Optimal swimming speeds reflect preferred swimming speeds of brook charr (*Salvelinus fontinalis* Mitchell, 1874)

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Abstract Several measures have been developed to quantify swimming performance to understand various aspects of ecology and behaviour, as well as to help design functional applications for fishways and aquaculture. One of those measures, the optimal swimming speed, is the speed at which the cost of transport (COT) is minimal, where COT is defined as the cost of moving unit mass over unit distance. The experimental protocol to determine the optimal swimming speed involves forced-swimming in a flume or respirometer. In this study, a 4.5-m-long tilted raceway with gradually increasing upstream water speed is used to determine a novel, behaviourally based swimming parameter: the preferred swimming speed. The optimal swimming speed and the preferred swimming speed of brook charr were determined and a comparison of the two reveals that the optimal swimming speed ($25.9 \pm 4.5 \text{ cm s}^{-1}$ or $1.02 \pm 0.47 \text{ bl s}^{-1}$) reflected the preferred swimming speed (between 20 cm s^{-1} or $0.78 \pm 0.02 \text{ bl s}^{-1}$ and 25 cm s^{-1} or $0.95 \pm 0.03 \text{ bl s}^{-1}$). The preferred

swimming speed can be advantageous for the determination of swimming speeds for the use in aquaculture studies.

Keywords Swimming behaviour · Brook charr · Optimal swimming speed · Preferred swimming speed · Raceway · Respirometry

Introduction

A number of swimming performance levels have been described for fishes: sustained, prolonged and burst (Beamish 1978). Each swimming level has its own energetic characteristics, but sustained and prolonged swimming are mainly powered by red aerobic muscles while burst swimming is powered by white anaerobic muscles (Beamish 1978). Aerobically powered swimming modes are used for volitional routine swimming, important in activities such as migration, foraging, courtship, agonistic interactions. (Beamish 1978; Videler 1993). They also constitute the largest portion of a fish’s energy budget (Brett 1964) and hence influence growth rates, energy available for reproductive effort, and in aquaculture, the amount of energy that can be transformed into fish meat. Such speeds are commonly small compared with the speed range of fishes and various measures of performance have been sought that pertain to such speeds.

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One such measure of performance at the low speed end of the spectrum at which volitional behaviour usually occurs is the optimal swimming speed defined at the speed at which the cost of transport (COT) is smallest (Tucker 1970). COT is in turn defined as the cost of moving unit mass over unit distance. Optimal swimming speed can be affected by various factors. Most commonly, U_{opt} is based on rates of oxygen consumption, and hence is affected by temperature, fish size, endothermy and other factors influencing standard metabolic rate (Weihs 1973a; Beamish 1978; Webb 2006; Tudorache et al. 2007a). Weihs (1973a) has also shown that net energy gain can be used in considering U_{opt} , when slightly different values are obtained reflecting an ecological factor, food density.

Because U_{opt} is a performance measure similar to speeds of fish during volitional activity, it has been used to evaluate the economics of routine activities and migration (e.g. Hinch and Rand 2000; Tudorache et al. 2007a; Palstra et al. 2008), behaviour maximizing net energy gain (Weihs 1973b) and hence is important in aquaculture in affecting growth for a given food intake (e.g. Totland et al. 1987; Christiansen et al. 1985; Davison 1997; Palstra et al. in prep.).

Several other measures of swimming performance are in common use, such as the critical swimming speed, U_{crit} , determined by forced-swimming increasing velocity tests (Brett 1964). However, there are both methodological difficulties in determining U_{crit} (e.g. Tudorache et al. 2007b; Peake and Farrell 2004) and conceptual uncertainties because of behavioural parameters that influence the results (Farrell 2007). The defining characteristic of speeds used in routine activities is, of course, that they are volitional, and hence, fish can choose the speed at which they swim. This leads to the concept that there are preferred speeds, U_{pref} , for fishes. For example, fishes in lotic situations typically choose locations within a small speed range and in lentic situations, swim for most of the time within a similar small speed range. U_{pref} is therefore a direct measure of performance relevant to behaviours central to fish ecology, and hence also to human-managed systems.

