Sustained swimming capacity of Atlantic salmon

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ABSTRACT: Sustained swimming in fish relies on aerobic metabolism alone and has been defined as swimming speeds that can be maintained for 200 min. However, few studies have tested swimming performances at constant velocities for such durations. Instead, the limits of sustainable swimming are often defined indirectly as speeds where anaerobic metabolism is required. Atlantic salmon *Salmo salar* aquaculture is currently expanding to more exposed locations that experience occasional strong current velocities, and thus a more practical assessment of the sustained swimming capacity is needed to ensure acceptable animal welfare. To this purpose, we performed swim tunnel respirometry experiments with groups of larger post-smolts (~800 g) at 13°C. First, the average critical swimming speed (U_{crit}) was determined (97.2 cm s^{-1}); then, sustained swimming trials were conducted in which fish were forced to swim up to 4 h at 60, 80 or 100% of the average U_{crit}. All fish endured 60 and 80% U_{crit} for 4 h, while only 2 avoided fatigue at 100% U_{crit} (n = 24 treatment^{-1}). A decrease in oxygen consumption rate over time at the sub-U_{crit} intensities indicated swimming became more efficient and aerobic. To explain variation in swimming performance within the group, U_{crit} and fatigue time were correlated with relative ventricular mass, condition factor and weight. However, these parameters were poor predictors of swimming performance. In conclusion, Atlantic salmon possess the aerobic capacity for continuous high-intensity swimming of at least 80% U_{crit} for several hours. This adds important temporal insight to welfare guidelines related to current velocities in aquaculture.

KEY WORDS: Endurance swimming · U_{crit} · Respirometry · Exposed aquaculture

INTRODUCTION

Sustained swimming does not result in fatigue and, in theory, can therefore be maintained indefinitely. Physiologically, this means that propulsion should be strictly aerobically fueled. In salmonids, this involves recruitment of the thin layer of slow red muscle fibres on the lateral sides, while fast white muscle fibres remain inactive (Hudson, 1973, Bone et al. 1978, Wilson & Egginton 1994). Homeostasis is then maintained with no accumulation of lactate, depletion of glycogen stores or other respiratory or osmotic disturbances.

Sustained swimming has been defined as swimming speeds that can be maintained for 200 min (Beamish 1978). Although this definition is widely

cited, studies on swimming capabilities rarely test fish at constant velocities for ≥200 min (e.g. Brett 1967, Cotterell & Wardle 2004). Instead, the most common assessment of swimming capacity is the critical swimming speed (U_{crit}), where a stepwise increase in swimming speed at intervals typically varying between 15 and 60 min is continued until the fish fatigues (Brett 1964, Plaut 2001, Farrell 2007). Therefore, U_{crit} represents the highest prolonged swimming speed a fish can maintain for a limited time (minutes) and is inherently powered by both aerobic and anaerobic metabolism at the final swimming velocities (Wilson & Egginton 1994).

To assess the speed limit of sustainable swimming in salmonids, several studies have used standard U_{crit} protocols while deploying various approaches

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to reveal when the transition from strictly aerobic to a mixture of aerobic and anaerobic metabolism occurs. Methods have involved calculations of aerobic swimming efficiency and power propulsion (Webb 1971), acid–base status and change in swimming behaviour (Kiceniuk & Jones 1977), measurements of intramuscular lactate and phosphocreatine (Burgetz et al. 1998), and electromyography to measure when large-amplitude white muscle traces are present (Sisson & Sidell 1987, Wilson & Egginton 1994, Beddow & McKinley 1999). These studies found that aerobic metabolism predominates in salmonids swimming up to 70 to 90% of their U_{crit} (e.g. Jones 1982, Burgetz et al. 1998, Beddow & McKinley 1999). This represents an impressive aerobic capacity for continued high-intensity swimming in salmonids compared to other groups of fish, such as cyprinids, that only sustain 30 to 50% of their U_{crit} aerobically (Jones 1982).

