Partition of aerobic and anaerobic swimming costs related to gait transitions in a labriform swimmer

Jon C. Svendsen[1,2,*], Christian Tudorache[3], Anders D. Jordan[2], John F. Steffensen[2], Kim Aarestrup[1] and Paolo Domenici[4]

[1]Technical University of Denmark, National Institute of Aquatic Resources, Freshwater Fisheries, Vejlsøvej 39, DK-8600 Silkeborg, Denmark, [2]University of Copenhagen, Marine Biological Laboratory, Biological Institute, Strandpromenaden 5, DK-3000 Helsingør, Denmark, [3]Laboratory for Ecophysiology, Biochemistry and Toxicology, University of Antwerp, Groenenborgerlaan 171, 2020 Antwerp, Belgium and [4]CNR – IAMC, Istituto per l'Ambiente Marino Costiero, Località Sa Mardini, 09072 Torregrande, Oristano, Italy

*Author for correspondence (jos@aqua.dtu.dk)

SUMMARY

Members of the family Embiotocidae exhibit a distinct gait transition from exclusively pectoral fin oscillation to combined pectoral and caudal fin propulsion with increasing swimming speed. The pectoral–caudal gait transition occurs at a threshold speed termed U_{p-c}. The objective of this study was to partition aerobic and anaerobic swimming costs at speeds below and above the U_{p-c} in the striped surfperch *Embiotoca lateralis* using swimming respirometry and video analysis to test the hypothesis that the gait transition marks the switch from aerobic to anaerobic power output. Exercise oxygen consumption rate was measured at 1.4, 1.9 and $2.3 L s^{-1}$. The presence and magnitude of excess post-exercise oxygen consumption (EPOC) were evaluated after each swimming speed. The data demonstrated that $1.4 L s^{-1}$ was below the U_{p-c}, whereas 1.9 and $2.3 L s^{-1}$ were above the U_{p-c}. These last two swimming speeds included caudal fin propulsion in a mostly steady and unsteady (burst-assisted) mode, respectively. There was no evidence of EPOC after swimming at 1.4 and $1.9 L s^{-1}$, indicating that the pectoral–caudal gait transition was not a threshold for anaerobic metabolism. At $2.3 L s^{-1}$, *E. lateralis* switched to an unsteady burst and flap gait. This swimming speed resulted in EPOC, suggesting that anaerobic metabolism constituted 25% of the total costs. Burst activity correlated positively with the magnitude of the EPOC. Collectively, these data indicate that steady axial propulsion does not lead to EPOC whereas transition to burst-assisted swimming above U_{p-c} is associated with anaerobic metabolism in this labriform swimmer.

Key words: energetics, kinematics, locomotor mode, median and paired fin swimming, respiratory physiology.

INTRODUCTION

The swimming performance envelope of fishes is usually partitioned into multiple propulsion systems to provide sufficient mechanical power (Webb and Fairchild, 2001). Labriform locomotion is a widespread swimming mechanism in fishes during which propulsive forces are generated by oscillating pectoral fins (Westneat and Walker, 1997). Members of the family Embiotocidae exhibit a distinct transition from exclusively pectoral fin oscillation to combined pectoral and caudal fin propulsion with increasing swimming speed (Drucker, 1996; Drucker and Jensen, 1996a; Drucker and Jensen, 1996b; Drucker and Jensen, 1997; Webb, 1973). Accumulating evidence suggests that the transition is driven by a need to supply additional mechanical power rather than to minimize swimming costs (Cannas et al., 2006; Jones et al., 2007; Kendall et al., 2007; Korsmeyer et al., 2002; Walker and Westneat, 2002a). As stated by Webb (Webb, 1998), only small amounts of muscle can be packed around the paired fins while larger amounts can be accommodated about the axial skeleton driving caudal propulsion.

The pectoral–caudal gait transition speed, termed U_{p-c}, has been considered a biomechanically equivalent speed, ideal for inter- and intra-specific functional and physiological comparisons of swimming performance in fishes using a labriform swimming mode (Drucker, 1996; Drucker and Jensen, 1997; Mussi et al., 2002). For this comparison, it has been assumed that the U_{p-c} marks the switch from aerobic to anaerobic power output and elicits physiologically relevant levels of activity (Drucker and Jensen, 1996b). Using a

critical swimming speed (U_{crit}) protocol, Cannas and colleagues (Cannas et al., 2006) found that oxygen consumption rate increased exponentially as a function of swimming speed up to $1.75 L_S s^{-1}$ (standard lengths per second) in the striped surf perch *Embiotoca lateralis* Agassiz. This speed coincided with the U_{p-c}. At higher speeds, no relationship between swimming speed and oxygen consumption rate was observed, possibly indicating anaerobic metabolism. Conventional U_{crit} protocols, however, do not permit accurate partitioning of aerobic and anaerobic components of the swimming costs (Reidy et al., 1995) and the relative contributions of the two components at increasing speeds remain unknown in labriform swimmers. Using a novel test protocol, the present study aimed at partitioning aerobic and anaerobic components of the swimming costs by measuring oxygen consumption rate in *E. lateralis* swimming at increasing speeds, each followed by measurements in the post-exercise state. Excess post-exercise oxygen consumption (EPOC) is evidence of anaerobic activity in intact fish (Beamish, 1978).

