JOURNAL OF EXPERIMENTAL ZOOLOGY 307A:296–300 (2007)

Estimating the Active Metabolic Rate (AMR) in Fish Based on Tail Beat Frequency (TBF) and Body Mass

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ABSTRACT Tail beat frequency (TBF) was measured for carp (*Cyprinus carpio*) and roach (*Rutilus rutilus*), during steady swimming at five different speeds and for fish of various body masses. A multiple stepwise linear regression analysis resulted in models for the prediction of TBFs depending on swimming speed as an independent variable. Speed explained 72 and 86% of the variance in TBF for carp and roach, respectively. By using these data to predict TBF from speed and substituting values into a model from a previous study that predicts active metabolic rates (AMR) from body mass and swimming speed, we can calculate AMR from only fish mass and TBF. Thus, the derived models can be used to estimate the AMR in fish by measuring TBFs in the field using biotelemetry. The approach presented here is a useful and relatively simple tool for estimating the activity metabolism in free-swimming fish. In future studies this method should be applied to a larger and more representative sample size to test the applicability and the validity for a broader range of species. *J. Exp. Zool. 307A:296–300, 2007.*

How to cite this article: Ohlberger J, Staaks G, Hölker F. 2007. Estimating the active metabolic rate (AMR) in fish based on tail beat frequency (TBF) and body mass. J. Exp. Zool. 307A:296–300.

The energetics and activity of free-swimming fish is of great interest to ecologists, because activity costs in fish are directly linked to food capture, predator avoidance, growth rate, reproduction and habitat shifts (Videler, '93; Webb, '94). As swimming activity accounts for the largest portion of the energy budget of a fish (Jobling, '94; Hölker and Breckling, 2002), accurate estimates of swimming costs are required for developing bioenergetics models in ecological fish studies.

The actual metabolism of free-ranging fish in the wild cannot be measured directly, because respiration measurements are not feasible under these conditions. Thus, metabolic rates of fishes in the field have to be determined based on laboratory measurements of the energy consumption of the fish.

Different methods have been proposed to estimate the metabolic rate of fish in the field, for example by doubling the standard metabolic rate (Winberg, '56) or by including spontaneous activity in laboratory tests of fish swimming (Jobling, '82). However, these methods only provide rough estimates, as the actual activity level of the fish cannot be considered. The actual activity metabolism in free-swimming fish has to be assessed based on laboratory-derived models combined with direct measurements of fish activity by telemetric field studies.

Biotelemetry represents a precise method to link field metabolic rates to laboratory-derived estimates of the energy expenditure. Radio or ultrasonic transmitters can be used to estimate field rates by measuring aspects of fish physiology such as heart rate, axial muscle activity, and ventilation rate or tail beat frequency (TBF) as indices of locomotor activity (Cooke et al., 2004a). TBF has proved to be an accurate indicator of the swimming activity in carangiform and subcarangiform swimmers (Bainbridge, '58; Hunter and Zweifel, '71; Steinhausen et al., 2005). Electromyogram (EMG) locomotory activity telemetry seems to be

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Received 5 January 2007; Accepted 9 February 2007
Published online 15 March 2007 in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/jez.384.

the most reliable method for measuring TBFs in free-swimming fish (Ross et al., '81; Hinch et al., '96; Briggs and Post, '97, for a review see Cooke et al., 2004b), but it has also been measured with pressure transducers (Webber et al., 2001). As the axial muscles are the main swimming muscles in most fusiform fish, EMGs can be used as reliable estimates of swimming costs by relating them to oxygen consumption rates measured under laboratory conditions.

In this paper, we provide measurements of TBFs related to the oxygen consumption of two morphologically distinct cyprinids. The derived models of swimming costs depending on tail beat rate and mass can be used in telemetric field studies to estimate the activity costs of carp (*Cyprinus carpio* L.) and roach (*Rutilus rutilus* (L.)). Using this method of TBF observation and respirometry measurements of fish swimming in the lab, it will be possible to develop such relationships for other fish species to estimate activity costs of free-swimming fish in the field.

Thus the aim of this study was to present a simple tool for estimating active metabolic rates in the field based on laboratory measurements. The two physiological parameters needed for these models, fish mass and tail beat rates, are relatively easy to measure. We hope that this paper will encourage researchers to use this method in more comprehensive studies of fish eco-physiology.