Interestingly, regardless of the experimental approach, these previous studies did not test whether the fish were able to maintain their highest sustainable swimming speed for ≥200 min, thereby not confirming whether those derived swimming speeds actually were truly sustainable. A less theoretical and more practical assessment of sustained swimming capabilities in farmed Atlantic salmon is now needed because of the current trend of establishing salmon sea cage farms at more exposed locations (Holmer 2010, Bjelland et al. 2015). With exposed sites positioned in high-energy environments with occasional strong water currents that potentially impact fish welfare, acceptable current velocities need to be defined. In this regard, U_{crit} was recently suggested as a useful welfare parameter for acceptable peak currents in sea cages (Remen et al. 2016). However, U_{crit} only represents the acceptable limit during short-duration strong current events and provides little information about whether the fish will cope or reach fatigue at intermediate current velocities if exposed for several hours.

The purpose of this study was to test the sustained swimming capacity of Atlantic salmon at U_{crit} and sub-U_{crit} speeds for durations of up to 4 h within a large swim tunnel respirometer. The oxygen consumption rate ($\dot{M}O_2$) here provides a measurement of the steady-state aerobic energy expenditure during prolonged swimming at constant velocities. A secondary objective was to assess the variation in swimming performance between individuals and whether this variation could be explained by size, condition factor (K) and relative ventricular mass (RVM).

MATERIALS AND METHODS

Animals

Prior to the experiments, farmed Atlantic salmon *Salmo salar* (Aquagen) had been kept for 6 mo at the Institute of Marine Research, Matre, Norway, in large circular tanks (3 m diameter, 5.3 m³ volume) with an inflow of 120 l min⁻¹ under a simulated natural photoperiod at low currents. Water temperature was maintained at 13°C, dissolved oxygen was not allowed to fall below 85% saturation and salinity was 34‰ (full-strength seawater). Feed was given in excess daily between 10:00 and 14:00 h through automatic feeding devices (Nutra, 3 mm pellet size; Skretting). Experiments were performed in November and December 2016 in accordance with Norwegian laws and regulations for procedures and experiments on live animals under permit number 9776.

Experimental setup

Swim trials were conducted in a large Brett-type swim tunnel respirometer with a swim section 248 cm long by 36 cm in diameter. The technical specifications and flow properties of this setup have previously been described (Remen et al. 2016, Bui et al. 2016, Hvas et al. 2017). To observe undisturbed fish behaviour, a camera was placed behind the rear grid of the swim section adjacent to an oxygen sensor (RINKO ARO-FT; JFE Advanced). Oxygen concentration was logged every 2 s (MiniSoft SD200W; SAIV A/S Environmental Sensors & Systems) and was kept above 85% saturation at all times by rapid intermittent flushing with water from a large, thermally controlled reservoir connected to the swim tunnel setup, which also served to keep the temperature constant at 13 ± 0.1°C. The top opening at the rear end could be partially removed when fish were placed in or taken out of the swim tunnel setup.

A large swim tunnel was chosen to better accommodate the natural swimming behaviour of Atlantic salmon and to prevent underestimations of the true swimming capacity of the fish, which has been known to occur in smaller setups (Tudorache et al. 2007, Deslauriers & Kieffer 2011, Remen et al. 2016). Groups of 8 fish were tested simultaneously per swim trial to reduce the volume-to-biomass ratio, so reliable O₂ traces could be made within 10 min. Furthermore, small, single-fish respirometers closely resemble the conditions for confinement stress trials of salmonids (Pottinger & Carrick 1999,

Vindas et al. 2016). Therefore, small groups of Atlantic salmon swimming together in a larger volume may reduce stress levels during experiments. Swimming in schools is also likely to reduce the cost of transport and therefore improve the swimming performance in some species (Hartwell & Otto 1978, Herskin & Steffensen 1998, Svendsen et al. 2003).

The fish rarely overlapped, meaning that for the most part they never exceeded 10% of the cross-sectional area of the swim tunnel. As a consequence, solid blocking effects were not corrected for (Bell & Terhune 1970, Plaut 2001).

Swim trial protocols

Fish were gently netted and quickly moved to the swim tunnel, which was placed in the same room as the holding tanks, and were allowed to acclimate to their new surroundings at 20 cm s^{-1} (~0.46 body lengths [BL] s^{-1}) overnight before the swim trials commenced the following day.