Two principal types of muscle used to power swimming are red-oxidative (slow) and white-glycolytic (fast) (Webb, 1998). Pectoral fin movements are powered and controlled by a number of pectoral girdle muscles whereas undulations of the body axis are powered by the segmented myotomal musculature (Kendall et al., 2007). The pectoral girdle muscles in labriform swimmers are mostly red (Westneat and Walker, 1997); however, they also have white components (Davison, 1988; Fernández et al., 1999) indicating

anaerobic capacity (Davison, 1988; Schaarschmidt and Jürss, 2003). The myotomal musculature is usually spatially divided into separate regions of red and white fibres (Sänger and Stoiber, 2001). In labriform swimmers, and other median and paired fin swimmers, the red myotomal musculature may be scarce (Fernández et al., 1999; Martinez et al., 2000) or absent (Davison, 1987; Kronnie et al., 1983).

Studies on axial undulation have demonstrated that the red muscles power steady swimming at slow to moderate speeds, whereas white muscles are increasingly recruited for unsteady swimming at higher speeds (Jayne and Lauder, 1994; Rome et al., 1984; Sänger and Stoiber, 2001). Energy for the white muscles is supplied almost exclusively from the anaerobic utilization of phosphocreatine (PCr), ATP and glycogen (Gibb and Dickson, 2002; Sänger and Stoiber, 2001). For every mole of glycogen used to support anaerobic metabolism, two moles of lactate are produced (Boutilier et al., 1993; Peake and Farrell, 2004). The transition from steady axial undulation to unsteady burst swimming is associated with decreasing levels of intracellular pH (Lurman et al., 2007) and muscle glycogen (Peake and Farrell, 2004), and increasing levels of lactate (Martinez et al., 2004; Peake and Farrell, 2004) and inorganic phosphate (Lurman et al., 2007). After exhaustive exercise, regeneration of muscle PCr, ATP and glycogen and clearance of the lactate load are necessary if muscles are to regain their ability to contract (Milligan, 1996; Milligan, 2004). Many of the physiological disturbances coupled to anaerobic metabolism are cleared during the period associated with EPOC (Peake and Farrell, 2004).

A few studies have quantified the magnitude of EPOC related to exhaustive swimming using U_{crit} protocols (Lee et al., 2003a; Lee et al., 2003b). Kaufman measured aerobic and anaerobic swimming costs in juvenile fish (Kaufman, 1990), but as far as we know, no study has partitioned aerobic and anaerobic swimming costs in adult fish at distinct sub-maximal speeds. Moreover, few studies (e.g. Pucket and Dill, 1984) have quantified the relationship between the magnitude of EPOC and swimming kinematics and behaviours.

The objective of this study was to partition aerobic and anaerobic swimming costs at sub-maximal speeds below and above the U_{p-c} in *E. lateralis* using swimming respirometry and video analysis to test the hypothesis that the gait transition from pectoral oscillation to axial undulation marks a switch from aerobic to anaerobic power output. Above the U_{p-c}, the analyses included a second gait transition occurring in *E. lateralis* shifting from steady to unsteady axial undulation. To partition aerobic and anaerobic swimming costs, exercise $\dot{M}_{O_2}$ (i.e. oxygen consumption rate during exercise) and EPOC were quantified in fish swimming at three different speeds, one below the U_{p-c} and two above the U_{p-c}. The last two swimming speeds included caudal fin propulsion in a mostly steady and unsteady (burst-assisted) mode, respectively. Components of aerobic and anaerobic metabolism were combined to estimate the total metabolic cost of swimming. Finally, correlation analysis was employed to examine whether pectoral and caudal fin beat frequencies (kinematic variables) and burst frequency (behavioural variable) influence the magnitude of the EPOC.

MATERIALS AND METHODS
Experimental animals
Eleven *E. lateralis* (fork length L_F=24.4±0.3 cm; standard length L_S=21.0±0.2 cm; mass 296.0±8.7 g; means ± s.e.) were seined at Jackson Beach, San Juan Island, WA, USA. They were kept under the ambient light regime (August) in flow-through tanks with filtered full strength sea water at Friday Harbor Laboratories, University of Washington, USA. The mean water temperature was 12.5°C (range: 11.6–13.4°C). Prior to experimentation, fish were acclimated to the laboratory conditions for at least 1 week. All methods were approved by the Animal Care and Use Committee at the University of Washington (IACUC protocol no. 3018-09).

Respirometry
A 31.45 l swimming respirometer was employed to measure oxygen consumption rate ($\dot{M}_{O_2}$) as a function of swimming speed (U) using water from the flow-through system (Cech, 1990). The working section in the respirometer was 47 cm long, 15 cm wide and 14.5 cm deep. Additional details have been published previously (Svendsen et al., 2003). Water temperature in the respirometer was maintained at 13.5°C (range: 13.4–13.6°C). Intermittent-flow respirometry was applied in accordance with previous studies (Steffensen, 1989; Steffensen et al., 1984). The software LoliResp (Loligo Systems Aps, Tjele, Denmark) was used to control the respirometric loops, each consisting of a flush (4 min), a wait (1 min) and a measurement (5 min) period (Cannas et al., 2006). Oxygen partial pressure in the respirometer was measured using fibre optic sensor technology (Fibox 3 connected to a dipping probe; PreSens, Regensburg, Germany), and $\dot{M}_{O_2}$ (mg O_2 kg^{-1} h^{-1}) was calculated based on standard equations (Schurman and Steffensen, 1997). Fish mass (to the nearest 0.1 g), length, depth and width (all to the nearest 1 mm) were determined to allow pre-experimental calculation and correction of the solid blocking effects (Bell and Terhune, 1970; Gehrke et al., 1990) ranging from 4.5% to 4.9%. The size of the experimental fish was chosen as a compromise between the potential wall effects (Webb, 1993) in the respirometer and the required size of the fish, allowing measurements of $\dot{M}_{O_2}$ (Herskin and Steffensen, 1998; Korsmeyer et al., 2002; Wardle et al., 1996).

