Journal of Fish Biology (2006) **69,** 1612–1625
doi:10.1111/j.1095-8649.2006.01225.x, available online at http://www.blackwell-synergy.com

Gait transition and oxygen consumption in swimming striped surfperch *Embiotoca lateralis* Agassiz

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(Received 8 July 2005, Accepted 23 June 2006)

A flow-through respirometer and swim tunnel was used to estimate the gait transition speed ($U_{p\text{-}c}$) of striped surfperch *Embiotoca lateralis*, a labriform swimmer, and to investigate metabolic costs associated with gait transition. The $U_{p\text{-}c}$ was defined as the lowest speed at which fish decrease the use of pectoral fins significantly. While the tail was first recruited for manoeuvring at relatively low swimming speeds, the use of the tail at these low speeds [as low as 0·75 body (fork) lengths s^{-1}, L_F s^{-1}) was rare (<10% of the total time). Tail movements at these low speeds appeared to be associated with occasional slow manoeuvres rather than providing power. As speed was increased beyond $U_{p\text{-}c}$, pectoral fin (PF) frequencies kept increasing when the tail was not used, while they did not when PF locomotion was aided by the tail. At these high speeds, the tail was employed for 40–50% of the time, either in addition to pectoral fins or during burst-and-coast mode. Oxygen consumption increased exponentially with swimming speeds up to gait transition, and then levelled off. Similarly, cost of transport (C_T) decreased with increasing speed, and then levelled off near $U_{p\text{-}c}$. When speeds $\geq U_{p\text{-}c}$ are considered, C_T is higher than the theoretical curve extrapolated for PF swimming, suggesting that PF swimming appears to be higher energetically less costly than undulatory swimming using the tail.

Key words: *Embiotoca lateralis*; gait transition; labriform; oxygen consumption; swimming.

INTRODUCTION

Different modes of swimming have been associated with differences in habitat, feeding styles and life-history characteristics. Webb (1984) defines two main classes of swimming, based on the principal fins used: 1) median-paired fin (MPF) swimming, where the paired fins (*i.e.* pectoral or pelvic fins) or the median fins (*i.e.* dorsal and anal fins) are the primary means of locomotion and 2) body-caudal fin (BCF) swimming, in which the body is used to generate

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waves that drive the caudal fin as the primary propulsor. MPF swimming is usually associated with complex habitats, where manoeuvrability is important, while BCF swimming is more common in fishes from open habitats where long distance swimming is used.

MPF swimming is divided into undulatory and oscillatory motion based on the motion of the fins. In undulatory motion, more than one wave is propagated down the chord of the fin at a time, whereas in oscillatory motion, a more basic 'rowing' mechanism occurs. Oscillatory fin swimming can be divided into two groups on hydromechanical grounds: drag-based swimming and lift-based swimming (Blake, 1983). Drag-based swimming occurs in fishes that use the pectoral fins as paddles, moving them along the axis of movement when oriented perpendicularly. Lift-based swimming is characterized by fishes that orient the pectoral fins in plane with the axis of movement and 'flap' them.

It has been suggested that MPF swimming is more energetically efficient than BCF swimming at low speeds, due to the reduced drag associated with the maintenance of a rigid body compared with BCF swimming, where significant drag is caused by undulatory motion of the body (Blake, 1980; Webb, 1984; Korsmeyer *et al.*, 2002). BCF swimming is generally associated with greater maximum speed and acceleratory abilities than MPF swimming (Webb, 1984).

One style of MPF locomotion is 'labriform' swimming. Labriform swimmers rely exclusively on lift-based pectoral fin (PF) locomotion for a wide range of speeds (Drucker & Jensen, 1996*a*; Westneat, 1996; Walker & Westneat, 1997), although they employ their caudal fins for burst swimming or at high speeds. In labriform swimmers, gait transition can be defined as the speed at which MPF swimming is augmented by BCF motion. This is an additive transition, as BCF motion is used as an accessory source of thrust in labriform swimmers.

Gait transition is traditionally thought of as a threshold point, at which the animal must 'shift gears' to achieve higher speeds (Drucker & Jensen, 1996*a*). The gait transition speed ($U_{\text{p-c}}$) is correlated with the size of the fish, and generally occurs at higher proportional speeds (measured in body lengths s^{-1}, $L\ \text{s}^{-1}$) in smaller fishes (Drucker & Jensen, 1996*a*; Mussi *et al.*, 2002). Previous work on the gait transition in labriform swimmers has shown that the kinematics involved in the fin beat and gait transition may indicate a physiological limit to the swimming speed (Drucker & Jensen, 1996*a*). It is thought that the $U_{\text{p-c}}$ may indicate a switch from aerobic to anaerobic power, and it is therefore a physiologically equivalent performance measurement that is conserved in labriform swimmers across sizes (Drucker & Jensen, 1996*b*). At low speeds (*i.e.* $<1{\cdot}00\ L\ \text{s}^{-1}$), both amplitude of the fin stroke and the fin beat frequency increase with speed. At higher speeds (up to $U_{\text{p-c}}$), PF frequency, but not amplitude, increases with speed (Drucker & Jensen, 1996*a*; Mussi *et al.*, 2002). At speeds $\geq U_{\text{p-c}}$, however, neither PF beat amplitude nor frequency changed, and it is mainly the tail power that modulates speed (Drucker & Jensen, 1996*a*).

