O_{2}}$ had almost completely returned to the routine level before the second $U_{crit}$ test. The wild adult Pacific salmon used in the present study typically swam at a much faster velocity than the sockeye salmon in the earlier study and the $RR$ was never significantly less than unity. This finding clearly establishes that a 45 min interval between successive $U_{crit}$ tests is indeed a sufficient recovery period for adult salmonids. Furthermore, the present study provides convincing evidence that repeat $U_{crit}$ performance is possible without full metabolic recovery prior to the second swim because $M_{O_{2}}$ was elevated above routine levels for both WVR sockeye salmon and STN pink salmon, though not for CHE coho salmon. In addition, $M_{O_{2}}^{max}$ and swimming economy were unchanged in the second swim in all three species, even though in two instances (WVR sockeye salmon and STN pink salmon) $M_{O_{2}}$ was elevated prior to the second swim $U_{crit}$ test. This suggests that $M_{O_{2}}$ values up to 4.2 mg O$_2$ kg$^{-1}$ min$^{-1}$ had no significant effect on $M_{O_{2}}^{max}$ even though factorial aerobic scope was quite low as a result. Consequently, $M_{O_{2}}^{max}$ for the second swim was unaffected by this type of metabolic load. These results contrast with an earlier suggestion that metabolic loading (i.e. an elevated metabolic rate) can limit maximum metabolic rate (Fry, 1971). It would seem that adult salmonids can compensate for the metabolic load associated with the excess post-exercise oxygen consumption of the first swim either by ‘deferring’ the load until after the second exercise bout, or by ‘repaying’ the load at the slower swimming velocities of the second swim. Both of these ideas could be easily tested in future studies.

Farlinger & Beamish (1977) found for largemouth bass Micropterus salmoides (Lacepède) that a second $U_{crit}$ swim was better than the first. For the six groups of adult Pacific salmon tested in the present study, only the STN pink salmon improved their performance on the second swim. Previous studies that similarly employed a habituation swim shortly after introducing the fishes to the swim tunnel also found no difference in the two $U_{crit}$ values (Farrell et al., 1998; Jain et al., 1998).

In conclusion, the tools are now available to make reliable field measurements of swimming performance and $M_{O_{2}}$ without having to move large adult salmonids long distances to laboratories. These mobile respirometer swim tunnels should enable future studies to carefully dissect the influences of fish stocks and species, water temperature, reproductive status and sex on swimming performance and migration energetics. In doing so, it may also be possible to assess the effect migration distance may have on salmonid energetics and swimming performance. Already, Hinch et al. (2002) have shown that important differences exist for pink and sockeye salmon in terms of their...
migration behaviours and their pattern of energy usage when migrating up the Fraser River.

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References