Each *E. lateralis* was introduced to the swimming section and given at least 10 h (overnight) to acclimate while swimming at 0.5 L_F s^{-1}. This period appears to be sufficient to allow $\dot{M}_{O_2}$ to return to normal levels following the increase induced by anaerobic exercise during handling and the unfamiliar surroundings (Jordan et al., 2001; Steffensen et al., 1984). Subsequently, each fish was exposed to an experimental swimming protocol consisting of nine 30 min periods with swimming speeds sequentially adjusted to 0.5, 0.8, 1.1, 1.4, 0.5, 1.9, 0.5, 2.3 and 0.5 L_F s^{-1}. Fish were not swum to fatigue (i.e. U_{crit} was not determined). $\dot{M}_{O_2}$ was measured once every 10 min, giving three $\dot{M}_{O_2}$ measurements (Scarabello et al., 1991) at each of the nine sequential swimming speeds. The speeds were chosen to examine $\dot{M}_{O_2}$, and thereby EPOC, after a swimming exercise that would not induce gait transition (1.4 L_F s^{-1}) and after two swimming exercises that would induce gait transition (1.9 and 2.3 L_F s^{-1}) following Drucker and Jensen (Drucker and Jensen, 1996a; Drucker and Jensen, 1996b). According to these studies, the mean gait transition speed is size dependent and occurs at 1.83±0.02 L_F s^{-1} in the *E. lateralis* tested in the present study. Using the 95% confidence interval (CI) of the allometric relationship provided by Drucker and Jensen (Drucker and Jensen, 1996b), the gait transition speed may range from 1.54 to 2.1 L_F s^{-1}. Preliminary trials indicated that *E. lateralis* employed the caudal fin in a steady and unsteady (burst-assisted) mode at 1.9 and 2.3 L_F s^{-1}, respectively. Detection of EPOC was carried out by comparing the mean $\dot{M}_{O_2}$ during the initial 0.5 L_F s^{-1} period (pre-exercise routine metabolic rate, RMR) (Bushnell et al., 1994; Lee et al., 2003a; Lee et al., 2003b) with the first $\dot{M}_{O_2}$ measurement during the 0.5 L_F s^{-1} period that followed each of the three different swimming exercises (i.e. post-exercise RMR). Experimentally, each fish was considered to be unaffected by EPOC after a swimming exercise if the post-exercise RMR was below the pre-exercise RMR +10% during

the subsequent $0.5 L_F s^{-1}$ periods. The threshold RMR +10% was chosen because preliminary data showed that the RMR over time typically varied within ±10% if the swimming speed was kept constant at $0.5 L_F s^{-1}$. Similar observations were reported by Kaufman (Kaufman, 1990).

Kinematic and behavioural variables

Fish in the working section of the respirometer were recorded laterally using a digital video camera (60 fields s^{-1}; GR-DVL 9800, JVC, Yokohama, Japan). Within the camera's field of view, a mirror ($395 \text{ mm} \times 573 \text{ mm}$) was mounted above the transparent respirometer at a 45 deg angle relative to horizontal to allow dorsal–ventral recordings. The floor and rear wall were covered with reflective material (3M, Scotchlite 6060, St Paul, MN, USA) to enhance the image contrast, and marked with a grid of 5 cm squares to be used as reference points. Analysis of the video recordings was conducted frame by frame using video editing software (Premiere Pro 2.0, Adobe, San Jose, CA, USA). Mean frequencies (Hz) of pectoral fin (f_p) and caudal fin (f_c) beats were determined as the average of two 1 min periods during each of the 10 min respirometric loops. The pectoral fin beat cycle includes pectoral fin movements that generate thrust, using both abduction and adduction, and a non-propulsive pause or refractory period, in which the fins are placed against the body (Drucker and Jensen, 1996a; Mussi et al., 2002). The present study considered the beating of pectoral fins including the refractory phase (Archer and Johnston, 1989; Mussi et al., 2002). A caudal fin beat was defined as a full oscillation of the tail (Hunter and Zweifel, 1971), i.e. a complete cycle of left and right lateral displacement (Drucker and Jensen, 1996a). The pectoral–caudal gait transition speed, U_{p-c}, was defined as the highest current velocity at which the fish could swim without regular use of the caudal fin: $f_c < 0.3 \text{ Hz}$ (Drucker and Jensen, 1996a). In addition, the mean frequency of bursts (f_b) was quantified in the two 1 min periods during each of the respirometric loops. A burst was defined as a forward excursion ($\geq 10 \text{ cm}$) assisted by the caudal fin.

