The Use of Gait Transition Speed in Comparative Studies of Fish Locomotion[1]

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SYNOPSIS. Physiological and biomechanical inquiries into the principles of vertebrate locomotion require comparison among animals of different size, habitat and phyletic association. In designing comparative studies of locomotion, a major challenge is to isolate the effects of experimentally imposed variation from the confounding effects of variation in animal activity level associated with differences in scale and life history. For swimming vertebrates, traditional measures of speed used for comparison, including sprint speed and critical swimming speed, should in theory each elicit similar efforts from different animals but have practical shortcomings that can limit their usefulness. This paper presents an alternative approach, adapted from the work of mammalian physiologists, which controls for differences in relative activity level among swimming animals of different size and habitat through comparison at gait transition speeds. The method is illustrated with examples from study of the teleost fish family Embiotocidae, whose members exhibit a distinct transition from exclusively pectoral fin oscillation to combined pectoral and caudal fin propulsion with increasing swimming speed. The pectoral-caudal gait transition speed, or any percentage thereof, is shown to be 'biomechanically equivalent' for swimmers of different size. When this performance limit is expressed in terms of body lengths traveled per unit time, a common normalization of swimming speed, it varies markedly across size and habitat within the family. This finding has the important implication that length-specific speeds may not induce comparable degrees of exercise from different fishes, and thus kinematic and physiological comparisons at such speeds can yield misleading results. The comparative approach described for pectoral fin swimmers, and the limitations of length-specific speed, should be generally applicable to studies of other swimming vertebrates.

INTRODUCTION

To navigate successfully in the aquatic environment, a swimming animal must be capable of propelling itself over a wide range of speeds. Fishes accomplish the demanding array of locomotor tasks involved in prey selection and capture, predator avoidance, and migration through an often dramatic modulation of speed (reviewed by Beamish, 1978; Videler, 1993). Early studies of fish locomotion in this century focused in large part on documentation of the maximum speeds achieved by species in the field (Stringham, 1924; Denil, 1937; Lane, 1941; Wales, 1950; Gero, 1952) and on analysis of the fin and body movements used during voluntary swimming in captivity (Breder, 1926; Magnan, 1930; Gray, 1933; Harris, 1937). The advent of water flumes in the laboratory provided a controlled environment for experimental studies of fishes' swimming abilities. With speed under the investigator's control, two important avenues of research could be fol-

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lowed: (1) descriptive study of the speed-dependence of swimming kinematics (*e.g.*, Bainbridge, 1958; Webb, 1971*a*; Hudson, 1973) and energetics (*e.g.*, Fry, 1957; Blazka *et al.*, 1960; Brett, 1964) in model species; and (2) complementary comparative study of these areas in swimmers of different size, sex and habitat (Bainbridge, 1958; Brett, 1965; Beamish, 1970; Hunter and Zweifel, 1971; Webb *et al.*, 1984; Taylor and McPhail, 1986; Williams and Brett, 1987).

The comparative approach has great utility in extending initial descriptive work through quantification of the effects of both experimentally induced and naturally occurring variation among different populations of fishes. In applying this approach, an important methodological question must be addressed: how can the effects of the variation being studied (*e.g.*, in animal size or ecological association) be isolated from the confounding effects of other sources of variation within the study group? In comparative studies of locomotion, particular attention must be paid to controlling for variation in animal activity level. The degree of exercise a swimming animal undergoes (whether defined kinematically or energetically) increases generally with the absolute speed of locomotion (Fry, 1947; Brett *et al.*, 1958; Dahlberg *et al.*, 1968; Webb, 1971*a*). Allometric studies have demonstrated that the highest level of activity, achieved at the top speed within a gait, is size-dependent (reviewed by Goolish, 1991) and thus at any given absolute speed different-sized fish may not be at similar relative levels of exercise (*i.e.*, equal fractions of their maximum speed). Similarly, comparison of ecologically distinct fishes reveals pronounced differences in maximum swimming performance, presumably related to the differing selective pressures imposed by their respective environments (Jones *et al.*, 1974; Taylor and McPhail, 1986; Graham *et al.*, 1990; Rome *et al.*, 1992; Stobutzki and Bellwood, 1994). It is reasonable to expect that species adapted to different habitats exhibit different stride frequencies and rates of oxygen consumption, for example, during locomotion. However, comparisons at absolute speeds do not al-

low one to separate the effect of ecological divergence on swimming kinematics and energetics from that of differences in locomotor activity level.

Thus the question arises: within a swimmer's normal scope for activity, what is an appropriate speed for making meaningful functional and physiological comparisons with other swimmers? The purpose of this paper is to review and reevaluate traditional measures of speed used in comparative studies of fish locomotion, and to present an alternative approach to the normalization of speed for activity level based on research I have conducted with Jeffrey Jensen of Harvard University. The general implications of this approach for swimming studies are illustrated with two specific examples from our work: allometric (ontogenetic) comparisons and ecological (interspecific) comparisons within the surfperches (Teleostei: Perciformes).

