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RESPIRATORY COST OF SWIMMING IN LARVAL AND JUVENILE CYPRINIDS

BY RUEDIGER KAUFMANN

Zoologisches Institut der Universität, Technikerstrasse 25, A-6020 Innsbruck, Austria

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Summary

The relationship between swimming speed and respiration rate for larvae and juveniles (1.5–600 mg fresh mass) of two cyprinid species, *Chalcalburnus chalcoides* and *Rutilus rutilus*, was measured in a flow-tunnel at 20°C.

1. A special tunnel respirometer with small volume and fast response had to be constructed to cope with the methodological difficulties encountered with the larvae.

2. The oxygen uptake increased quadratically with swimming speed if the oxygen debt incurred at the highest speeds was included in the calculations. The maximum speeds sustainable over 2 min were 6–8 lengths s^{-1}; the critical speed marking the onset of anaerobic processes was only 10–15 % lower. Energetics and performance were similar for both species. The cost of transport was much higher for larvae and juveniles than for adult fish and decreased rapidly during growth.

3. Standard and routine metabolic rates scaled with an allometry of $M^{-0.23}$, active rates with $M^{-0.15}$, where M is body mass in grams. In the smallest larvae, however, the standard rates were nearly independent of body mass. Their active rates of 80 μmol O_2 h^{-1} g^{-1} fresh mass were twice as high as those of adults.

4. The scope for activity was high on an absolute scale, but not when expressed as factorial scope, since the standard rate was also high. For the same reason, routine activity accounted for less than 25 % of the energy budget, despite the high cost of transport.

5. The data are discussed with respect to the changing swimming pattern during ontogeny, the shift from cutaneous to branchial respiration and the metabolic processes involved.

Introduction

In juvenile and adult fish, swimming activity is the most important factor influencing energy turnover (Brett and Groves, 1979). The same holds true for the larval and postlarval stages but, additionally, large amounts of energy are required for their extremely fast growth. The two cyprinid species investigated here, Danube bleak *Chalcalburnus chalcoides mento* (Agassiz) and roach *Rutilus rutilus*

Key words: *Chalcalburnus chalcoides*, *Rutilus rutilus*, swimming energetics, growth, cost of transport, scope for activity, tunnel respirometer.

(L.), differ in that roach start swimming and feeding within 3 days of hatching, but Danube bleak do not do so until the seventh day. Within 3 months they grow over nearly three orders of magnitude from 1.5 mg to 1 g (Wieser *et al.* 1988): this fast growth is necessary to reduce their vulnerability to predation. Thus, the energy budget seems to be finely balanced with the allocation of energy to growth and activity closely interrelated, since locomotion is a prerequisite for acquiring the food necessary for growth. In this context it is important to know more about the energetic costs of swimming: they can be expected to reflect the dramatic morphological and physiological changes occurring during the early life history (El-Fiky *et al.* 1987), the change of swimming style and the hydrodynamic situation.

The classic approach for assessing swimming energetics is to force the fish to swim in a flow-tunnel respirometer and to measure the relationship between swimming speed and oxygen uptake. Since the development of tunnel respirometers in the early sixties (Brett, 1964), extensive investigations have clarified the situation for larger fish, but very few similar data on larvae are to be found in the literature. Except for the results of Ivlev (1960*a*,*b*) and Dabrowski (1986*a*,*b*), most estimates of swimming costs are based on indirect evidence (Rombough, 1988). Hydrodynamic models for power requirements are also scarce (Webb, 1978). The present paper is intended to fill this gap in experimental evidence and to provide a link with the data on larger fish.

Investigations of this kind on larvae have been hampered by methodological problems. It proved difficult to force fish larvae to swim at a controlled speed and most respirometers were inadequate for the purpose. Nonetheless, the cyprinid larvae used here readily swim against an oncoming water current, provided they have enough space to move and that their short endurance times are taken into consideration. To meet these demands, a small Brett-type flow tunnel was constructed with special emphasis on a fast respirometer response. This apparatus made it possible to establish the power–performance relationships of swimming speed and respiration rate up to velocities where the larvae reach their aerobic capacity.

Materials and methods

Respirometric principles

In measuring respiration rates up to the maximum aerobic rate at high swimming speeds the primary methodological problem is the need for a rapidly responding respirometer. Especially in the case of fish larvae, with limited endurance, the apparatus should be able to resolve respiration changes in times well below 1 min. The usual designs, however, require measuring periods of around 15 min at a given swimming speed for reliable estimates of the respiration rate.

The only investigations so far made on the relationship between oxygen consumption and swimming speed for larvae and small juveniles employed the

optomotoric reflex to induce swimming, and this was restricted to relatively low speeds (Ivlev, 1960*a*,*b*; Dabrowski, 1986*a*,*b*). The classical methods for larger fish (reviewed by Beamish, 1978), in contrast, involve tunnel respirometers of various kinds (Blazka *et al.* 1960; Brett, 1964; Smith and Newcomb, 1970). With such methods higher swimming speeds are usually attained, since they make use of both the optomotoric response and the rheotactic behaviour of the animals. This approach is reasonable for larvae as well, provided the experimental apparatus is adapted to their needs.

Optimizing the performance of a respirometer always involves a compromise between opposing technical demands. Where response time is the primary concern, the flow-through principle using polarographic oxygen sensors should generally be preferred to closed or intermittent systems because it gives a continuous record of the respiration rate. To keep the time constants low, the measurement flow should be maximized and the volume of the animal chamber, in this case the recirculating flow-tunnel, should be minimized (Hughes *et al.* 1983; Kaufmann *et al.* 1989). However, the former impairs accuracy, while the latter makes it more difficult to achieve a satisfactory flow profile in the tunnel. Also, the animals require freedom of movement, and crowding effects have to be avoided.

In any case, the respirometric signal will be distorted by the lags within the system, a problem that can be overcome by employing signal correction techniques. These require, first, that the respirometer's response properties should be constant and reproducible, which is promoted by perfect mixing within a recirculating flow-tunnel and, second, that the oxygen recordings should be free of noise. The oxygen sensors therefore have to be shielded carefully against any disturbances, such as temperature fluctuations or pressure changes caused by the flow-tunnel.

The above demands were met by combining a flow-through respirometer of the 'twin-flow' type, as used by Gnaiger (1983) for continuous measurement, with a modified and miniaturized version of the flow-tunnel of Brett (1964), which may be classified as a low-volume, high-power device (Smith and Newcomb, 1970). This construction (Fig. 1) allows independent adjustment of the operating conditions for the respirometer and the flow-tunnel. The whole apparatus was built of polyvinylchloride and acrylic, and was submerged in a temperature-controlled water bath. A personal computer sampled the data and controlled the drive of the flow-tunnel and the calibration valve of the respirometer.

The tunnel respirometer

The recirculating flow-tunnel was driven by a centrifugal pump upstream of the swimming chamber (Fig. 1). With small larvae, a swimming chamber rectangular in cross-section (1.5 cm×3 cm×5.5 cm long) was used (Figs 1, 2). Adjustable vanes in the expansion cone upstream flattened the flow profile and gross turbulence was spoiled by a turbulence grid. Larger animals required higher speeds and more freedom to move in the longitudinal direction. For them, the tunnel was equipped with a longer chamber of circular cross-section (diameter 1.8 cm, 11.5 cm long). In