Data analysis

Differences in the pre- and post-exercise RMR were analysed using a one-way repeated measures ANOVA followed by pair-wise multiple comparison procedures (Holm–Sidak). For each swimming exercise, the analysis only included the first post-exercise RMR measurement. When this analysis indicated a difference, the individual relationship between time t (h) and post-exercise RMR was described using the following double exponential equation (Scarabello et al., 1991):

$$\dot{M}_{O_2} = ae^{k_1 t} + be^{k_2 t} + c , \qquad (1)$$

where a, k_1, b, k_2 and c are constants, and e is the base of the natural logarithm. All constants were estimated using non-linear regression (Levenberg–Marquardt), apart from c, which entered the model as the mean pre-exercise RMR. Data included the mean exercise $\dot{M}_{O_2}$ at $t=0$. The recovery period was terminated when the curve intercepted the 95% confidence limit of c (Bushnell et al., 1994). The equation was integrated to estimate the EPOC (Lee et al., 2003a; Lee et al., 2003b; Scarabello et al., 1991). At the individual level, EPOC was combined with the exercise $\dot{M}_{O_2}$ to provide the metabolic cost that included both the aerobic and anaerobic components as assumed by Lee and colleagues (Lee et al., 2003b).

The relationship between swimming speed and $\dot{M}_{O_2}$ was described using the hydrodynamics-based power equation (Videler, 1993):

$$\dot{M}_{O_2} = a + bU^c , \qquad (2)$$

where a, b and c are constants. Eqn 2 was transformed to estimate the optimal swimming speed (U_{opt}) according to the following equation (Videler, 1993):

$$U_{opt} = [a / (c-1)b]^{1/c} , \qquad (3)$$

where U_{opt} is the speed that minimizes the energy expenditure per unit of distance travelled.

At the individual level, the absolute number of pectoral and caudal fin beats and the number of bursts were derived from the mean frequencies and the length of each test period (30 min). Multiple regressions with stepwise backward elimination (removal criteria: $\alpha > 0.1$) were employed for individual EPOC as the dependent variable and pectoral and caudal fin beats and bursts as independent variables. Data were $\ln(x+1)$ transformed to meet the normality and homoscedasticity requirements of parametric analysis. Tests were carried out using Sigmastat 3.01 and SPSS 15.0 (SPSS Inc., San Rafael, CA, USA). Results were considered significant if $\alpha < 0.05$. All values are reported as means ± s.e.m. unless noted otherwise.

RESULTS

No fish showed signs of fatigue (i.e. resting against the bounding grid in the swimming respirometer) (e.g. McFarlane and McDonald, 2002). Cannas and colleagues (Cannas et al., 2006) exposed larger *E. lateralis* ($L_F=28.2 \text{ cm}$) to incrementally increasing swimming speeds until fatigue. Using their data and the relationship between size and U_{crit} for a generic fish (Wolter and Arlinghause, 2003), the U_{crit} for the *E. lateralis* tested in the present study was estimated to be $2.6 L_F s^{-1}$. Given this value, 1.4, 1.9 and $2.3 L_F s^{-1}$ corresponded to 54%, 73% and 88% of U_{crit}.

