How to build a pectoral fin: functional morphology and steady swimming kinematics of the spotted ratfish (*Hydrolagus colliei*)

K.L. Foster and T.E. Higham

Abstract: Aquatic flight is the primary locomotor mode for many animals, including penguins and other diving birds, turtles, and fishes, where labriform and rajiform swimming have been the focus of much interest. However, despite its interesting phylogenetic placement, little is known about the aquatic flight of the sister lineage to the elasmobranchs, the chimaerids. This study investigates the pectoral fin morphology of the spotted ratfish (*Hydrolagus colliei* (Lay and Bennett, 1839)) as a possible factor underlying the kinematics of their steady swimming by comparing muscle mass, distribution, and abductor to adductor ratio with those of a closely related shark (*Squalus acanthias* L., 1758). Despite fundamental differences in swimming mode, abductor to adductor muscle ratio did not differ between species ($P = 0.49$). However, the muscle ratio in the spotted ratfish was similar to the range determined in other flapping labriform swimmers. Ratfish had larger, distally placed pectoral fin muscles relative to body size than dogfish ($P < 0.0001$) possibly aiding in fine control. Stroke amplitude remained constant across body size ($P = 0.26$) and relative swimming speed ($P = 0.23$) in the ratfish, whereas the downstroke was significantly faster than the upstroke ($P = 0.006$). The similar muscle ratio, despite differences in stroke phases, may be explained by physiological or in vivo recruitment differences between abductors and adductors in the ratfish.

Résumé : Le vol aquatique est le mode principal de locomotion de plusieurs animaux, dont les manchots et autres oiseaux plongeurs, les tortues et les poissons, chez lesquels on s'est beaucoup intéressé à la nage labriforme et la nage rajiforme. Cependant, on connaît peu de choses sur le vol aquatique des chiméridés, la lignée sœur des élasmobranches, malgré leur position phylogénique intéressante. Notre étude examine la morphologie de la nageoire pectorale de la chimère d'Amérique (*Hydrolagus colliei* (Lay et Bennett, 1839)) comme facteur sous-jacent potentiel de la cinématique de leur nage régulière soutenue, en comparant la masse musculaire, la répartition des muscles et le rapport des abducteurs–adducteurs avec les mêmes caractères chez un requin fortement apparenté (*Squalus acanthias* L., 1758). Malgré des différences fondamentales dans le mode de nage, le rapport des abducteurs–adducteurs ne diffère pas entre les deux espèces ($P = 0{,}49$). Cependant, le rapport des muscles chez la chimère d'Amérique correspond à l'étendue observée chez d'autres nageurs labriformes qui battent des nageoires. Les chimères possèdent des muscles en position distale dans les nageoires pectorales de plus grande taille par rapport à la taille corporelle que les aiguillats ($P < 0{,}0001$), ce qui aide peut-être au contrôle à l'échelle fine. L'amplitude du battement reste constante quelles que soient la taille corporelle ($P = 0{,}26$) et la vitesse relative de nage ($P = 0{,}23$) chez la chimère, alors que l'abaissée est significativement plus rapide que la remontée ($P = 0{,}006$). Les rapports musculaires semblables, malgré les différences dans les phases du battement, peuvent s'expliquer par des différences physiologiques, ou in vivo, de recrutement entre les muscles abducteurs et adducteurs chez la chimère.

[Traduit par la Rédaction]

Introduction

Flapping flight has allowed birds, bats, and millions of species of insects to exploit a challenging niche and diverge from terrestrial species with such spectacular success that it is arguably the most successful locomotor strategy in the evolution of animals (Tian et al. 2006). In addition to the airborne flight of birds (Brown 1963) and bats (Tian et al. 2006), a diverse assemblage of vertebrate species engage in aquatic flight, propelling themselves through the water with wings, fins, or flippers. Several bird lineages, including penguins (Clark and Bemis 1979; Mill and Baldwin 1983; Hui 1988) and puffins (Johansson 2003) have secondarily specialized in aquatic flight, utilizing vertical oscillations of their wings to produce thrust. Sea turtles also swim by flapping their flippers (Davenport et al. 1984; Renous and Bels 1993), whereas freshwater species often employ a drag-based rowing or paddling motion where limbs move parallel, rather than perpendicular, to the body axis (Davenport et al. 1984; Pace et al. 2001). However, despite the tremendous diversity of animals employing this mode of locomotion, aquatic flight has been relatively understudied.

