

The morphological basis of labriform rowing in the deep-sea Bigscale *Scopelogadus beanii* (Percomorpha: Beryciformes)



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ABSTRACT

A recent shipboard video reveals that the deep-sea melamphaeid fish *Scopelogadus beanii* is capable of rowing labriform propulsion. These data indicate that *S. beanii* engages in powerful and highly maneuverable drag-based locomotion, an energetically expensive swimming mode in which the pectoral fin produces thrust from a fore-aft rowing stroke. The pectoral-girdle musculoskeletal morphology, including muscle insertions and origins is described herein, and estimations of isometric force produced by each division are reported based on calculations of physiological cross-sectional area. The study species possesses similar adductor muscle configuration but has one fewer abductor muscle as compared to previously studied rowers. In addition, girdle muscle masses are compared with a previously published morphospace of labriform swimmers. From this analysis, it is inferred that muscles occupying a portion of morphospace not yet described for rowing fishes, power the dynamic sculling of *S. beanii*. Placing these results in an ecomorphological context, the resource utilization of *S. beanii* is considered, specifically that it is a consumer of gelatinous zooplankton, a consistently distributed food resource. Although *S. beanii* resides in the dimensionless bathypelagic zone of the open ocean, a swimming mode that increases maneuverability is perhaps an adaptation to feed among dense aggregations of its prey.

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1. Introduction

The behavior of the biota that inhabits the largest ecosystem on Earth, the deep pelagic ocean, remains largely unexplored. Because of the inherent difficulties of studying or capturing animals at depth, in-situ and laboratory experiments focusing on the locomotion of deep-sea fishes are few (but see Cowles and Childress, 1995; Collins et al., 1999; Moore and Schaefer, 2002; Bailey et al., 2003; Luck and Pietsch, 2008). As a result, an understanding of the relationships between locomotor morphology, function, and behavior in these species remains elusive. A few studies, however, have addressed locomotor behavior in pelagic fishes. Both Moore and Schaefer (2002) and Luck and Pietsch (2008) described the swimming behavior of ceratioid anglerfishes of the genera *Gigantactis* and *Oneirodes*, respectively, and concluded that these species are carangiform swimmers, rapidly oscillating the caudal fin during bursts of dynamic propulsion. Referencing the luring behavior of ceratioids (see Pietsch, 2009), the authors of these studies inferred that the ecological importance of burst carangiform swimming was associated with a lie-and-wait foraging strategy. Although the data are limited, these studies indicate that the behavioral link between lie-and-wait foraging and caudal-driven locomotion exist in deep-sea taxa just as it does for shallow-water taxa (Webb, 1984).

Even less is known about the locomotor behavior of fishes utilizing other common foraging strategies in the pelagic deep-sea. To the authors' knowledge, no previous study has reported the locomotor type of a pelagic planktivore, another common feeding guild in the deep-sea (Gartner et al., 1997). Here, for the first time, the swimming behavior of a deep-sea zooplankton specialist is described based upon shipboard video of a freshly captured specimen of *Scopelogadus beanii* (Günther) taken in the western North Atlantic. *S. beanii* is a member of the beryciform family Melamphaeidae that is widely distributed in tropical to subtropical bathypelagic waters of the North Atlantic, South Pacific, and Indian Oceans (Ebeling and Weed, 1963). Video analysis demonstrates that this species is a strong labriform swimmer capable of powerful and highly maneuverable rowing, a behavior common to several groups of shallow-water fishes utilizing dense aggregations of food resources (Bellwood and Wainwright, 2001; Fulton et al., 2001; Werner and Hall, 1974). The objectives of this study were threefold: to establish (1) the morphological basis of sculling in *S. beanii*; (2) whether this specialized locomotor type is powered by pectoral-fin musculoskeletal anatomy similar to other labriform swimmers; and (3) whether the relationship between locomotor and foraging behavior of *S. beanii* is congruent with other fishes that inhabit less formidable environments. To achieve objectives 1 and 2, new osteological and myological data from *S. beanii* are integrated, including origin-insertion patterns and muscle mass and fin-architecture data, with previously published data for labriform swimmers. To quantify how the pectoral-fin musculoskeletal anatomy differs from other labriform swimmers,

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an analysis of muscle-mass morphospace was undertaken. Lastly, to address the relationship between swimming and foraging modalities (objective 3), novel locomotor and kinematic and behavioral data was combined with published diet data for *S. beanii*.

2. Materials and methods

2.1. Material examined and video analysis

Twenty-two specimens of *S. beanii* were captured with an international young gadoid pelagic trawl (YGP) at an approximate depth of 455 m in the vicinity of Bear Seamount in the western North Atlantic (39°50'17"N, 67°24'48"W) aboard the NOAA vessel R/V *Delaware II* on 5 June 2004. To retain the captured fish alive, the codend of the YGP was equipped with a light aluminum holding tank with an approximate volume of 10³ L (see Lacroix et al., 2005). One specimen (7.5 cm SL) taken alive was removed from the holding tank within 5 min of coming aboard and placed in a 18.9-L glass aquarium filled with seawater at approximately 20 °C. The specimen was then immediately filmed at 15 frames per second with a Nikon CoolPix 5400 (Nikon, Melville, NY) under the ship laboratory lighting and a 150-W fiber-optic light source (see Video S1). After video recording, all specimens were then fixed in sea-water buffered formalin for up to 10 days and later transferred to 70% ethanol for storage. The recorded specimens and 17 other individuals were deposited in the Museum of Comparative Zoology, Harvard University (MCZ 164310, 7.5–25 mm SL). Another three specimens from the same trawl were accessioned into the Yale Peabody Museum of Natural History (YPM ICH14962, 29–49 mm SL); while another five specimens of *S. beanii* captured from the same locality but taken in April, 2005 (MCZ 165261, 75–108 mm SL) were the source of all anatomical observations and morphological data.