Striped surfperch *Embiotoca lateralis* Agassiz as a model labriform swimmer was used. Striped surfperch are near-shore labriform swimmers that live in structurally complex habitats, although they may move offshore to deeper water during the autumn and winter months. They are generally found in loose schools from northern Baja California to southern Alaska (Eschmeyer *et al.*, 1983). Previous studies on fishes from the percid family Embiotocidae have investigated the kinematics associated with labriform swimming (Webb, 1973; Drucker & Jensen, 1996*a*, *b*, 1997; Mussi *et al.*, 2002). The aim of the present experiment was to describe the metabolic rate, *via* oxygen consumption, of a labriform swimmer in association with the pattern of propulsion across the gait transition. It is hypothesized that, as the tail is gradually recruited, there will be a speed at which the use of the pectoral fins (in proportion of time) decreases significantly compared with lower speeds. This speed will be defined as $U_{p\text{-}c}$. It is also hypothesized that the oxygen consumption curve will vary as a result of gait transition.

MATERIALS AND METHODS

Striped surfperch were collected at Jackson Beach, San Juan Island, Washington State, U.S.A. (48°31′ N; 123°01′ W). A beach seine was used to capture all specimens. Fish were kept in flow-through sea water in a circular tank (150 × 100 cm) at Friday Harbor Laboratories of the University of Washington. Six fish [mass (M) 0·48 ± 0·09 kg, mean ± S.E. fork length (L_F) 28·17 ± 2·04 cm] were tested after a minimum of 11 days in captivity. The water temperature was set at 11° C, range ±1° C. Females were excluded to avoid the effects of gravid fish on the measured respiration rate. Prior to being introduced in the respirometer, each specimen was measured for M, L_F, depth and width of body (without using any anaesthesia). Fish were left overnight in the respirometer at a current speed of 0·25 L_F s^{-1}.

ANALYSIS OF SWIMMING BEHAVIOUR

A CCD camera (Sony SSC S20, 30 frames s^{-1}) was used in conjunction with a videotape recorder to film a dorsal view of the fish. The bottom of the swimming chamber was coated with 3M 'Scotchlite' reflective tape to enhance the contrast for video applications and to assist in counting fin beats. Cardboard sheeting was used to cover the side of the respirometer to prevent any outside stimuli from affecting the fish during the experiment. In addition, the solid blocking effect (water speed increase due to the profile of the fish in the cross-sectional area of the respirometer) was corrected for each fish, based on each fish's L_F, depth and width according to the following equation (Bell & Terhune, 1970): $U_f = U_t(1 + \varepsilon_S)$, where U_f is the speed corrected for solid blocking effect and U_t is the speed in the flume without a fish in the respirometer chamber. The fractional error due to the solid blocking effect (ε_S) was calculated and corrected for, as: $\varepsilon_S = \tau\lambda(A_O A_T^{-1})^{1.5}$, where τ is a dimensionless factor describing the cross-sectional shape of the flume, λ is the shape-based constant of the fish, A_O is the maximal cross-sectional area of each test fish and A_T is the cross-sectional area of the swimming section. For any cross-sectional shape, τ is equal to 0·8, while λ for any streamlined object is equal to 0·5 body length:body thickness (Bell & Terhune, 1970; Korsmeyer *et al.*, 2002).

Fish were swum at nominal speeds (U_f) increasing every 30 min by 0·25 L_F s^{-1}. Data collection began at 0·5 L_F s^{-1}. At each swimming speed, captured video was analysed to calculate the relative proportion of time during which each fish used one of the following locomotor modes: the pectoral fins alone (PF), the caudal fin alone (T), the pectoral and caudal fins simultaneously (PF + T) or a glide phase (G). The $U_{p\text{-}c}$ was defined as the lowest speed at which fish decrease the proportion of time of pectoral fin use significantly. The pectoral and caudal fin beat frequencies in each of the three locomotor modes were counted in beats s^{-1}, *i.e.* PF frequency during PF locomotion (F_{PF}), PF frequency during PF + T locomotion (F_{PF+T}), tail beat frequency during T locomotion

(F_T) and tail beat frequency during PF + T locomotion (F_{T+PF}). Fin beat frequency, per individual and for each U_f step, was calculated as the ratio between the total numbers of fin beats of a locomotion style divided by the time during which that propulsive mode was used. Fish were swum until failure, *i.e.* when a fish contacted the grid at the rear of the experimental chamber and made no further effort to regain position. Upon failure, the current speed was reduced to 0·5 L_F s^{-1}.

A corrected speed (U_c) was also calculated in order to take into account the relative movements of the fish in the swimming chamber, as the fish was moving forward by a certain distance D over a given time T (*i.e.* at $U_c = U_f + DT^{-1}$) and backwards (*i.e.* at $U_c = U_f - DT^{-1}$). During each U_f step, U_c provided a more accurate measure of speed for the total time through which a certain locomotor mode was used. For each fish and each speed level, U_c was calculated by including periods of forward and backward swimming as well as steady positions in the swim chamber.

