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Energetics of median and paired fin swimming, body and caudal fin swimming, and gait transition in parrotfish (*Scarus schlegeli*) and triggerfish (*Rhinecanthus aculeatus*)

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Summary

To determine the energetic costs of rigid-body, median or paired-fin (MPF) swimming *versus* undulatory, body-caudal fin (BCF) swimming, we measured oxygen consumption as a function of swimming speed in two MPF swimming specialists, Schlegel's parrotfish and Picasso triggerfish. The parrotfish swam exclusively with the pectoral fins at prolonged swimming speeds up to 3.2 total lengths per second ($L\,s^{-1}$; 30 min critical swimming speed, U_{crit}). At higher speeds, gait transferred to a burst-and-coast BCF swimming mode that resulted in rapid fatigue. The triggerfish swam using undulations of the soft dorsal and anal fins up to $1.5\,L\,s^{-1}$, beyond which BCF undulations were recruited intermittently. BCF swimming was used continuously above $3.5\,L\,s^{-1}$, and was accompanied by synchronous undulations of the dorsal and anal fins. The triggerfish were capable of high, prolonged swimming speeds of up to $4.1\,L\,s^{-1}$ (30 min U_{crit}). In both species, the rates of increase in oxygen consumption with swimming speed were higher during BCF swimming than during rigid-body MPF swimming. Our results indicate that, for these species, undulatory swimming is energetically more costly than rigid-body swimming, and therefore support the hypothesis that MPF swimming is more efficient. In addition, use of the BCF gait at higher swimming speed increased the cost of transport in both species beyond that predicted for MPF swimming at the same speeds. This suggests that, unlike for terrestrial locomotion, gait transition in fishes does not occur to reduce energetic costs, but to increase recruitable muscle mass and propulsive surfaces. The appropriate use of the power and exponential functions to model swimming energetics is also discussed.

Key words: Scaridae, Balistidae, labriform, balistiform, aquatic locomotion, rigid-body swimming, undulatory swimming, respirometry, cost of transport.

Introduction

The study of fish swimming energetics has largely focused on one form of aquatic locomotion: the undulation of the body and caudal fin (Videler, 1993; Webb, 1994b). Many fishes, however, primarily swim using other forms of locomotion, with various combinations of median or paired fin movements, and most fish use a combination of different gaits depending on swimming speed (Blake, 1983; Webb, 1998). A 'gait', as defined by Webb (1998), is '*a unique combination of muscle-propulsor behavior which is recruited more or less discretely while moving over a portion of the total performance range of the animal*.' The common classification of fish swimming modes was made by Breder (1926), who recognized the diversity of styles and fin usage and the specialization within particular groups of fishes. The descriptions of these swimming modes, or gaits, have been refined, updated and placed on a continuum both within and among species (Lindsey, 1978; Blake, 1983; Webb, 1994a). Fish swimming gaits can be divided into two functional groups, median-paired fin (MPF) gaits and body-caudal fin (BCF) gaits (Webb, 1998). MPF gaits are powered by one or more median or paired fins, while the body is held rigid, and BCF gaits involve undulation of the body and caudal fin to create thrust. BCF swimming is the most common swimming style, and is the ancestral condition in vertebrates (Lauder, 2000). However, some more derived groups of fishes (e.g. order Tetraodontiformes and order Perciformes, suborder Labroidei) are specialized MPF swimmers (Webb, 1982; Lauder and Liem, 1983).

MPF swimming is generally considered to provide greater maneuverability and stability at slow swimming speeds, while BCF swimming provides greater power output for higher speeds and accelerations (Webb, 1998). The features of MPF swimming are presumably advantageous for movement through structurally complex habitats, such as coral reefs, where many

MPF specialists are found. Specialization in MPF swimming, however, is considered to come at the cost of reduced steady or BCF swimming performance in these fishes (Webb, 1982). The implication is that MPF swimming, while more effective for maneuvering behaviors, is energetically less efficient, and therefore BCF swimming is the ideal swimming mode for steady swimming at cruise speeds. Thus, fishes requiring slow maneuvering capabilities should be MPF swimmers, while open-water, cruise swimmers should use a BCF mode of propulsion.

Alternatively, it has been proposed that swimming with an MPF gait should have lower energetic costs, through a reduction in drag by keeping the body rigid (Webb, 1975; Gordon et al., 1989; Lighthill and Blake, 1990). Hydrodynamic models of fish swimming, and tracking water flows over both swimming and non-swimming fish, suggest that the thrust required for undulatory swimming is 1.5- to 5-fold higher than rigid-body drag (Lighthill, 1971; Webb, 1998; Anderson et al., 2001). The additional thrust required for undulatory swimming is attributed to increased friction drag, caused by boundary layer thinning, and energy loss in the lateral recoil of the body (Lighthill, 1971; Webb, 1982; Webb, 1992). In this study we tested the hypothesis that MPF swimming is more efficient than BCF swimming by measuring total metabolic rate during both steady, rigid-body (MPF) and undulatory (BCF) swimming in two species of fish specialized for MPF swimming.

In addition to specialization for certain swimming modes, most fish use a combination of gaits over their swimming performance range (Webb, 1998). If one mode of swimming is most efficient, then why do gait transitions occur? In terrestrial vertebrates, it has been shown that each gait optimizes transport costs over different ranges of speed, and that the animal chooses the gait that minimizes power requirements at their current speed (Alexander, 1989). As speed of locomotion increases, gait transition occurs to minimize energetic costs and maximize endurance. It has been proposed that the same rationale governs gait transition in fishes (Alexander, 1989; Webb, 1998). For example, MPF swimming may be more efficient only at slow swimming speeds, with BCF swimming becoming more efficient at higher speeds (Blake, 1980). An alternative hypothesis is that gait transition occurs because the different muscle-propulsor systems are effective over a limited range of performance (Rome, 1994). For example, MPF gaits may be more effective for low speeds (providing greater stability and maneuverability), while BCF swimming allows recruitment of additional muscle to provide the power needed to achieve higher speeds (Alexander, 1989; Webb, 1998). We measured metabolic rate over a range of swimming speeds and gaits, and tested whether or not the cost of transport decreases after the transition from MPF to BCF swimming as speed increases.

We studied two species of coral reef fishes considered to be MPF swimming specialists. Schlegel's parrotfish, *Scarus schlegeli* (order Perciformes, family Scaridae), uses labriform locomotion for routine swimming (named after their sister family Labridae, the wrasses). This MPF swimming mode involves flapping of the pectoral fins for propulsion. Although there have been numerous studies of the kinematics of this mode of swimming (Webb, 1973; Blake, 1983; Gibb et al., 1994; Lauder and Jayne, 1996; Westneat, 1996; Drucker and Jensen, 1997; Walker and Westneat, 1997; Westneat and Walker, 1997), there have been few measurements of the metabolic costs of labriform locomotion (Webb, 1974; Gordon et al., 1989; Parsons and Sylvester, 1992). The other species used in this study was the Picasso triggerfish, *Rhinecanthus aculeatus* (order Tetraodontiformes, family Balistidae), which is specialized for balistiform locomotion (named for the triggerfish family). This MPF swimming mode uses undulations of the soft dorsal and anal fins (Blake, 1978, 1983). We are aware of no previous measurements of swimming metabolic rate in fish using this type of locomotion. Both species switch gaits to body-caudal fin undulations (BCF gait) at higher swimming speeds.