Aquatic flight is also common, and has been studied extensively, in many lineages of fishes. For example, the kinematic and energetic advantages of flapping versus rowing

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propulsion (Webb 1973; Westneat 1996; Walker and Westneat 1997; Westneat and Walker 1997; Walker and Westneat 2000, 2002), as well as hydrodynamics (Drucker and Lauder 2000), of pectoral fin swimming in actinopterygian fishes have been the subject of intense investigation. The kinematics and functional morphology of the rajiform oscillation and undulation of the pectoral fins in skates and rays have also been analyzed (Daniel 1988; Rosenberger and Westneat 1999; Rosenberger 2001). These studies have vastly increased our knowledge of the morphological and kinematic diversity of pectoral fin propulsion in these lineages. However, the kinematics of the swimming of ratfishes, sister group to the more well-known elasmobranchs, have only briefly been explored by Combes and Daniel (2001).

Although it is not uncommon to see pectoral fin swimming in the chondrichthyans, as the dorso-ventrally flattened skates and rays rely on this form of locomotion, it is unusual to observe a reliance on labriform swimming in the ratfishes, chondrichthyans with a more fusiform body shape. The majority of sharks hold their pectoral fins rigid during routine swimming, only using them to initiate turns or changes in their vertical position in the water column (Fish and Shannahan 2000; Wilga and Lauder 2000). Instead, most sharks utilize axial undulations and oscillations of their caudal fin to generate thrust (Ferry and Lauder 1996; Lauder 2000; Wilga and Lauder 2002; Blake 2004). Chimaeras diverged from elasmobranchs approximately 400 million years ago (Grogan and Lund 2004), making them likely the oldest extant lineage to employ aquatic flight for routine swimming. It is, therefore, of particular interest to understand the morphological, kinematic, and hydrodynamic characteristics of the locomotion in these fishes and how they differ from both elasmobranchs and the actinopterygians that swim in a similar manner.

The first goal of this study is to compare the functional morphology of the spotted ratfish (*Hydrolagus colliei* (Lay and Bennett, 1839)), a representative chimaerid that is endemic to the west coast of North America (Quinn et al. 1980), and the spiny dogfish (*Squalus acanthias* L., 1758), a squaliform shark. The amount of force a muscle is able to generate is proportional to the size of the muscle (Powell et al. 1984). Thus, the differences in pectoral fin function in these two species suggest that the pectoral muscles of ratfish should be larger for increased power and (or) force generation. Similarly, as is seen in many birds and other aquatic fliers, the abductor muscles, responsible for drawing the fin down towards the midline of the body, are expected to play a greater role in thrust production than the adductor muscles, which draw the fin back up, and therefore the abductor to adductor muscle ratio should be greater than one in ratfish. The second goal of this study is to examine how the pectoral fin morphology of the ratfish relates to the steady swimming kinematics and how the use of their pectoral fins compares with the labriform swimming observed in other fishes.

Materials and methods

Subjects

Twenty-five spotted ratfish, 44.3 ± 0.05 to 659.3 ± 0.05 g (mean ± SE), were collected by trawling in Barkley Sound, off the west coast of Vancouver Island, at depths of 45–70 m (Trevor Channel) and 70–85 m (Imperial Eagle Channel). Animals were held at the Bamfield Marine Sciences Centre (BMSC) in large, covered, outdoor, continuously flow-through, unfiltered seawater tanks and were kept and handled in accordance with the animal care guidelines of the centre. High levels of oxygen were maintained through constant aeration using six air stones. Ratfish were maintained without feeding for a period of 2–3 weeks before being euthanized with an overdose of anaesthetic (MS-222; Animal Use Protocol No. UP09-SP-BMF-05).