RESPIROMETER

An intermittent-flow respirometer and swim tunnel with a volume of 31·45 l was used for all experiments (experimental chamber: size 15 × 15 × 45 cm). The respirometer was situated horizontally within a larger, continuously re-circulating water-bath (*c.* 100 l) to help maintain a constant temperature. Measurements of oxygen partial pressure (P_{O_2}) were taken every second for 10 min intervals using an electrode (Radiometer, E-5046) sampling water taken from the flushing chimney *via* tygon tubes connected to a Istmatec peristaltic pump. Laminar flow was induced by baffles and a Plascore honeycomb (6 mm cell diameter) placed at the water inlet beginning of the experimental chamber. Each of the three 10 min sampling periods (in 30 min at any given speed) consisted of 4 min of flushing, 1 min of closed mixing period and 5 min of data collection. The three rate of oxygen consumption (M_{O_2}) measurements at the same speed were averaged for individual fish (Korsmeyer *et al.*, 2002). The M_{O_2} was calculated (Steffensen *et al.*, 1984) from the slope of the linear regression of P_{O_2} decline over time for each measurement cycle, using the formula (Korsmeyer *et al.*, 2002): $M_{O_2} = sV\alpha M^{-1}$ where s is the slope, V is the volume of the respirometer minus the volume of the fish and α is the oxygen solubility (mgO_2 kg^{-1} h^{-1}). Only measurements that were equal to or exceeded a regression coefficient (r^2) of 0·98 were used (Korsmeyer *et al.*, 2002). Oxygen calibration was performed using air-saturated sea water prior to and after each experiment. Calibration of flow speed was performed using a Höntzh turbine flowmeter. Oxygen consumption was related to swimming speed (U_f) for speeds < and > $U_{p\text{-}c}$, separately. The U_c could not be used in conjunction with respirometer measurement, since the respirometry data required a much longer sampling period than the relatively short forward and backwards motions of the fish in the chamber. In this case, the speed of the flow was representative of the average speed of the fish over the sampling period. Each fish was used only once, at the various speed steps. Fish were video-taped while in the swim tunnel respirometer. Hence, the oxygen consumption and the kinematics of each fish were done simultaneously.

COST OF TRANSPORT

The predicted oxygen consumption, at different swimming speeds, was calculated based on a regression of the $\log_{10}$ of observed oxygen consumption values and swimming speed. The equation was: $\log_{10} M_{O_2} = \log_{10} a + bU_f$, where a corresponds to the standard metabolic rate (Herskin & Steffensen, 1998), and b is the slope of the semi-logarithmic regression. Cost of transport (C_T) for a certain distance was calculated by inserting values for the predicted M_{O_2}, based on the relationship between M_{O_2} and speed into the following equation: $C_T = M_{O_2} U_f^{-1}$, where M_{O_2} is the oxygen consumption at a given U_f .

M_{O_2} DURING THE RECOVERY PERIOD

Oxygen consumption during the 30 min swimming period at 0·5 L_F s^{-1} was compared with post-test M_{O_2}, during the first 30 min of the recovery period (also at 0·5 L_F s^{-1}).

DATA ANALYSIS

The percentage of use for each swimming mode (pectoral fins alone, pectoral fins + tail and tail alone) was analysed in order to provide an indication of the relative use of each locomotion style. The proportion of use of pectoral fins was analysed using a repeated measures ANOVA with a *post hoc* test (Tukey). Proportions were arcsine transformed following Zar (1984). The relationships between fin beat frequencies and U_c were tested for each swimming mode using linear regressions. Comparison of linear regressions (using a *t*-test as in Zar, 1984) was used to compare the relationship between fin beat frequency *v.* U_c for each propulsive system (tail or pectoral fins) when used alone *v*. when coupled with pectoral fins and the tail, respectively. The M_{O_2} data were tested for heteroscedasticity (increased variability in *y* with increasing values of *x*) following Zar (1984). As M_{O_2} data were significantly heteroscedastic, they were log$_{10}$-transformed as suggested by Zar (1984). Linear regressions were used to test the relationship between log$_{10}$ M_{O_2} and U_f. Data for linear regressions were divided into $<U_{p\text{-}c}$ and $\geq U_{p\text{-}c}$ based on the use of fin statistics. A comparison of M_{O_2} at 0·5 L_F s^{-1} before and after the test was done by using a paired *t*-test.

A single fish (27 cm L_F) was sacrificed (euthanasia with MS222 overdose) in order to measure the amount of red axial muscle. The cross-section at 75% of the L_F was analysed by using a digital camera and SigmaScan/Image analysis v. 1.20 (Jandel Scientific Software, San Rafael, CA, U.S.A.). The amount of red muscle in the cross-sectional area analysed was 0·3% of the total section.

RESULTS

SWIMMING BEHAVIOUR AND SPEED

Swimming behaviour in striped surfperch varied with swimming speed, and a number of propulsive styles in different combinations were observed (Fig. 1). At the lowest experimental speed (U_f = 0·5 L_F s^{-1}), striped surfperch used pectoral fins exclusively (PF locomotion). At intermediate speeds (U_f = 0·75–1·50 L_F s^{-1}), PF locomotion was accompanied by occasional tail beating (PF + T locomotion). This tail motion was, however, restricted to <10% of the total time, and it appeared to correspond to manoeuvring rather than propulsion. At $U_f \geq$ 1·75 L_F s^{-1}, fish started to use the tail alone (T locomotion), in addition to PF + T which occurred *c*. 20–35% of the time. Burst-and-coast swimming was used increasingly, up to *c*. 23% of the total time (burst and coast = tail 8·2% + glide 15·4% at the highest speed U_f = 2·25 L_F s^{-1}). At these high speeds, the use of pectoral fins alone was restricted to *c*. 50–60% of the time. The proportion of time during which the pectoral fins were used was affected by speed (repeated measures ANOVA, $F_{5,42}$, $P < 0·001$). A *post hoc* Tukey test showed that two statistically different groups can be identified, *i.e*. speeds $U_f <$ 1·75 L_F s^{-1}, and speeds $U_f \geq$ 1·75 L_F s^{-1} ($P < 0·001$ in all comparisons between proportions of the speeds of the two groups) (Fig. 1).

