



Gait transition speed, pectoral fin-beat frequency and amplitude in *Cymatogaster aggregata*, *Embiotoca lateralis* and *Damalichthys vacca*

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Surfperches are labriform swimmers and swim primarily with their pectoral fins, using the tail to assist only at higher speeds. The transition, from pectoral to pectoral and caudal fins, occurs at a threshold speed that has been termed physiologically and biomechanically 'equivalent' for fishes of different size. The gait transition (U_{p-c}) of *Cymatogaster aggregata* occurred at a higher speed (measured in bodylengths s^{-1}) for smaller fish than larger fish. At U_{p-c} , pectoral fin-beat frequency was size-dependent: smaller fish have a higher pectoral fin-beat frequency than larger fish. In contrast, at low speeds (i.e. <60% of U_{p-c}) the pectoral fin-beat frequency was independent of the size of the fish. Inter-specific comparisons of U_{p-c} , pectoral fin-beat frequency and amplitude among *C. aggregata*, *Embiotoca lateralis* and *Damalichthys vacca* showed that *C. aggregata* had a higher U_{p-c} than *E. lateralis* and *D. vacca*. The pectoral fin-beat frequency at U_{p-c} showed no significant differences among species. *Cymatogaster aggregata* achieved higher U_{p-c} , in part, through increased fin beat amplitude rather than frequency. These differences in performance may be related to the different habitats in which these species live.

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INTRODUCTION

Embiotocids, as typical labriform swimmers, primarily use oscillating pectoral fins for lift-based propulsion at slow and moderate speeds; at high speeds there is a gait transition to a caudal fin assisted swimming mode (Harris, 1937; De Martini, 1969; Webb, 1973; Drucker, 1996; Drucker & Jensen, 1996a,b). The hydrodynamic forces generated by the pectoral fins are related to kinematic variables of the fins, their surface area, shape and orientation (Harris, 1937; Drucker & Lauder 2000). In general, labriform propulsion is produced by dorso-ventral, and antero-posterior movements of the pectoral fins (Webb & Blake, 1985). Within a narrow range of speeds pectoral fin kinematics can be variable between species and within a single species (Webb, 1973; Gibb *et al.*, 1994; Drucker & Jensen, 1996a; Walker & Westneat, 1997). Investigating the inter- and intra-specific variation in the kinematics of pectoral fin swimming is an important first step in understanding the evolution of pectoral fin locomotion.

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Twenty-three of 24 embiotocid species are near-shore inhabitants of the north-eastern and north-western Pacific. A single species, *Hysteroecarpus traski* Gibbons, inhabits fresh water in California. The marine species are found in complex habitats, such as eelgrass beds, rocky reefs and kelp beds, and also in calm, deeper water, shallow, sandy bottoms and even surf zones. Differences in habitat distribution among these species may be correlated with a number of factors, e.g. fins and body shape, design of underlying functional systems and swimming ability. The swimming performance of certain labrids has been related to the habitat in which they live (Fulton *et al.*, 2001).

Swimming performance can be evaluated by focusing on gait at increasing speeds. An animal gait was defined by Alexander (1989) as discrete changes in muscle and fin-body combinations that propel the body with increasing speed. The gait transition speed (U_{p-c}) has been considered an ideal parameter for comparisons of swimming performance among fish of different size and between species (Drucker, 1996). In fact, U_{p-c} represents a step transition during steady swimming that elicits equivalent levels of exercise in fish of different sizes, as Drucker and Jensen (1996a,b) showed for striped surfperch *Embiotica lateralis* Agassiz. In this study the effect of size on U_{p-c} and frequency and amplitude of fin beats in an ontogenetic series of shiner perch *Cymatogaster aggregata* Gibbons was examined and ecologically relevant comparisons were made with two different species of embiotocids, *E. lateralis* and pile perch *Damalichthys vacca* Girard.

