The paired fins of bony fishes have long been considered critical components of the locomotor system (Schmalhausen, 1916; Breder, 1926; Harris, 1953; Aleev, 1969) yet comparatively little attention has been given to the musculoskeletal mechanics of paired-fin-based propulsion in this group. The role of appendicular musculature in fin control during swimming has been hypothesized from analysis of anatomical lines of action (e.g. Williamson, 1893; Jessen, 1972; Geerlink, 1989). Detailed patterns of fin movement, and their hydromechanical significance, have also been described (Magnan, 1930; Harris, 1937, 1938; Webb, 1973; Geerlink, 1983; Fricke and Hissmann, 1992; Gibb et al. 1994) but in the absence of correlated patterns of muscular activity. Apart from the preliminary work of Lauder (1995) and Westneat (1996), the functional connection between paired fin anatomy and kinematics (i.e. how muscles work to produce propulsive fin movements) has yet to be investigated directly in freely swimming fish.

The objective of this study was to examine the kinematics and neuromuscular control of the pectoral fins during labriform locomotion, a swimming mode exhibited by an enormous diversity of perciform fishes (Breder, 1926; Lindsey, 1978; Blake, 1983). Within this broad categorization, a number of mechanically distinct pectoral fin swimming modes exist. ‘Generalized’ labriform swimming (i.e. largely drag-based propulsion) is exhibited by both short-bodied forms, such as the Centrarchidae (Gibb et al. 1994) and Cichlidae (Blake, 1979), and long-bodied forms (Nototheniidae: Archer and Johnston, 1989). In these groups, the pectoral fins are used for propulsion over a relatively narrow range of low swimming speeds. By contrast, we aimed to characterize the specialized ‘embiotociform’ gait, named by Webb (1994) for the surfperches. Owing to the similar functional demands placed on the pectoral fins of many fishes, it is probable that the mechanistic details of embiotociform swimming are widely distributed within the Perciformes.

In spite of their phylogenetic and ecological divergence, the surfperches exhibit a number of mechanistic similarities which probably characterize the family. The timings of kinematic events and the maximal excursions of the fin tip, as well as the temporal order of muscle activation and the time to peak activity, are largely conserved. The predominant dorsoventral component of fin movement during the stride is consistent with a lift-based mechanism of propulsion. E. lateralis exhibits a greater anteroposterior range of motion and a more continuous period of fine motor control of the fin than A. rhodoterus, differences which may correspond to the species’ respective capacities for maneuvering. Mechanistic variation in the family is associated with rather minor structural differences (in fin shape and fin base orientation). Owing to the similar functional demands placed on the pectoral fins of many fishes, it is probable that the mechanistic details of embiotociform swimming are widely distributed within the Perciformes.

Key words: Embiotocidae, surfperch, Embiotoca lateralis, Amphistichus rhodoterus, pectoral fin locomotion, swimming, kinematics, electromyography.

Summary

The musculoskeletal mechanism of pectoral fin propulsion was investigated in representatives of the two subfamilies of the Embiotocidae (surfperches). Kinematic and electromyographic records of steady swimming by the open-water cruiser Amphistichus rhodoterus and the benthic maneuverer Embiotoca lateralis were compared at 80% of the species’ respective pectoral–caudal gait transition speeds. Synchronized records of fin movement and the intensity of pectoral muscle activity allowed previous hypotheses of muscle function, based on anatomical lines of action, to be tested. Divisions of the pectoral musculature inserting on the central and trailing-edge fin rays serve simple functions of abduction and adduction. Muscles controlling the fin’s leading edge, by contrast, play more complex roles during the fin stroke, including deceleration of the fin at the downstroke–upstroke transition and rotation of the adducted fin during the non-propulsive period between fin beats.

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surfperches (Embioticidae). This swimming mode is thought to involve primarily lift-based propulsion and is used as the primary means of locomotion over a wide range of speeds (Webb, 1973, 1993; Drucker and Jensen, 1996a,b). A similar mode is employed by members of the closely related Labridae (Westneat, 1996) and is probably important in other perciform families (e.g. Chaetodontidae, Pomacanthidae, Acanthuridae).

Rather than describe the mechanism of labriform swimming for a single species, we chose to study representatives of the two subfamilies within the Embiotocidae: the Amphistichinae, open-water cruisers that feed from the water column above structurally simple substrata, and the Embiotocinae, benthic maneuverers that feed from algal or rocky substrata (cf. Drucker, 1996). This subfamilial division represents the basal split within the Embiotocidae (Tarp, 1952; Jensen, 1993). Through an analysis of functional similarities between ecologically and phylogenetically divergent species, we attempted to infer the locomotor mechanism characteristic of the family. Mechanistic differences were interpreted in the light of the species’ distinct phylogenetic associations, as well as their divergent habitats and associated swimming behaviors.

Comparison of these taxa focused on (1) three-dimensional patterns of movement of the pectoral fin, (2) timing patterns of muscle activation, and (3) profiles of the intensity of muscular activity during steady swimming. Analysis of synchronized electromyographic and kinematic records allowed testing of hypotheses of pectoral muscle function based on observation of myological architecture.

Materials and methods

The substratum-associated striped surfperch Embiotoca lateralis Agassiz was collected by beach seine at Argyle Bay, San Juan Island, WA, USA, and the open-water redtail surfperch Amphistichus rhodoterus Agassiz by hook and line at Neah Bay, WA, USA. Fishes were maintained at the University of Washington’s Friday Harbor Laboratories in flow-through seawater tanks at 12 °C. Anatomical observations were made from fresh, formalin-preserved and cleared and stained specimens.

To control for size-related differences in swimming ability (see Drucker and Jensen, 1996a,b), similarly sized individuals of the two species (22.7–24.4 cm standard length, SL) were selected for study. These animals swam in the working area (34 cm wide×25 cm deep×80 cm long) of a large racetrack-shaped flow tank (Nowell et al. 1989). Collimation of the water current, determination of its velocity profile within the working area, and calibration of the paddle-wheel drive system are described elsewhere (Drucker and Jensen, 1996a).