Materials and methods

Animals

To measure the metabolic rate of fish swimming with various gaits, Schlegel's parrotfish, *Scarus schlegeli* (Bleeker 1861), and Picasso triggerfish *Rhinecanthus aculeatus* (L.), were swum in a recirculating flume respirometer. Seven parrotfish (mass 148–315 g, total length 20.1–25.3 cm) and five triggerfish (105–180 g, 16.0–19.0 cm) were caught by gill net and hook-and-line, respectively, and kept at ambient temperatures (26–27 °C) in flow-through seawater tanks at the Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus, Okinawa, Japan. The fish were not fed for 48 h prior to experiments and were used within 2 weeks of capture.

The swimming respirometer

The swimming respirometer, made of transparent Perspex, consisted of a 31-liter recirculation loop with flow generated by a propeller. Rectilinear flow was promoted by baffle screens and deflectors followed by a honeycomb flow-straightener (7 mm cell diameter), producing micro-turbulent flow through the working section (47 cm long, 15 cm wide, 14.5 cm deep). As with any swim-flume studies, we cannot rule out the possibility that wall effects influenced fish swimming performance (Webb, 1993), particularly for median or paired fin swimming in which the propulsors extend perpendicularly from the main body axis. Swimming respirometers must balance the need for a sufficiently small volume (relative to fish mass) for accurate oxygen consumption measurements with a large enough working section to minimize hydrodynamic problems. Fish sizes were chosen to minimize these problems, and data collected when the fish showed significant interactions with the flume walls were discarded. For the triggerfish, the maximum vertical distance from the tip of the soft dorsal to the tip of the anal fin ranged from 6.8 to 8.6 cm (flume depth 14.5 cm). For the parrotfish, pectoral fin span at maximal extension ranged from 9.9 to 12.5 cm (flume width 15.0 cm).

Water flow speed was calibrated according to the voltage output of the propeller's motor controller. The swimming respirometer was submerged in an aerated, flow-through seawater bath (26–27 °C), and could be alternately sealed or flushed with water from the bath *via* a computer-actuated pump. The working section was covered with a blind to prevent the fish being disturbed by outside movements, and its activity was viewed *via* a video monitor.

Oxygen partial pressure (P_{O_2}) in the respirometer was measured with an oxygen electrode (Radiometer, E 5046) housed in a thermostated cuvette. A continuous flow of seawater from the respirometer was maintained past the electrode by a peristaltic roller pump at a rate of 3.5 ml min^{-1}. The oxygen electrode was calibrated with air-saturated sea water several times a day.

Rate of oxygen consumption ($\dot{M}_{O_2}$) was measured using computerized, intermittent-flow respirometry (Steffensen et al., 1984). The respirometer was periodically flushed with clean, aerated sea water from the bath for 4 min followed by a 1 min closed mixing period and then 5 min of closed respirometry, during which the decline in P_{O_2} in the system was recorded every second. The flushing and measurement periods, and the data recording, were automated by computer, providing a measure of oxygen uptake every 10 min. This system has the advantage of providing frequent, high-resolution respirometry measurements without washout problems, while keeping oxygen levels high (>17 kPa, 80 % saturation) and preventing buildup of metabolic waste (Steffensen, 1989).

Experimental protocol

Each fish was introduced into the respirometer the day prior to the swimming speed test, and allowed to acclimate overnight at a water speed of 7–10 cm s^{-1}. This flow rate maintained adequate water mixing, but was not enough to induce swimming, and the fish eventually settled on the bottom of the working section. Oxygen consumption measurements began immediately, and continued overnight to obtain a measure of standard metabolic rate (SMR, $\dot{M}_{O_2}$ at zero swimming speed).

The following day, a critical speed (U_{crit}) swimming test was performed (Brett, 1964; Beamish, 1978) with step-wise increases in flow speed of approximately 0.5 total length s^{-1} ($L\,s^{-1}$) every 30 min (3×10 min $\dot{M}_{O_2}$ measurement periods) until the fish fatigued, i.e. could no longer maintain its position away from the downstream screen of the working section. Video recordings (50 fields s^{-1}) were made at each flow speed for analysis of fin-beat frequencies. Following the experiment, the fish were weighed and body dimensions were measured. The triggerfish were returned to the wild and the parrotfish were killed by an overdose of anesthetic (tricaine methanesulfonate) for subsequent confirmation of species identification. After each experiment, the oxygen consumption in the empty respirometer was measured to determine background levels (10.8±7.7 mg $O_2\,h^{-1}$, mean ± S.D., N=12), which were subtracted from the experimental values for $\dot{M}_{O_2}$.

Data calculations and analysis

Because water flow speed in the flume increases in the presence of a fish that occupies part of the cross-sectional area of the working section (solid-blocking effect), swimming speeds were corrected according to the equations of Bell and Terhune (1970):

$$U_F = U_T(1 + \varepsilon_S), \quad (1)$$

where U_F is the corrected flow speed and U_T is the speed in the flume without a fish in the swimming section. The fractional error due to solid blocking (ε_S) was calculated for each individual fish as:

$$\varepsilon_S = \tau\lambda(A_O/A_T)^{3/2}, \quad (2)$$

where τ is a dimensionless factor depending on flume cross-sectional shape, λ is a shape factor for the test object, A_O is the maximum cross-sectional area of the test fish, and A_T is the cross-sectional area of swimming section. For any sectional shape, τ=0.8 to one decimal place, and for a streamlined object λ=0.5 body length/body thickness (Bell and Terhune, 1970). Body thickness was calculated as the average of the fish depth and width, and the cross-sectional area of the fish was assumed to be an ellipse based on maximal depth and width measurements. The fractional cross-sectional area of the swimming section occupied by the fish (A_O/A_T) ranged from 6 to 11 %.

Swimming gait and fin-beat frequencies were measured from video recordings. At each swimming speed and for each gait used, three separate periods of steady swimming were analyzed and the time for 10 complete fin beat cycles determined and averaged to give fin-beat frequency (beats s^{-1}). Each swimming speed was analyzed over a 1 min time interval to determine the percentage of time spent using each gait.

The 30-min critical swimming speed (U_{crit}) was calculated as described by Beamish (1978):

$$U_{crit} = U_i + [(t_i/t_{ii})U_{ii}], \quad (3)$$

where U_i is the highest speed maintained for the entire prescribed time, U_{ii} is the speed increment, t_i is the length of time at the speed that produced fatigue, and t_{ii} is the prescribed time between speed increments.

Oxygen consumption rate ($\dot{M}_{O_2}$) was determined from the slope of a linear regression of the P_{O_2} decline over time for each measurement cycle, using the formula:

$$\dot{M}_{O_2} = sV_{resp}\alpha, \quad (4)$$

where s is the slope, V_{resp} is the volume of the respirometer minus the volume of the fish, and α is the solubility of oxygen in the water. Only measurements where the regression coefficient of determination (r^2) was greater than or equal to 0.98 were used. The slope was corrected for any signal drift that occurred between electrode calibrations by both adjusting for the rate of change and correcting P_{O_2} values for calibration error. This correction averaged 6.2±10.7 %, mean ± S.D. (N=875).

