

PARTITIONING THE EFFECTS OF TEMPERATURE AND KINEMATIC VISCOSITY ON THE C-START PERFORMANCE OF ADULT FISHES

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Accepted 20 April; published on WWW 11 June 1998

Summary

Temperature has been shown to have a significant effect on swimming performance in teleost fish. This thermal dependence has usually been attributed to correlated changes in muscle contractile physiology. However, the physical properties of all materials, including both water and living tissues, are profoundly affected by changes in temperature. In particular, both the kinematic viscosity of water and the flexible body dynamics of the fish (independent of muscle contractile activity) are substantially higher at lower temperatures. In this study, we investigated the extent to which the observed thermal dependence of locomotor performance of fish simply reflects changes in the biophysical properties of the aqueous medium independent of the changing physiology of the animals. C-starts (escape swimming) of adult goldfish (*Carassius auratus*, length approximately 8 cm) were video-taped (400 frames s⁻¹) at 5 °C and 20 °C in fresh water and at 20 °C in fresh water containing 1.2 % dextran (kinematic

viscosity equivalent to that of water at 5 °C). Temperature had a significant positive effect on maximum forward velocity (m s⁻¹), angular velocity (degrees s⁻¹) and total distance moved, but viscosity had no detectable effect on any kinematic parameters at 20 °C. Since viscous forces may have more pronounced effects on smaller fish, C-starts of adult guppies (*Poecilia reticulata*, length approximately 2 cm) were video-taped in fresh water and in fresh water containing 1.2 % and 3.6 % dextran at 20 °C. Viscosity had a significant effect on kinematic variables only at 3.6 % dextran; at 1.2 % dextran, the effects were marginal. It was concluded that most of the observed thermal dependence of C-starts at temperatures normally experienced by these fish was due to changes in physiological processes as opposed to physical changes in the environment.

Key words: fish, escape, swimming, C-start, temperature, kinematic viscosity, guppy, *Poecilia reticulata*, goldfish, *Carassius auratus*.

Introduction

Teleost fish are found in thermal environments ranging from 44 °C (desert pupfish, *Cyprinodon macularius*; Schoenherr and Feldmeth, 1993) to -1.9 °C (Antarctic fish; Eastman, 1993). Such a wide range of temperatures is known to have a highly significant effect on locomotor performance (Johnston *et al.* 1991). Since the physiological rate properties of muscle are profoundly affected by temperature, typically with a Q₁₀ of 2 or greater (see Bennett, 1985), it has traditionally been assumed that the thermal dependence of locomotor performance in ectotherms is primarily the consequence of changes in the physiological properties of the neuromuscular system. Both the biochemical and contractile properties of muscle show a significant thermal dependence in ectotherms. For example, goldfish fast muscle myofibrillar ATPase activity, a major determinant of maximum shortening speed (Barany, 1967), has been shown to more than double with a 10 °C increase in temperature (Johnston *et al.* 1975). Maximum swimming speed is also strongly thermally dependent (Johnson and Bennett, 1995). In addition, in carp fast muscle, the activity of Ca²⁺-

ATPase from isolated sarcoplasmic reticulum and twitch contraction kinetics are highly temperature-dependent (Fleming *et al.* 1990). Twitch contraction kinetics are believed to be an important determinant of maximum swimming speed (Wardle, 1975) and again have been equated with changes in maximum swimming speed associated with acute exposure to a change in temperature in a number of teleost species (see Johnson and Bennett, 1995).

Physiologists have typically focused on the functional role of these changes in muscle contractile properties with temperature through correlated studies of isolated muscle properties and organismal performance. However, the causation of the thermal dependence of locomotor performance is considerably more complex. It is not just the physiological properties of the neuromuscular system but also the actual physical properties (e.g. viscosity) of all materials, including living tissue and the aqueous environment, that change with temperature. For example, Antarctic fish living permanently at -1.9 °C will experience viscosities approximately three times

greater than desert pupfish living at 40 °C or above (see Denny, 1951). Thus, when investigating the effects of temperature on the swimming performance of aquatic ectotherms, one must consider changes in the physical properties of the surrounding environment and the organism itself in addition to the physiological properties of the neuromuscular system or its components.