MATERIAL AND METHODS

Roach were caught from Lake Müggelsee in Berlin, Germany. After capture, the fish were immediately transferred to laboratory aquaria. Carp were obtained from the Wageningen University, Netherlands, where they were cloned from one strain and were thus genetically identical. Before experiments, both species were kept under laboratory conditions for several weeks. The fish were held in glass aquaria with constantly aerated water at a temperature of $20.0 \pm 0.5^{\circ}C$ under a 12:12h photoperiod cycle. Specimens of roach 21–30 cm in total length, weighing 104–303 g, and carp 20–26 cm in total length, weighing 122–346 g, were used in this study.

Swimming activity of eight roach and carp was recorded using a CCD Video camera (25 frames per second) mounted above a swim tunnel for automated intermittent-flow respirometry designed after Hölker (2003). The used respirometer allowed short-interval measurements of fish swimming at different speeds over time periods of up to 1 week. It consisted of a measuring recirculation system (25 l) with a swimming chamber of 15 cm in diameter and 40 cm in length. An external ventilation system (125 l) supplied aerated fresh water in-between two measuring phases. The whole respirometer was temperature-controlled to a preset value of $20 \pm 0.2^{\circ}C$. Temperature and oxygen concentration were measured with a fixed TriOxmatic 701 sensor (WTW) coupled to an oximeter (WTW, Oxi 171) that allowed automated flushing and measuring periods.

To measure TBFs, the introduced fish were allowed to adapt to experimental conditions for at least 24 hr at a speed of $0.5\,BL\,s^{-1}$. Subsequently, swimming speeds of 0.5, 0.75, 1.0, 1.25 and $1.5\,BL\,s^{-1}$ were run for approximately 2 hr. At each swimming speed TBFs were counted for 10 not consecutive and randomly chosen minutes of swimming activity. One tail beat was defined, according to Hunter and Zweifel ('71), as a complete oscillation of the tail.

Mean values and standard deviations were calculated for each speed and individual fish. The set of TBF data for both species was analyzed by multiple stepwise linear regression. Swimming speed, body mass and tail beat amplitude were tested to evaluate which of these variables could contribute to the precision of the model. Candidates for independent variables were included in the model if the F statistics associated with those variables had a significant P-value. When testing the significance of the estimated parameters of the fitted model, t-statistics were calculated. Tail amplitude did not vary with swimming speed, which is in accordance with Hunter and Zweifel ('71) and Rome et al. ('90). As mass also did not correlate significantly with TBF, models only included swimming speed as an independent variable. Parameter estimates, standard errors, confidence intervals, t-values and significance levels of each parameter were calculated. An analysis of variance (ANOVA) was used to evaluate the overall significance of the model being fitted. Finally, the following simple linear model proved to fit the data best showing significance for the overall model as well as the discrete parameters:

$$\mathrm{TBF} = \alpha \times U + \beta \quad (1)$$

or

$$U = \frac{\mathrm{TBF} - \beta}{\alpha}, \quad (2)$$

where TBF is tail beat frequency (Hz), U is relative swimming speed ($BL\,s^{-1}$) and α and β are constants.

This model was then used to predict active metabolic rates by applying a previously derived model of the AMR based on fish mass and swimming speed of these species from Ohlberger et al. (2005):

$$\mathrm{AMR} = a \times M^{\mathrm{b}} \times U^{\mathrm{c}},$$

where M is body mass (g), U is swimming speed ($\mathrm{cm\,s^{-1}}$) and a, b and c are constants.

AMR is then calculated by:

$$\mathrm{AMR} = a \times M^{b} \times \left(\frac{\mathrm{TBF} - \beta}{\alpha}\right)^{\mathrm{c}} \qquad (3)$$

Statistical tests and regression analyses were performed using SPSS 9.0 (SPSS Inc.).

An error probability of 5% ($P = 0.05$) was defined as general significance level.

AMR was studied by Ohlberger et al. (2005) in the same intermittent respirometer system as it is described in this paper. Furthermore, the experimental fish belong to the same experimental group. For AMR measurements fish were introduced into the swimming chamber and a flow velocity of $0.5\,\mathrm{BL\,s^{-1}}$ was run for 2 days to acclimate the fish to experimental conditions. Subsequently, flow velocities of 0.75, 1.0, 1.25 and $1.5\,\mathrm{BL\,s^{-1}}$ were run for approximately 24 hr each. After removal of the fish a blank value was determined. Swimming speeds were corrected for solid blocking effects according to Bell and Terhune ('70).

