

Pectoral fin beat frequency predicts oxygen consumption during spontaneous activity in a labriform swimming fish (*Embiotoca lateralis*)

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Abstract The objective of this study was to identify kinematic variables correlated with oxygen consumption during spontaneous labriform swimming. Kinematic variables (swimming speed, change of speed, turning angle, turning rate, turning radius and pectoral fin beat frequency) and oxygen consumption (MO_2) of spontaneous swimming in *Embiotoca lateralis* were measured in a circular arena using video tracking and respirometry, respectively. The main variable influencing MO_2 was pectoral fin beat frequency ($r^2=0.71$). No significant relationship was found between swimming speed and pectoral fin beat

frequency. Complementary to other methods within biotelemetry such as EMG it is suggested that such correlations of pectoral fin beat frequency may be used to measure the energy requirements of labriform swimming fish such as *E. lateralis* in the field, but need to be taken with great caution since movement and oxygen consumption patterns are likely to be quite different in field situation compared to a small lab tank. In addition, our methods could be useful to measure metabolic costs of growth and development, or bioassays for possible toxicological effects on fish.

Keywords *Embiotoca lateralis* · Energetics · Labriform swimming · Metabolism · Oxygen consumption · Striped surfperch · Swimming performance

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Introduction

Locomotion represents a large component of the bioenergetic budget of many fish species (Koch and Wieser 1983; Boisclair and Leggett 1989; Boisclair and Sirois 1993). Nevertheless, this component remains poorly documented (Soofiani and Hawkings 1985; Lucas et al. 1991; Ney 1993). Locomotion can be described as steady or unsteady swimming. Steady swimming is defined as swimming in a straight line at a constant speed (Blake 1983; Viedeler 1993), mainly studied in swimming respirometers (Brett 1964; Beamish 1978; Korsmeyer et al. 2002). Unsteady

swimming involves manoeuvres, acceleration and deceleration (Blake 1983; Viedeler 1993), and is a major component of spontaneous swimming activity which includes common behaviours such as safeguarding territories, searching for food, avoiding predators and mating. The bioenergetics of spontaneous swimming activities are relevant to estimate the locomotion costs of free-ranging fish and therefore are ecologically important. While the kinematics of unsteady swimming has been studied extensively (Viedeler 1993; Domenici and Blake 1997), its energetic aspects are less well known (Webb 1991; Tang and Boisclair 1993; Krohn and Boisclair 1994; Steinhausen 2005).

Labriform swimming, i.e. using pectoral fins for lift-based propulsion at slow to moderate speeds (Webb 1973; Drucker and Jensen 1996a), is a widespread locomotion mode in structural complex habitats, where it is believed to provide greater manoeuvrability and stability at low speeds (Korsmeyer et al. 2002). Therefore, labriform swimming occurs in many groups of perciform fishes, including numerous families inhabiting coral reefs (Thorsen and Westneat 2005). However, the energy consumption of spontaneous swimming activity (involving both steady and unsteady components) of labriform fish is only poorly understood (Jones et al. 2007; Kendall et al. 2007). This is important because forced swimming models of steady activity are insufficient in explaining spontaneous activity (Tang et al. 2000).

The striped surfperch (*Embiotoca lateralis*) is an ideal subject species for studies of labriform swimming behaviour as they rely on pectoral fins for propulsion over a wide range of speeds (Drucker and Jensen 1996a). The objective of the study was to investigate the energetic costs of spontaneous swimming in striped surfperch, quantified by (a) speed (U), (b) acceleration and deceleration (A), (c) turning angle (A_T), (d) turning radius (R_T) and (e) the pectoral fin beat frequency (f_P). The aim was to find a potential predictor that can be used as a tool to measure the energy expenditure in the field at very low to moderate swimming speeds.

Materials and methods

Fish collection

The study was carried out at Friday Harbor Marine Laboratories of the University of Washington, Friday

Harbor, San Juan Island, Washington, USA, in summer 2005. Striped surf perch, *Embiotoca lateralis*, were collected by beach seining at Jackson Beach on San Juan Island. Fish were maintained unfed for at least 72 h prior to experimentation in holding tanks with a constant flow through of seawater at a temperature of $13 \pm 0.5^\circ\text{C}$. Sex and maturation of individual fish were not registered.