Therefore, we explored the use of U_{pref} as a volitional swimming speed, using a tilted raceway setup with gradually increasing upstream water speed to determine U_{pref} in a repeatable fashion (Peake and

Farrell 2004). We also compared U_{pref} with U_{opt} calculated from metabolic rate measured during forced-swimming tests in a Blazka-type respirometer.

Materials and methods

Fish

Brook charr (26.2 ± 0.6 cm, total length, L_T , mean $\pm$ SD, $N = 10$) were caught by means of angling with a barbless hook from a private fish pond (Nashwaak Village, New Brunswick, Canada). Upon transport to the aquaculture facilities at the University of New Brunswick (Fredericton campus, Fredericton, New Brunswick, Canada), they were kept in dechlorinated municipal water for 7–15 days prior to experimentation at 12.2°C (range $\pm 0.9^\circ\text{C}$) at a low current speed in the tanks ($0\text{--}10$ cm s^{-1}). Fish were fed a salmonid grower diet (Corey Feed Mills Ltd., Fredericton, NB, Canada) ad libitum. Fish fed and behaved naturally in captivity. The experiments were conducted between July and August, 2008.

Ten fish were used in both U_{pref} and U_{opt} trials. For five fish, U_{pref} was measured first followed by U_{opt} , and for the remainder, U_{opt} was determined before transfer to the tilted flume to determine U_{pref} . After a fish had completed both tests, each fish was anaesthetized in a 1% solution of tertiary amyl alcohol. Body mass and total length L_T were measured, averaging 200 ± 13 g and 26.2 ± 0.6 cm, respectively (mean $\pm$ SD).

Preferred swimming speed (U_{pref})

U_{pref} was determined in a Plexiglas raceway with gradually increasing water speed due to a 3.5° inclination (Fig. 1, see also Tudorache et al. 2010 for details). The raceway was 450 cm long, 12.5 cm wide and 50 cm deep. The 3.5° inclination resulted in an upstream water depth of 5 cm and water speed of 110 cm s^{-1} and a downstream water depth of 40 cm and speed of 10 cm s^{-1} . Water speed was measured every 10 cm (flow probe HFA-U276, Hoentzsch GmbH, Weiblingen, Germany) and showed a steady decrease towards the downstream end of the raceway. With the exception of the upstream 40 cm of the raceway, the water stream was free of turbulences, according to a dye test, which was performed by

Fig. 1 Water velocities at positions from start of flume (mean $\pm$ SD, $N = 3$)

dripping a few drops of ink in the water, and the turbulences noted in the upper 40 cm were minimal. The downstream end was fitted with a holding tank, 75 cm long, 50 cm wide and 50 cm deep (Fig. 2). Water was pumped from the downstream tank to the upstream end of the flume by means of a submersible pump (Alita Model PV-800; Aracadia, CA, USA). The total volume of water was 250 l. Water temperature was maintained at 15°C with an in-line chiller (Aqua Logic Model DS-7; San Diego, CA, USA) and dissolved oxygen concentration did not fall below 7.5 mg l⁻¹. Eight cameras (SNG SED-CAM-YC26S, Sharpe Electronics Corp., Osaka, Japan), connected to a digital video recorder (EDVR 16 D3, Everfocus, Taipei, Taiwan, see Tudorache et al. 2010 for comparison), were mounted ca 1 m below the

Fig. 2 Schematic three-dimensional drawing of the tilted raceway with downstream holding tank. The arrow indicates direction of the water flow

raceway so they could record images of a section of 70 cm with overlapping fields. A grid on the bottom over the entire length of the raceway facilitated orientation and scaling.