Morphometric measurements

Freshly euthanized individuals of spotted ratfish (n = 25) were measured, weighed, and photographed, using a Sony Cyber-shot DSC-S60 camera (Sony Corporation, New York, New York, USA) at a resolution of 1024 × 768 pixels, to obtain total body length and mass. Left pectoral fins were removed by cutting as close to the body as possible and fins were placed on a flat Styrofoam board and photographed, ensuring the fin was opened maximally, for subsequent determination of surface area. The left fins were used in all cases to be consistent. To determine the relative position of the most distal insertion points of muscle on the pectoral fins, the longest length of muscle in each of five fins was measured, in line with fibre direction, and expressed as ratios relative to the longest length of the fins from tip to base. Fins were skinned, and all muscle was removed from the underlying cartilaginous skeleton, up to the most distal insertion point at the end of the last row of radials, and weighed. In two individuals, the entire right pectoral adductor and abductor muscles were traced back to their points of origin on the scapula and coracoid bar and removed and dissected as with the left side. The masses of the entire right pectoral muscles were then divided by their matching left pectoral muscles, which only reflected the amount of muscle projecting into the fin. In this way these two fish were used to obtain a correction factor that could then be used to determine the entire pectoral muscle (including both the muscle found in the body and the muscle projecting into the fin) of all other ratfish.

Seven freshly killed and frozen spiny dogfish were obtained from the BMSC after being held in captivity for no more than 2 weeks. To compare their pectoral fin morphology with that of ratfish, total body length and mass were determined prior to pectoral fin removal and dissection as above.

Kinematics

Five spotted ratfish, of lengths ranging from 39 ± 0.05 to 53.4 ± 0.05 cm (mean ± SE), were placed in the flume (12 m long × 2 m wide × 1 m deep, filled to approximately 0.5 m with continuously flowing, unfiltered seawater) at the BMSC with one motor propelling water at approximately 40–50 cm·s^{-1}. Each ratfish was filmed in lateral view at 100 frames·s^{-1} using a Casio EXILIM EX-F1camera (Casio America, Inc., Dover, New Jersey, USA) at a distance of between 40 and 60 cm from the animal. Images were scaled using the known length of the fish as a reference.

Coordinates of the tip of the fin were digitized in each frame using ImageJ version 1.42q (National Institute of Health, Washington, D.C., USA). From these coordinates,

the path of the fin tip through the stroke was reproduced on an *x*–*y* coordinate system for visualization. In addition, the maximum displacement of the fin from the top of the stroke (the beginning of the downward, propulsive stroke) to the bottom (where the fin begins its ascent back to its original position) was quantified and averaged for each individual to obtain the mean stroke amplitude over the eight strokes analyzed per individual. The tip of the nose was also digitized to ensure that the fish swam at a constant speed and with minimal pitch and yaw. The duration of the upstroke and downstroke were determined, as were the mean velocities of the fin tip through these two stroke segments.

Data analysis

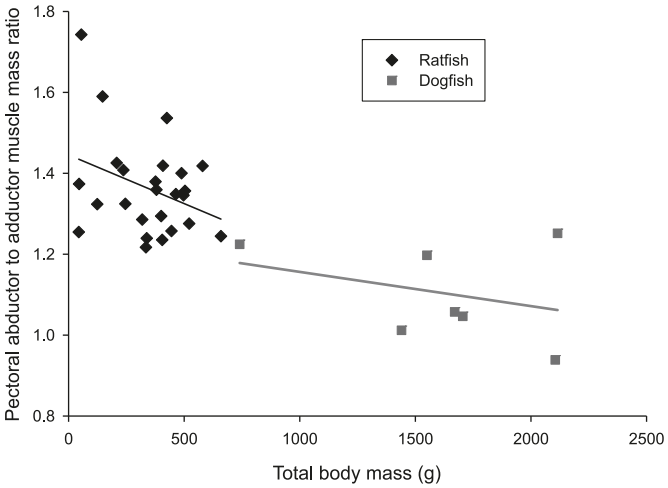
All statistical analyses were performed using MYSTAT version 12.02 (SYSTAT Software, Inc., Chicago, Illinois, USA). Least squares regressions were used to characterize the relationship between body mass and abductor to adductor muscle ratio, body mass and pectoral muscle mass, and mean stroke amplitude and body length in the ratfish. A two-sample *t* test was performed to compare the mean muscle length to fin length ratio of each species. For fin area – total body length comparisons in the ratfish, fin area and body length were both log-transformed. When appropriate, the slopes of the regressions for ratfish and dogfish were compared using an ANCOVA with species and body mass or length (covariate) serving as independent variables and abductor to adductor muscle ratio, pectoral muscle mass, or fin area as dependent variables. Mean downstroke and upstroke periods and velocities were compared using a paired *t* test. A *P* value of 0.05 was the criterion for statistical significance in all tests.

