PECTORAL FIN LOCOMOTION IN THE STRIPED SURFPERCH

II. SCALING SWIMMING KINEMATICS AND PERFORMANCE AT A GAIT TRANSITION

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Summary

In this study, we report the first allometric equations relating gait parameters and swimming speed to body size for fish employing pectoral fin locomotion. Comparisons of locomotor kinematics and performance among striped surfperch (Teleostei: Embiotocidae) are made at the pectoral–caudal gait transition speed ($U_{p\text{-}c}$). $U_{p\text{-}c}$ is considered to elicit physiologically equivalent levels of exercise in animals varying over 100-fold in body mass (M_b) by virtue of dynamically similar pectoral fin movements (constant duty factor, length-specific stride length and fin-beat amplitude) and size-independent propulsive efficiency. At $U_{p\text{-}c}$, pectoral fin-beat frequency scales in proportion to $M_b^{-0.12\pm0.03}$, a size-dependence consistent with that observed for stride frequency in fishes swimming by axial undulatory propulsion and in many running tetrapods. It is proposed that the similarity in the scaling of frequency in these vertebrate groups reflects an underlying similarity in the allometry of the maximal velocity of muscle shortening. Absolute $U_{p\text{-}c}$ ($m\,s^{-1}$) generally increases with body size, but the fastest speeds are not exhibited by the largest animals. A pattern of declining performance in fish 23 cm in standard length and longer may be related to their disproportionately small fin areas and aspect ratios. The pronounced negative allometry of $U_{p\text{-}c}$ expressed as standard body lengths per second indicates that a given length-specific speed does not induce comparable levels of activity in large and small fish. Thus, normalization of swimming speed to body length may not be a sufficient correction for kinematic comparisons across size.

Key words: striped surfperch, *Embiotoca lateralis*, labriform locomotion, pectoral fin, swimming performance, gait transition, physiologically equivalent speed, allometry, kinematics.

Introduction

During the past 30 years, the influence of body size on the kinematics of locomotion in vertebrates has been the subject of extensive study. Comparative physiologists have been particularly successful in relating the body mass of terrestrial tetrapods spanning a broad range of adult sizes to the temporal and spatial patterns of limb movement during running (e.g. Heglund *et al.* 1974; Pennycuick, 1975; Huey, 1982; Alexander and Maloiy, 1984; Heglund and Taylor, 1988; Marsh, 1988; Bennett *et al.* 1989; Strang and Steudel, 1990; White and Anderson, 1994; Zani and Claussen, 1994). One of the challenges for workers studying the scaling of locomotor mechanics is to select a speed at which meaningful comparisons among differently sized animals can be made. The concept of physiologically equivalent speed was developed by Heglund *et al.* (1974) and Heglund and Taylor (1988) specifically to allow comparisons of gait parameters among mammals of different sizes and geometric proportions. At equivalent speeds, differently sized mammals consume the same amount of metabolic energy per unit body mass during a stride (Taylor *et al.* 1982; Taylor, 1985; Heglund and Taylor,

1988) or incur a minimal energetic cost of locomotion (Pennycuick, 1975; Hoyt and Taylor, 1981) and experience similar levels of peak musculoskeletal stress in their limbs (Taylor, 1985; Biewener and Taylor, 1986; Perry *et al.* 1988). The similar stresses and power requirements for differently sized animals have been cited to justify kinematic comparisons at these speeds. An equivalent speed commonly used in studies of the scaling of running mechanics is the speed at the transition between two gaits (e.g. trot–gallop transition). Kinematic variables such as stride frequency and stride length change in a regular and predictable way with body mass at gait transitions (Heglund *et al.* 1974; Heglund and Taylor, 1988).

Studies of the scaling of oscillatory locomotor movements in aquatic vertebrates have placed less emphasis on comparisons of differently sized animals at gait transition speeds. Among bony and cartilaginous fishes, speeds selected for kinematic comparison across size include maximum sprint speed (Bainbridge, 1958; Wardle, 1975; Webb, 1977) and minimum stalling speed (Hunter and Zweifel, 1971), which can be difficult to induce and measure reliably, and similar body

length-specific speed (Webb and Keyes, 1982; Williams and Brett, 1987; Graham *et al.* 1990), which is unlikely to elicit comparable levels of activity. Webb *et al.* (1984) compared tail-beat kinematics of large and small trout at the critical swimming speed (U_{crit}), the speed at which fish are thought to make their maximum sustained (aerobic) effort. Although U_{crit} is intended to represent a physiologically equivalent speed for differently sized fish by reflecting the transition from aerobic to anaerobic metabolism (Webb *et al.* 1984), there is a debate as to whether it estimates this transition accurately (Wilson and Egginton, 1994).

To date, there has been very little work on the scaling of locomotor movements in fishes that use modes of swimming other than axial undulatory propulsion (but see Archer and Johnston, 1989). Despite this relative lack of study, swimming with the pectoral fins (labriform locomotion: Breder, 1926) is employed by a diversity of bony fishes (Lindsey, 1978; Blake, 1983*b*). Many species have been reported to swim at low speeds by oscillation of the pectoral fins and to switch at higher speeds to axial undulation (pectoral–caudal transition: reviewed by Webb, 1994*b*; see also Whoriskey and Wootton, 1987; Parsons and Sylvester, 1992; Gibb *et al.* 1994; Stobutzki and Bellwood, 1994; Drucker and Jensen, 1996). We view this change in swimming mode as a gait transition (*sensu* Alexander, 1989; Webb, 1994*a*) and argue that the speed at which it occurs (U_{p-c}) is physiologically equivalent for labriform swimmers of different size.