Dissections were performed under a Leica MZ7.5 stereoscope (Leica Microsystems, Wetzlar, Germany). All musculoskeletal terminology follows Winterbottom (1974). Dissection began by skinning each specimen then detaching the left pectoral girdle by removing the obscuring hypaxial muscle, separating the cleithrum at its anterior articulation with the contralateral element, and disarticulating the posttemporal from the neurocranium. Photographs of the lateral and medial aspects of the whole girdle were then taken with a Nikon D5 digital SLR camera; these images were then analyzed in estimates of physiological cross-sectional area (see below). The whole left girdle from a single specimen (97 mm SL) was set aside for visualization of in-situ muscle morphology by X-ray microtomography (micro-CT; see below). After digital imaging and micro-CT analysis, the origin and insertion for each girdle muscle were recorded before removal with blunt forceps. Dissected muscles were then immersed in 2.0 M phosphate-buffered saline for 30 h to rehydrate, then blotted dry with paper towels before being massed on a Mettler AE50 analytical balance scale to 0.0001 g. To estimate the relative contribution of each muscle to propulsion, the mass of each adductor and abductor muscle was divided by the total girdle-muscle mass. Recorded as percentages (means presented in Table 1, raw data in

Table 1

Estimations of and data used to calculate physiological cross-sectional area (PCSA) and maximal force (F_{muscle}) for pectoral-fin muscle of *Scopelogadus beanii*. Data are reported as mean ± standard error of the mean (s.e.). Mass and fiber-length data were taken from the left pectoral girdle of five specimens (75–108 mm SL; see Material examined and video analysis).

	Mass (g)	% girdle mass ^a	Fiber length (mm)	PCSA (cm ²)	F_{muscle} (N)	% total PCSA- F_{muscle}
ABS	0.0043 ± 0.0003	7.6%	5.51 ± 0.52	0.0075	0.15	12.2%
ABP	0.0074 ± 0.0008	13.0%	5.64 ± 0.26	0.0123	0.25	20.0%
ADS	0.0073 ± 0.0010	12.9%	8.66 ± 0.42	0.0080	0.16	13.0%
ADP	0.0333 ± 0.0050	60.5%	11.46 ± 0.60	0.0270	0.54	44.0%
ARRD	0.0057 ± 0.0009	9.8%	7.93 ± 0.51	0.0066	0.14	10.7%

ABS, abductor superficialis; ABP, abductor profundus; ADS, adductor superficialis; ADP, adductor profundus; and ARRD, arrector dorsalis.

Table S1), these data were compared to Thorsen and Westneat's (2005) dataset that included comparable data from labriform swimmers of the families Acanthuridae, Cichlidae, Chaetodontidae, Embiotocidae, Labridae, Mullidae, and Zanclidae. To assess how similar adductor and abductor muscle masses of *S. beanii* are to fishes of these families, a principle component analysis (PCA) was performed based on a covariance matrix of five muscle percentages: abductor superficialis (ABS), abductor profundus (ABP), adductor superficialis (ADS), adductor profundus (ADP), and arrector dorsalis (ARRD). The arrector ventralis (ARRV) was absent in *S. beanii* and a minor component of the species analyzed by Thorsen and Westneat (2005: Table 3); thus, data for this muscle were not included in the PCA. Before PCA, muscle percentages were arcsine transformed following Sokal and Rohlf's (1995) suggestion for proportions.

2.2. Muscle force estimations

To further characterize the contribution of each muscle to pectoral-fin propulsion, maximal force was estimated according to division-specific physiological cross-sectional area (PCSA). Maximal muscle force (F_{muscle}) was calculated as follows:

$$F_{muscle} = PCSA \cdot F_{iso},$$

where F_{iso} equals the maximal isometric force produced by muscle per unit of mass. A value of 20 N/cm² was used for F_{iso} , the maximal force produced by fish white muscle according to James et al. (1998). PCSA was calculated as:

$$PCSA = \frac{M_{muscle} \cdot \cos(\theta)}{\rho \cdot FL},$$

where M_{muscle} and θ are mass and pennation angle, respectively, and ρ and FL are muscle density and fiber length, respectively. Values for muscle masses are those reported in Table 1. All pectoral-girdle muscles observed in *S. beanii* were fusiform and parallel; thus, θ was 0 in all cases. For ρ , a value of 1.05 g/cm³ was used, the density of fish white according to Lowndes (1955). FL was computed as the average fiber length based on ten measurements taken across the muscle. Individual FL measurements were taken from adductor- and abductor-side images processed in ImageJ1.44p (Rasband, 2013). PCSA and F_{muscle} estimates are reported in Table 1.

2.3. Micro CT and double staining

To visualize in-situ muscle morphology, the pectoral girdle of a single specimen (97 mm SL) was dissected, removed from the body, and soaked in 0.3% phosphotungstic acid (PTA) for three days following Metscher (2009). After soaking the girdle in PTA for three days, the specimen was scanned in a SkyScan1173 high-energy spiral-scan micro-CT unit (Micro Photonics, Inc., Allentown, PA). Scan parameter values for amperage, voltage, exposure time, and image rotation were 55 μ A, 110 kV, 730 ms, and 0.5°, respectively. The scan produced a voxel size of 12 μ m. After slice reconstruction in NRecon (Micro Photonics, Inc.), segmentation and volume rendering were performed in Mimics 15.0 (Materialise, Leuven, Belgium).

To assess girdle osteology and fin-ray segmentation and bifurcation, parameters known to affect fin-ray stiffness and performance (Flammang et al., 2013), full girdles from three specimens (95–105 mm SL) were cleared and double-stained following Dingerkus and Uhler (1977). Images of the three girdles were taken under the stereoscope with a Nikon Coolpix 4500. Girdle images were then processed in ImageJ to enumerate segments and measure pre- and post-bifurcation lengths along the five longest rays taken following Flammang et al. (2013). Mean segment length and distal segmented and bifurcating portions of fin rays are reported in Table 3.

3. Results

3.1. Video analysis and swimming kinematics

A total of twenty-four discrete fin beats were recorded and analyzed. Fin-beat frequency was 2.0 ± 0.07 Hz, with a mean rest period of 0.28 ± 0.03 s between beats. Pectoral-fin beats were synchronous on the left and right sides of the fish (Fig. 1, Supplemental video).

Outstroke of the pectoral-fin beat was characterized by anterior rotation of the dorsal edge of the fin into the direction of travel. At onset of abduction, movement was initiated at the base of the fin and more distal fin elements remained in close association with the body. As the fin pulled away from the body, the flexible distal 50% of the fin was curved backwards and appeared to be dragged through the water by the more proximal portion of the fin. During this period, the midsection of the fin had a maximum curvature of 0.46 mm^{-1} (Fig. 2). As the pectoral fin reached maximum lateral excursion at an angle of approximately 85° from the long axis of the body, wave of curvature had progressed distally to the end of the now straight fin.