Results

The pectoral muscles and skeletal elements were similar in both spotted ratfish and spiny dogfish. Both species had three rows of radials projecting into the fin and the adductors (responsible for raising the fin) and abductors (responsible for depressing the fin), originating from the scapula and coracoid bar, respectively, inserted all along the radials, with the most distal insertion point at the end of the last row of radials. The length of these muscles, however, differed significantly between species so that the most distal insertion point in the ratfish was farther along the fin (33.69% ± 0.95% of fin length) than in the dogfish (24.75% ± 0.37% of fin length; $t_{[8]} = -8.44$, $P < 0.0001$).

The pectoral abductor to adductor muscle ratio (Fig. 1) was not correlated with body mass ($F_{[1,31]} = 2.78$, $P = 0.11$) and did not vary between species ($F_{[1,31]} = 0.49$, $P = 0.49$). Total pectoral muscle mass and body mass, however, were positively correlated ($F_{[1,31]} = 122.33$, $P < 0.0001$) and differed between species ($F_{[1,31]} = 20.97$, $P < 0.0001$), with ratfish having larger pectoral muscles relative to body mass than dogfish (Fig. 2*a*). The mass of pectoral muscle found within the confines of the fin (Figs. 2*b*, 3) also increased with body mass ($F_{[1,31]} = 190.02$, $P < 0.0001$) and was significantly greater in the ratfish than in the dogfish ($F_{[1,31]} = 119.56$, $P < 0.0001$). Pectoral fin area (Fig. 4) increased with body length in both species ($F_{[1,29]} = 262.64$, $P < 0.0001$) and was larger in the ratfish than in the dogfish ($F_{[1,29]} = 65.89$, $P < 0.0001$).

Fig. 1. Abductor to adductor muscle ratio relative to whole body mass (g). No significant difference (ANCOVA, $F_{[1,31]} = 0.49$, $P = 0.49$) was found in muscle ratio between the spotted ratfish (*Hydrolagus colliei*) ($r^2 = 0.11$) and the spiny dogfish (*Squalus acanthias*) ($r^2 = 0.11$). Muscle ratio did not correlate significantly with body mass (ANCOVA, $F_{[1,31]} = 2.78$, $P = 0.11$).



The ratfish pectoral fin created an oval fin tip trace, never crossing its path within a given stroke (Fig. 5). Fin stroke amplitude of ratfish was constant despite differences in body length ($r^2 = 0.019$, $P = 0.26$) and relative swimming speed (Fig. 6; $r^2 = 0.59$, $P = 0.23$); stroke frequency was not affected by body length ($r^2 = 0.74$, $P = 0.14$). The downstroke, however, was faster than the upstroke (Fig. 7; $t_{[3]} = -6.94$, $P = 0.006$).