Temperature has a dramatic effect on the viscosity of water and a somewhat smaller though significant effect on the density. Viscosity (dynamic) describes the degree to which a fluid particle will be retarded by any lack of synchronized activity of adjacent particles, or the 'interlaminar stickiness' (Vogel, 1983). In contrast, kinematic viscosity, which is simply the ratio of viscosity to density, describes the ease with which a fluid flows (i.e. the 'gooiness') (Vogel, 1983) and as such is the parameter that is most used when examining the effects of temperature on the fluid mechanics of biological systems. The question of how changes in kinematic viscosity associated with changes in temperature may affect hydrodynamic characteristics and swimming capacity has been discussed previously by a number of authors (e.g. Sidell and Moerland, 1989), but only recently investigated experimentally (Johnson *et al.* 1993; Podolsky and Emlet, 1993; Fuiman and Batty, 1997). Viscosity was found to have a significant effect on tail-beat frequency and tail-beat amplitude during routine swimming of small herring (*Clupea harengus*) larvae (Fuiman and Batty, 1997). The latter study questioned the validity of applying hydrodynamic models of inanimate geometric solids to swimming organisms and suggested that viscous forces may be more important than previously expected for animals swimming at higher Reynolds numbers ($Re \leq 450$) (Fuiman and Batty, 1997). The significance of changes in viscosity to the locomotor performance of larger fishes swimming at higher speeds ($Re \geq 450$) is investigated here.

In this investigation, C-start performance was studied in adult specimens of the goldfish (*Carassius auratus*) and the guppy (*Poecilia reticulata*) to examine the importance of viscous forces in the observed relationship between temperature and swimming performance. The C-start is characterized by an initial preparatory stroke (the 'C'), induced by the simultaneous activity of muscle along one side of the body (Fig. 1) (Eaton *et al.* 1977; Jayne and Lauder, 1993). This is followed by a propulsive (S-shaped) stroke during which the centre of mass of the animal is accelerated from its original position (Fig. 1) (Eaton *et al.* 1977). The C-start is a highly stereotyped behaviour, and the thermal dependence of this locomotor activity can therefore be tested relatively independently from possible changes in spontaneous (voluntary) swimming activity associated with changes in temperature (Cossins and Bowler, 1987). Changes in the biochemical and contractile properties of fast muscle associated with a change in temperature have recently been directly correlated with changes in C-start performance (Johnson and Bennett, 1995). However, the proportion of the observed thermal dependence of C-start performance

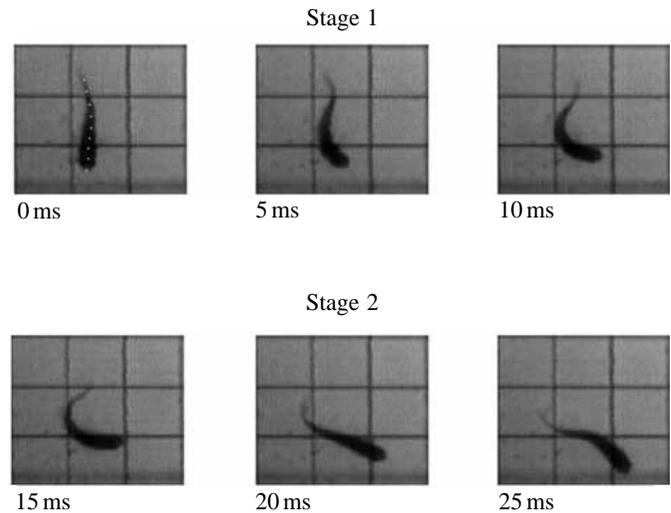


Fig. 1. The C-start of a guppy (*Poecilia reticulata*) in fresh water at 20 °C. Note that in stage 1 the body of the fish bends into the characteristic 'C'. Stage 2 consists of an S-shaped propulsive stroke during which the centre of mass of the body is accelerated from its original position. In the first video frame, the midline of the fish has been digitised. The grid is 2 cm×2 cm.

attributable to changes in the kinematic viscosity of the surrounding water or to changes in the internal properties (both physiological and physical) of the animal itself remained to be tested.