MATERIALS AND METHODS

FISHES

Shiner perch, pile perch, and striped surfperch were collected by beach seine at Jackson Beach (48°31' ; 123°01' W), San Juan Island, Washington, U.S.A, in July 2001. Shiner perch of various sizes (3.5–13.8 cm standard length, L_S , $n=23$) were used for the allometric study of gait transition. Individuals of uniform L_S (mean \pm s.d., *C. aggregata*, 6.3 ± 0.4 cm, $n=6$; *E. lateralis*, 6.1 ± 0.2 cm, $n=3$; *D. vacca*, 6.7 ± 0.2 cm, $n=5$) were used for inter-specific comparisons of pectoral fin kinematics. Fishes were held at the Friday Harbor Laboratories of the University of Washington in flow-through seawater tanks at 12° C.

EXPERIMENTAL PROCEDURE

Experiments were performed in a flume tank with a working section 50 cm long, 12 cm wide and water depth of 14 cm, for the smaller sizes (<10 cm). The trials for fishes >10 cm were carried out in a larger flume tank with a working section 100 cm long, 70 cm wide and 30 cm deep. Only trials in which fishes remained at least 2 cm from the walls, the bottom and the water surface of the working area were analysed to avoid boundary effects. The cross-sectional area of the largest fish was <10% of the cross-sectional area of the flume working area, thus making corrections for the blocking effect of the body unnecessary (Webb, 1975; Graham & Laurs, 1982). Current speed was controlled with repeatable precision by applying a constant voltage determined by a digital voltmeter to the driving motor. Flow speed was calibrated with dye injected in the fluid, and its trajectory through the working section of the flume captured on video. A mirror positioned at 45° above the flume provided a dorsal view of the propulsive movements of the fins. The flume was illuminated with Lowell video lights and lateral and dorsal views were recorded simultaneously with a JVC DVL9800U mini digital video camcorder at either 60 or 125 frames s^{-1} . The former was used for analysis of gait transition speed, the latter to establish pectoral fin beat frequency and amplitude.

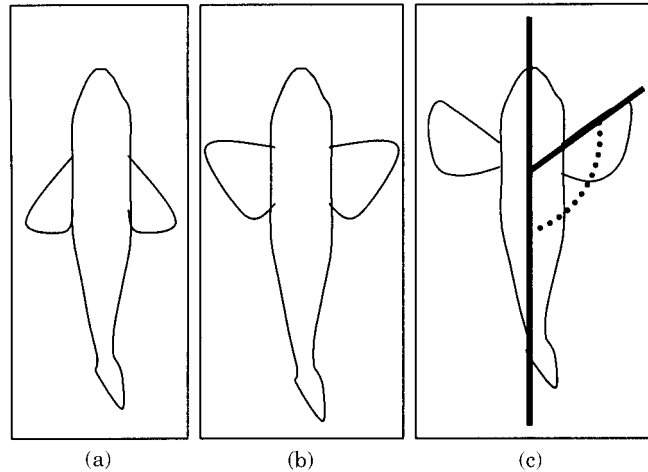


FIG. 1. Dorsal images of pectoral fin positions during swimming: (a) and (b) show two sequences of abduction and (c) represents the maximum excursion of the pectoral fin before the adduction movement. Amplitude of fin-beat was measured as the angle in degrees formed by the line through the body axis of the fish and the leading edge of the fin just before the adduction phase (••••).

The fishes did not require training to swim in the flume. Fishes were acclimated in the flume tank for 20 min at very low speed, *c.* $0.6 \text{ body lengths s}^{-1}$ ($L_S \text{ s}^{-1}$). Experiments on gait transition and scaling of fin kinematics were conducted by increasing current speed $0.2 L_S \text{ s}^{-1}$ every 2 min.

KINEMATICS ANALYSIS

Gait transition speed, pectoral fin beat frequency and amplitude, and frequency of the caudal fin motion in different sizes of *C. aggregata*, and in *C. aggregata*, *E. lateralis* and *D. vacca* of the same size were measured. These kinematic variables were measured frame-by-frame from the video recordings for each fish during steady swimming at each speed, from $1.0 L_S \text{ s}^{-1}$ to a speed that exceeded U_{p-c} by $0.6\text{--}1.0 L_S \text{ s}^{-1}$.