During instroke, the proximal portion of the fin was reduced in area while the distal half of the fin was spread in a fan-like shape. Fin rays appeared to be mostly straight during adduction, except for at the beginning of instroke when the distal 85–95% of the fin experienced high oscillatory maximum curvature of 1.11 mm^{-1} (Fig. 2).

3.2. Pectoral-girdle muscle architecture

The musculoskeletal components of the pectoral girdle of *S. beanii* were easily identified based on comparisons with published studies, including Winterbottom's (1974) survey of teleost fishes and Thorsen and Westneat's (2005) investigation of percomorph labriform swimmers. The differences, however, between *S. beanii* and other teleosts, specifically other labriform swimmers, are substantial, including the absence of several muscles. This includes the arrector ventralis (ARRV), adductor medialis (ADM), and adductor radialis (ADR). The ARRV is an adductor-side muscle present in a conservative pattern in labriform swimmers (Thorsen and Westneat, 2005). Medial to the abductor superficialis (ABS) and originating on the anterolateral surface of the cleithrum and the lateral face of the cleithrum and scapula, the ARRV inserts onto the anteromedial base of the first fin ray. The ADM is inconsistently present in teleosts in general (Winterbottom, 1974) and labriform swimmers in particular (Thorsen and Westneat, 2005). In the former, it lies between folds of the adductor superficialis (ADS) and inserts onto the middle fin rays (Thorsen and Westneat, 2005). The ADR, a minute muscle and the most medial adductor, originates on the coracoid and partly on the scapula and inserts variably onto a single or several fin rays (Thorsen and Westneat, 2005).

Descriptions of each muscle present in *S. beanii*, including positions of origin and insertion, are present below and in Fig. 3. The architecture of each muscle is compared to general patterns in other teleosts, especially those with labriform propulsion.

3.2.1. Abductor superficialis (ABS)

The abductor superficialis is the lateral-most muscle of the pectoral girdle. It originates along the entire length of the lateral side of the cleithrum in most teleosts (Thorsen and Westneat, 2005; Winterbottom, 1974), yet, in *S. beanii*, its origination is restricted to the posterior tip of the cleithrum only (Fig. 3). In *S. beanii* the ABS inserts onto all fin rays via tendons, including the first fin ray (Fig. 3). Other authors describe the insertion of the ABS as including all fin rays except the first (Thorsen and Westneat, 2005; Winterbottom, 1974). In some species, it has been noted that the ABS contains two subdivisions (Thorsen and Westneat, 2005). In *S. beanii*, however, there is but a single division of the ABS.

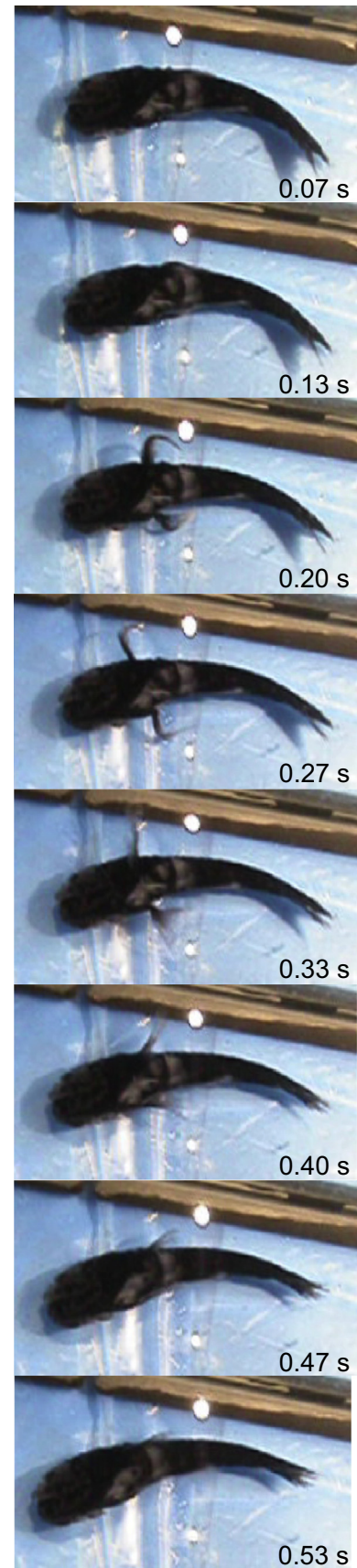


Fig. 1. Single fin beat of *Scopelogadus beanii* filmed at 15 frames per second.