Analysing pre- and post-exercise RMR, repeated measures ANOVA indicated a significant treatment effect (Fig. 1). Subsequent pair-wise comparisons demonstrated no effects of swimming at 1.4 and $1.9 L_F s^{-1}$ ($P > 0.39$), while the post-exercise RMR was higher than the pre-exercise RMR after swimming at $2.3 L_F s^{-1}$ ($P < 0.001$)
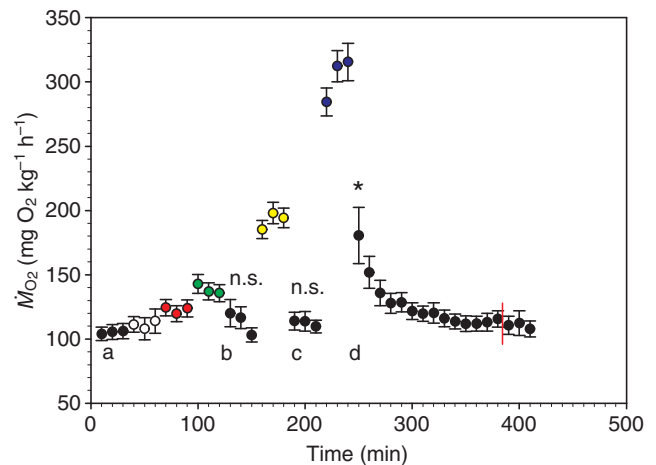
Fig. 1. Oxygen consumption rate ($\dot{M}_{O_2}$) in *Embiotoca lateralis* swimming at 0.5 fork lengths per second ($L_F s^{-1}$) (black symbols; routine metabolic rate, RMR) and at incrementally increasing swimming speeds adjusted to 0.8, 1.1, 1.4, 1.9 and $2.3 L_F s^{-1}$ denoted by white, red, green, yellow and blue symbols, respectively. RMR after swimming at 1.4 and $1.9 L_F s^{-1}$ (b,c) did not differ from pre-exercise RMR (a), while RMR after swimming at $2.3 L_F s^{-1}$ (d) was significantly higher than pre-exercise RMR (a), demonstrating the presence of excess post-exercise oxygen consumption (EPOC). The end of EPOC in an average fish is indicated by the red vertical line (at $t=384 \text{ min}$). *$P<0.001$; n.s., not significant.
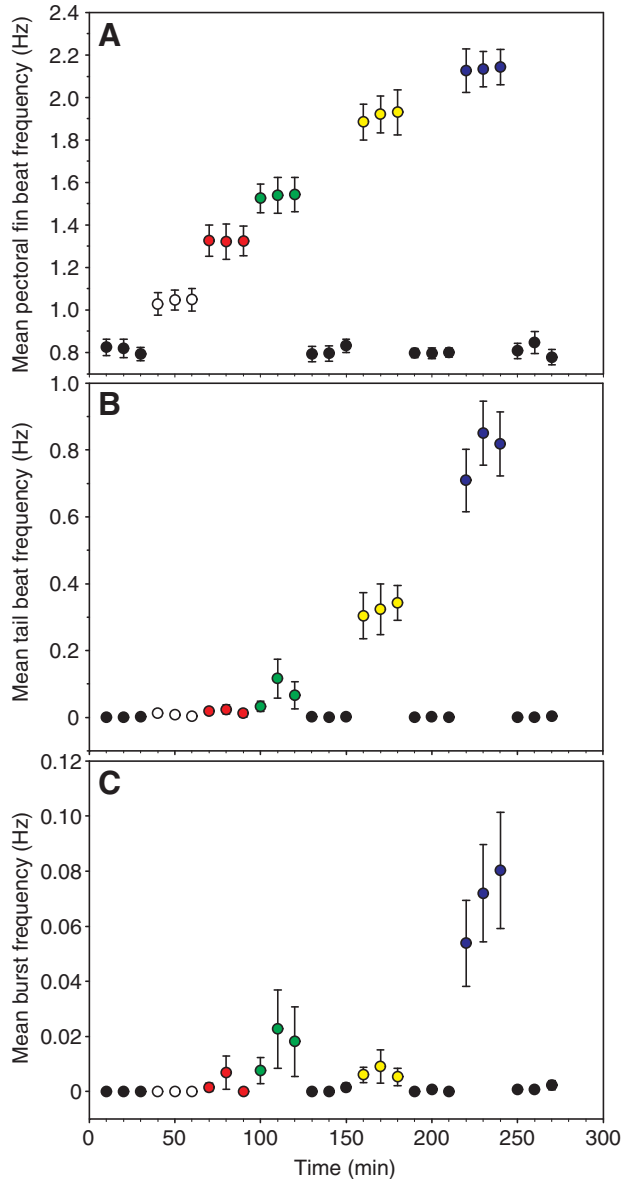
Fig. 2. Pectoral (A) and caudal (B) fin beat frequencies, and frequency of bursts (C), in *E. lateralis* in relation to swimming speed (*U*). Symbol colours correspond to the six swimming speeds described in Fig. 1.

Fig. 3. Linear relationship between EPOC and the number of bursts performed by individual *E. lateralis* swimming at 2.3 $L_F s^{-1}$ for 30 min. The relationship was described by Eqn 4 (see Results). The asterisk indicates two overlapping data points at 69.9 bursts.

2002a; Walker and Westneat, 2002b). Fast axial undulations resulted in rapid forward translation of the fish relative to the fixed tank while subsequent pectoral fin oscillation resulted in the slow backward translation of the fish relative to the tank (Walker and Westneat, 2002a; Walker and Westneat, 2002b; Cannas et al., 2006). Similar to the kinematic data, f_b returned to the pre-exercise level when the swimming speed was reduced to $0.5 L_F s^{-1}$ in the post-exercise periods (Fig. 2C).

Analysis of individual EPOC and burst activity revealed that the number of bursts performed while swimming at $2.3 L_F s^{-1}$ (Fig. 2C) correlated positively with the magnitude of the EPOC (Fig. 3). The intercept with the ordinate was not significantly different from zero ($P=0.53$) and thus was excluded from the equation. The resulting linear equation ($R^2=0.81$; $P<0.0001$) was:

$$EPOC = 0.45 \, (\pm 0.07) \times bursts \, . \qquad (4)$$

The regression analysis indicated no correlation between the pectoral and caudal fin beats and EPOC.

Exercise $\dot{M}_{O_2}$ correlated positively with swimming speed (Fig. 4). Data from the three post-exercise $0.5 L_F s^{-1}$ periods (Fig. 1) were excluded from this analysis. Eqn 2 was used to describe the relationship between swimming speed and exercise $\dot{M}_{O_2}$ (Fig. 4), and provided the following equation ($P<0.01$; $R^2>0.99$):

$$\dot{M}_{O_2} = 109.37 \, (\pm 3.53) + 6.16 \, (\pm 1.77) U^{4.14(\pm 0.34)} \, . \qquad (5)$$

Individual exercise $\dot{M}_{O_2}$ and EPOC were combined at $2.3 L_F s^{-1}$. This resulted in a 34.0% increase in the metabolic cost from 304.12 to 407.49 mg $O_2 kg^{-1} h^{-1}$ (Fig. 4). Thus, the anaerobic cost constituted 25.4% of the total metabolic cost. Eqn 2 was applied to describe the relationship between swimming speed and the total metabolic cost (i.e. exercise $\dot{M}_{O_2}$ + EPOC) ($P<0.01$; $R^2>0.99$):

$$\dot{M}_{O_2} = 115.04 \, (\pm 5.82) + 1.17 \, (\pm 0.74) U^{6.63(\pm 0.76)} \, . \qquad (6)$$