WHAT IS AN APPROPRIATE SPEED FOR LOCOMOTOR COMPARISONS?

One of the first formal methodologies proposed for making comparisons among fish swimming under different experimental conditions was devised by Brett (1964). The approach involves estimating the highest sustained speed, or *critical speed* (U_{crit}), of fish swimming in a flume. Current velocity is increased in increments at fixed time intervals (Δt) until fatigue occurs. From measurement of the penultimate speed achieved (U) and the time (t) spent in the final velocity increment (ΔU) before exhaustion, critical swimming speed may be calculated as follows:

$$U_{crit} = U + \frac{t}{\Delta t} \cdot \Delta U. \qquad (1)$$

It is reasonably assumed that fish make their maximum aerobic effort at U_{crit} and on this basis the speed has been used as a threshold level of performance for kinematic and energetic comparisons (Brett, 1964, 1965; Webb, 1971*a*; Webb *et al.*, 1984).

Since the largest locomotor muscle mass of fishes (*i.e.*, myotomal) is composed predominantly of rapidly fatigable, fast-twitch fibers, it has been argued that maximum

burst or *sprint speed* (U_{max}) is appropriate for the purpose of comparison (Webb, 1977). At U_{max}, the highest speed powered by anaerobic metabolism, temporal and spatial patterns of caudal fin movement have been studied in swimmers varying both in body size and in ecology (Bainbridge, 1958; Wardle, 1975; Taylor and McPhail, 1986; Wardle and He, 1988).

In theory U_{crit} and U_{max}, as measures of top speed, should each elicit comparable levels of activity in fishes of different size and habitat. In practice, however, it is difficult to demonstrate that a fish has reached the upper limit of its scope for activity (Bainbridge, 1958). Sprint speeds, maintained often for only seconds at a time, can vary substantially among individuals of a species according to both motivation and pre-exercise training (Blaxter and Dickson, 1959; Bainbridge, 1962; Wardle and He, 1988). Although U_{crit} reflects steady, sustained swimming performance, this speed too is subject to considerable intraspecific variation (Brett *et al.*, 1958; Beamish, 1970; Jones *et al.*, 1974). In general, measures of swimming endurance (*e.g.*, Eq. 1: t) range widely within species (Vincent, 1960; Bainbridge, 1962; Brett, 1964, 1967).

An alternative method for comparison which has seen widespread use in swimming studies involves correction of speed for variation in body length. Originally proposed by Bainbridge (1958) as a means of controlling for size-related differences in swimming ability, speed is expressed in terms of body lengths traveled per second (L/sec). *Length-specific speed* has been used by subsequent workers (*e.g.*, Beamish, 1966; Webb and Keyes, 1982; Graham *et al.*, 1990) in comparisons of gait parameters among fishes of different size. In the absence of detailed information about the relationship between swimming performance and ecology, like-sized fishes differing in habitat and life history have also been compared at similar length-specific speeds (Brett and Sutherland, 1965; Taylor and McPhail, 1986; Williams and Brett, 1987; Graham *et al.*, 1990). In contrast to U_{crit} and U_{max}, a given relative speed elicits an intermediate level of activity which can be induced repeatably and with little error in the

laboratory. Such speeds, however, are unlikely to demand *similar* levels of activity from fishes of different size or ecological association, as is argued below.

The ideal speed for comparison would both elicit similar relative levels of exercise in different swimmers, and mark a discrete, submaximal point within a gait so that the speed can be measured reliably. These criteria are met by *gait transition speed*. Heglund *et al.* (1974) posited that at the transition between gaits (*e.g.*, from the trot to the gallop) different-sized running vertebrates have the same relative power requirements and experience similar stresses in their limbs. Such speeds were termed 'physiologically equivalent' for animals of different size and have been used extensively to study the scaling of running mechanics and energetics (see review by Lindstedt and Thomas, 1994). A valid criticism of this approach (Garland, 1983) is that equivalent speed was not precisely defined in its original presentation and thus the notion that at gait transitions animals of different size are at comparable levels of activity was more of an assertion than an experimentally supported fact. Since its introduction, however, it has been shown that different-sized runners experience similar peak musculoskeletal stresses (Biewener and Taylor, 1986; Perry *et al.*, 1988) and have similar mass-specific power requirements at gait transition speeds (Heglund and Taylor, 1988). Such patterns have been cited to justify kinematic and physiological comparisons.

Biologists interested in allometric and ecological comparisons among swimming vertebrates stand to benefit by borrowing this concept developed for tetrapods: namely, controlling for differences in activity level by comparing animals at a gait transition speed. I adopt this approach for teleost fish which exhibit a change in gait with increasing swimming speed, and present kinematic evidence that the transition speed is 'biomechanically equivalent' for different swimmers.