SMR was calculated from a frequency histogram of the raw $\dot{M}_{O_2}$ data collected overnight, excluding the initially elevated

values immediately after the fish was introduced into the respirometer. Two normal curves were fit to the $\dot{M}_{O_2}$ frequency histogram to separate the SMR peak, when the fish was at rest, from the peak of elevated metabolism seen during spontaneous activity (routine metabolic rate) (Steffensen et al., 1994).

For the swimming speed test, periods of unsteady swimming (with the exception of the burst-and-glide swimming mode seen at the highest speeds in the parrotfish) and swimming against the sides of the flume were eliminated from analysis. Multiple $\dot{M}_{O_2}$ measurements at the same speed were averaged for individual fish.

Two models were used to describe the relationship between $\dot{M}_{O_2}$ and swimming speed U. The first is the traditional exponential function (Brett, 1964; Webb, 1975; Beamish, 1978):

$$\dot{M}_{O_2} = a10^{(bU)} \quad (5)$$

and its logarithm-transformed linear form:

$$\log\dot{M}_{O_2} = \log a + bU, \quad (6)$$

where a is SMR ($\dot{M}_{O_2}$ at zero speed) and b is the slope of the semi-logarithmic regression.

The second model is the hydrodynamics-based power function (Wu, 1977; Videler, 1993):

$$\dot{M}_{O_2} = a + bU^c, \quad (7)$$

and its linear form:

$$\log(\dot{M}_{O_2} - a) = \log b + c\log U, \quad (8)$$

where a is SMR, and therefore ($\dot{M}_{O_2}$–a) is the metabolic increment due to swimming, which we define here as the net cost of swimming. The exponent c, which is the slope of log–log regression of this metabolic increment as a function of swimming speed, contains information on the aerobic swimming efficiency (Wardle et al., 1996). The linear forms of both functions (equations 6, 8) were used to fit least-squares regressions. For the exponential function, SMR values were included in the regression at zero speed. In the case of the power function, the SMR determined for each individual was subtracted from the swimming $\dot{M}_{O_2}$ values to obtain $\dot{M}_{O_2}$–a.

To determine the effects of body mass, swimming gait, and swimming speed on $\dot{M}_{O_2}$, and to compare the slopes (analysis of covariance, ANCOVA), we used the General Linear Model procedures of SYSTAT (version 10, SPSS Inc. 2000). For the exponential model (equation 6), we used stepwise multiple regression analysis to test for any significant effects on $\log\dot{M}_{O_2}$ of swimming speed, log(mass), gait, and the interaction terms: log(mass)×speed and gait×speed. Variables and interaction terms that did not contribute significantly to the multivariate regression were dropped, one at a time, and a new regression was calculated until only variables with significant effects on $\log\dot{M}_{O_2}$ remained. The same procedure was repeated for the power model (equation 8), except that effects on $\log(\dot{M}_{O_2}$–$a)$ were tested, and log(speed) was substituted for speed. A significance level of $P<0.05$ was used in statistical tests unless otherwise noted. Error values are given as standard deviation (S.D.).

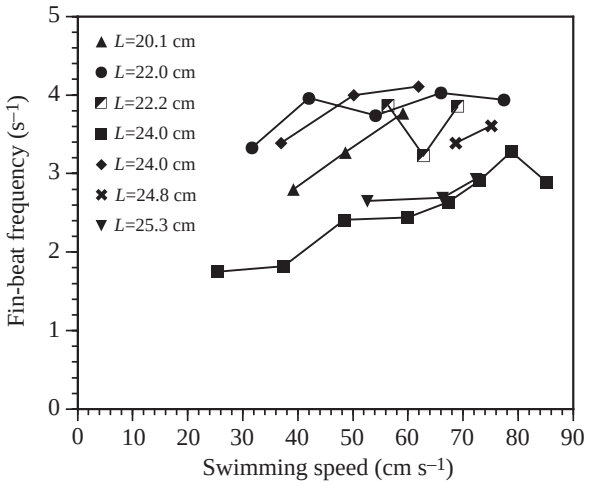

Fig. 1. Pectoral fin-beat frequencies as a function of swimming speed for seven parrotfish *Scarus schlegeli* during the critical speed swimming test. Total body lengths (L) are given for each individual.

Results

Swimming performance and gaits

The purpose of this study was not to make detailed kinematic descriptions of swimming; however, we did make observations on fin-beat frequencies and gait transitions in the triggerfish and parrotfish. Below about 1.5 L s^{-1}, or 35 cm s^{-1}, the parrotfish either did not swim or swam unsteadily (maneuvered or accelerated) using their pectoral fins (MPF gait, labriform swimming). Above this swimming speed, the pectoral fins were used synchronously, and fin-beat frequency tended to increase, in general, with swimming speed, although some fish showed little or no change in fin-beat frequency at the higher swimming speeds (Fig. 1). The parrotfish swam exclusively with the pectoral fins up to 70–90 cm s^{-1} (3–3.5 L s^{-1}). At higher speeds, the fish changed to body-caudal undulations in a burst-and-coast swimming mode (BCF gait) with the pectorals held flat against the body, but could not sustain this gait for more than 10 min before fatiguing. Critical swimming speeds (U_{crit}, the highest speed that can be sustained for a prescribed time period, in this case 30 min) ranged from 66 to 82 cm s^{-1} (mean=73±7 cm s^{-1}, N=7) or 2.8–3.7 L s^{-1} (mean=3.2±0.3 L s^{-1}, N=7).

At low swimming speeds, the triggerfish swam using undulations of the dorsal and anal fins (MPF gait, balistiform swimming). When swimming steadily, the dorsal and anal fins undulated at the same frequency. The pectoral fins were used only occasionally for maneuvering at the lowest speed (≤1.0 L s^{-1}) and were held against the side at higher swimming speeds. From 25 to 60 cm s^{-1} (1.5–3.0 L s^{-1}), body-caudal undulations (BCF gait) were used intermittently for increasing amounts of time as speed increased, and were used continuously above 65 cm s^{-1} (3.5 L s^{-1}) (Fig. 2A). During

