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Function of dorsal fins in bamboo shark during steady swimming

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ABSTRACT

To gain insight into the function of the dorsal fins in white-spotted bamboo sharks (Orectolobiformes: Hemiscylliidae) during steady swimming, data on three-dimensional kinematics and electromyographic recordings were collected. Bamboo sharks were induced to swim at 0.5 and 0.75 body lengths per second in a laminar flow tank. Displacement, lag and angles were analyzed from high-speed video images. Onset, offset, duration, duty cycle and asynchrony index were calculated from three muscle implants on each side of each dorsal fin. The dorsal fins were displaced more laterally than the undulating body. In addition, the dorsal tips had larger lateral displacement than the trailing edges. Increased speed was accompanied by an increase in tail beat frequency with constant tail beat amplitude. However, lateral displacement of the fins and duration of muscle bursts remained relatively constant with increased speed. The range of lateral motion was greater for the second dorsal fin (mean 33.3°) than for the first dorsal fin (mean 28.4°). Bending within the fin was greater for the second dorsal fin (mean 43.8°) than for the first dorsal fin (mean 30.8°). Muscle onset and offset among implants on the same side of each dorsal fin was similar. Three-dimensional conformation of the dorsal fins was caused by interactions between muscle activity, material properties, and incident flow. Alternating bilateral activity occurred in both dorsal fins, further supporting the active role of these hydrofoils in thrust production during steady swimming. The dorsal fins in bamboo sharks are capable of thrust production during steady swimming and do not appear to function as stabilizing structures.

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1. Introduction

Chiloscyllium plagiosum (Anonymous [Bennett] 1830) (Order Orectolobiformes, Family Hemiscylliidae), white-spotted bamboo sharks, are benthic ambush predators that rely on suction to draw prey from crevices around coral reefs but are also able to crush hard prey (Compagno, 1984; Ramsay and Wilga, 2007; Wilga et al., 2007; Wilga and Sanford, 2008). This species is commonly held in aquaria where they spend considerable time resting on the substrate; however, little is known about their locomotor routine in the wild. Bamboo sharks locomote mostly by anguilliform body undulation and have a very flexible body (Compagno, 1984; Maia et al., 2012). Bamboo sharks have a blunt head and a tapered body, which is markedly different from the streamlined shape of fast pelagic fishes. They also possess two posteriorly placed dorsal fins of similar dimension and shape.

Sharks are typically fusiform shaped and variation in body morphology is generally associated with head, fins and tail shape and placement (Maia et al., 2012). Fin placement and size differ between

bamboo sharks and spiny dogfish. Bamboo sharks have a more posteriorly placed first dorsal fin at 37% of the body length (BL) compared to 34% in spiny dogfish. The spacing between the two dorsal fins is also larger in spiny dogfish, 22% of body length versus 11% in bamboo sharks. In addition, bamboo sharks have a proportionally larger second dorsal fin, 30% smaller than the first dorsal fin compared to 50% smaller in spiny dogfish, and proportionally more muscle insertion into both dorsal fins (Maia and Wilga, unpublished data). However, the center of mass of the body in bamboo sharks is similar to that of spiny dogfish at 30% of body length (Domenici et al., 2004).

How does fin shape and placement influence fin function? Early manipulative studies of fin function in sharks used wooden models in a wind tunnel to conclude that median fins function to prevent roll (Harris, 1936). The model in that study was based on dusky smoothhounds, *Mustelus canis*, which have a body plan more similar to spiny dogfish than bamboo sharks, with a larger first dorsal fin placed more anteriorly.

In actinopterygians, the dorsal and anal fins have distinct functions in different species and these functions correlate with placement on the body. The anterior placement of the dorsal fin plays a crucial role as a stabilizer during steady swimming in brook trout, while the posteriorly placed dorsal and anal fins function as thrusters in bluegill sunfish (Drucker and Lauder, 2005; Standen and Lauder, 2005, 2007; Tytell et al., 2008). Much of this flexibility

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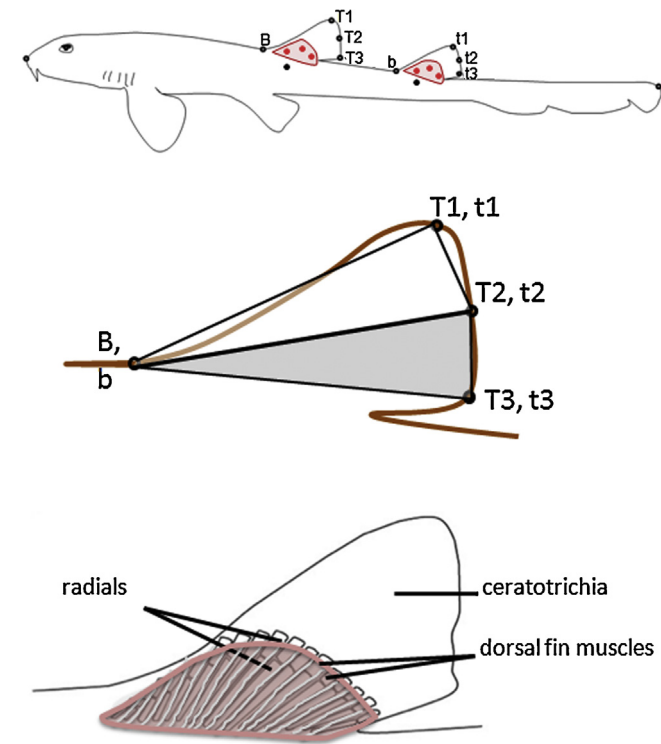