Respirometry of spontaneous swimming

Routine metabolic rates were measured in striped surf perch (body length, $L = 18.6 \pm 0.4$ cm, body mass, $M = 128 \pm 0.2$ g, $n = 7$). Single fish were introduced into a perspex circular arena respirometer (diameter 41.0 cm, height 11 cm, volume 14.2 l; Steinhausen 2005; Fig. 1) after being left to acclimatize for minimum of 6 h. This period appeared to be sufficient for other fish to settle to a routine oxygen consumption rate (Steffensen et al. 1984; Jordan et al. 2001). The respirometer was submerged in water to keep the temperature constant at 13°C . Two external pumps were connected to the respirometer by three ports on the side. One pump re-circulated the water continually at a slow flow rate (~ 0.7 l min^{-1}) to mix the water. Oxygen partial pressure was measured with the system closed using a sharp fibre optic sensor (Pst₃, PreSens, Germany, limit of detection (LOD), 15 ppb; measurement range, 0–45 ppm; accuracy at 20°C , $\pm 1\%$ at 100% air-saturation and $\pm 0.15\%$ at 1% air-

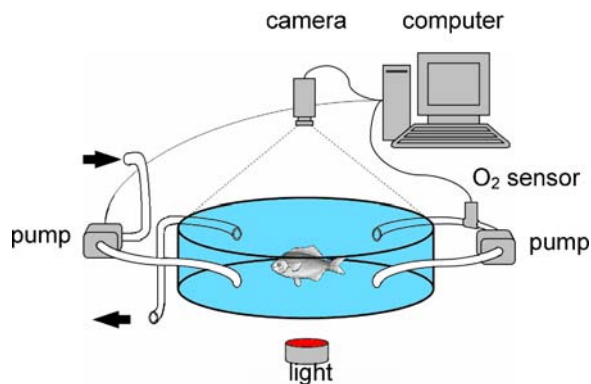


Fig. 1 Simplified illustration of the equipment used to determine the spontaneous swimming levels and routine metabolic rates in *Embiotoca lateralis*. During the flush period (10 min), the respirometer was refilled with water from a surrounding tank. During the measuring period, the decline in pO₂ was measured over 40 min. The position of the fish was tracked with 5 Hz with a mounted CCD camera

saturation), inserted in the recirculation tube so that the sensor measured the bypassing water. The sensor was connected to an oxygen meter (Microx TX3; PreSens, Regensburg, Germany). The second pump flushed the respirometer through two remaining ports prior to each measuring period. Each period was initiated by flushing the chamber with oxygenated water for 15 min, followed by a 1 min period to achieve a steady state in the chamber. Oxygen partial pressure (pO_2) was measured at a frequency of 1 Hz over the following 40 min before another cycle was started. Each trial consisted of 6 periods of fresh water recirculation and four measuring periods.

Video tracking and analysis

The fish were filmed at 25 frames per second (fps) with a CCD-camera (TVCCD 460; Monacor, Denmark) mounted at a height of 1 m above the respirometer. In order to synchronize the video of the swimming fish with the MO_2 , the onset of each measuring period was signalled by a brief flash of the infrared light source. Images were digitized by a video capture card (Pinnacle PCTV Rave) with a resolution of 640×480 pixels. Data were collected with Labtech Notebook Pro via a Measurement Computing PCMCIA-DAS16D/D interface board. An infrared light source (Monacor IR-10) illuminated the fish from below. The geometrical centre of the resulting digitized silhouette of the fish was tracked as a xy coordinate pair at a frequency of 5 Hz using LoliTrack software (Loligo Systems, Denmark). A script aligning xy coordinates and the simultaneous decline in pO_2 ($r^2=0.84 \pm 0.11$) into periods of 10 min was written with Lab-tech Notebook Pro-software.