In the first series of experiments, the average U_{crit} of the stock was defined by a stepwise increase in current velocity of 20 cm s^{-1} every 30 min until all fish reached fatigue. Fatigue was defined as when a fish was no longer able to continue swimming even when encouraged to do so by a touch to the tail. Three replicate U_{crit} trials were conducted with a total of 24 fish.

In the second series of experiments, sustained swimming capabilities were assessed by forcing fish from the same stock to swim for 4 h at a constant water current velocity, defined as a percentage of the average U_{crit} obtained in the previous experiment. A total of 3 replicate trials at 60, 80 and 100% of the average group U_{crit} were made. Swim speed was increased by 20 cm s^{-1} every 15 min until the desired velocity was reached. The time was noted when a fish fatigued and it was then quickly removed from the setup, while the fish that endured all 4 h were noted to have completed the swim challenge.

$\dot{M}O_2$ measurements were made during all swim trials. In the U_{crit} protocol, the system was closed for 20 min and then flushed for 10 min at each increment interval, while the closed and flush periods were reduced to 10 and 5 min respectively during the sustained swimming protocols. Dissolved oxygen saturation was never allowed to fall below 85%. To ensure this, the closed period was reduced to 8 min and the flushing period increased to 7 min during sustained swimming at 100% U_{crit}.

After swim trials, fish were removed from the experimental setup and immediately killed with a quick blow to the head. Fish weight (W) and fork length (L_f) were measured and the ventricle was dissected out and weighed.

Calculations

U_{crit} was calculated according to Brett (1964):

$$U_{crit} = U_f + \frac{t_f U_i}{t_i} \qquad (1)$$

where U_f is the last completed swim speed, t_f is the time where fatigue was reached at the final swim speed, t_i is the time interval at each speed, and U_i is the magnitude of the swim speed increment.

$\dot{M}O_2$ was calculated from the change in oxygen concentration over time for each of the closed periods in all the swim trials. The cost of transport (CoT) at the various swimming speeds during the U_{crit} trials was calculated as mg O_2 kg^{-1} km^{-1}. A parabola was fitted to these values to express CoT as a function of swimming speed. The minimum of this function then served as an approximation of the optimum CoT swimming speed. RVM was calculated as the percentage of the ventricular mass of the total body weight of the fish. K was calculated according to Ricker (1975) as $100(W / L_f^3)$.

Statistics

A 1-way ANOVA with Tukey's post hoc test was used to test for differences between groups in W, L_f, K and RVM, and a Shapiro-Wilk test was used to confirm equal variance in these data. A linear regression fit was made between swimming capacities and various parameters to explore possible correlation patterns. Pearson's correlation coefficient was used to determine the statistical significance and strength of these correlations (SigmaPlot v.12.3; Systat Software). The level of significance for all tests was set at $\alpha = 0.05$.

RESULTS

The values of W, L_f, K and RVM for the different test groups are summarized in Table 1. W and L_f were similar between groups. However, the 60% U_{crit} group had larger RVM and lower K compared to the other groups, indicating that their bodies were slightly leaner.

Table 1. Weight (W), fork length (L_f), relative ventricular mass (RVM) and condition factor (K) of the 4 test groups of Atlantic salmon (n = 24). Superscript letters indicate a significant difference (p < 0.05). Data are means ± SE

Groups	W (g)	L_f (cm)	RVM	K
U_{crit} test	849 ± 36	43.0 ± 0.6	0.085 ± 0.002[a]	1.06 ± 0.02[a]
60 % U_{crit} sustained	777 ± 50	42.9 ± 0.6	0.097 ± 0.003[b]	0.96 ± 0.03[b]
80 % U_{crit} sustained	836 ± 27	42.7 ± 0.5	0.089 ± 0.003[a]	1.07 ± 0.02[a]
100 % U_{crit} sustained	916 ± 40	43.9 ± 0.6	0.091 ± 0.003[a]	1.07 ± 0.02[a]

The average U_{crit} was 97.2 ± 1.6 cm s^{-1} (2.27 ± 0.04 BL s^{-1}, n = 24), where all fish fatigued while swimming at either 100 or 120 cm s^{-1}. The water current velocities for sustained swimming trials at 60, 80 and 100 % of the average U_{crit} were therefore set to 58, 78 and 97 cm s^{-1} respectively.