Fig. 1. (A) Landmarks used to determine the three-dimensional kinematics of bamboo shark dorsal fins during steady swimming and electrode position (red dots bilateral implantation, black dots left side implantation). (B) Detail on dorsal fin decomposition into bending planes. (C) Schematic representation of the dorsal fin anatomy in a bamboo shark. Uppercase letters refer to landmarks on the first dorsal fin (B, base; T1, distal tip of the fin; T2, midpoint between T1 and T3; T3, trailing edge tip) and lowercase letters refer to the second dorsal fin landmarks (b, base; t1, distal tip of the fin; t2, midpoint between t1 and t3; t3, trailing edge tip).

is thought to be due to the high level of muscular control of individual fin rays in bony fishes (Standen and Lauder, 2005; Lauder, 2006). Unilateral muscle contraction of a hemitrichia causes the fin ray to bend toward the opposite side of the active muscle (Jayne et al., 1996; Drucker and Lauder, 2001). In contrast, the ceratotrichia of chondrichthyan fishes are not controlled individually; rather, the dorsal fin muscle inserts into multiple ceratotrichia via a tendinous sheet (Geerlink and Videler, 1987; Compagno, 1999; Liem and Summers, 1999). Despite this, the ceratotrichia are still able to control conformation of the dorsal fins enough to produce thrust during steady swimming in spiny dogfish (Maia and Wilga, unpublished data). The first dorsal fin of spiny dogfish acts as a stabilizer, moving independently of the body as suggested by Harris (1936), while the second dorsal fin appears to function as a thruster and moves with the body (Maia and Wilga, unpublished data). Simultaneous activation of bilateral muscles in a dorsal fin is consistent with a stabilizing function, while alternating bilateral activity in a dorsal fin is expected from a thrust-producing structure, as was found in the first and second dorsal fins, respectively, of spiny dogfish (Maia and Wilga, unpublished data). Bilaterally asynchronous activity also occurs in the thrust-producing dorsal fin of bluegill sunfish when swimming steadily (Jayne et al., 1996).

Bamboo shark dorsal fins have two rows of rectangular radials that extend less than 50% into the fin area, as can be seen in Fig. 1. Between two radials in tandem there is a cartilaginous pad. The dorsal fin muscle originates from the stratum compactum of the skin, with each muscle bundle extending over a set of distal and proximal radials to insert onto the associated ceratotrichia (Maia and Wilga, unpublished data). The dorsal fin of bamboo sharks is thus very distinct from that of spiny dogfish, which retains the more basal

condition of basals and radials organized as plate-like structures with muscles that broadly insert over multiple basals and radials (Maia and Wilga, unpublished data).

In the present study, we investigate whether the dorsal fins of bamboo sharks function as stabilizers, as hypothesized by Harris (1936) and verified for the first dorsal fin of spiny dogfish, or as thrusters, as shown for the second dorsal fin of spiny dogfish (Maia and Wilga, unpublished data). Three-dimensional (3D) kinematics and muscle activation patterns of the dorsal fins of bamboo sharks are tested during steady swimming at two speeds. Based on the position of the dorsal fins in a posterior position on the trunk, the large fin and muscle area, and the derived condition of fan-like fin radials, we hypothesize that the dorsal fins in bamboo sharks function in thrust generation. If the fins are generating thrust, we expect the dorsal fins to have a large range of conformational change and bilaterally asynchronous activation of the dorsal fin muscles. We also expect an increase in the range of motion with increasing swimming speed to augment thrust.

2. Materials and methods

2.1. Experimental subjects

Four bamboo sharks were obtained from Sea World, Orlando and housed in a circular tank (1900 l) with 32 psu salinity, 22 °C (± 1 °C), on a 12 h light cycle and fed every other day on a natural diet of squid (*Illex* sp.) and fish (*Scomber* sp., *Clupea* sp., *Menidia* sp.). Total length ranged from 48.3 cm to 55.9 cm, with a mean of 50.7 ± 3.5 cm. To rule out sex bias, two males and two females were used. The experiments were approved under the University of Rhode Island IACUC protocol # AN05-07-001.

2.2. Experimental protocol

Individual sharks were placed in a flow tank (Model 1520; Rolling Hills Research Corp., El Segundo, CA, USA) (working section 1.5 m length \times 0.5 m height \times 0.38 m width) and trained to maintain steady, rectilinear swimming at speeds of 0.50 BL s^{-1} and 0.75 BL s^{-1} . The two speeds were chosen to reflect the range of speeds at which bamboo sharks could steadily swim in the flow tank (see supplementary online video in Appendix A). Reflective metal markers (2 mm diameter, approximately 2 mg each) were fixed onto the dorsal and caudal fins with cyanoacrylate glue to track fin movement (Fig. 1A). These markers were used to define four landmarks on each dorsal fin: anterior of base, distal tip, midpoint between the distal tip and trailing edge, and trailing edge. The individuals were anesthetized with tricaine methanesulfonate (MS-222; 1.75 g in 20 l) for placement of the markers, which took approximately 30 min. The individuals were allowed to recover for 90 min in the flow tank prior to starting the experiment. Two high-speed video cameras (Photron FastCam, 125 frames s^{-1} ; Photron USA, Inc., San Diego, CA, USA) were used to film simultaneous lateral and dorsal views of the swimming fish; the dorsal camera was aimed at a mirror positioned at an angle of 45° above the tank. Experiments were conducted in water temperatures of 22 °C (± 0.5 °C).

