

## RESEARCH ARTICLE

# The ontogenetic scaling of form and function in the spotted ratfish, *Hydrolagus colliei* (Chondrichthyes: Chimaeriformes): Fins, muscles, and locomotion

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**Abstract**

The alteration of form and function through the life of a fish can have profound impacts on the ability to move through water. Although several studies have examined morphology and function in relation to body size, there is a paucity of data for chondrichthyans, an ancient group of fishes. Ratfishes are interesting in that they utilize flapping pectoral fins to drive movement, and they diverged from elasmobranchs early in the gnathostome phylogeny. Using the spotted ratfish, *Hydrolagus colliei*, we quantified the scaling of traits relevant for locomotion, including median and paired fin external anatomy, the musculature of the pectoral and pelvic fins, and the kinematics of the pectoral fins. Whereas pelvic fins scaled with either positive allometry (fin span and area) or isometry (fin chord length at the base of the fin), pectoral fin measurements either scaled with negative allometry (fin span and aspect ratio) or isometry (fin area and chord length). Correspondingly, all pelvic fin muscles exhibited positive allometry, whereas pectoral muscles exhibited a mix of isometric and positively allometric growth. Caudal fin area and body frontal area both scaled with positive allometry, whereas dorsal fin area and span scale with isometry. Pectoral fin amplitude during swimming exhibited isometry, and fin beat frequency decreased with body size. Our results highlight the complex changes in form and function throughout ontogeny. Finally, we highlight that hierarchical differentiation in morphology can occur during growth, potentially leading to complex changes in performance of a functional system.

**KEYWORDS**

allometry, drag, Holocephali, pectoral fin, pelvic fin, swimming

## 1 | INTRODUCTION

The ontogenetic scaling of morphology and function has garnered extensive interest for centuries (Dubois, 1897; Gayon, 2000; Gould, 1966; Huxley & Teissier, 1936), and is of fundamental importance in the life of organisms (Schmidt-Nielsen, 1984). These traits may grow differentially, providing a window into the potential shifts in function that growing animals face. Thus, studies that examine the scaling of multiple propulsive surfaces with respect to body size will provide insight into the scaling of overall animal function. This will also reveal the integrated suite of traits that is often critical for effective function

(Kane & Higham, 2015), such as the multiple propulsors of swimming in fishes (Blake, 2004; Feilich, 2017; Standen & Lauder, 2005).

Fishes employ a range of surfaces to interact with the fluid environment, ranging from the body to median and paired fins (Blevins & Lauder, 2012; Harris, 1936; Harris, 1938; Harris, 1953; Higham, Malas, Jayne, & Lauder, 2005; Standen & Lauder, 2005; Standen & Lauder, 2007). Swimming behaviors are commonly divided into two categories, one driven primarily by movements of the body and caudal fin (BCF propulsion sensu; Webb, 1984), and the other driven primarily by movements of multiple or single sets of median or paired fins (MPF propulsion sensu; Webb, 1984). There is considerable diversity of movement within each of the categories.

For example, BCF swimmers can use only the caudal peduncle regions, whereas others may exhibit undulations that extend from the halfway point along the body (or even the head) to the tip of the caudal fin (Gillis, 1996; Lauder & Tangorra, 2015; Maia, Wilga, & Lauder, 2012). Within MPF swimmers, the majority of fishes utilize pectoral fin oscillations (flapping and rowing) or undulatory motions of the fins (Lauder & Madden, 2007; Rosenberger, 2001; Sfakiotakis, Lane, & Davies, 1999; Thorsen & Westneat, 2005; Wainwright, Bellwood, & Westneat, 2002; Walker & Westneat, 2002a, 2002b; Westneat, 1996; Westneat, Thorsen, Walker, & Hale, 2004). Associated with the diverse array of movement patterns is a wide range of fin morphologies (Fontanella et al., 2013; Fulton & Bellwood, 2004; Kane & Higham, 2012; Thorsen & Westneat, 2005). Despite our thorough understanding of fish swimming diversity, the scaling of fin and body morphology with ontogeny is poorly understood.

Within each mode of swimming, there is a dramatic range of intra- and inter-specific body sizes. Sharks tend to be isometric as they grow; however, in some instances, allometric relationships in the head and caudal fin shape have been associated with shifts in diet and migration (Fu et al., 2016; Irschick & Hammerschlag, 2015; Lingham-Soliar, 2005). Studies that examine both the scaling of morphology and swimming kinematics are rare. In one of the few studies that did examine the scaling of kinematics, Drucker and Jensen (1996) found that striped surfperch (*Embiotoca lateralis*), which uses only the pectoral fins for swimming, exhibits negative allometry in their pectoral fin span, area, and aspect ratio (AR). In addition, there was no relationship between body size and pectoral fin beat amplitude (Drucker & Jensen, 1996). The latter point was interpreted as supporting the hypothesis that pectoral fins are dynamically similar across body size. They also found that fin beat frequency declines with body size, which is also supported by previous work (Bainbridge, 1958). By contrast, zebrafish pectoral fin area and span both scale with positive allometry, although measurements of AR were not made (McHenry & Lauder, 2006). It is not currently understood why fishes would exhibit differences in the scaling of fin form and function (but see, e.g., Fish, 1990), but such observations reinforce that additional data are necessary.

Chondrichthyes (Holocephali + Elasmobranchii) represent an ancient group of fishes originating approximately 430 million years ago in the Silurian (Coates, Gess, Finarelli, Criswell, & Tietjen, 2017; Inoue et al., 2010), and are therefore in a critical position in the gnathostome phylogeny (Qiao, King, Long, Ahlberg, & Zhu, 2016). Holocephalans are in a significant evolutionarily position with ancestors originating at least 300 million years ago (Grogan & Lund, 2004). The earliest extant lineages likely arose approximately 167 million years ago in the Jurassic (Inoue et al., 2010). They are cartilaginous fishes that are mostly found in deep water (Didier, 1995), and they typically have relatively large heads and long, tapering bodies and caudal fins (Angulo, Lopez, Bussing, & Murase, 2014; Didier, Kemper, & Ebert, 2012). Locomotion of the spotted ratfish is primarily driven by motions of the highly flexible, and large, pectoral fins (Combes & Daniel, 2001; Foster & Higham, 2010; Maia et al., 2012), which in turn comprise large pectoral fin muscles (Foster & Higham, 2010) relative to other cartilaginous fishes. The caudal fin and body remain fairly rigid during routine swimming, and are unlikely to contribute significantly to propulsion.