In contrast to previous comparative studies of swimming mechanics, this paper focuses on the patterns of fin movement and muscle activity that occur in the two species at a fixed percentage of the pectoral-caudal gait transition speed (U_{p-c}). Earlier work (Drucker, 1996) has shown that the traditional approach of comparing ecologically distinct taxa at a given body-length-specific speed may not fully correct for differences in swimming ability. Here, the surfperches are compared at approximately 80% U_{p-c}, a high labriform cruising speed and one at which like-sized individuals of the two species should be at similar levels of exercise. Within the 23–24 cm size class, U_{p-c} is 2.40 SLS^{-1} on average for A. rhodoterus and 1.87 SLS^{-1} for E. lateralis (Drucker, 1996), and thus the species are compared below at 2.0 SLS^{-1} (83.3% of mean U_{p-c}) and 1.5 SLS^{-1} (80.2% of mean U_{p-c}), respectively.

Video image acquisition and analysis

Surfperches were video-taped during labriform locomotion simultaneously in dorsal and lateral views using Sony video cameras (60 fields s^{-1}; 1/2000 s shutter speed). A Panasonic digital video mixer (WJ-AVES) synchronized and combined partial fields from the dorsal and lateral S-VHS video signals. The resulting split-screen images were recorded through a Panasonic WJ-810 time–date generator to a Panasonic AG-1970 video cassette recorder.

Video tapes were reviewed for scenes of steady swimming in which the subject’s body and fins remained at least 5 cm from the walls of the working area. Individuals whose normal fin movements appeared altered by the surgical implantation of electrodes in the pectoral musculature (as described below) were excluded from the study group. Since the left and right pectoral fins oscillate synchronously in E. lateralis and A. rhodoterus at 80% U_{p-c}, patterns of fin movement were examined unilaterally. To improve their visibility, the pectoral fin tips were marked with small opaque spots of cyanoacrylate adhesive gel mixed with chalk dust. The position of the left fin marker in dorsal and lateral views was digitized using Image for Macintosh, version 1.51 (National Institutes of Health, USA) from individual video fields stored digitally with a Hotronics AP41-SF time base corrector.

Five complete pectoral fin stroke cycles were analyzed for each of three individuals per species from which anteroposterior, mediolateral and dorsoventral fin tip excursions were quantified. All excursions were measured as a percentage of head length (HL, the distance from the anterior angle of the dorsal head of the maxilla to the posterior margin of the operculum). Standardization of linear fin tip displacements to % HL minimized the measurement error that arises from the use of distance scales placed outside the immediate area in which the fin moves (e.g. a background centimeter grid). The video image sample rate of 60 Hz provided sufficient temporal resolution (24–41 fields per stride cycle) for three-dimensional reconstruction of the fin tip path. Following each experiment, a digital image of the subject’s left lateral aspect was collected to allow measurement of the aspect ratio of the pectoral fin (length^2/area) and the angle of the fin base with respect to the longitudinal axis of the body.

Electromyography

Patterns of electrical activity in the muscles investing the pectoral fin (Fig. 1) were recorded using fine-wire bipolar hook electrodes (Loeb and Gans, 1986). The electrodes were made from steel alloy wire (Evanohm S, 0.051 mm in diameter).
whose ends were bared for approximately 0.5 mm and laid 1 mm apart inside the tips of 27 gauge hypodermic needles. Small intercontact spacing was used to increase the selectivity of the electrodes during recording and reduce the potential for cross-talk with nearby muscles. An additional length of insulated wire (approximately 5 cm) with a small recurved tip was loaded into the barrel of each needle to serve as an independent marker of the muscle implantation site. This marker is designed to maintain its position upon tension on the electrode cable and migration of the tips (P. Motta, personal communication), as was often unavoidable at the end of each experiment when the subject was netted and removed from the flume. Following swimming trials, fishes were killed by an overdose of tricaine methanesulfonate (MS-222). Through post-mortem dissection, it was possible to verify the original locations of all the electrodes during recording.

With the fish under anesthesia (dilute solution of MS-222 in sea water), wire triplets (electrode + marker) were inserted percutaneously into the target muscles of the left fin. An effort was made to have the bipolar axis of each electrode parallel to the muscle fiber orientation (Loeb and Gans, 1986). Long needles (3.2 cm) were used to allow access to the deep adductors. The proper level of anesthesia was maintained by periodically flushing the gills with anesthetic or fresh sea water adductors. The proper level of anesthesia was maintained by periodically flushing the gills with anesthetic or fresh sea water as necessary. After implantation, each marker wire was trimmed to the skin surface, and the electrodes were glued into a single cable which was sutured (6-0 gauge silk) to the skin immediately posterior to the fin base and again dorsal to the lateral line. The fin tips were marked as described above, and the subject was allowed to recover in the working area of the flume for 1–2 h.

Electromyograms (EMGs) were recorded onto a TEAC multi-channel tape recorder at 19 cm s^{-1} (frequency response d.c. to 5000 Hz). The trailing ends of the electrodes were inserted into high-impedance probes and shielded from a.c. interference by a grounded wire cage. Signals were amplified 5000–20000 times by Grass P511J differential preamplifiers with 60 Hz notch filters and a bandpass of 100 Hz to 10 kHz. To allow correlation of electromyographic signals with the video record, a circuit was used to generate a square-wave synchronization pulse which was recorded by the TEAC tape recorder and which simultaneously powered a light-emitting diode within the video field.

In addition to meeting the kinematic criteria outlined above, the five fin strokes per individual selected for quantitative electromyographic analysis had a high EMG signal:noise ratio, which reduced the error involved in determining the onset and offset of muscle activity. Signals degraded by low-frequency motion artifact (e.g. from mechanical disturbance of the electrode cable) were not included in the analysis. EMGs recorded from adjacent muscles were inspected for correlation in timing and spike profile in order to test for the presence of cross-talk between electrodes (see Manguin et al. 1986).

Digital conversion of analog EMGs was performed using MacADIOS II hardware (12-bit accuracy) on a Power Macintosh 7100. The sample rate used (8333 Hz) is within the range which allows high-fidelity reproduction of vertebrate EMGs and accurate quantification of the intensity of muscle activity (Jayne et al. 1990). An analysis program was written with SuperScope II software (GW Instruments, Inc., Somerville, MA, USA) to measure the intensity (rectified integrated area) of each 5 ms bin comprising a digital EMG burst. Binwise analysis of EMG intensity \(I_{EMG}\) allowed the construction of average muscle activity profiles for each individual. The onsets and offsets of muscle activity were selected using an on-screen cursor. Because the sample period of analog-to-digital conversion was small (0.12 ms) relative to the video framing period (16.7 ms), the rising edge of the synchronization pulse could not be determined with equal accuracy in electromyographic and video records. The error associated with temporal correlation of EMGs and video events was no greater than 16.7 ms.