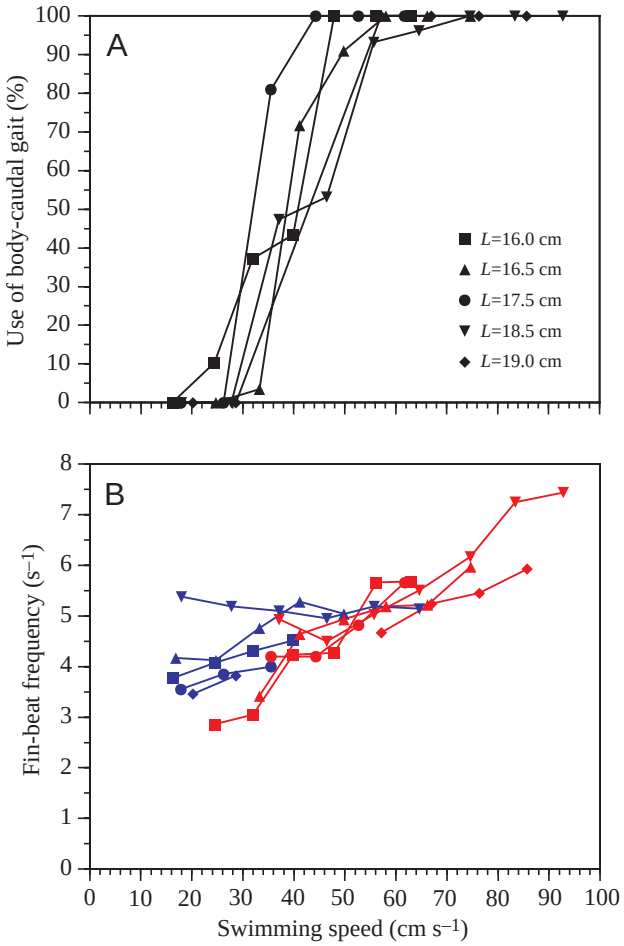

Fig. 2. Percentage of time using the body-caudal fin gait (A) and fin-beat frequencies (B) as a function of swimming speed for five triggerfish *Rhinecanthus aculeatus*. When not using body-caudal undulations, the triggerfish swam using only undulations of the dorsal and anal fins. In B, symbols in blue are frequencies of the dorsal and anal fins during swimming with only these median fins. Symbols in red are the frequencies of the dorsal, anal and caudal fins when body-caudal swimming was used. Total body lengths (L) are given for each individual.

body-caudal swimming, the dorsal and anal fins beat at the same frequency as the caudal fin, with deflections in the same direction as the adjacent body undulations. For the triggerfish, U_{crit} ranged from 55 to 93 cm s^{-1} (mean=76±14 cm s^{-1}, N=5), or 3.2–5.0 L s^{-1} (mean=4.1±0.7 L s^{-1}, N=5), although the high end of the range maybe an underestimate, as this was the maximal flow speed of the swim flume. With one exception, fin-beat frequencies increased with swimming speed (Fig. 2B). At the transitional swimming speeds, when MPF and BCF gaits were used alternately, fin-beat frequencies were generally lower during body-caudal swimming, than when using the dorsal and anal fins alone (Fig. 2B).

Energetics

After placing the fish in the swimming respirometer, $\dot{M}_{O_2}$ was typically slightly elevated for a few hours, but then settled

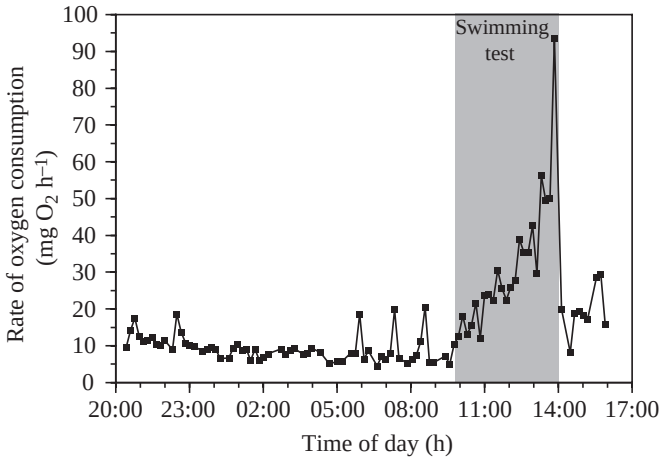

Fig. 3. Rate of oxygen consumption ($\dot{M}_{O_2}$) measurements throughout an experimental run with a 105 g triggerfish *Rhinecanthus aculeatus*. Measurements began shortly after placing the fish in the respirometer (19:50 h) and were made every 10 min. $\dot{M}_{O_2}$ stabilized overnight, allowing determination of standard metabolic rate (see text). Three periods of spontaneous activity appeared in the early morning hours, demonstrating the high resolution of the system. The shaded region indicates the period during the swimming speed test.

overnight, allowing the determination of SMR, after excluding occasional increases in $\dot{M}_{O_2}$ due to spontaneous activity (Fig. 3). Mean SMR for parrotfish was 31.5±11.4 mg O_2 h^{-1} (N=7) or 127±27 mg O_2 kg^{-1} h^{-1} (N=7), and for triggerfish was 10.2±4.4 mg O_2 h^{-1} (N=5) or 74.7±21.9 mg O_2 kg^{-1} h^{-1} (N=5). In both parrotfish and triggerfish, $\dot{M}_{O_2}$ increased significantly with increases in swimming speed (Figs 4A, 5A).

In the parrotfish swimming using the MPF gait, $\dot{M}_{O_2}$ increased significantly with swimming speed (Fig. 4A) and was also positively correlated with body mass (scaling exponent=0.81), but there were too few data to perform a regression for swimming speed during the burst-and-coast BCF gait. $\dot{M}_{O_2}$ during BCF swimming was, however, significantly higher than during MPF swimming (ANCOVA, Fig. 4A). After subtraction of SMR from the swimming $\dot{M}_{O_2}$ values to get the net cost of swimming, ($\dot{M}_{O_2}$–a), the effect of mass was no longer significant (Fig. 4B). The value ($\dot{M}_{O_2}$–a) in proportion to speed increased to the power 1.66 and also increased significantly with the transition to the BCF gait (ANCOVA, Fig. 4B).

For the triggerfish, swimming $\dot{M}_{O_2}$ values were grouped according to gait use; one set where *only* the MPF gait was used, and one where both the MPF and the BCF gaits were used. $\dot{M}_{O_2}$ increased with swimming speed in both sets (Fig. 5A). However, the rate of increase (slope of the semi-log regression) was significantly higher when the BCF gait was used (ANCOVA, Fig. 5A). The net cost of swimming also increased at a higher rate (to the power of 2.31) during BCF swimming compared with MPF swimming (to the power of 1.55), although these values were not significantly different (P=0.07) (Fig. 5B). The lower statistical significance is probably due to the loss of zero speed values after calculating

