

Anatomy and Muscle Activity of the Dorsal Fins in Bamboo Sharks and Spiny Dogfish During Turning Maneuvers

Anabela Maia* and Cheryl D. Wilga

Department of Biological Sciences, College of the Environmental and Life Sciences, University of Rhode Island, 120 Flagg Road, Kingston, Rhode Island 02881-0816

ABSTRACT Stability and procured instability characterize two opposing types of swimming, steady and maneuvering, respectively. Fins can be used to manipulate flow to adjust stability during swimming maneuvers either actively using muscle control or passively by structural control. The function of the dorsal fins during turning maneuvering in two shark species with different swimming modes is investigated here using musculoskeletal anatomy and muscle function. White-spotted bamboo sharks are a benthic species that inhabits complex reef habitats and thus have high requirements for maneuverability. Spiny dogfish occupy a variety of coastal and continental shelf habitats and spend relatively more time cruising in open water. These species differ in dorsal fin morphology and fin position along the body. Bamboo sharks have a larger second dorsal fin area and proportionally more muscle insertion into both dorsal fins. The basal and radial pterygiophores are plate-like structures in spiny dogfish and are nearly indistinguishable from one another. In contrast, bamboo sharks lack basal pterygiophores, while the radial pterygiophores form two rows of elongated rectangular elements that articulate with one another. The dorsal fin muscles are composed of a large muscle mass that extends over the ceratotrichia overlying the radials in spiny dogfish. However, in bamboo sharks, the muscle mass is divided into multiple distinct muscles that insert onto the ceratotrichia. During turning maneuvers, the dorsal fin muscles are active in both species with no differences in onset between fin sides. Spiny dogfish have longer burst durations on the outer fin side, which is consistent with opposing resistance to the medium. In bamboo sharks, bilateral activation of the dorsal fin muscles could also be stiffening the fin throughout the turn. Thus, dogfish sharks passively stiffen the dorsal fin structurally and functionally, while bamboo sharks have more flexible dorsal fins, which result from a steady swimming trade off. *J. Morphol.* 274:1288–1298, 2013. © 2013 Wiley Periodicals, Inc.

KEY WORDS: elasmobranchs; electromyography; functional morphology; inclinometer; dorsal fin muscle; maneuvering

INTRODUCTION

Chondrichthyan fishes have a strikingly different muscle and skeletal arrangement in the dorsal fins compared to actinopterygian fishes. The fin rays in actinopterygians are composed of bilaterally paired

hemitrichia with bilateral muscles attached to each (Geerlink and Videler, 1987; Taft et al., 2008; Taft, 2011). Contraction of muscles on one side causes the hemitrichia to slide along each other putting the contralateral side in tension and bending the fin ray towards the contracted muscle (Lauder, 2006; Taft et al., 2008; Taft, 2011). Instead of hemitrichia, chondrichthyan fishes have ceratotrichia supporting the fin web (Compagno, 1999), where muscles do not attach to individual ceratotrichia but rather to a tendinous sheath that connects all the ceratotrichia (Goodrich, 1904). Although chondrichthyan fishes have only ipsilateral muscle insertion onto the ceratotrichial tendon sheath, recent 3D kinematic studies on the dorsal fin during steady swimming in spiny dogfish and bamboo sharks suggest that the range of movement is similar to actinopterygian fishes (Maia and Wilga, 2013). In bamboo sharks, both of the dorsal fins act as thrusters during steady swimming (Maia and Wilga, 2013). Variation in the function of the two dorsal fins also exists among actinopterygian taxa. The dorsal fin in bluegill sunfish generates primarily posterior forces that function mainly for thrust (Drucker and Lauder, 2001), while the dorsal fin in rainbow and brook trout produce larger lateral forces, which contribute to stabilization (Drucker and Lauder, 2005; Standen and Lauder, 2007). During steady swimming, the dorsal fin in the bluegill sunfish bends

Contract grant sponsor: Fulbright-Portugal (A.M.); Contract grant number: MCTES/FCT/SFRH/BD/36852/2007; Contract grant sponsor: University of Rhode Island Graduate Fellowship (A.M.); Contract grant sponsor: National Science Foundation (C.W.); Contract grant numbers: IOS-0542177, IOS-0344126.

*Correspondence to: Anabela Maia, Department of Biology, Tufts University, 200 Boston Ave., Medford, MA 02155.
E-mail: Anabela.Maia@tufts.edu

Received 20 November 2012; Revised 9 June 2013;
Accepted 18 June 2013.