**Statistical analyses**

From selected sequences of the synchronized kinematic and electromyographic recordings, the following variables were measured: for each fin stroke, the maximal anteroposterior, mediolateral and dorsoventral excursions of the fin tip, and the timings of the events illustrated in Fig. 2 (fin positions b–f); for each pectoral muscle, the onset and offset of electrical activity, and the time at which the greatest intensity of activity in a 5 ms bin was recorded \(t_{max}\). Since \(HL\) was not significantly different in similarly sized individuals of the two species (Table 1), direct comparison between \(E.\ \text{lateralis}\) and \(A.\ \text{rhodoterus}\) of maximal excursion variables (% \(HL\)) was possible. The timings of kinematic and electromyographic events were measured relative to the onset of fin abduction (i.e. when the fin tip reaches its most dorsal position prior to the downstroke; see Fig. 2, a). For the purpose of interspecific comparison, timings were standardized to a percentage of the stride period, \(T\), defined as the time between consecutive onsets of fin abduction.

Two-level nested analyses of variance (ANOVAs) were conducted to test for significant variation in these variables between species and among individuals within species (SuperANOVA software, Abacus Concepts, Inc., Berkeley, CA, USA). F-statistics for the fixed effect (species) were calculated by dividing the species mean square value by that of the random effect (individual). The effect of individuals within species was tested over the residual (Sokal and Rohlf, 1981). Significance was evaluated at the \(P<0.01\) level because multiple comparisons were made for each fin stroke (cf. Lauder and Shaffer, 1988).

**Results**

**Anatomy**

The embiotociform mode of swimming is not associated with gross anatomical specializations of the pectoral girdle or fin musculature. As in the generalized teleost condition, the pectoral fin of surfperches is invested by two primary muscle masses: the abductors on the lateral surface of the pectoral...
girdle and the adductors on the medial surface (Fig. 1; see also Pychlau, 1908; Shann, 1920; Grenholm, 1923; Starks, 1930; Jessen, 1972; Winterbottom, 1974; Geerlink, 1989).

The adductor superficialis (Fig. 1A) extends from the flange of the anterolateral cleithrum to the base of the pectoral fin. Individual fascicles of this muscle insert tendinously onto the lateral bases of the central and trailing-edge fin rays (2–23 in Embiotoca lateralis; 2–27 in lateral bases of the central and trailing-edge fin rays (2–23 in Amphistichus rhodoterus). The arrector ventralis (Fig. 1B) is a strap-like muscle that originates from the anterolateral cleithrum and converges into a stout tendon which inserts onto the anteromedial surface of the expanded base of the first fin ray. The truncated first ray together with the second ray comprise the anterior margin, or leading edge, of the pectoral fin. The adductor profundus (Fig. 1A,B) is the largest of the laterally situated muscles, originating broadly from the lateral coracoid and the connective tissue between the ventral tips of the cleithrum and coracoid, and inserting tendinously onto the lateral bases of all but the most posterior two fin rays. Divisions of the adductor profundus that insert onto the first two fin rays are separate along their entire length from the rest of the muscle. Portions serving the remainder of the fin form progressively less discrete muscle bundles towards the fin’s trailing edge (Fig. 1B).

The architecture of the pectoral adductors is grossly similar to that of the corresponding abductor muscles. The arrector dorsalis and adductor profundus are roughly parallel in orientation to their lateral antagonists (cf. Fig. 1B,C). The former arises from the anteroventral part of the medial surface of the cleithrum to insert by a very short tendon onto the medial base of the first fin ray (Fig. 1D). The latter originates from the medial coracoid and ventromedial cleithrum and attaches via tendons to the posteromedial bases of the central lepidotrichia.

The adductor radialis, arising from the posterior margin of the last radial, inserts onto the trailing-edge fin rays not served by the adductor profundus (Fig. 1D). The adductor superficialis (Fig. 1C,D) differs in orientation from its lateral counterpart. The superficial adductor is comprised of two continuous sections, arising from the anteromedial cleithrum, with distinct lines of action. The dorsal portion of the adductor superficialis serves the posterior fin rays (5–23 in E. lateralis; 5–27 in A. rhodoterus; Fig. 1C, adductor superficialis posterior) and ‘crosses over’ the ventral portion of the muscle, which serves the anterior rays (2–4 in both E. lateralis and A. rhodoterus; Fig. 1D, adductor superficialis 2,3,4) (cf. Winterbottom, 1974). At their extremes in orientation, the fibers of these two muscle regions run almost at right angles to one another. Both portions of the muscle insert via tendons onto the anteromedial surface of the lepidotrichia, well distal to the fin ray bases (Fig. 1C,D).

Although activity in the arrector dorsalis, which serves the marginal fin ray (Fig. 1D), was not recorded in this study, implantation of the divisions of the adductor superficialis serving fin rays 2 and 3 (Fig. 1D, AD.S. 2,3) allowed investigation of the neuromuscular control of the pectoral fin’s leading edge during aduction.

In spite of their distinct swimming habits in nature, A. rhodoterus and E. lateralis show no obvious differences in pectoral osteology or myology. The species do differ

### Table 1. Summary of kinematic and electromyographic variables measured from Embiotoca lateralis and Amphistichus rhodoterus during embiotociform locomotion

