

PECTORAL FIN LOCOMOTION IN THE STRIPED SURFPERCH

I. KINEMATIC EFFECTS OF SWIMMING SPEED AND BODY SIZE

ELIOT G. DRUCKER* AND JEFFREY S. JENSEN

Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA

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Summary

Swimming trials at increasing velocity were used to determine the effects of steady swimming speed on pectoral fin kinematics for an ontogenetic series of striped surfperch *Embiotoca lateralis*, ranging from 6 to 23 cm in standard length (*SL*). The fin stroke cycle consisted of a propulsive period, the duration of fin abduction and adduction, and a 'refractory' period, during which the fin remained adducted against the body. Pectoral fin-beat frequency (f_p) measured as the inverse of the entire stride period, as in past studies, increased curvilinearly with speed. Frequency, calculated as the reciprocal of the propulsive period alone, increased linearly with speed, as shown previously for tail-beat frequency of fishes employing axial undulation. Fin-beat amplitude, measured as the vertical excursion of the pectoral fin tip during abduction, increased over a limited range of low speeds before reaching a plateau at 0.35–0.40 *SL*. Pectoral fin locomotion was supplemented by intermittent caudal fin undulation as

swimming speed increased. At the pectoral–caudal gait transition speed (U_{p-c}), frequency and amplitude attained maxima, suggesting that the fin musculature reached a physiological limit. The effects of body size on swimming kinematics differed according to the method used for expressing speed. At a given absolute speed, small fish used higher stride frequencies and increased frequency at a faster rate than large fish. In contrast, the relationship between f_p and length-specific speed ($SL s^{-1}$) had a greater slope for large fish and crossed that for small fish at high speeds. We recommend that comparisons across size be made using speeds expressed as a percentage of U_{p-c} , at which kinematic variables influencing thrust are size-independent.

Key words: striped surfperch, *Embiotoca lateralis*, labriform locomotion, pectoral fin, gait transition speed, body size, swimming, kinematics.

Introduction

The speed and size of an animal are important determinants of its locomotor behavior. For bony fishes, the influence of these variables on patterns of propulsor movement during swimming has been extensively documented (e.g. Bainbridge, 1958; Hunter and Zweifel, 1971; Webb *et al.* 1984). This work, however, has focused to a great extent on a single mode of swimming, axial undulatory propulsion (Webb and Blake, 1985), in which thrust is generated by waves of bending of the body and tail. Although it has been less well studied, swimming with the pectoral fins, termed labriform locomotion by Breder (1926), is widespread among bony fishes. Labriform swimming is the primary mode of locomotion for many substratum-associated taxa and is particularly common among the vast assemblage of reef-dwelling perciform fishes (Lindsey, 1978; Blake, 1983). Modulation of pectoral fin kinematics with increasing swimming speed has been described for adult perciforms which use labriform locomotion over a narrow range of low speeds prior to the initiation of axial undulation (Parsons and

Sylvester, 1992; Gibb *et al.* 1994; Webb, 1994). Apart from the studies of Webb (1973) and Westneat (1996), the relationship between speed and swimming kinematics has not been examined in fishes that rely primarily on the pectoral fins for generating thrust. In addition, the influence of body size on the temporal and spatial patterns of fin movement by pectoral fin swimmers remains largely unexplored (cf. Archer and Johnston, 1989).

Among teleosts employing labriform locomotion, the surfperches (family Embiotocidae) utilize a specialized swimming mechanism involving the generation of positive and negative lift forces during each pectoral fin-beat cycle in a fashion analogous to that proposed for the wing-beat cycle of some birds in flight (Webb, 1973). Compared with other labriform swimmers studied, surfperches swim over an unusually wide range of speeds using pectoral fin propulsion alone (Drucker and Jensen, 1996). From birth, the large, well-developed young are capable labriform swimmers which come to occupy the same general spatial and trophic niche as

*e-mail: edrucker@oeb.harvard.edu.

adults (Holbrook and Schmitt, 1984; Schmitt and Holbrook, 1984). Reliance on the paired fins for propulsion over their entire range of swimming speeds, and throughout their entire life history, makes the surfperches ideal subjects for studying the effects of speed and scale on labriform swimming behavior.