Published online 2 August 2013 in
Wiley Online Library (wileyonlinelibrary.com).
DOI 10.1002/jmor.20179

toward the ipsilateral side, consistent with a function for thrust augmentation (Jayne et al., 1996; Drucker and Lauder, 2001).

Stability and procured instability characterize two opposing types of swimming, steady and maneuvering respectively (Webb, 2006). Steady swimming is easily studied in the controlled environment of a flow tank, and has been used for many locomotion studies in sharks (Wilga and Lauder, 2002, 2004; Donley and Shadwick, 2003; Donley et al., 2005; Flammang et al., 2011). In contrast, maneuvers are more difficult to study under controlled conditions due to less predictable movements such as braking, vertical maneuvers, routine turns and fast starts in the field of view (Webb, 2006). Only a few studies have looked at unsteady swimming in sharks, namely at escape responses (Domenici et al., 2004), foraging turns (Kajiura et al., 2003), routine turning maneuvers (Porter et al., 2009, 2011) and vertical maneuvers (Wilga and Lauder, 2001, 2002) in sharks. Pectoral fins are used to generate thrust during vertical maneuvers in sharks, where activation of the epaxial, cucullaris, fin adductor, fin protractor, fin abductor, and hypaxial muscles result mainly in changes in camber (Wilga and Lauder, 2000, 2001). Similar to the pectoral fins, the dorsal fins might be capable of actively generating thrust or adjusting stability for the fine control necessary for maneuvering. That is, produce enough force to overcome the water pushing on the fins. Maximal muscle force can be predicted using muscle cross sectional area (CSA) (Powell et al., 1984).

This study investigates the anatomy and muscle function of the dorsal fins in two species, *Squalus acanthias* (Linnaeus, 1758; Order Squaliformes, Family Squalidae) commonly known as spiny or piked dogfish, and *Chiloscyllium plagiosum* (Bennett 1830; Order Orectolobiformes, Family Hemiscylliidae) or white-spotted bamboo sharks. Spiny dogfish occur in inshore and offshore waters from temperate and subarctic regions (Compagno, 1984). Although spiny dogfish can be found frequently near the substrate on continental and insular shelves, as well as on the upper continental slope, they also cruise in the water column and feed mainly on fish and squid (Compagno, 1984). White-spotted bamboo sharks are a bottom-dwelling species found off the coast of Indonesia and in surrounding Pacific waters in coral reef habitats and feed primarily on benthic invertebrates (Compagno, 1984). The two species have distinctly different body types and distinct dorsal fin morphologies that may reflect habitat preference and locomotor strategies. The dorsal fins of white-spotted bamboo sharks, *C. Plagiosum*, lack basal pterygiophores while the dorsal fins of spiny dogfish have one or more basal pterygiophores with supraneurals connecting to the vertebral column (Shirai, 1996). Spiny dogfish not only have a variable number of basal and radial pterygiophores among individuals, but the basals and the

radials are often indistinguishable from each other (Benzer, 1944).

We hypothesize that bamboo sharks, which inhabit complex reef habitats, will have more extensive subdivisions of the muscle and skeletal arrangement that will result in higher freedom of movement of the dorsal fins and higher theoretical muscle force that confers greater turning maneuverability. Muscle activity of the dorsal fins during turns in bamboo sharks is expected to be finely controlled with alternating activity on the left and right sides of the fin; while spiny dogfish will use the fins as rudders, which is characterized by simultaneous contraction on both sides with higher magnitude on the outer side of the turn.

MATERIALS AND METHODS

Anatomy

Seven mature fresh frozen bamboo sharks, *C. plagiosum*, Bennett, 1830; Total length (TL) 51–78 cm, and nine mature fresh frozen spiny dogfish individuals *S. acanthias*, Linnaeus, 1758; TL 74–87 cm, were used for the morphometric analysis. The bamboo shark specimens were obtained from Sea World Orlando, FL, while the spiny dogfish were caught by trawl in the Narragansett Bay, RI, Graduate School of Oceanography Fish Trawl Survey, R/V Cap'n Bert, with Rhode Island Division of Environmental Management permission. Data was collected for the following variables: distance from snout to first dorsal fin base (SD1), interdorsal distance (D1D2), distances between second dorsal and caudal fin (D2T), first and second dorsal fin base (B1, B2), height (H1, H2), and total length of the shark (Fig. 1A). The variables were standardized for size effects by dividing by total length and converting to a percentage. Fin area and percentage of fin planar area occupied by muscle (Fig. 1B) were obtained through orthophotography using Image J software, v. 1.43u (Rasband, 1997–2012). These area variables are presented as a ratio of the first to the second dorsal fin to minimize size effects.