2.3. Kinematics

Four randomly chosen tail beats from sequences where the fish was swimming steadily horizontally were analyzed for each individual and speed using Photron Motion Tools 1.0.1.3. A tail beat cycle was defined from the point of maximum excursion of the tail from one side to the other with the return of the tail to that same point after passing the midline twice. Reflective markers were tracked in every frame and 3D coordinate data were exported to

Excel (Microsoft Office, v. 2007) where macros (written by A. Maia) were run to calculate the following kinematic variables: tail beat amplitude, tail beat frequency, fin excursion rate, total displacement, and time of maximal displacement to each side. Tail beat amplitude was calculated as the displacement of the tip of the upper lobe of the tail during a tail beat, while tail beat frequency was calculated as the inverse of the duration for that same movement. Fin excursion rate is defined as the distance in 3D space the fin spans per unit time. Total displacement is defined as the absolute displacement of the fin in 3D space. Time of maximal displacement is calculated as the time that the fin tip is at the most lateral position during a tail beat cycle. Range of motion (ROM) is defined as the angle swept by the dorsal fin during a tail beat and was calculated for the first and second dorsal fins relative to the earth frame of reference and the fish frame of reference. These planar angles were calculated relative to the vertical position of the fin in the natural position (line of insertion of the fin at the midline) and were defined by the following landmarks: anterior point of the fin base, distal tip of fin, and trailing edge (Ferry and Lauder, 1996). The fin was further divided into two smaller triangles representing the leading edge and trailing edge (Fig. 1B), with the angle between these two triangles used to test for conformational changes within the fin during a tail beat. The predicted phase lag of each fin tip was determined assuming the leading fin to be a stiff structure. This value was obtained by determining the horizontal distance between the base of the fin (B, b) and the tip of the fin (T1, t1) and then dividing that distance by the wavelength of the locomotor wave and multiplying by the wave period to obtain values of predicted lag of the fin tip. This was then compared with the observed phase lag to determine if the fin is moving as expected by the propagation of the locomotor wave (Standen and Lauder, 2005). Differences between observed and predicted phase lag (fin moving in phase with the trunk) can indicate whether the fin is moving differently from the body, and thus independently (Standen and Lauder, 2005).

Paired *T*-tests were used to test for differences in caudal fin amplitude and frequency at the two swimming speeds, as well as differences between fin landmarks and the respective base (Zar, 2009). Expected and observed phase lag for T1 and t1 landmarks were also tested using paired *T*-tests (Zar, 2009). If the data were not normally distributed, Mann-Whitney tests (Zar, 2009) were used. Two-way ANOVAs were used to test for differences in excursion rates, angles, and timing of maximal displacement by fin and speed (Zar, 2009). Bonferroni corrections were used to compensate for the lack of independence of the variables being tested (Zar, 2009). We tested normality and homoscedasticity of variance and when the parameters were not met we used ANOVA on ranks followed by Dunn comparison tests instead (Zar, 2009). All statistical analyses were run using SAS software v. 9.2 (SAS Institute Inc., Cary, NC, USA).

2.4. Muscle activity

Three individuals were tested for muscle activity. Each individual was anesthetized and intubated with seawater with MS-222 (1.75 g in 20 l) for the duration of the surgery (<60 min). Bipolar stainless steel electrodes were implanted bilaterally using a 25-gauge needle at three locations along each dorsal fin muscle: leading edge, middle of the fin, and trailing edge (Fig. 1A). Two additional electrodes were implanted in the red epaxial muscle below each fin on the left side (Fig. 1A). Electrode leads were sutured to a loop between the two dorsal fins and inserted into a pin connector that transmitted data to a computer during the experiments. The shark was allowed to recover in the flow tank for 2 h after surgery. The temperature in the experimental tank was 22 °C (±0.5 °C). Electromyography (EMG) signals were recorded with differential amplifiers 1700 (A-M Systems, Sequim, WA, USA), with a high-pass

filter setting of 10 kHz and a low-pass filter setting of 3 Hz. Analog muscle signals were converted to digital using a PowerLab/16sp (ADInstruments, Colorado Springs, CO, USA) and stored in a computer. EMG signals were filtered with digital high-pass filters of 50 Hz in Chart software (v.5.4.2, ADInstruments).

Waveform analyses were conducted using Chart software on four trials for each individual at each speed. To determine onset and offset of muscle activity, the EMG trace was filtered, rectified and integrated. Muscle activity was defined when the post-processed signal reached 2.5 of the baseline value (Roberts et al., 2007). Activity in the red epaxial muscle near the first dorsal fin was used as the reference. The magnitude of an individual muscle burst was determined relative to the maximum peak overall for that muscle implant. Duty cycle for each muscle was defined as the percentage of the duration of a motor activation pattern (epaxial and dorsal fin muscle activity) wherein that muscle was active. A motor activation pattern (MAP) is defined from the onset of epaxial muscle activation (the reference muscle) to the next onset of the epaxial, which is expected to be equivalent to a tail beat.

The asynchrony index (AI) is a measure of how much the left and right sides of a muscle are active simultaneously (Gerry et al., 2008). This index was calculated for left and right muscle pairs with the following formula:

$$AI = 1 - \frac{dur1/TE + dur2/TE}{2},$$

where *dur1* and *dur2* are the durations of the left and right muscles and *TE* is the total duration of the event, from the onset of activity of the first of these two muscles to the offset of the last muscle to be active during a particular behavior (Gerry et al., 2008).

All summary statistics are reported as mean ± standard deviation. To test for the effect of fin (1st and 2nd dorsal), a two-way mixed model analysis of variance (ANOVA) was performed, with individual as a random effect and fin as a fixed effect (Zar, 2009). Paired *T*-tests were used to test for differences between left and right muscle pairs (Zar, 2009). Statistical tests were conducted using SAS v.9.1.2.