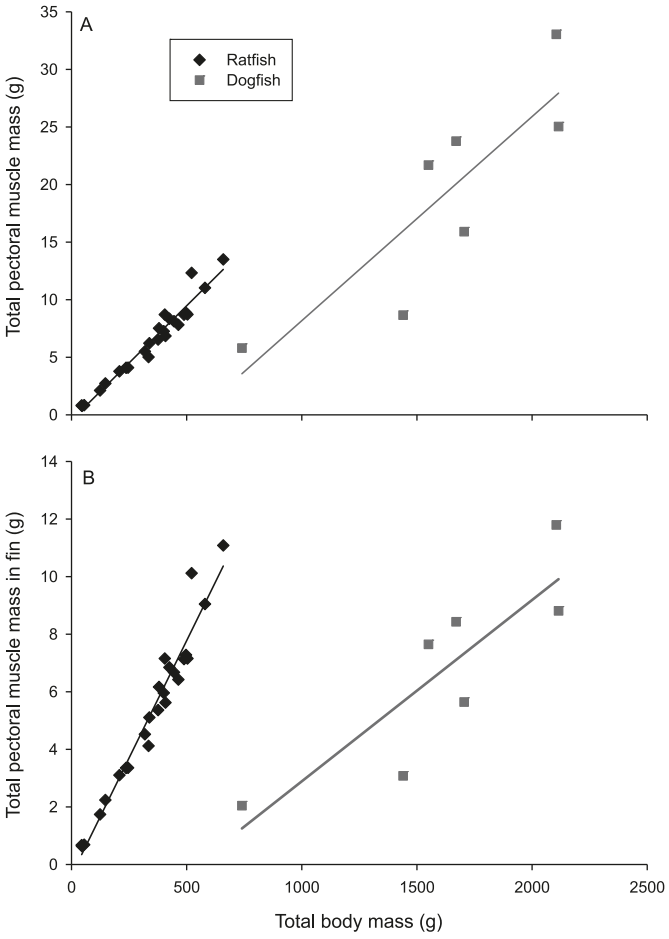
Discussion

Compared with the spiny dogfish, the spotted ratfish have both larger pectoral fin muscles relative to their body size and a greater proportion of pectoral fin muscle is found in the fin rather than remaining within the confines of the body wall. This distribution pattern may be linked to the ecology of the ratfish, playing a role in increasing manoeuvrability and fine control. In addition, although the abductor to adductor muscle ratio of ratfish was close to one and did not differ with that of the dogfish, we found a significant difference between the two stroke phases in the ratfish, with the downstroke progressing faster than the upstroke. Stroke amplitude, however, did not vary with body size.

Morphometrics

Contrary to our expectations, we found no difference in pectoral abductor to adductor muscle ratio between ratfish (1.36 ± 0.02; mean ± SE) and dogfish (1.10 ± 0.05; mean ± SE). This is surprising because in contrast with dogfish, which are known to maintain a rigid pectoral fin position during routine swimming (Fish and Shannahan 2000), and the leopard shark (*Triakis semifasciata* Girard, 1855), which likely show little or no EMG activity during steady swimming (Wilga and Lauder 2004), ratfish are known to rely exclusively on their pectoral fins for propulsion during steady swimming (Combes and Daniel 2001). However, Thorsen

Fig. 2. (A) Total pectoral muscle mass (g) relative to body mass (g). Spotted ratfish (*Hydrolagus colliei*) ($r^2 = 0.95$) had significantly larger pectoral muscles than spiny dogfish (*Squalus acanthias*) ($r^2 = 0.74$) relative to body size (ANCOVA, $F_{[1,31]} = 20.97$, $P < 0.0001$). Muscle mass correlated significantly with body mass (ANCOVA, $F_{[1,31]} = 122.33$, $P < 0.0001$). (B) Pectoral muscle mass found in fin (g) relative to body mass (g). Ratfish ($r^2 = 0.95$) had significantly larger pectoral muscles than dogfish ($r^2 = 0.74$) relative to body size (ANCOVA, $F_{[1,31]} = 119.56$, $P < 0.0001$). Muscle mass in the fin was positively correlated with body mass (ANCOVA, $F_{[1,31]} = 190.02$, $P < 0.0001$).



and Westneat (2005) found that the lift-based labrids have muscle ratios similar to that found in the ratfish in this study (abductor to adductor ratios between 1.395 and 1.071). This modest muscle ratio may be explained by one of two possibilities. First, the approximately equal size of abductors and adductors in these fishes may suggest that relatively equal forces are being generated on both the upstroke and the downstroke, a possibility that could be explored with hydrodynamic analyses of pectoral-based swimming. Second, although mass is conserved between abductors and adductors, it is possible that muscle physiology and in vivo fibre recruitment differs between these muscle groups. Future work needs to be done to explore these two possibilities.

Although the ratio of abductor to adductor pectoral muscle mass did not differ between the two species, the physiological characteristics of the pectoral muscles are largely unknown and may be a source of variation between the species. A single study examined the distribution of fibre types in the pectoral muscle of *Chimaera monstrosa* L, 1758, a species of ratfish (Kryvi and Totland 1978). They found that the pectoral muscles of this species consisted of an outer, mixed region of red and pink fibres with a more deeply situated white region. In addition, a previous study showed that the major profundus muscle (within the pectoral fin) of a labriform swimmer, the pumpkinseed sunfish (*Lepomis gibbosus* (L., 1758)), contained 55% anaerobic muscle fibres and 45% fibres of mixed aerobic capacity (Luiker and Stevens 1993). Thus, considerable physiological variation can exist within a single pectoral fin muscle, although this is relatively unexplored. Although we have no data regarding the physiology of pectoral muscles of spotted ratfish, there does appear to be variation in color (red and white) within single muscles (K.L. Foster and T.E. Higham, personal observation). Future work should examine whether the characteristics (e.g., fibre type) of abductor muscles differ from adductor muscles, which may help explain the lack of a difference in muscle mass ratio.