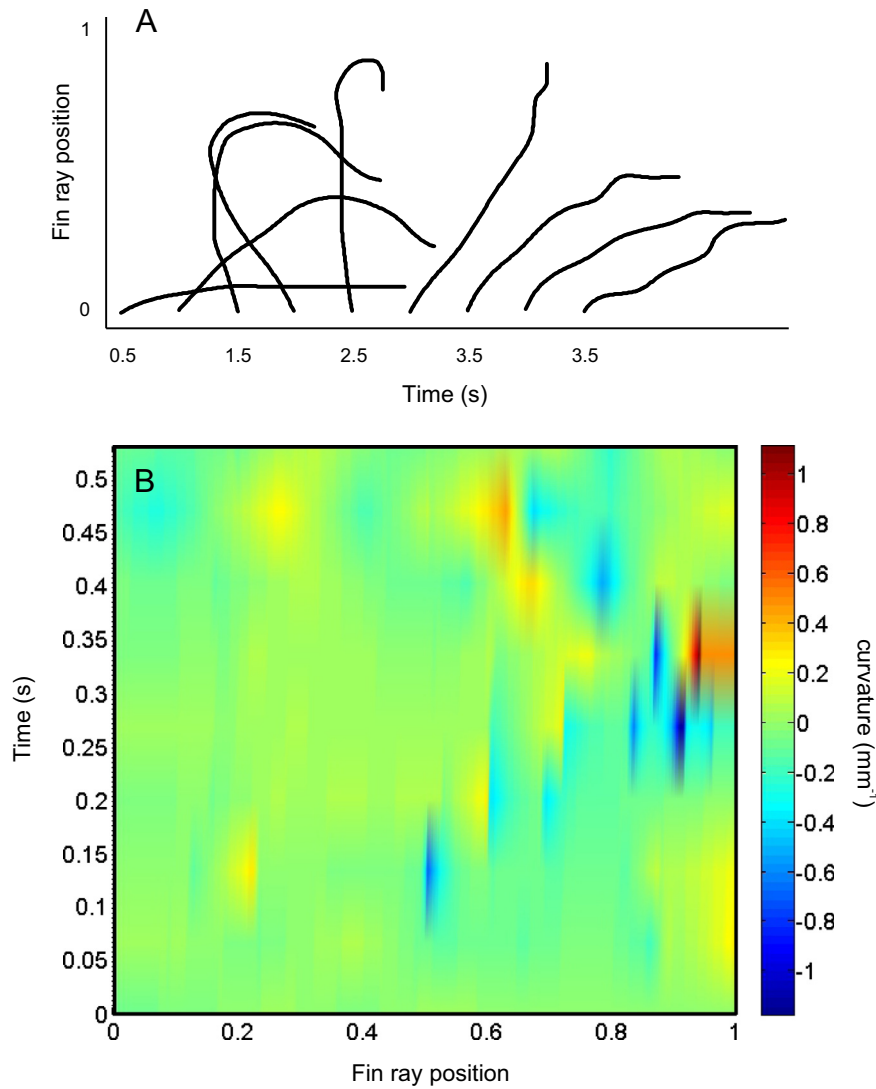


Fig. 2. Curvature of longest pectoral-fin ray of left pectoral fin of *Scopelogadus beanii* during a single propulsive fin beat. A: Spline curves representing fin ray shape over time. The y-axis represents the position of the fin ray in proportion of total fin-ray length from the base (0, proximal) to tip (1, distal). Spline curves were fitted by a custom MATLAB program fitting 200 points over the length of the fin ray throughout the duration of the video sequence (see Flammang et al., 2013). B: Colormap showing magnitude and direction of curvature of the longest left pectoral-fin ray from the base (0, proximal) to tip (1, distal) over time (y-axis).

3.2.2. Abductor profundus (ABP)

In *S. beanii*, the abductor profundus lies ventral to the ABS and originates at the posterolateral face of the coracoid and inserts onto tendons that in turn insert onto all fin rays, including the first (Fig. 3). In other species, this muscle has a much more anterior and broad insertion along the lateral face of the cleithrum and is often composed of two or more subdivisions (Thorsen and Westneat, 2005; Winterbottom, 1974). In *S. beanii*, this is but a single division.

3.2.3. Adductor superficialis (ADS)

The adductor superficialis is the most medial muscle of the pectoral girdle (Thorsen and Westneat, 2005). It is composed of a set of lateral bundles that folds over a separate set of medial bundles in such a way that the muscle appears triangular in shape. The lateral set of bundles originates dorsally on the medial face of the coracoid while the medial set originates more anteriorly on the coracoid. The insertions of the bundles are distinct; the lateral bundles insert onto tendinous processes of the bases of the distal rays while the medial bundles insert similarly onto the medial rays. Neither set of bundles inserts onto the marginal ray (Winterbottom, 1974). The fold created by the “criss-cross” of the

lateral and medial bundles positions the muscle fibers in a right angle to one another (Thorsen and Westneat, 2005; Winterbottom, 1974). In *S. beanii*, the origin of the lateral division extends dorsally along the medial face of the supracleithrum, and from there, extends to the dorsal region of the cleithrum. The insertion of the lateral division is remarkable, with muscle bundles anchored directly to the hemitrichs of the ventral-most fin rays at approximately 15% of the fin length. To the authors' knowledge, this is the first time that such a distal insertion for the ADS has been described (Fig. 3). The medial bundles of *S. beanii* are conserved in that they maintain the traditional origin and insertion patterns: originating along the medial side of the cleithrum, extending ventrally along the posterior end of the coracoid, and inserting on fin rays 8–14.

3.2.4. Arrector dorsalis (ARRD)

Like the ARRv, the ARRD is composed of tightly bound muscle fibers. In other labriform swimmers, these divisions originate ventral to the ADS and dorsal to the ADP and insert at the base of the first marginal ray, a pattern that is conserved in *S. beanii* (Thorsen and Westneat, 2005; Fig. 3).

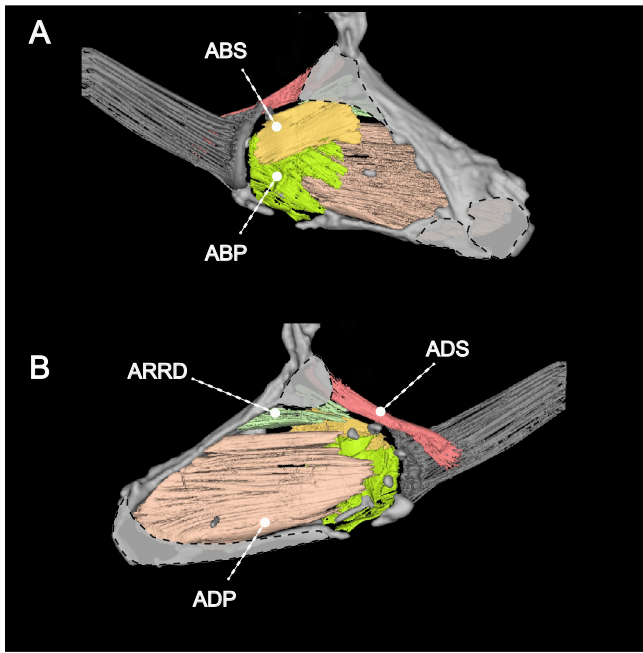


Fig. 3. Volume renderings of a microCT scan of the left pectoral girdle of *Scopelogadus beanii* (MCZ 165261, 97 mm SL) with nonmineralized soft tissue stained with phosphotungstic acid. Voxel size = 12 μ m. Areas of mineralized elements (grey) without clear definition in reconstruction are outlined with transparent grey with a dashed border. Abbreviations: ABS, abductor superficialis; ABP, abductor profundus; ADS, adductor superficialis; ADP, adductor profundus; and ARRD, arrector dorsalis.

3.2.5. Adductor profundus (ADP)

The adductor profundus lies ventral to the ADS. Its origin in *S. beanii* is similar to other teleosts, attaching at the anteroventral tip of the cleithrum where it meets the anterior edge of the coracoid, on the medial side of the girdle. Insertion patterns vary considerably in other fishes (Winterbottom, 1974). In their sample of labriform swimmers, Thorsen and Westneat (2005) observed that the ADP inserted via tendons onto rays P3–16. However, in *S. beanii*, the ADP inserts onto processes of all fin rays, including the dorsal most rays (Fig. 3).