The pectoral-caudal gait transition speed (U_{p-c}), as defined by Drucker (1996), was the highest current velocity at which the fish could swim using pectoral fin propulsion alone. At higher speeds, the caudal fin movement begins to supplement pectoral oscillation. The pectoral fin beat cycle includes pectoral fin movements that generate thrust, using both abduction and adduction, and a pause or refractory period, in which the fins are placed against the body. This study considered the beating of pectoral fins including the refractory phase. The fin beat amplitude was measured as the angle in degrees formed by the body axis of the fish and the leading edge of the fin at maximum extension before the adduction phase (Fig. 1). This measurement is a component (i.e. in the horizontal plane) of the true amplitude, since the fin beat of surfperches has a large dorsoventral component.

RESULTS

GAIT TRANSITION SPEED AND PECTORAL FIN BEAT FREQUENCY IN *C. AGGREGATA*

There was a significant relationship between gait transition speed and L_S ($P < 0.001$, $n = 23$) in shiner perch. The absolute U_{p-c} in cm s^{-1} in relation to L_S showed that the fastest speeds were reached by larger fish. The relationship was not isometric [Fig. 2(a)]. Length-specific gait transition speed, U_{p-c} in L_S decreased linearly with increasing L_S [Fig. 2(b)].

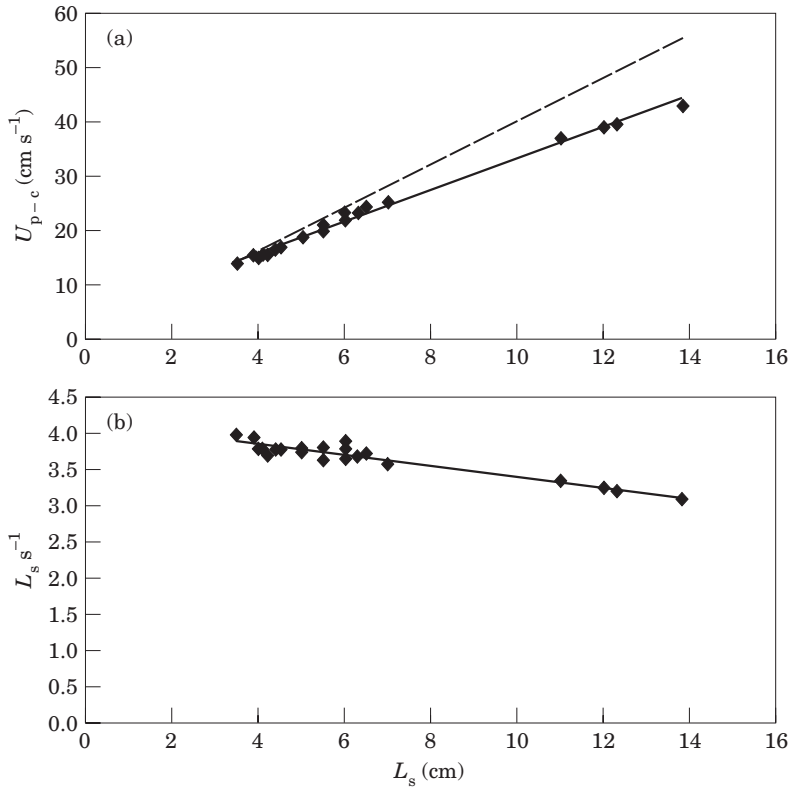


FIG. 2. The relationship between (a) absolute gait transition speed U_{p-c} and (b) $L_s \text{ s}^{-1}$ and the L_s for *Cymatogaster aggregata*. (a) U_{p-c} increases with increase in L_s . The line was fitted by: $y = 2.88x + 4.40$ ($r^2 = 0.99$). The deviation from the isometric relationship (— —) is significant ($t = 2.08$, $P < 0.01$, d.f. = 21). (b) U_{p-c} decreases with increasing L_s . The line was fitted by: $y = -0.076x + 4.16$ ($r^2 = 0.90$).

The frequency of pectoral fin beating increased with speed for all sizes studied, attaining a maximum at U_{p-c} , and then decreased when the caudal fin started to supplement pectoral fin oscillations (Fig. 3).