RESULTS

TBFs increased with increasing swimming speed in all fish. Minimum TBF occurred at $0.5\,\mathrm{BL\,s^{-1}}$ and maximum TBF at $1.5\,\mathrm{BL\,s^{-1}}$. Absolute minimal and maximal beat rates were similar for carp (0.84–1.42 Hz) and roach (0.9–1.47 Hz). The increase of TBF was best described by a simple linear function that only included swimming speed as independent variable ($\mathrm{TBF} = \alpha \times U + \beta$; Fig. 1, Table 1). Relative swimming speeds ($\mathrm{BL\,s^{-1}}$) explained 72 and 86% of the variance in TBF in carp (ANOVA: $F(1,38) = 97.20$; $P < 0.001$) and roach (ANOVA: $F(1,38) = 240.53$; $P < 0.001$), respectively. The regressions proved to be significantly different between the species ($F = 3.86$; $P = 0.025$). In both species the increase in TBF with swimming speed was similar, but carp showed a significantly lower intercept compared to roach.

Using the energetic models derived in Ohlberger et al. (2005), we computed the following equations for the active metabolic rates of the two species depending only on TBF and fish mass:

$$\mathrm{AMR_{carp}} = 0.021 \times M^{0.8} \times \left(\frac{\mathrm{TBF} - 0.290}{0.060}\right)^{0.95}$$

$$\mathrm{AMR_{roach}} = 0.024 \times \mathrm{M}^{0.93} \times \left(\frac{\mathrm{TBF} - 0.684}{0.048}\right)^{0.6}$$

These models are shown on a 3D plot to illustrate the differences between them (Fig. 2).

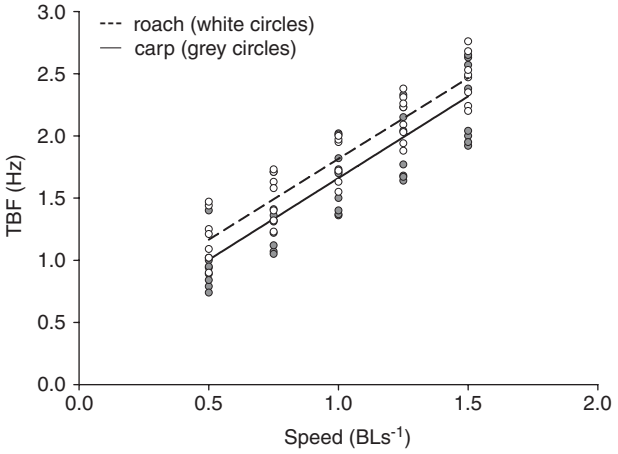

Fig. 1. Linear models of TBF (Hz) over U ($\mathrm{BL\,s^{-1}}$) for carp (dashed) and roach (solid). Single TBF values of roach are represented by white circles and those of carp by gray circles. The models were derived according to $\mathrm{TBF} = \alpha^{*}U + \beta$. The equations for carp and roach differ significantly ($F = 3.86$; $P = 0.025$) showing similar slope but a lower intercept for carp compared to roach.

TABLE 1. Linear models of TBF (Hz) depending on relative swimming speed U ($\mathrm{BL\,s^{-1}}$) for carp and roach

	Estimates and standard errors				Model		
Species	α	SE	β	SE	TBF = $\alpha^{*}U+\beta$	r^2	N
Carp	1.31	0.13	0.35	0.14	$1.31^{*}U+0.35$	0.72	8
Roach	1.30	0.08	0.52	0.09	$1.30^{*}U+0.52$	0.86	8

DISCUSSION

Our models show that the TBFs of carp and roach are significantly different, with values being higher for roach over the whole investigated speed range. The intercepts of the linear models differ amongst them but the slopes are similar, pointing out slightly different swimming characteristics of these cyprinids. When combining these TBF to

