

RESEARCH ARTICLE

Rainbow trout provide the first experimental evidence for adherence to a distinct Strouhal number during animal oscillatory propulsion

Robert L. Nudds*, Emma L. John, Adam N. Keen and Holly A. Shiels

ABSTRACT

The relationship between tail (or wing) beat frequency (f_{tail}), amplitude (A) and forward velocity (U) in animals using oscillatory propulsion, when moving at a constant cruising speed, converges upon an optimum range of the Strouhal number ($St=f_{\text{tail}} \cdot A/U$). Previous work, based on observational data and supported by theory, shows St falling within the broad optimum range ($0.2 < St < 0.4$) and considers this adequate to indicate its importance in governing wing or tail kinematics. This study presents the first evidence using an experimental manipulation that supports the importance of maintaining kinematics at a single optimum (or preferred) St . The tail beat kinematics of rainbow trout, *Oncorhynchus mykiss*, were disturbed by increasing water temperature (T_{water}) from 11 ± 1 to $20 \pm 1^\circ\text{C}$. Elevated T_{water} increased f_{tail} and decreased A , whilst St at any given U was conserved. St increased with U , driven by concomitant increases in A , whilst f_{tail} was unaffected by U . An increase in T_{water} also increased basal metabolic costs, but did not affect the incremental increase in metabolic cost with increasing U . Predicted future changes to T_{water} of lakes and rivers ($5\text{--}10^\circ\text{C}$ over the next 100 years) may not present major locomotory problems to salmonids.

KEY WORDS: Fish, Locomotion, Respirometry, Salmonid, Swim flume, Swimming

INTRODUCTION

The relationship between movement and forward velocity (U) in animals moving at a constant cruising speed using oscillatory propulsion is thought to converge upon an optimum range of a dimensionless parameter, the Strouhal number (St) (Nudds et al., 2004; Taylor et al., 2003; Triantafyllou et al., 1993). Geometrically similar organisms moving in dynamically similar ways should converge on a single St and it is intuitive to expect that number to relate to efficiency of movement. St is defined as:

$$St = \frac{f_{\text{tail}} \cdot A}{U}, \quad (1)$$

where, for fish, f_{tail} is tail beat frequency (Hz), A is peak-to-peak stroke amplitude of the tail tip (m), and U is equal to swimming speed (m s^{-1}), which are representative of vortex shedding frequency, wake width and free-stream velocity, respectively. St appear to peak within $0.2 < St < 0.4$ for both swimming and flying animals (Taylor et al., 2003; Triantafyllou et al., 1993; Triantafyllou et al., 1991), indicating that animals are evolutionarily constrained

to a narrow optimum range for high propulsive efficiency. A closer look at the data and subsequent measurements (Rohr and Fish, 2004), however, shows that the range of St measured in animals varies considerably. Indeed, the optimum range of $0.2 < St < 0.4$ is actually a large target in itself. Of course, the broader the range of organisms, the less geometrically similar they are; therefore, it is not surprising that variations in St are evident across taxa. In fish and cetaceans, St appears to change with body size (Eloy, 2012; Kayan et al., 1978). St also differs between animals depending on whether they are mainly thrust producers (such as most fish and insects) or also need to produce lift as in birds (Nudds et al., 2004; Taylor et al., 2003). St also varies with U , generally decreasing with increasing U in fish (Hunter and Zweifel, 1971; Lauder and Tytell, 2005; Webb, 1971), birds (Tobalske et al., 1999) and bats (Lindhe Norberg and Winter, 2006). In contrast, Tytell (Tytell, 2004) found that eels, *Anguilla rostrata*, maintained a constant St across a range of speeds. All previous work on animal St , however, is observational (Eloy, 2012; Nudds et al., 2004; Taylor et al., 2003; Triantafyllou et al., 1993; Triantafyllou et al., 1991); there is no evidence for an organism adhering to a given St when its kinematics are directly manipulated. Therefore, whether St is really an important governor of oscillatory propulsion kinematics and, hence, the explanations for variation in the measured values valid, is not certain.

Reproductive success for many salmonid species depends on completion of a return migration to natal riverine spawning grounds (Farrell et al., 2008; Finstad et al., 2005). During these migrations, fish cope with changes in salinity, water temperature (T_{water}) and water speed (Hodgson and Quinn, 2002; Klemetsen et al., 2003). Elevated T_{water} linked to climate change, however, is thought to be having a negative impact on migration success in some river systems (Karppinen et al., 2002; Laine et al., 2002; Thorstad et al., 2008). Reports show that salmon temporarily cease migration in water over 21°C (Farrell et al., 2008), and there is no evidence of successful migrations being established by a population at a temperature in excess of 19°C (Hodgson and Quinn, 2002). Fish are ectotherms, so increased T_{water} elevates metabolic rate, resulting in a reduced aerobic capacity (the difference between maximum and minimum metabolic rate) (Farrell, 2009; Wang and Overgaard, 2007). Because locomotion is energetically costly, the reduced aerobic scope at warm temperatures, coupled with a decreased oxygen carrying capacity of water, may have implications for the biomechanical efficiency of swimming.