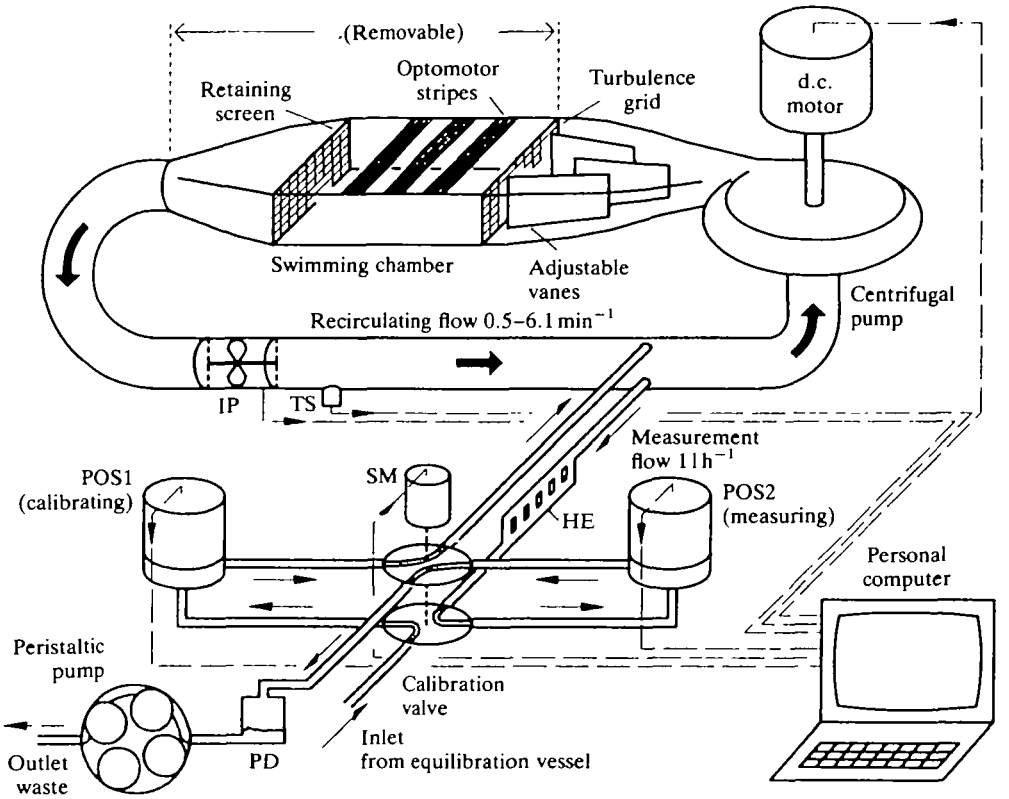

Fig. 1. The experimental apparatus combines a small Brett-type flow-tunnel (total volume 100 ml) with a twin-flow respirometer (Gnaiger, 1983) which is a two-sensor flow-through device. A personal computer acquires the data and controls the experimental protocol. POS, polarographic oxygen sensor; IP, indicator propeller; TS, temperature sensor; HE, heat exchanger; SM, servomotor of valve; PD, pulsation damping.

this chamber avoidance of the rear tunnel region could be enforced by charging the retaining screen with electric pulses (5 V 100 ms, 2 Hz) which caused no irritation to the animals. The total volume of the tunnel amounted to about 100 ml, with 25 ml in the smaller chamber and 29 ml in the larger one.

The whole swimming chamber could be conveniently removed from the apparatus for insertion of the animals. It was lit from above; stripes to induce the optomotor response helped the fish to keep their position. A mirror at an angle of 45° facilitated observation and video recordings were made through a window in the temperature-controlled bath.

With the help of injected dye, video recordings revealed a flat flow profile for both chambers. Since the animals blocked less than 7% of the tunnel's cross-section, the swimming speed could be estimated directly from the volume flow measured by an indicator propeller (type W16, Höntsch Instruments, Germany) in

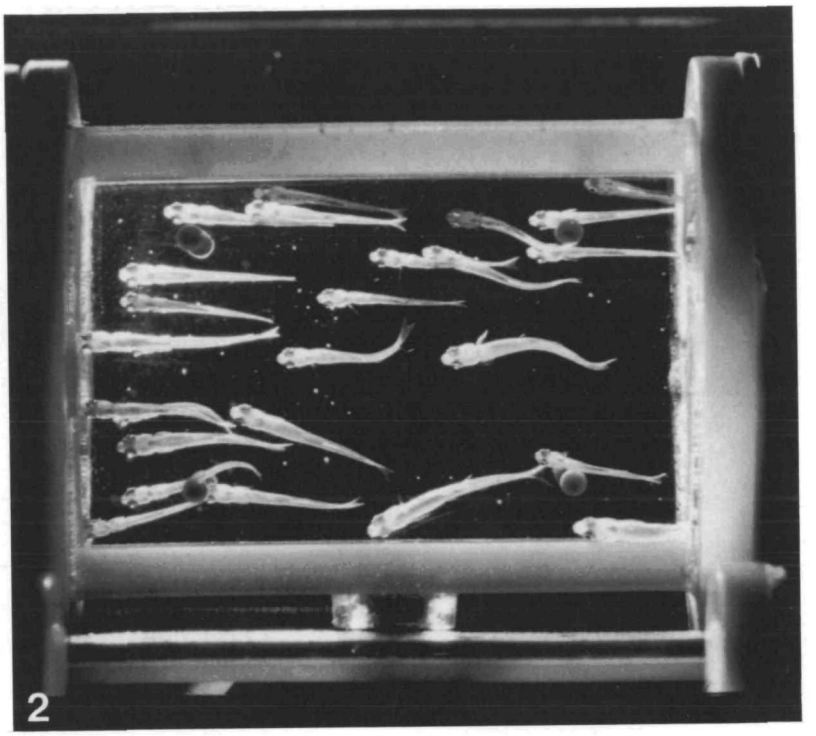

Fig. 2. Postlarval roach *Rutilus rutilus* (25 mg fresh mass, 17 mm total length) swimming in the flow-tunnel at moderate speed (viewed from below). The swimming chamber measures 55 mm by 30 mm (depth 15 mm).

the return path. The working speed range was 1–30 cm s^{-1}, the lower limit being set by the need for good mixing for respirometry and the upper limit by the onset of turbulence and cavitation.

The twin-flow respirometer, after Gnaiger (1983), is a flow-through type which measures the respiration rate from the difference in oxygen content between the inlet and the outlet of an animal chamber (here the whole flow-tunnel) continuously flushed by a slow measurement flow. A calibration valve alternates the position of the two polarographic oxygen sensors (model 2120, Orbisphere, Switzerland) with respect to the flow (Fig. 1). Thus, one sensor may be recalibrated with the incoming water while the other takes over measurement of the outlet water.

To avoid out-gassing, the respirometer was connected to the return path of the tunnel where the static pressure is lowest. A heat exchanger removed residual frictional heat caused by the tunnel before the water reached the oxygen sensor.

Air-saturated inlet water was drawn from an equilibration vessel and the measurement flow was kept constant at 1 l h^{-1} by a peristaltic pump at the outlet. With the biomass used (300–600 mg fresh mass) the oxygen concentration in the tunnel always remained normoxic above 85 % of air saturation.

Data recording and evaluation

A personal computer (Commodore C64) equipped with an analog/digital interface designed by the author was used to record the data. Signals from the oxygen sensors were sampled at intervals of 5 s. Averages over 15 s were stored on disk for later evaluation, together with measurements of the flow velocity in the tunnel, the temperature and the barometric pressure.

The product of the oxygen difference signal and the measurement flow yielded the rate of oxygen uptake, which was, however, affected by the inertia of the system. Several correction formulae have been proposed for recovering the real time course using estimates of the major time constants based on volumes and turnover rates (e.g. Evans, 1972; Niimi, 1978; Belaud *et al.* 1979; Propp *et al.* 1982; Hughes *et al.* 1983), but it must be emphasized that for maximum accuracy the respirometer's dynamic response should be determined experimentally. This was done here by injecting oxygen-free water into the swimming chamber. The resulting impulse responses revealed two time constants ($\tau_1 \approx 6$ min, $\tau_2 \approx 0.25$ min), regardless of the flow velocity in the tunnel. Thus, the actual time course could be reconstructed by using the differential equation (Jenkins and Watts, 1968; Randzio and Suurkuusk, 1980):

$$y(t) = x(t) + (\tau_1 + \tau_2)\frac{dx}{dt} + \tau_1\tau_2\frac{d^2x}{dt^2}, \quad (1)$$

with $y(t)$ denoting the corrected result and $x(t)$ the original respiration rate.