THE MODEL SYSTEM

Like tetrapods, many fishes exhibit gait transitions (Alexander, 1989; Webb,

1994*a*). Species that swim by passing waves of bending of the body from head to tail often switch from steady axial undulation to a saltatory "burst-and-coast" mode of propulsion at high speeds (Weihs, 1974; Videler and Weihs, 1982; Rome *et al.,* 1990). To illustrate the value of comparing swimmers at gait transition speeds, I focus on a less well-studied group, the pectoral fin swimmers. Many percomorph fishes, as well as some less-derived actinopterygians, swim over low speeds by pectoral fin propulsion (termed labriform locomotion by Breder, 1926) and with increasing speed supplement paired fin movements with caudal fin oscillation (reviewed by Drucker and Jensen, 1996*b*). At the pectoral-caudal gait transition speed (U_{p-c}), it is proposed that valid kinematic and physiological comparisons of different swimmers may be made.

A group of fishes particularly well-suited to comparative study of labriform locomotion is the surfperches (Embiotocidae). The family occupies near-shore marine habitats of the North Pacific and is comprised of two ecologically distinct subfamilies (Fig. 1). Members of the Amphistichinae are found in structurally simple habitats (*e.g.,* open water above a sandy ocean floor) and exhibit ram feeding, a mode of prey capture which requires high-speed cruising in the water column. By contrast, embiotocins are largely substrate-associated, occurring in structurally more complex habitats such as rocky reefs, and employ suction feeding, a strategy favoring high maneuverability (De Martini, 1969; Jensen, 1993). In addition, the family is viviparous, producing large well-developed young that employ pectoral fin locomotion from the moment of parturition. Throughout ontogeny and across habitat, the surfperches exhibit a distinct transition from purely pectoral to primarily caudal fin swimming, and thus are ideal subjects for examining the influence of scale and ecology on labriform swimming performance.

BIOMECHANICALLY EQUIVALENT SPEED

To justify comparisons at a gait transition speed, one must demonstrate that it elicits equivalent levels of activity in different animals. In studies of 'physiologically equiv-
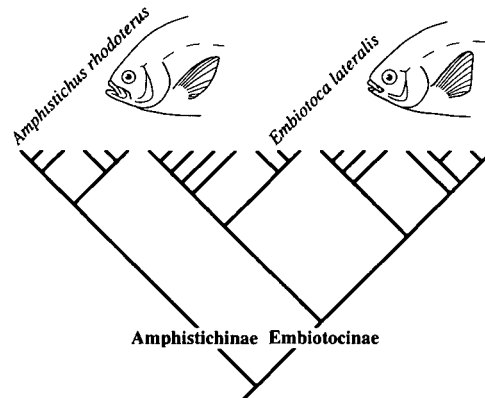

FIG. 1. Proposed intrarelationships of the Embiotocidae (from Jensen, 1993) highlighting the species used in comparative studies of pectoral fin locomotion. The striped surfperch, *Embiotoca lateralis,* varies 5-fold in body length and over 100-fold in body mass throughout ontogeny and served as a model for investigation into the intraspecific scaling of labriform swimming performance. This species and the redtail surfperch, *Amphistichus rhodoterus,* were used as representatives of the two ecologically distinct basal sister groups of the family. Members of the Amphistichinae occur in open water and use a ram feeding strategy while members of the Embiotocinae are largely substrate-associated and feed by suction from benthic substrates.

alent' running speed, activity level has been gauged by the energetic cost of locomotion (*e.g.,* Heglund and Taylor, 1988) or by the level of force generated within the limbs (Biewener and Taylor, 1986; Farley and Taylor, 1991). Here, 'biomechanically equivalent' speed is defined in terms of simple kinematic criteria applicable to swimming vertebrates. At a biomechanically equivalent speed, swimmers of different size exhibit kinematically similar fin movements with size-independent propulsive efficiency.

The requirements of kinematic similarity are adopted from those described by Alexander and Jayes (1983) for tetrapods running in a "dynamically similar" fashion. First, the proportion of the stride period occupied by propulsive fin movements (the duty factor, D) must be the same in different-sized fish. Second, dimensionless stride length, the distance traveled in one complete fin beat period (λ_s, or [speed/propulsive frequency]) expressed as a multiple of propulsor length (L_p) must be size-indepen-

dent. For oscillatory propulsors (either paired as in labriform swimmers or unpaired as in thunniform axial swimmers), L_p is taken as fin span, the distance from fin base to tip (*cf.*, Daniel, 1984). The characteristic length of undulatory propulsors may alternatively be measured as fin base length in the case of median fin swimmers (Blake, 1983) or as body length for anguilliform axial swimmers.

The mechanical efficiency of an aquatic propulsor represents the fraction of the total muscle power generated that is used to produce forward thrust (Webb, 1971*b*, 1975). A kinematic measure of the efficiency of an undulatory propulsor is "slip," the ratio of forward swimming speed of the animal to rearward speed of the propulsive wave of bending of the body or undulating fin. For oscillatory propulsors an important determinant of efficiency is the comparable quantity termed advance ratio (*J*). This is a dimensionless parameter which measures forward swimming velocity relative to mean fin tip velocity (*cf.*, Ellington, 1984):

$$J = \frac{U}{2\phi f L_p},\qquad(2)$$

where U is swimming speed, ϕ is angular fin beat amplitude (rad), and f is fin beat frequency. At a biomechanically equivalent speed, slip and advance ratio are expected to be size-independent.