Rainbow trout, *Oncorhynchus mykiss* (Walbaum 1792), are subcarangiform swimmers relying on oscillations of their tail (caudal fin) driven by muscle to produce thrust for forward propulsion. It is well established that vertebrate skeletal muscle function is affected by temperature, with Q_{10} reported to range from 1.5 to 3.0 (Bennett, 1984; James, 2013), and, as fish are ectotherms, changes to T_{water} will directly affect muscle temperature (Johnston and Temple, 2002;

Faculty of Life Sciences, University of Manchester, Manchester M13 9PT, UK.

*Author for correspondence (robert.nudds@manchester.ac.uk)

Received 9 January 2014; Accepted 20 March 2014

List of symbols

A	peak-to-peak stroke amplitude of the tail tip
f_{tail}	tail beat frequency
l_{body}	body length
M_b	fish body mass
St	Strouhal number
T_{opt}	optimum temperature
T_{water}	water temperature
U	forward velocity (swimming speed)
U_{crit}	maximum aerobic swimming speed of the fish
V	swim tunnel volume
V_m	fish volume
\dot{V}_{O_2}	rate of oxygen consumption

Rome et al., 1984). Previous studies have shown tail beat kinematics to be affected by T_{water} changes (Stevens, 1979). Consequently, T_{water} manipulations may provide a potential mechanism for experimentally testing the importance of adherence to a given optimum St , as well as being of importance in identifying the effects of temperature upon migratory swimming ability.

In the present study, \dot{V}_{O_2} (rate of oxygen consumption) and tail beat kinematics were quantified in rainbow trout swimming at two temperatures over a range of increasing U . Using the same individuals of a single species in both temperature treatments obviates the aforementioned variation in St that is due to body size, species and U . The hypotheses tested were that the St used at a given U would not be affected by temperature, as the fish would strive to maintain optimum swimming kinematics. St may vary across U , however, and of course, whether this hypothesis is truly tested was also dependent upon an observable change in kinematics. The second hypothesis was that the metabolic stress caused by the increased T_{water} would lead to an increase in \dot{V}_{O_2} , which would be more marked at higher, more physiologically demanding speeds.

RESULTS

St increased with U , but did not differ between temperature treatments across all speeds (Fig. 1, Table 1). The increase in St with U based upon the lines of best fit from the GLM (Fig. 1A) was slight, however, being 0.19 for both treatments at 0.68 m s^{-1} , and 0.22 and 0.23 at 1.11 m s^{-1} for control and warm treatments, respectively (Fig. 1A).

A increased concomitantly with, and at the same incremental rate as, U in both treatments (Fig. 1B). A , however, was higher (by 4 mm) in the control group at all speeds. A did not differ between individual fish (Table 1). In contrast, f_{tail} was not affected by U , but was higher in the warm temperature treatment ($4.70 \pm 0.08 \text{ Hz}$) than in the control treatment ($4.17 \pm 0.09 \text{ Hz}$) (Table 1). f_{tail} also varied among individual fish. The increased St with U is therefore modulated through an increase in A . The warm temperature induced a change in fish kinematics whereby St was maintained at control temperature levels through a trade-off between f_{tail} , which was increased, and A , which was decreased.

\dot{V}_{O_2} increased with increasing U at the same incremental rate in both treatments (Table 1). \dot{V}_{O_2} , however, was higher at all speeds in the warm temperature treatment than at the control temperature (Fig. 2). The same absolute increase across all speeds at the warm temperature suggests that the increased metabolic cost is focused on basal processes and not necessarily swimming locomotion per se. \dot{V}_{O_2} differed between individual fish (Table 1).

Fore–aft positional change (accelerations) within the working section was small for both T_{water} treatments (means were 0.005 ± 0.001 and $0.003 \pm 0.001 \text{ m s}^{-2}$ for control and warm