3. Results

3.1. Kinematics

Bamboo sharks power steady swimming by means of body caudal locomotion with a traveling wave of decreased amplitude from tail to snout. The tail fin moves in a figure eight. Bamboo sharks increase speed by increasing tail beat frequency from 1.57 s⁻¹ at 0.5 BL s⁻¹ to 1.95 s⁻¹ at 0.75 BL s⁻¹ (Mann-Whitney ANOVA: *U* = 211.5, *n* = 16, *p* < 0.05), while maintaining a constant tail beat amplitude of 12.6 ± 5.8 cm (Mann-Whitney ANOVA: *U* = 298, *n* = 16, *p* = 0.207). Most of the movement in the dorsal fins occurs in the horizontal plane, although three-dimensional motion occurs in both fins at both speeds (Fig. 2). Representative traces of the first and second dorsal fins are shown in 3D plots with projections onto the three planes at 0.5 BL s⁻¹ and at 0.75 BL s⁻¹ in Fig. 2.

The dorsal fin tips trail the base closely with larger lateral excursion (Fig. 3). The lag of fin tip movement relative to the base ranged from 40 to 80 ms. Lag in the first dorsal fin was larger than the lag in the second dorsal fin at 0.75 BL s⁻¹ (*H* = 13.091, d.f. = 3, *p* < 0.05). Lag at 0.5 BL s⁻¹ was more variable than at 0.75 BL s⁻¹, as evidenced by the higher coefficients of variation (0.5 BL s⁻¹, 1.03 for first dorsal fin, 4.36 for second dorsal fin; 0.75 BL s⁻¹, 0.72 for first dorsal fin and 0.86 for second dorsal fin).

Dorsal fin displacement was consistently larger than the adjacent trunk for both fins and speeds (*H* = 111.9, d.f. = 8, *p* < 0.05; Fig. 4A). Dorsal fin tips (T1, t1) had larger lateral excursions than the trailing edges (T3, t3) for both fins and speeds (T1 vs. T3: *q* = 4.89,

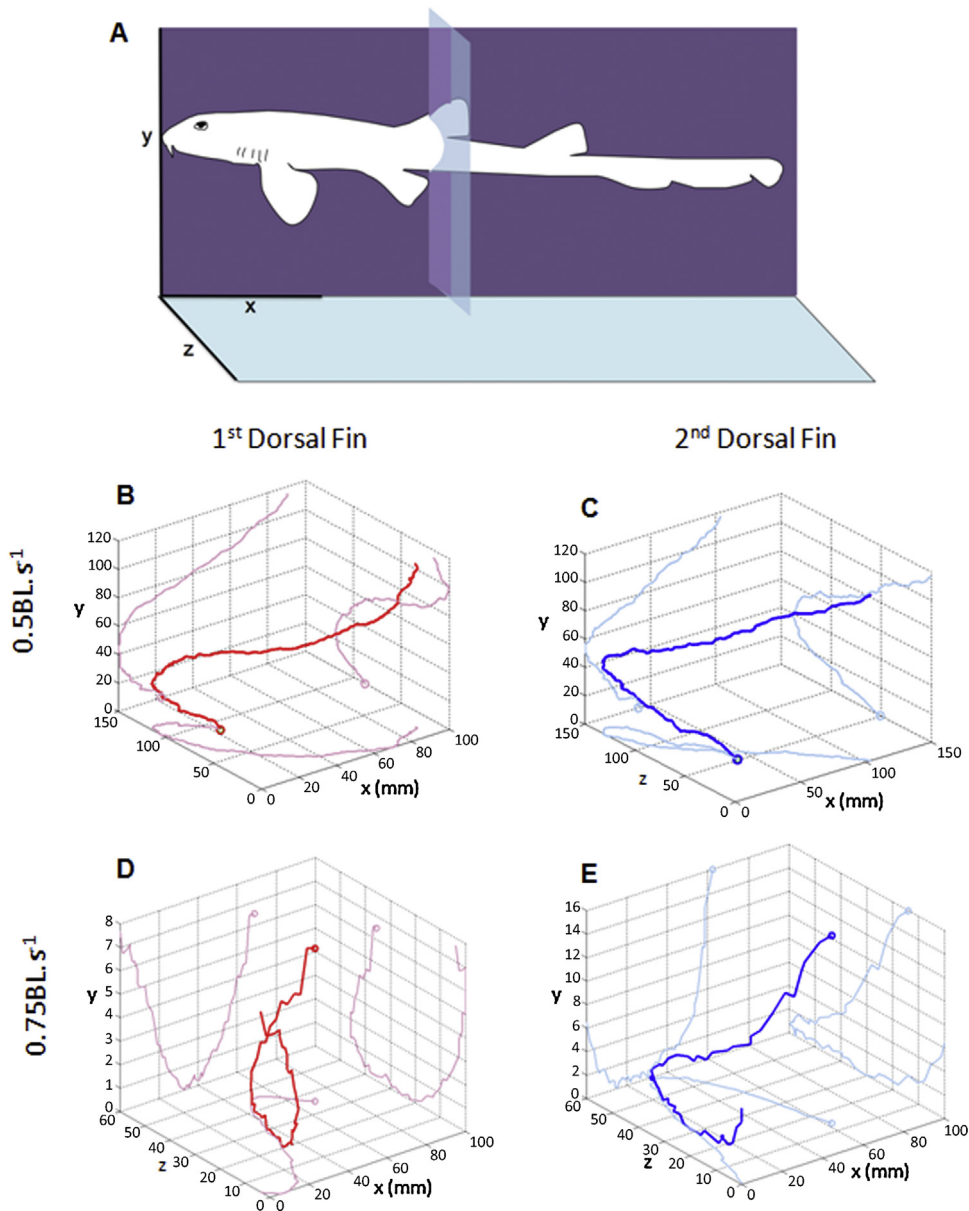


Fig. 2. Three-dimensional decomposition of dorsal fin kinematics during one tail beat. (A) Planes that intersect the fish transversally at the level of the two fins. (B) 3D decomposition of the first dorsal fin tip at 0.5 BL s^{-1} ; (C) 3D decomposition of second dorsal fin tip kinematics at 0.5 BL s^{-1} ; (D) 3D decomposition of the first dorsal fin tip at 0.75 BL s^{-1} ; (E) 3D decomposition of second dorsal fin tip kinematics at 0.75 BL s^{-1} . Open circles represent the beginning of the tail beat. Red colors refer to the first dorsal fin and blue colors to the second dorsal fin throughout all the figures. Lighter lines represent the projections on the referential planes.