At U_{p-c} , the frequency of pectoral fin beating (F_p) in *C. aggregata* was size-dependent ($P < 0.001$, $n = 17$, Fig. 4). Smaller fish had a higher pectoral fin-beat frequency at U_{p-c} than larger fish. In contrast, at low speeds the frequency of pectoral fin beating was independent of L_s (Fig. 5). Regression analysis for each swimming speed expressed in percentage of U_{p-c} revealed that at 30, 40 and 50% U_{p-c} , pectoral frequency was independent of size, while $>60\%$ the relationship was significant (Table I).

GAIT TRANSITION SPEED, PECTORAL FIN BEAT FREQUENCY AND AMPLITUDE AMONG EMBIOTOCIDS

The transition from pectoral to caudal-associated fin propulsion of shiner perch, striped surfperch and pile perch of the same size was analysed. The U_{p-c} among these species occurred at significantly different velocities [Fig. 6(a); one-way ANOVA $P < 0.001$, Tukey's test for the comparison of all three groups to each other, $P < 0.001$]. The U_{p-c} in shiner perch was higher than striped

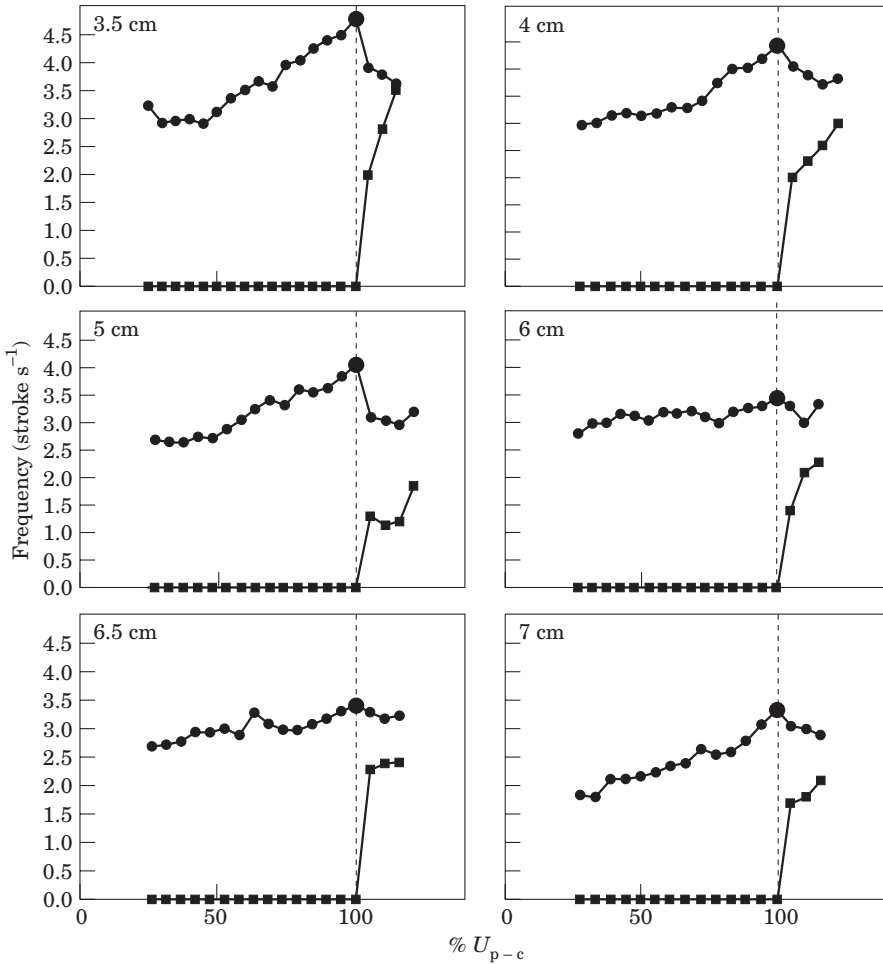


FIG. 3. Pectoral (●) and caudal fin-beat (■) frequencies for *Cymatogaster aggregata* of increasing L_S . The pectoral fin frequency increases with increasing current speed attaining a maximum at U_{p-c} (●), and decreases again once the caudal fin starts to support the pectoral oscillation.

surfperch and pile perch; the latter two species switched from exclusively pectoral fin to caudal-assisted propulsion at lower velocities than for the shiner perch by 15 and 32%, respectively.