3.3. Muscle-mass morphospace and force contributions

The muscular components of the pectoral girdle differ in varying degrees in their relative masses from other labriform swimmers (Thorsen and Westneat, 2005; Table 1, Fig. 4). As a proportion of total girdle musculature, the adductor profundus of *S. beanii* is most dissimilar. At 56.8%, the ADP contributes 21% more mass than the species with the largest ADP in Thorsen and Westneat’s (2005) dataset (Table 1, Fig. 4). The adductor superficialis is smaller than many other other labriform swimmers, however, at 12.9%, it is comparable to several species, including *Zanclus cornutus*, *Amphistichus argenteus*, *Stethojulis trilineata*, and *Gomphosus varius*, all species with ADS masses less than 18% the total girdle musculature (Table 1, Fig. 4). Like other labriform swimmers, the ARRD is small in *S. beanii* (9.8% versus 2.4–10.4%; Table 1, Fig. 4). On the abductor side, *S. beanii* differs more subtly. At 12.9%, the abductor profundus is only slightly smaller than the smallest ABP in Thorsen and Westneat’s (2005) dataset: 15.5% for *Thorichthys meeki* (Table 1, Fig. 4). The other species included in the previous study, however, all had ABP masses considerably larger than *S. beanii* at 22.3–35.6% of the girdle

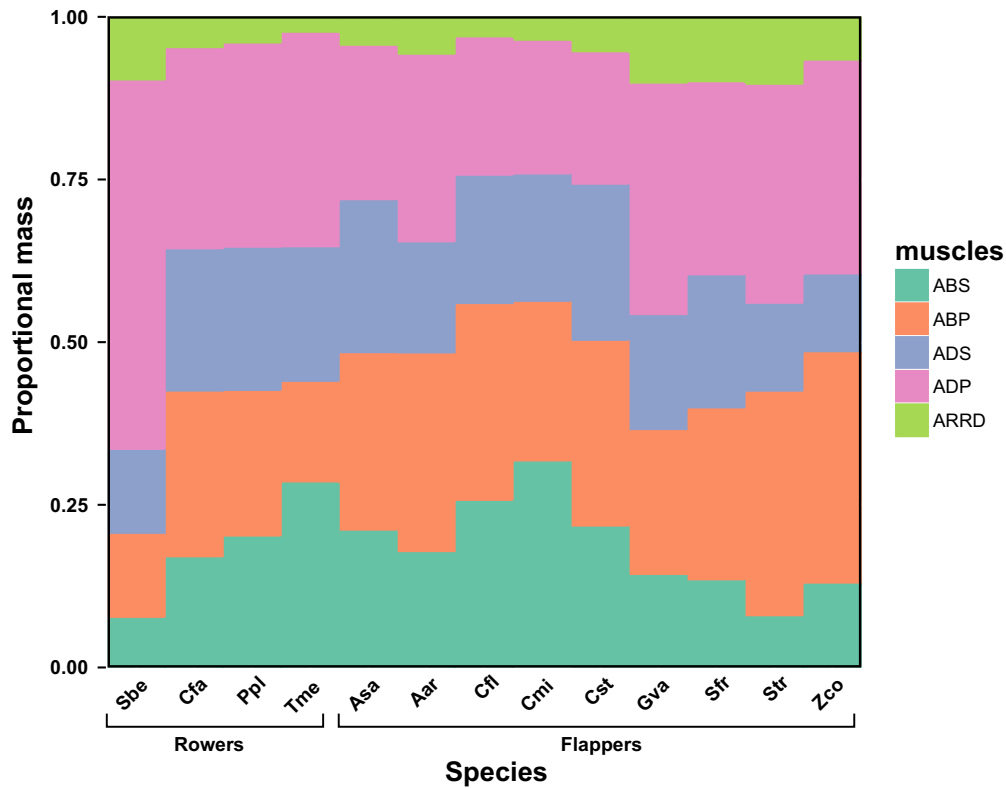


Fig. 4. Muscle mass contributions of *Scopelogadus beanii* and 12 other labriform swimmers according to Thorsen and Westneat (2005). Abbreviations (muscle divisions): ABS, abductor superficialis; ABP, abductor profundus; ADS, adductor superficialis; ADP, adductor profundus; and ARRD, arrector dorsalis. Abbreviations (species): Sbe, *Scopelogadus beanii*; Cfa, *Centropyge flavissimus*; Ppl, *Parupeneus pleurostigma*; Tme, *Thorichthys meeki*; Asa, *Abudefduf saxatilis*; Aar, *Amphistichus argenteus*; Cfl, *Centropyge flavissimus*; Cmi, *Chaetodon miliaris*; Cst, *Ctenochaetus striatus*; Gva, *Gomphosus varius*; Sfr, *Scarus frenatus*; Str, *Stethojulis trilineata*; and Zco, *Zanclus cornutus*.

muscle mass (Table 1, Fig. 4). The abductor superficialis of *S. beanii* is similarly small. At 7.6%, only slightly smaller than *S. trilineata* (7.9%), but considerably smaller than the remainder of labriform reef fishes (12.9–31.7%; Table 1, Fig. 4). The balance of adductor mass versus abductor mass is much different than any of the labriform swimmers reported in Thorsen and Westneat (2005). A 20.5%–79.5% ratio of adductor-to-abductor mass represents a skewed ratio relative to these other fishes. The most skewed ratio reported in this former study was 39.8%–60.2%, adductor–abductor, for the labrid *G. varius*. All other species were much closer to an even division between adductor and abductor masses (Table 1, Fig. 4).