As an extension of the study by Webb (1973) which describes the effects of swimming speed on patterns of pectoral fin movement in the adult shiner surfperch *Cymatogaster aggregata*, we examine below the relationship between body size and the speed-dependent kinematics of pectoral fin swimming in an ontogenetic series of striped surfperch *Embiotoca lateralis*. We focus on this developmental size series rather than making cross-taxonomic comparisons of differently sized adults in order to avoid the confounding effects of interspecific variation in body form, habitat and locomotor ability (Huey and Hertz, 1982; Nee *et al.* 1991; Promislow, 1991). Specifically, we address the following questions: (1) how do the gait parameters affecting swimming speed and thrust (in particular, fin-beat frequency and amplitude) change with speed and (2) how are these kinematic functions influenced by body size? The answers to these basic questions contribute to a general model for comparing kinematic and physiological variables among labriform swimmers of different size (Drucker and Jensen, 1996).

Materials and methods

Fish

Striped surfperch (*Embiotoca lateralis* Agassiz) were collected by beach seine at Argyle Bay, San Juan Island, Washington, USA. Fish were housed at the Friday Harbor Laboratories of the University of Washington in 2601 and 23501 flow-through seawater tanks at 12 °C. In order to avoid any effects of prolonged pregnancy on swimming performance in these viviparous fish (Dorn *et al.* 1979), we used only males for experimentation. Individuals bearing gill parasites or exhibiting frayed fins were excluded from the study group. The fish were fed shrimp and squid every other day for 2 weeks prior to swimming trials.

Experimental procedure

Surfperch swam individually in a large racetrack-shaped flume against a current generated by a motor-driven paddle wheel (Nowell *et al.* 1989). The working area (34 cm wide × 25 cm deep × 80 cm long) was situated at the end of an 8 m long straightaway on the side of the racetrack opposite the paddles. Over the relatively large distance between the paddles and the working area, turbulence in the current was substantially attenuated. To collimate the flow further, plastic baffles (1.3 cm square grid) were positioned perpendicular to the floor of the channel upstream from the working area. These design features resulted in nearly rectilinear horizontal and vertical velocity profiles in the area where the fish swam. At distances greater than 5 cm from the walls and floor of the

working area, the flow velocity was within 5% of the mean free-stream velocity. Velocity profiles and the relationship between flow velocity and paddle motor speed were determined by timing drops of Methylene Blue introduced into the working area. The water temperature was maintained at 12 °C by a continuous low-volume flow of fresh sea water through the flume.

Four size classes of fish were selected for study from the population maintained in the laboratory ($N=3$ per size class; mean standard length, $SL \pm$ S.D.: 5.7±0.3, 11.9±0.3, 16.9±0.2 and 23.2±0.2 cm). None of the individuals was trained to swim in the flume. Each fish was starved for 24 h prior to its swimming trial and then anesthetized lightly with tricaine methanesulfonate and its body length measured. To improve the precision of kinematic measurements, the translucent tips of the pectoral fins were marked with small spots (approximately 1 mm diameter) of an opaque solution of cyanoacrylate adhesive gel and chalk dust. Fish recovered in the working area of the flume and were acclimated for 30–60 min at a low speed (approximately $0.6 SL s^{-1}$).

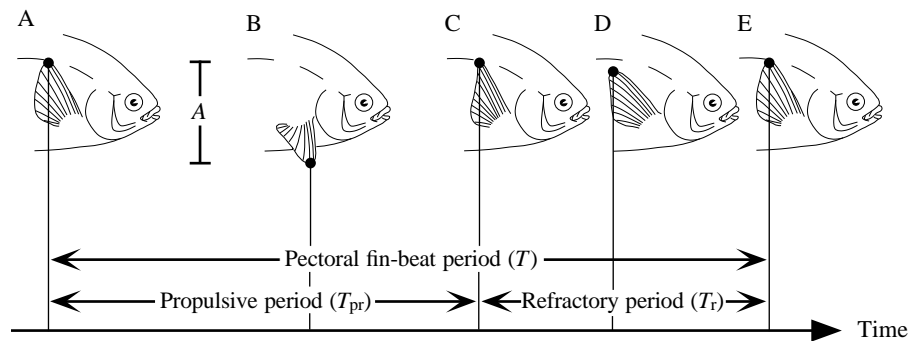
Swimming speed was increased in $0.2 SL s^{-1}$ steps from $0.6 SL s^{-1}$ to the speed at which the fish could no longer prevent itself from contacting the downstream baffle of the working area. The interval between velocity increments was 3 min. As has been reported for other species during swimming trials at increasing velocity (Bainbridge, 1962; Brett, 1964; Brett and Sutherland, 1965; Videler, 1981), striped surfperch exhibited spontaneous unsteady swimming behavior at initial low speeds. In order to allow accurate kinematic measurements at these speeds, the initial portion of the swimming trial was repeated after the subject had reached its maximum speed and had become accustomed to forced swimming in the flume. Visual and auditory cues were occasionally used to encourage steady swimming in the center of the working area.