The equivalency of $U_{p\text{-}c}$ for labriform swimmers was investigated in an ontogenetic series of striped surfperch, *Embiotoca lateralis*, varying over 100-fold in body mass. Fish underwent increasing velocity swimming trials with 0.2 L/sec speed increments at 3 min time intervals. The pectoral-caudal gait transition speed was taken as the highest speed a fish could maintain for 3 min by pectoral fin oscillation alone (*cf.*, Drucker and Jensen, 1996*a*). The kinematic variables D, λ_s/L_p (where L_p is pectoral fin span) and J show a clear dependence upon swimming speed (Fig. 2A), but when measured at $U_{p\text{-}c}$ do not show a significant dependence upon body mass (Fig. 2B). Thus $U_{p\text{-}c}$ is considered a sound choice for allometric comparisons of kinematic gait parameters (*e.g.*, stride frequency, fin beat am-

plitude and others influencing swimming thrust: Drucker and Jensen, 1996*b*) as well as physiological variables such as metabolic rate and intensity of locomotor muscle activity.

ONTOGENETIC AND ECOLOGICAL VARIATION IN $U_{p\text{-}c}$: IMPLICATIONS FOR SWIMMING STUDIES

With evidence that $U_{p\text{-}c}$ is a comparable speed for different-sized swimmers, one can evaluate whether other measures of speed used for allometric comparisons successfully correct for differences in activity level. Figure 3 illustrates the allometry of $U_{p\text{-}c}$ with swimming speed expressed in terms of body lengths traveled per second, a common standardization in studies of aquatic locomotion. For a length-specific speed to demand comparable levels of activity in different-sized animals, it must remain a fixed proportion of $U_{p\text{-}c}$, a biomechanically equivalent performance limit. That is, the transition speed expressed as L/sec must be scale-independent.

Because $U_{p\text{-}c}$ (L/sec) in fact declines with body size, it follows that a given length-specific speed does not elicit the same level of activity in fish of different sizes. Consider, for example, that 2.5 L/sec is the highest labriform swimming speed for intermediate-sized striped surfperch (17 cm), but for fish only slightly smaller is 80% of $U_{p\text{-}c}$ (Fig. 3A) and induces a relatively lower level of activity. Thus, kinematic or physiological comparisons made at 2.5 L/sec would have these fish at quite different fractions of their scope for activity within the labriform gait.

In general, this limitation of length-specific speed in controlling for size-related differences in activity level is evidenced by 'gait compression' (*cf.*, Webb, 1994*b*). When swimming speed is expressed in terms of L/sec, the labriform gait is restricted to an increasingly narrow range of speeds as body size increases (Fig. 4). Accordingly, comparisons of gait parameters at a given length-specific speed have the effects of body size confounded by the effects of variation in locomotor activity level.

It is suggested, therefore, that the long-standing practice of normalizing swimming
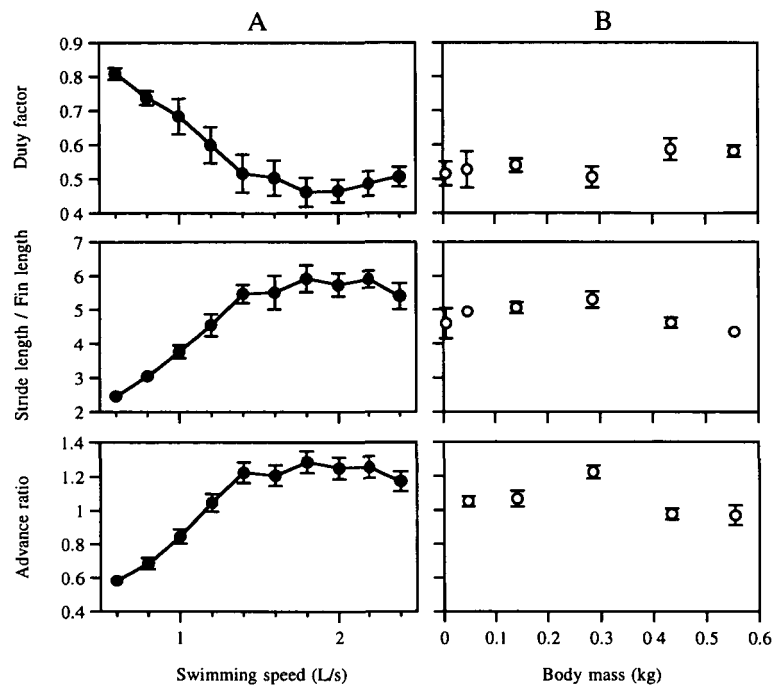
FIG. 2. (A) Duty factor, relative stride length and advance ratio for pectoral fin oscillation are speed-dependent in *Embiotoca lateralis*. Representative curves are shown for individuals 16.9 ± 0.2 cm mean standard length (L) ± SD, n = 3. The last point in each plot is at the average pectoral-caudal gait transition speed (U_{p-c}). (B) When measured at U_{p-c}, these gait parameters do not vary significantly with body mass, a finding which supports the hypothesis that the transition speed is biomechanically equivalent for swimmers of different size. Kinematic values are plotted as mean ± standard error. After Drucker and Jensen (1996b).