At $U_f \geq$ 1·75 L_F s^{-1}, all swimming styles (PF, PF + T, T and G) were observed. These resulted in cycles of swimming modes where PF swimming was associated with a backward motion in the swim tunnel, while during T

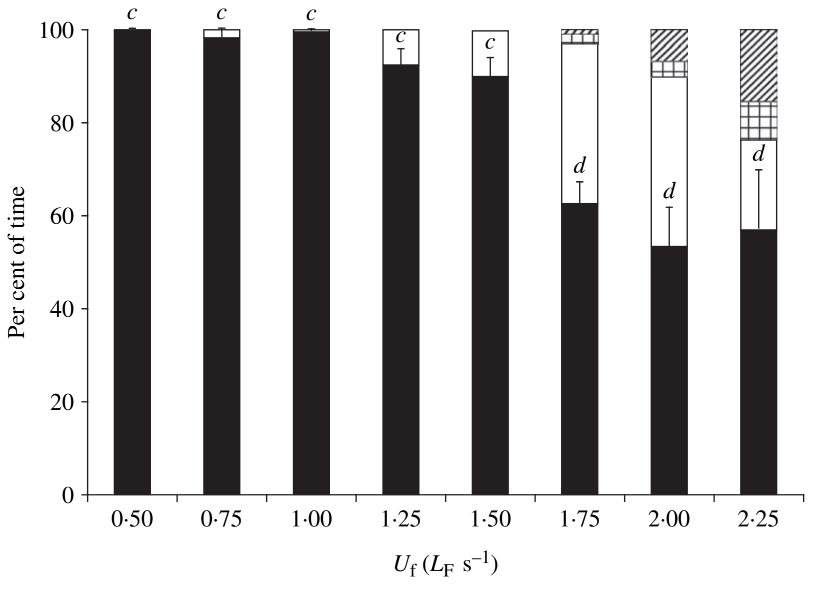

FIG. 1. Average time spent (in % of the total) in each swimming style at different speeds (U_f) [■, pectoral fin only (PF); □, pectoral fin + tail (PF + T); ▦, tail only (T); ▨, glide (G)]. At $U_f = 0·75\ L_F\ s^{-1}$, fish started using the tail in combination with the pectoral fin. At $U_f \geq 1·75\ L_F\ s^{-1}$, the proportion of time during which the fish used the tail (with and without pectoral fins) and gliding, increased beyond 40% of the total. The percentage of time during which the pectoral fins were used with or without the tail is indicated as mean + S.E. Repeated measures ANOVA ($P < 0·001$) followed by a *post hoc* Tukey test showed that two different groups of pectoral fin use can be identified, *i.e.* speeds $U_f < 1·75\ L_F\ s^{-1}$, and speeds $U_f \geq 1·75\ L_F\ s^{-1}$, identified with *c* and *d*, respectively, in the column bar.

locomotion fish moved forward in the swim tunnel. An example is given in Fig. 2, where fish using their pectoral fins alone maintained an actual speed (U_c) that was slightly lower than U_f. As a result, fish were moving backwards in the swim tunnel. Once the tail was recruited (PF + T), U_c increased, approaching U_f. Fish then accelerated up to speeds higher than U_f once burst-and-coast locomotion occurred. After the glide phase (G), fish resumed PF locomotion at $U_c < U_f$. Therefore, at relatively high speeds fish tended to move backwards in the swim chamber when using their pectoral fins with or without the tail, while they tended to move forward in the chamber when using the tail. Consequently, U_c was lower than U_f in PF swimming (*c*. 3% slower at 2·25 L_F s^{-1}) and in PF + T swimming (*c*. 6% slower at 2·25 L_F s^{-1}) while U_c was higher than U_f when fish were using the tail (*c*. 12% at 2·25 L_F s^{-1}; Fig. 3).

PECTORAL FIN FREQUENCY, TAIL BEAT FREQUENCY AND SPEED

At the lowest speeds, only pectoral fins were used for locomotion. The caudal fin was used occasionally at speeds between 0·75 and 1·5 L_F s^{-1}, and more consistently at higher speeds. The relationship between PF frequencies and U_c showed that only F_{PF} were significantly related to U_c ($F_{PF} = 0·76\ U_c + 0·81$;

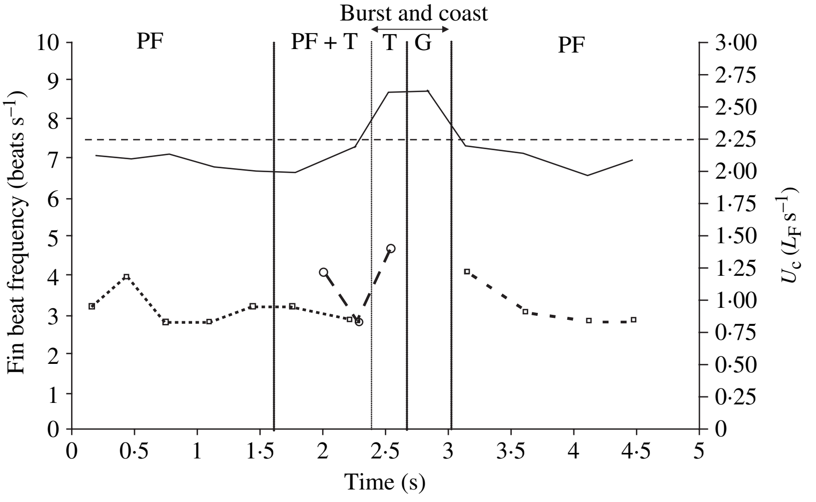

FIG. 2. Example of fin beat frequency (··□··, pectoral fins and -○- tail) and speed U_c (—) through time at $U_f = 2·25\ L_F\ s^{-1}$. Fin beat frequency was calculated throughout each fin beat cycle (power stroke and return stroke) and is represented in the middle of each fin beat cycle period by ○; in this burst there were three tail beats. ---, the U_f at $2·25\ L_F\ s^{-1}$. Vertical lines divide various swimming modes: PF (pectoral fins) and PF + T (pectoral fins plus tail), T (tail) and G (glide). The successive use of tail and glide is indicated as burst and coast by ↔.