The fish were illuminated by two 500 W tungsten lamps and video-taped simultaneously with two Sony video cameras (60 fields s^{-1} , shutter speed $1/2000 \text{ s}$) in lateral view through the clear acrylic wall of the working area and in dorsal view by means of a mirror mounted at 45° above the working area. A floating plate glass roof over the working area eliminated turbulence at the water surface and distortion of the subject's dorsal aspect. Live video signals were sent to a Panasonic digital video mixer (WJ-AVE5) which synchronized and combined partial fields from both dorsal and lateral views. The resulting split-screen images were recorded through a time code generator to S-VHS format video tape for analysis.

Kinematic analysis

From video-taped records of swimming trials, several kinematic variables were measured for each fish during steady locomotion. The pectoral fin-beat cycle was defined as beginning and ending with consecutive onsets of pectoral fin abduction. Each fin-beat period (T) consisted of a period of propulsive fin movements (T_{pr}), from the onset of abduction to the end of adduction, and a non-propulsive pause or 'refractory' period (T_r) between the end of adduction and the

Fig. 1. Sequential lateral images of *Embiotoca lateralis* during one complete pectoral fin stroke cycle at a constant labriform swimming speed. The propulsive period of pectoral fin abduction and adduction (T_{pr} , A–C) is followed by a pause or 'refractory' period (T_r , C–E) during which the fins rotate posteriorly and then anteriorly slightly while fully adducted against the body. A, pectoral fin-beat amplitude.



beginning of the following abduction (Fig. 1). Field-by-field analysis of dorsal video images allowed measurement of stride frequency (pectoral fin-beat frequency, f_p), which was taken as the number of pectoral fin beats performed during a selected analysis period divided by the total time elapsed in seconds. Similarly, caudal fin-beat frequency (f_c) was calculated from the number of tail beats (complete cycles of left and right lateral displacement) observed in the analysis period.

Because T includes a refractory period, pectoral fin-beat frequency calculated in this study and others (e.g. Archer and Johnston, 1989; Gibb *et al.* 1994) as T^{-1} underestimates the rate of force development by the pectoral musculature. To provide a more accurate measure of the average rate of thrust generation, we also calculated a corrected pectoral fin-beat 'frequency' (f_p') as T_{pr}^{-1} (cf. Webb, 1973), a term analogous to the reciprocal of ground contact time for the feet of running vertebrates (Taylor, 1994). Uncorrected frequency, f_p , is reported in addition to f_p' to facilitate comparison with earlier studies.

Pectoral fin-beat amplitude (A) was digitized from lateral video images using an Apple Macintosh computer and the program Image, version 1.51 (National Institutes of Health, USA). Amplitude was measured as the excursion (in cm) of the pectoral fin tip perpendicular to the horizontal swimming path from the onset of abduction to the onset of adduction (Fig. 1). Amplitude could not reliably be determined for the smallest individuals and is reported below for fish of 12 cm and longer. The pectoral-caudal gait transition speed (U_{p-c}) was the highest swimming speed at which the fish could hold station in the current for 3 min by pectoral fin oscillation alone (i.e. without regular use of the caudal fin: $f_c < 0.3 \text{ s}^{-1}$).

The video sequences selected for analysis met the following criteria. At speeds up to the gait transition, the fish had to swim steadily (i.e. remain stationary relative to a fixed reference point) for three or more consecutive pectoral fin beats. At speeds above the gait transition, at which pectoral fin oscillation was supplemented by unsteady axial undulation, the fish had to match the current velocity ($\pm 5\%$) for at least three consecutive bursts of tail beating. We further required that the pectoral and caudal fin tips remained at least 5 cm from the walls of the working area. At this distance, the gap:span ratio of the fins was 2.3 or greater, indicating that hydrodynamic wall effects had a negligible influence on swimming performance (Lighthill, 1979; Webb, 1993).