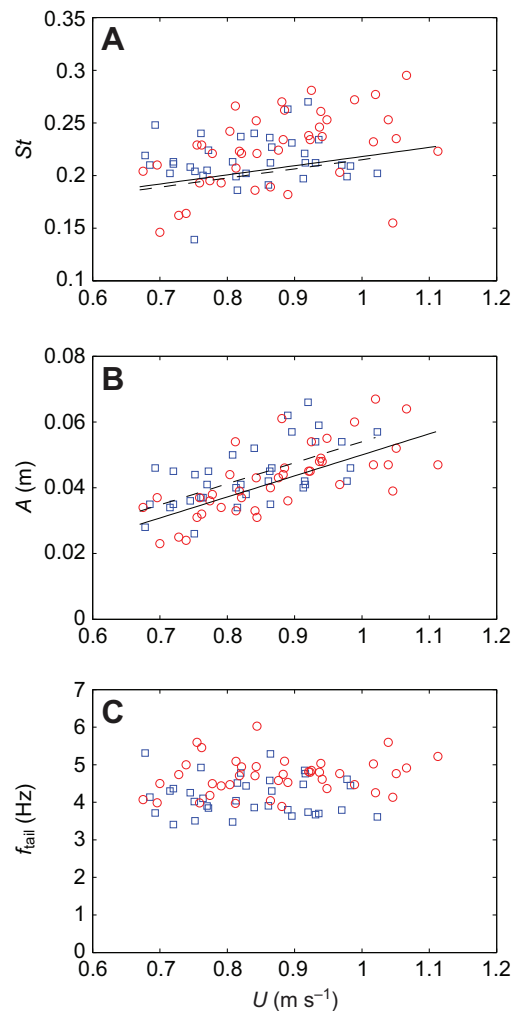


Fig. 1. Scatter plots of kinematics parameters against swimming speed (U). Blue squares and dashed lines represent the cold temperature data, and red circles and solid lines represent the warm temperature data. (A) For Strouhal number (St), the lines of best fit calculated from the general linear model (GLM) are $y=0.128+0.087x$ and $y=0.131+0.087x$ for cold and warm temperature data, respectively. (B) For tail beat amplitude (A), the lines of best-fit calculated from the GLM are $y=-0.010+0.064x$ and $y=-0.014+0.064x$ for cold and warm temperature data, respectively. (C) There was no predictable relationship between tail beat frequency (f_{tail}) and U .

temperatures, respectively). Furthermore, there was no interaction effect between T_{water} and U ($F_{1,65}=0.80$, $\eta_p^2<0.01$, $P=0.375$) on the accelerations during the recorded swimming bouts, and they did not differ between fish, T_{water} treatment or with U (fish, $F_{7,66}=1.44$, $\eta_p^2=0.13$, $P=0.204$; T_{water} , $F_{1,66}=0.909$, $\eta_p^2=0.01$, $P=0.344$; U , $F_{1,66}=3.34$, $\eta_p^2=0.05$, $P=0.072$). Hence, fore–aft positional change was both minimal and consistent throughout all of the experimental trials. This, coupled with the fact that data were only collected when the fish remained in the centre of the working section, means that the fish were swimming at a steady and near-constant U .

DISCUSSION

As hypothesised, when the locomotor system of the trout was disturbed, they adhered to the same St at any given U (Fig. 1A). Which variable the temperature directly affected (Fig. 1B,C) is not evident, but St was maintained through a trade-off between an increase in f_{tail} and decrease in A . Nonetheless, this is the first experimental (involving a manipulation) evidence for an apparent

Table 1. Statistical output from the general linear models (GLMs) for each of the three kinematic measures and the rate of oxygen consumption

y	Removed terms	Final GLM
St	$T_{\text{water}} \times U$, $F_{1,65}=3.21$, $\eta_p^2=0.05$, $P=0.078$	T_{water} , $F_{1,66}=0.25$, $\eta_p^2<0.01$, $P=0.618$ Fish, $F_{7,66}=2.47$, $\eta_p^2=0.21$, $P=0.026$ U , $F_{1,66}=7.01$, $\eta_p^2=0.10$, $P=0.010$
A	$T_{\text{water}} \times U$, $F_{1,65}=0.07$, $\eta_p^2<0.01$, $P=0.791$	T_{water} , $F_{1,66}=5.94$, $\eta_p^2=0.08$, $P=0.018$ Fish, $F_{7,66}=1.32$, $\eta_p^2=0.12$, $P=0.253$ U , $F_{1,66}=38.86$, $\eta_p^2=0.37$, $P<0.001$
f_{tail}	$T_{\text{water}} \times U$, $F_{1,65}=0.79$, $\eta_p^2=0.01$, $P=0.376$ U , $F_{1,66}=1.47$, $\eta_p^2=0.02$, $P=0.230$	T_{water} , $F_{1,67}=22.70$, $\eta_p^2=0.25$, $P<0.001$ Fish, $F_{7,67}=2.24$, $\eta_p^2=0.19$, $P=0.041$
\dot{V}_{O_2}	$T_{\text{water}} \times U$, $F_{1,48}=2.90$, $\eta_p^2=0.06$, $P=0.095$	T_{water} , $F_{1,49}=72.24$, $\eta_p^2=0.60$, $P<0.001$ Fish, $F_{7,49}=7.87$, $\eta_p^2=0.53$, $P<0.001$ U , $F_{1,49}=112.29$, $\eta_p^2=0.70$, $P<0.001$

Removed terms are presented in order of deletion from the GLMs.

y, dependent variable; St , Strouhal number; A , tail-beat amplitude; f_{tail} , tail-beat frequency; \dot{V}_{O_2} , rate of oxygen consumption; U , swimming speed; T_{water} , water temperature.

adherence to a preferred (perhaps optimum) St for an animal using oscillatory propulsion. At both temperatures, a slight increase in St with U was driven by increases in A , whilst f_{tail} was constant across all velocities. Invariant f_{tail} suggests that muscle contraction frequency may be optimised within very narrow bounds (James, 2013), with the centre of these bounds increasing with temperature (Fig. 1C). The contractile properties of vertebrate muscle function are widely agreed to show high temperature dependence (Bennett, 1984; James, 2013), and muscle contraction kinetics are slowed and maximum power output of red muscle decreased at lower temperatures in a number of bony fish and shark species (Altringham and Block, 1997; Bernal et al., 2005; Bernal and Sepulveda, 2005; Bernal et al., 2009; Donley et al., 2012; Donley et al., 2007; Shadwick et al., 2004).