All oxygen consumptions are given as mass-specific quantities (μmol $O_2\,h^{-1}\,g^{-1}$ fresh mass). Applying the correction of equation 1 improved the effective temporal resolution to about 30 s and step changes of the respiration rates (see Fig. 3) could be estimated to $\pm 2\,\mu$mol $h^{-1}\,g^{-1}$ within that time. Absolute accuracy of measurement, in contrast, was mainly limited by the blank oxygen uptake in the respirometer and should be considered as $\pm 10\,\%$ of the routine rates for all experiments (± 1–$3\,\mu$mol $h^{-1}\,g^{-1}$). Blanks were recorded before and after experiments and interpolated linearly for correction (Dalla Via, 1983).

For all nonlinear curve fits the Levenberg–Marquardt algorithm (Press *et al.* 1986) was used, an iterative procedure taking into account the standard deviations of the individual data points. The residual standard deviation indicates the quality of the fit; error estimates of the parameters are given only when statistically meaningful.

Animals

Parent animals of *R. rutilus* and *C. chalcoides* were caught in Austrian lakes during spring 1988 and the eggs fertilized artificially in the laboratory. Larvae of *C. chalcoides* start swimming on or around the sixth day after hatching and those of *R. rutilus* within the first 3 days, and 2 days later the larvae are feeding. The total fresh mass at the time of hatching is 1.4 mg for *R. rutilus* and 1.9 mg for *C. chalcoides*. The yolk accounts for less than 10 % (S. Hinterleitner, personal communication) and is absorbed within 6–7 days. By this time the swim bladder

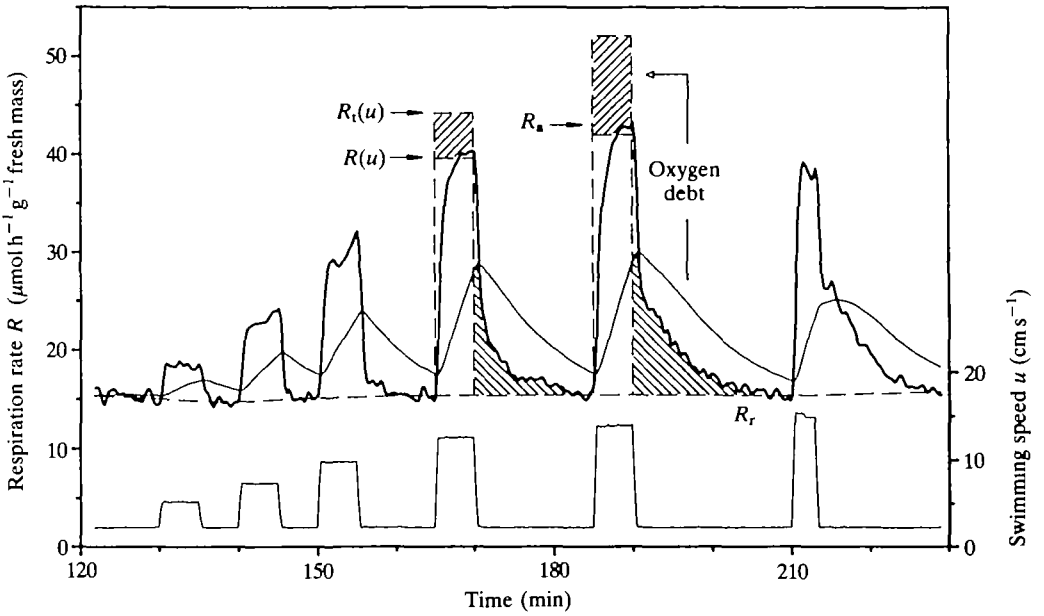

Fig. 3. Section of an experiment with roach *Rutilus rutilus* (2 months old, 100 mg) showing the response of the respiration rate R (heavy line) to changes in the swimming speed u (bottom trace). Corrections for the respirometer's time constants were applied to the original respiration signal (fine line). An oxygen debt (hatched area), where present, was added to the actual respiration level $R(u)$ to estimate the total respiratory demand of swimming $R_t(u)$. The resting periods yielded the routine respiration R_r; the active rate R_a is given as the maximum oxygen uptake inducible by exercise.

has become functional (El-Fiky and Wieser, 1988). Dry mass is 17 % of fresh mass in larvae and increases to 23 % in juveniles (Hinterleitner *et al.* 1987).

The larvae were fed *Artemia* nauplii during the first weeks and *Tubifex* later on. Animals were kept at the experimental temperature of 20 °C, which is close to the temperature of their natural environment (Rheinberger *et al.* 1987).

Experimental protocol

Experiments started shortly after hatching and continued until the juveniles outgrew the flow-tunnel. They covered a mass range of 1.4–280 mg for *R. rutilus* (eight experiments) and 2–570 mg for *C. chalcoides* (24 experiments), which corresponds to a total length of 7.5–45 mm. The first measurements on *C. chalcoides* included prefeeding larvae, whereas in all experiments on *R. rutilus* feeding animals were used.

Rapid growth of over 2.5 orders of magnitude during the first months makes it difficult to ensure comparable conditions with one respirometer. The number of animals in the experiments decreased from 250 of the youngest larvae to a single individual of the largest juveniles. Above 200 mg they were able to keep their position only in the longer chamber (see above). Experiments comparing both

types of swimming chambers with animals of this size yielded identical results for the respiration rates, but slightly better performance in the larger chamber. Above 600 mg most fish became too confined to attain a steady swimming pattern.

The animals were left unfed for 8–12 h prior to experiments to obtain postabsorptive respiration rates and to avoid defecation within the respirometer. Duration of an experiment was typically 4 h. After insertion into the swimming chamber the animals were allowed to adapt to changing flow velocities for about 1 h. The handling stress subsided rapidly and the initially high respiration rates at low speeds declined to routine levels, which then remained constant throughout the experiments (to within ±10 %). At the lowest flow velocity used (1–1.5 body lengths s^{-1}) the animals just oriented themselves to the water current, at still lower velocities they moved around freely in the chamber and respiration was independent of water speed.

The animals were exercised at a series of constant speeds, from low to high speeds, usually for periods of 5 min interrupted by resting periods of routine swimming (Fig. 3). At high speeds the exercise periods were shortened and the speed was further increased until the animals failed to swim for at least 2 min, which is the time required to reach a steady exercise respiration level. The acceleration during the stepwise changes of speed was limited to 1 cm s^{-2} to allow the animals to keep pace. When strenuous swimming caused an oxygen debt, the resting periods were extended until the respiration rates had dropped back to the routine level. Since it is known from larger fish that the apparent swimming capacity may depend on the experimental protocol (Farlinger and Beamish, 1977; Beamish, 1978), reduction of performance due to fatigue or exhaustion was ruled out by repeated swimming trials. After a final period of routine swimming over 30–45 min the animals were removed from the respirometer and anaesthetized for weighing.