Results

Speed effects

Striped surfperch exhibit two distinct locomotor patterns during swimming trials at increasing velocity. These patterns are qualitatively similar to those described by Webb (1973) for the shiner surfperch *Cymatogaster aggregata*. At low to intermediate swimming speeds, pure labriform locomotion is employed in which the pectoral fins move synchronously through repeated cycles of abduction and adduction to generate forward thrust (Fig. 1). The trunk and tail do not undergo undulatory bending. At higher speeds, the pectoral-caudal gait transition occurs: undulation of the posterior trunk and caudal fin begins to supplement oscillation of the pectoral fins (see also Archer and Johnston, 1989; Gibb *et al.* 1994; Webb, 1994). Although the pectoral and caudal fins are occasionally used at the same time above U_{p-c} , the typical pattern is one of alternating pectoral and caudal fin oscillation. This swimming mode resembles the 'burst-and-coast' swimming behavior exhibited by axial undulators (Weihs, 1974; Videler and Weihs, 1982). Each intermittent burst of tail beating propels the fish forward and allows a period of coasting during which the body remains straight and the pectoral fins are fully adducted. Prior to the next burst phase, as the fish drifts backwards in the current, the pectoral fins oscillate rapidly. As opposed to most other labriform swimmers studied, which utilize body undulation alone at the highest swimming speeds (Archer and Johnston, 1989; Webb, 1994), surfperch employ pectoral fin oscillation, at least intermittently, over their entire range of swimming speeds.

For all sizes of *Embiotoca lateralis* studied, the relationship between uncorrected pectoral fin-beat frequency and swimming speed is non-linear (Fig. 2). Stride frequency increases slowly at low labriform swimming speeds and more rapidly at intermediate speeds, attaining a maximum at or soon after the pectoral-caudal gait transition. In contrast to f_p , the corrected pectoral fin-beat frequency f_p' increases linearly with swimming speed up to U_{p-c} . As caudal fin-beat frequency increases and axial undulation becomes the primary means of generating thrust, both measures of pectoral fin-beat frequency reach a plateau or decrease slightly.

Pectoral fin-beat amplitude expressed as a proportion of standard body length (A/SL) increases up to approximately 60% U_{p-c} and then reaches a plateau, prior to the gait transition

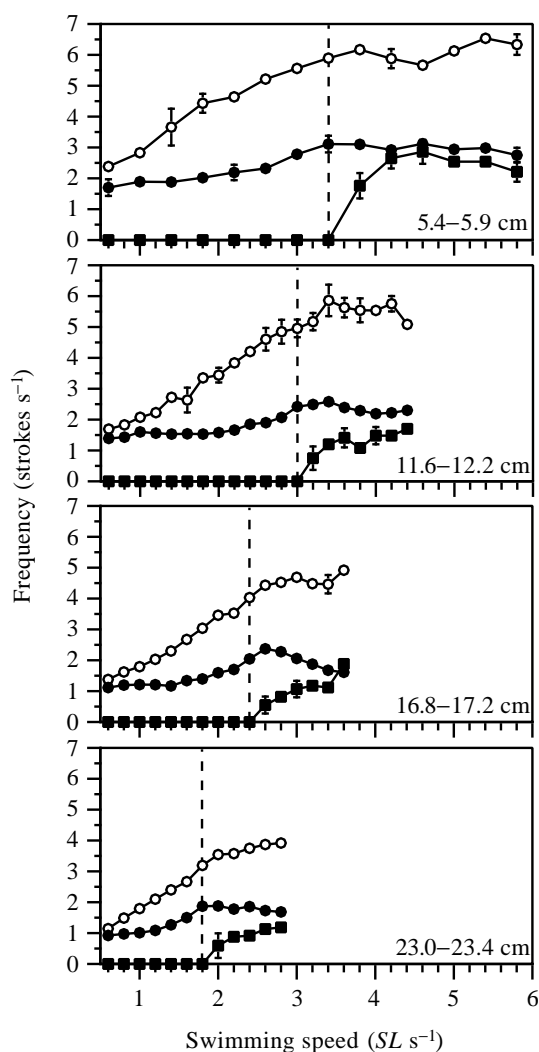


Fig. 2. Relationship between fin-beat frequency and swimming speed. Size ranges for the four groups ($N=3$) are given in terms of standard body length (SL). Vertical dashed lines indicate the mean pectoral-caudal gait transition speed (U_{p-c}). The last point in each curve is at the maximum speed achieved before exhaustion. Note that uncorrected pectoral fin-beat frequency (\bullet) (i.e. $1/\text{pectoral fin-beat period}$, see Fig. 1) increases curvilinearly with speed, while the corrected frequency (\circ) (i.e. $1/\text{propulsive period}$, see Fig. 1) rises linearly up to U_{p-c} . Both measures of frequency reach a plateau or decrease slightly just above the gait transition, which is marked by a rise in caudal fin-beat frequency (\blacksquare). For each individual, 3–30 fin beats were analyzed per speed increment. Mean frequencies are shown \pm S.E.M.