Comparison of pectoral fin-beat frequencies at U_{p-c} revealed no significant differences between the species [Fig. 6(b); one-way ANOVA, $P > 0.05$]. In contrast, the amplitude of the pectoral fin was significantly different [Fig. 6(c); one-way ANOVA, $P < 0.001$]. Tukey's *post-hoc* test showed that fin beat amplitude of shiner perch was significantly higher than the other two species ($P < 0.001$ in both cases), but not between striped surfperch and pile perch ($P > 0.05$).

DISCUSSION

The data confirm the importance of the gait transition speed (U_{p-c}) as a performance measure in labriform swimmers. Most studies of swimming

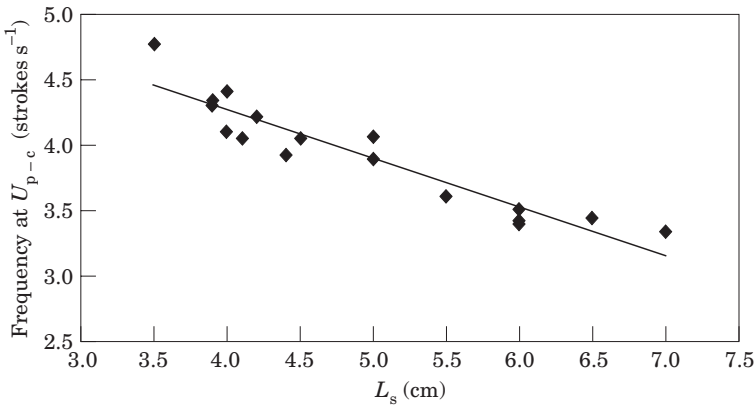


FIG. 4. The relationship between pectoral fin beat frequency at U_{p-c} and L_S in *Cymatogaster aggregata*. The line was fitted by: $y = -0.37x + 5.75$ ($r^2 = 0.88$).

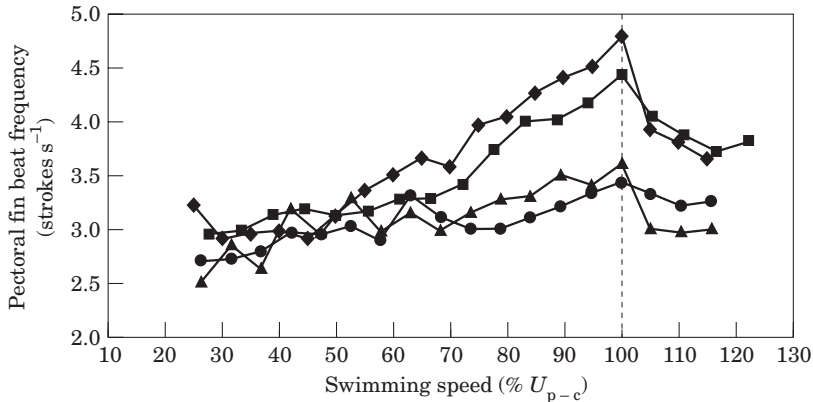


FIG. 5. The relationship between pectoral fin beat frequency and swimming speed for four *Cymatogaster aggregata* of arbitrarily chosen L_S (●, 3.5 cm; ▲, 4.5 cm; ■, 5.5 cm; ◆, 6.5 cm). Frequency is not related to size at slower speeds, but $>70\%$ of U_{p-c} frequency is consistently higher for smaller fish. U_{p-c} is represented by a solid vertical line.

performance have focused on the maximum speed (U_{max}), the critical swimming speed (U_{crit}), the maximum sustained speed (U_{ms}) and the maximum prolonged speed (U_{mp}) (Bainbridge, 1958, 1962; Blaxter, 1969; Pedley, 1976; Wardle, 1977; Weihs, 1977; Beamish, 1978; Webb *et al.*, 1984; Videler, 1993; Domenici & Blake, 1997).