Results

Respiratory response to swimming

The relationship between respiration rate and swimming activity is shown in Fig. 3, together with estimates for the oxygen demand of swimming. A stepwise increase of speed caused the oxygen uptake to rise sharply and to attain within 1–2 min a steady, speed-dependent level $R(u)$, for which the averages over the swimming periods (leaving out the first minute) were calculated. In some cases where the routine respiration R_r, measured at the low speeds, drifted slightly during experiments, this drift was subtracted from the $R(u)$ values. After strenuous exercise there was a slow return to the routine rates, revealing an oxygen debt due to anaerobic processes. Pre-exercise levels were reached within 15 min, which is much faster than found in larger fish (Heath and Pritchard, 1962; Brett, 1964; Soofiani and Priede, 1985). An estimate of the total oxygen uptake evoked by swimming $R_t(u)$ was obtained by adding the oxygen debt to the actual respiration rates $R(u)$, a procedure that makes two assumptions: first, that there is

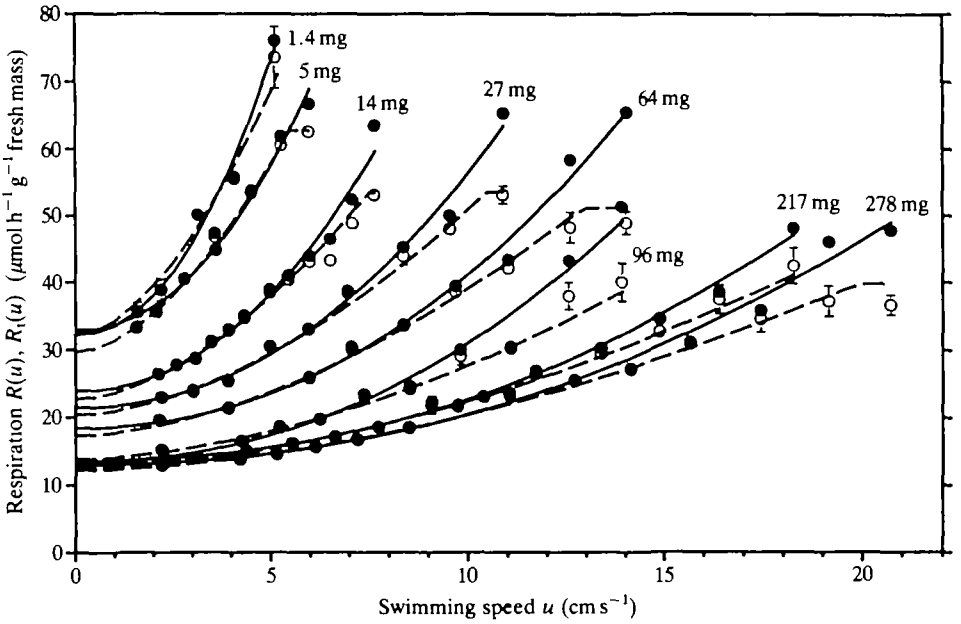

Fig. 4. Power–performance relationships between swimming speed and oxygen uptake of developing roach *Rutilus rutilus* at 20°C. Original data together with the fitted power functions ($a+cu^b$) are given for the respiration levels $R(u)$ (○---) and the total respiration $R_t(u)$ including the oxygen debt (●——). Each line corresponds to one experiment, the number of individuals decreased from 140 of the smallest larvae to three of the largest juveniles (average fresh mass is given). Lines for $R(u)$ are drawn levelling off at the observed active rates R_a.

a constant basal metabolism to which any activity-related respiration is added and, second, that the size of the oxygen debt represents the anaerobic work done.

Power–performance relationship

Plotting the respiration rates $R(u)$ and $R_t(u)$ against swimming speed (Figs 4, 5) gives the well-known pattern of a curvilinear increase with speed and a tendency for the oxygen uptake $R(u)$ to level off at the highest speeds, where anaerobic processes and the concomitant oxygen debt begin to contribute to the total metabolism $R_t(u)$ (Brett, 1964). The scatter of these data is quite small compared with many similar investigations on larger fish (e.g. Brett, 1964; Smit *et al.* 1971; Priede and Holliday, 1980), which is attributed to the steady swimming pattern and the unexcited behaviour of the larvae and juveniles.

For an empirical description of these power–performance relationships between respiration (R) and swimming speed (u), functions of the form:

$$R(u) = a + cu^b \tag{2}$$

were chosen, where a is the standard metabolic rate at zero swimming speed, and b and c are constants. Such power functions were also used in the earliest

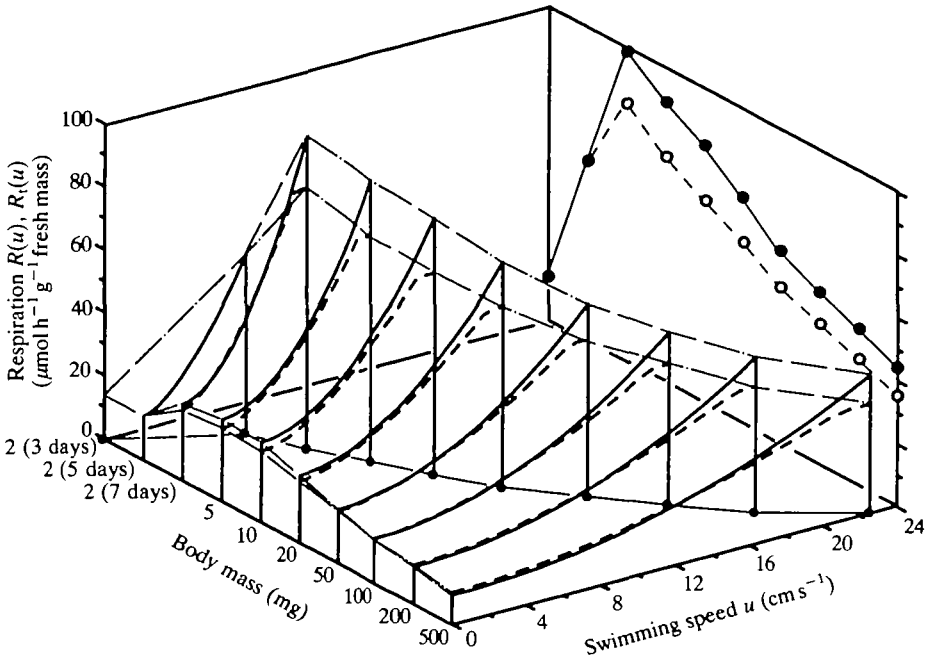

Fig. 5. Power–performance relationships of developing Danube bleak *Chalcalburnus chalcoides*. The respiration levels $R(u)$ (broken lines) and the respiration $R_t(u)$ (solid lines) are drawn according to the model of Table 1 (based on 24 experiments with 1–250 individuals, numbers decreasing with body mass). The maximum values attained are outlined on the back plane, the development of swimming ability is shown for the 2-mg larvae (five experiments, days after hatching given in brackets).

investigations of this kind on fish larvae (Ivlev, 1960*a*,*b*) but were very soon replaced by exponential functions (Brett, 1964):

$$R(u) = ae^{bu}, \tag{3}$$

which have since been used throughout the literature. The shapes of these functions are very similar at higher speeds, but differ considerably at low speeds, which is especially important when using them to extrapolate to the standard metabolic rate at zero swimming speed (parameter a). Fitting exponential curves (equation 3) always gives lower estimates, and with the cyprinid larvae these curves consistently fell too low even at routine speeds. Extrapolations from power functions (equation 2), however, coincided with values from inactive fish, measureable in a few cases when the animals rested at the retaining screen of the tunnel. Therefore, the preference for power functions is justified here. They have the additional advantage that the velocity-dependent term is analogous to that in models for the hydromechanic thrust power (Webb, 1978) and that the standard rate (parameter a) does not interfere with the slope. Using the exponential form the estimated standard rates in the present study would have been 25 % lower, but

Table 1. *Dependence of the total metabolic intensity* R_t *(μmol O_2 h^{-1} g^{-1} fresh mass) on swimming speed* u *(cm s^{-1}) and fresh body mass* M *(mg) for feeding larvae and juveniles*

$R_t(u)=a+cu^b$	*R. rutilus* (1.4–280 mg)	*C. chalcoides* (2–570 mg)
a (standard rate)	31.9 (<5 mg) $46.2M^{-0.23}$ (≥5 mg)	$23.2M^{0.07}$ (<8 mg) $45.5M^{-0.25}$ (≥8 mg)
b (exponent)	2.15	$1.77+0.10\log M$
c (factor)	$2.04M^{-0.63}$	$3.90M^{-0.67}$
u_{max}	$4.10M^{0.29}$	$5.72M^{0.22}$
L (total length)	$0.68M^{0.27}$	$0.60M^{0.31}$

The parameters (a,b,c) of the power relationship $R_t(u)=a+cu^b$ are given as functions of body mass (fitted to estimates from 8 and 24 experiments for *Rutilus rutilus* and *Chalcalburnus chalcoides*, respectively).