No fish fatigued while swimming at 60 and 80 % U_{crit} for 4 h (Fig. 1). Only 2 out of 24 fish endured 4 h at 100 % U_{crit}, with the majority fatigued within the first 2 h (Fig. 1). L_f in the 100 % group ranged from 36 to 49.5 cm, meaning that fish were swimming at relative speeds between 2.69 and 1.96 BL s^{-1}, which may have explained differences in endurance time at this absolute current speed. However, the linear regression of BL s^{-1} against fatigue time had an almost horizontal slope and an R^2 of 0.006 (Fig. 1), which suggests that fatigue time was independent of the differences in relative swimming speeds of individual fish in this group. Fish approaching fatigue showed increasingly unsteady swimming behaviour
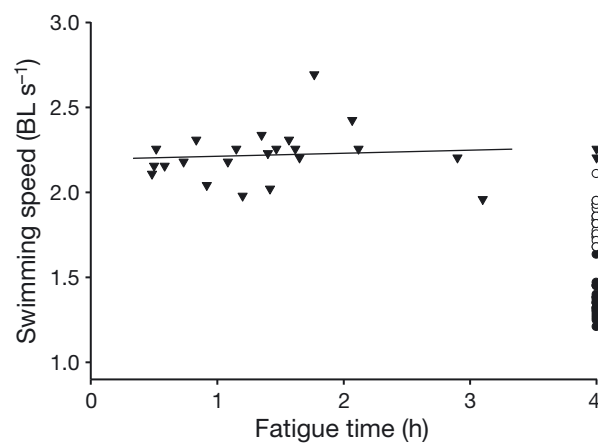
with occasional burst and glide movements and a tendency to fall back until they hit the rear grid.

$\dot{M}O_2$ during sustained swimming had distinct curve profiles at each of the intensities, averaging 509.9, 415.5 and 306.3 mg O$_2$ kg^{-1} h^{-1} at 100, 80 and 60 % U_{crit} respectively (Fig. 2). Since most fish fatigued in the 100 % group, the measured $\dot{M}O_2$ should be a good approximation of the average maximum rate of oxygen consumption ($\dot{V}O_{2max}$). This implies that sustained $\dot{M}O_2$, expressed as a percentage of $\dot{V}O_{2max}$ in the 60 and 80 % groups, on average corresponded to 60.1 and 81.4 % of $\dot{V}O_{2max}$ respectively.

There was a tendency for $\dot{M}O_2$ to slightly decrease over time during sustained swimming. A linear regression of $\dot{M}O_2$ versus time produced negative slopes of −5.35 and −7.44 mg O$_2$ kg^{-1} h^{-1}, with corresponding highly significant Pearson correlation factors of −0.77 and −0.74 respectively (p < 0.001). The pattern in $\dot{M}O_2$ at 100 % was more ambiguous since fish had to be removed from the setup between most measurement periods, and since too few fish eventually remained to obtain a proper oxygen trace in the latter periods.
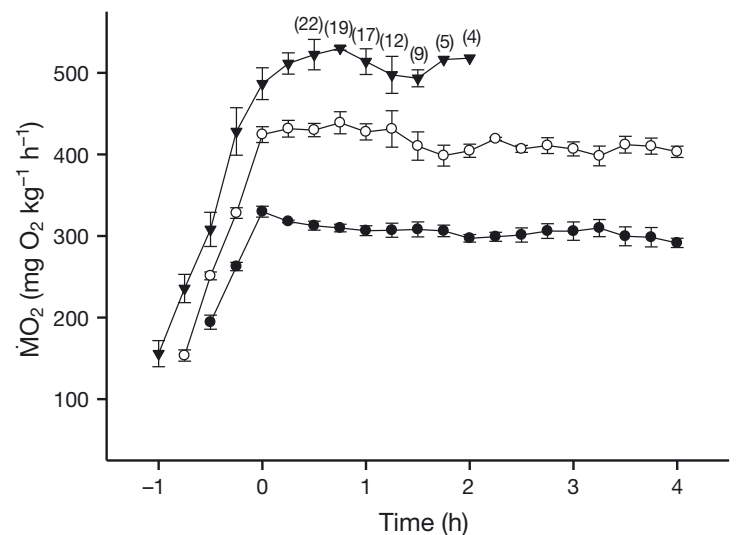