$p < 0.05$; t_1 vs. t_3 : $t = 8.59$, $p < 0.05$; Fig. 4A). Lateral excursion was similar for the same point at the two different speeds, except for the first dorsal fin trailing edge that moved more at the lower speed (Fig. 4A). The pattern of lateral excursion for each fin is similar for both speeds, indicating that the kinematics remain unchanged with speed. The same pattern occurs for three-dimensional displacement, although there is greater variability (Fig. 4B). Also, there is a reversal in the displacement of t_2 relative to t_3 in the 3D displacement, which could be indicative of movement of t_2 in the vertical or frontal plane (Fig. 4).

The range of motion in the dorsal fin was similar between speeds, but was greater for the second dorsal fin relative to the earth referential, although there was also an individual effect (Table 1). The mean range of motion was 28.4° for the first dorsal fin and 33.3° for the second dorsal fin ($F = 4.54$, d.f. = 1, $p < 0.05$). Conformational changes within the fin were similar between speeds but greater in the second dorsal fin (30.8° for first dorsal

Table 1
Mean range of motion (ROM) in the earth frame of reference and p -value results from 3-way ANOVA with fin, speed and individual as factors.

Variable	Mean ($^\circ$)	p
Fin		
1st dorsal	28.41	0.038
2nd dorsal	33.25	
Speed (BL s^{-1})		
0.5	30.06	N.S.
0.75	31.61	
Shark		
1	35.61	<0.001
2	23.56	
3	25.36	
4	38.79	

BL, body length; N.S., non-significant differences.

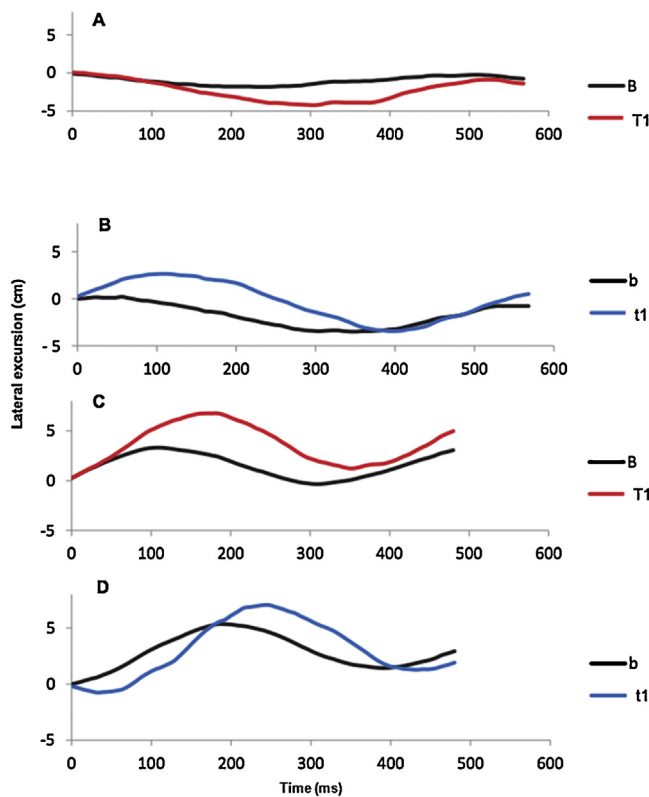


Fig. 3. Representative plot of lateral fin excursion over time for (A) first dorsal fin tip and base at 0.5 BL s^{-1} ; (B) first dorsal fin tip and base at 0.75 BL s^{-1} ; (C) second dorsal fin tip and base at 0.5 BL s^{-1} ; and (D) second dorsal fin tip and base at 0.5 BL s^{-1} . Uppercase letters refer to landmarks on the first dorsal fin (B, base of the fin; T1, distal tip of the fin) and lowercase letters refer to the second dorsal fin landmarks (b, base of the fin; t1, distal tip of the fin).

fin, 43.8° for second dorsal fin; Table 2). The bending angle within the fin varied within a tail beat.

3.2. Muscle activity

All of the dorsal fin and epaxial muscles were active during most of the MAP cycle. Motor activity among the three implants on a side was similar for onset and duration variables. However, sporadically the timing and magnitude of motor activity among the three implants on the same side of a fin differed.

Cyclical activation was found for all the muscles implanted during a MAP. Burst duration was similar between swimming speeds (Figs. 5 and 6). However, swimming speed influenced

Table 2

Mean bending angles within the fin and p -value results from 3-way ANOVA with fin, speed and individual as factors.

Variable	Mean ($^\circ$)	p
<i>Fin</i>		
1st dorsal	30.81	0.005
2nd dorsal	43.78	
<i>Speed (BL s^{-1})</i>		
0.5	39.45	N.S.
0.75	35.14	
<i>Shark</i>		
1	35.16	<0.001
2	27.69	
3	31.95	
4	54.39	

BL, body length; N.S., non-significant differences.