$r^2 = 0·80$, $n = 44$, $P < 0·001$), while F_{PF+T} were not ($r^2 = 0·09$, $n = 26$, $P > 0·05$) [Fig. 4(a)]. Since one of the two regressions was not significant, the difference between these two relationships was not tested. The relationship between tail beat frequencies and U_c showed that both F_T and F_{T+PF} are significantly related to U_c ($F_T = 0·95\ U_c + 1·11$; $r^2 = 0·36$, $n = 13$, $P < 0·05$; $F_{T+PF} = 0·60\ U_c + 1·13$; $r^2 = 0·35$, $n = 26$, $P < 0·01$) [Fig. 4(b)]. These two regressions

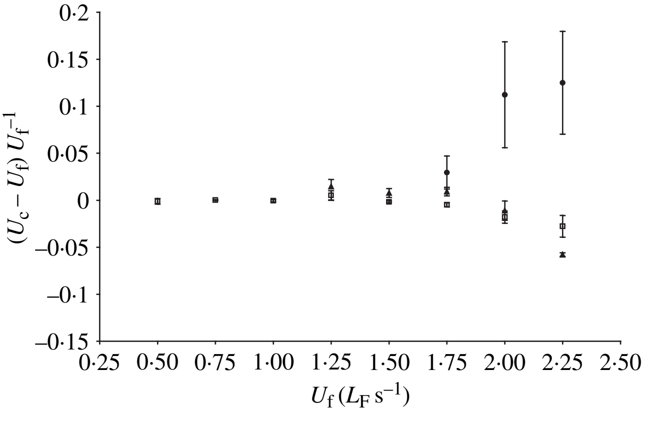

FIG. 3. The difference between corrected speed (U_c) and nominal speed (U_f) as a proportion of U_f. At high speeds, $U_c < U_f$ when pectoral fins are used alone (□) or with the tail (▲) while $U_c > U_f$ when the tail is used (●). Values are means ± S.E.

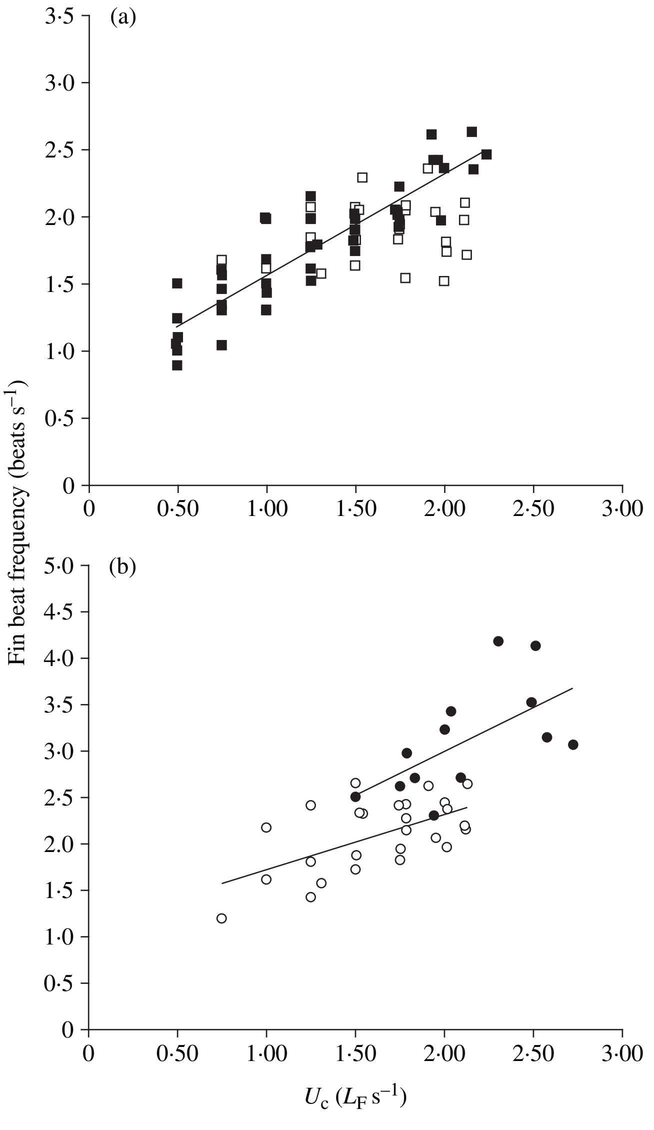

FIG. 4. (a) The relationship between pectoral fin frequencies [■, pectoral fin (F_{PF}); □, pectoral fin + tail (F_{PF+T})] and corrected speed (U_c). Only F_{PF} were significantly related to U_c ($y = 0{\cdot}76x + 0{\cdot}81$; $r^2 = 0{\cdot}80$; $n = 44$; $P < 0{\cdot}001$), while F_{PF+T} were not ($r^2 = 0{\cdot}09$, $n = 26$, $P > 0{\cdot}05$). (b) The relationship between tail beat frequencies [●, tail (F_T); ○, tail + pectoral fin (F_{T+PF})] and U_c. Both F_T ($y = 0{\cdot}95x + 1{\cdot}11$: $r^2 = 0{\cdot}36$, $n = 13$, $P < 0{\cdot}05$) and F_{T+PF} ($y = 0{\cdot}6x + 1{\cdot}13$: $r^2 = 0{\cdot}35$, $n = 26$, $P < 0{\cdot}01$) were significantly related to U_c.

showed no significant difference in their slopes ($F_{1,35}$, $P > 0{\cdot}05$), but had different elevations ($F_{1,36}$, $P = 0{\cdot}001$) (Zar, 1984). This suggests that, for any given speed, F_T was higher than F_{T+PF}. The F_T was calculated based on one to five consecutive tail beats.