Pectoral fin beat frequency (f_p) was measured by counting fin beats from movie file sequences of 10 min in AVI format, collected simultaneously with respirometry and swimming data during the closed respirometry cycles. Each of the 24 periods per individual (six experimental runs of each 1 h; four measuring periods of each 10 min in each experimental run) were ranked relative to each other; i.e. low, medium or high MO_2 . From each category, three periods of each 10 min were randomly assigned for analysis of f_p . This resulted in nine periods captured video sequences per individual ($n=63$ for all fish). For illustration, in one randomly selected case, the effect of f_p on MO_2 was counted during the entire

experimental period of 6 hours (i.e. four periods times 6 h, Fig. 2).

Quantification of activity

Swimming speed (U) was calculated as the displacement of geometrical centre of mass of the fish over time and expressed as the average body length per second ($bl\ s^{-1}$) over 10 min. For every consecutive frame, acceleration and deceleration (A) was calculated as the derivative of U , and expressed in absolute values because the positive and negative accelerations would have cancelled out and resulted in average A close to 0. The turning angle (A_T) was calculated as the angle between two consecutive vectors characterising the direction of the fish in a horizontal plane, given by $\cos \theta_i = u_{i-1} \times u_i / (|u_{i-1}| \times |u_i|)$. The turning radius (R_T) was determined according to Domenici and Blake (1991) as the radius of the circle that can be calculated from three consecutive positions of the centre of mass. f_p was adjusted to a standard body mass of 0.1 kg according to:

$$f_{p(0.1kg)} = f_p (M 0.1^{-1})^{(1-0.12)}$$

where $f_{p(0.1\ kg)}$ is pectoral fin beat frequency of a 0.1 kg fish, M is the body mass in kilogram and 0.12 is a scaling exponent (Drucker and Jensen 1996b).

Calculation of oxygen consumption

Mass specific oxygen consumption (MO_2) was calculated using the formula:

$$MO_2 = \alpha V_{resp} \beta M^{-1}$$

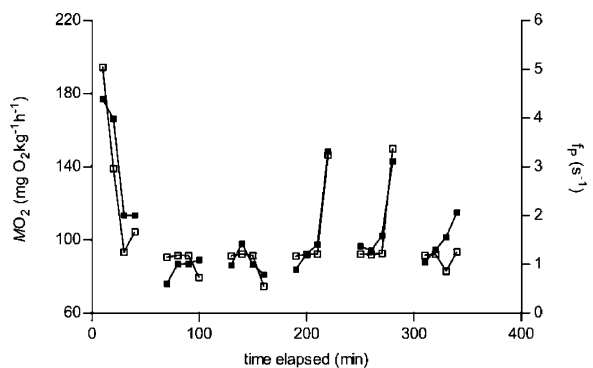


Fig. 2 Simultaneous recording of oxygen consumption (MO_2 =□) and fin beat frequency (f_p =■) of a single surfperch at spontaneous swimming. Each symbol represents a 10 min average

where MO_2 is the oxygen consumption ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$), α is the slope of the linear regression ($\Delta O_2 \text{ sat} \Delta t^{-1}$), V_{resp} is the volume of the respirometer minus the volume of the fish (l) where body mass is equalised body volume (1 $\text{kg}=1$ l), β is oxygen solubility ($\text{mg O}_2 \text{ mmHg}^{-1} \text{ l}^{-1}$) and M is the body mass of the fish (kg). To correct for mass specific oxygen consumption, metabolic rates were adjusted to a standard body mass of 0.1 kg using the formula

$$MO_{2(0.1\text{kg})} = MO_2 (M 0.1^{-1})^{(1-0.79)}$$

where $MO_{2 0.1 \text{ kg}}$ is the corrected consumption, M is fish body mass and 0.79 is a scaling coefficient (Clarke and Johnston 1999).

Oxygen consumption as a function of a predicting kinematic variable, i.e. U , A , A_T , R_T , or $f_P(x)$ can be described using a power function

$$MO_2 = a + b x^c$$

with a being the estimate of the standard metabolic rate (SMR), i.e. the MO_2 at zero activity, and b and c being constants.

Statistics

The total number of fish was seven. The combined influence of all variables (U , A , A_T , R_T , and f_P) on MO_2 was explored using forward stepwise regression ($p < 0.05$, $n=7$, STATISTICA 6.0, StatSoft, Inc., 2001). MO_2 was log transformed ($\log MO_2$) for linear regression analysis. Data used for statistical analysis were average data over 10 min.