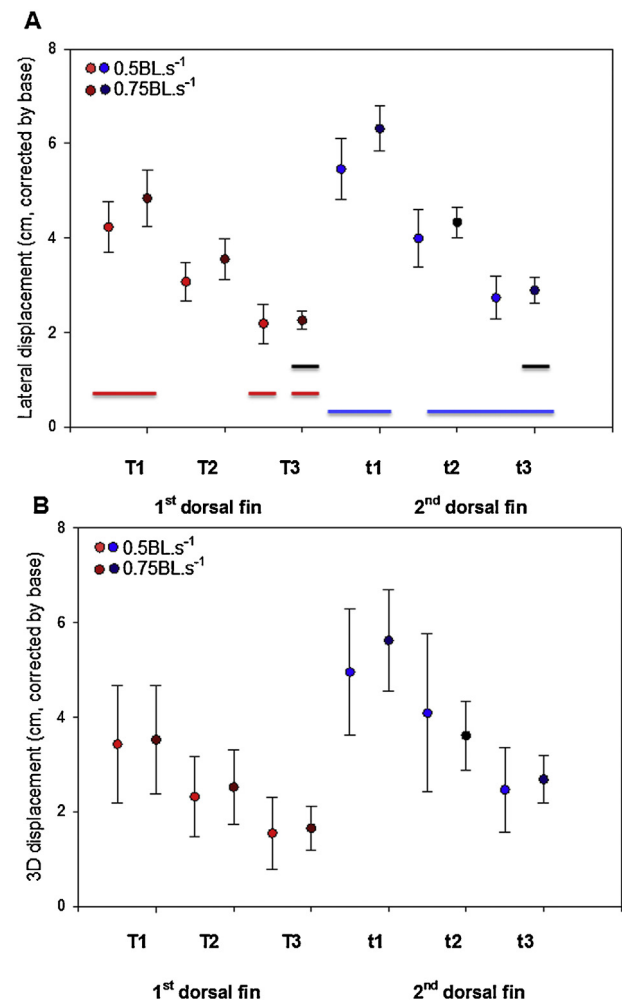


Fig. 4. Plot of mean displacement of fin landmarks for all trials corrected by base (bars represent standard error), at 0.5 BL s^{-1} and 0.75 BL s^{-1} . (A) Mean lateral displacement and (B) mean three-dimensional displacement. Lines of the same color and same level represent differences found through ANOVA on ranks at 0.05 level of significance. Uppercase letters refer to landmarks on the first dorsal fin (T1, distal tip of the fin; T2, midpoint between T1 and T3; T3, trailing edge tip) and lowercase letters refer to the second dorsal fin landmarks (t1, distal tip of the fin; t2, midpoint between t1 and t3; t3, trailing edge tip).

burst duration in certain muscle bundles: left middle and right trailing edges of the first dorsal fin, and right leading edge of the second dorsal (two-way ANOVA, $F_{\text{speed}} = 8.49$, $F_{\text{muscle}} = 2.014$, $p < 0.05$). Duty cycle was similar and varied from 22% to 55% for all of the muscles ($31 \pm 15\%$, two-way ANOVA, $p > 0.05$). Comparing the onset of bilateral pairs for the same muscle revealed some differences between speeds ($Z = -2.338$, $p < 0.05$; Fig. 6), with more differences between left and right muscle activations in the first dorsal fin at 0.5 BL s^{-1} and in the second dorsal fin at 0.75 BL s^{-1} . However, the asynchrony index did not reflect this trend and was similar between speeds (overall mean: 0.42 ± 0.18 , two-way ANOVA, $p > 0.05$). Onset and duration were similar among unilateral implants within a muscle. Magnitude was similar among implants, muscles, speeds, and individuals.

4. Discussion

Three-dimensional kinematics reveals that both dorsal fins in white-spotted bamboo sharks oscillate in phase with the undulating body during swimming. However, the dorsal fins have larger lateral displacement than the trunk. Larger oscillation patterns

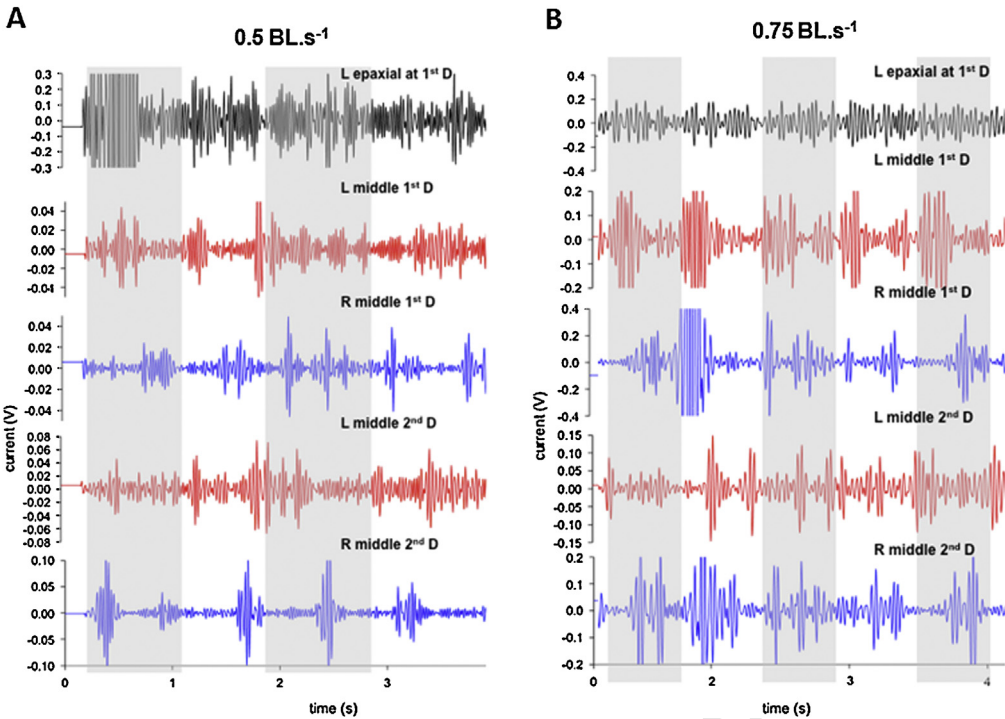


Fig. 5. Representative traces of muscle activation in the dorsal fin of a bamboo shark during steady swimming at (A) 0.5 BL.s⁻¹ and (B) 0.75 BL.s⁻¹ through consecutive tail beats. For clarity purposes only the middle of each fin is represented; every other tail beat is represented by a shaded area.