Agreement with experimental data is within ±10 % of predicted values. This applies for speeds from 1 length s^{-1} to u_{max} (cm s^{-1}); the allometry of the total length L (cm) is included for conversion of absolute speed to lengths s^{-1}.

The number of experiments was N=8 for *Rutilus rutilus* and N=24 for *Chalcalburnus chalcoides*.

recalculation of data from Webb (1971) showed that the difference could be as much as 50 % with large fish.

Fitting curves of the form of equation 2 to the data from individual experiments yielded a rather large scatter of the exponents b. Nonetheless, they showed that the total energy expenditure $R_t(u)$, including the oxygen debt, grows nearly quadratically with swimming speed for all sizes of *C. chalcoides* and *R. rutilus* (b=1.91±0.67, N=22 and b=2.15±0.41, N=8, respectively, mean±standard deviation), possibly with a slight increase of the exponent during growth in *C. chalcoides* (P<0.1). Estimates from values for $R(u)$ restricted to the speed range of aerobic swimming gave slightly lower exponents.

Table 1 gives the mass-dependences of parameters a, b and c from equation 2 for a model approximating the total metabolic intensity $R_t(u,M)$ as a function of swimming speed u and fresh body mass M. To express speed in terms of lengths s^{-1}, the allometry of the total length is included. The only difference of biological significance between the two species appears during the yolk-sac stages: whereas *R. rutilus* starts swimming very soon and attains high aerobic powers (Fig. 4), *C. chalcoides* develops its swimming ability gradually during the first week (Fig. 5).

Swimming speeds

The maximum speeds sustainable for 2 min (u_{max}) were 6–8 length s^{-1}, with no clear dependence on animal size when given in these relative units (Fig. 6, Table 1). The swimming capacity of adult fish is usually characterized by the 'critical speed' determined from their stamina when subjected to a strictly

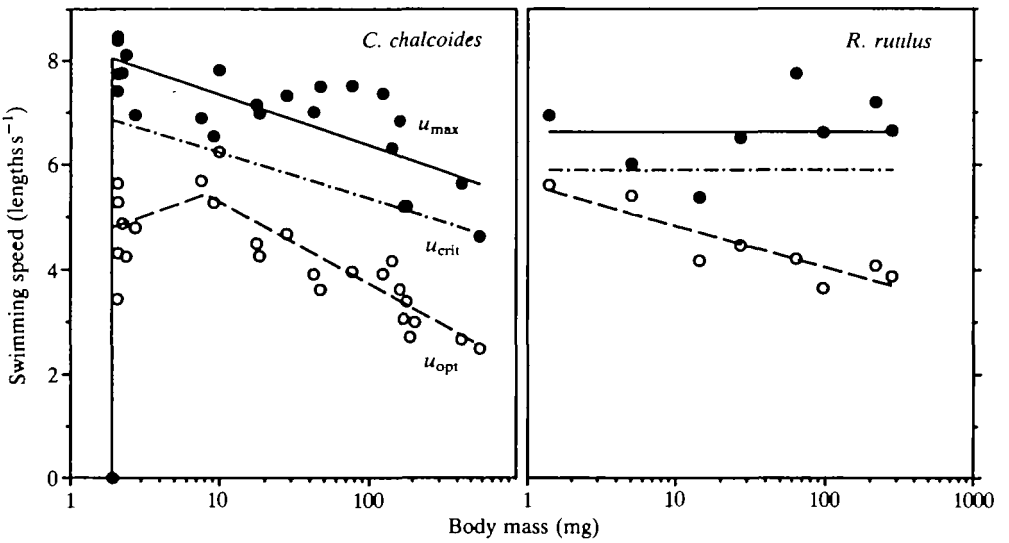

Fig. 6. Swimming speeds of Danube bleak (*Chalcalburnus chalcoides*) and roach (*Rutilus rutilus*). u_{max} (●——) is the maximum speed sustainable for 2 min, u_{crit} (–·–) denotes the limit of aerobic swimming where the oxygen demand R_t reaches the aerobic capacity R_a, and u_{opt} (○– –) refers to the speed with the minimum gross cost of transport (see Fig. 8). Points give data for each experiment (N=24 for *C. chalcoides*, N=8 for *R. rutilus*).

observed swimming protocol (Farlinger and Beamish, 1977; Beamish, 1978). This approach is difficult with the very fragile larvae, and especially so in the present investigation, since it was important to avoid exhaustion to obtain reliable respiration measurements. Therefore, the term critical speed (u_{crit}) is used here for the speed at which the metabolic energy demand $R_t(u)$ meets the aerobic capacity R_a (see below) and above which any further speed increase has to be powered by anaerobic processes. For *C. chalcoides* and *R. rutilus* u_{crit} values were 85 and 89 %, respectively, of the speed maintainable over 2 min (u_{max}). Around u_{crit} the fatigue times started to decrease sharply, indicating the transition from prolonged to burst swimming (Beamish, 1978). The maximum burst speeds of larvae are known to be much higher: 25 length s^{-1} over 100 ms are documented on high-speed films of *C. chalcoides* measuring 10 mm (see Fig. 10A) and speeds up to 55 length s^{-1} have been reported from other species (Hunter, 1972; Webb and Corolla, 1981; Fuiman, 1986).

Standard, routine and active respiration

The terms standard (R_s), routine (R_r) and active (R_a) metabolic rates are commonly defined in conjunction with relationships between metabolism and activity (Beamish and Mookherjii, 1964; Brett, 1964; Brett and Groves, 1979). Standard and active metabolic levels have been difficult to determine for fish larvae for want of power–performance relationships allowing an extrapolation

down to inactivity and extending up to maximum aerobic capacity. Estimates for the standard rates were obtained from anaesthetized animals (e.g. De Silva and Tytler, 1973; De Silva *et al.* 1986) or immediately before hatching (e.g. Gruber and Wieser, 1983), and active rates were assessed during bursts of activity induced by electric shocks (Wieser *et al.* 1985; Wieser and Forstner, 1986). The minimum and maximum respiration rates observed during long experiments have frequently been used as approximations (e.g. Cetta and Capuzzo, 1982; Wieser *et al.* 1988). But with all these approaches it remained questionable whether they isolated the energy demand of locomotion.

The respiration rates given in Fig. 7 follow more closely the original definition. Routine rates (R_r) are averages for resting periods throughout the experiments. They refer to the postabsorptive state (at least for the post-yolk-sac stages) and to swimming speeds of 1–2 length s^{-1}, which is within the range of natural cruising speeds (Wanzenböck and Schiemer, 1989). The values given here agree with oxygen consumptions measured in animals swimming freely in larger respiration chambers (Wieser and Forstner, 1986; Wieser *et al.* 1988). Standard rates (R_s) were extrapolated from the power–performance relationships (equation 2). Since estimates based on the total metabolic rates $R_t(u)$ and on the actual respiration rates $R(u)$ yielded slightly different results (see Figs 4, 5), averages of both are given. Active rates (R_a) are the highest 1-min averages measured in the experiments. They occurred at speeds where stamina was around 2 min; higher