Fish were introduced to the downstream holding tank at the low velocity end of the raceway 16 h before the experiment. Access to the raceway was blocked with a grid. After the acclimation period, the grid was removed and fish locations and behaviour were recorded for the following 4 h. At the end of the experiment, fish were gently removed from the raceway by means of netting (hand net, 30 $\times$ 15 $\times$ 15 cm) for recovery prior to measuring U_{opt} or for mass and length measurement.

Video footage in mp4 format (25 fps) was analysed using the program ImageViewer (Everfocus, Taipei, Taiwan). Locations of the centre of mass (determined according to Tudorache et al. 2008) of each fish were recorded along the raceway. Swimming speeds (i.e. position holding against water speeds) were categorized in intervals of 5 cm s⁻¹ and indicated as $U \pm 2.5$ cm s⁻¹, so that, for example, all speeds between 7.75 and 12.25 cm s⁻¹ were categorized as 10 cm s⁻¹, between 12.5 and 17.5 as 15 cm s⁻¹, etc. If a fish spent more than 3 s within an interval, then it was defined as being swimming at a 'steady' speed. Shorter durations or variable ground speeds were defined as 'transient' associated with fishes changing location along the raceway. These observations resulted in time (min) spent swimming at specific current speed intervals.

The choice for 3 s as a threshold between steady and transient swimming behaviour is arbitrary. A different time interval would lead to different proportions of total time spent in steady and transient swimming. However, the distributions of time spent at different speeds would be resulting in similar values for U_{pref} .

Optimal swimming speed (U_{opt})

A 35 l Blazka-type respirometer (as described by Kutty and Saunders 1973) was used to determine U_{opt} . The inner tunnel (108 cm length $\times$ 12.8 cm diameter) served as a swim chamber in which the fish were contained by means of screens located at either end. Oxygen concentration of the water was measured with a probe (Oxyguard Standard Probe, Oxyguard

International A/S, Brikerød, Denmark) that was inserted in the outer tunnel connected to a data collecting system (Oxyguard Multichannel System) and data-logger system (Oxyguard Multilog) connected to a PC. Data were collected with Windows Hyperterminal.

Fish were allowed 2 h acclimation in oxygen-saturated ($>10 \text{ mg l}^{-1}$) flow-through water at 10 cm s^{-1} at 15°C after transfer into the inner tunnel. An acclimation of 2 h is sufficient for repeatable performance measures in increasing velocity trials (Farrell et al. 1998; Jain and Farrell 2003). After acclimation, oxygen consumption was measured from changes in dissolved oxygen levels over 20-min period when water throughput was turned off followed a 30-min period flushing period to replace the oxygen used. Oxygen levels never dropped below 7.5 mg l^{-1} . Oxygen consumption was measured at current speeds of 10, 20, 30, 40 and 50 cm s^{-1} imposed in random order to avoid a possible habituation effect on the results. However, direct observation of the fish in the swimming tunnel revealed an unstable swimming behaviour, characterized by deployment of pectoral fins, irregular position holding and exploring the tunnel, at 10 cm s^{-1} , therefore the $\dot{M}\text{O}_2$ data at 10 cm s^{-1} were not taken into account.

Various models have been used to describe the relationship between metabolic rate and swimming speed: linear, power and exponential (Webb 1997). Equations using various models were explored and that with largest r^2 was selected as that with the best fit. This was a polynomial function for these data: ($r^2 = 1$)

$$\dot{M}\text{O}_2 = aU^3 - bU^2 - cU + \text{SMR},$$

where $\dot{M}\text{O}_2$ is oxygen consumption rate ($\text{mg g}^{-1} \text{ h}^{-1}$), SMR is standard metabolic rate ($\text{mg g}^{-1} \text{ h}^{-1}$) and determined by extrapolating the curve to zero swimming speed (Tudorache et al. 2007a), U is swimming speed (cm s^{-1}) and a , b and c are constants.