An invariant f_{tail} and increasing A with increasing U is contrary to previous findings. Earlier work in fish suggests that f_{tail} is modulated (increased) whilst A remains constant with increasing U (Bainbridge, 1958; Hunter and Zweifel, 1971; Rome et al., 1990; Rome et al., 1984; Stevens, 1979; Tytell, 2004; Webb, 1971), although at very low speeds A may also be modulated (Bainbridge, 1958; Webb, 1971). A similar increasing f_{tail} and invariant A with U was also found across seven species of cetaceans (Rohr and Fish, 2004). In birds, f_{wing} also appears to increase with U , but A decreases with U [e.g. see table 2 in Tobalske et al. (Tobalske et al., 1999)].

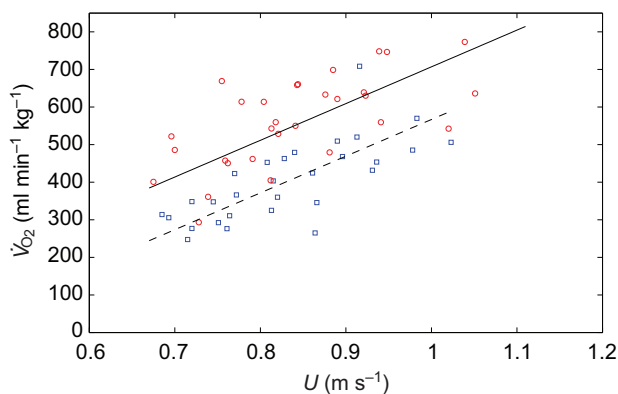


Fig. 2. Rate of oxygen consumption (\dot{V}_{O_2}) plotted against swimming speed (U) for cold temperature (blue squares) and warm temperature (red circles) treatments. The lines of best fit calculated from the GLM output are $y=-410.33+977.10x$ and $y=-270.27+977.10x$ for cold (dashed line) and warm (solid line) temperature data, respectively.

There are, however, many differences between the present study and those previously conducted: the specification and design of the flume, the method for persuading the fish to swim (light versus electric grid), the camera resolution and the species studied. For example, the cetaceans were swimming freely around a large elliptical pool, in a broad range of temperatures from 12 to 20°C and were cajoled into swimming at maximum U , which may not be their preferred cruising speed (Rohr and Fish, 2004). Also, it is intuitive to expect differences in tail beat kinematics across species, relating to habitat (i.e. still water versus flowing water species) and swimming form (i.e. carangiform, sub-carangiform, anguilliform or thunniform). Therefore, without a multi-species study under standardised conditions, which remains a priority for future work, it is perhaps premature to speculate at length about the incongruence in speed effects on tail-beat kinematics.

The majority of calculated St for the rainbow trout were between 0.20 and 0.40, within the hypothesized optimum range for high propulsive efficiency (Triantafyllou et al., 1993). Nevertheless, several values fell below the optimum range (Fig. 1). Thrust, however, is still produced outside of the optimum range, albeit with a much reduced propulsive efficiency (Anderson et al., 1998; Barrett et al., 1999; Read et al., 2003; Triantafyllou et al., 1991). Perhaps the low St recorded here were due to unpreferred kinematics resulting from stress effects. St was previously shown to decrease with U , ranging from 0.45 to 0.30 in rainbow trout (Webb, 1971) and ~0.41 to 0.30 in jack mackerel (Hunter and Zweifel, 1971), and was found to be independent of U in seven species of cetacean (Rohr and Fish, 2004), which is contrary to the findings of the present study. Previous studies on temperature change and fish tail kinematics are limited and the effects are not consistent, which again may be species dependent. For example, increased T_{water} increased f_{tail} in bass (Stevens, 1979), decreased f_{tail} in rainbow trout (Stevens, 1979) and had no effect on f_{tail} in carp, *Cyprinus carpio* (Rome et al., 1990). T_{water} also did not affect A in carp (Rome et al., 1990). Therefore, although the previous data for rainbow trout (Webb, 1971) are contrary to the findings of the present study, those for bass are congruent (Stevens, 1979). Again, these differences are likely to be species specific, as a result of different data analysis approaches or differences in methodology. Indeed, A is generally chosen as a proxy for wake width. Although this is a reasonable assumption, it is likely that tail shape and other kinematic parameters (for example, the phase angle between tail heave and pitch) will subtly affect the relationship between A and wake width, which in turn would lead to differences in St calculations between species. If hydrodynamics

dominate, however, then for an individual fish, St should not vary as significantly as other parameters, as shown in this present study.

\dot{V}_{O_2} increased with U and was higher at the higher T_{water} treatment (Fig. 2). The incremental change in \dot{V}_{O_2} with U was similar at both T_{water} values and, therefore, the hypothesised greater increase in \dot{V}_{O_2} at higher T_{water} was not observed. The increased metabolic costs at increased T_{water} appear to be a consequence of an increase in basal/routine processes. An increase in \dot{V}_{O_2} with increasing U until U_{crit} – defined as the maximum aerobic swimming speed of the fish (Jain et al., 1997) – is in agreement with previous studies (Brodeur et al., 2001; Gamperl et al., 2002; Steinhausen et al., 2008). Furthermore, acute temperature changes (increasing T_{water} by a rate of 2°C h^{-1}) leading to increased \dot{V}_{O_2} is well documented (Altimiras et al., 2002). Here, \dot{V}_{O_2} continued to rise towards U_{crit} , instead of levelling off at high U (Gamperl et al., 2002; Thorstad et al., 2008). This result may be explained if the fish were not fully reaching U_{crit} . Indeed, fish refusing to swim at U_{crit} is frequently reported in swim flumes that do not employ electric grids (Rodnick et al., 2004).