speed to body length may not be a sufficient correction for functional comparisons across size (*cf.*, Drucker and Jensen, 1996a, b). This conclusion has important implications for both allometric and ecological comparisons of aquatic gait parameters.

Allometric comparisons

In allometric swimming studies, gait parameters measured for different-sized fish are commonly plotted as functions of length-specific speed on the same axes to facilitate comparison (*e.g.*, Hunter and Zweifel, 1971; Graham *et al.*, 1990). To illustrate this approach, the product of corrected pectoral fin beat frequency and linear fin beat amplitude, as defined by Drucker and Jensen (1996a), is plotted against relative swimming speed for three size classes of *Embiotoca lateralis* (Fig. 5A). This product is assumed to reflect pectoral muscle shortening velocity (Webb, 1973) and the square of the term should be proportional

to mean thrust generated during steady swimming (Wu, 1977). It would be of interest, therefore, to determine how such a quantity varies with body size. At a given length-specific speed, a distinct size-dependence of the product is apparent (Fig. 5A). It is important to appreciate, however, that this dependence is an artificial one, since the animals are not at equivalent speeds. The top length-specific speed for the largest fish (Fig. 5A: U_{p-c} = 1.8 L/sec) is an intermediate speed for the smallest fish (approximately 50% U_{p-c}) and induces a correspondingly lower relative level of activity.

How then should speed be standardized to allow accurate assessment of the impact of body size on swimming mechanics? In an allometric study of oxygen consumption rates in salmon, Brett (1965) proposed that fish of different sizes may be compared at any fraction of their respective critical swimming speeds. This procedure is employed under the assumption that U_{crit} is an
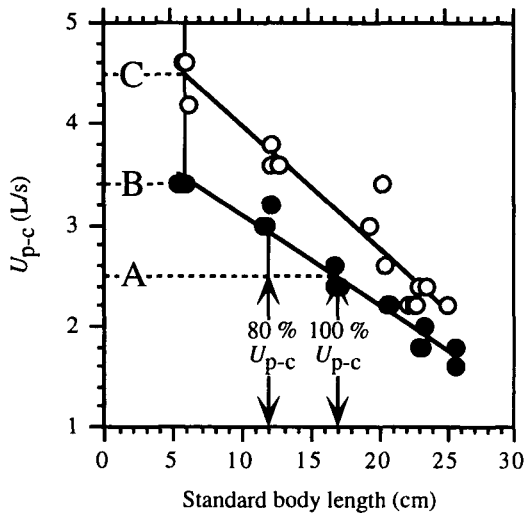
FIG. 3. Scaling of pectoral-caudal gait transition speed in the open-water surfperch *Amphistichus rhodoterus* (○) and the substrate-associated *Embiotoca lateralis* (●). Swimming speed is expressed in terms of standard body lengths traveled per second (L/sec). The negative allometry of U_{p-c} indicates that, within a species, a given length-specific speed does not elicit comparable levels of activity in different-sized fish. For example, in *E. lateralis* 2.5 L/sec (A) is 100% U_{p-c} for a 17 cm fish but is approximately 80% U_{p-c} for an individual only 5 cm shorter. The consistent difference in U_{p-c} between ecologically distinct taxa suggests that length-specific speeds also fail to correct for interspecific variation in activity level. The relative U_{p-c} for young of the year *E. lateralis* (B) is on average 75% of the transition speed for like-sized *A. rhodoterus* (C). Comparisons at B have the fish at a 25% difference in scope for activity within the labriform gait.

equivalent speed (*i.e.*, at which all fish make their maximum aerobic effort: Webb, 1971*a*; Webb *et al.*, 1984) and so similar intermediate levels of activity should be elicited at any given percentage of U_{crit}. For labriform swimmers, this approach can be applied using U_{p-c}. In general, comparisons at speeds expressed as a proportion of an equivalent speed must be validated explicitly. For surfperch, the three gait parameters used to test for similarity in fin kinematics and propulsive efficiency (Fig. 2B) vary with % U_{p-c} in a size-independent fashion (Fig. 6). Accordingly, any fraction of the top pectoral fin swimming speed is biomechanically equivalent for fish of different size.