Fig. 1. Relative swimming speed (body length [BL] s^{-1}) versus time to fatigue during sustained swimming trials of Atlantic salmon. Points at the 4 h mark represent individual fish that completed the trial. Filled circles, open circles and triangles correspond to swimming speeds of 58, 78 and 97 cm s^{-1} respectively. Line represents a linear regression for fatigued fish ($y = 0.017x + 2.194$, R^2 = 0.006)

Fig. 2. Oxygen consumption rate ($\dot{M}O_2$) during 4 h sustained swimming trials at 60 % (closed circles), 80 % (open circles) and 100 % (triangles) of the average critical swimming speed (U_{crit}) for this batch of Atlantic salmon corresponding to 58, 78 and 97 cm s^{-1} respectively. Before 0 h, O$_2$ values correspond to the initial velocities prior to the desired swim speed being reached. Numbers in brackets: number of fish remaining; total number of fish at all other points is 24. Data are means ± SE
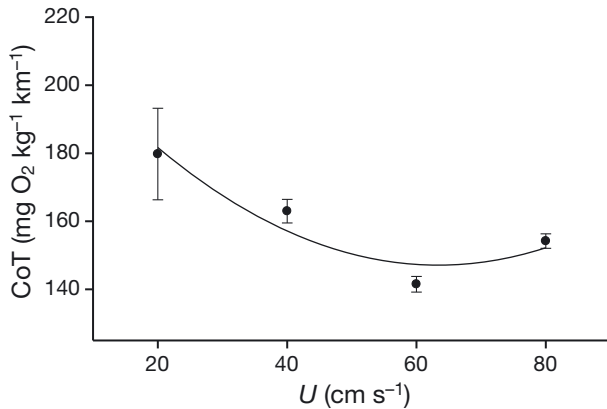
Fig. 3. Cost of transport (CoT) at intermediate swimming speeds calculated from the critical swimming speed (U_{crit}) trials (n = 3) for Atlantic salmon. The parabola fit is $y = 0.019x^2 - 2.333x + 221$, $R^2 = 0.903$, and the minimum is 147 mg O_2 kg^{-1} km^{-1} at 63.3 cm s^{-1}, which marks the theoretical optimum CoT. Data are means ± SE

The CoT plotted against what can be considered aerobic swimming speeds had a U-shaped curve, where the minimum of a parabola regression fit was 147 mg O_2 kg^{-1} km^{-1} at 63.3 cm s^{-1} (1.47 BL s^{-1}) (Fig. 3). This minimum CoT represents a theoretical optimal cruising speed for long distance swimming.

Some variation in swimming performance was found, with U_{crit} ranging from 1.84 to 2.79 BL s^{-1}, and fatigue time at 100% U_{crit} ranging between 30 and 186 min (2 fish endured 240 min). Plots with RVM, W and K versus either relative U_{crit} or fatigue time during sustained swimming can be seen in Fig. 4 with their corresponding Pearson's correlation coefficient and p-value. RVM and K were not correlated with U_{crit} (p = 0.632 and 0.492 respectively), although W was negatively correlated with the relative U_{crit} (p = 0.006). Fatigue time was independent of W and K (p = 0.606 and 0.218 respectively), while fish with larger RVM were associated with earlier fatigue times (p = 0.024).

DISCUSSION

Sustained swimming capacity

The average U_{crit} of 97 cm s^{-1} (2.27 BL s^{-1}) found here is similar to earlier studies on reared Atlantic salmon when considering slight differences in fish size, temperature and experimental setups (Wagner et al. 2003, 2004, Wilson et al. 2007, Remen et al. 2016). In the 24 fish tested, U_{crit} ranged from 80.5 to 107.3 cm s^{-1}. This implies that during the sustained swimming trials at speeds derived from the group average U_{crit}, individual fish experienced varying

relative intensities centred on this group average. Using the minimum and maximum from the U_{crit} trials, an estimate can be made for the range of individual variation in relative intensities experienced during the sustained trials: at 60% it would range from 54 to 72%, at 80% from 73 to 97%, and at 100% from 91 to 121%. Therefore, some appreciable individual differences in experienced swimming intensity are likely to have occurred in the sustained swimming trials.