The spotted ratfish, *H. colliei*, ranges from the intertidal to just over 900 m depth (Barnett, Earley, Ebert, & Cailliet, 2009), and is found in

relatively shallow water compared to other chimaeroid fishes. It can reach sizes of approximately 100 cm in total length (Love, Mecklenberg, Mecklenberg, & Thosteinsson, 2005). We examined their ontogenetic scaling of fin external morphology, internal muscular anatomy of the fins, and locomotor kinematics. Using an unprecedented body size range of 8 g (15 cm length) to 1,056 g (60 cm length), including up to 76 individuals (depending on the analysis), we addressed the following questions: (a) Given the importance of pectoral fins for steady swimming, how do internal and external pectoral fin morphology scale with body size? We predict that scaling will either be isometric or positively allometric, given the reliance on these fins for swimming. (b) Do kinematics, muscle morphology, and external body and fin morphology exhibit comparable scaling patterns? We expect that muscles of the pectoral fins will exhibit isometric or positive allometric growth, in accordance with the reliance on the pectoral fins for locomotion. Kinematics, as well as body and other fin traits, are expected to scale with isometry. Fin ARs should be independent of body size.

## 2 | MATERIALS AND METHODS

Seventy-six spotted ratfish (*H. colliei*; Lay & Bennett, 1839) were collected by trawling in Barkley Sound off the west coast of Vancouver Island near the Bamfield Marine Sciences Centre (BMSC) during the summers of 2016 and 2017. There was a mix of males and females, but seven individuals were too small to sex. Thus, we did not separate the sexes in our analyses. Depths of capture ranged from 74 to 100 m (Trevor Channel, 48.839115, -125.163503) and from 88 to 100 m (Imperial Eagle Channel, 48.890214, -125.186419). Bottom temperatures range from 6 to 7 °C while the bottom trawls each lasted approximately 30 min. Body mass ranged from 8 to 1,056 g, and body length ranged from 14.7 to 59.7 cm. Healthy fish were immediately transferred to large outdoor holding tanks at the BMSC, and each tank was supplied with continuous seawater and air stones to assist with the maintenance of oxygen level. Tanks had opaque walls and were covered with dark tarps to minimize stress. Following locomotor experiments (in the subset of fish that were used for this part of the study), fish were euthanized with an overdose of buffered MS-222. Unhealthy fish from the trawls were immediately euthanized and used for morphological analyses. All dissections were then carried out on freshly euthanized specimens. All experiments were approved by the Animal Care Committee at the BMSC under protocols UP16-FE-SP-05 and UP17-SP-BMF-05.

### 2.1 | Locomotor experiments

In order to quantify the kinematics of the pectoral fins, a sample of *H. colliei* were recorded swimming in a flowing unfiltered seawater tank, with a GoPro Hero4 Black video camera filming at 120 fps (GoPro Inc, San Mateo, CA). The seawater tank was equipped with a grid made out of 2 cm × 2 cm squares on the wall opposite the camera in order to scale the fin motions digitally. This also allowed us to correct for any distortion from the lenses.

Using ImageJ (bundled with 64-bit Java 1.8.0\_112, Wayne Rasband Developers 1997), five cycles of fin movement, tracking the tip of the pectoral fin, were measured for each of the eight individuals. Fin beat

**TABLE 1** Scaling relationships for the variables examined in this study

Variable	N	R <sup>2</sup>	p-Value	Exp slope	Obs slope	SE slope	Lower CI	Upper CI	Scaling
Pec span	72	0.95	<.001	0.33	0.296	0.008	0.280	0.311	Negative
Pec area	73	0.95	<.001	0.66	0.642	0.060	0.582	0.701	Isometric
Pec AR	72	0.13	.002	0	-0.049	0.015	-0.079	-0.019	NA
Pec chord 12.5%	63	0.93	<.001	0.33	0.329	0.012	0.305	0.352	Isometric
Pelv span	51	0.90	<.001	0.33	0.400	0.028	0.344	0.456	Positive
Pelv area	74	0.94	<.001	0.66	0.759	0.023	0.712	0.805	Positive
Pelv AR	51	0.01	.463	0	-0.024	0.047	NA	NA	NA
Pelv chord 12.5%	37	0.89	<.001	0.33	0.370	0.022	0.325	0.416	Isometric
First Dors span	52	0.91	<.001	0.33	0.347	0.016	0.316	0.379	Isometric
First Dors area	74	0.91	<.001	0.66	0.632	0.023	0.587	0.677	Isometric
First Dors AR	52	0.03	.118	0	0.043	0.036	NA	NA	NA
Pec ADDS mass	20	0.98	<.001	1.00	1.088	0.038	1.008	1.168	Positive
Pec lev 3 mass	20	0.97	<.001	1.00	1.064	0.043	0.975	1.154	Isometric
Pec lev 2 mass	19	0.92	<.001	1.00	1.037	0.072	0.886	1.188	Isometric
Pec AbDS mass	20	0.99	<.001	1.00	1.143	0.032	1.076	1.210	Positive
Pelv ADDS mass	20	0.99	<.001	1.00	1.172	0.032	1.105	1.240	Positive
Pelv AbD pro	20	0.99	<.001	1.00	1.278	0.035	1.205	1.352	Positive
Pec amplitude	8	0.83	<.001	0.33	0.390	0.072	0.213	0.567	Isometric
Pec frequency	8	0.65	.016	Neg <sup>a</sup>	-0.181	0.054	-0.314	-0.048	NA
Frontal area	52	0.94	<.001	0.66	0.763	0.028	0.707	0.819	Positive
Caudal fin area	42	0.63	<.001	0.66	1.053	0.128	0.794	1.312	Positive

Pec = pectoral; pelv = pelvic; AR = aspect ratio; dors = dorsal; ADDS = adductor superficialis; AbDS = abductor superficialis; lev = levator; AbD Pro = abductor proximalis.