Ratfish have significantly larger pectoral muscles than dogfish. This result was expected because of the reliance on pectoral fins for propulsion in the ratfish, which would require increased power, and possibly force, generation. Because dogfish rely on axial undulations and oscillations of their caudal fin for routine swimming (Ferry and Lauder 1996; Lauder 2000; Wilga and Lauder 2002; Blake 2004), little force and power are expected to be generated by their pectoral fins (Wilga and Lauder 2004), and thus pectoral muscle involvement and size is minimized. Accompanying this increased movement and power generation from the pectoral fins of ratfish is a need to control how the fins are actually being moved. We found that although the underlying skeletal elements of the pectoral fin (propterygium, mesopterygium, metapterygium, three rows of radials; Wilga and Lauder 2001) are similar and pectoral muscle extends approximately to the end of the last row of radials in both species, the pectoral muscle's most distal insertion point is located farther from the body in ratfish relative to overall fin length. Additionally, we found that a greater proportion of the ratfish pectoral muscle is found distally. These characteristics might serve as mechanisms for the increased requirement for control over fin movement and shape given that distal muscle placement will increase mechanical advantage (in this third-class lever system), resulting in less movement of the fin for a given muscle strain or force. Such control over fin movement and shape may be essential to the ecology of the spotted ratfish, as they inhabit benthic waters and thus may need to manoeuvre around obstacles littering the ocean bottom. Future work examining the link between pectoral fin movements, morphology, and manoeuvrability will provide insight into this interesting question.

The significantly larger fins of the ratfish, which also appear to be more flexible than those of the dogfish (K.L. Foster and T.E. Higham, personal observation), may also play a role in the ecology of this species. It is likely that the large flexible fins, coupled with the arrangement of the muscles that we found in the fins (see above), indicate the importance of fine control. Preliminary experiments suggest that different parts of the fin can be controlled independently. For example, the trailing edge of the fin does not appear to

Fig. 3. Dorsal view of left pectoral fin of the spotted ratfish (*Hydrolagus colliei*; left) and the spiny dogfish (*Squalus acanthias*; right). Muscle projecting into fin is outlined in white.

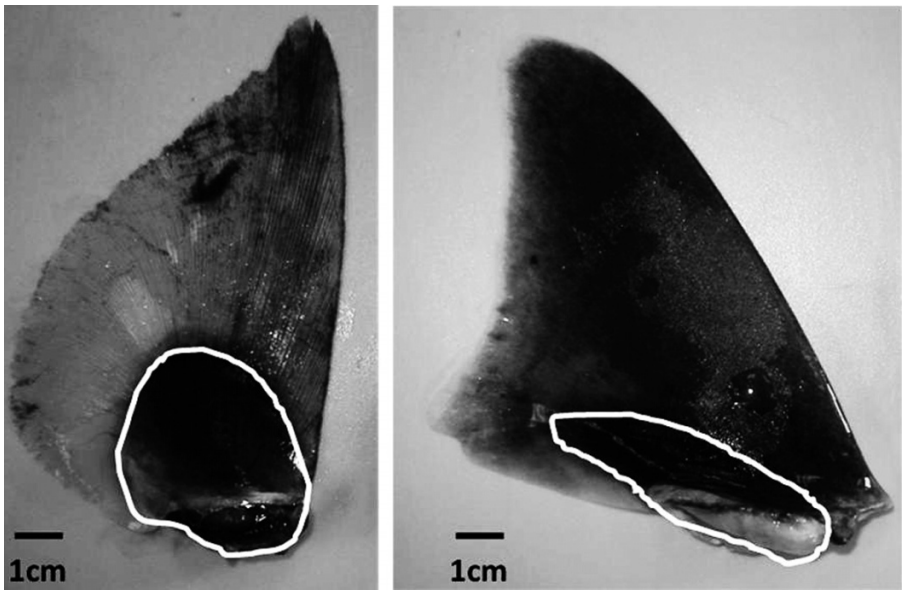
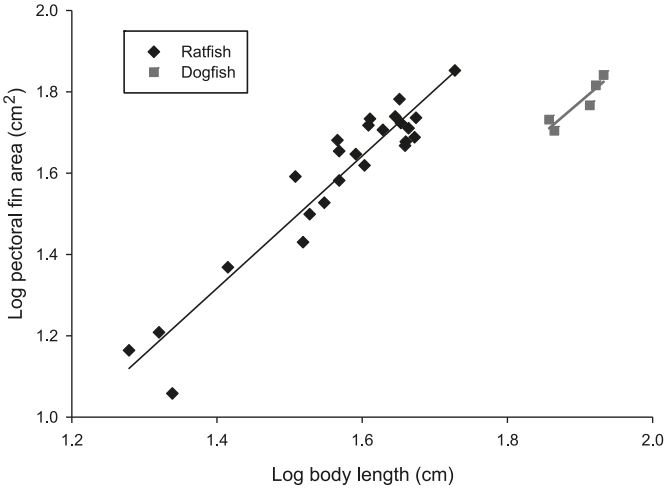