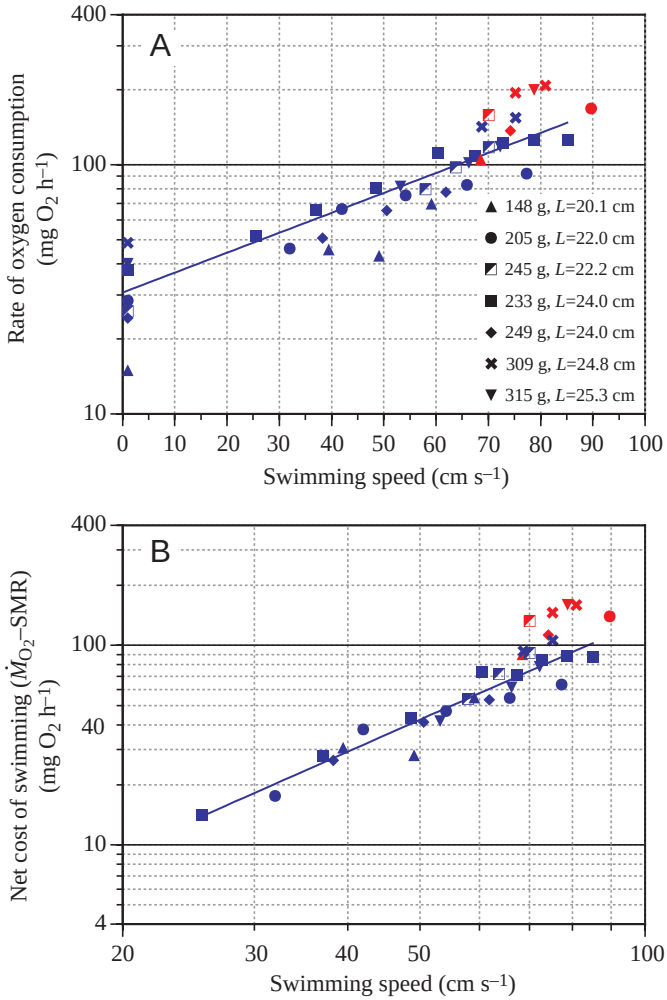

Fig. 4. Total rate of oxygen consumption $\dot{M}_{O_2}$ (A) and net swimming costs (B) as a function of swimming speed for the parrotfish *Scarus schlegeli*. Blue symbols, oxygen uptake during labriform (rigid-body) swimming; red symbols, during body-caudal undulations. Both $\dot{M}_{O_2}$ and net swimming costs were significantly higher during body-caudal undulations (ANCOVA, $P<0.05$). Mass and total length (L) are given for each individual. Standard metabolic rates (SMR, a) are shown at zero speed (A). Total $\dot{M}_{O_2}$ (A) during rigid-body swimming was positively related to swimming speed (U) and body mass (M) by the equation: $\log\dot{M}_{O_2}=1.984+0.008U+0.809\log M$, $r^2=0.92$, $N=7$. For clarity, only a single regression line is shown for the mean mass of 0.243 kg. Net swimming costs (B) were calculated as $\dot{M}_{O_2}$–SMR for each individual, and during rigid-body swimming were positively related to speed by the equation $\log(\dot{M}_{O_2}–a)=–1.193+1.660\log U$, $r^2=0.91$, $N=7$.

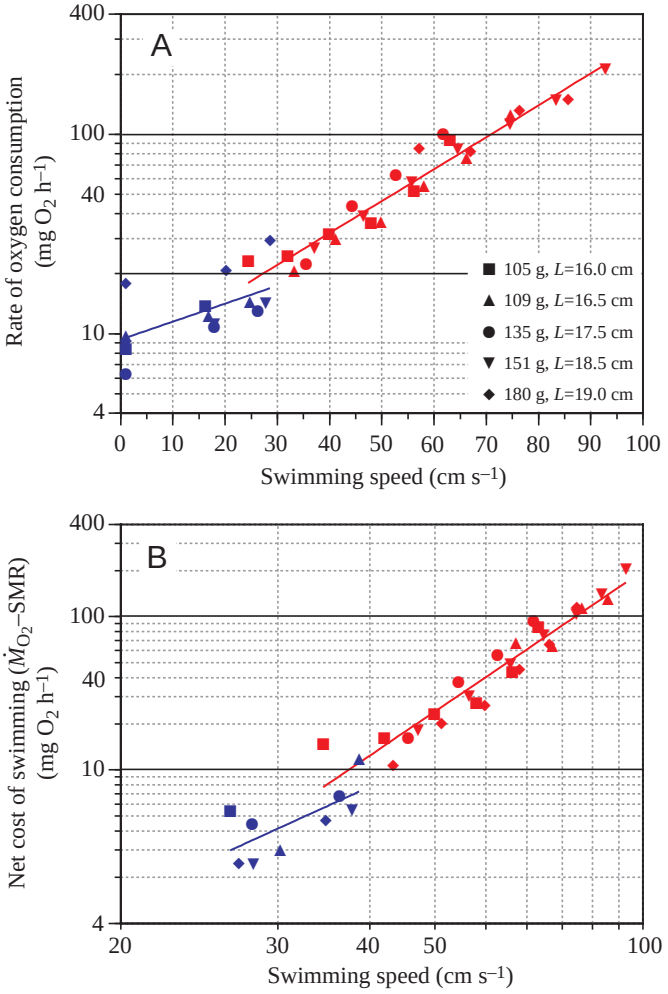

Fig. 5. Total rate of oxygen consumption $\dot{M}_{O_2}$ (A) and net swimming costs (B) as a function of swimming speed for the triggerfish *Rhinecanthus aculeatus*. Blue symbols, oxygen uptake during balistiform (rigid-body) swimming; red symbols, during swimming with the use of body-caudal undulations in addition to the dorsal and anal fins. The rate of increase (slope) in total $\dot{M}_{O_2}$ was significantly higher during body-caudal swimming (ANCOVA, $P<0.05$). Mass and total length (L) are given for each individual. Standard metabolic rates (SMR, a) are shown at zero speed (A). Total $\dot{M}_{O_2}$ (A) during rigid-body swimming was positively related to swimming speed (U) by the equation: $\log\dot{M}_{O_2}=0.971+0.009U$, $r^2=0.42$, $N=5$. For body-caudal swimming, the relationship was: $\log\dot{M}_{O_2}=0.865+0.016U$, $r^2=0.94$, $N=5$. Net swimming costs (B) were calculated as $\dot{M}_{O_2}$–SMR for each individual. During rigid-body swimming, net swimming costs were positively related to swimming speed by the equation: $\log(\dot{M}_{O_2}–a)=–1.403+1.553\log U$, $r^2=0.49$, $N=5$, and during body-caudal swimming by the equation: $\log(\dot{M}_{O_2}–a)=–2.306+2.302\log U$, $r^2=0.91$, $N=5$.

($\dot{M}_{O_2}–a$). The effect of body mass on either $\dot{M}_{O_2}$ or ($\dot{M}_{O_2}–a$) was not significant for the relatively narrow range of triggerfish body masses investigated.

The total cost of transport (TCOT, Fig. 6), the amount of oxygen used per unit mass per unit distance, was calculated for both species from the exponential relationships shown in Figs 4A and 5A. The relationship between TCOT and swimming speed is typically U-shaped, with the swimming speed where TCOT is at a minimum defined as the optimal speed (U_{opt}). Parrotfish U_{opt} occurred during MPF swimming at 53 cm s^{-1} (approximately 2.3 L s^{-1}), with a minimum TCOT of 176 mg O_2 kg^{-1} km^{-1} (Fig. 6). As with total $\dot{M}_{O_2}$, TCOT during BCF swimming in the parrotfish was higher than during MPF swimming at the same speeds. For the triggerfish,