The results of the principal component analysis of muscle-mass percentages of total girdle musculature are presented in Fig. 5. The first three components explain 96.6% of the variance with 59.3%, 27.1%, and 10.2% of the variance explained by PC1, PC2, and PC3 respectively (Table 2). Variance in the relative masses of the ABS, ADS, and ADP, and ARRD is captured by PC1 (Table 2, Fig. 5a). Much of PC2 captures variance in the masses of the ABP and ADP and PC3 captures variance in ABS, ADS, and ARRD (Table 2, Fig. 5b). The flappers in Thorsen and Westneat's (2005) dataset are characterized by a small ADP (PC1) and medium to large ABP (PC2) muscle masses (Tables 1,2; Figs. 4,5a). By contrast, rowers, including *S. beanii*, have medium to large ADP and small to medium ABP muscle masses (Tables 1,2; Figs. 4,5a). Driven largely by this ABP–ADP relationship, *S. beanii* occupies a unique portion of muscle-

Table 2

Eigenvalues and eigenvector loadings for a principal component analysis of the proportion of five common muscle masses in *Scopelogadus beanii* and labriform swimming reef-fishes from Thorsen and Westneat (2005). Data represent analysis of percent total muscle mass of left pectoral-fin girdle.

	PC1	PC2	PC3	PC4	PC5
Eigenvector	2.967	1.355	0.508	0.169	0.000
Proportion of variance	0.593	0.271	0.102	0.034	0.000
Cumulative proportion	0.593	0.864	0.966	1.000	1.000
<i>Factor loadings</i>					
ABS	−0.534	−0.178	0.334	0.568	0.499
ABP	−0.043	0.850	0.098	−0.234	0.459
ADS	−0.467	−0.165	−0.770	−0.286	0.282
ADP	0.487	−0.440	0.166	−0.348	0.649
ARRD	0.508	0.154	−0.508	0.648	0.201

ABS, abductor superficialis; ABP, abductor profundus; ADS, adductor superficialis; ADP, adductor profundus; and ARRD, arrector dorsalis.

mass morphospace relative to all other species considered (Fig. 5a). In addition, the ADS and ABS is smaller than all other labriform swimmers. *S. beanii* (Table 2; Fig. 5a). Relative to other rowers, *S. beanii* is distinguished by exceptional ADP and and ARRD masses (Table 2; Fig. 5a).

Of the five pectoral-girdle muscles, the ADP of *S. beanii* has the largest PCSA and, thus, produces the greatest amount of force: 44.0% of the total (Table 1). The next most powerful muscle according to this analysis is the ABP at 20% of the total force. The three remaining muscles, the ADS, ABS, and ARRD, produce relatively low magnitudes of force at 13.0%, 12.2%, and 10%, respectively (Table 1). The two larger adductors (ADP + ARRD) alone produce 54.8% of the total muscle force compared to 45.2% produced by the abductors (Table 1).

3.4. Pectoral-girdle osteology and fin-ray architecture

The cleithrum of *S. beanii* is reduced in its anteroposterior thickness relative to other labriform swimmers (Fig. 6b; Thorsen and Westneat, 2005; Figs. 1–4). The anterior tip of the long coracoid articulates with the cleithrum within the ventral fold of its horizontal limb (Fig. 6b). Posteriorly, the posterior body of the coracoid meets the anterior edge of the scapula (Fig. 6b). The scapula is rhomboidal with a single foramen, a shape similar to many other labriform swimmers (Fig. 6b,d; Thorsen and Westneat, 2005). The posterior margin of the scapula anchors proximal articulations with the four proximal radials. The anterodorsal margin of the scapula articulates with the cleithrum within the ventral fold of its dorsoposterior lobe. The four radials increase in size ventrally and articulate distally with the cartilage pad at the bases of the fin rays (Fig. 6b,d). The first, dorsal-most lepidotrichia articulates directly with the scapula and is unsegmented and nonbifurcating (Fig. 6b,c).

Serial segments account for more than two-thirds (69.5%) of the distal length of the pectoral fin lepidotrichia in *S. beanii* (Table 3; Fig. 6a). The mean length of each segment was 0.39 mm; segments were of equal length along the length of the lepidotrichia. Bifurcation in the fin rays occurs slightly distal to the beginning of the segmented portion with the post-bifurcated rays representing 65.9% of the distal length of the ray (Table 3, Fig. 6a,b).

4. Discussion

4.1. Summary

This study reports for the first time labriform swimming in a deep-sea fish. *S. beanii* is a strong rower, capable of a high degree of maneuverability. Through morphological analysis, it is established that this stroke is actuated by a portion of muscle-mass morphospace not yet described for labriform swimmers in general and other rowers in particular. The musculoskeletal architecture of *S. beanii* also differs significantly

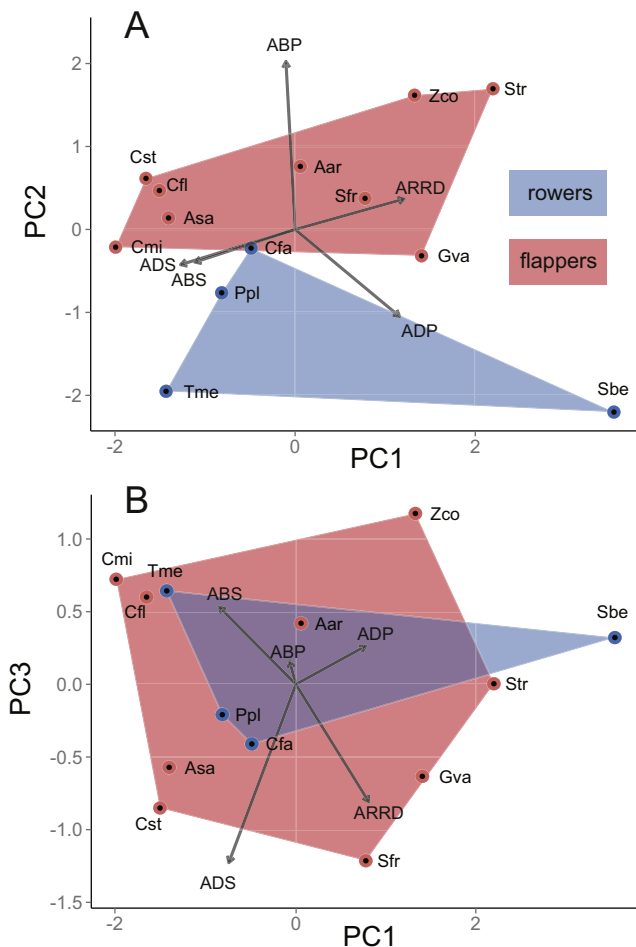


Fig. 5. Biplot representing a principal-component analysis of muscle-mass composition in *Scopelogadus beanii* and 12 reef fishes that demonstrate labriform locomotion. Arrows represent projections of the muscle-mass variable loadings. (A) Plot of species scores on principal component 2 versus principal component 1. (B) Scatterplot of species scores on principal component 3 versus principal component 1. See caption to Fig. 4 for abbreviations.