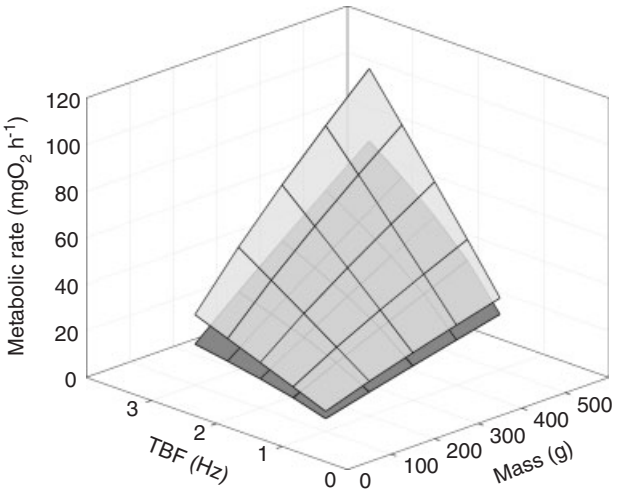

Fig. 2. Models of the active metabolic rate of carp (light gray) and roach (dark gray) according to equation (3). Metabolic costs are lower in roach over the whole investigated mass and tail beat range. Moreover, the increase of the metabolic rate with increasing TBF is lower in roach compared to carp.

speed relationships with our energetic models from Ohlberger et al. (2005), it can be seen that the energy expenditure of carp, at any TBF and body mass, is distinctly higher during swimming compared to roach (Fig. 2, Table 1). If we calculate the energetic costs at a given TBF and body mass, the difference between the species becomes even clearer. For example, a 200 g carp swimming at a TBF of 2.0 Hz is predicted to consume 35.08 $mgO_2\,h^{-1}$, whereas a roach of the same mass at the same TBF would consume 24.15 $mgO_2\,h^{-1}$, which is only 69% of the energy expenditure of the carp.

The difference between the two species can be explained by different morphological characteristics, which highly influence the swimming energetics in fishes (Lighthill, '69; Weihs and Webb, '83). Carp encounter higher swimming costs due to the deeper and more compact body form compared to the slender roach. This is also reflected in the species ecological demands as carp are generally associated with slower moving water profiles (Ohlberger et al., 2006).

A number of authors previously had shown that a relationship between TBF and swimming speed exists (Bainbridge, '58; Hunter and Zweifel, '71; Wardle et al., '89). The debate, however, weather TBF is a sufficient indicator for swimming velocity is quite controversial. Bainbridge ('58) described the relationship between swimming speed, TBF, and tail beat amplitude and size for three species of freshwater fish. According to his publication tail beat amplitude increased with frequency up to five beats per second. But Hunter and Zweifel ('71) later showed that his evidence was weak, because only two of the seven studied fish showed such a relationship. They, by contrast, found no evidence for a consistent change in tail beat amplitude with swimming speed. TBF showed a linear relationship to velocity in all fish species studies by Hunter and Zweifel ('71). They conclude that during steady swimming tail beat amplitude is a constant proportion of body length at any speed. Videler ('93) again disputed this statement and recent evidence for tail amplitude modulation during steady swimming can be found in Webber et al. (2001). They used ultrasonic differential pressure transmitter in cod (*Gadus morhua*) and showed that tail beat amplitude and TBF both were related to swimming speed. Tail beat amplitude increased at lower but levelled of at higher speeds in their tests. TBF, on the other hand, was related to swimming speed linearly showing a high regression analysis correlation ($r^2 = 0.85$). This value from Webber et al. (2001) is similar to the regression analysis correlations found in this study, which are 0.72 and 0.86 for carp and roach, respectively. Up to date no clear picture can be drawn about the modulation of tail beat amplitude during steady swimming.

In our study, we present validation of the relationship between TBF and swimming speed without influence of the tail beat amplitude and we suggest that TBF represents an accurate measurement of AMR in these cyprinids. Moreover, EMG signals corresponding to the intensity of fish exercise are correlated with swimming velocity (Kaseloo et al., '92; Briggs and Post, '97) and it has been assumed that EMGs generated by muscle contractions in the tail are highly correlated to the oxygen consumption in fishes (Weatherley et al., '82; Weatherley and Gill, '87).

In conclusion, our models suggest that active metabolic rates in free-swimming fish might be estimated by using physiological biotelemetry data on the basis of TBF models derived in laboratory experiments.

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