However, no fish became fatigued in either of the sub-U_{crit} groups when forced to continue swimming for 4 h, despite some individuals potentially swimming close to their U_{crit}, particularly in the 80% group. This result is somewhat surprising considering a previous study on rainbow trout *Oncorhynchus mykiss*, which has respiratory physiology similar to Atlantic salmon, found significant intramuscular lactate production and phosphocreatine depletion within 30 min at 70 to 80% U_{crit} (Burgetz et al. 1998), while the aerobic limit for sustained swimming in salmonids is generally believed to be ~80% U_{crit} (Webb 1971, Jones 1982). On the contrary, another study on Atlantic salmon found that white muscles were not recruited until speeds above 85.5% U_{crit} (Beddow & McKinley 1999), which, together with the present study, suggest that Atlantic salmon possess a higher relative aerobic swimming capacity than other salmonids such as rainbow trout. Regardless, by testing sustained swimming capabilities for ≥200 min according to the original definition by Beamish (1978) at a predefined sub-percentage of the average group U_{crit}, it has now been confirmed that Atlantic salmon are able to sustain at least 80% of U_{crit} for several hours.

Oxygen consumption during sustained swimming

$\dot{M}O_2$ while swimming at 80% U_{crit} for 4 h corresponded to ~81.4% of the VO_{2max}. It is therefore not surprising that no fish reached fatigue here, since the aerobic capacity was far from fully utilized at this swimming intensity.

Since intramuscular lactate accumulation was found at sub-U_{crit} speeds in rainbow trout, and the fact that only 3 ATP molecules are produced when glycogen is converted to lactate while 5 ATP molecules are needed to convert lactate back into glycogen, it has been argued that anaerobic metabolism constitutes a notable component of the energy budget during salmonid migration (Burgetz et al. 1998). Furthermore, lactate recovery is slow in fish, ranging
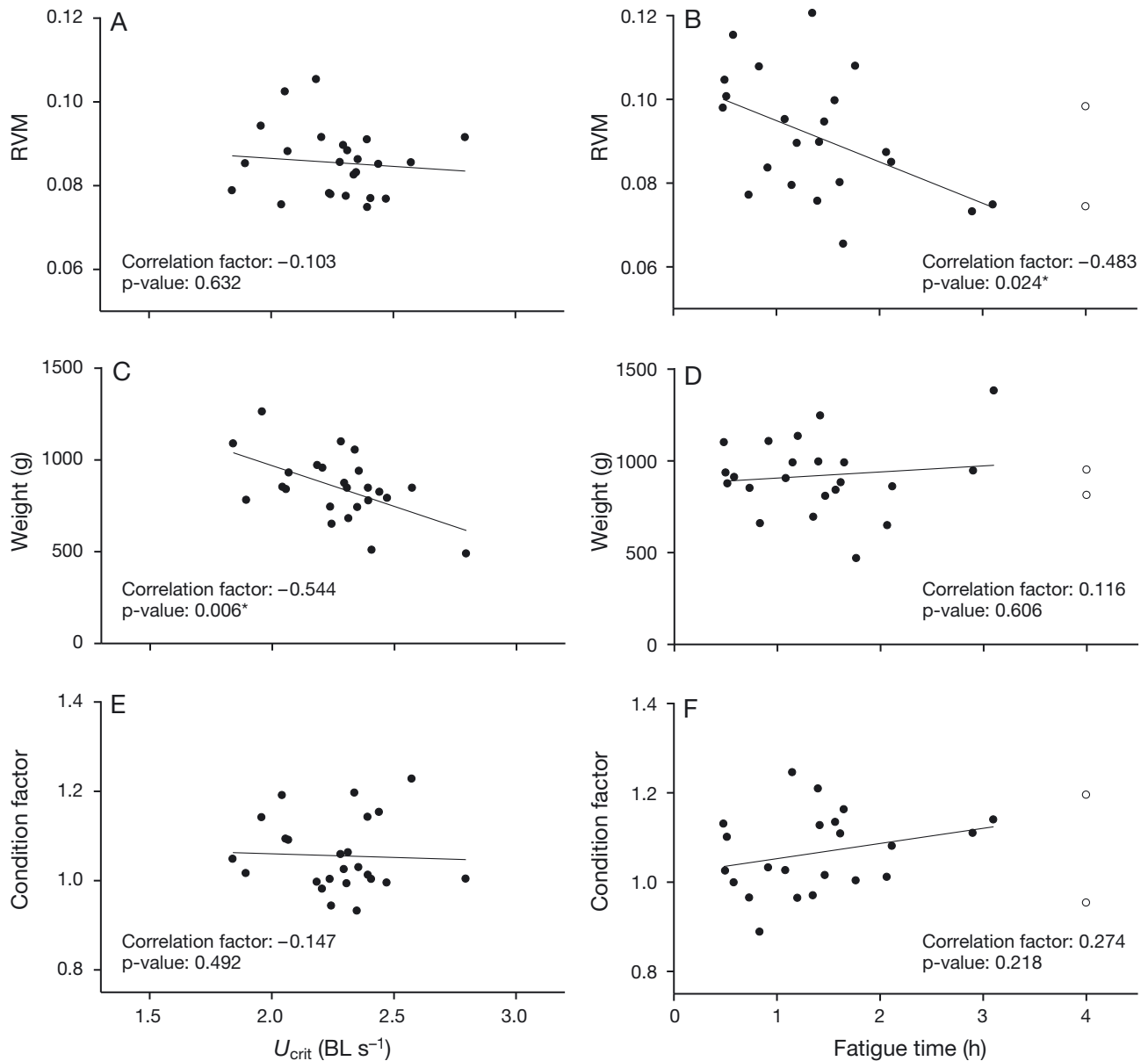
Fig. 4. Relative ventricular mass (RVM), weight, and condition factor versus either the relative critical swimming speed (U_{crit}) (left panels) or fatigue time of Atlantic salmon during the sustained swimming challenge at 97 cm s^{-1} (right panels) (n = 24). Open circles on right panels: fish that completed the swimming trial and were therefore omitted from the correlation analyses. *p < 0.05