The surfperches (family Embiotocidae) are unusual among bony fishes in their sole reliance on the pectoral fins for propulsion over a wide range of swimming speeds. In this paper, we describe the relationship between body size and (1) pectoral fin dimensions, (2) gait transition speed and (3) the kinematics of labriform locomotion in an ontogenetic series of striped surfperch *Embiotoca lateralis*. Focusing on patterns of pectoral fin excursion at U_{p-c}, we develop the first allometric equations for labriform swimmers relating the kinematic variables affecting swimming speed to body mass. Analysis of the allometry of U_{p-c} allows testing of the hypothesis (Drucker and Jensen, 1996) that length-specific labriform swimming speeds do not elicit comparable levels of exercise in fish of different sizes.

Materials and methods

Surfperch (*Embiotoca lateralis* Agassiz) were collected by beach seine at Argyle Bay, San Juan Island, Washington, USA, and maintained in large flow-through seawater aquaria at 12 °C at the University of Washington's Friday Harbor Laboratories. Seventeen male fish comprising six discrete yearly size classes (5.4–25.6 cm standard length, *SL*; 6.8–32.6 cm total length, *TL*; 4.0–557.5 g body mass, M_b) were selected for experimentation (Table 1). The flow tank used in this study and details of the experimental protocol have been described previously (Drucker and Jensen, 1996). Briefly, each fish underwent an exercise trial at increasing velocity designed to induce the transition from labriform to combined pectoral and caudal fin locomotion. Swimming speed was increased in $0.2\,SL\,s^{-1}$ increments at 3 min intervals until the fish reached its maximum speed and quickly became exhausted. The dorsal and lateral aspects of each subject were video-taped simultaneously at 60 fields s^{-1}. Field-by-field viewing of video tapes allowed measurement of kinematic gait parameters at U_{p-c}.

Following its swimming trial, each member of the study group was anesthetized in a dilute solution of tricaine methanesulfonate in order to allow measurement of pectoral fin dimensions. The length of the pectoral fin (L_p), taken as the distance (in cm) from the tip to the midpoint of the base, fin area (*S*, in cm^2) and fin aspect ratio (*AR*), defined as L_p^2/S, were measured using the program Image, version 1.51 (National Institutes of Health, USA) running on an Apple Macintosh computer.

Gait parameters

The pectoral fin-beat period (*T*) was partitioned into two distinct phases: a propulsive period (T_{pr}) extending from the onset of abduction to the end of adduction, and a pause or 'refractory' period, beginning at the end of adduction, during which the fin remains fully furled against the body in preparation for the following abduction (see Fig. 1 in Drucker and Jensen, 1996). The proportion of the fin stroke cycle occupied by propulsive fin movements was defined as T_{pr}/T. Fin-beat frequency (s^{-1}) was measured as described in Drucker and Jensen (1996). Both uncorrected frequency (f_p) taken as

Table 1. *Mass and body dimensions of* Embiotoca lateralis *studied*

Size class	N	M_b (g)	SL (cm)	TL (cm)	L_p (cm)	S (cm^2)	AR
1	3	4.8±0.72	5.7±0.25	7.1±0.31	1.4±0.06	0.8±0.09	2.5±0.03
2	3	46.5±0.78	11.9±0.31	15.1±0.29	2.8±0.11	3.6±0.34	2.2±0.06
3	3	140.9±7.57	16.9±0.23	21.5±0.15	3.7±0.15	7.0±0.14	2.0±0.20
4	3	285.5±2.43	20.8±0.06	26.2±0.31	4.4±0.15	9.6±0.25	2.0±0.12
5	3	435.0±8.87	23.2±0.20	29.5±0.32	5.0±0.18	13.8±0.20	1.8±0.15
6	2	554.5±4.31	25.6±0	31.8±1.13	5.6±0.23	17.5±1.06	1.8±0.04

Values given as mean ± standard deviation.

N, sample size; M_b, wet body mass; *SL*, standard body length (measured from anterior tip of snout to posterior hypural margin); *TL*, total body length (anterior tip of snout to posterior-most point of caudal fin); L_p, pectoral fin length; *S*, fin area; *AR*, fin aspect ratio.

Size classes 1, 2, 3 and 5 were studied in Drucker and Jensen (1996).

T^{-1} and corrected, or propulsive, frequency (f_p') defined as T_pr^{-1} were determined at $U_\mathrm{p\text{-}c}$. Fin-beat amplitude (ϕ) was measured as the angle (rad) subtended by the fin tip during abduction in the plane perpendicular to the incident water current.

Stride length (λ_s) is the distance (in m) traveled by the fish during one complete pectoral fin-beat cycle (cf. Wardle, 1975) and was calculated at $U_\mathrm{p\text{-}c}$ using the equation:

$$\lambda_\mathrm{s} = U/f_\mathrm{p}, \tag{1}$$

where U is the swimming speed (in m s^{-1}) and f_p is in s^{-1}.