Results

Spontaneous swimming activity over time

The trends of f_P and MO_2 of an individual over the period of 5 h and 40 min appear to be similar, suggesting that the two are correlated (Fig. 2). No measurements were taken when the respirometer system was flushed for 30 min after a measuring period of 40 min to ensure oxygen saturation of the water.

Oxygen uptake and kinematic variables modelling

MO_2 in striped surfperch in the circular arena respirometer ranged between 72 and 334 $\text{mg kg}^{-1} \text{ h}^{-1}$.

The mean swimming speeds were $0.21 \pm 0.1 \text{ bl s}^{-1}$ and ranged between 0.16–0.38 bl s^{-1} ($n=174$). A multi-linear regression model for log-transformed MO_2 was computed:

$$\log MO_2 = 1.59 + 0.95 U + 0.003 A + 0.001 A_T + 0.003 R_T + 0.047 f_P$$

From the analysis, only f_P and A_T were significantly contributing to $\log MO_2$ with an r^2 of 0.66 and 0.32, respectively (forward stepwise regression, $r^2=0.76$, $p < 0.05$, $n=54$). Plotting MO_2 against f_P (Fig. 3a) resulted in an exponential curve described by the formula:

$$MO_2 = \text{SMR} + b f_P^c$$

with SMR being $85.93 \pm 11.59 \text{ mg kg}^{-1} \text{ h}^{-1}$, b being 17.37 ± 9.18 and c being 1.08 ± 0.25 ($p < 0.05$, $r^2=0.71$,

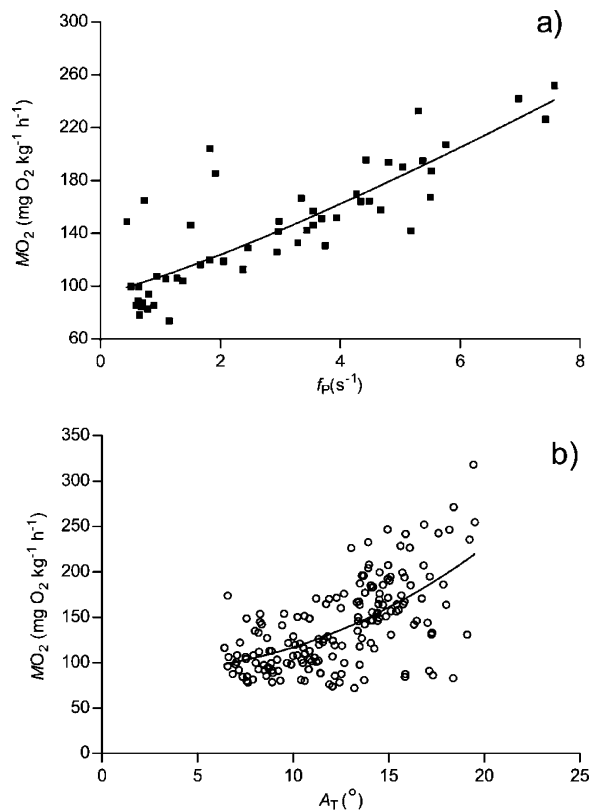


Fig. 3 **a** Relationship of pectoral fin beat frequency (f_P) on $\log MO_2$ at spontaneous swimming ($MO_2 = \text{SMR} + b f_P^c$, $r^2=0.80$, $p < 0.05$). **b** Relationship of turning angle (A_T) on $\log MO_2$ at spontaneous swimming ($MO_2 = a + b A_T^c$, $r^2=0.38$, $p < 0.05$)

$n=54$). When plotting MO_2 against A_T (Fig. 3b), the exponential formula:

$$MO_2 = SMR + bA_T^c$$

arose, with SMR being $87.20 \pm 16.41 \text{ mg kg}^{-1} \text{ h}^{-1}$, b being 0.17 ± 0.38 and c being 2.24 ± 0.73 ($p < 0.05$, $r^2 = 0.38$, $n = 174$).

