

## A NOTE ON INTERACTIONS BETWEEN TEMPERATURE, VISCOSITY, BODY SIZE AND SWIMMING ENERGETICS IN FISH LARVAE

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*Accepted 26 January; published on WWW 20 April 1998*

### Summary

In a previous study, it was shown that at a given speed the larvae of a species of freshwater fish, the Danube bleak *Chalcalburnus chalcoides*, expended considerably more metabolic energy at 15 °C than at 20 °C. We applied hydromechanical arguments to our previous data in order to determine whether the higher cost of swimming at the lower temperature might be due to the effects of viscous forces. However, even under the unrealistic assumption of the larvae swimming in the viscous regime at Reynolds numbers as high as 2000, we show here that hydromechanical forces cannot

explain the high energy cost of swimming at 15 °C. Instead, we offer a new hypothesis that the 'two-gear system' of the swimming muscles operating in juvenile and adult fish is not yet functional in the larvae, with the consequence that, when these fish are swimming at high speeds in cold water, the muscle fibres have to operate over an increasingly inefficient range of shortening velocities.

Key words: fish, swimming, fish larvae, hydrodynamics, metabolic rate, Danube bleak, *Chalcalburnus chalcoides*.

### Introduction

The effects of temperature on swimming in aquatic animals have been studied by recording the kinematics and/or energy expenditure of the animals. Since, in water, changes in temperature are obligatorily linked to changes in viscosity, attempts have been made to separate the effects of these two variables. This can be achieved by altering the viscosity of water independent of temperature by the addition of an osmotically inactive substance such as methyl cellulose, dextran or polyvinyl pyrrolidone (Linley, 1986; Podolsky, 1994; Podolsky and Emler, 1993). Recently, Fuiman and Batty (1997) applied this method to small (9.6 mm) and large (18.2 mm) herring larvae *Clupea harengus*. They recorded kinematic variables from spontaneously swimming larvae at 6, 9 and 13 °C, and artificially altered viscosity from  $1.2 \times 10^{-6}$  to  $2.0 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$ . Their major findings were (1) that voluntary swimming speeds of small larvae are strongly affected by viscosity but relatively little by temperature at equal viscosities, and (2) that the viscous hydrodynamic regime for larval herring extends further up the scale of Reynolds number (to approximately 450) than is usually assumed (Weihs, 1980; Webb and Weihs, 1986; Osse, 1990). The effect of the viscosity of water on the swimming behaviour of small herring larvae is demonstrated best by the observation (Fig. 2 in Fuiman and Batty, 1997) that voluntary swimming speed declined linearly from approximately 15 to 5 mm s<sup>-1</sup> as viscosity increased from  $1.2 \times 10^{-6}$  to  $2.0 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  and that this relationship was totally unaffected by water temperature.

These experiments with spontaneously swimming fish raise

questions regarding the energetic consequences of such a behaviour. If, as the results of Fuiman and Batty (1997) show, small herring larvae select an optimal swimming speed at a constant level of energy expenditure, how would energy expenditure be affected if the fish were forced to swim outside their selected (optimal?) range of speeds? The major question of physiological interest here is the extent to which it is possible to separate direct from indirect effects of temperature on the swimming energetics of the larvae.

On the basis of a fairly complete set of data from a previous study on the swimming energetics of the larvae of a species of freshwater fish, the Danube bleak *Chalcalburnus chalcoides* (Kaufmann, 1990; Kaufmann and Wieser, 1992), we are able to show that temperature exerts an indirect influence on the swimming energetics of fish larvae not so much *via* its effect on the viscosity of water but *via* its effect on the contractile properties of swimming muscles.

### Materials and methods

The original data were derived from experiments in which larvae of the Danube bleak *Chalcalburnus chalcoides mento* (Agassiz) were swum in a flow-through respirometer at 15 and 20 °C and at a wide range of velocities which allowed calculation of total ( $R_t$ ) and standard ( $R_s$ ) metabolic rates as well as the active metabolic rate ( $R_a$ ) at maximum ( $U_{\text{max}}$ ) and critical ( $U_{\text{crit}}$ ) swimming velocity (Kaufmann and Wieser, 1992). Stimulated by the study of Fuiman and Batty (1997),