(Fig. 3). Unlike frequency and amplitude, the proportion of each pectoral fin stroke period occupied by propulsive fin movements (T_{pr}/T) decreases over low swimming speeds, falling from 0.78 ± 0.05 to 0.45 ± 0.04 on average (\pm S.D.) across the four size classes. This minimum coincides with the plateauing of fin-beat amplitude. Plots of T_{pr}/T versus speed show a second inflection point at U_{p-c} , at which speed a local maximum is attained (Fig. 3).

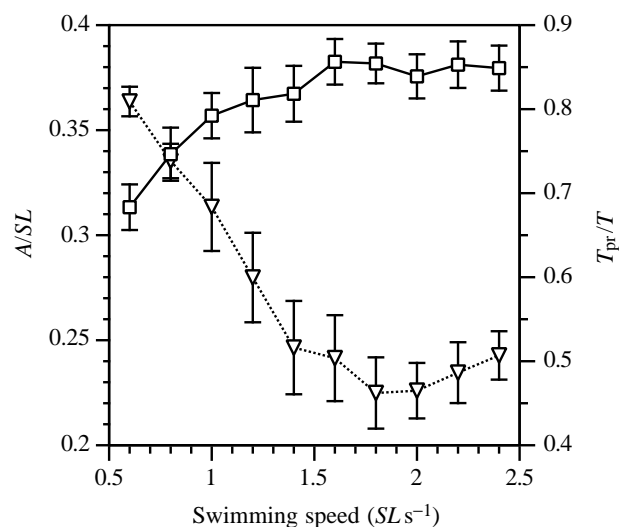


Fig. 3. Body length-specific pectoral fin-beat amplitude, A/SL (\square), and propulsive period expressed as a proportion of the fin-beat period, T_{pr}/T (∇), plotted as functions of swimming speed for a representative size class (mean SL 16.9 ± 0.2 cm). The last points in each curve are measurements at the pectoral-caudal gait transition speed, U_{p-c} . Amplitude increases over low to intermediate speeds and reaches a maximum prior to U_{p-c} . As A/SL reaches a plateau, T_{pr}/T increases to augment thrust. Data shown as means \pm S.E.M. ($N=9$).

Size effects

The influence of body size on the frequency of pectoral fin movement during labriform swimming is illustrated in Fig. 4. To maintain a given absolute swimming speed, smaller fish generally require higher f_p than larger fish (Fig. 4A). Similarly, the corrected pectoral fin-beat frequency is inversely related to body size. The rate of increase in f_p' with absolute speed decreases with size, but for all sizes is linear up to U_{p-c} (Fig. 4B). When speed is expressed in terms of standard body lengths traveled per second, however, these trends are altered: large fish (17 and 23 cm) exhibit a higher f_p than do smaller fish (12 cm) at speeds approaching U_{p-c} (Fig. 4C). As body size increases, the range of speeds ($SL s^{-1}$) over which the pectoral fins are used for propulsion is reduced. This gait compression (cf. Webb, 1994) is accompanied by an increase in the rate of change in f_p with swimming speed. Consequently, the curves describing the relationship between f_p and length-specific speed for the largest fish studied tend to cross those for smaller fish (Fig. 4C).