are indicative of controlled movement to increase the volume of water moved for thrust production. The dorsal fins in bluegill sunfish also have higher lateral excursion when producing thrust and may be cupped to push the water more efficiently (Drucker and Lauder, 2001; Standen and Lauder, 2005). Fin cupping is powered by bending individual fin rays in actinopterygians (Standen and

Lauder, 2005). Such fine control was thought to be absent in elasmobranchs (Liem and Summers, 1999). The complex musculoskeletal arrangement in white-spotted bamboo sharks should allow multiple ceratotrichia to function as analogs to the sliding hemitrichia of bony fishes (Maia and Wilga, unpublished data), by independently activating selected muscle fibers in the fin. However, no differences

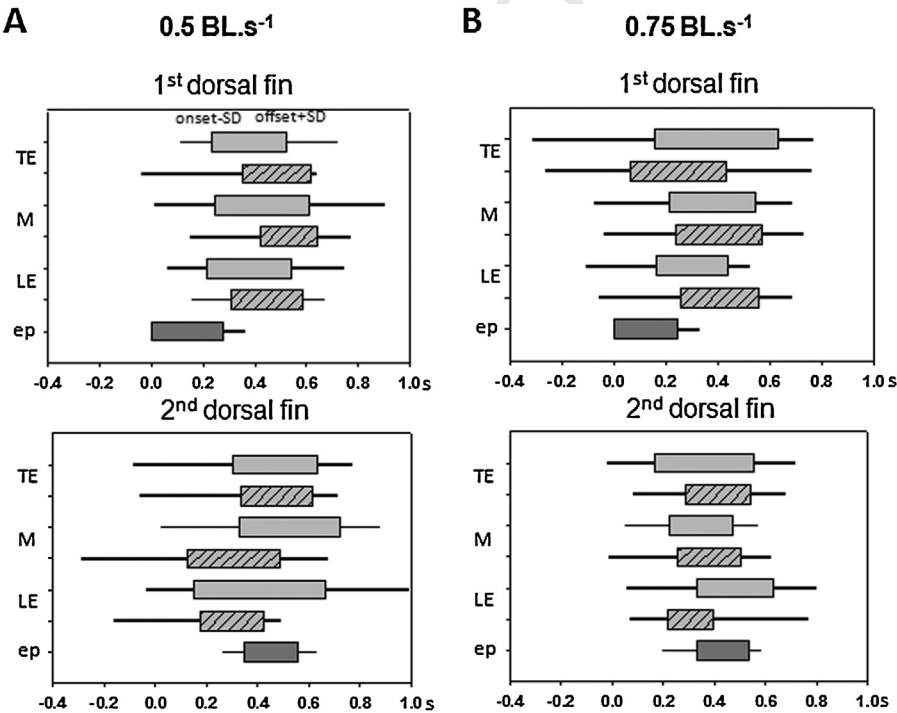


Fig. 6. Temporal variables (onset and offset) for dorsal fin muscle activation in bamboo sharks during steady swimming for all individuals and trials combined at (A) 0.5 BL.s⁻¹ and (B) 0.75 BL.s⁻¹. Striped bars represent muscles on the left side and solid bars represent muscles on the right side. Abbreviations: ep, left red epaxial; LE, leading edge; M, middle; and TE, trailing edge.

were found in the magnitude or onset of motor activity among implants along the same side of the fin in the swimming bamboo sharks studied here. Fin cupping, as observed in the videos and verified by 3D kinematics showing that bending occurs within the fins of bamboo sharks during steady swimming, could be the result of flow interaction with fin mechanical properties that merit further study.

White-spotted bamboo sharks and bluegill sunfish have other anatomical similarities; both species have a posterior placement of the dorsal fins, which is beneficial for thrust production. Appendage placement relative to the center of mass plays a key role in determining fin function as thrusters or stabilizers by directing force differently (Drucker and Lauder, 2001). Laterally oriented forces that produce torque are more effective at counteracting destabilizing forces when located around the center of mass. A fin with a large moment arm located above the center of mass is capable of producing strong torque to counteract destabilizing forces that could perturb normal locomotion, such as tidal currents or passing fish. On the other hand, a fin located farther back from the center of mass can produce force with a larger thrust component that will propel the fish forward. In bamboo sharks and bluegill sunfish, the dorsal fins are positioned farther back on the body, at the optimal position for thrust generation. In contrast, the dorsal fins of rainbow and brook trout and the first dorsal fin in spiny dogfish are positioned closer to the center of mass, thus generating torque that will have a larger impact on the stability of the fish (Drucker and Lauder, 2005; Standen and Lauder, 2007).

The pattern of bending within the fin was complex and could not be completely discerned by the methods used here. Bending can result from a combination of muscle activation, anisotropic biomechanical properties of the fin, and passive resistance to fluid motion (Lauder, 2006). The distal tips of the dorsal fins had greater lateral displacement than the trailing edge, which remains closer to the trunk. The majority of the dorsal fin muscle mass was positioned anteriorly in the fin with fibers oriented at a dorsoposterior angle that pulls the dorsal skeletal structures more.