<table>
<thead>
<tr>
<th>Variable</th>
<th>E. lateralis</th>
<th>A. rhodoterus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximal dorsoventral excursion of fin tip (% HL)</td>
<td>139.2±0.97</td>
<td>145.9±2.60</td>
</tr>
<tr>
<td>Maximum mediolateral excursion (% HL)</td>
<td>71.9±2.66</td>
<td>65.8±3.24</td>
</tr>
<tr>
<td>Maximum anterior excursion (% HL)</td>
<td>32.5±2.22</td>
<td>6.0±1.33</td>
</tr>
<tr>
<td>Maximum posterior excursion (% HL)</td>
<td>49.8±1.87</td>
<td>12.6±1.49</td>
</tr>
<tr>
<td>Stride period, T (ms)</td>
<td>598.9±13.05</td>
<td>447.7±10.78</td>
</tr>
<tr>
<td>Time to mid-downstroke, b (% T)</td>
<td>23.6±0.76</td>
<td>21.0±0.99</td>
</tr>
<tr>
<td>Time to downstroke–upstroke transition, c (% T)</td>
<td>39.1±0.80</td>
<td>41.3±1.35</td>
</tr>
<tr>
<td>Time to mid-upstroke, d (% T)</td>
<td>52.6±0.99</td>
<td>54.5±1.77</td>
</tr>
<tr>
<td>Time to end upstroke, e (% T)</td>
<td>63.0±0.92</td>
<td>75.6±1.44</td>
</tr>
<tr>
<td>Time to mid-pause, f (% T)</td>
<td>74.0±1.07</td>
<td>88.6±1.61</td>
</tr>
<tr>
<td>Arrector ventralis t\textsubscript{max} (% T)</td>
<td>–5.7±0.75</td>
<td>–7.5±0.98</td>
</tr>
<tr>
<td>Abductor superficialis t\textsubscript{max} (% T)</td>
<td>–3.2±0.93</td>
<td>–6.9±0.70</td>
</tr>
<tr>
<td>Abductor profundus t\textsubscript{max} (% T)</td>
<td>–2.0±0.93</td>
<td>–4.6±0.55</td>
</tr>
<tr>
<td>Adductor superficialis 2,3 t\textsubscript{max} (% T)</td>
<td>47.5±2.10</td>
<td>45.3±1.72</td>
</tr>
<tr>
<td>Adductor profundus t\textsubscript{max} (% T)</td>
<td>45.3±1.19</td>
<td>47.5±1.53</td>
</tr>
</tbody>
</table>

Three individuals per species; five fin beats per individual. Measurements reported as mean ± S.E.M. pooled within species (N=15).

Maximal posterior excursion measured relative to fin position at end of propulsive period; other maxima measured relative to fin position at onset of propulsive period. Mean HL ± s.d. = 6.4±0.24 and 6.3±0.29 cm for E. lateralis and A. rhodoterus, respectively (not significantly different, t-test, d.f.=9).

Letters following timing variables (b–f) correspond to the kinematic events labeled in Fig. 2; all timings are measured relative to the start of downstroke (Fig. 2, a). The time to the end of upstroke (e) is equivalent to the propulsive period, T\textsubscript{pr}.

HL, head length; T, stride period; t\textsubscript{max}, time to peak EMG activity.
Fig. 1. Pectoral girdle and associated musculature of *Embiotoca lateralis*. (A) Right lateral aspect. (B) Same, abductor superficialis removed. (C) Right medial aspect. (D) Same, adductor superficialis posterior removed. Gross anatomical differences between *E. lateralis* and *Amphistichus rhodoterus* in the pectoral region were not observed. AB.S., abductor superficialis; AB.P., abductor profundus; AB.P. 1,2, divisions of abductor profundus serving the first two fin rays; ARR.V., arrector ventralis; AD.S. 2,3,4, ventral portion of adductor superficialis serving fin rays 2–4; AD.S. post., dorsal portion of adductor superficialis serving posterior fin rays; AD.P., adductor profundus; ARR.D., arrector dorsalis; AD.R., adductor radialis; CL, cleithrum; COR, coracoid; R₁, first pectoral fin ray. Activity in ARR.D. and AD.R. was not examined in this study.
conspicuously, however, in fin shape and fin base orientation. The open-water *A. rhodoterus* has a significantly longer, more slender fin than the substratum-associated *E. lateralis* (mean aspect ratio ± s.d. = 2.8±0.26 and 1.8±0.15, respectively; *t*-test, d.f.=6, *P*<0.001). The orientation of the fin base relative to the longitudinal axis of the body is significantly lower (*P*<0.05) in *A. rhodoterus* (26±3.9°) than in *E. lateralis* (36±5.3°) (cf. Fig. 2A,B).

**Patterns of fin movement**

The pectoral fin stroke of *Embiotoca lateralis* is qualitatively similar to that of the closely related surfperch *Cymatogaster aggregata* (Webb, 1973). Downstroke is initiated by abduction of the anterior margin of the pectoral fin, which precedes movement of the trailing fin rays (Fig. 2A, a). As the fin peels away from the body, the tip is depressed and protracted. At mid-downstroke, the fin appears distinctly bowed in lateral view, and the leading edge is inclined at a slight angle to the incident current (Fig. 2A, b). Upstroke begins similarly with elevation and retraction of the leading edge and ends as the remainder of the fin assumes an adducted position (Fig. 2A, c–e). This period of propulsive fin movements (*T*<sub>pr</sub>) is followed by a kinematic pause period during which the fin rotates posteriorly and ventrally while pressed against the body (Fig. 2A, e–f). In preparation for the next stroke, the adducted fin then rotates anteriorly and dorsally (Fig. 2A, f–a).

*Amphistichus rhodoterus* exhibits the same sequence of pectoral fin excursions with minor variations in the three-dimensional path of the fin tip (Fig. 2B). The relative degree of dorsoventral and mediolateral fin tip excursion during the propulsive period is not significantly different in the two species (Fig. 3A,B; Table 2). The kinematic profile of *E. lateralis* is, however, characterized by significantly greater fin protraction (by 26 % *HL*, on average) during the downstroke (cf. Fig. 2A,B, a–c in dorsal view; see Tables 1, 2). In addition, *E. lateralis* exhibits asymmetrical anteroposterior fin excursions: the fin tip is retracted during the upstroke on average by 17 % *HL* more than it is protracted during the downstroke (Fig. 3A; Table 1). *A. rhodoterus*, by contrast, protracts and retracts the fin tip more equally (approximately 6–12 % *HL*; Fig. 3B).

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**Fig. 2.** Lateral and dorsal views of the pectoral fin strokes of *Embiotoca lateralis*, a benthic maneuverer (A), and *Amphistichus rhodoterus*, an open-water cruiser (B). The timings of electromyographic activity and kinematic events (fin positions b–f) were measured relative to the onset of the downstroke (a, at left). Both species exhibit a predominant dorsoventral component of fin movement. By virtue of a more obliquely oriented fin base, *E. lateralis* is capable of greater anteroposterior fin excursions than *A. rhodoterus* (cf. A and B in dorsal view: degree of fin protraction, a–c, and retraction, d–f).
The timings of kinematic events during the downstroke also show interspecific similarities. The fin tip reaches its most lateral and ventral positions (Fig. 2, b,c, respectively) at non-significantly different proportions of the stride periods of the two species (Table 2). The upstroke, however, is executed more rapidly in *E. lateralis*, such that remaining kinematic events (Fig. 2, e–f) occur relatively sooner (Table 2; cf. Fig. 3A,B). Accordingly, the percentage of the stride period occupied by propulsive fin movements \( \left( \frac{T_{pr}}{T} \times 100 \right) \) is lower in *E. lateralis* than in *A. rhodoterus* (by an average of 13 %: Fig. 3A,B; Table 1). At 80 % \( U_{p-c} \), the species use fin beat frequencies (mean ± S.D.) of 1.7 ± 0.14 and 2.2 ± 0.20 Hz, respectively.