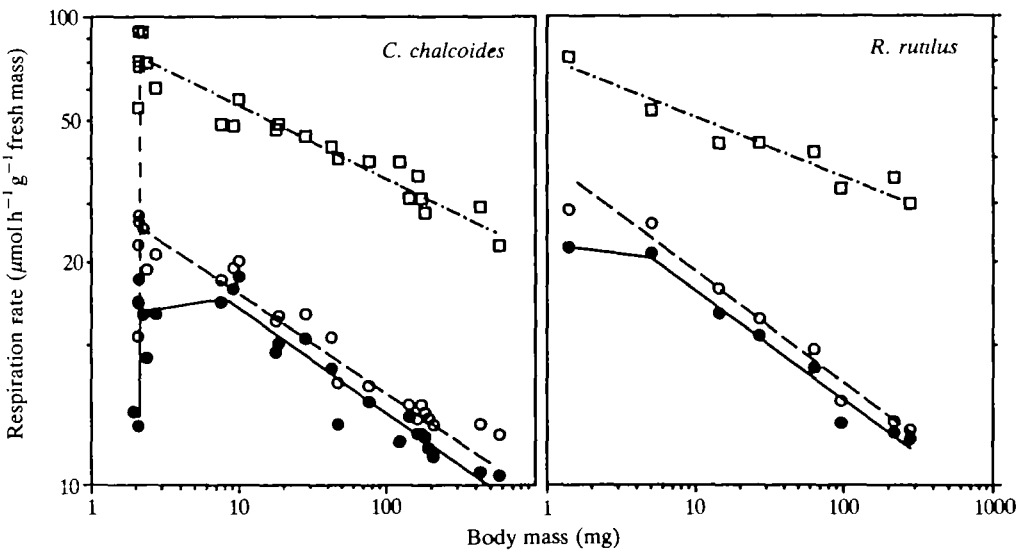

Fig. 7. Size scaling of the standard (R_s, ●——), routine (R_r, ○--) and active (R_a, □-·-) respiration rates of *Chalcalburnus chalcoides* and *Rutilus rutilus* (number of experiments N=24 and N=8, respectively). Routine and active levels are measured values, standard rates are extrapolated from the power–performance relationships ($a+cu^b$). The corresponding scaling allometries are given in Table 2.

Table 2. *Scaling of standard, routine and active respiration rates (μmol O_2 h^{-1} g^{-1} fresh mass) with body mass* M *(mg) for feeding larvae and juveniles*

	R. rutilus (1.4–280 mg)			*C. chalcoides* (2–570 mg)		
$R=AM^B$	*A*	*B*	S.D.	*A*	*B*	S.D.
Standard rate*			±0.82			±1.88
(R_s)	32.58	−0.041	(<5 mg)	22.69	0.048	(<8 mg)
	(±1.64)			(±1.05)		
	44.32	−0.232	(≥5 mg)	39.97	−0.224	(≥8 mg)
	(±2.23)	(±0.018)		(±1.85)	(±0.018)	
Routine rate			±2.19			±2.67
(R_r)	49.34	−0.237		41.78	−0.213	
	(±1.24)	(±0.012)		(±1.65)	(±0.009)	
Active rate			±4.98			±3.18
(R_a)	92.12	−0.156		81.14	−0.126	
	(±2.84)	(±0.011)		(±3.18)	(±0.013)	

The parameters of allometric functions AM^B are given with their standard deviations (estimated from nonlinear curve fitting).

The number of experiments was $N=8$ for *Rutilus rutilus* and $N=24$ for *Chalcalburnus chalcoides*.

S.D. denotes the standard deviation of the fit; * fitted to log-transformed data.

speeds over shorter periods caused only a larger oxygen debt and no further increase of the respiration rates. Hence these values are interpreted as the maximum aerobic turnover.

Metabolic levels during growth can be described by the allometric function $R=AM^B$ (Table 2). These functions are usually applied to metabolic rates of individuals, whereas here the mass-specific metabolic intensities are used and therefore the mass exponents (B) are lower by 1.

The basic trends were deduced from the abundant data on *C. chalcoides* and then applied in an analogous form to the data on *R. rutilus*. Most remarkable are the extremely high aerobic capacities R_a, around 80 μmol h^{-1} g^{-1}, found immediately after the larvae start swimming. They then decline in a uniform manner with mass exponents near −0.15. This is significantly higher than the exponents around −0.23 for the routine rates R_r. The standard rates R_s develop biphasically. From the onset of swimming to a mass between 5 and 10 mg they are nearly constant, but no reliable allometry can be given for this range. As the fish grow, the standard rates decline in the same manner as the routine rates.

Thus far the results for both species are quite similar, apart from slightly higher routine and standard rates in *R. rutilus*, but experiments with the late-swimming *C. chalcoides* during development of locomotor activity revealed an interesting effect. Until the fifth day after hatching the oxygen uptake of the immobile larvae was 14 μmol h^{-1} g^{-1} ($N=3$). Then, when they started swimming and before the onset of feeding and rapid growth, not only did the routine and active rates

increase as expected but the standard metabolic rate also rose to about $23\,\mu mol\,h^{-1}\,g^{-1}$ ($N=2$).

Scaling of routine and standard metabolism of fish has been intensively studied. There are, however, large variations in the mass exponents given for different species and developmental stages. It is generally believed that, for individual metabolic rates, 0.80–0.85 is a good estimate for mass exponents for juveniles and adults (Winberg, 1961; Brett and Groves, 1979), whereas for fish larvae the value may be closer to the isometric value of 1.0 (Rombough, 1988; Giguere *et al.* 1988). The routine rates with scaling exponents around 0.8 found here agree well with earlier results from cyprinid larvae (Kudrinskaya, 1969; Karpenko and Proskurina, 1970; Wieser and Forstner, 1986). Nonetheless, exponents approaching 1 are probably more appropriate for the standard rates of the earliest developmental stages. Similar changes in the allometry during development have been reported for other species (Kamler, 1976; Dabrowski, 1986*c*) and may be a general feature (Rombough, 1988).

Comparable data on the size-dependence of active metabolic rates are scarce. In salmonids, active rates scale with higher mass exponents than standard rates, and for juveniles may even be above the isometric value of 1 (Brett, 1964, 1965; Wieser, 1985). To a lesser extent this also holds true for the larval cyprinids, with exponents of 0.87 and 0.84, but here the mass-specific active rates clearly decline with mass. This is hardly surprising as they are 2.5-fold higher than those of adult fish (Blaxter, 1969; Beamish, 1978) and are, moreover, among the highest respiration rates ever recorded for fish. Higher oxygen consumptions have only been found in clupeid larvae (Holliday *et al.* 1964; Eldridge *et al.* 1977), disregarding the unbelievably high values of Ivlev (1960*a*,*b*).

Cost of transport

For comparative purposes, the metabolic cost of swimming is expressed as the energy required for a unit mass of animal to travel a unit distance. This cost of transport is much higher for small animals than for large ones and has been shown to decrease allometrically with body mass for all forms of locomotion (Schmidt-Nielsen, 1972). For juvenile and adult fish (3–1500 g) the allometry is well documented (Beamish, 1978). A decreasing trend has also been found for fish larvae (Ivlev, 1960*a*; Dabrowski, 1986*b*,*c*).

The cost of transport is calculated from the power–performance relationships (equation 2) and may be given as a gross cost by including the maintenance metabolism or as a net cost by considering only the energy expenditure for swimming:

$$\text{gross cost} = \frac{R_t(u)}{u}, \tag{4}$$

$$\text{net cost} = \frac{R_t(u) - R_s}{u}. \tag{5}$$

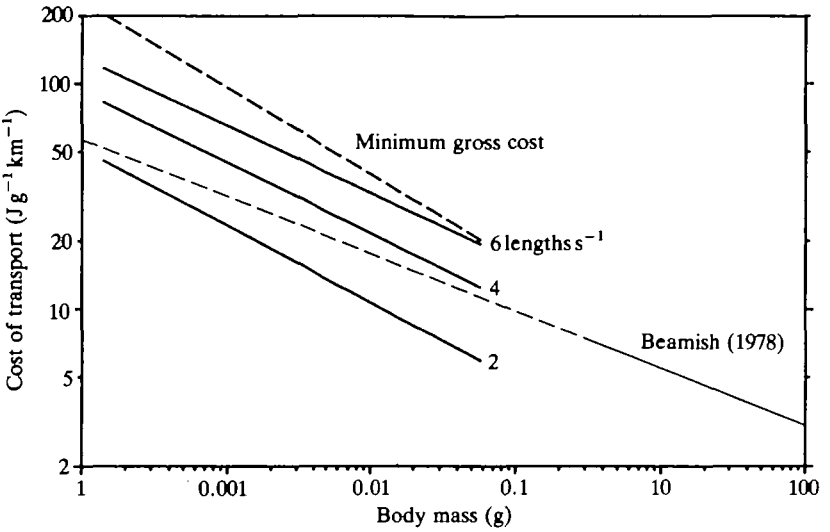

Fig. 8. Scaling of the cost of transport (estimated from pooled data of both species, N=32) compared with the trend given by Beamish (1978) for fish heavier than 3 g (fine line). The net costs (solid lines) are given for speeds of 2, 4 and 6 lengths s^{-1}, the minimum gross cost (broken line) refers to the speed u_{opt} (see Fig. 6).