An increase in the range of motion that would augment thrust was expected in the faster swimming speed. However, range of motion, lateral displacement, and magnitude of muscle activity were similar between speeds within fins. This suggests that bamboo sharks are not augmenting thrust by recruiting more muscle fibers to increase fin stroke and produce more thrust, the way some labriform fishes use their pectoral fins (Walker and Westneat, 2002). However, thrust force can also be augmented in other ways: by increasing flapping frequency or by increasing burst duration (Walker and Westneat, 2002). Higher flapping frequency can increase the energy in the wake over the same duration, while longer burst durations can produce higher integrated force. Bamboo sharks are indeed increasing stroke frequency of the dorsal fin with increasing tail beat frequency, since lag values relative to the body were similar between speeds. Burst duration was also longer at the faster speed for three of the seven implants in the first dorsal fin muscle. Although bamboo sharks are not using the same dorsal fin mechanics as bony fishes to augment force, they still appear capable of producing higher forces at increased speeds.

The 3D kinematics and motor activity patterns indicate a thrusting function for the first and second dorsal fins in bamboo sharks. The bilateral dorsal fin muscles show alternating activation of the left and right sides. To the best of our knowledge, the activation pattern of dorsal fin muscles has only been investigated in bluegill sunfish (Jayne et al., 1996) and spiny dogfish (Maia and Wilga, unpublished data). Bluegill sunfish have a spiny and a soft dorsal fin, with the soft portion located more posteriorly on the trunk. Muscle activation of the soft dorsal fin is independent of the adjacent red epaxial muscle during steady swimming in bluegill sunfish (Jayne et al., 1996), which is similar to the dorsal fins in steady-swimming

bamboo sharks. In addition, in the aforementioned study, activity in the dorsal fin muscles during steady swimming only occurred at tail beat frequencies above 4 Hz. In bamboo sharks, the dorsal fins were active during steady swimming at the two speeds tested, as they were in spiny dogfish (Maia and Wilga, unpublished data). During slow maneuvers and fast starts the dorsal fins also show lateral movement (Maia, pers. obs.), which indicates active motion during most modes of swimming. Motor activity in the dorsal fins of spiny dogfish was nevertheless distinct from that in bamboo sharks. In spiny dogfish, the bilateral muscles of the first dorsal fin are simultaneously active, indicating active stiffening of the fin (Maia and Wilga, unpublished data). In addition, 3D kinematics shows that the first dorsal fin of spiny dogfish moves independently from the base of the fin and in the opposite direction of axial motion (Maia and Wilga, unpublished data). In contrast, the second dorsal fin of spiny dogfish moves in phase with axial motion and has asynchronous bilateral motor activation, indicative of a thrust-producing fin (Maia and Wilga, unpublished data). These two studies on bamboo sharks and spiny dogfish present evidence that contradicts the classical theory that shark dorsal fins are only capable of passively stabilizing the fish (Harris, 1936).

No differences were detected for the onset or duration of motor activity among the implants in the dorsal fins within one side of a fin. This was not expected as bamboo sharks have distinct muscle bundles associated with each row of radials, which had been hypothesized to function in an analogous manner to muscles controlling independent fin rays in actinopterygian fishes. Nonetheless, multiple regions of the dorsal fin muscles were simultaneously recruited in bluegill sunfish (Jayne et al., 1996). In other fins that are also required to overcome high fluid forces, such as the pectoral fins of labrids during steady swimming or the pectoral fins of leopard sharks during vertical maneuvers, we observe a similar pattern of simultaneous activation of different muscles on the same side of the fin (Westneat and Walker, 1997; Drucker and Jensen, 1997; Wilga and Lauder, 2000; Maia et al., 2012). Simultaneous activation of muscles along the fin may be necessary to resist relatively higher fluid forces in some swimming behaviors.

Bamboo sharks inhabit complex reef environments in close association with the benthos (Compagno, 1984). Little is known about their locomotor habits in the wild. In aquaria, bamboo sharks are normally found resting on the substrate or foraging for food. Bamboo sharks are also capable of very fast acceleration, especially during escape responses (Maia, pers. obs.). Posteriorly placed dorsal fins are advantageous in fast acceleration behaviors (Webb, 1984). Bamboo sharks are anguilliform locomotors with a very flexible body (Compagno, 1984; Maia et al., 2012). By adding thrust produced by the dorsal fins, bamboo sharks can increase swimming efficiency. In addition, since bamboo sharks spend so much time resting on the bottom and have a low body profile, stability requirements are bound to be low. This is in contrast to the benthopelagic spiny dogfish that have a high-profile body and routinely swim in the water column (Maia and Wilga, unpublished data).

Our data indicate that the dorsal fins are actively being oscillated laterally to create forward thrust with some lateral loss due to fin orientation. Further investigation of the flow around the dorsal fins will enable quantification of the thrust components. The placement of the dorsal fins, with an interdorsal distance of approximately the length of a dorsal fin poses another question: are vortices shed at the first dorsal fin interacting with the second dorsal fin?

5. Conclusions

Contrary to traditional theory that the dorsal fins in sharks function as stabilizers (Harris, 1936), the fins appear to act as thrusters during steady swimming in bamboo sharks. A large range of motion

and lateral displacement, as can be observed in bamboo sharks, are requisite for a thrusting function of the dorsal fins. Accordingly, the dorsal fin muscles have motor activity patterns with bilateral asynchronous activation. The capacity to create complex 3D conformations like fin cupping suggests that the complexity of the dorsal fin skeletal structures in bamboo sharks confers a function that is analogous to the flexible fins of bony fishes.

This study improves our understanding of bamboo shark locomotion and the role of the dorsal fins during steady swimming, and reveals a surprising diversity in the form and function of the dorsal fins among shark taxa. From an ecological standpoint, relating how fin function and swimming performance reflect the requirements of ecological niche and the constraints of anatomy will allow inferences to be made about habitat use, establishing a bridge that is currently lacking between laboratory studies and nature (Maia et al., 2012).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.zool.2013.05.001>.

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