Fig. 4. Log-transformed pectoral fin area (cm^2) relative to log-transformed body length (cm). Spotted ratfish (*Hydrolagus colliei*; $r^2 = 0.91$) had significantly larger pectoral fins than spiny dogfish (*Squalus acanthias*; $r^2 = 0.85$) relative to body size (ANCOVA, $F_{[1,29]} = 65.89$, $P < 0.0001$). Fin area correlated significantly with body length (ANCOVA, $F_{[1,29]} = 262.64$, $P < 0.0001$).



flow passively behind the leading edge (Bestor 1993). Thus, future investigations examining in vivo muscle function (using electromyography and sonomicrometry) in relation to three-dimensional fin movements will determine how much fine control ratfish actually have over their fins.

Kinematics

Spotted ratfish employ a flapping motion of the pectoral fins to generate thrust. Rather than moving in a figure eight pattern, as seen in other studies of labriform swimming (Westneat 1996) and the aquatic flight in birds (Clark and Bemis 1979), the path of the fin tip of the spotted ratfish never crosses (Fig. 5), proceeding instead in a oval manner. The manner in which fins move can be linked to the direc-

Fig. 5. Fin tip trace showing the path of the tip of the right pectoral fin of a swimming spotted ratfish (*Hydrolagus colliei*). Trace is superimposed over an image of a ratfish and shows a counterclockwise motion beginning with the upstroke at the bottom right.

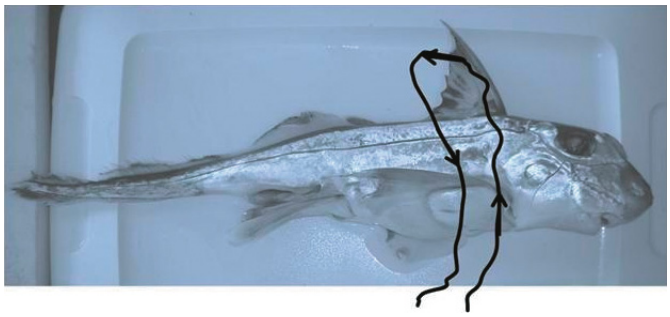


Fig. 6. Stroke amplitude (cm; mean ± SE) relative to swimming speed (body length (BL) · s^{-1}) of the spotted ratfish (*Hydrolagus colliei*). The amplitude did not vary significantly across swimming speed ($r^2 = 0.59$, $P = 0.23$).