Discussion

The results suggest that energy requirements of a labriform fish during spontaneous swimming activity can be accurately predicted ($r^2 = 0.71$) using the pectoral fin beat frequency (f_p). Although turning angle (A_T) also contributed to oxygen uptake, the correlation was low ($r^2 = 0.32$). Therefore, future studies of metabolic rates and activity of free labriform swimming fish may benefit from including techniques that allow direct measurements of f_p in the field. For example, a number of laboratory and field studies have applied electromyography EMG to correlate muscular recruitment with axial swimming kinematics (Jayne and Lauder 1995a; Jayne and Lauder 1995b) and to determine swimming costs of axial swimmers (Hinch and Rand 1998; Standen et al. 2002). Cooke et al. (2004) predicted that some of the most interesting future findings in ecology will be derived from studies involving biotelemetry (i.e. remote measurement of physiology, behaviour and/or energetics). Given our results, we suggest that EMG records of the pectoral activity may be used to measure fin beat frequency (rather than speed and distance) and hence to estimate oxygen consumption in striped surf perch and other labriform fishes.

The minimum metabolic rates found by extrapolating f_p (Fig. 3a) and A_T (Fig. 3b) to zero activity resulted in values of 85.93 ± 11.59 and $87.20 \pm 16.41 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$, respectively. These values closely resemble the results by Cannas et al. (2006) reporting an SMR of $82 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ (adjusted to a body mass of 0.1 kg) for striped surf perch in a conventional swimming respirometer. Thus, the similarity among the SMR estimates suggests a sufficient accuracy of the oxygen consumption measurements in the circular arena respirometer.

Commonly, MO_2 is measured in swimming respirometers at relatively higher swimming speeds than those observed in this study. Work on forced linear

swimming may be particularly relevant for pelagic fish that show long periods of relatively steady swimming in nature. However, various authors have shown that the costs of locomotion during spontaneous swimming in non-pelagic fish species are higher than that of forced swimming (Weatherly and Gill 1987; Webb 1991; Steinhausen 2005). This is most likely due to the additional resistance components of the spontaneous swimming (Webb 1991). Relatively low speed swimming (spontaneous) as it occurs in nature may imply a high degree of manoeuvring, stability control and accelerations/decelerations with loss of momentum, especially in fish that live in structurally complex environments (Domenici 2003). This issue may apply to labriform swimmers, such as *Embiotocidae*, which rely on pectoral fin activity for all types of locomotion as well as a synchrony with their ventilation rates (Webb 1975). As a result, the relationship between speed and MO_2 during such activity patterns may be weak, as found already by Gordon et al. (1998). This implies that the use of pectoral fins in striped surf perch in our experiment is mainly related to behaviours other than forward locomotion, including manoeuvring, stability control and hovering.

The observed low swimming speeds in the circular arena respirometer ($0.21 \pm 0.1 \text{ bl s}^{-1}$) may be due to a number of factors. Considering a potential effect of laboratory confinement, it is possible that our results may be influenced by the artificial confinement of the fish. The tank was relatively small (tank diameter $\approx 2.2 \text{ bl}$) due to restrictions imposed by respirometry techniques. Space availability favours higher speeds (Tang and Boisclair 1993). Another explanation of the low speeds observed during spontaneous swimming may be the social behaviour of striped surf perch. Grouping behaviour may have discouraged the solitary fish to swim actively within the arena respirometer, compared to fish swimming in a group. This is in agreement with previous studies on cyprinid fishes showing social facilitation (reviewed by Smith 1991). It remains to be established if the preferred swimming speed and perhaps swimming kinematics are influenced by the presence of conspecifics. Also, the chamber was relatively large for respirometric measurements. Therefore, it was necessary to close the respirometer for 40 min to measure oxygen consumption. This suggests that the fidelity of the measurements is relatively small and may not detect

peak values. Instead it shows mean oxygen consumption over a 40 min period.

In conclusion, these results on the metabolic costs of spontaneous activity in a labriform fish suggest that f_p (in combination with EMG record) may be used as a field indicator of swimming energetics. However, the relevance for the field needs to be taken with great caution since movement and oxygen consumption patterns are likely to be quite different in field situation compared to a small lab tank. In addition, our methods could be useful to measure metabolic costs of growth and development, or bioassays for possible toxicological effects on fish.

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