Swimming performance also appeared to be influenced by T_{water} , with faster top speeds being measured at higher T_{water} in five out of eight fish (Fig. 2), which is in agreement with previous work (Farrell, 2002; Rome et al., 1990; Rome et al., 1984; Taylor et al., 1997). This finding suggests that warmer T_{water} may aid swimming performance, at least within the thermal tolerance zone of the fish.

In conclusion, rainbow trout at any given U adhered to the same St , even though their tail beat kinematics were disrupted by a T_{water} change. This is the first experimental evidence for the potential importance of maintaining kinematics at a single optimum (or preferred) St . An increase in T_{water} did increase basal metabolic costs, but contrary to hypothesised, it did not affect the incremental cost (changes in \dot{V}_{O_2} with U) of swimming. It would appear that rainbow trout, and perhaps other fish species, possess the plasticity to maintain their movement patterns at a biomechanical optimum when faced with thermal adjustments to muscle function and increases in basal energy expenditure. In fact, marginal increases in T_{water} may actually improve swimming performance in terms of the top speed attainable, which may be advantageous for migration, foraging or predator avoidance. Furthermore, future predictions of changes to T_{water} of lakes and rivers are only $5\text{--}10^\circ\text{C}$ over the next 100 years (Sharma et al., 2007), and it appears that rainbow trout, at least, can cope with this easily in terms of swimming biomechanics.

MATERIALS AND METHODS

Ethics statement

All experimental procedures were covered by a UK Home Office project licence (40/3584) held by H.A.S. and were under the ethical approval of the University of Manchester.

Fish

Eight sexually immature female rainbow trout (mean length= 0.29 ± 0.003 m, mean body mass= 262.20 ± 0.03 g) (Chirk Trout Farm, Wrexham, UK) were housed on a 12 h:12 h dark:light cycle in aerated 500 l re-circulated freshwater tanks at $11\pm 1^\circ\text{C}$. Temperature, pH, ammonia and nitrate levels were closely monitored and 30% water changes were conducted every 3 days. Fish were fed to satiation on commercial trout pellets three times a week, but were fasted for 24 h prior to experimentation. All husbandry and housing conditions were in accordance with the local handling protocols and adhere to UK Home Office legislation.

Respirometry

\dot{V}_{O_2} was measured using stop-flow respirometry in a Brett-style swim flume respirometer (~ 67.2 l volume; Loligo Systems, Denmark). Water velocity (equal to U) was calibrated using a handheld HFA flow meter (Höntzsch

GmbH, Germany) and U was measured in the centre of the working section ($0.17\times 0.17\times 0.65$ m) of the flume. Water oxygen content was measured with a fibre-optic oxygen meter (model FIBOX 3 LCD, PreSens, Germany) and a temperature-calibrated dipping probe, situated in the respirometry chamber of the swim tunnel and connected to a PC running OxyView[®] software (LCDPST3 V1.16). Logger Pro[®] (Version 3.4; Vernier Software and Technology, USA) was used to calculate the rate of decline in O_2 content ($\text{mg } O_2 \text{ l}^{-1} \text{ min}^{-1}$) by fitting a linear regression to the O_2 -time data. \dot{V}_{O_2} was then calculated using the formula:

$$\dot{V}_{O_2} = \frac{\text{Rate of } O_2 \text{ decline} \cdot (V - V_m) \cdot 60}{M_b}, \quad (2)$$

where V is swim tunnel volume (l), V_m is fish volume (assuming $1 \text{ kg}=1 \text{ l}$ of water) and M_b is fish body mass (kg).

Kinematic data collection

Tail beat kinematics were captured using an HDR-SR8E (Sony, Japan) video camera filming at $100 \text{ frames s}^{-1}$ positioned on a tripod above the working section so that the sensor plane was parallel to the water surface. The working section was briefly illuminated by a single halogen lamp during filming. To determine A , the position of the tail tip was digitized and tracked using Tracker 4[®] video analysis software (Open Source Physics, Java framework). Data were only collected from fish that were swimming in the centre of the working section. U was adjusted to account for fore-aft positional variations within the working section between the beginning and end of the video clip. No corrections to U were made to account for either fish buoyancy or blockage effects. Of course, these were the same in both treatments so do not compromise the validity of the comparison between the two temperature treatments.

Experimental protocol

Experiments were conducted on individual fish over the course of 3 weeks. Experiments were run on all fish at $11\pm 1^\circ\text{C}$, which was also the acclimation (control) temperature and then at $20\pm 1^\circ\text{C}$. This temperature was chosen because 20°C is below the critical thermal maximum for rainbow trout, but above optimum temperature (T_{opt}) and thus should cause a reduction in their aerobic capacity (Farrell, 2009) and affect swimming kinematics. All aspects of the respirometry and kinematic evaluation were kept constant between the two temperatures.