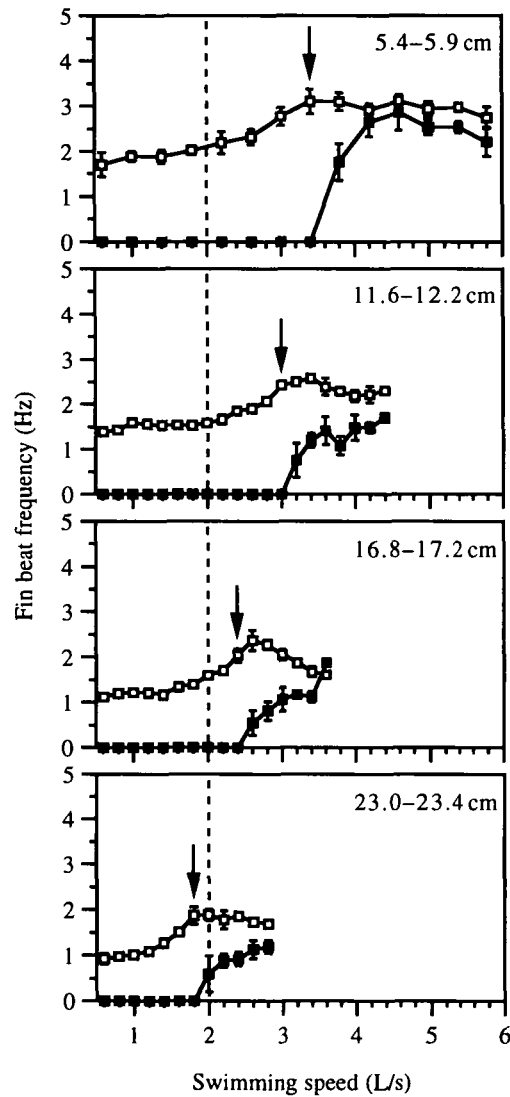With speed expressed in terms of % U_{p-c} the apparent size-dependence of the product

FIG. 4. Relationship between fin beat frequency (□: pectoral; ■: caudal) and length-specific swimming speed in *Embiotoca lateralis* illustrating compression of the labriform gait with increasing body size. The size ranges for each group (n = 3) are in standard length. Arrows indicate average U_{p-c}. The last point in each curve is at the maximum speed achieved before exhaustion. Average frequencies are shown with SEM error bars. At a given length-specific speed (*e.g.*, 2 L/sec, dashed line), allometric comparison of stride frequency is complicated by the fact that different-sized animals are not at similar fractions of U_{p-c}. After Drucker and Jensen (1996*a*).
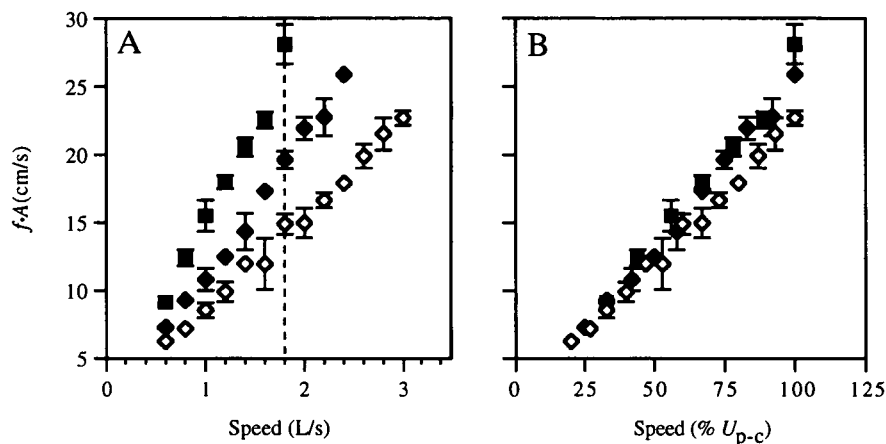
FIG. 5. The size-dependence of swimming kinematics varies with the speed selected for allometric comparison. The product of corrected pectoral fin beat frequency and fin beat amplitude ($f \cdot A$) for three size classes of *Embiotoca lateralis* is plotted as a function of (A) body length-specific swimming speed and (B) speed expressed as a percentage of the pectoral-caudal gait transition speed. At a given length-specific speed (*e.g.*, 1.8 L/sec, dashed line), $f \cdot A$ appears to be proportional to body length but different-sized fish are not at equivalent levels of activity. Comparisons at any percentage of U_{p-c} do not indicate a significant size-dependence of this quantity. Data given as mean ± SEM. Symbols same as in Figure 6. From Drucker and Jensen (1996a).

of frequency and amplitude disappears (Fig. 5B). This example illustrates that the effects of body size on aquatic gait parameters, and the underlying mechanical quantities they reflect, can be obscured by comparisons at length-specific speeds.