The advance ratio (J) is a dimensionless quantity which measures the ratio of forward swimming velocity to mean fin tip velocity (see Ellington, 1984) and is related to the mechanical efficiency of the pectoral propeller (von Mises, 1945; Vogel, 1981). In order to assess its scale-dependency, the advance ratio of the pectoral fin at the gait transition was calculated from Ellington (1984) using fin length (in m) as a characteristic length:

$$J = U/2\phi f_\mathrm{p} L_\mathrm{p}. \tag{2}$$

Statistical analyses

Morphometric and kinematic variables that changed through ontogeny according to the power-law function $y=aM_\mathrm{b}^b$, where M_b is body mass (in kg), were log$_{10}$-transformed and related to log$_{10}M_\mathrm{b}$ using the least-squares linear regression model. Allometric equations then took the form: log$y$=log$a$+$b$logM_b. Although simple linear regression analysis is generally unsuitable for describing scaling relationships (Rayner, 1985),

its use in this case is justified because animals were selected for experimentation to fill discrete size classes. Thus, the independent variable, body mass, was under investigator control (Sokal and Rohlf, 1981). The statistical significance of regressions was determined with F-tests. Student's t-tests were used to assess whether sample regression coefficients differed significantly from hypothesized parametric slopes (Sokal and Rohlf, 1981).

Results
Allometry of body dimensions

Geometrically similar animals have linear dimensions that scale with $M_\mathrm{b}^{1/3}$ and measures of body area proportional to $M_\mathrm{b}^{2/3}$. Dimensionless parameters calculated from morphological measurements are expected to be size-independent. In *Embiotoca lateralis*, all body proportions measured deviated significantly from the expectations of geometric similarity. The deviation was relatively slight for standard body length (Table 2: b=0.32), but larger fish had substantially shorter pectoral fins (b=0.29), smaller fin areas (b=0.63) and lower fin aspect ratios (b=−0.069) than predicted by geometric similarity.

Scaling of swimming kinematics and performance at $U_\mathrm{p\text{-}c}$

Several gait parameters measured at the pectoral–caudal gait transition speed exhibit a clear size-dependency. Small fish switch gaits at higher pectoral fin-beat frequencies and with shorter stride lengths than large fish (Fig. 1A,B). Corrected and uncorrected fin-beat frequency scale similarly: f_p and f_p' at

Table 2. *Allometric relationships for body proportions, swimming performance and gait parameters measured at the pectoral–caudal gait transition speed in* Embiotoca lateralis

y	r	P	a	b	95 % confidence interval for b	β	t
Body proportions							
SL (cm)	0.99	<0.001	30.8	0.315	0.308 to 0.321	1/3	−6.7***
L_p (cm)	0.99	<0.001	6.45	0.286	0.271 to 0.301	1/3	−6.7***
S (cm^2)	0.99	<0.001	23.4	0.629	0.601 to 0.657	2/3	−2.8*
AR	0.88	<0.001	1.75	−0.0689	−0.0907 to −0.0472	0	−6.8***
Swimming performance							
$U_\mathrm{p\text{-}c}$ (TL s^{-1})	0.97	<0.001	3.16	−0.0559	−0.0631 to −0.0487		
Gait parameters at $U_\mathrm{p\text{-}c}$							
f_p (s^{-1})	0.92	<0.001	1.72	−0.116	−0.143 to −0.0895		
f_p' (s^{-1})	0.95	<0.001	3.07	−0.135	−0.161 to −0.110		
T_pr/T	0.40	NS	0.514	0.118	−0.0312 to +0.267		
$\lambda_\mathrm{s}/L_\mathrm{p}$	0.22	NS	4.96	−0.521	−1.81 to +0.768		
ϕ (rad)	0.19	NS	2.35	−0.141	−0.599 to +0.318		
J	0.31	NS	1.11	−0.185	−0.545 to +0.174		

T_pr/T, $\lambda_\mathrm{s}/L_\mathrm{p}$, ϕ and J were related to body mass M_b (kg) by least-squares linear regression: y=a+bM_b. $U_\mathrm{p\text{-}c}$=a+bTL (cm). All other dependent variables were log$_{10}$-transformed and regressed against log$_{10}M_\mathrm{b}$: log$y$=log$a$+$b$logM_b; N=14–17. NS, non-significant regression.

t-tests compare sample slopes (b) with parametric slopes (β) expected assuming geometric similarity; *P<0.05; ***P<0.001.

Abbreviations for body proportions as in Table 1. $U_\mathrm{p\text{-}c}$, pectoral–caudal gait transition speed; TL, total body length; f_p, pectoral fin-beat frequency (T^{-1}); f_p', corrected pectoral fin-beat frequency (T_pr^{-1}); T_pr/T, proportion of fin-beat period occupied by propulsive fin movements (duty factor); $\lambda_\mathrm{s}/L_\mathrm{p}$, fin length-specific stride length; ϕ, angular fin-beat amplitude; J, fin advance ratio.