**Patterns of muscular activity**

Pectoral fin movements observed during swimming in the surfperches are generated by a temporally conservative pattern of muscle activation (Fig. 4; Table 3). The timings of the onsets and offsets of pectoral EMGs, measured relative to the onset of fin downstroke, were pooled among the three individuals of each species and used to construct summary diagrams of the mean duration of muscle activity (Fig. 5). For some muscles, these timings show significant interindividual variation (Table 3), but the differences among fish of each species are minor (Fig. 5).

Contraction of the arrector ventralis initiated every fin stroke analyzed, although the lag time between the onset of activity in this muscle and the onset of activity in the next abductor to fire is consistently greater in *E. lateralis* (Fig. 4, 5). Activity in the superficial and deep abductors begins nearly simultaneously in both species and ends significantly earlier in *A. rhodoterus* (Fig. 4; Table 3). The upstroke is preceded by contraction of the adductor superficialis 2,3. In *E. lateralis*, two out of three individuals displayed a brief burst of activity in this muscle during the end of abductor activity (Figs 4, 5). In the other striped surfperch and in all of the redtail surfperch studied, activity in the adductor superficialis 2,3 was limited to a second, prolonged contraction (duration approximately 35–90 % \( T \)). The other adductors show more consistent patterns of firing: the adductor superficialis posterior was inactive at 80 % \( U_{p-c} \) (despite being successfully implanted), and the adductor profundus contracted during the initial phase of fin upstroke. The offset of the latter muscle occurs significantly

### Table 2. F-statistics from nested analyses of variance conducted on kinematic variables measured from *Embiotoca lateralis* and *Amphistichus rhodoterus*

<table>
<thead>
<tr>
<th>Variable</th>
<th>Between species d.f.=1</th>
<th>Among individuals d.f.=3–4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum dorsoventral excursion of fin tip (% HL)</td>
<td>1.04</td>
<td>21.50**</td>
</tr>
<tr>
<td>Maximum mediolateral excursion (% HL)</td>
<td>0.57</td>
<td>6.88**</td>
</tr>
<tr>
<td>Maximum anterior excursion (% HL)</td>
<td>22.10*</td>
<td>23.00**</td>
</tr>
<tr>
<td>Maximum posterior excursion (% HL)</td>
<td>147.80**</td>
<td>1.78</td>
</tr>
<tr>
<td>Stride period, ( T ) (ms)</td>
<td>21.66*</td>
<td>6.65**</td>
</tr>
<tr>
<td>Time to mid-downstroke, ( b ) (% ( T ))</td>
<td>1.83</td>
<td>3.08</td>
</tr>
<tr>
<td>Time to downstroke–upstroke transition, ( c ) (% ( T ))</td>
<td>2.55</td>
<td>0.70</td>
</tr>
<tr>
<td>Time to mid-upstroke, ( d ) (% ( T ))</td>
<td>0.32</td>
<td>4.19</td>
</tr>
<tr>
<td>Time to end upstroke, ( e ) (% ( T ))</td>
<td>25.15*</td>
<td>1.92</td>
</tr>
<tr>
<td>Time to mid-pause, ( f ) (% ( T ))</td>
<td>57.90*</td>
<td>0.63</td>
</tr>
</tbody>
</table>

*P\( \leq 0.01 \); **P\( \leq 0.001 \).

Abbreviations as in Table 1.

### Table 3. F-statistics from nested analyses of variance conducted on electromyographic variables measured from *Embiotoca lateralis* and *Amphistichus rhodoterus*

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Between species d.f.=1</th>
<th>Among individuals d.f.=3–4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arrector ventralis (% ( T ))</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onset</td>
<td>1.07</td>
<td>4.98*</td>
</tr>
<tr>
<td>Offset</td>
<td>1.35</td>
<td>13.97**</td>
</tr>
<tr>
<td>( t_{max} )</td>
<td>0.57</td>
<td>6.88**</td>
</tr>
<tr>
<td>Abductor superficialis (% ( T ))</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onset</td>
<td>1.90</td>
<td>10.56**</td>
</tr>
<tr>
<td>Offset</td>
<td>9.68*</td>
<td>10.02**</td>
</tr>
<tr>
<td>( t_{max} )</td>
<td>4.29</td>
<td>3.00</td>
</tr>
<tr>
<td>Abductor profundus (% ( T ))</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onset</td>
<td>13.18</td>
<td>0.61</td>
</tr>
<tr>
<td>Offset</td>
<td>27.71*</td>
<td>0.46</td>
</tr>
<tr>
<td>( t_{max} )</td>
<td>4.38</td>
<td>1.35</td>
</tr>
<tr>
<td>Adductor superficialis 2,3 (% ( T ))</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onset</td>
<td>8.57</td>
<td>1.36</td>
</tr>
<tr>
<td>Offset</td>
<td>0.26</td>
<td>4.41</td>
</tr>
<tr>
<td>( t_{max} )</td>
<td>0.16</td>
<td>5.52*</td>
</tr>
<tr>
<td>Adductor profundus (% ( T ))</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onset</td>
<td>0.87</td>
<td>1.58</td>
</tr>
<tr>
<td>Offset</td>
<td>51.15*</td>
<td>0.49</td>
</tr>
<tr>
<td>( t_{max} )</td>
<td>0.62</td>
<td>2.68</td>
</tr>
</tbody>
</table>

*P\( \leq 0.01 \); **P\( \leq 0.001 \).