from 2 to 8 h (Schulte et al. 1992, Pagnotta et al. 1994). If swimming at sub-U_{crit} required a substantial anaerobic component for Atlantic salmon, lactate would have to be metabolized 'on the run' to sustain homoeostasis, which should lead to an increase in $\dot{M}O_2$ over time when the fish were forced to swim at a high intensity for 4 h. Theoretically, it could be assumed that during continued high intensity swimming an escalating excess post-exercise oxygen consumption (EPOC)-effect would eventually cause $\dot{M}O_2$ to approach VO_{2max} with a subsequent lactate

accumulation and thereby cause fatigue. On the contrary, while swimming at 60 and 80 % U_{crit} for 4 h, $\dot{M}O_2$ decreased significantly over time, meaning that the energy requirements of a potential anaerobic component were negligible in the energy budget for Atlantic salmon at these swimming intensities.

The observed decrease in $\dot{M}O_2$ over time may have been caused by more efficient swimming in the latter periods when the fish became more accustomed to the current velocity and optimised their swimming gait. Salmonids are dependent on anaerobic meta-

bolism at the beginning of swimming and when swimming speeds increase, which is associated with lactate production and a small oxygen debt at intermediate velocities (Webb 1971, Jones 1982). Thus, some anaerobic metabolism may have occurred initially until a new steady-state rate of oxygen delivery to the working muscles was established. The decrease in $\dot{M}O_2$ over time could then, in part, also be ascribed to a decreasing need for lactate metabolism in the latter periods of the sustained swimming trials.

The minimum CoT can be interpreted as the optimum cruising speed for foraging or migration (Weihs 1973, Drenner et al. 2012). At 63.3 cm s^{-1} (1.47 BL s^{-1}), the minimum CoT found in this study for Atlantic salmon corresponded to 65% of the U_{crit}, and was far below the highest sustainable swimming speeds. This indicates that in theory, the optimum cruising speed should be achievable for an indefinite amount of time with no risk of fatigue. The minimum CoT reported here is similar to previous studies on salmonids (e.g. Lee et al. 2003, Hvas et al. 2017).