<sup>a</sup> This is based on previous studies (Drucker & Jensen, 1996; Mussi et al., 2002) and biomechanical theory.

frequency was quantified as the number of fin beats (over five cycles) divided by the duration. The maximum amplitude was defined by the top of the stroke (peak), where the fin begins its descent, and the bottom of the stroke (trough), where the fin begins to move up again. We only assessed movement in the vertical plane, which may impose a limitation on our results. The average velocity of pectoral fins was quantified as the amplitude divided by duration of movement. Swimming speed was comparable among all trials (held station in flowing water), but the exact flow rate of the water was not quantified. Based on fin beat frequency and body size measurements, it is likely that the speeds of the ruffin in our study approximated 0.15 m/s, as in Combes and Daniel (2001). The speed of flowing water elicited a steady and sustainable speed.

## 2.2 | External fin and body morphology

Digital images (Panasonic Lumix DMC-FZ1000, Panasonic Corporation, Osaka, Japan) were obtained of intact pectoral, pelvic, caudal, and dorsal fins on euthanized animals, and were analyzed using ImageJ. Sample sizes for morphological traits varied (see Table 1) due to unforeseen damage to fins due to the trawling procedure. Pectoral and pelvic fins were measured from dorsal view images, whereas the first dorsal fin and the upper lobe of the caudal fin were measured from lateral view images (Figure 1). For each fin, we calculated the span ( $L$ ), defined as the distance from the base of the midpoint of the fin, at the fin-body junction, to the farthest tip of the fin (Figure 1). Also calculated were fin surface area ( $S$ ) and fin AR, defined as  $L^2/S$ . Finally, we quantified the chord length of the pectoral and pelvic fins at 12.5% of the span (Figure 1). We selected this location because it closely

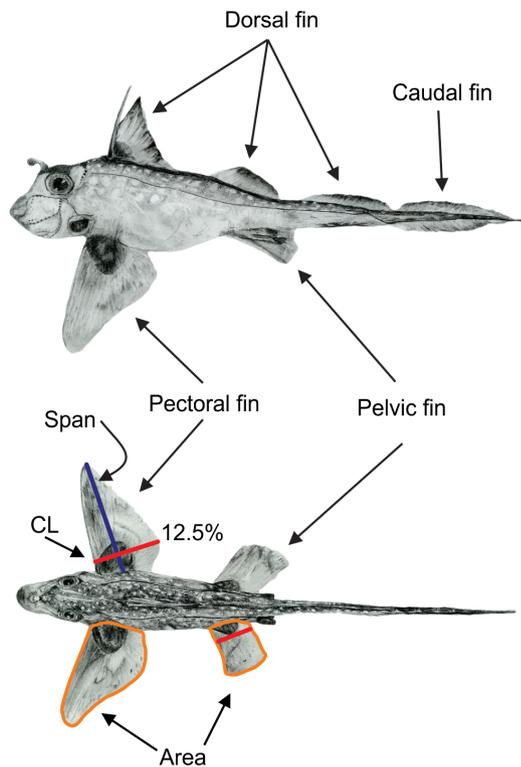
represents the greatest distance between the leading and trailing edge of the fin. The frontal area of the body was quantified using an anterior image of freshly euthanized specimens; the dorsal and pectoral fins were not included in this measurement. Of note, frontal area and fin area can be used as proxies for profile and fin drag, respectively; profile drag is expected to be the dominant drag force acting on the body.

## 2.3 | Fin muscle morphology

Seventeen individuals, ranging from  $23.7 \pm 0.1$  to  $538.2 \pm 0.1$  g, were euthanized (as above), weighed (OHAUS EP2102  $\pm 0.1$  g), and then dissected for fin muscles. Left pectoral and pelvic fins were skinned and six muscles were measured for each fish. The four pectoral muscles were the adductor superficialis, abductor superficialis, levator 3, and levator 2 (Figure 2). The two pelvic fin muscles were the adductor superficialis and the abductor proximalis, as described by Diogo and Ziermann (2015). Fascicle lengths were measured using Mastercraft electronic calipers ( $\pm 0.02$  mm), and each muscle was extracted from the body and weighed (Adventure Pro AV264  $\pm 0.0001$  g). Pectoral fin muscles that originated within the body wall were followed to their points of origin and extracted in order to determine the total mass.

## 2.4 | Scaling and statistics

Ontogenetic changes in morphology and kinematics were assessed according to the power-law function  $y = aM_b^b$ , where  $M_b$  is body mass (in grams) and  $b$  is the scaling exponent. All data were  $\text{Log}_{10}$



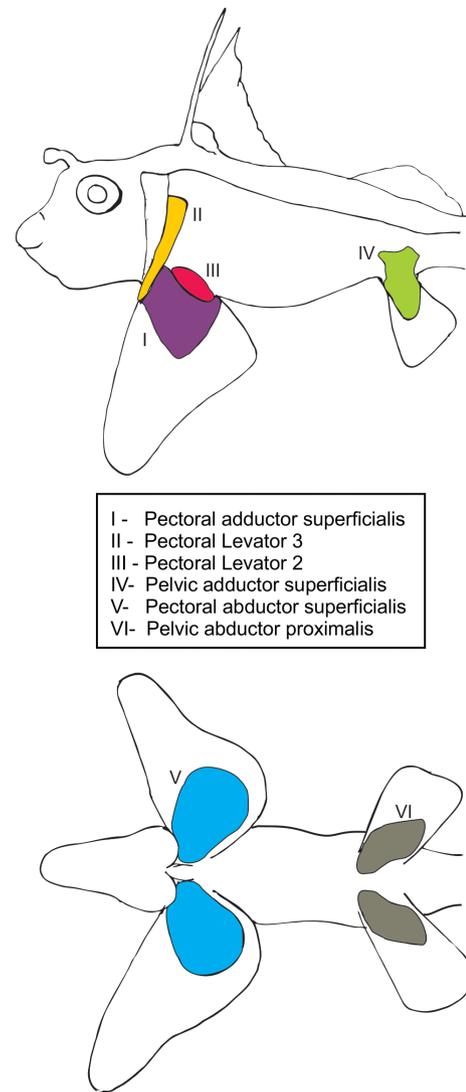
**FIGURE 1** Illustrations of a ratfish in lateral (top) and dorsal (bottom) showing the measurements in our study. The dorsal fin has three lobes, although we only assessed the span, aspect ratio, and area of the first dorsal (anterior). The caudal fin has an upper and lower lobe, although we only quantified the area of the upper lobe. Chord length was quantified in both the pectoral and pelvic fins at 12.5% of the total span of the fin, and was perpendicular to the span