Fig. 1. Gait parameters and swimming performance measured at the pectoral–caudal gait transition speed ($U_{p\text{-}c}$) plotted as functions of body mass on logarithmic coordinates. Regression lines (A) are for corrected fin-beat frequency (1/propulsive period) f_p' (○) and uncorrected fin-beat frequency (1/fin-beat period) f_p (●) of *Embiotoca lateralis* and do not differ significantly in slope (see Table 2). Other labriform swimmers studied use stride frequencies consistent with the scaling relationship observed for f_p: ⊕, *Cymatogaster aggregata*, 15 °C (Webb, 1973); □, *Pomoxis annularis*, 25 °C (Parsons and Sylvester, 1992); △, *Lepomis macrochirus*, 20 °C (Gibb *et al.* 1994). Absolute stride length (B) and absolute $U_{p\text{-}c}$ (C) generally increase with body size, but the largest animals achieve disproportionately low stride lengths and speeds. Length-specific $U_{p\text{-}c}$ ($SL\,s^{-1}$), by contrast (D), declines curvilinearly with body mass.
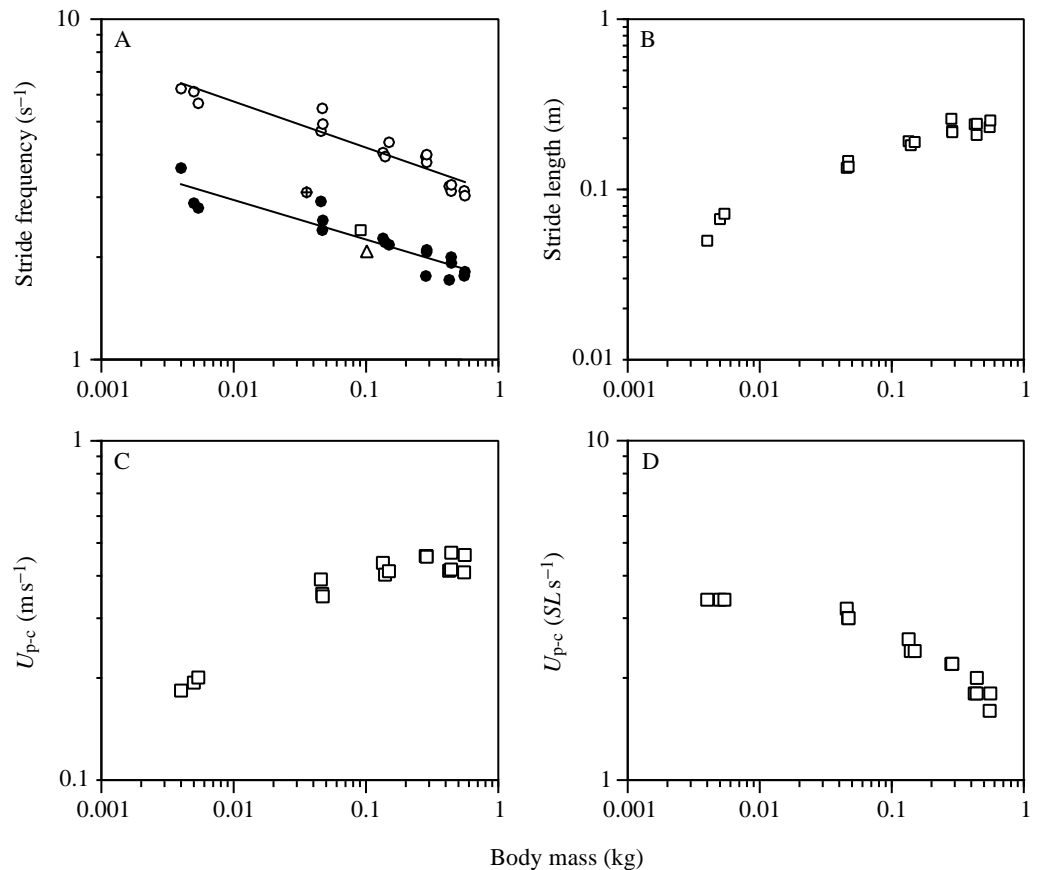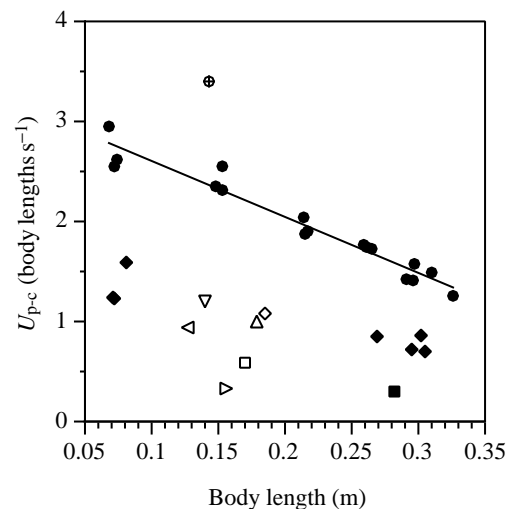
$U_{p\text{-}c} \propto M_b^{-0.12}$ to $M_b^{-0.14}$ (Table 2). Unlike frequency, $U_{p\text{-}c}$ is not a simple function of M_b. Absolute $U_{p\text{-}c}$ ($m\,s^{-1}$) generally increases with size, but the largest fish switch gaits at disproportionately low speeds (Fig. 1C). Length-specific $U_{p\text{-}c}$ ($SL\,s^{-1}$) declines curvilinearly with M_b when plotted on logarithmic coordinates (Fig. 1D). $U_{p\text{-}c}$ expressed as total body lengths per second ($TL\,s^{-1}$) does, however, decline linearly with body length (Table 2). At a given total length, surfperches achieve higher relative pectoral–caudal gait transition speeds than other labriform swimmers studied within a 5–10 °C temperature range (Fig. 2).