COT was determined by dividing $\dot{M}\text{O}_2$ values by the swimming speed. The U_{opt} (m s^{-1} and bl s^{-1}), where the COT ($\text{mg O}_2 \text{ kg}^{-1} \text{ m}^{-1}$) reached a minimum (Tucker 1970), was determined by plotting the polynomial trend line through COT values versus swimming speeds per individual fish. The point on this trend line with the lowest COT (COT_{min}) was

calculated by setting the first derivative to zero (Palstra et al. 2008).

Statistics

Normality of the data used for analysis was determined by Kolmogorov–Smirnov tests. U_{pref} data $>5\%$ steady swimming time were compared with each other using one-way ANOVA ($P < 0.05$). U_{opt} and U_{pref} were compared with each other using the non-parametric Wilcoxon matched pairs test with a significance level of 0.05. Results are as means $\pm$ standard deviation (SD).

Results

Preferred swimming speed (U_{pref})

After opening the grid, fish spent about 10 min in the holding tank before entering the raceway. All fish tested entered the raceway eventually spontaneously, without external motivation. Then, the fish spent about 20–30 min exploring the raceway, especially upstream, and below the upstream water entrance where water flow was turbulent.

Fish spent $178.0 \pm 12.1 \text{ min}$ (mean $\pm$ SD; $73.6 \pm 4.4\%$ of the total time) at a steady speed and $63.6 \pm 10.2 \text{ min}$ ($26.3 \pm 4.4\%$ of the time) transitioning from steady swimming at various locations. Most time was spent at swimming speeds of the speed category of 20 cm s^{-1} ($0.78 \pm 0.02 \text{ bl s}^{-1}$) and 25 cm s^{-1} ($0.97 \pm 0.02 \text{ bl s}^{-1}$; each representing approximately 25% of the steady speed time, statistically not different, one-way ANOVA, $P > 0.05$), followed by 15 cm s^{-1} (10%) and 30 cm s^{-1} (5%) (Fig. 3). Fish did not swim at other speeds for more than 5% of the time spent in steady swimming; therefore, those data were not considered for analysis.

Optimal swimming speed (U_{opt})

After introduction in the respirometer, swimming at speeds of 10 cm s^{-1} , swimming was not steady for the entire period of swimming at 10 cm s^{-1} during which fish explored the respirometer. Only at a swimming speed of 20 cm s^{-1} did swimming behaviour become steady.

Fig. 3 The time (% total steady swimming time) spent swimming steadily plotted against clusters of swimming speeds of 5 cm s⁻¹ (see text for details). Letters indicate significant differences between values >5% of total steady time (one-way ANOVA, $P < 0.05$)

Figure 4 shows $\dot{M}O_2$ values plotted polynomially against swimming speeds. The best-fit equation revealing $\dot{M}O_2$ to U was the following: $\dot{M}O_2 = -0.0104U^3 + 1.010U^2 - 18.671U + 258.81$ ($r^2 = 1$; $P < 0.05$). COT_{min} at a U_{opt} averaged 25.9 ± 8.9 cm s⁻¹ (1.01 ± 0.35 bl s⁻¹) is 0.97 ± 0.06 mg g⁻¹ m⁻¹.

When comparing U_{opt} with the U_{pref} categories with the highest time values, i.e., 20 and 25 cm s⁻¹, Wilcoxon matched pairs test revealed a significant difference between U_{opt} and U_{pref} of 20 cm s⁻¹ ($P < 0.05$) but no difference between U_{opt} and U_{pref} of the speed category of 25 cm s⁻¹ ($P > 0.05$).