Maximum speed is a measure of the maximum swimming performance fuelled anaerobically; U_{ms} and U_{mp} can be used to reconstruct the endurance curve (Videler, 1993). Maximum sustained speed is the maximum speed that can be sustained aerobically. Critical swimming speed represents a transition speed, and Wilson & Eggington (1994) have shown that anaerobic musculature is recruited at speeds lower than U_{crit} . The gait transition speed represents an equivalent level of exercise which is useful for comparison of performance between fishes of different species and sizes. Drucker (1996) showed that various locomotor parameters, such as advance ratio (a measure of locomotor efficiency

TABLE I. The coefficients and significance of regression analysis of pectoral fin-beat frequency and standard length measured for swimming speeds at increasing intervals up to U_{p-c} , where $U_{p-c} = a + bL_S$ (cm), $n = 10$

U_{p-c}	b	a	r^2	F	P
30%	-0.05154	3.098	0.1673	1.607	>0.1
40%	-0.1442	3.671	0.2392	1.572	>0.1
50%	-0.16283	3.820	0.3276	2.436	>0.1
60%	-0.1277	3.846	0.6659	15.95	<0.01
70%	-0.1571	4.083	0.7446	23.32	<0.01
80%	-0.3351	5.218	0.9489	148.5	<0.001
90%	-0.3833	5.635	0.9469	142.8	<0.001
100% (U_{p-c})	-0.4372	6.097	0.9046	75.87	<0.001

in labriform swimmers), duty factor, and intensity of electromyographic activity were independent of size at U_{p-c} . Therefore, U_{p-c} represents a valid alternative to measuring the locomotor performance of labriform locomotion, as suggested by Drucker & Jensen (1996a). Further work is needed in order to ascertain whether U_{p-c} also represents the upper limits of aerobic activity. Recent work by Korsmeyer *et al.* (2002) on triggerfish *Rhinacanthus aculeatus* (L.) shows that at speeds higher than U_{p-c} oxygen consumption actually increased, showing that for this species U_{p-c} is not a measure of maximum aerobic swimming speed.

The significant correlation between U_{p-c} and L_S (Fig. 2) is similar to the correlation seen between U_{max} and L_S in fishes that normally proceed by caudal undulation. In addition, speed and L_S are more closely correlated as speed approaches U_{p-c} (Table I) indicating that there is a physiological limit to how fast the fish can swim by pectoral undulation alone. These results are the first confirmation of the assertion of Drucker & Jensen (1996a) that the gait transition speed is an important physiological 'breakpoint' for labriform swimmers.

The present study, as in several previous studies on U_{max} , U_{mp} and U_{ms} (Videler, 1993), found that as size increased the absolute U_{p-c} also increased. As in the other studies, when speed is normalized to the length of the fish (U_{p-c} in lengths per second), the speed decreased with increasing size. In fact, the smallest fish showed an U_{p-c} of $4.0 L_S s^{-1}$, while the U_{p-c} of the largest sizes was *c.* $3.0 L_S s^{-1}$, a 25% decrease. This is exactly paralleled by results for striped surfperch (Drucker & Jensen, 1996a,b). The higher relative velocity of small fish has been related to muscle twitch frequencies, which are size and temperature dependent (Wardle, 1975, 1977), and also to decreasing aerobic capacity of the musculature at increasing fish size (Goolish, 1991).

Pectoral fin movement is a kinematically variable parameter among different species, and within species, across a large range of speeds (Gibb *et al.*, 1994; Drucker & Jensen, 1996a; Walker & Westneat, 1997). The fin beat frequency is an important kinematic parameter that was measured across a range of sizes of shiner perch. For each individual fish, the pectoral fin-beat frequency generally increased with speed (Fig. 3), attaining a maximum at U_{p-c} , suggesting that the fin musculature reached a physiological limit, and decreased once the caudal fin