Four other important kinematic variables measured at $U_{p\text{-}c}$

are independent of body size in *Embiotoca lateralis*. Despite moderate to weak degrees of correlation between these gait parameters and M_b (Table 2), the absolute variation in each dependent variable is low. At $U_{p\text{-}c}$, the proportion of the fin-beat period occupied by propulsive fin movements (T_{pr}/T) does not vary significantly with body mass (Fig. 3A; mean ± S.D. 0.54±0.06), a result that follows from the constancy of f_p/f_p' at $U_{p\text{-}c}$ (Fig. 1A). Similarly, the slope of the relationship between length-specific stride length at $U_{p\text{-}c}$ and body mass is not
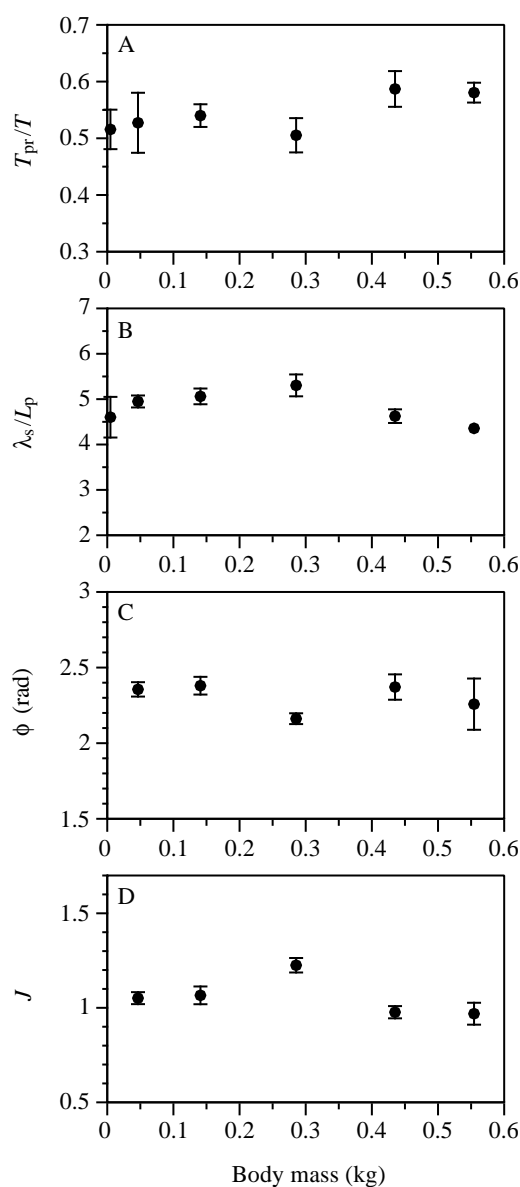
Fig. 2. Relationship between body length-specific pectoral–caudal gait transition speed ($U_{p\text{-}c}$) and body length in labriform swimmers. Note that surfperches (*Embiotoca lateralis*, ●, this study, and *Cymatogaster aggregata*, ⊕) switch to axial undulatory propulsion at relatively higher speeds than other species studied. Body length is total length (*TL*) except for *Pomoxis annularis*, for which standard length (*SL*) is reported. For studies examining a single size class, average body length is plotted. The regression line for the striped surfperch is also shown (see Table 2). ◆, *Notothenia neglecta*, 2 °C (Archer and Johnston, 1989); ◁, *Lepomis gibbosus*, 20 °C (Brett and Sutherland, 1965); ▷, *Lepomis macrochirus*, 15 °C (Webb, 1994*b*); ▽, *Lepomis macrochirus*, 15 °C (Webb, 1993); ◇, *Stenotomus chrysops*, 10 °C (Rome *et al.* 1992); ■, *Oncorhynchus mykiss*, 15 °C (Webb, 1971*a*). Other symbols are as in Fig. 1.

Fig. 3. Duty factor T_{pr}/T (A), specific stride length λ_s/L_p (B), pectoral fin-beat amplitude ϕ (C) and fin advance ratio J (D) measured at the pectoral–caudal gait transition speed plotted as functions of mean body mass for each size class of *Embiotoca lateralis*. Kinematic values are given as mean ± S.E.M., N=6–9. The lack of significant dependence of these variables on body mass (see Table 2) supports the hypothesis that the gait transition speed is physiologically equivalent for labriform swimmers of different size.

significantly different from zero at α=0.05 (Fig. 3B; 4.84±0.47). Angular fin-beat amplitude (2.31±0.14 rad) and pectoral fin advance ratio (1.06±0.11) also show no significant dependence on M_b at the gait transition (Fig. 3C,D; Table 2).

Discussion
Equivalence of the pectoral–caudal gait transition speed
Below, we argue that U_{p-c} is physiologically equivalent for

labriform swimmers of different size. As originally defined, an equivalent speed is one at which the metabolic cost of locomotion incurred per gram per stride and the peak musculoskeletal stresses experienced are scale-independent (Taylor *et al.* 1982; Perry *et al.* 1988). Although the energetics and mechanics of labriform locomotion are not investigated here, the size-independence of key gait parameters at the pectoral–caudal gait transition speed provides evidence that surfperch of different sizes are at comparable levels of exercise at U_{p-c}.

An expectation for differently sized animals moving in a kinematically similar fashion is that the fraction of the stride period in which forward thrust is generated should be constant. For terrestrial tetrapods, this fraction is the duty factor, D, defined as the relative period of contact of a given limb with the ground (McGhee, 1968). As predicted by theory, D is size-independent at gait transition speeds (McMahon, 1977; Alexander and Jayes, 1983; Biewener, 1983). The quantity T_{pr}/T for labriform swimmers, which is comparable to the duty factor of running animals, shows a similar independence of body mass at U_{p-c} (Fig. 3A).

It is also predicted that animals at equivalent speeds should exhibit constant length-specific stride lengths. Expressed as a multiple of hip height, λ_s varies little at the trot–gallop transition in quadrupedal mammals spanning five orders of magnitude in M_b (Alexander and Jayes, 1983: Froude numbers of 2–3). Similarly, surfperch at the pectoral–caudal gait transition use a size-independent relative stride length, λ_s/L_p (Fig. 3B). This result, together with the scale-independence of T_{pr}/T and angular fin-beat amplitude (Fig. 3A,C), supports the hypothesis that pectoral fins of different size have 'dynamically similar' motions at U_{p-c} (cf. Alexander and Jayes, 1983).