Discussion

This study sought to evaluate the utility of measuring preferred swimming speeds (U_{pref}) in comparison with the more common reference of optimal swimming speed (U_{opt}) for low-speed behaviours. U_{pref}

Fig. 4 Relative oxygen consumption ($\dot{M}O_2$) plotted against swimming speed of brook charr swimming in a confined respirometer. The fitting curve is provided by the polynomial function $\dot{M}O_2 = -0.0105U^3 + 1.006U^2 - 18.665U + SMR$ ($r^2 = 0.99$, $N = 10$) with U being swimming speed (cm s⁻¹) and SMR, the standard metabolic rate, has a value of 258.77 mg O₂ kg⁻¹ l⁻¹

chosen volitionally by fasted trout in the current speed gradient of the raceway was reflected by U_{opt} determined from metabolic rates measured during forced-swimming in a flume, which was within the range of U_{opt} found in salmonids of 10–29 cm body length at 15°C water temperature, i.e., U_{opt} of 1–2 body lengths s⁻¹ (Brett 1964; Webb 1971a, b). Additionally, in aquaculture, growth for various salmonids is maximized at a constant swimming speed of 1.5 bl s⁻¹ (Davison and Goldspink 1977; Jørgensen and Jobling 1993). Also, spontaneous activity data from migration and aquaculture studies at similar water temperatures and size classes suggest a range of speeds from 0.5 to 3 bl s⁻¹ (Cooke et al. 2000; Thorstad et al. 2004; Babaluk et al. 2001). This indicates that the calculated U_{opt} is not necessarily the only speed at which fish migrate (Standen et al. 2002) or swim in aquaculture facilities (Cooke et al. 2000).

The time spent swimming steadily is strongly skewed to lower speeds between 10 and 40 cm s⁻¹. The skew arises from a small cluster of speeds between 50 and 60 cm s⁻¹ which in practice represents less than 5% of the total time spent swimming

steadily. These speeds occurred primarily after fish first entered and explored the flume when initially they tended to explore the upstream end of the system. This was the area where flow tended to be more turbulent as noted during dye tests. The fish may have been attempting to use the energy in the eddies that comprise turbulence (Breder 1965; Webb 1998; Lupandin 2005), but found the scale was not well matched to their size (Webb et al. 2010; Webb and Cotel 2010). Thus, these observations were considered qualitatively different from those after the initial exploration and were excluded from the analysis. The resulting time intervals spent swimming steadily at various speeds were then normally distributed.

It can be objected that fish chose a specific location along the raceway not for the water speeds encountered but for the water depths. Unpublished observations during a pilot study to another published research using the same set-up (Tudorache et al. 2010) revealed that smaller brook charr (ca. 12 cm L_T) were showing the same behaviour of settling at a certain swimming speed after exploring the raceway. When altering the water discharge of the pump and therefore the water speeds at different locations along the raceway, fish chose similar speeds, independent of water depth, which remained always the same due to the inclination of the raceway. This observation gave the original idea to the present study. Therefore, it is unlikely that the specific position along the raceway was chosen for its water depth.

The results show that for the determination of U_{opt} speeds below 20 cm s⁻¹ could not be used due to unsteady swimming behaviour of the fish. Direct observation of the swimming behaviour at such low speeds suggested that velocities were too low to be held in steady swimming mode, and the fish was confined in too small space to fully express volitional swimming behaviour. The described erroneous swimming behaviour, involving deployment of pectoral fins, irregular position holding etc., can be interpreted as a reaction to this situation. Therefore, the usefulness of U_{opt} , conceptually an ecologically important reference speed, is diminished because of the low sensitivity to speeds in the range seen during routine activity, foraging and migration. Linear swimming at such low speeds in limited space can be obstructed by their own unsteady nature and reduce the reliability of the results. Alternatively, U_{pref} , as measured in the

present study, is based on volitional swimming behaviour at a variety of velocities. Also, space is not a restrictive factor. Hence, U_{pref} may be a preferable measure for swimming speeds in the field and aquaculture facilities. However, the method applied in the present study reveals a very broad result of U_{pref} , i.e., a value spanning from 17.5 to 27.5 cm s⁻¹ as the speed categories of 20 and 25 cm s⁻¹ are approximations ± 2.5 cm s⁻¹. A more accurate result could be obtained using next to the present set-up an automated cine installation, similar to the one used by Tudorache et al. (2009), where swimming speeds and resting times/positions can be detected automatically. This could facilitate the process of data collection and make the resulting U_{pref} more accurate.