we have now used the information summarized in Table 1 of Kaufmann and Wieser (1992) to calculate Reynolds number ( $Re$ ), hydromechanical power and the metabolic rates indicated above for three size classes of Danube bleak larvae at 15 and 20 °C (Table 1). All the fish had been acclimated to 20 °C so that the measurements at 15 °C involved an acute change of environmental temperature. Information given in the literature can be used to estimate the hydromechanical forces that the fish must overcome when swimming at a given speed in water of a given temperature. Following Vogel (1981) and Fuiman and Batty (1997), total power  $P_h$  (drag force times velocity) during steady swimming can be represented by:

$$P_h \propto \rho U^3 L^2, \quad (1)$$

in the inertial regime, and by:

$$P_h \propto \mu U^2 L, \quad (2)$$

in the viscous regime, where  $\rho$  is density,  $\mu$  is dynamic viscosity,  $U$  is swimming speed and  $L$  is total length. The density of water is practically independent of temperature, whereas viscosity decreases with temperature. In consequence, it is only in the viscous regime that a temperature effect on hydrodynamic power should be expected. Since our original data had shown that at a given speed fish larvae expended significantly more metabolic energy when swimming in cold (15 °C) than in warm (20 °C) water, we investigated which fraction of the excess energy was due to hydromechanical forces and which fraction to physiological constraints forcing the fish to work harder when swimming in the cold. To be on the safe side, we made the unrealistic assumption that, even at Reynolds numbers up to 2000 (Table 1), the fish swam in the

viscous regime. This sets an upper boundary to the expected effects of temperature on hydromechanical power.

## Results

As discussed extensively by Kaufmann (1990), the total metabolic rate ( $R_t$ ) of fish swimming at a given speed is composed of the standard rate  $R_s$  and the active rate  $R_a$ , which is a power function of swimming velocity ( $U$ ), that is:

$$R_t = R_s + R_a = R_s + aU^b, \quad (3)$$

where  $a$  and  $b$  are constants.

Thus, the effects of temperature on the active and standard metabolic rates can be derived separately. Note, however, that it is assumed that  $R_s$  is constant. If, during swimming, maintenance functions included in  $R_s$  were temporarily suppressed – and there are indications that this may sometimes be the case (Kaufmann and Wieser, 1992; Wieser, 1995) – results regarding the metabolic ‘efficiency’ of swimming would have to be reconsidered. From equation 2, we calculated the hydromechanical power for the three size classes of larvae swimming at 15 °C and 20 °C (Fig. 1B). The excess hydromechanical power required at 15 °C compared with that at 20 °C for larvae of exactly the same length would be proportional to the change in dynamic viscosity, i.e. 13.7 % (see footnote to Table 1). This corresponds to a  $Q_{10}$  of 0.77 under the viscous regime, irrespective of swimming speed (Fig. 1C). In consequence, this would be the value expected for the active metabolic rate  $R_a$  if the difference in energy expended by our fish at the two temperatures were due solely to hydromechanical constraints. If the fish are assumed to have swum in the inertial regime,  $Q_{10}$  would be close to 1.0 (Fig. 1C).

Our measurements of active metabolic rate (Fig. 1A) show

Table 1. Summary of experimental variables at two temperatures for three size classes of larval and juvenile Danube bleak *Chalcalburnus chalcoides*

	9 mm		13 mm		17 mm	
	15 °C	20 °C	15 °C	20 °C	15 °C	20 °C
Mean fresh mass (mg)	3.9±0.2	3.4±0.2	10.1±0.9	10.3±0.9	25.3±2.2	24.4±2.2
Mean total length, $L$ (mm)	9.5±0.5	9.1±0.5	12.7±0.5	12.8±0.5	17.0±0.7	16.8±0.7
$U_{crit}$ (mm s <sup>-1</sup> )	63	78	73	100	87	116
$Re$ at $U_{crit}$	525	708	814	1277	1299	1945
$R_s$ (W kg <sup>-1</sup> )	2.57	4.09	2.29	3.66	2.16	2.82
$R_a$ at $U_{crit}$ (15 °C) (W kg <sup>-1</sup> )	5.44	4.63	3.93	3.10	3.07	2.36
$Q_{10}$ ( $R_s$ )		2.54		2.56		1.70
$Q_{10}$ ( $R_a$ ) at $U_{crit}$ (15 °C)		0.72		0.62		0.59
$Q_{10}$ (hydromechanical)		0.77		0.77		0.77

Fresh mass and total length are mean values ( $\pm$ S.D.) for animals for 1–3 experiments each. Between 25 and 150 individuals were used in experiments, such that total fresh mass was in the range 300–600 mg.

$U_{crit}$  is sustained aerobic swimming speed,  $Re$  is the Reynolds number at this speed.