RESPIROMETRY

The relationship between oxygen consumption ($\log_{10} M_{O_2}$) and swimming speed was tested separately for speeds $<U_{p\text{-}c}$ and $\geq U_{p\text{-}c}$, in order to investigate the relationship between M_{O_2} and speed for each gait separately. The relationship between $\log_{10} M_{O_2}$ and speeds $<U_{p\text{-}c}$ was significant ($\log_{10} M_{O_2} = 0 \cdot 24U_f + 1 \cdot 77$; $r^2 = 0{\cdot}83$; $n = 30$, $P < 0{\cdot}001$), while the relationship between $\log_{10} M_{O_2}$ and speed $\geq U_{p\text{-}c}$ was not ($r^2 = 0{\cdot}04$; $n = 14$, $P > 0{\cdot}05$) (Fig. 5). This is because M_{O_2} plateaus at speeds $\geq U_{p\text{-}c}$. The *y*-intercept of the regression line for speeds $<U_{p\text{-}c}$ was also used to estimate standard metabolic rate (Herskin & Steffensen, 1998), which was found to be 58·9 mgO_2 kg^{-1} h^{-1}.

The C_T decreased with increasing speed, and then levelled off near $U_{p\text{-}c}$ (Fig. 6). This was the lowest point on the curve, indicating the most efficient speed (using *i.e.* the minimum amount of oxygen consumed per unit mass and unit distance), or U_{opt} for speeds $<U_{p\text{-}c}$, where the main propulsive system was the pectoral fin. At speeds $\geq U_{p\text{-}c}$, C_T was extrapolated from the C_T curve for PF-based locomotion (calculated using the regression between speed and M_{O_2} for speeds $<U_{p\text{-}c}$), in order to provide a comparison with the actual C_T values calculated from oxygen consumption. The C_T at speeds $\geq U_{p\text{-}c}$ appeared to be higher than the PF-extrapolated curve, except for the highest speed measured (2·25 L_F s^{-1}).

Oxygen consumption before and after each trial was compared at $U_f = 0{\cdot}5$ L_F s^{-1} to test if an increase in oxygen consumption occurred after the test. An increase was expected due to the recruitment of axial muscle (anaerobic muscle) at the highest speeds. Oxygen consumption during the first 30 min of recovery was found to be 1·97 times higher than before the swimming test (paired *t*-test, number of pairs = 6, $P < 0{\cdot}05$).

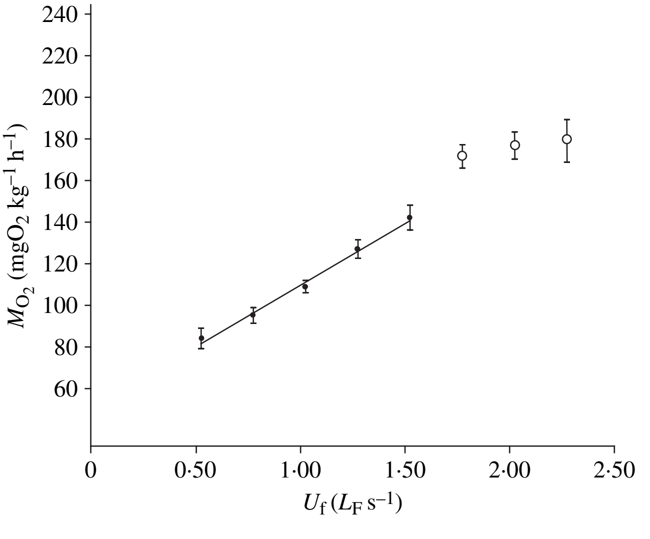

FIG. 5. Relationship between rate of oxygen consumption (M_{O_2}) and swimming speed (●, speeds $< U_{p\text{-}c}$; ○, speeds $\geq U_{p\text{-}c}$). The points are mean values at each speed. The regression line was significant only for speeds $<1{\cdot}75$ L_F s^{-1} ($y = 0{\cdot}24x + 1{\cdot}77$). Values are means ± S.E.

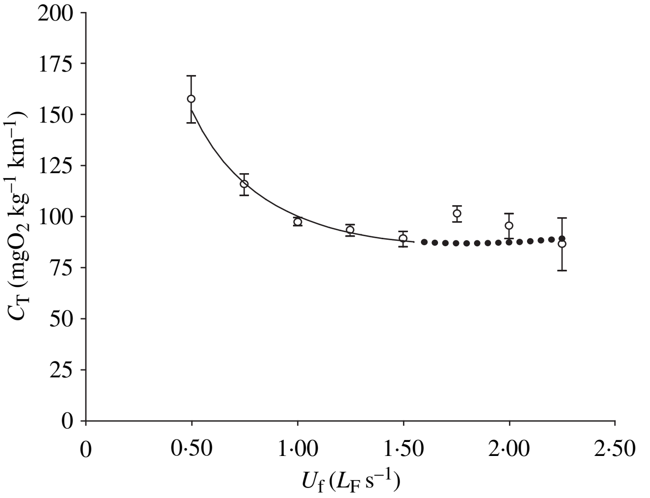

FIG. 6. Cost of transport (C_T) at different swimming speeds (U_f). —, C_T at speeds $<U_{p\text{-}c}$ obtained using the regression between M_{O_2} and speed (see Fig. 5). •••, the extrapolation of C_T to speeds $>U_{p\text{-}c}$ using the values for C_T at speeds $<U_{p\text{-}c}$. ○, the mean ± S.E. C_T calculated for all speeds.