Abbreviations as in Table 1.
Fig. 3. Profiles of fin movement and pectoral muscle activity during embiotociform swimming at 80% of the pectoral–caudal gait transition speed. Fin tip excursions (expressed as a percentage of head length, HL) and intensity of muscular activity (rectified integrated EMG area: $I_{EMG}$) are shown as means ± S.E.M. for five consecutive strides of a representative individual of each species. Arrows indicate the direction of fin tip movement in three dimensions (0% HL = position of anterior angle of pectoral fin base). $I_{EMG}$ values are for the unamplified signal. Dotted lines designate the mean timings of kinematic events (a–f, see Fig. 2). (A) Embiotoca lateralis (HL=6.3 cm). Note the relatively high-intensity activity in the abductors superficialis and profundus through mid-downstroke (b) and in the adductor profundus through the end of
the propulsive period (e). At no point during the average stride period are all the pectoral muscles silent. (B) *Amphistichus rhodoterus* (*HL*=6.4 cm). Note that abductor activity is concentrated in the period preceding the onset of downstroke (a) and becomes greatly diminished thereafter. Between the middle and end of downstroke (b–c), a period of 40–80 ms elapses during which none of the studied pectoral muscles is active. The adductor profundus becomes silent soon after mid-upstroke (d). See text for discussion. No activity was recorded in the adductor superficialis posterior. Muscle abbreviations as in Fig. 1. P, posterior; A, anterior; L, lateral; M, medial; D, dorsal; V, ventral; T, stride period.
upstroke. The offset of the latter muscle occurs significantly later in *E. lateralis* (Fig. 5; Table 3).

Analysis of the intensity of electromyographic activity, in addition to onset and offset, was critical to the interpretation of pectoral muscle function. Since the intensity of the electrical signal detected by bipolar electrodes can vary substantially with slight differences in electrode orientation within a muscle (Loeb and Gans, 1986), interspecific comparison of absolute $I_{\text{EMG}}$ was not undertaken here. Instead, average profiles of contraction intensity were examined (Fig. 3A,B).

*E. lateralis* and *A. rhodoterus* exhibit no significant differences in the timing of peak muscle activity (Table 3, $t_{\text{max}}$), but show important differences in $I_{\text{EMG}}$ profile. In both species, the motor pattern is initiated by a high-intensity burst of activity in the arrector ventralis. This muscle is recruited 40–70 ms before the onset of abduction of the leading edge of the fin. During the period of propulsive fin movements which follows, the ventral arrector exhibits a greatly diminished $I_{\text{EMG}}$ (Fig. 3A,B). The activity profiles of the abductors superficialis and profundus in *E. lateralis* are roughly symmetrical in shape and maintain broad peaks after maximum activity is attained by the arrector ventralis (Fig. 3A). By contrast, in *A. rhodoterus*, these muscles show skewed profiles like that of the arrector ventralis; all three abductors show their most concentrated activity at approximately the same time (Fig. 3B). Low-level activity in the adductor superficialis 2,3 begins up to 105 ms before the onset of the upstroke in *E. lateralis* (Fig. 3A, c). In *A. rhodoterus*, the mean electromechanical delay is 10 ms. Bimodal activity follows in both species, with $I_{\text{EMG}}$ peaks occurring before the fin reaches its most lateral and dorsal positions (Fig. 3A,B, d,e, respectively). The deep adductor fires as the fin begins moving dorsally and continues high-intensity contraction through mid-upstroke. In *E. lateralis*, this muscle remains active until the end of the propulsive period (Fig. 3A, e).

Highly amplified electromyographic recordings from small muscles are prone to degradation by cross-talk from electrical activity in adjacent muscles (O’Donovan *et al.* 1982; Mangun *et al.* 1986). To assess whether the signals recorded in this study were contaminated by cross-talk, raw EMGs for the abductor and adductor muscle groups were inspected for coincidence in timing (correlated onset and offset of activity) and similarity in spike profile (see Loeb and Gans, 1986). Although the pectoral abductors appear to fire simultaneously at the beginning of downstroke (Fig. 4), invariant phase relationships in the onset of the muscles’ activity were present in both species (Fig. 5). Abductor offsets, and adductor activity in general, showed pronounced temporal differences within individuals. In addition, consistent correlation in the shape and polarity of EMG waveforms across channels was not discernible (Fig. 4). Thus, we believe that the electrodes used in this study sampled from distinct populations of motor units and that the recorded EMGs accurately represent the electrical activity within the pectoral musculature.

### Discussion

#### Inference of muscle function

Inspection of the bony origins and insertions of the appendicular musculature reveals potential lines of action along which the paired propulsors may move during locomotion. Recent studies of vertebrate locomotor mechanics (e.g. Dial, 1992; Jayne and Lauder, 1995; Reilly, 1995) have emphasized, however, that additional analysis of the timing and intensity of muscular activity is required for the inference of complex muscle function. Summaries of EMG onset and offset (e.g. Fig. 5) illuminate periods during the stride in which the locomotor muscles may influence propulsive kinematics. $I_{\text{EMG}}$ analysis provides important additional information about the roles muscles play in propulsion, and how these roles may vary over the course of the locomotor cycle, by revealing time-dependent variation in the intensity of muscular activity. Below, hypotheses of pectoral muscle function based on muscle architecture are evaluated in the light of profiles of the intensity of muscular activity recorded during fin movement.

The roles assigned to the pectoral abductors during swimming, as deduced from their lines of action, have until now been rather general (but see Geerlink, 1989). The arrector

| Table 4. Locomotor functions of pectoral musculature in the Embiotocidae inferred from synchronized kinematic and electromyographic records |
|----------------------------------|-------------|
| Muscle                           | Function                                                                 |
| Adductors                        |                                                        |
| Arrector ventralis               | Rotates adducted fin anteriorly during non-propulsive pause period; initiates downstroke by abducting leading edge; limited role in further abduction |
| Abductor superficialis           | Protracts and depresses fin                                                                                  |
| Abductor profundus               | Protracts and depresses fin                                                                                  |
| Adductors                        |                                                        |
| Adductor superficialis 2,3       | Decelerates fin at downstroke–upstroke transition; initiates upstroke by retracting, elevating and adducting leading edge of fin; rotates adducted fin anteriorly during non-propulsive period |
| Adductor superficialis posterior*| Retracts and elevates abducted fin on upstroke; protracts adducted fin during pause period                    |
| Adductor profundus               | Retracts and elevates fin                                                                                  |

*No activity recorded at 80% $U_{p_e}$; functions proposed are for higher speeds.*
ventralis (or ventral ‘marginal muscle’ of Jessen, 1972) has been labeled a simple ‘erector’ of the fin’s leading edge. The superficial and deep abductors have been predicted to ‘flex’ and depress the fin lobe or to draw it forward (Williamson, 1893; Danforth, 1913; Ganguly and Nag, 1964). In general, these hypothesized roles are supported by the results of this study (Table 4). However, the data presented in Fig. 3 allow the functions of the muscles to be resolved in much finer detail. The arrector ventralis is the first abductor to show high-intensity activity in the period prior to the downstroke. On the basis of its line of action (Fig. 1B), it is thus probably responsible for anterior rotation of the adducted fin at the end of the pause period (Fig. 3A, B, f–a). In addition to this non-propulsive role, the muscle initiates abduction (i.e. lateral and ventral excursion) of the leading edge of the fin. Since the ventral arrector’s activity is concentrated in the period before downstroke begins, however, its role in subsequent modification of the fin tip’s trajectory would seem limited.