There is growing awareness among that forced-swimming tests are influenced by fish behaviour (see Farrell 2007, for a review). For example, Peake and Farrell (2004) showed that swimming smallmouth bass (*Micropterus dolomieu*; 24–38 cm fork length) reach a much higher gait transition speed (U_{gt}) when swimming freely up a 50 m long raceway compared with U_{crit} values obtained from a forced swim tunnel experiment. Similarly, Tudorache et al. (2007b) showed that U_{crit} of common carp (*Cyprinus carpio*; 5–26 cm standard length) in swimming tunnels is influenced by tunnel length. Taken together, these data indicate that tests of performance with fewer constraints on behaviour provide results more relevant to understanding fish biology, and applying results to managed systems such as in aquaculture. Given the recognized relationship between exercise and optimum growth and condition in cultured fish, whether for stocking programs or meat production (Davison 1997; McDonald et al. 1998), the results of this study suggest a biomechanical and behavioural basis contributing at least in part to for these observations.

Perspectives

Rearing aquaculture fish under exercise conditions improves growth and food conversion efficiencies and thus leads to better economic returns (Davison 1997). It enhances muscle growth (Davison and Goldspink 1977; Johnston and Moon 1980; Totland et al. 1987) and flesh quality (Totland et al. 1987; Tsuchimoto et al. 1988), reduces aggressive

interactions between fish (Adams et al. 1995; Christiansen and Jobling 1990; Christiansen et al. 1991, 1992; East and Magnan 1987; Jobling et al. 1993) and leads to a reduction in stress response (Woodward and Smith 1985; Young and Cech 1993, 1994). It is advisable to keep water speeds applied in aquaculture facilities near U_{opt} , as U_{opt} is the swimming speed with the lowest COT (Videler 1993). However, there is no indication, yet, that fish given the choice between swimming speeds would volitionally chose for swimming velocities near U_{opt} , the U_{pref} , a fact that is confirmed by the present study.

Volitional swimming tests have been shown to be a good alternative to forced-swimming tests, due to the effect of the forced character on the results (see Farrell 2007 for a review). The present study presents an alternative measurement of U_{opt} , merely based on behavioural observation. It is less invasive as traditional U_{opt} tests and based on volitional swimming instead of the traditional forced-swimming tests. This volitional swimming test can be used to compare different species, strains, size classes or ploidies, in order to find perfect rearing conditions for aquaculture fish. Also, it can be argued biomechanically that different muscle types have different optimal swimming speeds for growth (Davison 1997). Therefore, it would be advantageous to present cultured fish with the opportunity of choosing between different water speeds. During the present study, fish in the raceway chose one speed interval at which they remained steady, for the longest period during the observation time of 6 h. However, this is only a short-time window, and it is possible that other speeds would have been chosen, depending on the time of the day, feeding regime, rearing density and other factors typical for an aquaculture environment. Additionally, it has been shown by Weihs (1973a) that U_{opt} , measured in a traditional way using forced-swimming tests, depends strongly on physiological and environmental conditions, and in the recent past behavioural, factors are increasingly made responsible for physiological parameters of fish swimming (Farrell 2007).

When building aquaculture facilities, a variation of water velocities can be presented for fish to choose. Possibly, a tilted rearing tank can be considered, based on the design of the flume in the present study. Different positions with similar water velocities, including dead zones, turbulent zones and high velocity zones within these tanks can help to reduce

agonistic behaviour and lead to a more efficient and less stressful rearing situation for aquaculture fish. The results can be a significant increase in flesh quality and therefore economically interesting.

In conclusion, this study presents a new, volitional-based swimming speed, the preferred swimming speed, which should be explored in more detail in future studies and which can be taken into account for the improvement of aquaculture applications.

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