transformed prior to analyses and then related to  $\log_{10}M_b$  using the least-squares linear regression model. This model was chosen over a reduced major axis regression because we selectively maximized variation in the independent variable (body size), as in Drucker and Jensen (1996). Allometric equations then took the form:  $\log y = \log a + b \log M_b$ . To compare the scaling exponents to those expected from isometry, the 95% confidence interval of the slope was first calculated. If the expected value fell within the confidence interval, the relationship was considered isometric, but an exponent below or above the expected value was considered negative allometry or positive allometry, respectively. Geometrically similar organisms are expected to have linear dimensions that scale with  $M_b^{1/3}$ , measures of area proportional to  $M_b^{2/3}$ , and measures of mass proportional to  $M_b^1$ . Stride frequency was expected to scale negatively with body mass (Drucker & Jensen, 1996). Similar to previous studies (e.g., Drucker & Jensen, 1996), we predicted that AR should be independent of body size. All statistics were performed in Systat Version 13.

### 3 | RESULTS

#### 3.1 | Scaling of internal muscle morphology

The pectoral adductor superficialis ( $\alpha$  to  $M_b^{1.09}$ ) and the pectoral abductor superficialis ( $\alpha$  to  $M_b^{1.14}$ ) exhibited positive allometry

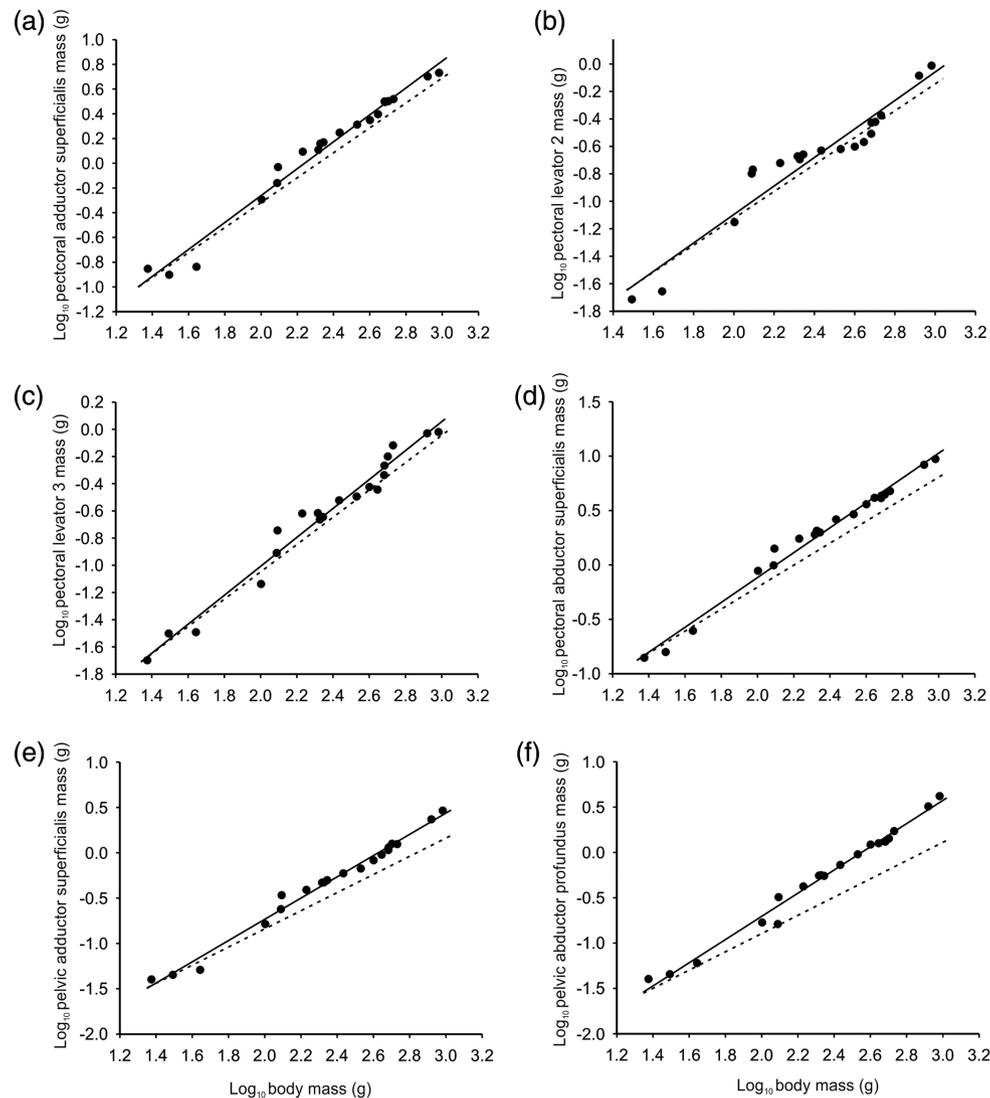


**FIGURE 2** Illustrations of the muscles examined in our study. The top illustration is a lateral view and the bottom is a ventral view. We examined four pectoral fin muscles (I, II, III, and V), and an abductor and adductor of the pelvic fins (IV and VI)

(Figure 3a,d), whereas the Pectoral levator 3 ( $\alpha$  to  $M_b^{1.06}$ ) and pectoral levator 2 ( $\alpha$  to  $M_b^{1.04}$ ) displayed isometry (Figure 3b,c; Table 1). For the pelvic fin muscles, both the adductor proximalis ( $\alpha$  to  $M_b^{1.28}$ ) and abductor superficialis ( $\alpha$  to  $M_b^{1.17}$ ) exhibited positive allometry (Figure 3e,f; Table 1).