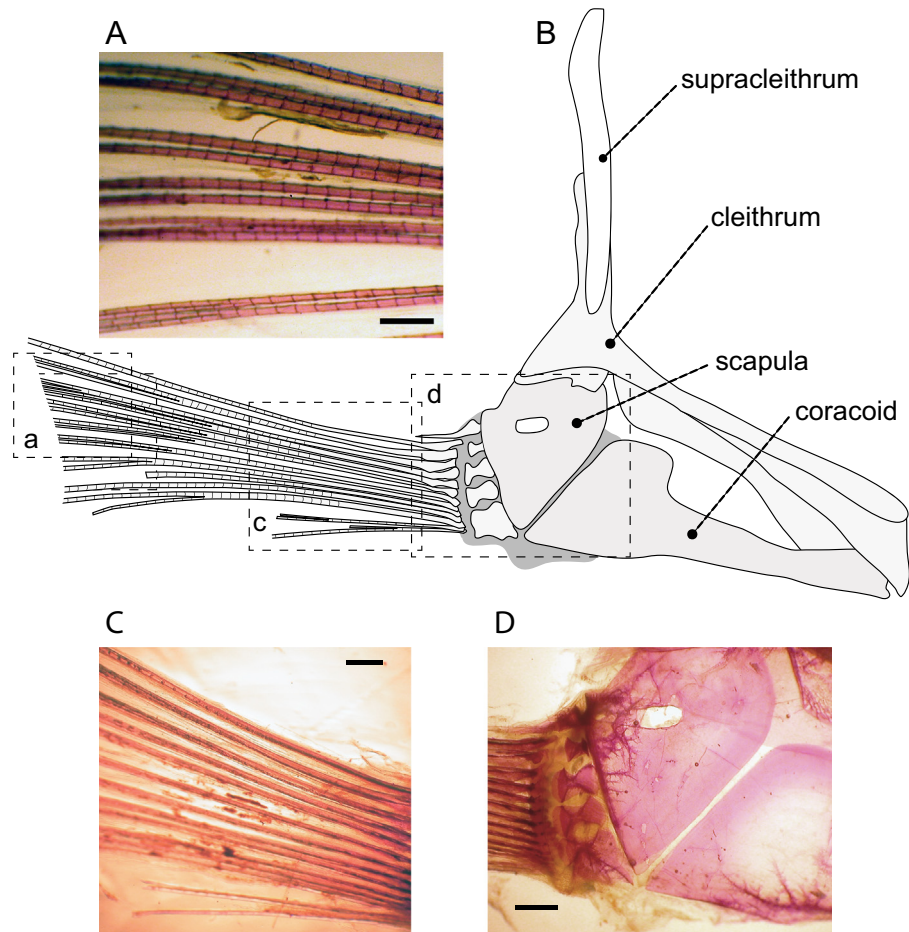


Fig. 6. Right lateral pectoral girdle and fin rays of *Scopelogadus beanii*. (A) Bifurcations of fin rays; (B) lateral view of entire girdle and proximal half of pectoral fin; (C) unbranched, proximal sections of pectoral fin; (D) proximal bases of fin rays, radials, scapula, and posterior coracoid. Inset boxes on B correspond to A, C, and D.

from other fishes that engage in similar locomotor behavior. The study species lacks several muscle divisions present in other labriform swimmers and possesses muscle insertions peculiar for a rower. These results demonstrate that dissimilar morphological arrangements may result in similar locomotor behavior and that labriform swimming and rowing has a separate evolutionary origin in the deep sea. What follows is a discussion of the stroke hydrodynamics and kinematics, how the musculo-skeletal anatomy contributes to specialized labriform swimming in *S. beanii* and, based on its feeding ecology, how this locomotor behavior contributes to resource utilization in the bathypelagic realm.

4.2. Hydrodynamic interpretation of kinematics

Although the chance opportunity to observe the swimming kinematics of this deep-sea fish did not permit a thorough investigation of hydrodynamic properties, a number of previous studies have demonstrated that fluid dynamics of labriform swimming is fairly consistent across taxa (Drucker and Lauder, 1999, 2002; Lauder and Jayne, 1996; Walker

and Westneat, 2002). Thus, this permits generalized statements concerning the pectoral-fin kinematics of *S. beanii*. For example, it can be expected that rotation of the leading dorsal edge of the pectoral fin on the outstroke produces lift. The extremely high mid-fin curvature during abduction is likely a result of hydrodynamic loading on the extremely long and flexible fin rays (Table 3); as a comparison, the maximum curvature of distal, segmented portion of fin ray in a hovering bluegill sunfish (*Lepomis macrochirus*) is 0.065 mm^{-1} (Flammang et al., 2013). It is hypothesized that the posteriorly oriented distal half of the fin may leave a trailing vortex on the outstroke that would potentially interact with the midsection of the fin during adduction and add momentum to the propulsive vortex generated during instroke. While fluid dynamics studies of living *Scopelogadus* may not be feasible, research employing bioinspired robotics is a good substitute for future studies of this phenomenon.

4.3. Musculoskeletal morphology and rowing propulsion

S. beanii occupies an as yet undocumented portion of muscle mass morphospace. Thorsen and Westneat (2005) asserted that their estimation of pectoral-fin functional morphospace was limited and would be expanded by analyses of non-labriform swimmers; however, *S. beanii* expands the known morphospace as a species relying on labriform propulsion. Despite this expansion, axes of variation for the study species accords with some aspects of the rowing–flapping continuum. Specifically, with a large adductor profundus and small abductor profundus (PC2; Fig. 5), the muscle mass of *S. beanii* differs similarly from the more balanced distribution of adductor–abductor masses of flapping swimmers (Thorsen and Westneat, 2005). Interpretation of the

Table 3

Pectoral-fin ray segmentation and bifurcation properties of *Scopelogadus beanii*. Data reflect samples from five middle rays of left pectoral fins of three specimens.