At equivalent speeds, we expect further that the Froude efficiency (η) of the pectoral propulsor is constant despite variation in body size. Froude (or propeller) efficiency is the ratio of useful work to total work done by a propulsor (McCutchen, 1977). The pectoral fin propeller efficiency is formally defined by Webb (1975) as:

$$\eta = P_D/P_m, \qquad (3)$$

where P_D is the mechanical thrust power developed by the pectoral muscle to overcome drag and P_m is the total pectoral muscle power generated.

In the absence of direct measurement of muscle power, propulsive efficiency of paired, oscillating appendages may alternatively be related to their advance ratio (von Mises, 1945; Vogel, 1981). This parameter has been determined for the wings of flying animals (e.g. Vogel, 1966; Ellington, 1984; Pennycuick, 1990) and here is calculated for the pectoral fins of the surfperch (equation 2). As noted by Webb (1975), J is a quantity comparable to 'slip', the ratio of U, the forward swimming speed of a fish relative to the current, and c, the backward speed of the propulsive wave generated relative to the fish's body. U/c has been used in studies of axial undulation to reflect the propulsive efficiency of the caudal propeller

(Lighthill, 1960; Webb, 1971b; Videler and Wardle, 1978). Since c is unknown for the pectoral fins of *Embiotoca lateralis*, J is taken in this study as an indicator of mechanical efficiency.

For the size range of surfperch examined in this study, the advance ratio at the gait transition speed does not vary significantly with body mass (Fig. 3D; Table 2). Thus, until direct measurement of P_D/P_m is made (equation 3), we estimate that at U_{p-c} the efficiency of converting muscle power to thrust power is size-independent, and valid comparisons of kinematics and performance may be made across size.

Scaling of gait transition speed

In studies of the energetics of fish locomotion, it is commonly reported that the aerobic muscle power available for steady swimming (P_{aerob}) increases with swimming speed at a slower rate than the power required to overcome drag (P_D). Thus, ($P_{aerob}-P_D$) decreases with U (Webb, 1975). When P_D exceeds P_{aerob}, a change in gait involving recruitment of more powerful, anaerobic muscle fibers is expected. Since the mass-specific energetic demand (P_D/M_b) of a swimming fish increases with body size, but the mass-specific aerobic capacity of the locomotor muscle (P_{aerob}/M_b) decreases with body size, maximum aerobic swimming performance tends to exhibit pronounced negative allometry (Goolish, 1991). Such a pattern is observed not only in fish employing axial undulation (Webb et al. 1984) but also in the labriform swimmer *Embiotoca lateralis*. The pectoral–caudal gait transition speed (body lengths s⁻¹), above which anaerobic myotomal muscle is recruited, declines regularly with body size (Figs 1D, 2).

The absolute gait transition speed generally increases with body mass, but the fastest speeds are not exhibited by the largest animals (Fig. 1C). Fish in the largest two size classes (23–26 cm SL) exhibit lower average absolute U_{p-c} values than does the 21 cm size class. A similar pattern of declining performance at the largest sizes is observed in aquatic and terrestrial vertebrates at maximum anaerobic speed and may stem from energetic or structural limitations imposed on large animals (reviewed by Goolish, 1991). In addition, the relationship between swimming speed and body size may be influenced by the allometry of propulsor dimensions. In *Embiotoca lateralis*, pectoral fin area, S, increases through ontogeny at a significantly slower rate than expected by models of geometrically similar growth (Table 2). Since the thrust power generated by a pectoral fin during drag-based propulsion is directly related to S (Blake, 1979), disproportionately smaller fins may limit the maximum labriform swimming speed achieved by larger fish. Since *E. lateralis* probably also derives thrust from the production of pectoral lift forces, as proposed for the shiner surfperch *Cymatogaster aggregata* (Webb, 1973), it is expected that absolute U_{p-c} would decline in the largest fish as a result of their relatively low pectoral fin aspect ratios (Table 2) and hence coefficients of lift (Blake, 1983a).

An area of interest for future investigation is the mechanism by which surfperches attain consistently higher U_{p-c} values than similarly sized labriform swimmers from other families

(Fig. 2). *Embiotoca lateralis* has a relatively narrow range of high speeds over which it can swim by axial undulation before rapidly fatiguing (Drucker and Jensen, 1996), a limitation that may be attributed to a reduced capacity for anaerobic power production of the myotomal muscle (Davison, 1988). The pectoral musculature of surfperch may thus be specialized for increased aerobic performance. At U_{p-c}, embiotocids and other pectoral fin swimmers of a given size use the same fin-beat frequency (Fig. 1A). Surfperches may generate more mechanical power per fin stroke at a given f_p by virtue of a greater pectoral muscle volume. In such a case, higher swimming speeds may be attained before recruitment of myotomal muscle and a change in gait are required. The scaling of pectoral muscle volume and its influence on the allometry of swimming performance remain to be investigated in the Embiotocidae.