Cost of transport (COT) was derived from the swimming speed and exercise $\dot{M}_{O_2}$ (Fig. 5). Mean COT at 1.4 and $1.9 L_F s^{-1}$ was 0.11 and 0.12 mg $O_2 kg^{-1} m^{-1}$, respectively. Using the exercise $\dot{M}_{O_2}$ data, Eqns 3 and 5 estimated U_{opt} to be $1.52 L_F s^{-1}$. When exercise $\dot{M}_{O_2}$ and EPOC were combined at $2.3 L_F s^{-1}$, COT increased 33.5% from 0.15 to 0.20 mg $O_2 kg^{-1} m^{-1}$ (Fig. 5). Thus, the anaerobic cost constituted 25.1% of the total COT. The U_{opt}, based on the total

(Fig. 1). Mean recovery time was 2.4(±1.0) h, and the resulting EPOC was 51.7(±18.8) mg $O_2 kg^{-1}$.

The kinematic data demonstrated that f_p increased with speed and returned to the pre-exercise level when the swimming speed was brought back to $0.5 L_F s^{-1}$ (Fig. 2A). There was very limited use of the tail at speeds $\leq 1.4 L_F s^{-1}$ (Fig. 2B). At higher speeds, f_c increased with the swimming speed. Following the definition proposed by Drucker and Jensen (Drucker and Jensen, 1996a), *E. lateralis* underwent gait transition at $1.9 L_F s^{-1}$, and made even further use of the tail at $2.3 L_F s^{-1}$ (Fig. 2B). In the post-exercise periods, f_c returned to the pre-exercise level (Fig. 2B). While there was erratic burst activity at swimming speeds $\leq 1.4 L_F s^{-1}$, f_b dropped to a relatively low level at $1.9 L_F s^{-1}$ (Fig. 2C). In contrast, *E. lateralis* switched to a consistent use of bursts at $2.3 L_F s^{-1}$ (Fig. 2C). This swimming mode corresponded to the burst and flap gait described by Walker and Westneat (Walker and Westneat,
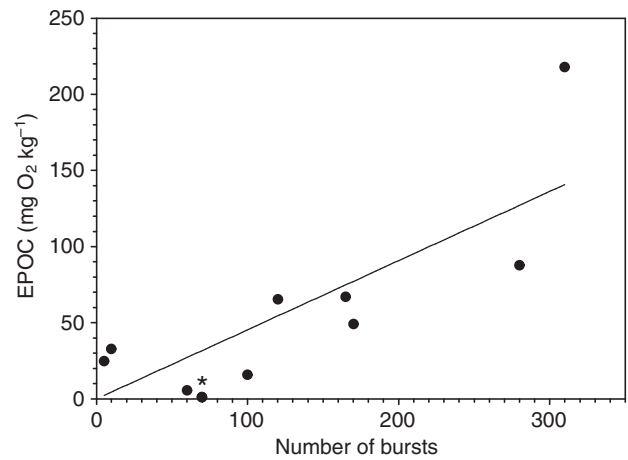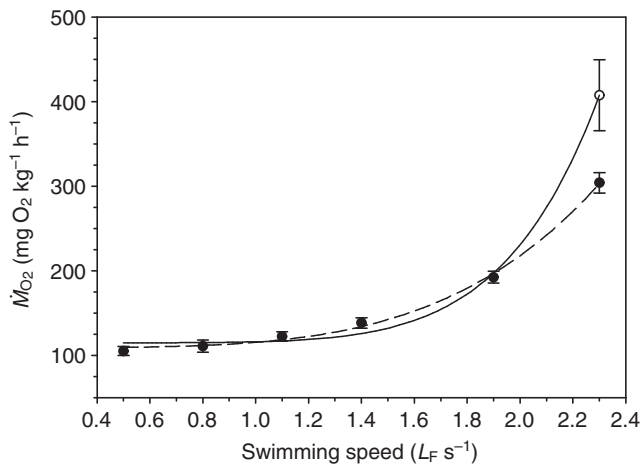
Fig. 4. $\dot{M}_{O_2}$ as a function of swimming speed (U) in *E. lateralis*. Black symbols correspond to the exercise $\dot{M}_{O_2}$ measured in the swimming fish. EPOC (Fig. 1) was added to the exercise $\dot{M}_{O_2}$ at 2.3 $L_F s^{-1}$ to provide the metabolic swimming cost that included both the aerobic and anaerobic components (white symbol). The two lines are Eqn 5 (dashed) and Eqn 6 (solid) describing the relationship between swimming speed and exercise $\dot{M}_{O_2}$, respectively excluding and including the EPOC.

Fig. 5. Cost of transport (COT) in relation to swimming speed (U) in *E. lateralis*. COT was derived from the swimming speed and exercise $\dot{M}_{O_2}$ (black symbols). At 2.3 $L_F s^{-1}$, EPOC (Fig. 1) and exercise $\dot{M}_{O_2}$ were combined to estimate the total COT (white symbol).

metabolic cost (i.e. exercise $\dot{M}_{O_2}$ + EPOC), was estimated to be 1.54 $L_F s^{-1}$ using Eqns 3 and 6.