DISCUSSION

Striped surfperch use a variety of swimming modes in various combinations. At relatively low speeds ($<1{\cdot}75\ L_F\ s^{-1}$), primarily pectoral fins were used, and tail beats occurred only rarely (<10% total time). As described by Korsmeyer *et al.* (2002) for MPF swimming in parrotfish *Scarus schlegeli* (Bleeker) and by Hove *et al.* (2001) for MPF swimming in boxfishes (Ostraciidae), striped surfperch may become unstable at lower speeds, necessitating the occasional use of the caudal fin for stabilizing manoeuvres rather than to aid in propulsion. In this study, pectoral fin use increased significantly at speeds $\geq 1{\cdot}75\ L_F\ s^{-1}$. Interestingly, PF frequency (when pectoral fins are used alone) increased continuously at speeds $>U_{p\text{-}c}$. The results obtained differs from Drucker & Jensen's (1996*a*) work, in which they found that PF frequency reached a plateau or a slight decrease at speeds $>U_{p\text{-}c}$. Previous studies on other MPF swimmers found a decrease in PF frequencies at speeds $>U_{p\text{-}c}$ (Parsons & Sylvester, 1992; Gordon *et al.*, 1996; Mussi *et al.*, 2002). Here, PF frequencies were separated when used with (F_{PF+T}) and without the tail (F_{PF}), and it was found that F_{PF} keeps increasing with speed, while F_{PF+T} does not significantly increase with speed and appears reduced, at high speeds [Fig. 4(a)], compared to F_{PF}, possibly due to the additional power provided by the tail. Similarly, tail beat frequency is reduced when aided by the pectoral fins. Korsmeyer *et al.* (2002) also observed that the fin beat frequencies of dorsal and anal fins in triggerfish *Rhinecanthus aculeatus* (L.) were higher when the fins were used alone than when they were used together with the tail at the transitional swimming speeds.

Drucker & Jensen (1996*a*) suggest that pectoral beat frequency reaches a physiological limit at $U_{p\text{-}c}$. Beyond this limit, higher speed would have to be generated by PF frequencies that far exceed the optimum muscle shortening velocity, and therefore to increase speed further, the tail would need to be recruited. Results shows that *E. lateralis* is capable of increasing PF frequencies further even at speeds $>U_{p\text{-}c}$, although in these cases the use of PF swimming is reduced in percentage of time to *c.* 50–60%. The present results do not contradict Drucker & Jensen's (1996*a*) general conclusions although additional explanations are required for the swimming behaviour observed.

While it is possible that PF frequencies higher than those observed at speeds $<U_{p\text{-}c}$ would imply suboptimal muscle shortening velocities, it is also possible that a similar argument be true for the axial muscles that need to be recruited in order to provide the power required for speeds near $U_{p\text{-}c}$. Speeds around gait transition may be relatively distant both from the optimal shortening speed of aerobic pectoral fin muscle (whose optimal shortening speed is probably lower than $U_{p\text{-}c}$) and of anaerobic axial muscle (whose optimal shortening speed occurs probably at speeds $>U_{p\text{-}c}$). This would concur with the cyclic swimming behaviour observed at speeds $\geq U_{p\text{-}c}$ (Fig. 2), going from speeds $U_c < U_f$ powered by PF swimming, to speeds $U_c > U_f$ powered by axial locomotion. Therefore, *E. lateralis* appears to behaviourally avoid a 'steady' swimming pattern at speeds near $U_{p\text{-}c}$. Perhaps cyclic swimming using both MPF and BCF propulsion at these speeds results in higher efficiency of locomotion than continuous swimming in a given locomotor mode. Work on smallmouth bass *Micropterus dolomieu,* Lacepède, an axial swimmer, shows that at transitional speeds, fish were unable (or unwilling) to swim through exclusive use of an unsteady gait, and alternated between steady and unsteady swimming modes (Peake & Farrell, 2004). As in the present work, these authors suggested that a reason for this behaviour might be that speeds around (or just above) gait transition were too low for optimal power production in the faster contracting anaerobic muscle (Rome *et al.*, 1990). Therefore, the observed phenomenon does not appear to occur only in transitions within axial locomotory gaits, as shown by Peake & Farrell (2004), but also among transitions between pectoral and axial swimming modes, as shown here.

The highest PF frequency observed (2·6 beats s^{-1}) occurred at $U_c = 2{\cdot}16\ L_F\ s^{-1}$. It is possible that this frequency and its relative speed attained represent a limit for PF locomotion in surfperches of this size. If surfperches can beat their pectoral fins at such high frequency and speed, it is not clear why they start using the tail extensively at 1·75 $L_F\ s^{-1}$. The use of the tail at speeds $\geq U_{p\text{-}c}$ may be explained by the relatively short time intervals surfperches can sustain PF locomotion at such high speeds.

Although past work (Drucker & Jensen, 1996*a*) have assumed that gait transition implied a shift from aerobic to anaerobic swimming, it is possible that some of the axial locomotion at low speed may be fuelled aerobically, given the (albeit small) presence of red axial fibres. The value found in *E. lateralis* (0·3% of red muscle) is low compared with other marine species analysed, including BCF and MPF swimmers (0–29·8% of red muscle, with 90% of the values >0·5% of red muscle; cross-section at 0·67 L_F; Greer-Walker & Pull, 1975; McLaughlin & Kramer, 1991).