#### 3.2 | Scaling of external fin and body morphology

Body frontal area scales with  $M_b^{0.76}$ , reflecting positive allometry (Table 1, Figure 4b). Pectoral fin area ( $M_b^{0.64}$ ) and chord length ( $M_b^{0.33}$ ) increased with isometry, while span (Figure 5a) increased with negative allometry. Pectoral fin AR decreased with body size (Figure 5d). Pelvic fin area ( $M_b^{0.76}$ ) and span ( $M_b^{0.40}$ ) increased with positive allometry, while chord length ( $M_b^{0.37}$ ) and AR was size invariant (Figure 6). Dorsal fin span (Figure 4d) and area (Figure 4e) scaled with isometry, while caudal fin area increased with positive allometry (Figure 4f). Dorsal fin AR was size invariant (Figure 4c).



**FIGURE 3** The scaling of pectoral (a–d) and pelvic (e, f) muscle mass with body mass. Isometric growth was observed for the levator 2 and levator 3 muscles of the pectoral fin, whereas positive allometric growth was observed in the remaining four muscles. All axes were  $\log_{10}$ -transformed. The dashed line represents the expected slope under isometry, and the solid line represents the regression using our data

### 3.3 | Scaling of locomotion

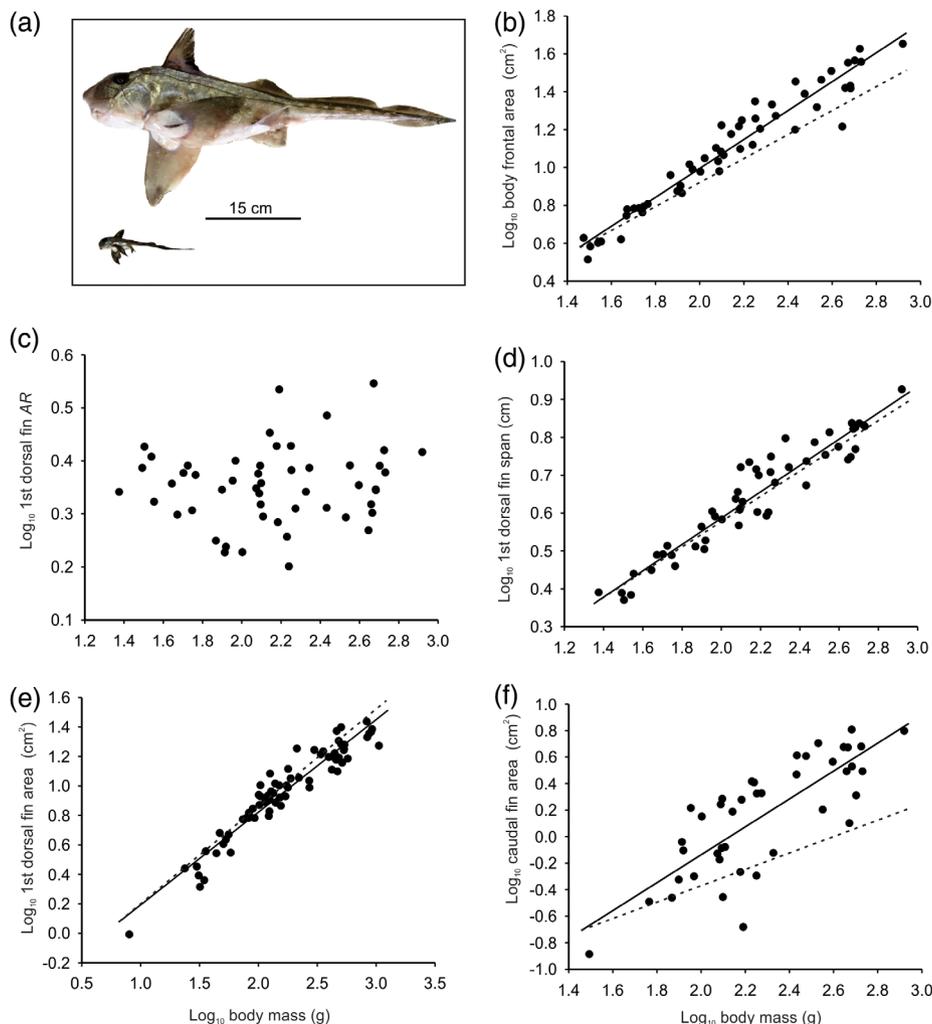
Pectoral fin amplitude during steady swimming exhibited an isometric pattern of growth with respect to body mass ( $\alpha$  to  $M_b^{0.39}$ ; Figure 7a), whereas pectoral fin beat frequency exhibited a negative relationship with body mass ( $\alpha$  to  $M_b^{-0.18}$ ) (Figure 7b; Table 1). Furthermore, pectoral fin velocity increased with body size, despite a constant swimming velocity ( $R^2 = 0.35$ ,  $p < .05$ ).

## 4 | DISCUSSION

The locomotor system of the spotted ratfish exhibits a complex pattern of growth. We found that, although some internal and external structures within a functional unit exhibited differential growth patterns (e.g., pectoral fin), some exhibited similar patterns (e.g., pelvic fin). Several of these patterns may be related to hydrodynamic shifts, including thrust generation and efficiency (e.g., lift-to-drag ratio).