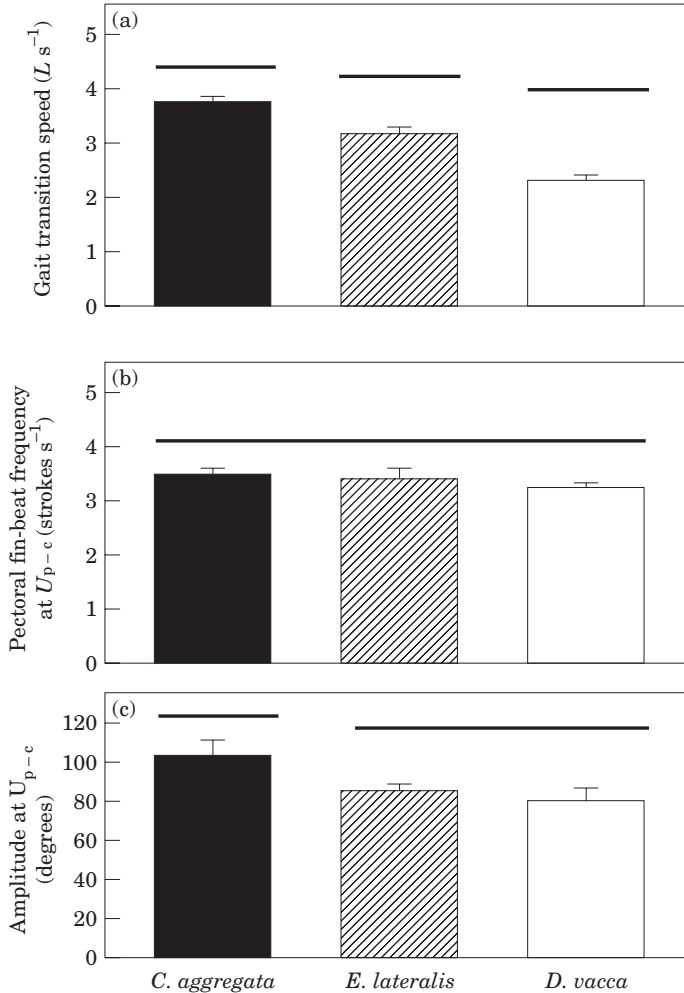


FIG. 6. (a) Relative speed of three embiotocids of similar size, at the gait transition speed (*C. aggregata*: $n=6$, 6.3 ± 0.4 cm L_S ; *E. lateralis*: $n=3$, 6.17 ± 0.28 cm L_S ; *D. vacca*, $n=5$, 6.77 ± 0.26 cm L_S). (b) Pectoral fin beat frequency for three embiotocids of similar size (*C. aggregata*: $n=3$, 6.0 ± 0.5 cm L_S ; *E. lateralis*: $n=3$, 6.1 ± 0.2 cm L_S ; *D. vacca*: $n=3$, 6.7 ± 0.2 cm L_S), at the gait transition speed. (c) Fin beat amplitude at U_{p-c} measured from the same fishes as in (b). In (a), (b), and (c), species united by horizontal lines are not significantly different.

motion started to supplement pectoral oscillation. At U_{p-c} , the pectoral fin-beat frequency was dependent on size: the small fish required higher pectoral fin-beat frequencies (Figs 4 and 5). This was consistent with similar scaling studies on fishes performing equivalent speeds of locomotion (Bainbridge, 1958; Parsons & Sylvester, 1992; Gibb *et al.*, 1994). Such a scaling relationship in shiner perch did not occur at current speeds $<60\%$ of the U_{p-c} . At these speeds, F_p for all sizes remained relatively constant at about three strokes s^{-1} (Fig. 5). A significant increase in F_p in relation to size occurred only at speeds $>60\%$ of the U_{p-c} (Table I).

The independence of pectoral fin beat frequency from length at lower speeds may be related to the underlying swimming behaviour of shiner perch. The

pectoral fin oscillation in shiner perch includes three phases, adduction, abduction and a refractory period; at low speeds each phase has approximately the same temporal proportion. The refractory period depends on swimming speed, and decreases at higher current velocities (Webb, 1973). At *c.* 60% of the U_{p-c} the proportion of time occupied by the refractory phase decreased dramatically (Webb, 1973), and this may be part of the reason why at this speed the pectoral fin beat frequency is size independent.