Muscular anatomy was described using five of the mature bamboo sharks and six of the mature spiny dogfish (same specimens used above for morphometrics). The skin was removed and fascicle length, muscle mass and angle of insertion relative to the horizontal septum were quantified. Fascicle length was measured using a stereomicroscope, insertion angle was calculated from orthophotography using Image J software and wet muscle mass was obtained by removing the muscle mass and weighing it on a precision scale. Anatomically relevant CSA was computed (Powell et al., 1984) using the equation:

$$CSA = \text{muscle mass}(\cos \phi) / (FL \times \text{muscle density}),$$

where FL is the average fascicle length, and ϕ is the fiber angle. Muscle density is considered 1.05 g cm^{-3} , a value derived from several elasmobranch species (Bone and Roberts, 1969). Unilateral theoretical maximum tetanic tension (P_o) was computed (Powell et al., 1984):

$$P_o = CSA \times T_{SP},$$

where the specific tension (T_{SP}) is assumed to be similar to that of shark white muscle 289.2 kN m^{-2} obtained from *Scyliorhinus canicula* (Lou et al., 2002).

T-tests were used to test for differences in anatomical variables between the two species. A principal components analysis explored whether morphometric variables differ between the two species using SPSS 12 (IBM, Corp. Armonk, NY). When normality and equality of variance criteria were not met, a

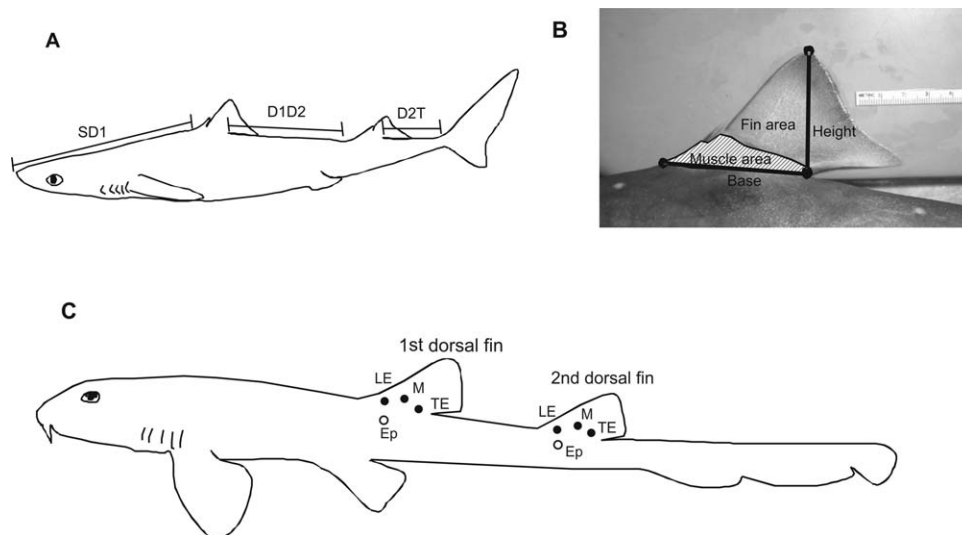


Fig. 1. Morphometric measurements (A, B) and electrode placement (C) for bamboo and spiny dogfish shark dorsal fins. SD1-distance between snout and first dorsal fin, D1D2-distance between first and second dorsal fins, D2T-distance between second dorsal fin and tail. In (C), black dots represent bilateral implantation and open circles represent left side only implantation (Ep-red epaxial; LE-leading edge; M-middle; TE-trailing edge).

Mann-Whitney test on ranks was used. CSA was regressed over total length and an analysis of covariance was used to test for differences in the two species regression intercepts and slopes. T-tests and analysis of covariance procedures were run using SAS statistical software.