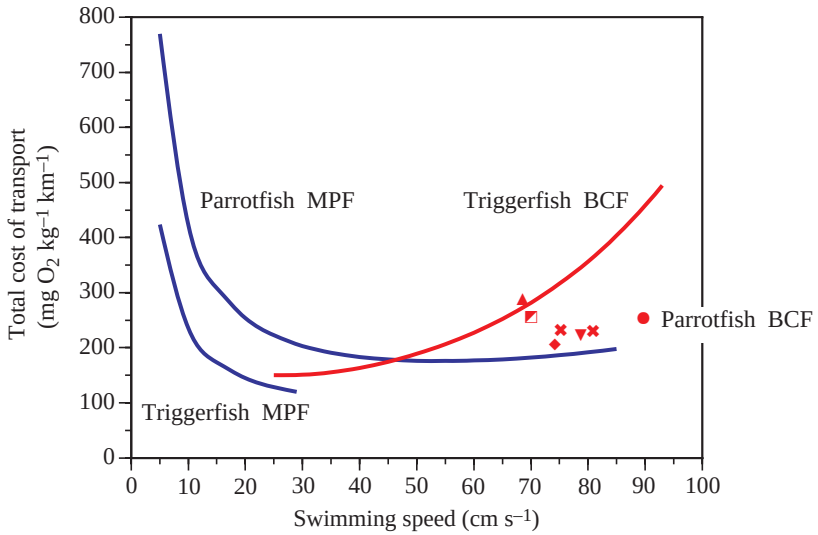

Fig. 6. Total cost of transport (TCOT), the amount of energy expended per unit mass per unit distance, as a function of swimming speed for the triggerfish *Rhinecanthus aculeatus* and the parrotfish *Scarus schlegeli*. TCOT was calculated from the relationship between total $\dot{M}_{O_2}$ and swimming speed presented in Figs 4A and 5A. Lines in blue are for median-paired fin (MPF), rigid-body swimming, and the line (triggerfish) and symbols (parrotfish) in red are for body-caudal (BCF), undulatory swimming. Symbols for parrotfish BCF swimming are the same as in Fig. 4.

U_{opt} occurred at the highest speed obtained with the MPF gait alone (25–29 cm s^{-1}, or approx. 1.5 L s^{-1}) at a TCOT of 120 to 128 mg O_2 kg^{-1} km^{-1} (Fig. 6). Upon switching to the BCF gait, TCOT increased and continued to increase with swimming speed.

Discussion

Swimming performance of MPF gait specialists

Most teleosts use MPF swimming at very low speeds, where stability and maneuverability are enhanced through use of multiple, flexible fins that can produce thrust independently in many different directions (Webb, 1998). Several radiations of specialization for MPF gait use during routine swimming have evolved within the Acanthopterygii, and are associated with changes in paired-fin positions to locations around the center of body mass and advancement of the anal fin to become symmetrical with the dorsal fin (Webb, 1982). Precise maneuverability and stability at low swimming speeds are presumably advantageous in structurally complex habitats such as coral reefs, where both parrotfish and triggerfish are found (Blake, 1978; Webb, 1994a). MPF specialization is thought to reduce caudal swimming performance because of trade-offs when optimizing for a particular gait (Blake, 1978; Webb, 1982; Webb, 1994a), although this may not be a disadvantage for MPF specialists which typically feed on prey that do not require high speeds for capture (Webb, 1982).

Although specialized as MPF swimmers, both the parrotfish and triggerfish could achieve high, prolonged swimming speeds (U_{crit}) that were comparable with similarly sized BCF swimmers (3–4 L s^{-1}) (Videler, 1993). These two species use different gaits to reach these high swimming speeds. Parrotfish, and some other labriform swimmers, have replaced BCF swimming with MPF swimming for cruise swimming, and the body and caudal fin are only used for short-duration burst swimming (Fig. 4) (Webb, 1974, 1982). At low swimming speeds, the parrotfish appeared to be unstable, as we were unable to get them to swim steadily below about 1.5 L s^{-1}. Similar swimming performance was found in another labriform swimmer, the bird wrasse *Gomphosus varius* (family Labridae), which uses MPF swimming at speeds up to 6 L s^{-1}, but will not swim steadily below 1.2 L s^{-1} (Westneat, 1996; Walker and Westneat, 1997). These fishes are adapted for MPF swimming to obtain high, sustained swimming speeds, and show poor swimming stability at low speeds, despite the MPF swimming mode. Labriform swimmers show a range of swimming capabilities from those that use labriform swimming for low-speed maneuverability to those capable of high speed, sustained swimming. Drucker and Lauder (2000) found a possible trade-off in pectoral fin morphology and kinematics between designs that permit high swimming speeds (generation of high posteriorly directed thrust), and those that permit a high degree of stability and maneuverability at low speeds (generation of large lateral forces). Similarly, from simulations of fin mechanics, Walker and Westneat (2000) concluded that fish using the pectorals in a lift-based swimming mode, by 'flapping' to generate thrust on both the upstroke and downstroke, should be more energy efficient, permitting high sustained swimming speeds, than those that use a drag-based 'rowing' mode. However, labriform swimmers using rowing mechanics should be more effective at low speeds, although at greater energetic cost, because more thrust is generated, facilitating maneuvering behaviors (Walker and Westneat, 2000). These two extremes of labriform swimming also correlate with fin morphology; high-speed lift-based swimmers possess elongate, high aspect-ratio fins, and those that are slow, drag-based swimmers have more rounded, low aspect-ratio fins (Webb, 1994b; Walker and Westneat, 1997, 2000, 2002; Wainwright et al., 1999).

This correlation between labriform swimming performance and fin morphology is consistent with analyses of maneuverability and habitat use among coral reef labriform swimmers. Those fishes with low aspect-ratio pectoral fins are superior maneuverers, inhabiting low-wave energy areas of the reef or remaining close to the substratum, while fish with high aspect-ratio fins are predominant in areas with high water

movement and at higher positions in the water column (Gerstner, 1999; Bellwood and Wainwright, 2001; Fulton et al., 2001). Consistent with their high sustainable swimming speeds, the parrotfish *S. schlegeli* have high aspect-ratio pectoral fins and are often found above the reef, swimming over large areas to forage, rather than within the reef complex where precise maneuverability would be more advantageous (Bellwood and Wainwright, 2001; K. E. Korsmeyer, J. F. Steffensen and J. Herskin, personal observations).

In contrast to the parrotfish, the triggerfish recruited body-caudal undulations to achieve high, prolonged swimming speeds (Fig. 5). This high-speed endurance was particularly surprising because triggerfish are typically considered to be highly adapted for low speed maneuverability at the expense of achieving high, sustained swimming speeds (Blake, 1978; Webb, 1982, 1998). Balistids, and the Tetraodontiforms in general, show a high degree of morphological specialization (Lauder and Liem, 1983), including a truncate body with limited flexibility, which is thought to limit BCF swimming, and development of defensive armor, which is thought to compensate for lack of high-speed swimming ability to escape predators (Lighthill and Blake, 1990; Webb, 1994a; Brainerd and Patek, 1998). The limited flexibility of tetraodontiform fishes is a result of reduced vertebral number (Brainerd and Patek, 1998), which limits maximal body curvature in these fishes, and probably reduces startle-response escape speeds (C-starts) that involve extreme bending of the body from a stationary position (Brainerd and Patek, 1998). At slow swimming speeds, triggerfish are clearly highly maneuverable and stable using balistiform locomotion. The large, flexible dorsal and anal fins can move independently and produce thrust in many different directions (Webb, 1998). These fish can hover, swim backwards, and turn about their own axis with little lateral translation of the body (Blake, 1978). In addition, we found they are capable of sustaining swimming speeds of about $4\,L\,s^{-1}$ (for at least 30 min) using body-caudal undulations, in addition to the undulations of the dorsal and anal fins (Figs 2 and 5). For sustainable swimming speeds at least, there appears to be no reduction in BCF swimming performance in the triggerfish. Any limitation in body and caudal fin undulation, if present, might be offset by the simultaneous use of the median fins. This high-speed swimming ability may be advantageous for the triggerfish to hold station in strong surge currents produced by wave action on the reef. Other tetraodontiform MPF specialists, boxfish (family Ostraciidae), puffers (family Tetraodontidae) and burrfish (family Diodontidae), are also highly maneuverable at low swimming speeds, and through a combination of gaits using pectoral, median and caudal fins can reach high, prolonged swimming speeds (Arreola and Westneat, 1996; Gordon et al., 1996, 2000; Walker, 2000; Hove et al., 2001).