Ecological comparisons

Just as swimming performance may vary with body size within a species, it is expected also to be correlated with the ecological associations of different species. Segregation into benthic and pelagic niches is a recurring pattern among bony fishes (Schluter and McPhail, 1993; Robinson and Wilson, 1994) and, within the Embiotocidae, provides an opportunity to examine the influence of habitat on labriform swimming ability. The substrate-associated striped surfperch (*Embiotoca lateralis*) and the open-water redtail surfperch (*Amphistichus rhodoterus*) were selected as representatives of the ecologically distinct embiotocid subfamilies (Fig. 1). In light of their extreme differences in physical and trophic habitat, it is not surprising that these fishes differ significantly in U_{p-c}. Across a 5-fold range in body length, the open-water species achieves consistently higher gait transition

speeds than does the substrate-associated species (Fig. 3).

The fact that U_{p-c} expressed in terms of L/sec varies between like-sized individuals of different species indicates that interspecific comparisons at a given length-specific speed may be problematic. As is the case for striped surfperch of different sizes (Figs. 3A, 4), a length-specific speed does not represent for different species the same fraction of the maximal labriform swimming speed (Fig. 3B, C).

Without knowledge of the interspecific difference in U_{p-c} (L/sec), one might be inclined to compare the two surfperches at intermediate length-specific speeds, at which *Embiotoca* exhibits significantly higher pectoral fin beat frequency than does *Amphistichus* (Fig. 7A). This pattern has been noted in other groups of fishes which contain both slow, substrate-associated and fast, open-water labriform swimmers (*e.g.*, the two typical life history forms of the stickleback *Gasterosteus aculeatus*: Taylor and McPhail, 1986). The conclusion that has been drawn from the elevated fin beat frequency of the benthic form is that it must "work harder" than the conspecific pelagic form to maintain position in a current (Taylor and McPhail, 1986).

Mean body length (cm)

—◇— 11.9

—◆— 16.9

—□— 20.8

—■— 23.2

Duty factor

1.2

1

0.8

0.6

0.4

Stride length / Fin length

6

5

4

3

2

1

Advance ratio

1.5

1

0.5

0   25   50   75   100   125
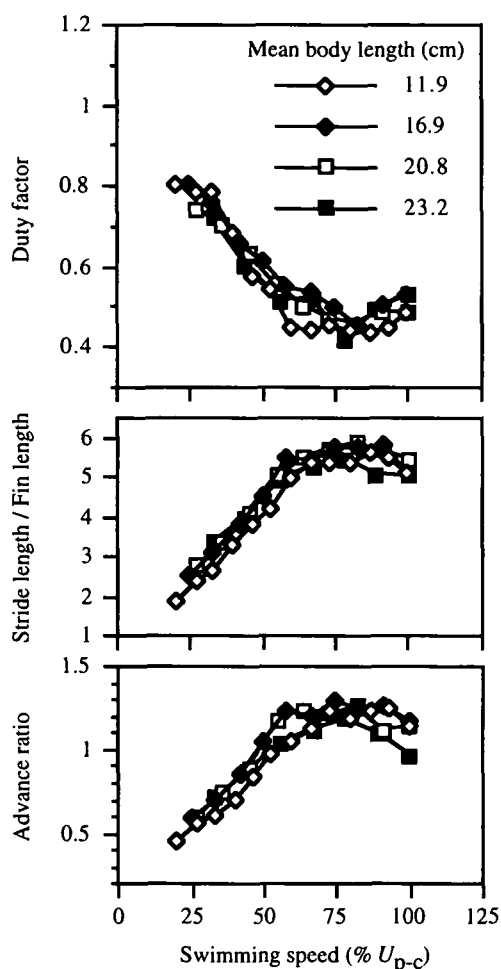
Swimming speed (% U_{p-c})

FIG. 6. Mean duty factor, relative stride length and advance ratio as functions of swimming speed as a percentage of U_{p-c} for *Embiotoca lateralis* (n = 3 per size class). Each gait parameter varies with speed in a size-independent fashion indicating that any fraction of U_{p-c} is a biomechanically equivalent speed for different-sized animals. Speed expressed as % U_{p-c} thus may be used for comparisons at intermediate levels of activity.

However, when speed is expressed as a percentage of the pectoral-caudal gait transition speed, in order to control for interspecific variation in swimming ability, one is led to a substantially different conclusion. The functions describing the relationship between fin beat frequency and speed are shifted so that they largely overlap each other at speeds up to U_{p-c} (Fig. 7B). The most conspicuous difference between *Em-*

biotoca and *Amphistichus* is in the fin beat frequencies used above the gait transition. Thus, in this case the elevated frequency seen in benthic swimmers (Fig. 7A) is an artifact of the measure of speed used for comparison.

The misleading kinematic patterns that stem from comparisons at length-specific speeds are mirrored by patterns of electrical activity in the pectoral musculature. Underlying propulsive fin movements during labriform swimming is the coordinated contraction of pectoral girdle muscles. For both *Embiotoca* and *Amphistichus*, the intensity of electromyographic signals (IEMG) recorded from the pectoral musculature is speed-dependent, increasing over low to intermediate swimming speeds and plateauing at the pectoral-caudal gait transition (Fig. 7C). Across most length-specific speeds, the substrate-associated surfperch exhibits higher relative IEMG than does the open-water species (Fig. 7C). Again, when speed is expressed as % U_{p-c} this interspecific difference is no longer evident (Fig. 7D).