Fish were netted from the holding tank and transferred into the swim flume respirometer. Fish length was measured so that speed increments relative to each individual's body length (l_{body} ; m) could be calculated as l_{body}/U . l_{body} increments were used to keep individual fish effort constant, but actual U (0.28 m s^{-1} to 1.11 m s^{-1}) was used in the data analyses. Note that slight changes in water viscosity between the two temperatures (~ 1.2 and 1.0 mPa s at 11 and 20°C , respectively) were unlikely to have any effects on the fish (Danos and Lauder, 2012).

Fish were then held in the respirometer for 12 h prior to the start of the swimming speed trial. During this period, U was maintained at 0.28 m s^{-1} ($\sim l_{\text{body}} \text{ s}^{-1}$) to provide a current for the fish to orientate towards whilst remaining quiescent and to ensure continuous mixing within the respirometer. For experiments at 20°C , the fish was placed in the swim flume at $11\pm 1^\circ\text{C}$ and the water was gradually heated to $20\pm 1^\circ\text{C}$ over the 12 h period prior to the start of the swimming trial. Water oxygen saturation in the swim tunnel was always maintained at $>90\%$ by air stones positioned in the reservoir.

For the swimming trial, the fish was subjected to a ramp increase in U , where U was increased from $l_{\text{body}} \text{ s}^{-1}$ (resting) in increments of $0.0033 l_{\text{body}} \text{ s}^{-1}$ until the fish was swimming at a rate of $2.5 l_{\text{body}} \text{ s}^{-1}$, which is approximately 70–75% of U_{crit} . Studies have shown that fish swimming at 70–75% of U_{crit} have a near-maximal aerobic capacity (Lee et al., 2003; Steinhausen et al., 2008). U was then increased at a rate of $0.2 l_{\text{body}} \text{ s}^{-1}$ every 30 min until exhaustion (indicative of U_{crit}). Kinematics and \dot{V}_{O_2} were recorded at each U . Exhaustion was defined as the point at which the fish stopped swimming, and did not respond to a bright light stimulus by recommencing swimming. At the point of exhaustion, U was decreased to $l_{\text{body}} \text{ s}^{-1}$ and after an hour of recovery the fish was removed from the respirometer and weighed to determine M_b .

Data analyses

The data distribution of each of the kinematics variables did not differ from normality (Shapiro–Wilk test): St ($W=0.985$, $n=76$, $P=0.535$), A ($W=0.978$, $n=76$, $P=0.214$), f_{tail} ($W=0.984$, $n=76$, $P=0.431$) and \dot{V}_{O_2} ($W=0.972$, $n=59$, $P=0.185$).

Possible effects of the two temperature (T_{water}) treatments (warm and control) upon the kinematics variables (and fore–aft positional change within the working section) were investigated using general linear models (GLMs). T_{water} was included as a factor, individual fish as a random factor and U as a covariate. Individual was included in the GLM because of the repeated measures taken for each fish. Although all the fish swam at a range of U values in both temperature treatments, the number of increments varied, rendering the data unsuitable for a repeated-measures model. The interaction term $T_{\text{water}} \times U$ was included to test for differences in the slope of the relationship between the kinematics variable and U . If not statistically significant, the interaction term ($T_{\text{water}} \times U$) was removed from the final GLM.

All statistical analyses were performed using IBM® SPSS® Statistics v.20 and means are displayed \pm s.e.m. In some cases within the GLMs unequal group variances were encountered. In these cases, SPSS implements a Satterthwaite's correction of the denominator degrees of freedom and it is this value that is noted in the statistical outputs in the subsequent text (Table 1).

Acknowledgements

The authors would like to thank Prof. Pat Butler, University of Birmingham, for the generous donation of the swim-flume respirometer. We would also like to thank two anonymous reviewers for their helpful comments on an earlier version of the manuscript.

Competing interests

The authors declare no competing financial interests.

Author contributions

R.L.N. and H.A.S. were involved in conception, design and execution of the study, interpretation of the findings, and drafting and revision of the manuscript. E.L.J. and A.N.K. conducted the study, and were involved in interpretation of the findings and drafting and revising the manuscript.

Funding

A University of Manchester Investing in Success Award to H.A.S. supported the study, and provided funds for swim-flume peripherals.