Materials and methods

Fish origin and maintenance

Specimens of goldfish (*Carassius auratus*) were purchased from a local fish farm (Bayou Aquatics, Ontario, CA, USA). Guppies (*Poecilia reticulata*) were obtained from laboratory stocks of wild populations maintained by D. Reznick at the University of California, Riverside. Animals were maintained in fresh water at 20 °C, under ambient light conditions (12 h:12 h dark:light) and fed *ad libitum* with fish flake. Goldfish measured 7.7 ± 0.3 cm (mean \pm s.d., $N=5$) and guppies measured 2.0 ± 0.2 cm (mean \pm s.d., $N=5$) total length.

Manipulation of the kinematic viscosity of aquarium water

The kinematic viscosity ($\text{m}^2 \text{s}^{-1}$) of 0–5 % dextran solutions at 20 °C and aquarium water at 5 °C was determined in the laboratory using an Ostwald viscometer. Dextran is a large (molecular mass 242 000) non-toxic carbohydrate polymer that had no detectable effect on the long-term health of experimental animals. Aqueous solutions of 1.2 % and 3.6 % dextran (w/v) increase the kinematic viscosity of water 1.6 and 3.4 times, respectively (Table 1). A reduction in temperature from 20 to 5 °C also increases kinematic viscosity 1.6 times (Table 1), and thus a solution of 1.2 % dextran was used to produce the environmental viscosity of low-temperature water while retaining the internal biophysics and physiology of the fish at the higher temperature.

Table 1. *Temperature and kinematic viscosity of the aquarium water used for C-start swimming in guppies and goldfish*

% Dextran (w/v)	Temperature (°C)	Kinematic viscosity (m ² s)
0	20	10 ⁻⁶
0	5	1.55×10 ⁻⁶
1.2	20	1.55×10 ⁻⁶
3.6	20	3.35×10 ⁻⁶

C-start performance

C-starts were video-taped using a NAC-HSV400 video system at 400 frames s⁻¹ in a custom-built glass aquarium (25 cm×20 cm×15 cm). Animals were viewed ventrally by placing a mirror at 45° to the horizontal below the tank. Illumination was provided from above through a 5 mm thick opaque strip of Perspex by a synchronized strobe system (NAC) or two 500 W tungsten photofloods (Smith Victor). A scale for the video images was provided by a 2 cm×2 cm grid drawn onto the base of the experimental arena. C-starts were reliably elicited by dropping a weight into the tank.

Fish were placed in the experimental arena for at least 1 h prior to the trials. For both species, C-starts were video-taped in normal water at 20 °C and in water at 20 °C containing 1.2 % dextran (which artificially increases kinematic viscosity to that observed at 5 °C). For guppies only, C-starts were also performed in water containing 3.6 % dextran (kinematic viscosity increased by a factor of 3.4). All individuals remained in good condition during and for several weeks after experimentation and were apparently unaffected by exposure to dextran. Five individuals of each species were used, and at least three C-starts were recorded for each fish in each 20 °C situation. Trials were always separated by at least 10 min. Owing to difficulties in eliciting numerous responses at 5 °C, only one or two C-starts were recorded at this temperature. Animals were allowed to accommodate to a change in kinematic viscosity for at least 4 h or overnight. The order in which fish were exposed to different kinematic viscosities was randomized. Following the completion of kinematic viscosity experiments, goldfish were acclimated to normal water for at least 48 h, cooled to 5 °C from 20 °C over 2 h and video-taped performing C-starts at this temperature.

Video analyses

Video frames were downloaded to a Dell 386 PC using a PC-VISION^{plus} frame-grabber card (Imaging Technology, MA, USA). Consecutive frames were downloaded from the frame previous to the first detectable movement in the C-start to a point at which the fish had visibly slowed following stage 2 of the response (animals typically brake using their pectoral fins following the completion of the C-start). The images from each sequence were analysed using customised software ('Measurement television', Garr Updegraff, Data-Crunch, San Clemente, CA, USA). The midlines of the fish were digitized using ten (goldfish) or nine (guppies) equally spaced points from the tip of the head to the tip of the tail. The coordinates

of these points were entered into a table and downloaded to Microsoft Excel, version 5.0 for Windows. Using a customised macro for Microsoft Excel, sequences were analysed to determine the three kinematic parameters described below.