METHODOLOGICAL RECOMMENDATIONS

The approach of investigating the effects of body size and habitat on locomotor mechanics at gait transition speeds has value in studies of fish swimming. The examples presented above call into question the validity of kinematic and physiological comparisons at length-specific speeds between (1) different-sized individuals of a single species and (2) like-sized individuals of ecologically distinct species. Alternatively, for labriform swimmers, comparisons may justifiably be made at U_{p-c} or any percentage thereof.

These conclusions have bearing not only on studies of appendage-based swimming, but also on those focusing on axial undulatory propulsion. Since estimates of equivalent speed (*e.g.*, U_{crit}, U_{max}) expressed in L/sec vary with both the size and ecology of caudal fin swimmers (Jones *et al.*, 1974; Graham *et al.*, 1990; Goolish, 1991), length-specific speeds seem inappropriate for comparisons within this extensively studied group of fishes. Caudal fin swimmers have been noted to undergo a distinct
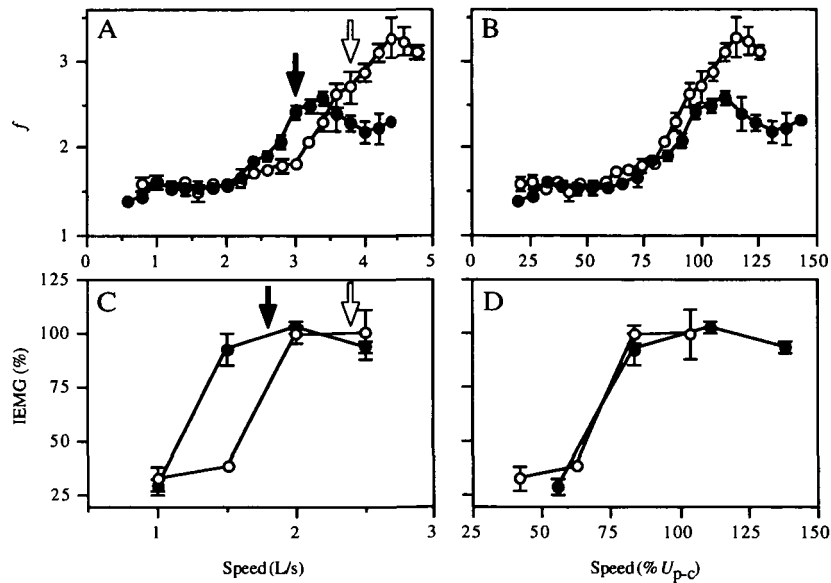
Fig. 7. Kinematic and physiological comparisons of ecologically distinct swimmers at length-specific speeds can yield misleading results. (A) The substrate-associated *Embiotoca lateralis* (●) exhibits higher average pectoral fin beat frequency (f) than does the open-water *Amphistichus rhodoterus* (○) between 2.4–3.4 L/sec. Average U_{p-c} indicated by arrows. (B) With speed normalized to U_{p-c}, this interspecific difference is no longer apparent. n = 3 per species; L = 12.1–12.7 cm. (C) The intensity of electromyographic activity in the pectoral abductor profundus (IEMG: rectified integrated burst area), expressed as a percentage of the intensity measured at U_{p-c}, is higher in *Embiotoca* across most length-specific speeds. (D) At any % U_{p-c}, however, the species do not differ substantially in relative IEMG. Five bursts at each speed analyzed for 24 cm individual of each species. All values plotted as mean ± SEM.

transition in gait from steady axial undulation at aerobically sustainable speeds to intermittent "burst-and-coast" swimming at higher speeds. This transition can be defined either kinematically in terms of a discrete change in spatial patterns of body movement (Videler and Weihs, 1982) or electromyographically, since it corresponds with the onset of white myotomal muscle recruitment (Rome *et al.*, 1990; Jayne and Lauder, 1994). Through a rather simple kinematic analysis (Fig. 2), it should be possible to determine whether the speed marking the switch from steady to burst axial undulation (U_{s-b}), or the threshold velocity for white muscle recruitment (U_{WMcrit}: Wilson and Egginton, 1994), is biomechanically equivalent for different caudal fin swimmers.

A recognized shortcoming of Heglund *et al.* (1974) was the failure to specify the precise requirements of physiological equivalency for running vertebrates. The resulting generality of the concept, however, affords

the comparative biologist an opportunity to develop equivalency criteria for non-terrestrial modes of locomotion. The kinematic requirements presented here for labriform swimmers should be applicable to fishes employing other modes of locomotion, but are not intended to represent the only relevant indicators of similarity in activity level. Information about the energetics and musculoskeletal stresses of swimming at gait transition speeds will undoubtedly refine the definition of equivalent speed for fishes and expand its utility in comparative studies of aquatic locomotion.

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