![Graph](image)

Fig. 4. Representative electromyograms recorded simultaneously from the pectoral musculature during three consecutive fin beats at 80% of the pectoral–caudal gait transition speed. Note adductor activity (at arrows) overlaps that of abductors in *Embiotoca lateralis*, whereas a period of electrical inactivity (indicated by asterisks) separates abductor and adductor bursts in *Amphistichus rhodoterus*. Muscle abbreviations as in Fig. 1. Dotted lines designate kinematic events a, c and e illustrated in Fig. 2.
Further fin depression is powered by the abductors superficialis and profundus, which in *E. lateralis* show high-intensity contractions through mid-downstroke (Fig. 3A, b). In *A. rhodoterus*, the activity of these muscles becomes greatly diminished early in the downstroke (Fig. 3B), reducing the period during which the fin is under direct muscular control.

Hypothesized functions of the pectoral adductors may also be refined through analysis of *I*\textsubscript{EMG}. Anatomical studies have proposed that these muscles are either unqualified ‘adductors’ (Danforth, 1913; Shann, 1920; Ganguly and Nag, 1964; Jessen, 1972) or that they act to draw the fin upwards and against the body (Williamson, 1893). Fig. 3 indicates that the adductor superficialis 2,3 in fact serves a multiple function during steady labriform swimming. That its activity begins prior to the onset of upstroke (Fig. 3A,B, c) is evidence that the muscle acts to decelerate the fin as it approaches the transition from downstroke to upstroke. An analogous role in the control of the wing beat upstroke has been noted for the avian pectoralis (Goslow and Dial, 1990; Biewener *et al.* 1992). Activation of the superficial adductor while the fin is being depressed suggests that the muscle undergoes a lengthening contraction. Stretching of the muscle and its associated tendons may allow for storage and subsequent recovery of strain energy in the tissue as the fin changes direction (see Biewener, 1989; Alexander, 1990). In addition, the lengthened muscle may be capable of more economical force production (Alexander, 1991). The significance of the bimodal *I*\textsubscript{EMG} profile is unclear, but trailing activity in the adductor superficialis 2,3 through the end of the propulsive period (Fig. 3A,B, e) is certain to power the adduction of the leading edge of the fin. Given its insertion on the anterior surface of the fin rays (Fig. 1D), further activity of adductor superficialis 2,3 indicates the muscle’s final role during the stride: anterior rotation of the adducted fin during the pause period prior to the next fin beat (Fig. 3A,B, f–a).

The onset of the adductor profundus as the upstroke begins precludes its involvement in braking the momentum of the abducting fin. Instead, this muscle shows high activity through mid-upstroke (Fig. 3A,B, d), a pattern consistent with its

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*Embiotoca lateralis*

![Diagram](image)

*Amphistichus rhodoterus*

![Diagram](image)

**Fig. 5.** Summary diagrams of the duration of pectoral muscle activity recorded during the fin stroke cycle at 80% of the pectoral–caudal gait transition speed (*U*\textsubscript{p-c}). The onsets and offsets of EMGs for each muscle were pooled among the three individuals of each species (*N*=10–15). Mean timings, represented by the ends of black bars, are shown with s.e.m. (dark gray bars). The order of muscle activation is conserved in the two species, but *Embiotoca lateralis* shows relatively later offsets of the superficial and deep abductors, and the adductor profundus. In two out of three *E. lateralis* studied, the adductor superficialis 2,3 showed activity (light gray bar) which broadly overlapped that of the adductor muscles. Activity in the adductor superficialis posterior was not detected in either species at 80% *U*\textsubscript{p-c}. Muscle abbreviations as in Fig. 1. Lines labeled a, c and e designate the mean timings of kinematic events illustrated in Fig. 2. *T*, stride period.
simple role as a fin adductor. An unexpected finding from analysis of correlated kinematic and electromyographic records was the inactivity of the adductor superficialis posterior (Fig. 4). This muscle is of particular interest because its line of action differs substantially from that of the other adductors (Fig. 1C). Preliminary analysis indicates that at swimming speeds greater than 80 % $U_{p-c}$ this muscle becomes active to serve a dual function: (1) to retract and elevate the abducted pectoral fin (Fig. 2, c–e); and (2) to rotate the adducted fin anteriorly during the pause period (Fig. 2, f–a). Thus, although nominally an adductor, this muscle may also play the important secondary role of an adductor in protracting the fin to the position at which downstroke begins (Table 4).

Mechanics of embiotociform swimming

At a comparable cruising speed, the surfperches *Amphistichus rhodoterus* and *Embiotoca lateralis* exhibit marked similarities in the musculoskeletal mechanism of pectoral fin propulsion. In particular, the fin beat cycle is characterized by large dorsoventral and mediolateral fin tip excursions (approximately 140 % HL and 70 % HL, respectively) and relatively minor anteroposterior movements (Fig. 3; Table 1). The timings of kinematic events during the downstroke show no significant interspecific differences (Table 2). Although the upstroke occupies a smaller percentage of the stride period in *E. lateralis* than in *A. rhodoterus*, the overall kinematic profile of fin adduction is quite similar in the two species (Fig. 3A,B). In addition, the temporal order of pectoral muscle activation, the timing of peak activity and the kinematic functions of the musculature during swimming are conserved (Fig. 5; Tables 3, 4).

Since *E. lateralis* and *A. rhodoterus* represent extremes of both phylogenetic and ecological divergence within the Embiotocidae, mechanistic similarities between the species are interpreted as features primitive for the family and possibly synapomorphic for a higher taxonomic group within the order Perciformes. Several labriform swimmers, both closely and more distantly related to the surfperches, exhibit the same three general phases of propulsive downstroke, upstroke and pause during which the adducted fin is rotated into position for the following stride (Webb, 1973; Geerlink, 1983; Archer and Johnston, 1989; Gibb et al., 1994; Westneat, 1996).