Some differences in the present results when compared with Drucker & Jensen (1996*a*) may also be ascribed to the different definitions of $U_{p\text{-}c}$. In their work, Drucker & Jensen (1996*a*) defined U_{p-c} as the highest swimming speed at which the fish could hold station in the current for 3 min by pectoral fin oscillation alone, while here the definition is based on statistical comparison of the time during which the pectoral fins are used. Therefore the two definitions are based on different criteria and, while they both define a transition, here U_{p-c} is defined as the lowest speed of the newly recruited gait, while Drucker & Jensen (1996*a*) define U_{p-c} as the highest speed before the gait change. Using the same species (*E. lateralis*), Drucker & Jensen (1996*b*) found U_{p-c} (in L_F s^{-1}) to decrease with size. Using their equation, an U_{p-c} of *c.* 1·6 L_F s^{-1} would occur in 28 cm fish, approximately the same size as the ones used in this study. If 1·5 L_F s^{-1} is considered the highest speed before the transition, then the calculation of U_{p-c} appears comparable to that of Drucker & Jensen (1996*b*).

Oxygen consumption increased exponentially for speeds $<U_{p-c}$, as was expected for aerobic swimming. Literature data on MPF swimming are scarce, but Webb (1975; *Cymatogaster aggregata* Gibbons), Gordon *et al.* [1989; *C. aggregata* and *Oxyjulis californica* (Günther)] and Korsmeyer *et al.* (2002; *S. schlegeli* and *R. aculeatus*), show a similar increase in oxygen consumption with swimming speed, although the slope of this increase is quite shallow in Gordon *et al.* (1989), and in some cases not significantly different from zero. For swimming speeds $\geq U_{p-c}$, M_{O_2} did not increase significantly, suggesting a shift from aerobic to anaerobic activity at speeds $>U_{p-c}$. The M_{O_2} at U_{p-c} (1·75 L_F s^{-1}), however, appears to be in line with the regression for lower speeds. Therefore, it is possible that at least some of the axial activity at U_{p-c} is aerobic. At high speeds the tail was used in conjunction with glides phases, in burst-and-coast swimming (Fig. 1). The recovery time associated with a burst-and-coast style of swimming, wherein the pectoral fins are used aerobically at maximum forward speed, but ground is lost (*i.e.* $U_c < U_f$), may be very important for long-term swimming at high speeds as it may enable the white axial muscle to partially recover before the next burst. This mechanism may allow the fish to swim at speeds slightly higher than U_{p-c} without exhaustion, at least within the time frame used here (30 min at each speed).

The C_T for speeds $\geq U_{p-c}$ appears higher than the extrapolated curve based on M_{O_2} at speeds $<U_{p-c}$ (largely based on PF locomotion) suggesting that PF locomotion is relatively more efficient than locomotion involving the tail. The value of the extrapolated curve and the measured value of C_T are similar at the highest speed (2·25 L_F s^{-1}). This may be due to increasing proportions of anaerobic swimming provided by the tail, which would not be shown on the graphs of C_T since this measurement is based on oxygen consumption. A similar pattern of transition between MPF swimming and burst-and-coast mode of swimming in *S. schlegeli* has been described (Korsmeyer *et al.*, 2002). Korsmeyer *et al.* (2002) found similar results when comparing MPF-extrapolated C_T with actual C_T for speed $\geq U_{p-c}$. *Scarus schlegeli* employs a median-fin based swimming style that changes to burst-and-coast at high speeds, and is followed rapidly by fatigue. This was explained by the lack of red muscle fibres in the myotomal axial muscle. In addition, it was argued that the total energy expenditure of the fish at speeds $\geq U_{p-c}$ may be underreported due to the use of anaerobic swimming that was not discerned by measurement of M_{O_2} (Korsmeyer *et al.*, 2002). Results show similar patterns in *E. lateralis*. The small amount of red

axial muscle found in surfperches suggests that at least some of the axial locomotion observed at low speeds may be fuelled aerobically. As noted above, anaerobic muscle recruitment may be responsible for the lack of an increase in the C_T at highest swimming speeds in *E. lateralis* (Fig. 6). The repayment of the oxygen debt after the swimming test is confirmed by the comparison of oxygen consumption at low ('resting') speed before and after the test. Previous work on other MPF swimmers has suggested that multi-propulsor MPF swimming may be more efficient than BCF swimming (Gordon *et al.*, 2000).

In conclusion, the use of different types of propulsive mechanisms in striped surfperch appears to be a relatively complex phenomenon. When the oscillatory frequency of each propulsive system is measured separately, both PF and tail beat frequency increase with swimming speed. This occurs when they are used as single propulsive systems, below and above $U_{p\text{-}c}$. Therefore, gait transition is not the result of a physiologically strict upper threshold in the oscillatory frequency of the pectoral fins. Gait transition may therefore be related to a progressive decrease in muscle efficiency of the PF system (*i.e.* oscillatory frequencies that correspond to suboptimal muscle shortening velocities) and an increase in the efficiency of tail locomotion. This shift in propulsive system is reflected in a change in the pattern of oxygen consumption, possibly due, at least in part, to the use of anaerobic axial musculature at the higher speeds. Further studies on a variety of labriform swimmers, combining kinematics and oxygen consumption, are needed in order to test the possibility that these findings may be a general feature of labriform locomotion.

We wish to thank Friday Harbor Laboratories (FHL), University of Washington, for giving us the opportunity to work on this project within the summer course 'Fish swimming: Kinematics, Ecomorphology, Behaviour and Environmental physiology' (instructors P. Domenici, J. Steffensen and G. Claireaux). M. Cannas and J. Schaefer were supported through an FHL fellowship. Thanks are due to D. Willows (FHL Director), G. Claireaux and the staff for providing research space, equipment and logistic support. Moreover, we wish to thank all the participants in the 'Fish class' of summer 2002 for help and support throughout our stay at Friday Harbor. This research was approved by the Animal Care and Use Committee of the University of Washington (Protocol IACUC #3429-02).

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