References

- Altimiras, J., Axelsson, M., Claireaux, G., Lefrancois, C., Mercier, C. and Farrell, A. P. (2002). Cardiorespiratory status of triploid brown trout during swimming at two acclimation temperatures. *J. Fish Biol.* **60**, 102–116.
- Altringham, J. D. and Block, B. A. (1997). Why do tuna maintain elevated slow muscle temperatures? Power output of muscle isolated from endothermic and ectothermic fish. *J. Exp. Biol.* **200**, 2617–2627.
- Anderson, J. M., Streitlien, K., Barrett, D. S. and Triantafyllou, M. S. (1998). Oscillating foils of high propulsive efficiency. *J. Fluid Mech.* **360**, 41–72.
- Bainbridge, R. (1958). The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *J. Exp. Biol.* **35**, 109–133.
- Barrett, D. S., Triantafyllou, M. S., Yue, D. K. P., Grosenbaugh, M. A. and Wolfgang, M. J. (1999). Drag reduction in fish-like locomotion. *J. Fluid Mech.* **392**, 183–212.
- Bennett, A. F. (1984). Thermal dependence of muscle function. *Am. J. Physiol.* **247**, R217–R229.
- Bernal, D. and Sepulveda, C. A. (2005). Evidence for temperature elevation in the aerobic swimming musculature of the common thresher shark, *Alopias vulpinus*. *Copeia* 146–151.
- Bernal, D., Donley, J. M., Shadwick, R. E. and Syme, D. A. (2005). Mammal-like muscles power swimming in a cold-water shark. *Nature* **437**, 1349–1352.
- Bernal, D., Syme, D., McGillivray, D., Donley, J. and Sepulveda, C. (2009). The effect of temperature on the muscle contractile properties in the common thresher shark. *Integr. Comp. Biol.* **49**, E199.
- Brodeur, J. C., Dixon, D. G. and McKinley, R. S. (2001). Assessment of cardiac output as a predictor of metabolic rate in rainbow trout. *J. Fish Biol.* **58**, 439–452.
- Danos, N. and Lauder, G. V. (2012). Challenging zebrafish escape responses by increasing water viscosity. *J. Exp. Biol.* **215**, 1854–1862.
- Donley, J. M., Shadwick, R. E., Sepulveda, C. A. and Syme, D. A. (2007). Thermal dependence of contractile properties of the aerobic locomotor muscle in the leopard shark and shortfin mako shark. *J. Exp. Biol.* **210**, 1194–1203.
- Donley, J. M., Sepulveda, C. A., Aalbers, S. A., McGillivray, D. G., Syme, D. A. and Bernal, D. (2012). Effects of temperature on power output and contraction kinetics in the locomotor muscle of the regionally endothermic common thresher shark (*Alopias vulpinus*). *Fish Physiol. Biochem.* **38**, 1507–1519.
- Eloy, C. (2012). Optimal Strouhal number for swimming animals. *J. Fluids Structures* **30**, 205–218.
- Farrell, A. P. (2002). Cardiorespiratory performance in salmonids during exercise at high temperature: insights into cardiovascular design limitations in fishes. *Comp. Biochem. Physiol.* **132A**, 797–810.
- Farrell, A. P. (2009). Environment, antecedents and climate change: lessons from the study of temperature physiology and river migration of salmonids. *J. Exp. Biol.* **212**, 3771–3780.
- Farrell, A. P., Hinch, S. G., Cooke, S. J., Patterson, D. A., Crossin, G. T., Lapointe, M. and Mathes, M. T. (2008). Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. *Physiol. Biochem. Zool.* **81**, 697–709.
- Finstad, A. G., Okland, F., Thorstad, E. B. and Heggberget, T. G. (2005). Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. *J. Fish Biol.* **67**, 919–930.
- Gamperl, A. K., Rodnick, K. J., Faust, H. A., Venn, E. C., Bennett, M. T., Crawshaw, L. I., Keeley, E. R., Powell, M. S. and Li, H. W. (2002). Metabolism, swimming performance, and tissue biochemistry of high desert redband trout (*Oncorhynchus mykiss* ssp.): evidence for phenotypic differences in physiological function. *Physiol. Biochem. Zool.* **75**, 413–431.
- Hodgson, S. and Quinn, T. P. (2002). The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. *Can. J. Zool.* **80**, 542–555.
- Hunter, J. R. and Zweifel, J. R. (1971). Swimming speed, tail beat frequency, tail beat amplitude, and size in jack mackerel, *Trachurus symmetricus*, and other fishes. *Fishery Bull. Fish Wildl. Serv. U.S.* **69**, 253–266.
- Jain, K. E., Hamilton, J. C. and Farrell, A. P. (1997). Use of a ramp velocity test to measure critical swimming speed in rainbow trout (*Oncorhynchus mykiss*). *Comp. Biochem. Physiol.* **117A**, 441–444.
- James, R. S. (2013). A review of the thermal sensitivity of the mechanics of vertebrate skeletal muscle. *J. Comp. Physiol. B* **183**, 723–733.
- Johnston, I. A. and Temple, G. K. (2002). Thermal plasticity of skeletal muscle phenotype in ectothermic vertebrates and its significance for locomotory behaviour. *J. Exp. Biol.* **205**, 2305–2322.
- Karppinen, P., Mäkinen, T. S., Erkinaro, J., Kostin, V. V., Sadkovskij, R. V., Lupandin, A. I. and Kaukoranta, M. (2002). Migratory and route-seeking behaviour of ascending Atlantic salmon in the regulated River Tuloma. *Hydrobiologia* **483**, 23–30.
- Kayan, V. P., Kozlov, L. F. and Pyatetskii, V. E. (1978). Kinematic characteristics of the swimming of certain aquatic animals. *Fluid Dyn.* **13**, 641–646.
- Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F. and Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecol. Freshwat. Fish* **12**, 1–59.
- Laine, A., Jokivirta, T. and Katopodis, C. (2002). Atlantic salmon, *Salmo salar* L., and sea trout, *Salmo trutta* L., passage in a regulated northern river – fishway efficiency, fish entrance and environmental factors. *Fish. Manag. Ecol.* **9**, 65–77.
- Lauder, G. V. and Tytell, E. D. (2005). Hydrodynamics of undulatory propulsion. In *Fish Physiology*, Vol. 23 (ed. E. S. Robert and V. L. George), pp. 425–468. Waltham, MA: Academic Press.
- Lee, C. G., Farrell, A. P., Lotto, A., MacNutt, M. J., Hinch, S. G. and Healey, M. C. (2003). The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *J. Exp. Biol.* **206**, 3239–3251.
- Lindhe Norberg, U. M. and Winter, Y. (2006). Wing beat kinematics of a nectar-feeding bat, *Glossophaga soricina*, flying at different flight speeds and Strouhal numbers. *J. Exp. Biol.* **209**, 3887–3897.
- Nudds, R. L., Taylor, G. K. and Thomas, A. L. R. (2004). Tuning of Strouhal number for high propulsive efficiency accurately predicts how wingbeat frequency and stroke amplitude relate and scale with size and flight speed in birds. *Proc. Biol. Sci.* **271**, 2071–2076.
- Read, D. A., Hover, F. S. and Triantafyllou, M. S. (2003). Forces on oscillating foils for propulsion and maneuvering. *J. Fluids Structures* **17**, 163–183.
- Rodnick, K. J., Gamperl, A. K., Lizars, K. R., Bennett, M. T., Rausch, R. N. and Keeley, E. R. (2004). Thermal tolerance and metabolic physiology among redband trout populations in south-eastern Oregon. *J. Fish Biol.* **64**, 310–335.
- Rohr, J. J. and Fish, F. E. (2004). Strouhal numbers and optimization of swimming by odontocete cetaceans. *J. Exp. Biol.* **207**, 1633–1642.
- Rome, L. C., Loughna, P. T. and Goldspink, G. (1984). Muscle fiber activity in carp as a function of swimming speed and muscle temperature. *Am. J. Physiol.* **247**, R272–R279.
- Rome, L. C., Funke, R. P. and Alexander, R. M. (1990). The influence of temperature on muscle velocity and sustained performance in swimming carp. *J. Exp. Biol.* **154**, 163–178.
- Shadwick, R. E., Bernal, D., Syme, D. A. and Donley, J. M. (2004). Hot shark in cold water: contractile properties of muscle from the endothermic Alaskan salmon shark, *Lamna ditropis*. *Integr. Comp. Biol.* **44**, 746.
- Sharma, S., Jackson, D. A., Minns, C. K. and Shuter, B. J. (2007). Will northern fish populations be in hot water because of climate change? *Glob. Chang. Biol.* **13**, 2052–2064.
- Steinhausen, M. F., Sandblom, E., Eliason, E. J., Verhille, C. and Farrell, A. P. (2008). The effect of acute temperature increases on the cardiorespiratory