During stage 1 of the C-start, fish bend about a stationary point known as the 'stretched-body centre of mass' (SBCM) (Nissanov and Eaton, 1989). This is an important point both biomechanically and ecologically as it is believed to represent the target for predatory strikes (Nissanov and Eaton, 1989). Maximum velocity (U_{\max}) (m s⁻¹) was determined from the maximum distance moved by the SBCM in 5 ms (two video frames); maximum angular velocity (ω_{\max}) (degrees s⁻¹) was determined from the maximum change in the angle between the tip of the head and the SBCM during stage 1, measured in two consecutive video frames (5 ms). Finally, the total distance moved by the SBCM in 40 ms for goldfish or 25 ms for guppies (D_{Total}) was also recorded (guppies typically completing the C-start manoeuvre in less time).

Statistics

For each performance trait (U_{\max} , ω_{\max} and D_{Total}), comparisons among different environmental conditions were made using two-way mixed-model analysis of variance (ANOVA) (with 'individual' as the second, random factor), followed by *post-hoc* tests of differences in least-squares means. To facilitate visual presentation of the data, values for each performance trait were also normalized by dividing each value, for each individual under each condition, by the mean of the 20 °C (no dextran) trait value.

To quantify the possible contribution of viscosity changes to overall changes in performance due to temperature, an additional calculation was carried out with the data for the goldfish. This calculation took the following form for each trait of each individual:

$$F_{\text{viscosity}} = (\text{Trait}_{20} - \text{Trait}_{\text{Dextran}}) / (\text{Trait}_{20} - \text{Trait}_5), \quad (1)$$

where $F_{\text{viscosity}}$ is the fraction of the temperature effect explained by changes in water viscosity, Trait_{20} is the trait value for the individual in 20 °C water without dextran, $\text{Trait}_{\text{Dextran}}$ is the trait value in 1.2 % dextran at 20 °C and Trait_5 is the trait value in 5 °C water. A positive value for this fraction indicates that a portion of the inhibitory effect of lower temperature may be due to the viscous component; a negative value indicates that the viscous component may enhance performance.

Results

Values for goldfish C-start traits under the different test conditions are shown in Fig. 2. Temperature had a significant depressant effect on all three kinematic parameters, similar to that reported previously for this species (Johnson and Bennett, 1995). U_{\max} decreased by 34 % ($P=0.045$), ω_{\max} by 28 % ($P=0.001$) and D_{Total} by 44 % ($P=0.003$) following acute exposure to 5 °C from 20 °C ($Q_{10}=1.3-1.4$). However, artificially changing viscosity at 20 °C with 1.2 % dextran did

not significantly reduce C-start performance (Fig. 2; U_{\max} , $P=0.49$; D_{Total} , $P=0.68$). In fact the only significant effect of increased viscosity was an increase in ω_{\max} ($P=0.020$).