### 4.1 | Pelvic and pectoral muscle morphology

The pectoral fins of ray-finned fishes are typically actuated by a complex suite of muscles that can control the position of the fin relative to the body and also the conformation of the fin surface (Lauder & Drucker, 2004). These include, among others, the abductor complex that drives the downstroke and an adductor complex that drives the upstroke (Westneat, 1996; Westneat et al., 2004). Across chondrichthyans, pectoral fin muscles can vary considerably in morphology, depending on the role that the pectoral fins play (Diogo & Ziermann, 2015; Goto, Nishida, & Nakaya, 1999; Maia et al., 2012). In ratfish, the levator 3 elevates and adducts the pectoral fin, but also rotates it laterally (Diogo & Ziermann, 2015). By contrast, levator 2 elevates, adducts, and rotates it medially (Diogo & Ziermann, 2015). The adductor and abductor superficialis muscles generally elevate and depress the pectoral fin, respectively (Didier, 1987). The broad abductor superficialis and adductor superficialis of the ratfish in our study both exhibited positive allometry, and the pectoral musculature comprises



**FIGURE 4** (a) Photographs of the largest and smallest ratfish used in this study. The ratfish above is just over 1 kg (approximately 60 cm in length) and the ratfish below is 8 g (approximately 15 cm in length). Also shown is the scaling (with respect to body mass) of (b) body frontal area, (d) dorsal fin span, (e) dorsal fin area, and (f) the area of the upper lobe of the caudal fin. Dorsal fin aspect ratio is shown in (c). For detailed results, see the manuscript text. All axes were  $\log_{10}$ -transformed. Frontal area and caudal fin area exhibited positive allometry. Dorsal fin span and area exhibited isometry, whereas there was no relationship between dorsal fin aspect ratio and body mass. The dashed line represents the expected slope under isometry, and the solid line represents the regression using our data

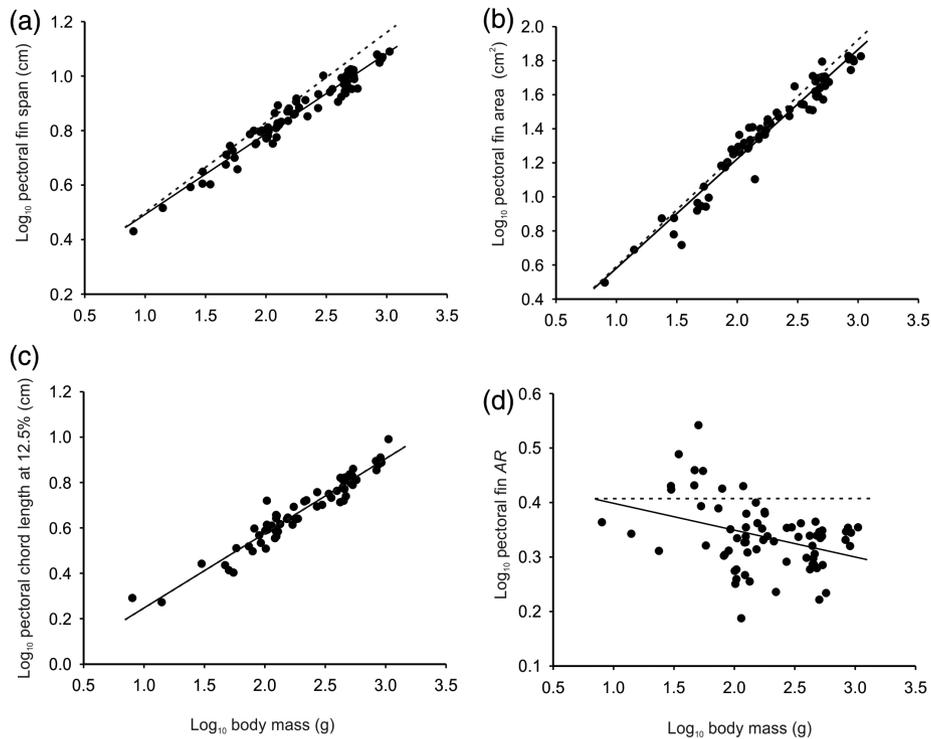
1.0–2.2% of total body mass. Given that the mass of the muscle can reflect its force-generating capability (Thorsen & Westneat, 2005), the relative increase in mass may assist ratfish with the increased velocity of the pectoral fins, as discussed below. Furthermore, it may also compensate for the reduced AR and increased chord length, both of which will decrease thrust and efficiency, and consequently increase acceleration performance (Combes & Daniel, 2001; Webb, 1984).

Pelvic fins, although understudied (Lauder & Drucker, 2004), are critical for locomotion in fishes (Harris, 1936; Harris, 1938; Standen, 2008; Standen, 2010). Similar to the pectoral fins, muscles of the pelvic fins control both movement and surface conformation (Lauder & Drucker, 2004). In rainbow trout, they help control speed and stabilize the body position during slow speed locomotion (Standen, 2010). Among holocephalans, the role of the pelvic fin is unknown. We found positive allometric growth of the adductor superficialis and abductor proximalis muscles of the pelvic fins, which likely contribute to an increased reliance on these fins for maneuvering, stability, and perhaps even making contact with the benthos.

## 4.2 | Scaling of external fin morphology

For spotted ratfish, there are shifts in fin shape and function with growth. Pectoral fin span exhibited negative allometry, leading to a relative decrease in the moment arms of these fins. This could depress the ability to execute and stabilize angular maneuvers and disturbances (e.g., yawing or rolling), respectively, although this would require further research. Furthermore, pectoral fin area scaled with isometry, and hence, larger ratfish likely experience less total fin drag. This, combined with the negative allometry of fin span, results in a decreased AR with body size. The lower AR likely promotes increased acceleration performance while sacrificing efficiency (Combes & Daniel, 2001; Webb, 1984). This may relate to the types of predators that are consuming large versus small ratfish. Smaller ratfish may face somewhat slower predators, whereas larger ratfish may face relatively fast predators.