Respiration rates were converted to units of power assuming an oxycaloric equivalent of 450 kJ mol<sup>-1</sup> O<sub>2</sub>; precision for these rates estimated from calibration experiments and from regression statistics is  $\pm 0.1$  W kg<sup>-1</sup> for  $R_s$  and  $\pm 0.2$  W kg<sup>-1</sup> for  $R_a$ .

Dynamic viscosities  $\mu$  used in calculations were  $1.139 \times 10^{-3}$  kg m<sup>-1</sup> s<sup>-1</sup> (15 °C) and  $1.002 \times 10^{-3}$  kg m<sup>-1</sup> s<sup>-1</sup> (20 °C).  $Q_{10}$  (hydromechanical) reflects the ratio of these viscosities independent of swimming speed.

$R_s$ , standard metabolic rate;  $R_a$ , active metabolic rate.

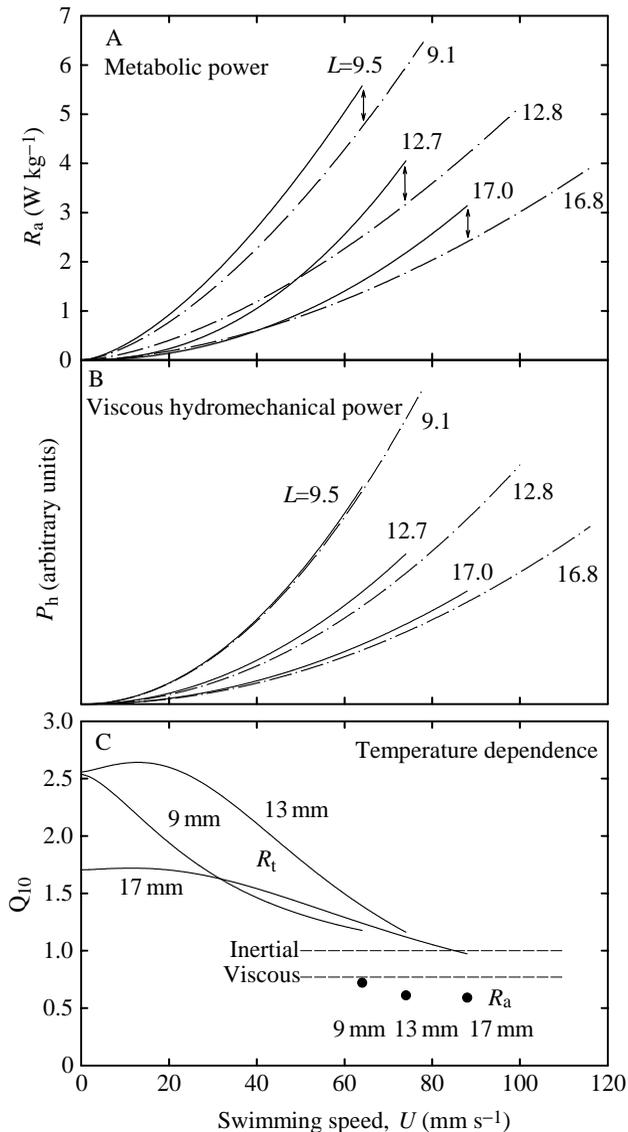


Fig. 1. (A) Active metabolic rate versus swimming speed, (B) hydromechanical power  $P_h$  according to the viscous model (equation 2) and (C)  $Q_{10}$  relationships for active ( $R_a$ ) and total ( $R_t$ ) metabolic rates for three size classes (9, 13, 17 mm total length  $L$ ) of Danube bleak *Chalcalburnus chalcoides* larvae swimming at 15°C (solid lines) and 20°C (broken lines). In A, curves are shown up to the critical swimming speed  $U_{\text{crit}}$ . Curves shown are averages from 1–3 experiments each. Arrows indicate the points at which  $Q_{10}$  values were calculated. In C, the curves show  $Q_{10}$  for  $R_t$ , and the filled circles show  $Q_{10}$  values for  $R_a$  at  $U_{\text{crit}}$  for the three size classes as indicated in A. The  $Q_{10}$  values expected for the hydromechanical power under viscous (0.77) and inertial (1.0) regimes are also shown (dotted lines).

that at higher speeds the fish larvae expended considerably more energy at 15°C than can be explained by hydromechanical forces (compare Fig. 1A and B). Moreover,  $R_a$  at 20°C increased less steeply with swimming speed (values of  $b$  in equation 3 were less than 2.0) than did the corresponding curves representing hydromechanical power

(exponent of 2.0 in equation 2). The difference between the metabolic and hydromechanical temperature effects is expressed by the  $Q_{10}$  values summarized in Table 1 and plotted in Fig. 1C. At  $U_{\text{crit}}$  (15°C), the  $Q_{10}$  of  $R_a$  ranged from 0.72 to 0.59 over the three size classes. These values are lower than the  $Q_{10}$  values calculated for the hydromechanical power under viscous (0.77) or inertial (1.0) regimes.