Muscle Activity

Three additional bamboo sharks were obtained from Sea World, Orlando, FL, and kept in a circular tank (1900 L) with 32 psu salinity, 22°C ($\pm 1^\circ\text{C}$), 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 41 to 81 cm. Three additional spiny dogfish were obtained from the Graduate School of Oceanography (University of Rhode Island) trawl cruises in Narragansett Bay, RI. Individuals were kept in 8,900 L round tank (3 m diameter and 1.20 m tall). The tanks were maintained at 32 psu salinity, 18°C ($\pm 1^\circ\text{C}$) and a 12 h:12 h light: dark cycle. Sharks were fed every other day on a natural diet of fish (*Scomber* sp., *Clupea* sp.) and squid (*Illex* sp.). Total length ranged from 48 to 86 cm.

Experiments were conducted at the University of Rhode Island during 2009 and 2010, under the IACUC protocol # AN05-07-001. Sharks were anesthetized using MS222 and intubated with sea water with MS222 at a diluted concentration (1.75 g in 20 L for 5 min) for the duration of the surgery (<60 min). Bipolar stainless steel electrodes were implanted bilaterally using a 25-gauge needle into three locations along each dorsal fin muscle: leading edge, middle of the fin and trailing edge locations (Fig. 1C). Two additional electrodes were implanted in the red epaxial muscle below each fin on the left side (Fig. 1C). Electrode leads were sutured to a loop between the two dorsal fins and pins were attached to the opposite end and inserted in a pin connector that transmitted data to a computer during the experiments. The shark was allowed to recover in the experimental tank for 2 h after surgery. The temperature in the experimental tank was kept at the same temperature as the holding tank and was the same for all trials for each species, 22°C ($\pm 0.5^\circ\text{C}$) for bamboo sharks and 18°C ($\pm 0.5^\circ\text{C}$) for spiny dogfish.

The experimental tank was an 8' diameter circular tank with tall polyvinyl chloride pipes to simulate a complex environment that induced spontaneous turning. The water level was maintained at 60 cm high. Turns were performed in front of the 1.2 m wide \times 0.6 m tall observation window and the animal would turn

around the polyvinyl chloride pipes (taller than the water level) spaced approximately 25 cm. Four routine turns were selected for each individual, which met the following criteria: 1) the animal turned in front of the window and around the polyvinyl chloride pipes, 2) the animal did not accelerated markedly from its routine swimming speed around the tank (escape responses, rapid accelerations were visually excluded), 3) the animal did not touch the pipes, 4) the initial and final position of the animal in the water column differed by less than two head heights. A high-speed camera positioned in the tank window was used to simultaneously record lateral video, necessary to identify behaviors and exclude fast starts and turns with high vertical components. An equal number of left and right turns were used for all the animals tested. Electromyography (EMG) signals were recorded with differential amplifiers 1700 (AM Systems, Sequim), 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) and stored in a computer. EMG signals were filtered with high pass filters of 50 Hz. Waveform analyses were conducted using Chart software (v.5.4.2, ADInstruments, Colorado Springs) for four trials for each individual.

Onset and offset of EMG activity was determined from the rectified, integrated EMG signal using a signal to noise ratio of 2.5 times the baseline value (Roberts et al., 2007). The magnitude of an individual muscle burst was determined relative to the maximum peak for that muscle implant. Cycle duration is defined from the onset of the reference implant to the next onset of the same implant, while duty cycle is defined as the percentage of the cycle duration in which the muscle was active. No differences were detected between left and right turns, thus the reference was the dorsal fin muscle leading edge implant on the inside of the turn. Four events were analyzed, for or each individual.

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 muscle pairs with the following equation,

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

where dur1 and dur2 are the durations of left and right muscles and TE is the total duration of the event, from onset of the first of these two muscles activity to the offset of the last

TABLE 1. Morphometric variables for dorsal fins in bamboo shark and spiny dogfish

Variable	Bamboo shark		Spiny dogfish		P-value
	Mean	Std. error	Mean	Std. error	
Distance to first dorsal fin	37.43	0.44	33.90	0.22	<0.001
First dorsal fin base	8.38	0.33	7.76	0.19	N.S.
First dorsal fin height	7.41	0.39	6.10	0.08	0.002
Second dorsal fin base	7.57	0.13	6.32	0.30	0.006
Second dorsal fin height	5.81	0.43	3.81	0.15	<0.001
First dorsal: second dorsal area	1.42	0.06	2.00	0.12	<0.001
Interdorsal space	11.07	0.39	22.23	0.87	<0.001
distance from second dorsal to tail	9.94	0.38	10.91	0.28	N.S.
First dorsal: second dorsal muscle area	1.36	0.10	1.29	0.10	N.S.
First dorsal muscle insertion angle	51.17	2.22	41.73	1.45	0.007
Second dorsal muscle insertion angle	54.23	0.71	42.30	2.29	0.016
First dorsal: second dorsal CSA	1.49	0.13	1.73	0.25	N.S.

muscle to be active during a particular behavior (Gerry et al., 2008). This index is useful to confirm or reject the hypothesis that during turns fins have alternate activation for thrust or simultaneous activation to be held against the flow and act like a rudder.