It appears that MPF gait specialization does not necessarily limit sustainable, steady swimming performance, although the gaits used to achieve high swimming speeds vary. Within a given gait, however, there is a trade-off for specialization within a certain range of swimming performance, as discussed above for labriform swimmers. In the parrotfish, the MPF gait appears to be adapted for moderate to high sustainable swimming speeds, limiting slow speed maneuverability, but permitting specialization of the BCF gait for high speed sprints and accelerations (Webb, 1982). Conversely, in the triggerfish, the MPF gait allows a high degree of stability and maneuverability at low speeds, but the fish must rely on BCF swimming to support high sustainable swimming speeds. Rapid sprints (burst swimming) by the triggerfish may be limited, however, as predicted for startle-response maneuvers (Brainerd and Patek, 1998).

Use of models to predict swimming energetic costs

The exponential equation (equations 5 and 6) is a valid model for relating total $\dot{M}_{O_2}$ with swimming speed in numerous fish species (Webb, 1975). With only two constants to derive, it is more robust than the power function, and more reliable for making predictions beyond the range of measured values. This is particularly true for estimating SMR by extrapolating the $\log\dot{M}_{O_2}$ values as a function of speed to zero speed (Brett, 1964; Bushnell et al., 1984; Dewar and Graham, 1994).

The slope of the semi-log transformation of the exponential function (factor *b* in equation 6; Figs 4A, 5A) indicates how quickly total energetic costs increase as swimming velocity increases, and has been used as a comparison of swimming efficiencies among species (Bernatchez and Dodson, 1985; Gordon et al., 1989; Dewar and Graham, 1994). However, this slope can be misleading because it is highly dependent on the *y*-intercept, or SMR. Two different fish with the same net cost of swimming (swimming $\dot{M}_{O_2}$–SMR) but different SMRs will have different slopes (*b*) (Korsmeyer and Dewar, 2001). Although suitable for comparing swimming costs among fish of the same or similar SMR (e.g. among the same group of fish as in Fig. 5A), the slope of the exponential relation cannot be used for comparison of swimming costs in fishes with different SMRs (e.g. different species).

In contrast, the power function (equation 7) takes into account differences in SMR (factor *a* in equation 7), so that the power to which velocity is raised (factor *c*) can be used to compare incremental swimming costs among species. However, unlike the exponential function, fitting the power equation to total $\dot{M}_{O_2}$ (equation 7) will overestimate SMR because iterative least-squares regression with this equation tends to place more weight on the higher speed values (Videler and Nolet, 1990). The transformation of the power equation (equation 8) results in a linear relationship between the log of the net cost of swimming ($\dot{M}_{O_2}$–SMR) and the log of speed (Figs 4B, 5B). Fitting to this linear form of the power equation (equation 8) is preferable because it avoids overestimation at the lower values, but it also requires an accurate measure of SMR in order to calculate ($\dot{M}_{O_2}$–SMR) (see Steffensen, 1989, for a discussion of common errors in respirometry).

Because it is the energy expended beyond the maintenance metabolism that is related to the energy to produce thrust, comparison of the net cost of swimming is more appropriate than of total $\dot{M}_{O_2}$. In addition, the power function follows

standard hydrodynamic laws, where the log of thrust (= the power to overcome drag) is directly related to the log of speed (Brett, 1964; Wu, 1977; Videler, 1993). The rate at which the log of the net swimming cost increases with the log of speed is found in factor *c* (the slope, or the power to which speed is raised in the untransformed form of the equation, equation 7). This value provides information on the aerobic swimming efficiency (Wardle et al., 1996) and best represents 'delta efficiency', the incremental costs above resting, or maintenance, metabolic costs (Blake, 1991; Full, 1991). It should be noted, however, that this model assumes that maintenance costs remain the same at different swimming speeds, and this may not be the case (Farrell and Steffensen, 1987). Nevertheless, it is the slope from the best-fit power function (equation 8) that we recommend be used for comparisons of swimming efficiency among different groups or species of fishes.

Energetics of MPF versus BCF swimming

For the triggerfish and parrotfish, it appears that undulatory BCF swimming entails a higher cost than rigid-body MPF swimming. When the parrotfish switched to a BCF gait, they also used a burst-and-coast mode of swimming. This swimming pattern is associated with use of the fast glycolytic (FG, or white) muscle (Videler and Weihs, 1982; Rome et al., 1990), which is consistent with the fish's rapid fatigue at these speeds. Other labriform swimmers, including many labrids and the threespined stickleback (*Gasterosteus aculeatus*), show the same swimming pattern, switching from pectoral fin use to BCF bursts at maximal sustained swimming speeds, and rapid fatigue results because the myotomal muscle lacks slow oxidative (SO, or red) fibers (te Kronnie et al., 1983; Whoriskey and Wootton, 1987; Davison, 1988; Walker and Westneat, 2002). Swimming costs in the parrotfish, as measured by oxygen consumption, increased during burst-and-coast swimming compared with that predicted for MPF swimming at the same swimming speeds (Fig. 4). Actual swimming costs were probably much higher, as only aerobic metabolism was measured, and the additional anaerobic contribution from use of FG muscle is not included in $\dot{M}_{O_2}$.

The triggerfish used BCF swimming at sustainable (aerobic) speeds, indicating the primary use of SO muscle. It is not surprising that total $\dot{M}_{O_2}$ and net swimming costs increased at a faster rate with swimming speed once the muscles powering body-caudal undulations were recruited in addition to those powering the undulations of the dorsal and anal fins (Fig. 5). Although *R. aculeatus* has a significant amount of myotomal SO muscle to power sustained BCF swimming (K. E. Korsmeyer, unpublished observations), in other balistids SO fibers are only found in the fin muscles, and the body musculature is composed entirely of FG fibers (Davison, 1987). In these species, sustainable swimming speeds would be limited to those that could be powered by balistiform locomotion alone. Among balistiform swimmers, there may be a range of performance specializations within this swimming mode equivalent to that seen in labriform swimmers (see above).