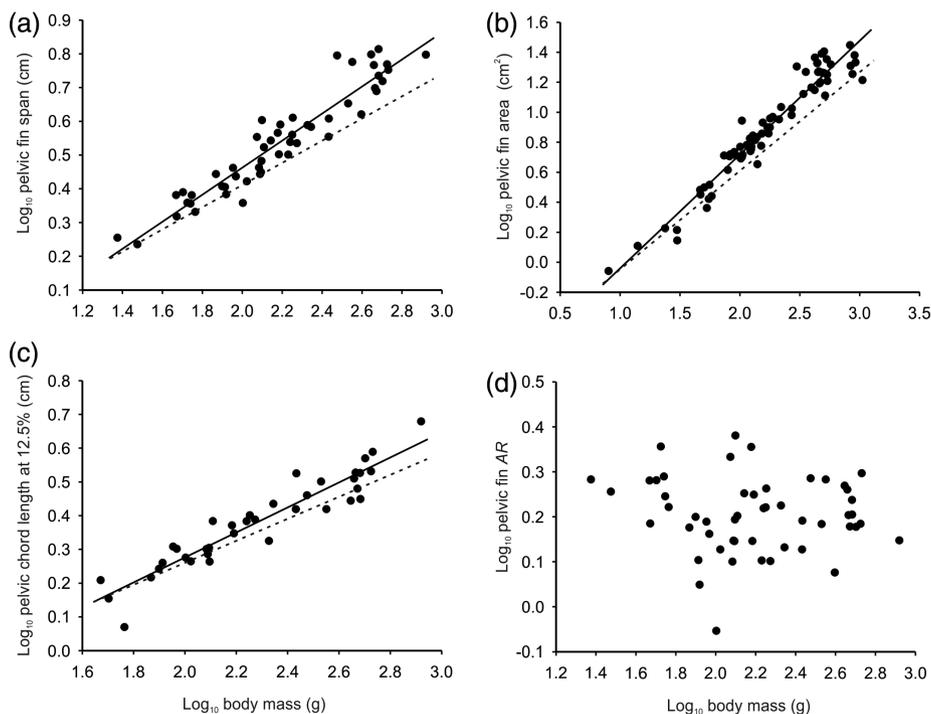
As ratfish grow, pelvic fin area and span increased more than expected from isometry. This, coupled with isometric growth of chord length, resulted in a fin shape that can generate more thrust by vortex



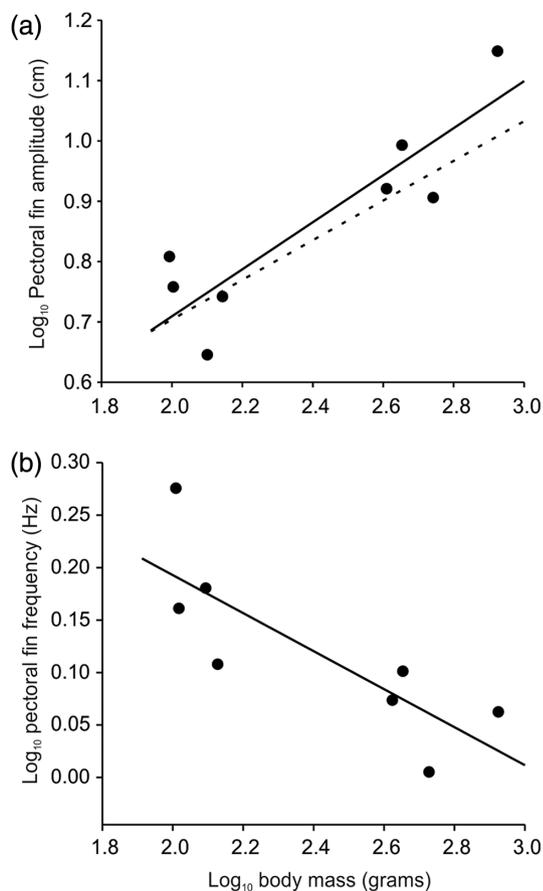
**FIGURE 5** The relationships between (a) pectoral fin span, (b) area, (c) chord length, and (d) aspect ratio, and body mass. All axes were  $\log_{10}$ -transformed. Span exhibited negative allometry, whereas area and chord length exhibit isometry. Aspect ratio was negatively related to body size. The dashed line represents the expected slope under isometry, and the solid line represents the regression using our data

shedding (Drucker & Lauder, 1999; McHenry & Lauder, 2006). Pelvic fin AR was not impacted by body size (Figure 6). In addition, the increased span, although with a slope less than 1, will increase the moment arm and drag, which may be important for maneuvers such

as braking (Geerlink, 1987; Higham, 2007a, 2007b; Higham et al., 2005). These increases in thrust and moment arm are accompanied by positive allometric growth of the adductor superficialis and abductor proximalis muscles of the pelvic fin. As noted by Maia et al. (2012),



**FIGURE 6** The relationships between (a) pelvic fin span, (b) area, (c) chord length, and (d) aspect ratio, and body mass. All axes were  $\log_{10}$ -transformed. Pelvic fin span and area exhibit positive allometry, whereas pelvic fin chord length exhibited isometry. Aspect ratio was not significantly correlated with body mass. The dashed line represents the expected slope under isometry, and the solid line represents the regression using our data



**FIGURE 7** The relationship between (a) pectoral fin amplitude and body mass and between (b) pectoral fin beat frequency and body mass. Amplitude increased with body size (isometry), whereas frequency decreased. The dashed line represents the expected slope under isometry, and the solid line represents the regression using our data

pelvic fin function is poorly understood among holocephalans and requires mechanical investigations. At this point, the role of the pelvic fins in ratfish is not understood, although it appears that they are potentially used for steering and braking and gliding (pers. obs.).

The role of the dorsal and caudal fins in ratfish is not entirely clear, although they likely contribute to rotational maneuverability and stability, as observed in closely related sharks (Domenici & Blake, 1997; Domenici, Standen, & Levine, 2004). Dorsal fin span and area increased with isometry and, consequently, the moment arm and fin drag are relatively less in larger ratfish. The AR of the dorsal fin also increased with isometry, and hence, the lift-to-drag ratios of these fins are constant. Furthermore, caudal fin area increased with positive allometry, and accordingly, drag is greater relative to mass in larger ratfish. Given that the tail does not appear to be involved in routine swimming, if ratfish perform C-starts (for review, see Domenici & Blake, 1997), this fin may have a role in maintaining the capacity to yaw a body with greater mass in fast-start swimming to escape predators.