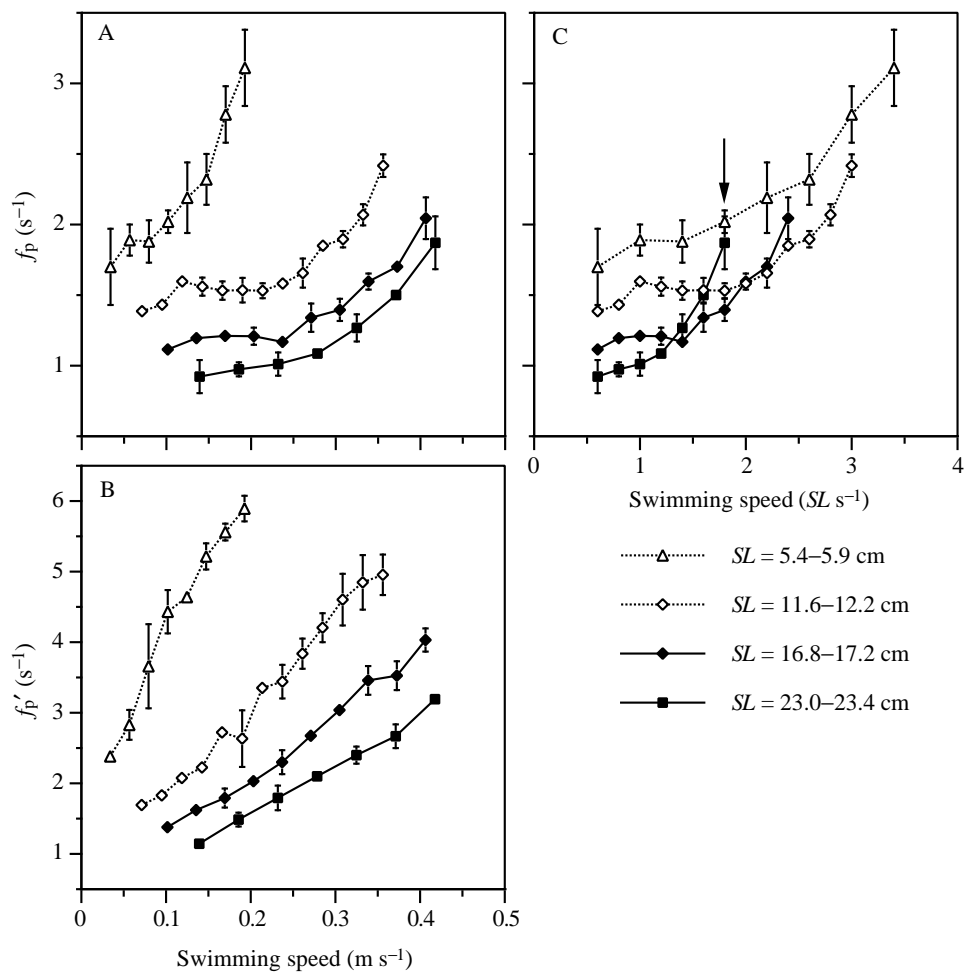
Unlike fin-beat frequency, length-specific amplitude does not vary substantially with body size at a given absolute or relative swimming speed. In fish varying twofold in length, A/SL increases at a roughly size-independent rate and reaches a plateau at 0.35 – 0.40 (Fig. 5).

Discussion

General kinematic patterns

The timing and magnitude of propulsor excursions in surfperch change with swimming speed in a manner generally

Fig. 4. Plots of pectoral fin-beat frequency as a function of swimming speed illustrating the kinematic effects of body size (standard length, SL) and their speed-dependence. The last points in each curve are measurements at the pectoral–caudal gait transition speed (U_{p-c}). Uncorrected frequency, f_p (i.e. $1/\text{pectoral fin-beat period}$, see Fig. 1), is inversely related to body length at a given absolute swimming speed (A). Exclusion of a kinematic refractory period from the fin stroke period allows calculation of a corrected frequency, f_p' (i.e. $1/\text{propulsive period}$, see Fig. 1), which shows a similar size-dependence (B). The influence of size on the linear rate of increase in f_p' matches that observed for the tail-beat frequency of caudal fin swimmers. When swimming speed is expressed as body lengths traveled per second (C), the apparent effects of size differ: large fish swim with the pectoral fins over a narrower range of speeds and achieve higher stride frequencies than small fish near U_{p-c} (example at arrow, $1.8 SL s^{-1}$). Data shown as means \pm S.E.M. ($N=3-30$ per individual).



similar to that reported for fishes employing axial undulation. For species relying on caudal fin propulsion, it has been demonstrated that length-specific fin tip amplitude is nearly speed-independent (Webb, 1975; Videler, 1993) whereas stride frequency increases linearly over a fish's entire range of swimming speeds (Bainbridge, 1958; Hunter and Zweifel, 1971; Webb *et al.* 1984). For *Embiotoca lateralis* swimming in the labriform mode, increases in speed are also achieved by a steady increase in stride frequency (Fig. 2) while amplitude remains a roughly constant proportion of body length at all but the lowest speeds (Fig. 5).