The power to which net swimming costs increased with speed was similar for both the parrotfish (1.66) and the triggerfish (1.55) when swimming in an MPF gait (Figs 4B and 5B). When the triggerfish added BCF swimming, the rate at which total $\dot{M}_{O_2}$ increased nearly doubled, and net swimming costs increased to the power of 2.31 (Fig. 5). Few studies comparable with this study of fish swimming energetics have used the power equation (equation 7). In a study of swimming metabolism of the horse mackerel, *Trachurus trachurus* (family Carangidae, a BCF carangiform swimmer), where SMR was also measured, swimming costs increased with speed to the power 2.56 (Wardle et al., 1996). This value is similar to that determined for the triggerfish during BCF swimming, and much higher than our MPF swimming values (Figs 4B, 5B).

Gordon et al. (1989) measured swimming $\dot{M}_{O_2}$ in two labriform swimmers, the shiner surfperch *Cymatogaster aggregata* (family Embiotocidae) and the señorita wrasse *Oxyjulis californica* (family Labridae). The rates of increase in total $\dot{M}_{O_2}$ with swimming speed in that study were extremely low, and in many cases not significantly different from zero. Although this suggests very low costs of swimming, the authors caution that their results could be due to confounding factors (Gordon et al., 1989). Variability in $\dot{M}_{O_2}$ was very high, suggesting that metabolism was elevated due to stress or excitement, particularly at low swimming speeds. SMR was not measured, and the power function, which was difficult to fit to their data, gave highly variable exponents (0.16–5.8), and is therefore difficult to compare with our results. A previous study using one of the same species (*C. aggregata*) found significant increases in $\dot{M}_{O_2}$ with swimming speed, and although a power function was not fit to the data, the results show increases in net swimming costs similar to those we found for the parrotfish (Webb, 1974).

In contrast to our results, Parsons and Sylvester (1992) found that total $\dot{M}_{O_2}$ decreased with a switch in swimming gait from MPF (labriform) to BCF swimming in white crappie *Pomoxis annularis* (family Centrarchidae). Unlike the parrotfish, the crappie use labriform swimming only up to about $1\,L\,s^{-1}$, before switching to BCF swimming for higher sustained swimming speeds (Parsons and Sylvester, 1992). The higher costs of labriform swimming in these fish may be due to fin specialization for stability and maneuverability at low speeds, which is associated with less efficient fin mechanics (Walker and Westneat, 2000). In addition, the costs to control stability increase as speed decreases, often resulting in elevated metabolic rates at low speeds (Webb, 1998). Such elevation was seen for the labriform swimmer *C. aggregata* below $1\,L\,s^{-1}$ (Webb, 1974). We did not measure $\dot{M}_{O_2}$ in either the parrotfish or triggerfish at water speeds below $1\,L\,s^{-1}$ because the fish would not swim, or only swam unsteadily, so that we could not determine swimming speed. It is reasonable to predict that $\dot{M}_{O_2}$ would be elevated because, for example, the triggerfish have higher than expected fin-beat frequencies at very low swimming speeds ($<0.5\,L\,s^{-1}$) (Blake, 1978). These higher costs for stability at very low speeds may obscure energetic advantages of MPF swimming.

The apparent energy savings with MPF swimming were similar in both the parrotfish and triggerfish, which supports the hypothesis that MPF swimming is more efficient than BCF swimming, possibly due to the reduced drag of rigid-body swimming (Webb, 1975; Lighthill and Blake, 1990). In addition, Lighthill (1990; Lighthill and Blake, 1990) calculated that balistiform propulsion by median fins attached to a deep, rigid body would increase the efficiency of thrust production. Among labriform swimmers, those with high aspect-ratio pectoral fins are also predicted to benefit from a high mechanical efficiency (Walker and Westneat, 2000).

One consequence of a lower increase in swimming costs using an MPF gait is that the minimum cost of transport occurs at a higher speed (Fig. 6). Although the triggerfish change gaits before reaching the minimum, the parrotfish have a very high U_{opt} (approximately $2.3\,L\,s^{-1}$) compared to the expected U_{opt} for fish of this size (approximately $1.3\,L\,s^{-1}$) (Videler, 1993), which suggests that they are adapted for relatively high routine swimming speeds. Also, the parrotfish TCOT-U curve is very flat above 30 cm s^{-1} (approximately $1.5\,L\,s^{-1}$), meaning that distance-specific transport costs change little over a broad range of swimming speeds. A similarly shallow TCOT curve was found for another MPF swimmer, the boxfish *Ostracion meleagris* (Gordon et al., 2000), suggesting this may be a common feature of rigid-body MPF swimmers. However, the minimum TCOTs for the triggerfish and parrotfish, and also the boxfish, are similar to that of other fishes (Videler, 1993; Gordon et al., 2000). Using the minimum TCOT to compare swimming energetics among fishes does include the costs of SMR, which are not directly related to swimming costs, however, and differences in U_{opt} (which are also highly dependent on SMR) mean that comparisons are made at different relative swimming speeds. Perhaps as a result of this, most of the variation in TCOT among fishes is explained by differences in body mass (Videler, 1993).

Energetics of gait transition

Unlike terrestrial vertebrates, the change of gait at higher speeds in the parrotfish and triggerfish does not appear to be a mechanism to reduce costs, but may occur because of a limitation in achievable thrust in any one particular gait. The similar rates of increase in MPF swimming costs in the parrotfish and triggerfish (Figs 4B, 5B) result in similarly shaped TCOT-U curves (Fig. 6). While the parrotfish is able to achieve high swimming speeds within the MPF gait, keeping TCOT low, the triggerfish must switch to BCF swimming, with its higher transport costs (Fig. 6). Why don't the triggerfish use MPF swimming at higher speeds, if swimming costs would be lower?

Minimization of energetic cost is not the only explanation for a change in gait. There are potential limitations in the amount of muscle and propulsors for thrust production that accompany use of median or paired fins (Alexander, 1989; Webb, 1998). In addition, there are several distinct muscle types, ranging from high-endurance, low-power SO fibers to low-endurance, high-power FG fibers, which also differ in the contraction rates at which they produce optimal power (Rome et al., 1988, 1990). To achieve the highest speeds and accelerations, most fish use the large mass of FG axial, myotomal muscle, which powers body and caudal fin undulations (Webb, 1998). Likewise, when the parrotfish reach maximal prolonged swimming speeds, they must switch to BCF undulations to recruit a large amount of FG muscle. These burst swimming speeds are used to escape from predators, where high propulsive efficiency is not as important as rapid acceleration.

The triggerfish, therefore, may not be able to power higher swimming speeds using only the dorsal and anal fins, because of limitations in recruitable muscle mass or fin-propulsive mechanics. Limits in thrust production are supported by the observed fin-beat frequencies during transitional swimming speeds. Dorsal and anal fin-beat frequencies were higher when swimming with an MPF gait than when swimming with the added use of the caudal fin, at the same swimming speed (Fig. 2). In other words, the additional fin use permitted a lower fin-beat frequency to produce the same forward speed. Our results suggest that gait transition does not occur to minimize power requirements, as is the case for terrestrial locomotion (Alexander, 1989), but instead to meet the greater power requirements required at these higher swimming speeds. For aquatic locomotion, gait transition may have more to do with generating the rapidly increasing thrust necessary to swim faster in such a dense and viscous medium.

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