Comparing the low-temperature and 1.2% dextran values

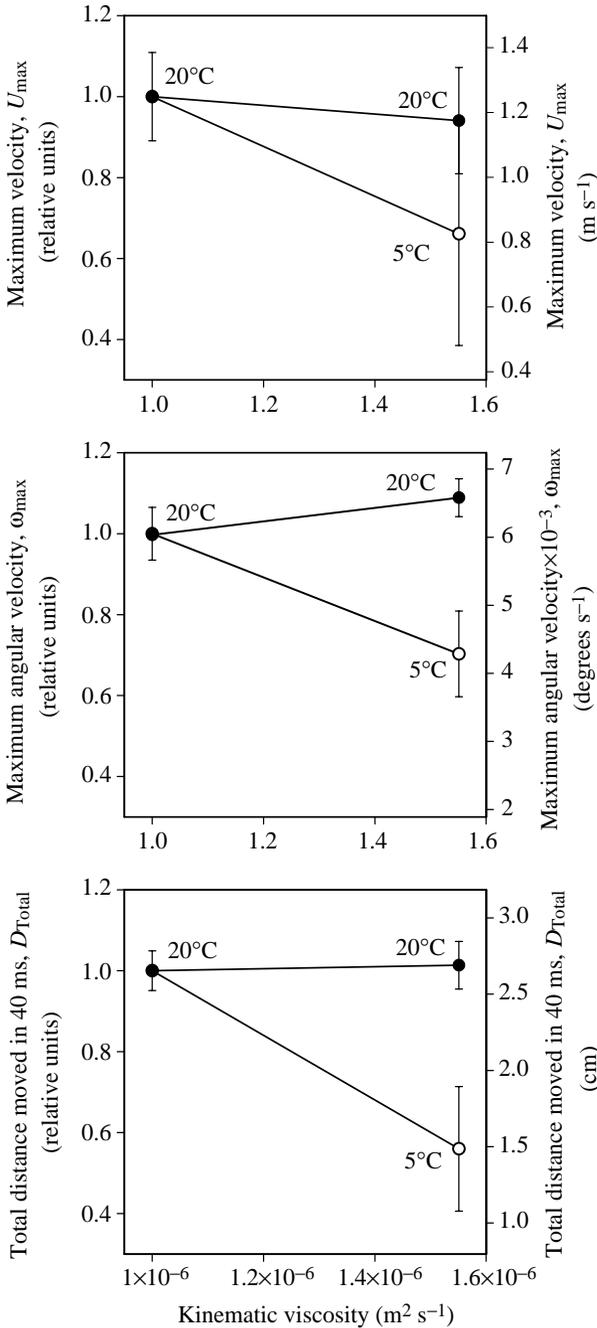


Fig. 2. The maximum velocity (U_{\max}), maximum angular velocity (ω_{\max}) and total distance moved in 40 ms (D_{Total}) for goldfish (*Carassius auratus*) during C-starts as a function of kinematic viscosity and temperature. Filled symbols represent C-starts performed in water at 20°C, open symbols in water at 5°C. Kinematic viscosity was increased at 20°C using 1.2% dextran. Left axes show values normalised to the mean at 20°C in normal water (viscosity $10^{-6} \text{m}^2 \text{s}^{-1}$); right axes show absolute values. Values are least-squares means \pm 95% confidence limits ($N=5$).

by means of the $F_{\text{Viscosity}}$ calculation indicates a marginal, but potentially significant, viscous component to low-temperature inhibition of goldfish swimming performance. $F_{\text{Viscosity}}$ of the U_{\max} of each goldfish had a mean value (\pm s.d., $N=5$) of 0.19 ± 0.41 , indicating that increased water viscosity might represent a moderate portion of the overall inhibitory effect of