A notable kinematic difference between the two swimming styles exists in the speed-dependence of stride frequency. Unlike caudal fin swimmers, surfperches increase this gait parameter non-linearly (Fig. 4A; Webb, 1973). An important distinction, however, must be drawn between the stride frequencies traditionally measured for axial and appendicular swimmers. The pectoral fin-beat period T includes a non-propulsive refractory period of variable duration, and thus f_p (T^{-1}) reflects the time-averaged frequency of fin oscillation, but not the rate at which forward thrust is generated. The tail-beat period of axial swimmers, by contrast, does not ordinarily contain a kinematic refractory period during steady locomotion (e.g. Bainbridge, 1963) and thus is more directly comparable

with T_{pr} than with T . In contrast to f_p , the corrected pectoral fin-beat frequency (T_{pr}^{-1}) shows a linear increase with speed up to the gait transition (Fig. 4B), similar to the pattern reported for tail-beat frequency of caudal fin swimmers. This example illustrates that analysis of the timing of the propulsive phase of the stride cycle is required to select appropriate measures of frequency for interspecific comparisons.

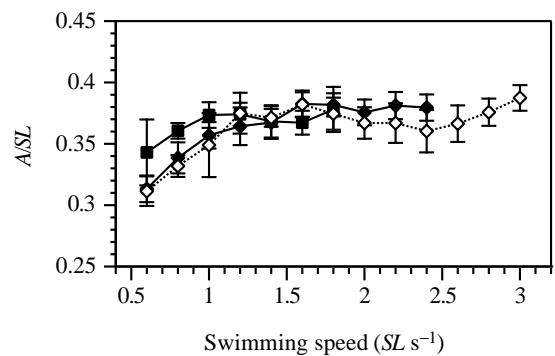


Fig. 5. Length-specific fin-beat amplitude (A/SL) versus swimming speed up to the pectoral–caudal gait transition speed in surfperch ranging twofold in standard length. A/SL varies with speed in a size-independent fashion. Symbols as in Fig. 4. Data shown as means \pm S.E.M. ($N=9$).

Embiotoca lateralis increases swimming speed by modulating gait parameters in two distinct phases. Despite a decrease in the proportion of each pectoral fin-beat period occupied by propulsive fin movements, fin-beat amplitude and f_p' rise over speeds up to approximately 60% U_{p-c} (Figs 2, 3). As amplitude reaches its maximum, f_p' continues to increase linearly (Fig. 2) and T_{pr}/T rises (Fig. 3), presumably to augment thrust at speeds nearing U_{p-c} . The plateauing of A/SL , followed by f_p' at higher speeds, and the peaking of T_{pr}/T at U_{p-c} may signify that *E. lateralis* can no longer effectively modulate pectoral fin kinematics to increase swimming speed and must instead switch to axial undulatory propulsion.

The physiological limit reached at the gait transition speed is probably related to the optimal velocity of shortening of the pectoral musculature. In fishes employing slow axial undulation, the shortening velocity (V) of aerobic myotomal muscle fibers increases with swimming speed over a narrow range in which mechanical power output is maximized (20–40% V_{max} , the maximum contraction velocity: Rome *et al.* 1990). At higher swimming speeds (i.e. when V exceeds the upper limit of the optimal velocity range), the power generated by red muscle decreases substantially and a change in gait occurs involving the recruitment of white myotomal muscle to supplement the power output of the red fibers (Rome *et al.* 1988, 1990). Thus, axial undulators switch gaits when the major aerobic muscle fiber type being used can no longer generate power sufficient to sustain locomotion.

We hypothesize that the pectoral–caudal gait transition of labriform swimmers is driven by a similar mechanism. The product $f_p'A$ reflects the shortening velocity of pectoral muscle fibers (cf. Webb, 1973) and increases linearly with swimming speed (Fig. 6), as has been demonstrated for V of the red myotomal fibers of axial undulators (Rome *et al.* 1990, 1992). In contrast to myotomal fibers, for which V increases by a factor of two within a gait (from $0.2V_{max}$ to $0.4V_{max}$), surfperch pectoral muscle undergoes a three- to fourfold increase in $f_p'A$ (Fig. 6), indicating that fibers of increasing speed may be recruited as swimming speed increases. At U_{p-c} , the fastest aerobic fibers used probably exceed the value of V for peak power and reach a limiting velocity at which power begins to decline. To swim faster without a further decrease of

mechanical power output, labriform swimmers recruit anaerobic myotomal muscle and initiate tail beating.