Drucker & Jensen (1996a) found that $>c.$ 60% U_{p-c} , fin beat amplitude reached a plateau, while fin beat frequency continued to rise. Therefore, amplitude can modulate speed $<60%$ U_{p-c} , while fin beat frequency is the only factor affecting speed $>60%$ U_{p-c} .

At different swimming speeds, Webb (1973) observed two patterns of pectoral fin movements in *C. aggregata*, termed A and B, differing only in length of the wave propagated over the fin. At speeds up to 60% of U_{p-c} , pattern B probably occurs, which is more effective at high current speeds because the fin operates at higher pectoral fin-beat frequencies. Therefore the use of pattern B and the decreasing of the refractory period may be a factor affecting the strength of the relationship between pectoral fin-beat frequency and size.

The gait transition speed also proved to be a useful parameter for evaluating different surfperch ecomorphs. The structural complexity of the natural habitat is related to the swimming performance of fishes (Domenici, 2002), and the three species chosen in the present study vary widely in their preferred habitat. Shiner perch is the most pelagic species, capable of performing relevant vertical migration to depths of *c.* 120 m (Eschmeyer *et al.*, 1983), and seasonal onshore-offshore movements (Morrow, 1980). The striped surfperch represents a species with a broad habitat range, occurring in rocky coasts and kelp beds, but occasionally also in sandy surf near-shore areas. Pile perch are substratum associated species, inhabiting rocky bottom and kelp beds (DeMartini, 1969; Eschmeyer *et al.*, 1983; Ebeling & Laur, 1986). Microhabitat preferences among surfperches correlate with different foraging behaviours (Holbrook & Schmitt, 1992), and these differences are even reflected in photoreceptor sensitivity (Cummings & Partridge, 2001). In short, these fishes inhabit very different environments and this is reflected in the significant differences in gait transition among the three species (Fig. 6). Shiner perch show the highest swimming performance and are the most pelagic species. Pile perch live in structurally complex habitats and show the lowest swimming performance. In such habitats, manoeuvring ability may be more advantageous than steady swimming performance (endurance) (Domenici, 2002). Striped surfperch appear to be a 'generalist' species showing an intermediate swimming performance between the more pelagic shiner perch and the substratum-associated pile perch.

Although the type of habitat could be affected by additional factors (e.g. inter-specific competition, microhabitat availability, food distribution and predation risk), swimming ability differs markedly among the three Embiotocidae, and must be a relevant factor constraining habitat use. These results are consistent with data from other cross species comparisons in other families of labriform swimmers (Bell & Galzin, 1984; Choat & Bellwood, 1985; Wainwright, 1988; Connell & Jones, 1991; Green 1996; Fulton *et al.*, 2001).

Two kinematic variables, fin beat frequency and amplitude, which are important for labriform locomotion for each of the three species, were examined to determine if the variation in U_{p-c} varied with one or both. While there are certainly other important parameters, both kinematic and morphological, the variables chosen are easily measured and have explanatory potential. Fin beat frequency did not vary among species at U_{p-c} , a situation also found in the surf zone specialist, the redbill surfperch *Amphistichus rhodoterus* (Agassiz) (Drucker 1996). The U_{p-c} was highest in shiner perch, intermediate in striped surfperch and lowest in pile perch. The larger fin beat amplitude of the shiner perch when compared to the other two species may partly explain these differences since higher amplitude is one way to increase swimming performance at a given fin beat frequency. Amplitude, however, was measured only in the horizontal plane, and it is possible that differences in 'flapping' angles between species may affect the results. Further underlying mechanisms explaining performance differences may lie in other kinematic parameters, or more likely, in differences in fin morphology such as shape and angle of insertion. Yet another possible explanation lies in the physiology and morphology of the fin musculature. It is possible that pile perch have reduced performance relative to the other two species because of a conflict between two functional parameters. Pile perch are strong crushers, supplied with large pharyngeal musculature. Hypertrophy of this musculature reduces the space for gill tissue, making it more difficult for these fish to sustain a high level of aerobic exercise (J. Jensen, pers.comm.).

Shiner perch are mature at 7 cm L_S , the length tested, while the other two species are still juveniles. This difference may have affected the results though there is no evidence that maturity affects swimming performance independently of size.

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