- performance of resting and swimming sockeye salmon (*Oncorhynchus nerka*). *J. Exp. Biol.* **211**, 3915-3926.
- Stevens, E. D.** (1979). Effect of temperature on tail beat frequency of fish swimming at constant velocity. *Can. J. Zool.* **57**, 1628-1635.
- Taylor, E. W., Egginton, S., Taylor, S. E. and Butler, P. J.** (1997). Factors which may limit swimming performance at different temperatures. In *Global Warming. Implications for Freshwater and Marine Fish* (ed. D. G. McDonald and C. M. Wood), pp. 105-133. Cambridge: Cambridge University Press.
- Taylor, G. K., Nudds, R. L. and Thomas, A. L. R.** (2003). Flying and swimming animals cruise at a Strouhal number tuned for high power efficiency. *Nature* **425**, 707-711.
- Thorstad, E. B., Okland, F., Aarestrup, K. and Heggberget, T. G.** (2008). Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Rev. Fish Biol. Fish.* **18**, 345-371.
- Tobalske, B. W., Peacock, W. L. and Dial, K. P.** (1999). Kinematics of flap-bounding flight in the zebra finch over a wide range of speeds. *J. Exp. Biol.* **202**, 1725-1739.
- Triantafyllou, M. S., Triantafyllou, G. S. and Gopalkrishnan, R.** (1991). Wake mechanics for thrust generation in oscillating foils. *Phys. Fluids A* **3**, 2835-2837.
- Triantafyllou, G. S., Triantafyllou, M. S. and Grosenbaugh, M. A.** (1993). Optimal thrust development in oscillating foils with application to fish propulsion. *J. Fluids Structures* **7**, 205-224.
- Tytell, E. D.** (2004). The hydrodynamics of eel swimming II. Effect of swimming speed. *J. Exp. Biol.* **207**, 3265-3279.
- Wang, T. and Overgaard, J.** (2007). Ecology. The heartbreak of adapting to global warming. *Science* **315**, 49-50.
- Webb, P. W.** (1971). The swimming energetics of trout. I. Thrust and power output at cruising speeds. *J. Exp. Biol.* **55**, 489-520.