Indicators of individual variation in swimming performance

Differences in swimming capacity within groups of farmed Atlantic salmon may be related to differences in overall health and growth potential, and a thorough understanding of the magnitude and cause of this variation could be valuable in aquaculture practices. In a previous study, by screening the swimming capacity in a large group of Atlantic salmon parr and dividing them into 'good' and 'bad' swimmers, it was found that after smoltification, good swimmers had larger RVM, taller secondary lamellae, a thicker compact myocardial layer, higher maximum cardiac output and improved growth rates (Anttila et al. 2014).

In the present study, U_{crit} ranged from 1.84 to 2.79 BL s^{-1} while time to fatigue at 97 cm s^{-1} ranged from 30 min to ≥4 h in samples of 24 larger post-smolts, which represents an appreciable variation in swimming capacity. However, RVM was not correlated with U_{crit}, and surprisingly, RVM was negatively correlated with fatigue time in the sustained swimming trial. Although a crude indicator for cardiac function on its own, larger RVM are, however, associated with thicker compact myocardium which improves coronary circulation and assists in contractile power in Atlantic salmon (Anttila et al. 2014). Still, larger RVM was not associated with improved swimming performance in the present study. Too few fish may have been assessed to obtain robust pat-

terns, or RVM may be less important in predicting swimming performance in larger Atlantic salmon.

Furthermore, K and W differences were also poor indicators of the observed variation in swimming performance within the size class tested here. Thus, the cause of variation in swimming performance is difficult to predict and is likely explained by numerous variables including cardio-respiratory traits. The relative role of various components in the swimming capacity variation in farmed Atlantic salmon deserves a more thorough and systematic assessment in future studies.

Implications for exposed aquaculture

The finding that farmed Atlantic salmon are able to sustain at least 80% U_{crit} for 4 h adds another important temporal dimension in the ongoing development of welfare guidelines for acceptable current velocities in exposed aquaculture. However, being forced to swim at intensities close to the sustainable limit chronically is not optimal in terms of production performance. When rainbow trout are swimming at 80% U_{crit}, blood flow is redistributed in systemic circulation to favour working muscles while blood flow to the liver, spleen and stomach is decreased (Randall & Daxboeck 1982). Continuous high-intensity aerobic swimming is therefore likely to inhibit digestion and growth (Farrell et al. 2001). This was recently demonstrated in Atlantic salmon post-smolts, where 6 wk of forced swimming at 1.5 BL s^{-1} had a significantly negative impact on growth rate (Solstorm et al. 2015).

Furthermore, an important environmental factor to consider is low temperatures, since strong current events are more likely to occur during winter. In striped bass *Morone saxatilis*, carp *Cyprinus carpio* and rainbow trout, white muscles were recruited at lower swimming speeds at lower temperatures, which reduced the maximum sustainable swimming speed (Sisson & Sidell 1987, Rome et al. 1990, Taylor et al. 1996). Similarly, U_{crit} was significantly reduced at 3 and 8°C compared to 13°C in Atlantic salmon, where reduced tail beat frequencies and earlier transition to burst and glide swimming at lower temperatures suggested earlier white muscle recruitment (Hvas et al. 2017). Since the present study was conducted at 13°C, the reported absolute values for sustainable swimming capacities are not representative of colder waters. Furthermore, it is unclear whether salmonids also are able to sustain ~80% U_{crit} aerobically in sub-optimal thermal environments.

Finally, the original 200 min definition for sustainable swimming (Beamish 1978) may be inadequate for welfare assessment in salmonid aquaculture. The aetiology of fatigue can be either the inability to supply sufficient metabolites (U_{crit} protocols) or exhaustion of metabolite supply (fixed velocity tests) (Jones 1982). Like marathon runners, fish could therefore eventually 'hit the wall' due to substrate depletion, despite swimming within their aerobic limit. Current velocities that can be endured aerobically for 200 min may therefore still result in fatigue if exposures last for several days. Future studies should therefore seek to define swimming capabilities during periods of days or weeks at intermediate current exposure.

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