	Mean \pm s.e.
Segment length (mm)	0.39 \pm 0.008
Segmented portion (%)	69.5 \pm 0.010
Bifurcated portion (%)	65.9 \pm 0.008

morphology of the adductor superficialis, abductor superficialis, and the arrectors within the context of the flapping–rowing continuum is more difficult and complicated. First, all rowing reef fishes share similar ADS, ABS, and ARRD mass configurations (PC1) with some flappers (Fig. 5a). This pattern indicates that the ADS, ABS, and ARRD may function similarly in rowing and flapping. Alternatively, similar ADS, ABS, and ARRD configurations may reflect the continuous nature of these two behaviors and indicate these fishes utilize both of them. However, *S. beanii*, a strong rower, aligns with flappers with respect to PC1 (Fig. 5a) in that it possesses a relatively large ARRD and small ADS and ABS. Rowers typically have reduced arrectors relative to flappers, the latter requiring a high degree of leading edge control (Thorsen and Westneat, 2005; Westneat, 1996) and the ADS and ABS are important actuators of up and down strokes during flapping (Drucker and Jensen, 1997). The relatively large ARRD and line of action similar to flappers suggests that leading-edge control may therefore be important in the rowing instroke of *S. beanii* and perhaps aids in lift generation. Although the smaller ABS and ADS of *S. beanii* are unique among rowers, this configuration may reflect that *S. beanii* does not regularly engage in flapping unlike other labriform swimmers considered and, thus, muscles associated with this behavior have been reduced and perhaps coopted in other functional roles.

The muscular force that powers strong sculling in *S. beanii* is dominated by the adductor profundus. According to the analysis presented here, this division accounts for 44% of the total force output of the pectoral girdle muscles (Table 1). By contrast, the next largest muscle, the abductor profundus, produces only 20% of the total force. The action of both the ADP and ABP is in line with the pectoral-fin rays (Fig. 3). Thus, the majority of forces produced by these muscles likely result in the anterior–posterior rotation of the pectoral fin about the radials (Fig. 2). The abductor superficialis and arrector dorsalis have either oblique lines of action (Fig. 3) or low PCSA (Table 1) or both. The line of action of the adductor superficialis suggests that his muscle is a minor source of in-stroke actuation; however, ADS bundles insert much more distally than the ADP insertion to the fin-ray bases. This more distal insertion of the ADS on the fin rays (Fig. 3) provides greater mechanical advantage and therefore more efficient force transmission relative to the other more proximal insertions of other fishes. Although this is unlikely to result in a dominant propulsive input comparable to the ADP, it is nonetheless perhaps a configuration that represents a modification of pectoral-fin musculature that optimizes propulsive force during the rowing instroke.

Lastly, although a goal of this study was to decipher the functional relationships between the unique muscular inputs and labriform swimming behavior in *S. beanii*, it must be noted that the opportunistic nature of this study limits the depth of its interpretations. Without a combination of detailed kinematic muscle activation analysis, however, the precise function of these motor components in *S. beanii* will remain elusive.

4.4. Ecomorphology of rowing propulsion in *S. beanii*

At bathypelagic depths, biomass is typically very scarce and patchily distributed (Marshall, 1954). Thus, it has been assumed that the fishes that inhabit the bathypelagic realm typically engage in behaviors associated with opportunistic utilization of prey resources. These include a lie-and-wait predation strategy and ingestion of large prey items (Gartner et al., 1997). Although, no observations of in-situ feeding behaviors exist for a bathypelagic fish, a few studies have documented non-feeding locomotor behavior in deep-sea ceratioid anglerfishes, a dominant and diverse lineage of deep-sea predatory taxa (Pietsch, 2009). Moore and Schaefer (2002) described the luring and locomotor behavior of a gigantactinid anglerfish and Luck and Pietsch (2008) analyzed the swimming kinematics and behavior of a species of *Oneirodes*. In both instances, the authors concluded that their study species relies on burst-carangiform swimming behavior driven by the caudal fin to rapidly overtake evasive prey and that this behavior was a strategy

suited to the sparsely aggregated food resources of the deep sea. Although these data are limited, they indicate archetypal relationships between foraging and locomotor behavior by fishes that inhabit the dimensionless bathypelagic realm; that is that fishes specializing in the capture of widely dispersed, evasive prey items engage in caudal-driven locomotion during ambush predation (Webb, 1984).

Under classic models of the relationship between prey type and distribution and locomotor behavior, how can the strong rowing behavior of *S. beanii* be interrupted? Rowing labriform locomotion is typically associated with slow-swimming fishes that maneuver frequently (Walker and Westneat, 2000, 2002). Furthermore, fishes utilizing rowing propulsion are often associated with highly complex structured habitats (Bellwood and Wainwright, 2001; Fulton et al., 2001). These patterns, drawn from previous studies of reef fishes, seem to be at odds with respect to the bathypelagic environment of *S. beanii*. Specifically, a foraging strategy driven by a low-speed, high-maneuverability locomotor strategy appears poorly suited for an unstructured habitat defined by low prey densities. However, if the prey choice of *S. beanii* is considered, the behavioral and ecomorphological relationship of feeding and locomotion becomes clearer.

In the western North Atlantic, the collection locality, *S. beanii* occupies depths from 400 to over 2000 m and is most abundant between 1500 and 2000 m (Gartner and Musick, 1989; Moore et al., 2003). Gartner and Musick (1989) reported that, although often captured in pelagic waters, *S. beanii* is associated with epibenthic slope waters over the continental margin. In the bathypelagic, *S. beanii* consumes a variety of prey, including many crustacean taxa (Mauchline and Gordon, 1991). In the epibenthic, *S. beanii* consumes mostly salp components of gelatinous zooplankton (Gartner and Musick, 1989; Mauchline and Gordon, 1991). Gelatinous zooplankton communities form extremely dense swarms over continental slopes (Graham et al., 2001; Madin et al., 2006; Wiebe et al., 1979). Dense aggregations such as these form a complex, three-dimensional field of prey (Graham et al., 2001). Gartner and Musick (1989) also reported that *S. beanii* feeds acyclically on salps over diel time scales. Thus, under long-standing models of the relationship between prey distribution and motility and locomotor behavior (Webb, 1984), the drag-based propulsion system involving the pectoral fins of the study species is expected given the Gartner and Musick's (1989) diet data. The drag-based pectoral-fin propulsion of *S. beanii* conveys high maneuverability at the cost of speed, two parameters which permit effective utilization of abundant, persistent, and three-dimensionally distributed prey (Walker and Westneat, 2000, 2002).

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