Scaling of stride frequency

Negative scaling of stride frequency at equivalent speeds of locomotion has been predicted by biomechanical theory (Hill, 1950; McMahon, 1975; Goldspink, 1977) and demonstrated empirically for a diversity of vertebrates (e.g. Bainbridge, 1958; Greenewalt, 1962; Heglund and Taylor, 1988; Marsh, 1988; Clark and Fish, 1994). In striped surfperch, pectoral fin-beat frequency at the pectoral–caudal gait transition speed also declines with body size ($f_p \propto M_b^{-0.12}$; Table 2). Fin-beat frequencies observed at U_{p-c} in the shiner surfperch (mean M_b 36 g) and two species of centrarchids (91–101 g) appear to follow the same scaling relationship (Fig. 1A). Archer and Johnston (1989) report pectoral fin-beat frequencies at the transition from labriform swimming to axial undulation in juvenile and adult notothenioid fish. With the assumption that length scales as $M_b^{1/3}$, we calculate for this species a scaling relationship very similar to that determined for striped surfperch: f_p at $U_{p-c} \propto M_b^{-0.13}$.

The size-dependence of stride frequency for labriform swimmers is consistent with that observed for fishes swimming by axial undulation. Although f_p' (1/propulsive period) is more directly comparable to tail-beat frequency than is f_p (1/pectoral fin-beat period) at a given speed (Drucker and Jensen, 1996), f_p is proportional to propulsive frequency at U_{p-c} (Fig. 1A). Caudal fin-beat frequency (f_c) at estimated maximum aerobic and anaerobic swimming speeds for a range of species scales approximately with $M_b^{-0.1}$ to $M_b^{-0.2}$ (excluding *Carassius auratus*, Table 3). The variability in the mass exponent for f_c may reflect recognized uncertainty in eliciting top speed in the laboratory (Bainbridge, 1958). The general agreement of scaling exponents between the labriform and undulatory swimmers (Table 3) is suggestive of a common physiological mechanism, but must be interpreted with caution (Marsh, 1988). We suggest the following testable explanation for the observed similarity in the allometry of stride frequency.

The velocity (V) at which a skeletal muscle fiber shortens during locomotion may be related to stride frequency (f) as follows:

$$V \propto (\Delta l/l)f, \tag{4}$$

Table 3. *Scaling exponents (b) for the allometric relationship* $y \propto M_b{}^b$, *where y is stride frequency (Hz) measured at a physiologically equivalent speed and* M_b *is body mass (kg)*

Locomotor mode	Species	Speed	b (95 % confidence interval)	Reference
Swimming	Bony fish			
Labriform	*Embiotoca lateralis*	$U_{p\text{-}c}$	−0.12 (±0.03)	Present study
	Notothenia neglecta	$U_{p\text{-}c}$	−0.13*	1
Axial undulatory	*Trachurus symmetricus*	U_{max}	−0.12*	2
	Oncorhynchus mykiss	U_{max}	−0.07*	3
	Leuciscus leuciscus	U_{max}	−0.11*	3
	Carassius auratus	U_{max}	−0.29*	3
	Oncorhynchus mykiss	U_{crit}	−0.23*	4
Running				
Quadrupedal	Primates	$U_{t\text{-}g}$	−0.22 (±0.16)	5
	Cursorial and non-cursorial			
	mammals excluding primates	$U_{t\text{-}g}$	−0.14 (±0.03)	5
		$U_{t\text{-}g}$	−0.15 (±0.03)	6
		U_{max}	−0.16 (±0.03)	6
Bipedal	Birds and man	U_{max}	−0.18 (±0.01)	7
	Lizard			
	Dipsosaurus dorsalis	U_{max}	−0.19 to −0.24	8

*Exponent from relationship between stride frequency and body length (*L*) re-expressed in terms of M_b under the assumption $L \propto M_b{}^{1/3}$.

$U_{p\text{-}c}$, pectoral–caudal gait transition speed; U_{max}, maximum speed; U_{crit}, critical swimming speed; $U_{t\text{-}g}$, trot–gallop gait transition speed.

1, Archer and Johnston (1989), Table 1; 2, Hunter and Zweifel (1971), Fig. 4; 3, Webb (1977) from Bainbridge (1958); 4, Webb *et al.* (1984), equations 3, 10; 5, Alexander and Maloiy (1984); 6, Heglund and Taylor (1988); 7, Gatesy and Biewener (1991); 8, Marsh (1988).

where Δl is the absolute fiber length excursion and l is the fiber's resting length (McMahon, 1984, p. 274). Assuming muscle strain ($\Delta l/l$) is independent of body size, V and f at an equivalent speed of locomotion should scale with the same power of body mass (Rome *et al.* 1990*b*; Rome, 1992). The implication, then, of similar allometry of stride frequency at the respective speeds of labriform and axial swimmers is that the shortening velocity of the muscle fibers used by the two groups scales similarly.

Although the pectoral–caudal gait transition speed of labriform swimmers and the maximum speed of axial swimmers represent dramatically different levels of exercise, the mechanical properties of the muscle driving locomotion in both cases may be similar. An important determinant of muscle performance (i.e. force and power output) is the value of V for active fibers expressed as a fraction of their maximal shortening velocity, V_{max} (reviewed by Rome, 1994). In axial swimmers, both red and white myotomal fibers operate within a narrow range of velocities (V/V_{max} is approximately 0.2–0.4) over which the mechanical power produced is maximal. We expect that the pectoral musculature of labriform swimmers works at a similar V/V_{max} at the gait transition speed. The similarity in the scaling of stride frequency in the two types of swimmers then may reflect a common size-dependence of V_{opt}, the shortening velocity yielding peak power (equation 4). The shortening velocity for maximal power output of myotomal fiber bundles undergoing oscillatory contractions *in vitro* scales in proportion to M_b to the −0.17 power (Anderson and

Johnston, 1992), a mass exponent within the range of those observed for tail-beat frequency at maximum swimming speed (Table 3). The power–velocity relationship of surfperch pectoral fin muscle is presently unknown, but it is predicted that V_{opt} has a similar size-dependence.