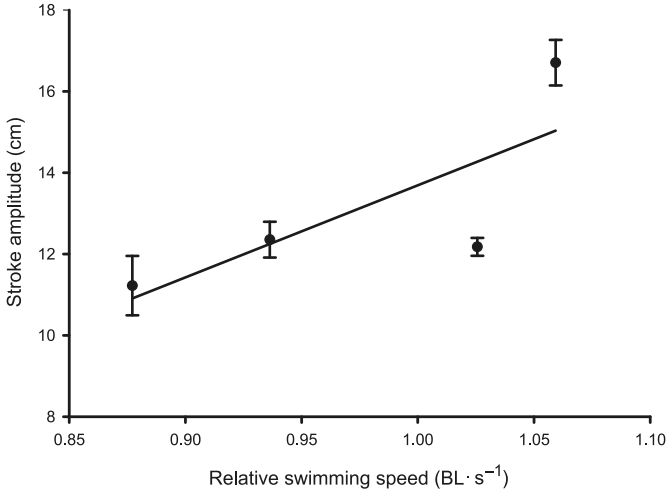
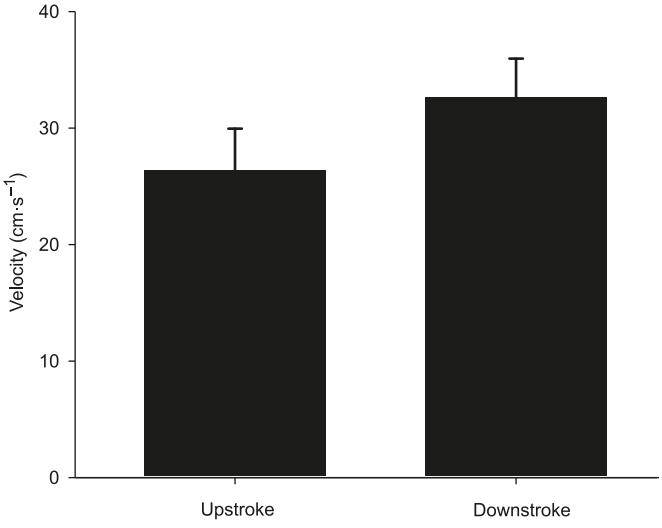


Fig. 7. Velocity ($cm \cdot s^{-1}$; mean ± SE) of the fin upstroke and downstroke of the spotted ratfish (*Hydrolagus colliei*). The downstroke was significantly faster than the upstroke (paired *t* test, $t_{[3]} = -6.94$, $P = 0.006$).



tion of the forces that are generated (Drucker and Lauder 2002). Thus, although the significance of this unique fin tip path is unclear at present, it appears that ratfish may generate forces in a different direction from that of other fishes.

A single study has previously investigated the kinematics of ratfish swimming. Combes and Daniel (2001) used two spotted ratfish, an adult and juvenile, to build a model to test the impact of planform fin (or wing) shape and flexibility on performance. The ratfish in that study swam at approximately a quarter of the speed (8–15 $cm \cdot s^{-1}$) compared with those used in this study (45 $cm \cdot s^{-1}$), and the larger ratfish was found to have both a larger stroke amplitude and lower stroke frequency than the smaller individual. These data are not consistent with our results. We found no significant relationship between body length and stroke frequency or amplitude. Although any conclusions we make from these data must be made cautiously because of the small sample size, it may be that these discrepancies can be explained by the different swimming speeds between the two studies. In addition, the differences in body size were likely smaller in our study compared with the study by Combes and Daniel (2001).

The bird wrasse (*Gomphosus varius* Lacépède, 1801) also swims using a flapping movement of its pectoral fins (Westneat 1996; Walker and Westneat 1997; Westneat and Walker 1997). However, the duration of the downstroke in the bird wrasse is longer than the upstroke, which is opposite to what we found in that the downstroke is significantly faster than the upstroke in the spotted ratfish. The slight negative buoyancy in the ratfish (K.L. Foster and T.E. Higham, personal observation) compared with the neutrally buoyant bird wrasse may contribute to this kinematic difference, as ratfish must produce some lift as well as thrust, potentially increasing the speed of the downstroke relative to the upstroke. Although thrust is generated mostly during the downstroke of the bird wrasse (Westneat 1996), bluegill sunfish (*Lepomis macrochirus* Rafinesque, 1819) produce thrust during both the downstroke and the upstroke (Drucker and Lauder 1999). Penguins, and perhaps other diving birds with essentially equal durations of upstroke and downstroke, likely produce approximately equal propulsion forces during both stroke phases (Clark and Bemis 1979). Our study did not quantify force production in the spotted ratfish, so it is unclear how force is generated during the stroke cycle.

Quantification of force production during labriform swimming has been investigated in bluegill sunfish and black surfperch (*Embiotoca jacksoni* Agassiz, 1853), using digital particle image velocimetry (Drucker and Lauder 1999, 2000). These studies not only determined the proportion of thrust and lift forces generated during each half of the stroke cycle, but they visualized the resulting vortex rings and related the characteristics and orientation of these rings to swimming performance. Digital particle image velocimetry would, therefore, be an interesting and essential next step in understanding the locomotion of the spotted ratfish and allow for a more comprehensive comparison of force generation patterns with those of other labriform swimmers.

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