### 4.3 | Aspect ratio

The shape of fins, especially pectoral fins, plays a major role in the locomotor performance and mechanics of pectoral swimming fishes (Higham et al., 2005; Walker & Westneat, 2002b). Fin AR, reflecting

the ratio of lift to drag, is an important measure of fin shape, and has been implicated in the divergence of fishes along key axes of ecological variation (Fulton & Bellwood, 2004; Wainwright et al., 2002). Surprisingly, few studies have examined the ontogenetic scaling of fin AR and compared this to predictions based on geometric similarity. Among reef fishes from the Pomacentridae and Labridae, pectoral fin AR either remains constant or increases with body size (Fulton, 2010; Wainwright et al., 2002). In addition, those adult fishes that are found in high-flow environments tend to have higher values of AR, which conveys the ability to swim faster. By contrast, surfperches exhibit a decrease in AR with increased body size (Drucker & Jensen, 1996). We found that pectoral fin AR, but not pelvic fin AR, was impacted by body size, with a negative relationship being observed for the pectoral fins. This is in contrast to previous work in reef fishes, but the habitat of these groups is vastly different. Ratfish are not likely contending with high flow speeds, and the decreased AR with body size may reflect the need for greater drag-based motions.

### 4.4 | Scaling of kinematics

In a previous study of ratfish kinematics, Foster and Higham (2010) found no relationship between body length and pectoral fin amplitude or fin beat frequency. By contrast, we found that both amplitude and frequency were correlated with body mass, although the former increased with body mass (isometry) and the latter decreased with body mass. It is unclear why the two studies might differ, although the previously published paper used only four individuals. In addition, although we did not determine the exact speeds of the ratfish in our study, estimations based on the body size and fin beat frequency suggest that the fish were swimming close to 0.15 m/s, as in Combes and Daniel (2001). This is much slower than the speeds (0.4–0.5 m/s) of the ratfish in Foster and Higham (2010), potentially leading to different results. Future studies should determine the scaling of frequency at different locomotor speeds.

The scaling of fin beat frequency among fishes has received very little attention. Shiner perch (*Cymatogaster aggregata*) exhibit a range of negative relationships between frequency and body length that depend on the speed of swimming relative to the gait transition speed (Mussi, Summers, & Domenici, 2002). Among striped surfperch, frequency scales with  $M_b^{-0.14}$  (Drucker & Jensen, 1996). For the ratfish in our study, pectoral fin beat frequency scales with  $M_b^{-0.18}$ . The similarity to striped perch is striking, and is potentially related to the underlying muscle physiology. In a study of Atlantic cod axial muscle fibers, the frequency required to produce optimum muscle power in vitro scales with  $M_b^{-0.17}$  (Anderson & Johnston, 1992). Thus, the scaling of frequency in ratfish may be directly tied to the ability of the pectoral muscles to generate optimum muscle power. To determine if muscle function is influencing the scaling of frequency in ratfish, future work should determine power output in relation to frequency in the main pectoral fin muscles of the ratfish, such as the adductor superficialis. The negative relationships between frequency and body mass are also observed among terrestrial quadrupeds. In a study that combined experimental and modeling data, stride frequency of galloping quadrupedal mammals scaled with  $M_b^{-0.13}$  (Herr, Huang, & McMahon, 2002). This has been attributed to mechanical constraints.

In addition, Heglund, Taylor, and McMahon (1974) studied a range of mammals, from mice to horses, and found that stride frequency scaled with  $M_b^{-0.14}$ . This relationship is very similar to that expected from elastic similarity, rather than geometric similarity (McMahon, 1975). Therefore, it appears that fin beat/stride frequency of aquatic and terrestrial vertebrates are comparable, despite the fact that elastic similarity is typically associated with terrestrial locomotion where supporting structures risk elastic failure due to body weight (Gunther & Morgado, 1983).

Pressure drag depends on the frontal area of the fish's body, and this increased for ratfish, but with negative allometry. Therefore, for a given swim speed, there appears to be a relative decrease in pressure drag that must be overcome by the pectoral fins. Furthermore, fin beat velocity increased in larger ratfish, and in conjunction with increased and decreased fin beat amplitude and frequency, respectively, positive allometry in the pectoral fin muscles, and pectoral fins that are shaped for relatively better burst acceleration performance, it seems likely that larger ratfish may be shifting to a burst and coast swimming behavior, which has been modeled to improve the economics of swimming in koi carps by up to 45% (Wu, Yang, & Zeng, 2007).

The increased burst acceleration performance might also be linked to predation shifts throughout ontogeny, although it is unclear whether specific predators will select for different sized ratfish. For example, the sixgill shark, *Hexanchus griseus*, is a predator of ratfish (Andrews & Quinn, 2012), and they can likely consume ratfish of any size. Other predators include elephant seals (*Mirounga angustirostris*), Pacific halibut (*Hippoglossus stenolepis*), and Spiny dogfish (*Squalus acanthias*; Andrews & Quinn, 2012). Given the size range of these predators, it is unclear whether shifts in predation will occur as ratfish grow. In addition, the attack performance of these predators, including scaling parameters, is poorly understood. More work is needed to assess how escape responses and behaviors might differ with ontogenetic shifts in body size among ratfish, as well as attack performance among predators. We predict that larger predators of larger ratfish will exhibit greater acceleration and velocity during attacks, given the ontogenetic shifts toward greater acceleration performance in ratfish.

#### 4.5 | Conclusions and future directions

Holocephalans diverged from elasmobranchs over 400 million years ago (Inoue et al., 2010), although it is unclear whether early holocephalans resembled extant groups. However, all extant species appear to use similar locomotor modes involving pectoral fin flapping as the primary mode of propulsion. Our results highlight the complex growth patterns, both internally and externally, of the locomotor system of the spotted ratfish. Although we lack information regarding locomotor function in other species of holocephalans, and for fins other than the pectorals, it is likely that the pelvic fins increase in importance as ratfish grow. The caudal fin is very thin compared to other fishes, but does exhibit positive allometric growth. This suggests that the caudal fin may play a greater role in adult fish, potentially during escape maneuvers. As noted earlier, ratfishes are interesting in that they utilize flapping pectoral fins to drive movement, and they diverged from elasmobranchs early in the gnathostome phylogeny. Thus, examining these species will provide great insight into the evolution of

mechanisms underlying pectoral-driven aquatic movement. This must be coupled with detailed studies of ecology throughout ontogeny.

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