Thus, the costs follow the rise of the power–performance relationships (Figs 4, 5), and their decrease during development is apparent from the flattening of these curves. Owing to the convex shape, the net cost increases steadily with swimming speed, whereas the gross cost attains a minimum at a particular speed u_{opt} (Fig. 6). Respiration rates were converted to energy units using an oxycaloric equivalent of 450 kJ mol^{-1} O_2 (Brett and Groves, 1979). The very similar costs for both species, *C. chalcoides* and *R. rutilus*, were pooled for the regressions shown in Fig. 8.

The gross costs at steady swimming speeds for animals of 0.6 g are double, and for the smallest larvae even four times, those obtained by extrapolating the relationship given by Beamish (1978). Qualitatively this is similar to the findings of Dabrowski (1986*c*) for coregonid larvae. At swimming speeds of around 4 lengths s^{-1} the net costs are also higher than expected from the trend in large fish, but only by a factor of 1.5. Since, in larvae, the gross cost is totally dominated by their very high standard rates, it is probably more reasonable to use net costs for comparisons between small and large fish. Moreover, the net cost is the more relevant quantity for the planktivorous cyprinids, which have to optimize the energy gained by catching prey (Wanzenböck and Schiemer, 1989).

Scope for activity

The difference between active and standard metabolism ($R_a - R_s$), which gives the aerobic power (per unit mass) available for locomotor activity, was termed the 'scope for activity' by Fry (1947). Owing to the problems connected with these metabolic levels the meaning of scopes given for fish larvae is unclear in many

cases. Sometimes they are interpreted as a 'relative scope' (R_a-R_r), proposed by Wieser (1985) as an alternative, or as 'routine scopes' (R_r-R_s), referring to the energy employed for routine activity. Many authors prefer to express the respiration increase over the standard rate as factorial scopes (R_a/R_s). These are, however, mostly governed by the development of the standard rates and therefore give little insight into the context of swimming energetics (see Rombough, 1988).

The scope in terms of aerobic power (Fig. 9, R_a-R_s) is highest for the smallest larvae and then, after a rapid decline, remains fairly constant for body masses above 10 mg. Even at this lower level, the scope is similar to that of powerful adult swimmers like salmonids (Brett, 1964; Blaxter, 1969; Beamish, 1978). The factorial scopes (Fig. 9, R_a/R_s), in contrast, are relatively low in the larvae, because of their high standard rates. They range from 2.5 to 4, with a minimum for the early feeding stages of 5–8 mg, and are within the variability of relative scopes (R_a/R_r) reported for larvae of various species (Rombough, 1988).

In assessing the cost of routine activities, the factorial representation of routine scope (R_r/R_s) is informative, since it indicates the contribution made to the energy budget. Values around 2 are thought to be representative for fish larvae (Rombough, 1988), which means that 50 % of the routine metabolism is caused by locomotion. In the case of the cyprinid larvae, this seems to be a gross

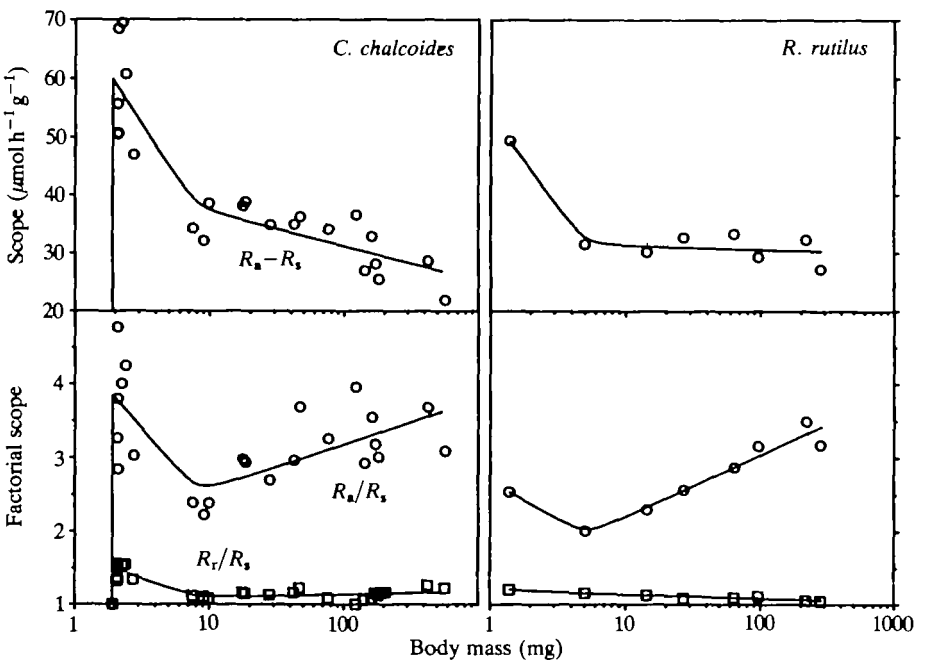

Fig. 9. Scope for activity of *Chalcalburnus chalcoides* and *Rutilus rutilus*. Top, scope in terms of metabolic power (R_a-R_s). Bottom, factorial scope (R_a/R_s, ○) and factorial scope for routine activity (R_r/R_s, □). The number of experiments was N=8 for *R. rutilus* and N=24 for *C. chalcoides*.

overestimation. Their routine scopes reached 1.50 only for the newly hatched *C. chalcoides* (Fig. 9), which suggests that activity never accounts for more than 30 % of the routine respiration, but that 10–15 % is a more realistic figure for feeding larvae and juveniles. The data thus indicate that, despite the high cost of transport, routine activity does not play such an important role in the energy budget of the larvae as is generally assumed. This may also be the case in other species, but it would not be expected for negatively buoyant larvae lacking a functional swim bladder, in which additional energy is required for lifting the fish off the substratum (Priede and Holliday, 1980).

Discussion

Swimming styles and swimming efficiency

Owing to their fast growth and to morphological changes, fish larvae encounter dramatic changes in their hydrodynamic environment, often with a concomitant shift from an anguilliform to a subcarangiform or carangiform swimming style (Hunter, 1972; Batty, 1981, 1984; Dabrowski, 1986*b*). The flow-tunnel experiments with speeds up to 8 length s^{-1} covered a range of Reynold's numbers (*Re*) from 50–500 for the smallest larvae to 10^3–10^4 for juveniles of 500 mg. Thus, the cyprinid larvae are too large to be dominated by viscous effects ($Re<10$), but at routine speeds they experience an intermediate situation ($10<Re<200$) where both frictional and inertial forces play a role (Weihs, 1980) until, as they reach a length of 15 mm ($Re>200$), swimming is governed by the inertia of the water alone.

Small larvae of *C. chalcoides* and *R. rutilus* swim in a continuous manner using flexing movements of the whole body (Fig. 10A). Very soon, with the development of the fins, the larvae change to a typical subcarangiform pattern of swimming, concentrating the propulsive movements towards the tail region (Fig. 10B), and adopting a 'burst-and-coast' swimming style. This change during growth conforms with predictions on theoretical grounds that the subcarangiform burst-and-coast style becomes more efficient with increasing Reynold's numbers (Weihs, 1974, 1980; Videler and Weihs, 1982; Webb, 1988). As found by Batty (1981) for plaice larvae, the cyprinids use their pectoral fins to counteract recoil of the tail and to reduce yaw of the head. At higher speeds the pectoral fins are inactive and a continuous swimming mode is employed.