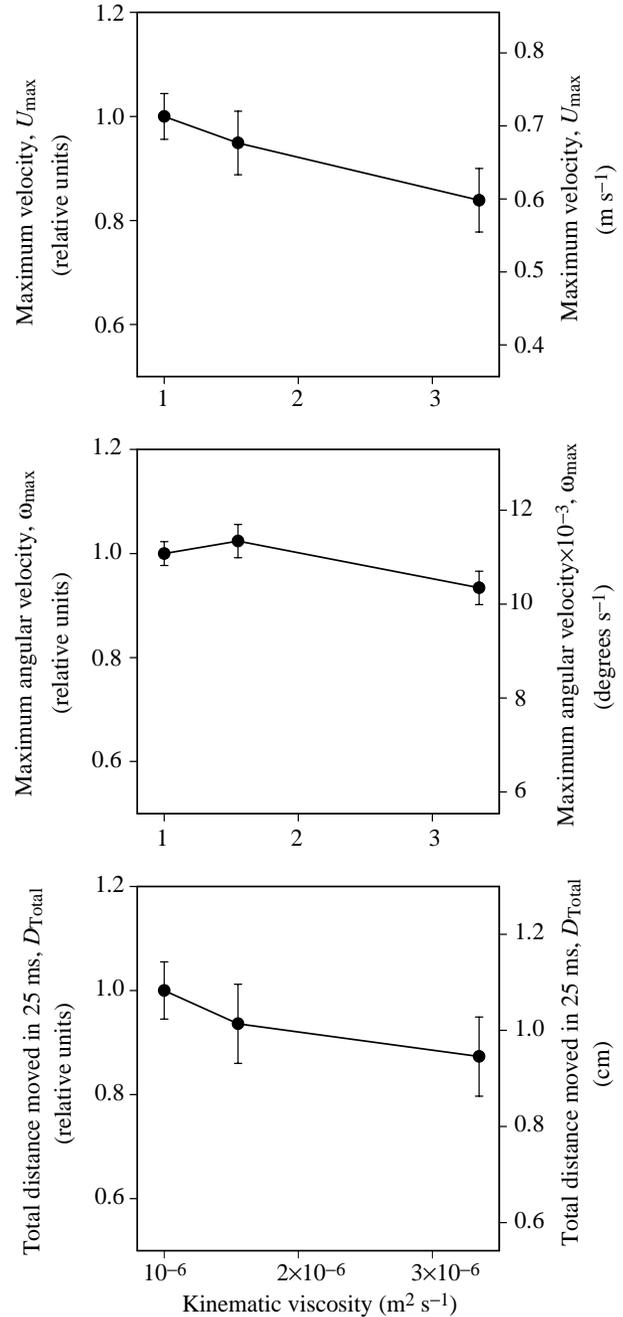


Fig. 3. The effects of kinematic viscosity on maximum swimming speed (U_{\max}), maximum angular velocity (ω_{\max}) and total distance moved in 25 ms (D_{Total}) during C-starts of guppies (*Poecilia reticulata*) at 20°C. Kinematic viscosity was increased 1.6-fold and 3.4-fold using 1.2% and 3.6% dextran respectively. Left axes show values normalised to the mean at a kinematic viscosity of $10^{-6} \text{m}^2 \text{s}^{-1}$ (i.e. normal water) right axes show absolute values. Values are least-squares means \pm 95% confidence limits ($N=5$).

Table 2. Maximum velocities attained during C-starts in goldfish as a function of temperature and/or viscosity

Kinematic viscosity, ν (m ² s ⁻¹)	Temperature (°C)	Maximum velocity, U_{\max} (m s ⁻¹)	Reynolds number, Re	Drag coefficient, C_f	
				Laminar	Turbulent
10 ⁻⁶	20	1.25	96 250	4.29×10 ⁻³	7.26×10 ⁻³
1.55×10 ⁻⁶	20	1.18	58 619	5.49×10 ⁻³	8.01×10 ⁻³
1.55×10 ⁻⁶	5	0.83	41 232	6.55×10 ⁻³	8.60×10 ⁻³

Reynolds numbers and frictional drag coefficients (assuming turbulent or laminar flow) are also shown (calculated according to Sidell and Moerland, 1989).

$Re = lU_{\max}/\nu$, where l is the total length of the fish.

$C_f = 1.33Re^{-0.5}$ (laminar); $C_f = 0.072Re^{-0.2}$ (turbulent).

low temperature on U_{\max} . However, this value was not significantly different from zero (one-sample t -test, $P=0.42$). $F_{\text{viscosity}}$ for ω_{\max} , in contrast, is -0.42 ± 0.33 , $N=5$). Although this is again not statistically significant ($P=0.085$), it suggests a possible positive effect on this performance trait, particularly given that a similar trend is seen in smaller fish (see below). $F_{\text{viscosity}}$ for D_{Total} is -0.07 ± 0.14 , $N=5$, indicating little if any viscous component to this trait.

Values for guppy performance are shown in Fig. 3. Over the range examined, kinematic viscosity appeared to have an almost linear effect on U_{\max} and D_{Total} , with these values decreasing by 16% and 13%, respectively, as kinematic viscosity increased from 10⁻⁶ m² s⁻¹ (normal water) to 3.4×10⁻⁶ m² s⁻¹ (3.6% dextran). The differences between these extreme kinematic viscosities were significant in both cases (U_{\max} , $P=0.002$; D_{Total} , $P=0.024$), but differences between normal water and 1.2% dextran were not (U_{\max} , $P=0.21$; D_{Total} , $P=0.20$). Values of ω_{\max} were also significantly lower in 3.6% dextran than normal water (7% decrease, $P=0.009$), but for this trait the trend does not appear to be linear (Fig. 3), with the suggestion of an increase in ω_{\max} at a kinematic viscosity of 1.55×10⁻⁶ m² s⁻¹ (normal water *versus* 1.2% dextran, $P=0.25$).