Furthermore, a number of taxa other than *A. rhodoterus* and *E. lateralis* exhibit a predominant dorsoventral component of fin motion during swimming (e.g. in the Labridae: Geerlink, 1983; Westneat, 1996). Such propulsor movements perpendicular to the axis of progression are consistent with a lift-based mechanism of propulsion (Webb and Blake, 1985; Daniel and Webb, 1987). By contrast, labriform swimmers that make use of drag and acceleration reaction forces show more anteroposterior fin movements. The fin blade is feathered during protraction and is oriented broadside to the flow during retraction (Blake, 1979, 1980; Archer and Johnston, 1989). The latter pattern is not exhibited by surfperches (Fig. 2). The pectoral fin of *E. lateralis* and *A. rhodoterus* assumes a changing, complex shape during the fin stroke which frustrates reliable measurement of angle of attack. Nevertheless, the inclination of the fin during both upstroke and downstroke (Fig. 2, b,d) indicates that lift production should be possible in these species, as has been suggested for the shiner surfperch *Cymatogaster aggregata* (Webb, 1973).

Undoubtedly the basic mechanism of hydrodynamic lift generation by ‘embiotociform’ swimmers (Webb, 1973, 1994) is not unique to the Embiotocidae. The extent to which patterns of neuromuscular control of the pectoral fins are shared among other perciform families remains to be determined.

Because *A. rhodoterus* and *E. lateralis* are distinct both genealogically and ecologically, differences between the species in locomotor mechanics cannot be unequivocally attributed to divergent adaptation. However, a number of these differences are consistent with the surfperches’ radiation into distinct habitats and adoption of species-specific swimming behaviors. The stride cycle of *E. lateralis*, which involves substantial anteroposterior excursion of the fin, is not typical of a continuous, steady labriform swimmer (see also the ‘downward–forward type’ fin abduction of the wrasse *Coris formosa*: Geerlink, 1983). In addition to producing lift, protraction of the fin into the flow during abduction is likely to generate drag forces which impede the fish’s forward progress. Such a downstroke, performed with fins of low aspect ratio, reflects the species’ capacity to maneuver slowly in physically complex habitats (see Blake, 1981; Webb, 1988). In particular, anterior extension of the paired fins should play an important role in backwards swimming and braking (Breder, 1926; Harris, 1937, 1938; Bainbridge, 1963; Geerlink, 1987; Fricke and Hissmann, 1992). Pronounced fin retraction on the upstroke (Fig. 3A), if performed unilaterally, should also aid in drag-based turning maneuvers.

The more limited anteroposterior range of motion of the fins in *A. rhodoterus* may correspond to a reduced potential for maneuverability. Primarily dorsoventral strokes of fins with a relatively high aspect ratio provide this species with a mechanism for rapid, lift-based locomotion in open water (see Webb, 1988). The greater proportion of the stride period occupied by propulsive fin movements in *A. rhodoterus* (Table 1, e) may explain in part this species’ ability to swim to higher absolute speeds with the labriform gait than *E. lateralis*.

Despite their kinematic differences, the surfperches exhibit no obvious variation in gross pectoral myology (Fig. 1) or in the relative timing of muscle activation during swimming (Fig. 5; Table 3). The degree of anteroposterior excursion of the pectoral fin seems to be determined simply by the orientation of the fin base. In *E. lateralis*, the articulation between the fin rays and the supporting radials lies at an angle to the longitudinal axis of the body 10° greater on average than in *A. rhodoterus*. As a result, when the temporally conserved motor program for fin oscillation is initiated, the paired fins of the benthically oriented species *E. lateralis* are protracted, while those of the open-water cruiser *A. rhodoterus* are depressed (Fig. 2A,B, a–c). Thus, a rather minor structural difference is associated with the species’ distinct fin movements and primary swimming behaviors (cf. Geerlink, 1989).
Detailed comparison of $I_{\text{EMG}}$ profiles of the two taxa reveals fine-scale interspecific variation in the motor program controlling locomotion. In *A. rhodoterus*, all three pectoral abductors show peaks of activity prior to the onset of the downstroke and sharply tapering levels of activity thereafter. Between the middle and end of downstroke (Fig. 3B, b–c; Fig. 4), a period of 40–80 ms elapses during which none of the six pectoral muscles studied is active. Similarly, intense contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually extend beyond mid-upstroke (Fig. 3B, d). In effect, fin abduction and contraction of the adductor profundus does not usually

By contrast, the fin stroke of *E. lateralis* is under continuous motor control. At no time during the average stride period are all six pectoral muscles silent (Figs 3A, 4). The superficial and deep abductors show high-level activity throughout most of the downstroke and substantially later offsets than in *A. rhodoterus* (Figs 3A, 5). Their activity is overlapped broadly by that of the adductor superficialis 2.3, which provides increased control of fin deceleration. Following its activation at the beginning of the upstroke, the deep adductor remains active until the end of the propulsive period (Fig. 3A, c–e). These activity profiles may be typical of maneuvering swimmers capable of spontaneous modification of fin movement during the stride. Additional work on unrelated taxa sharing the same habitats as *A. rhodoterus* and *E. lateralis* is required to determine the adaptive nature, if any, of these motor patterns.

Constant-velocity rectilinear swimming, as examined in this study, is infrequently demonstrated by most fishes in nature. Even for taxa specialized for open-water cruising, most swimming tasks require acceleration and changes of direction (Hoar and Randall, 1978; Webb, 1991). This investigation of steady labriform locomotion, however, provides information about the basic musculoskeletal mechanism of fin control that may be shared by phylogenetically and ecologically distinct teleost fishes. Owing to the generally similar functional demands placed on the pectoral fins in most perciforms, mechanistic features of embiociform swimming are likely to be widely distributed. In the case of *E. lateralis*, study of fin movements during steady locomotion also provides insight into the ways the fins may be used during unsteady swimming, a behavior which comprises a substantially greater portion of a fish’s time and energy budget. Analysis of the neuromuscular control of maneuvering is critical to a more complete understanding of the mechanics of paired-fin propulsion.

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References

Kinematic and electromyographic analysis of surfperch locomotion


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