The high cost of transport does not necessarily mean that the larvae are inefficient in a hydrodynamical sense; it is usually thought that their propeller efficiency is lower than that of larger fish (Weihs, 1980). For the smallest larvae it is impossible to evaluate the hydrodynamic power without kinematic data (Vlymen, 1974). In larvae above 20 mg, however, the Reynold's numbers are sufficiently high for a rough estimate of the thrust power, which can be used for a qualitative comparison with the metabolic energy expenditure (Webb, 1988). According to such simple models (Smit *et al.* 1971; Webb, 1978), the hydromechanical power increases faster with swimming speed (exponents 2.6–2.8) than the metabolic

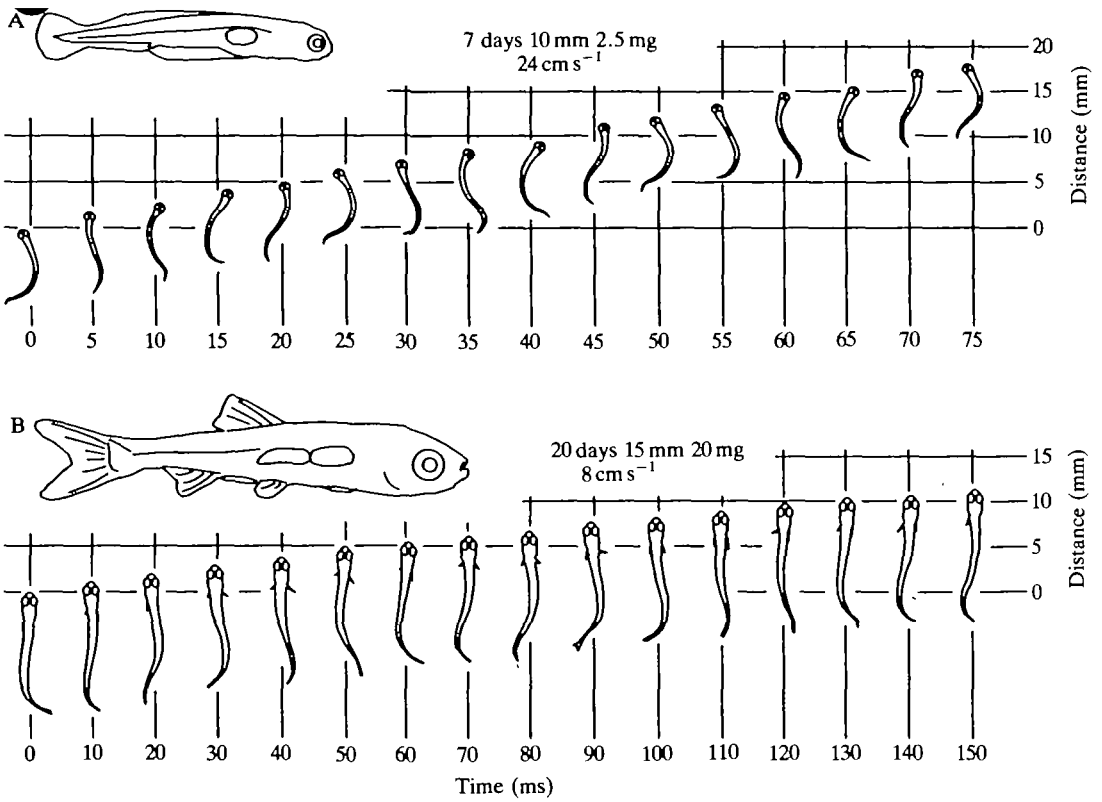

Fig. 10. Swimming styles of *Chalcalburnus chalcoides* for larval (A) and postlarval (B) stages (sequences redrawn from high-speed film at 200 frames s^{-1}). Age, total length and fresh mass are indicated, together with the swimming speed (burst speed in A, near critical speed in B).

power (exponent 2; Table 1), and it decreases more slowly with the size of the animals. This indicates an increase of the overall efficiency, consisting of the muscular and the hydrodynamic efficiency, with speed and with body mass. Probably the development of both the swimming muscles and efficient propulsive movements contribute to this improvement during growth.

Oxygen supply by cutaneous and branchial respiration

It is known that the mechanism of oxygen supply shifts from cutaneous to branchial respiration during larval ontogeny (Rombough, 1988). This is obvious from the relative amount of surface available for gas exchange on the body and the gradually differentiating gills (De Silva, 1974) and from experiments with carbon monoxide poisoning (Holeton, 1971). Moreover, a thin layer of red muscle fibres beneath the body surface may improve skin respiration in larvae (El-Fiky and Wieser, 1988). It is uncertain when and to what extent gill respiration takes over (Rombough, 1988). In various cyprinid species the gills appear to be fully

functional at 40 days (El-Fiky and Wieser, 1988), but the importance of cutaneous respiration may extend far into the juvenile stages (Oikawa and Itazawa, 1985).

Since the active respiration rates are limited by the oxygen transport to the tissues, as shown by their dependence on the oxygen concentration (R. Kaufmann, in preparation), they can be expected to reflect the capacity of the respiratory mechanism. The uniform development of active rates during growth (Fig. 7) therefore corroborates the suggestion that the shift from cutaneous to branchial respiration proceeds gradually (Oikawa and Itazawa, 1985; El-Fiky and Wieser, 1988). Moreover, the aerobic capacity of the larvae with their large body surface is superior to that of juveniles and would probably not be improved by earlier development of the gills, which could be costly to irrigate at a small size (Osse, 1989).

Metabolic energy sources for swimming

It has to be kept in mind that the metabolic energy expended for swimming was estimated on the assumption that there is a constant maintenance metabolism, even during strenuous activity. This seems to be the only reasonable assumption in the absence of additional information, although it may be challenged on the grounds that blood flow to the internal organs can be reduced during swimming (Randall and Daxboeck, 1982) and that the apparent respiratory cost of swimming in some cases depends on the feeding state (Furnell, 1987) and on environmental conditions (R. Kaufmann, in preparation). It is thus also possible that energy usually employed for maintenance can be re-allocated for locomotion upon demand (Wieser, 1989).

One of the advantages of an experimental protocol allowing the animals to rest between periods of exercise is that it facilitates measurement of the oxygen debt as an indicator of anaerobic processes during swimming. No oxygen debt was incurred up to quite high speeds and swimming therefore seems to be fully aerobic over a wide speed range. This is not surprising for the larvae, which have additional oxidative activity in the bulk musculature (El-Fiky *et al.* 1987; Hinterleitner *et al.* 1987), but adults of some cyprinid species progressively use their anaerobic white muscles even at moderate speeds (Johnston and Goldspink, 1973).

The highest speeds used here caused an oxygen debt amounting to 30 % of the total swimming respiration for both species. Even after such strenuous exercise, the animals recovered rapidly and there was no deterioration of performance during subsequent swimming trials. The time course of the oxygen debt repayment gives no clue to the anaerobic energy sources. Phosphocreatine levels are restored within the same time (Lackner *et al.* 1988), but the usually slower removal of lactate from anaerobic glycolysis may also be fast when complete exhaustion is avoided (R. Lackner, in preparation). From the activities of glycolytic enzymes measured *in vitro* it was deduced that the anaerobic capacity is higher in larval *C. chalcoides* than in larval *R. rutilus* (Hinterleitner *et al.* 1989). A corresponding

difference in performance, however, could not be found in the present flow-tunnel experiments.

Estimation of the power employed for burst swimming at the observed speed of 25 length s^{-1} (Fig. 10A) by extrapolating the power–performance relationships is mere speculation, but similar values, equivalent to an oxygen uptake of 1000 μmol h^{-1} g^{-1}, were deduced from the oxygen debt after burst swimming in small salmon (Puckett and Dill, 1984). Therefore, it is reasonable to assume that the burst power surpasses the aerobic capacity severalfold. The remaining anaerobic power requirement is high compared with the activity of glycolytic enzymes (Hinterleitner *et al.* 1989), making phosphocreatine breakdown the most likely energy source for burst swimming.

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