Discussion

Partitioning the effects of temperature and viscosity on C-start performance

Temperature has a highly significant effect on locomotor performance of fish (Fig. 2; Johnson and Bennett, 1995). The

greater proportion of this thermal dependence may be attributable to the influence of temperature on the physiological properties of the neuromuscular system. Maximum swimming speed (U_{\max}) decreases by 34% following a decline in temperature from 20 to 5 °C in goldfish (Fig. 2); up to one-fifth of that change might be attributable to changes in kinematic viscosity. Maximum angular velocity (ω_{\max}) also decreases by a similar amount (28%) with this decline in temperature (Fig. 2). However, in this case, increasing viscosity 1.6-fold independent of temperature might actually increase turning speed, a trend seen in both species studied here (Figs 2, 3). The total distance moved by the SBCM in 40 ms (D_{Total}) in goldfish decreased by 44% with decreasing temperature (Fig. 2). Possible contributions of viscosity to performance for this parameter were of a much smaller order of magnitude.

Trade-offs associated with changes in pressure and frictional drag

When one considers the effects of increased viscosity on the hydrodynamics of swimming, the initial inference might be to expect speed to decline as a result of the increase in drag. In the C-start, all available power is being used in the generation of swimming movements, and thus a reduction in maximum swimming speed might be predicted. However, one must first consider the fact that total drag is a function not only of frictional drag, which results from the intercohesion between water molecules (and therefore quantified by kinematic viscosity), but also of pressure drag. Pressure drag is the drag that results from 'unfavourable pressure gradients created by

Table 3. Maximum velocities attained during C-starts in guppies as a function of kinematic viscosity

Kinematic viscosity, ν (m ² s ⁻¹)	Temperature (°C)	Maximum velocity, U_{\max} (m s ⁻¹)	Reynolds number, Re	Drag coefficient, C_f	
				Laminar	Turbulent
10 ⁻⁶	20	0.71	14 200	1.11×10 ⁻³	1.06×10 ⁻³
1.55×10 ⁻⁶	20	0.68	8 774	1.42×10 ⁻³	1.17×10 ⁻³
3.35×10 ⁻⁶	20	0.60	3 582	2.22×10 ⁻³	1.40×10 ⁻³

Reynolds numbers and frictional drag coefficients (assuming turbulent or laminar flow) are also shown (calculated according to Sidell and Moerland, 1989).

$Re = lU_{\max}/\nu$, where l is the total length of the fish.

$C_f = 1.33Re^{-0.5}$ (laminar); $C_f = 0.072Re^{-0.2}$ (turbulent).

the distortion of flow about an object' (Sidell and Moerland, 1989). In Tables 2 and 3, a number of parameters have been calculated from the mean maximum swimming speeds attained by goldfish and guppies in the different experimental situations. The calculations and following arguments, although somewhat crude, have been carried out to highlight the potential importance of pressure drag on C-start performance (see also p. 148, Sidell and Moerland, 1989).

As expected, Reynolds numbers vary with temperature because of the increase in kinematic viscosity, even if the fish were able to attain the same swimming speed (Tables 2, 3). The frictional drag coefficient (C_f) may be calculated from these Reynolds numbers. Frictional drag (D_f), calculated from the standard Newtonian equation, is as follows:

$$D_f = \frac{1}{2} \rho S U^2 C_f \quad (2)$$

(Sidell and Moerland, 1989), where S is the wetted surface area, U is swimming velocity and ρ is the density of the surrounding environment. The density of water changes only fractionally with an increase in the concentration of dextran to 1.2% (see Lide, 1992). For this study of C-start swimming, wetted surface area remained constant and there was no statistically significant change in the velocity achieved by the fish with a 1.6-fold increase in kinematic viscosity (Tables 2, 3). Thus, for the purpose of this investigation, we may assume that frictional drag (D_f) is proportional to the drag coefficient (C_f). It would therefore appear that, despite a 28% increase in fractional drag (assuming laminar flow) or a 10% increase in frictional drag (assuming turbulent flow), fish are able to attain the same maximum swimming speed (Tables 2, 3). There may be two ways of explaining this unexpected result.