The transition from slow to fast swimming at the two temperatures is strikingly illustrated by the trajectories of the  $Q_{10}$  values of total metabolic rate ( $R_t$ ) in relation to swimming speed (Fig. 1C). Calculated  $Q_{10}$  values for the standard metabolic rate  $R_s$  ranged from 1.7 (large larvae) to approximately 2.5 (medium and small larvae) (Table 1). The increasing total metabolic cost of swimming  $R_t$  at the lower temperature (due to increases in  $R_a$ ) is reflected by the negative slope of the  $Q_{10}$  curves in Fig. 1C.

### Discussion

Our data demonstrate that, in fish larvae swimming at 15°C, or 5°C below their acclimation temperature, their net energy expenditure  $R_a$ , and thus their net cost of transport ( $COT$ ), is higher than can be explained by increased hydrodynamic forces, even under the unrealistic assumption that they are swimming in the viscous regime at Reynolds numbers as high as 2000. This is in contrast to the situation for large fish, in which  $COT$  remains constant or decreases with temperature (e.g. Brett, 1964; Beamish, 1970, 1981; Smit *et al.* 1971). A possible explanation for this difference in swimming energetics between larvae and adult fish can be derived from recent findings on the mechanics and energetics of isolated muscle fibres at different temperatures (Rome, 1990; Rome *et al.* 1990).

Since the work of Hill (1964), it has been known that the efficiency of muscle (the ratio of mechanical power produced to metabolic energy utilized) depends greatly on the ratio  $V/V_{\text{max}}$  (shortening velocity as a proportion of maximum shortening velocity), maximum efficiency being reached at values between 0.2 and 0.4. In consequence, animals moving at different speeds would benefit from the use of different muscle fibre types which reach optimal  $V/V_{\text{max}}$  ratios at different speeds. It is now well known (Rome *et al.* 1988) that fish achieve this goal with a two-gear system of red and white fibres, the former being optimized for slow speeds, the latter for fast speeds (Rome, 1990; Videler, 1993). There is a striking effect of temperature on the energetics of muscle fibres. At shortening velocities below the efficiency maximum ( $V/V_{\text{max}}$  approximately 0.3), efficiency is relatively unaffected by temperature, whereas at higher velocities efficiency decreases much more rapidly in cold-exposed than in warm-exposed muscle fibres. In consequence, in fish swimming at low temperatures, the fast white fibre type is activated at lower swimming speeds than in fish swimming at high temperatures. This has been called ‘compression of recruitment order theory’ (Rome, 1990). In fish larvae, the arrangement of muscle fibres differs from that in adult fish in several respects. Red fibres are

represented by a unicellular red layer which envelops the whole body, receiving oxygen largely by diffusion across the skin. The central muscle mass is composed of fibres much richer in mitochondria than are the white fibres of adult fish. The result of this arrangement is that, in fish larvae, swimming is almost entirely aerobic up to the highest speeds (Kaufmann, 1990; Wieser, 1995). Thus, we suspect that the 'two-gear system' is not yet functional in fish larvae, the consequence being that when these fish are swimming at high speeds in cold water the muscle fibres have to operate over an increasingly inefficient range of shortening velocities. The intricate relationships between swimming speed, temperature, muscle mechanics and energy metabolism explain the shape of the  $R_a$  curves in Fig. 1A, the metabolic cost of swimming at 15 °C increasing more rapidly with swimming speed than that of swimming at 20 °C.

Fuiman and Batty (1997) concluded that when studying the effects of temperature on the active metabolic rate of fish larvae the physical effect of viscosity has to be taken into account. We extend this with the caveat that in these animals any hydromechanical effects may be overwhelmed both by developmental constraints, particularly with respect to differentiation of the swimming muscles, and by the effects of temperature on the mechanics of muscle function.

This work was supported by the 'Fonds zur Förderung der wissenschaftlichen Forschung' of Austria, project no S-35/04. We thank Lee Fuiman for helpful comments on an earlier version.

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