DISCUSSION

A number of studies have quantified EPOC associated with complete exhaustion induced by chasing or electrical stimuli (Fu et al., 2007; Fu et al., 2009; Scarabello et al., 1991); however, few studies have quantified exercise $\dot{M}_{O_2}$ and EPOC to estimate the total metabolic costs of swimming (Lee et al., 2003a; Lee et al., 2003b). Using U_{crit} protocols, these studies estimated EPOC after fatigue. As far as we know, the present study is the first to partition aerobic (exercise $\dot{M}_{O_2}$) and anaerobic (EPOC) components of metabolic swimming costs at fixed sub-maximal speeds in adult fish. There was no evidence of EPOC at speeds $\leq 1.9 L_F s^{-1}$, whereas the anaerobic component constituted 25% of the total metabolic costs at 2.3 $L_F s^{-1}$ (Figs 4 and 5). In support of earlier studies (Farrell, 2007; Lee et al., 2003a; Lee et al., 2003b), these findings provide experimental evidence for a substantial anaerobic component at swimming speeds below U_{crit}.

The pectoral–caudal gait transition speed has been considered a biomechanically equivalent speed, ideal for inter- and intra-specific functional and physiological comparisons of swimming performance in fishes using a labriform swimming mode (Drucker, 1996; Mussi et al., 2002). For example, Drucker and Jensen (Drucker and Jensen, 1997) reported a comparative kinematic and electromyographic analysis of pectoral fin swimming in two different labriform swimmers, an open-water cruiser and a benthic manoeuvrer. The two species were compared at 80% of the species' respective pectoral–caudal gait transition speed. It has been assumed that the U_{p-c} marks the switch from aerobic to anaerobic power output and elicits physiologically relevant levels of activity (Drucker and Jensen, 1996b). In agreement with previous studies (Drucker and Jensen, 1996a; Drucker and Jensen, 1996b), the swimming speed of 1.9 $L_F s^{-1}$ induced pectoral–caudal gait transition in the present study (Fig. 2B). Based on Drucker and Jensen's findings (Drucker and Jensen, 1996b), it was hypothesized that the caudal propulsion would induce EPOC; however, there was no evidence for this
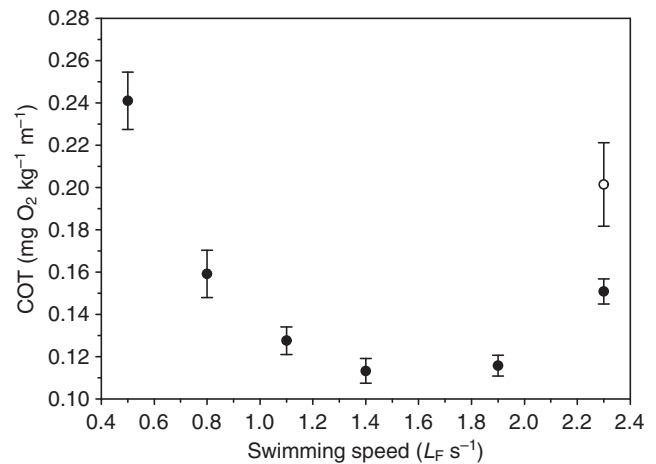
assumption (Fig. 1). These data suggest that U_{p-c} is not a threshold speed above which anaerobic metabolism occurs in *E. lateralis*. While caudal propulsion was employed at 1.9 $L_F s^{-1}$ (Fig. 2B), there was only limited burst activity (Fig. 2C), indicating steady swimming. This was in contrast to the swimming mode observed at 2.3 $L_F s^{-1}$ (Fig. 2B,C). At this speed, *E. lateralis* switched to a burst and flap gait (Walker and Westneat, 2002a; Walker and Westneat, 2002b) with fast axial undulations resulting in rapid forward translation of the fish followed by pectoral fin oscillations that led to slow backward translation. This unsteady swimming mode indicated accumulating EPOC (Fig. 1) that correlated positively with the burst activity (Fig. 3). Collectively, these data suggest that steady caudal propulsion is aerobic whereas unsteady caudal propulsion is anaerobic in this labriform swimmer. These findings do not exclude the idea of U_{p-c} as a biomechanically equivalent speed, ideal for inter- and intra-specific comparisons of swimming performance. However, provided a comparison assuming a switch from aerobic to anaerobic metabolism, it is more relevant to apply the transition to burst-assisted caudal propulsion (i.e. the burst and flap gait), which occurred at a speed faster than the U_{p-c} in the present study. The U_{p-c} remains useful for studies of the speed that is achievable and maintainable using pectoral fin-powered swimming. Moreover, certain labriform swimmers are unable to swim using steady caudal propulsion and may switch directly from steady pectoral fin oscillation to the burst and flap gait.