First, although we are unable to quantify pressure drag, the results of this investigation could support the idea that there may be at least some positive consequences to increased viscosity in cold water (Sidell and Moerland, 1989). For example, large bluefin tuna *Thunnus thynnus* will choose to swim in cooler water below the thermocline, presumably to reduce drag (Wardle, 1977). It is possible that a slight increase in viscosity serves to dampen disturbances at the boundary layer and thereby reduce pressure drag (Webb, 1975). Alternatively, since the C-start involves the rapid acceleration of the fish body, the majority of the force produced is employed in overcoming inertia as opposed to drag. One might therefore predict only a small effect of kinematic viscosity on maximum swimming speed (3% or less in this case).

The effects of kinematic viscosity on swimming performance are clearly complex and may, therefore, represent the response of the animal to a trade-off between the negative effects imposed by an increase in frictional drag and the positive consequences of increased kinematic viscosity on the stability of the boundary layer (and therefore pressure drag). Observed changes in angular velocity (Figs 2, 3) and the amplitude and frequency of tail beats (Fuiman and Batty, 1997) with increasing kinematic viscosity may also indicate changes in propeller efficiency during undulatory swimming.

Ecological and evolutionary implications of changes in environmental viscosity

Many teleost fish species are often exposed to quite large changes in temperature over periods of just a few hours or to seasonal changes lasting several months. For example, killifish (*Fundulus heteroclitus*) experience a seasonal change in sea temperature from -1 to 15°C , and during the warm summer months may be isolated in pools where temperatures may exceed 30°C and plummet to 12 – 14°C in less than an hour during tidal inundation (Sidell *et al.* 1983). Pupfish (*Cyprindodon* sp.) inhabit streams with a seasonal fluctuation of up to 40°C (Schoenherr, 1988). It is therefore possible that at least some species of teleost may naturally experience 2.5- to threefold changes in kinematic viscosity. In this respect, it is interesting that guppies (similar in size to *Cyprinodon*) are significantly affected by changes in kinematic viscosity of this magnitude. Maximum swimming speed, angular velocity and the total distance moved in 25 ms are significantly affected by a 3.4-fold increase in viscosity in this species (Fig. 3). A threefold change in kinematic viscosity could clearly affect escape performance and therefore survival.

In evolutionary terms, many species of teleost have evolved to live at extremes of temperature from 44 to -1.9°C and presumably may have had to adapt to the functional consequences of hydrodynamically different environments. Is it therefore possible that the greater tailbeat amplitude of juvenile (7 – 8 cm long) compared with that of adult Antarctic *Notothenia neglecta* (25 – 30 cm total length) during bouts of fast subcarangiform swimming at 2°C is a response to viscous forces (Archer and Johnston, 1989). It is also interesting that all Antarctic notothenids, both pelagic and demersal, appear to adopt only labriform locomotion for low-speed (endurance) swimming (Archer and Johnston, 1989). This may reflect some purely phylogenetic constraint within the Antarctic notothenids or an increase in the efficiency of drag-based forms of locomotion at high viscosity and low temperature.

It has also been generally assumed that viscous forces associated with a decline in temperature are significant only for fish larvae and not for larger fish (see Fuiman and Batty, 1997). From the results of this study, however, it is clear that, for at least some species of fish, the consequences of a change in the kinematic viscosity associated with a change in the thermal environment may have a real and significant impact on the ability to perform escape manoeuvres in the adult animal. Here (Table 3), we demonstrate that viscous forces may significantly inhibit locomotor performance even at Reynolds numbers as high as 3500, nearly an order of magnitude greater than previously supposed. Kinematic viscosity may also have had a direct effect on the evolution of vertebrate design in animals living in extremely cold, and therefore more viscous, environments.

We are grateful to Berenice Perez for the help in analysing video sequences. This work was supported by grants from the

National Science Foundation (IBN-9118346 and IBN-9420155).

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