The allometry of stride frequency for fishes is strikingly similar to that observed for terrestrial vertebrates during steady locomotion. For many bipedal and quadrupedal runners, f measured at the trot–gallop gait transition and maximum running speed scales with $M_b{}^{-0.14}$ to $M_b{}^{-0.24}$ (Table 3; but see Huey, 1982; Bennett *et al.* 1989). Unlike swimmers, however, animals running at a constant speed propel themselves by muscle contractions that are likely to be nearly isometric (Taylor, 1994). Rather than optimize mechanical power ($V/V_{max}=0.2–0.4$), runners are thought to maximize the force developed by locomotor muscle ($V/V_{max}\approx0$) (Roberts, 1995; cf. James *et al.* 1995). Regardless of the relative velocity of muscle shortening, however, at an equivalent speed of locomotion, animals of different sizes are expected to have a constant V/V_{max} for a fixed level of muscle performance. Accordingly, stride frequency at an equivalent speed should be proportional to V_{max} as well as to V (equation 4). Thus, the general similarity in the scaling of f in vertebrates utilizing fundamentally different locomotor modes and, as is likely, distinct muscle fiber types may stem from an underlying constancy in the allometry of V_{max}. The maximum shortening velocity of muscle fibers from the limbs of runners varying widely in body mass shows a size-dependence similar to that

of stride frequency: $V_{max} \propto M_b^{-0.13}$ (McMahon, 1975; Seow and Ford, 1991; cf. Marsh, 1988; Bennett *et al.* 1989). Although V_{max} of myotomal fibers was found to be independent of body size in the dogfish *Scyliorhinus canicula* (Curtin and Woledge, 1988), the scaling of this property is yet to be measured from the locomotor muscle of other axial swimmers or from the pectoral muscle of any labriform swimmer.

The comparison of kinematic allometries between ontogenetic series of fish and taxonomically diverse ranges of other animals requires validation. Development causes increases in body size as well as changes in the twitch kinetics of single fiber types (Marsh, 1988), the proportion of different fibers within a muscle (Kugelberg, 1976) and whole-muscle mechanical advantage (Dodson, 1975; Carrier, 1983). There is presently no information about the ontogenesis of contractile properties and fiber type composition of pectoral fin musculature or the allometry of relevant muscle lever arms, and thus the effects of neuromuscular and skeletal maturation and of body size cannot be separated in this study. Additional study of the pectoral fin musculoskeletal system is required to address the potential complications in comparing intra- and interspecific scaling of gait parameters.

Implications for swimming studies

Swimming performance is commonly expressed as speed in body lengths traveled per second after Bainbridge (1958) in order to allow comparisons among fishes of different size. In the absence of detailed data on the effects of body size on swimming performance, workers have compared gait parameters such as stride frequency among fishes of different size at similar length-specific swimming speeds (e.g. Webb and Keyes, 1982; Williams and Brett, 1987; Graham *et al.* 1990). This study demonstrates that normalization of speed to body length may not be a sufficient correction for comparisons of kinematics across size. In *Embiotoca lateralis*, $U_{p\text{-}c}$, the maximum speed sustainable by pectoral fin oscillation, when expressed in body lengths s^{-1} declines sharply with body size (Figs 1D, 2). Thus, for larger fish, a given length-specific speed represents a greater percentage of $U_{p\text{-}c}$ and requires a relatively higher level of activity than for smaller fish. For example, $2.0\,TL\,s^{-1}$ represents approximately 80 % $U_{p\text{-}c}$ for a 15 cm striped surfperch, but is 100 % $U_{p\text{-}c}$ for a fish only 7 cm longer (Fig. 2). Kinematic comparisons at such a speed may not be appropriate.

For studies investigating the effects of body size on swimming kinematics, we advocate the comparison of fishes of different size at a physiologically equivalent speed at which locomotor movements are dynamically similar and have the same propulsive efficiency. Kinematic patterns at intermediate levels of activity may be compared at swimming speeds expressed not as a certain number of body lengths per second but as a percentage of the equivalent speed (cf. Drucker and Jensen, 1996). For labriform swimmers, an equivalent speed for comparison across size is the pectoral–caudal gait transition speed.

Traditionally, patterns of swimming movements in axial undulators of different size have been compared at the critical swimming speed (U_{crit}), at which fish are thought to make their maximum aerobic effort (Webb, 1971a; Webb *et al.* 1984). Wilson and Egginton (1994) recently noted that U_{crit} does not precisely estimate the transition from aerobic to anaerobic metabolism in trout and that rapidly fatiguable glycolytic myotomal fibers are probably recruited at sub-critical speeds. Electromyography was used to determine the swimming speed at which anaerobic white muscle activity was initiated during swimming trials at increasing velocity. This threshold velocity for white muscle recruitment (U_{WMcrit}), like $U_{p\text{-}c}$ for labriform swimmers, represents a gait transition speed. The onset of white myotomal electrical activity corresponds to the switch from steady axial undulation to intermittent 'burst-and-coast' swimming behavior (Rome *et al.* 1990a; Wilson and Egginton, 1994). Whether defined electromyographically or kinematically, this transition speed should be useful as an equivalent speed for comparison of axial swimmers of different sizes. The extensive past use of U_{crit} as an equivalent speed may not be discounted, since the Froude efficiency of the caudal propeller is largely size-independent at this speed (Webb *et al.* 1984). However, gait transition speeds marking the switch from aerobic to anaerobic power output may elicit more physiologically relevant equivalent levels of activity for comparisons of swimming fish of different sizes.

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