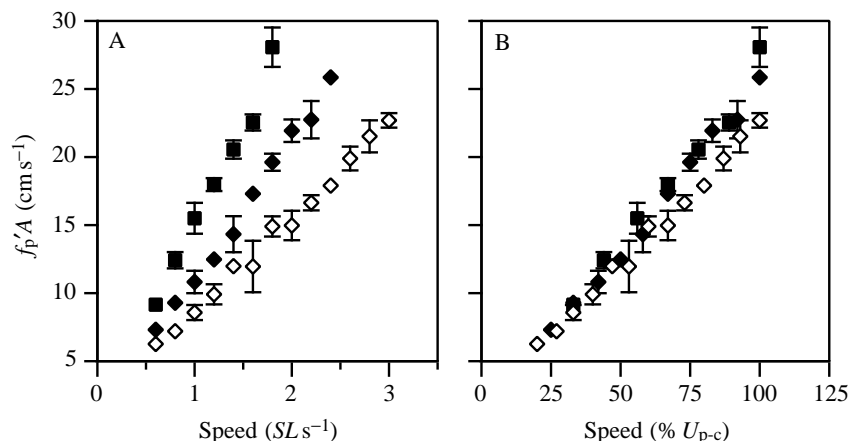
Kinematic effects of body size are speed-dependent

The influence of body size on the linear rate of increase in the frequency of propulsive pectoral fin movements (Fig. 4B) matches that observed for tail-beat frequency in axial undulators (Hunter and Zweifel, 1971; Webb *et al.* 1984). The curvilinear relationship between the time-averaged frequency of pectoral fin oscillation and absolute swimming speed shows a similar general size-dependence (Fig. 4A). This pattern differs, however, when frequency is plotted against speed expressed in terms of body lengths per second, a common practice in studies of fish locomotion (e.g. Bainbridge, 1958). In particular, large surfperch exhibit higher f_p values than do smaller ones at high speeds (Fig. 4C).

The central messages of the present paper are that kinematic comparisons across body size yield different information according to the speed at which the comparison is made and that, furthermore, not all measures of speed allow valid comparisons. At an absolute speed at which large fish swim slowly, small fish approach the pectoral–caudal gait transition (Fig. 4A,B: 0.15 – 0.20 $m\ s^{-1}$). Even when speed is corrected for body length, fish of different sizes may not be at comparable levels of activity. A speed of $1.8\ SL\ s^{-1}$, for example, represents for small striped surfperch (6 cm SL) an intermediate labriform swimming speed at which f_p increases relatively slowly, but for larger fish (23 cm) is U_{p-c} at which the fastest rate of increase in f_p occurs (Fig. 4C). At such a speed, the stride frequencies of fish of different sizes cannot be meaningfully compared.

How then may the impact of body size on swimming kinematics be assessed? At the pectoral–caudal gait transition speed, labriform swimmers of different sizes are assumed to be at equivalent levels of exercise (Drucker and Jensen, 1996). Kinematic comparisons across size may accordingly be made at U_{p-c} or any percentage thereof (cf. Brett, 1965; Webb, 1971). The effect of body size on gait parameters differs markedly when speed is expressed as a percentage of U_{p-c} as opposed to $SL\ s^{-1}$. As an example, the product $f_p'A$ shows a distinct, but misleading, dependence on body length when plotted against

Fig. 6. The product of corrected fin-beat frequency (f_p' , $1/\text{propulsive period}$, see Fig. 1) and amplitude (A) as a function of (A) length-specific swimming speed and (B) speed measured as a percentage of the pectoral–caudal gait transition speed, U_{p-c} . The influence of body size (standard length, SL) on patterns of change in $f_p'A$ depends directly on how swimming speed is expressed. At a given length-specific speed, the term appears to be proportional to SL , but fish of different sizes may not be at equivalent levels of activity. Comparisons at a given percentage of U_{p-c} indicate no size-dependence of $f_p'A$ (see text). Data are given as means \pm S.E.M. ($N=9$). Symbols are as in Fig. 4.



length-specific swimming speed (Fig. 6A). The term increases in a size-independent fashion when plotted against speed in terms of percentage U_{p-c} (Fig. 6B). Assuming that the relevant muscle lever arms remain in proportion to body length, $f_p'A$ should reflect muscle shortening velocity in labriform swimmers of different sizes (Webb, 1973). The square of the term is also expected to be related to the thrust generated by the propulsive wave of pectoral fins of different sizes (Webb, 1971; Wu, 1977). Thus, the method used to express swimming speed influences both the conclusions that may be drawn about the effects of size on kinematic trends and the predictions that may be made about the size-dependence of the underlying physiological and mechanical patterns.

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