In support of previous studies on *E. lateralis* (Drucker and Jensen, 1996a; Drucker and Jensen, 1996b), the present study demonstrated that 1.9 $L_F s^{-1}$ is above U_{p-c} as indicated by f_c (Fig. 2B). While there was no evidence of EPOC after swimming at 1.9 $L_F s^{-1}$ (Fig. 1), it remains unclear how *E. lateralis* powered swimming at this speed. The red oxidative component in the myotomal musculature is usually limited in labriform swimmers (Kronnie et al., 1983). In *E. lateralis*, only about 0.3% of the axial muscles is red (Cannas et al., 2006). It is possible that the red muscles powered the axial undulations at 1.9 $L_F s^{-1}$. However, given the low percentage of red muscle, it is surprising that *E. lateralis* is capable of swimming using caudal fin propulsion without evident EPOC at this speed. There are at least two factors involving white muscles that may help explain the observations. First, although white muscles are assumed to be performing

anaerobically (e.g. Sänger and Stoiber, 2001), the literature is replete with speculation that contraction in axial white muscles might have a small aerobic component (Farrell, 2007; McFarlane and McDonald, 2002; Mosse, 1979; Parkhouse et al., 1988; Peake and Farrell, 2004) and may be used during sustained swimming (Johnston and Goldspink, 1973; Johnston and Moon, 1980) at least in some species. Second, the dynamics of lactate produced in the white musculature are unknown in *E. lateralis*. Few studies have examined the fate of lactate following sub-maximal activity. However, glycogenesis is the dominating fate of lactate in reptiles, amphibians and fish following exhaustive exercise (Milligan and Girard, 1993). In the winter flounder (*Pseudopleuronectes americanus*), the majority of the lactate is retained within the working muscle, where it is utilized for *in situ* glycogenesis (Girard and Milligan, 1992). The amount of lactate appearing in the blood space of pleuronectids represents less than 1% of the total produced, whereas in salmonids, lactate in the blood space typically amounts to 10–20% of the total (Milligan and Girard, 1993). The lactate potentially serves as a significant oxidative fuel for the heart and red muscles (Milligan and Girard, 1993; Richards et al., 2002; Wieser et al., 1987), possibly occurring during the swimming trial as speculated by previous studies (Burgetz et al., 1998; Cannas et al., 2006; McFarlane and McDonald, 2002). This may be particularly relevant in fish species swimming in a burst and flap gait where propulsion is only partly covered by the caudal fin. Although speculative, lactate from the axial white muscles in *E. lateralis* might fuel the heart and red muscles elsewhere (e.g. pectoral girdle muscles), which perhaps explains the lack of EPOC at $1.9 L_F s^{-1}$. If that is the case, the locomotor system consisting of paired fin locomotion and axial locomotion may not be completely biochemically decoupled (see Domenici, 2003). These are intriguing issues that require further enquiry.

Recent studies have suggested that the pectoral–caudal gait transition is driven by a need to supply additional mechanical power rather than to minimize swimming costs (Cannas et al., 2006; Jones et al., 2007; Kendall et al., 2007; Korsmeyer et al., 2002; Walker and Westneat, 2002a). A number of these studies examined $\dot{M}_{O_2}$ as a function of swimming speed and concluded that the pectoral–caudal gait transition is not associated with a drop in the COT (Kendall et al., 2007; Korsmeyer et al., 2002). None of the previous studies have evaluated the presence of EPOC when estimating the COT in relation to the pectoral–caudal gait transition. Thus, these studies may have underestimated the swimming costs because the potential influence of anaerobic metabolism was unknown. In the present study, there was no indication of EPOC at 1.4 and $1.9 L_F s^{-1}$ (Fig. 1), representing speeds lower and higher than $U_{p–c}$. These findings suggest that the present comparison of COT at speeds lower and higher than $U_{p–c}$ (Fig. 5) was unaffected by anaerobic metabolism. In support of the previous studies (Kendall et al., 2007; Korsmeyer et al., 2002), the present study found no decrease in the COT as a consequence of the transition from pectoral fin oscillation to combined pectoral and caudal fin propulsion (Fig. 5). These findings corroborate the conclusion that the pectoral–caudal gait transition is driven by a need to supply additional mechanical power rather than to minimize swimming costs. At $2.3 L_F s^{-1}$, *E. lateralis* switched to an unsteady burst and flap gait (Fig. 2B,C). This transition did not result in reduced swimming costs; in fact, COT increased markedly, in particular when the aerobic and anaerobic costs were combined (Fig. 5). Similar to the pectoral–caudal gait transition, these observations suggest that the gait transition to unsteady axial propulsion occurs not to minimize swimming costs but to provide additional

mechanical power from the white fibres in the myotomal musculature.

In summary, the results of this study indicate that steady axial propulsion does not lead to EPOC whereas the transition to burst-assisted swimming above $U_{p–c}$ is associated with anaerobic metabolism in *E. lateralis*. Previous work has started to unveil the complex relationships between morphology, swimming performance and ontogenetic habitat use in fishes using the labriform swimming mode (Bellwood and Wainwright, 2001; Fulton and Bellwood, 2002). Further research on species-specific characteristics focusing on the partitioning of aerobic and anaerobic costs can add a relevant dimension to our understanding of habitat use, particularly in relation to different flow regimes because local hydrodynamic conditions, including wave-induced water motions, can be major determinants of habitat selection in labriform swimmers (Fulton, 2010; Fulton et al., 2005).

LIST OF ABBREVIATIONS

COT	cost of transport
EPOC	excess post-exercise oxygen consumption
f_b	burst frequency
f_c	caudal fin beat frequency
f_p	pectoral fin beat frequency
L_F	fork length
L_S	standard length
$\dot{M}_{O_2}$	oxygen consumption rate
RMR	routine metabolic rate
U	swimming speed
U_{crit}	critical swimming speed
U_{opt}	optimum swimming speed
$U_{p–c}$	pectoral–caudal gait transition speed

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