All summary statistics are reported as mean \pm standard deviation. To test for the effect of fin (first and second dorsal), a two-way mixed model analysis of variance (ANOVA) was performed, with individual as the random effect and fin as the fixed effect (Zar, 2009). Paired T-tests were used to test for differences between left and right muscle pairs (Zar, 2009). Another two-way ANOVA was also run with species random effect and muscles as the fixed effect. Statistical tests were conducted using SAS v. 9.1.2 (SAS Institute, Cary, NC).

RESULTS

Anatomy

Interspecific differences in several morphometric variables were found. Table 1 shows the statistical data on the morphometric variables for spiny dogfish and white-spotted bamboo shark dorsal fins corrected for body length. Most of the variables differ between the two species except for length of the second dorsal fin base and ratio of the planar muscle area between fins. Bamboo sharks have more posteriorly placed dorsal fins, longer dorsal fin bases and taller first dorsal fins than spiny dogfish. First and second dorsal fins are more dissimilar in size in spiny dogfish and the two fins are spaced further apart than in bamboo sharks. Dorsal fin muscle insertion angle is greater for bamboo sharks by over 10° compared to spiny dogfish, indicating more vertically oriented fibers.

The principal components analysis revealed several groups of variables that distinguish the two species (Fig. 2). The first two components represent 77.1% of the variation with four components explaining 90.9%. Distance to the first dorsal fin, length of first fin base, height of first fin base, and height of second dorsal fin loaded negatively on the first axis, while the ratio of first to second dorsal fin area, interdorsal distance, and distance between second dorsal fin and tail loaded positively. Fewer variables loaded highly on the second

axis, with planar area occupied by muscle loading negatively. The first axis was successful in distinguishing the two species (Fig. 2).

Gross anatomical examination of the musculo-skeletal system of the dorsal fins in spiny dogfish, *S. acanthias*, revealed that the dorsal fin muscle mass originates from the stratum compactum lying over the epaxial musculature and inserts onto the tendinous sheath connecting to the ceratotrichia at the distal row of radials (Figs. 3A,B). The single muscle mass is tightly packed and tapers toward the insertional end.

Covering the dorsal fin spine and spreading laterally to the fin in spiny dogfish is a ligamentous band that connects to the stratum compactum

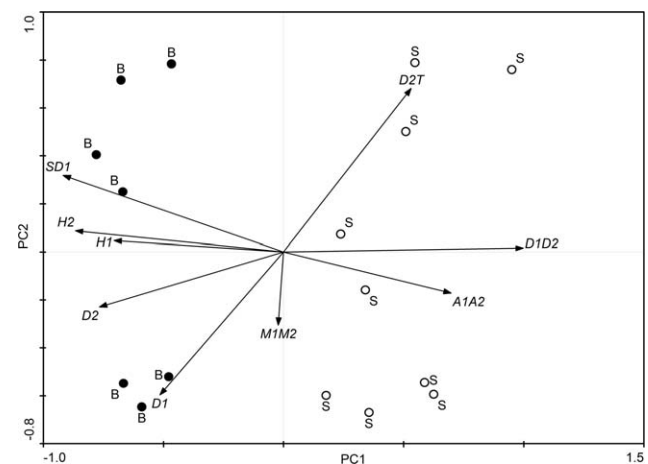


Fig. 2. Principal component analysis with PC2 (18.6%) loaded on PC1 (58.5%) separates the two species based on PC1. Variables used as predictors, as percent of body length or ratio: A1:A2-ratio of first dorsal fin area to second dorsal fin area; D1D2-distance between dorsal fins; D1-length of first dorsal fin base; D2-length second dorsal fin base; D2T-distance between second dorsal fin and tail; H1-height of first dorsal fin; H2-height of second dorsal fin; M1:M2-ratio of first to second dorsal fin area occupied by muscle; SD1-distance from snout to first dorsal fin. Samples: B-bamboo shark individuals; S-spiny dogfish individuals.

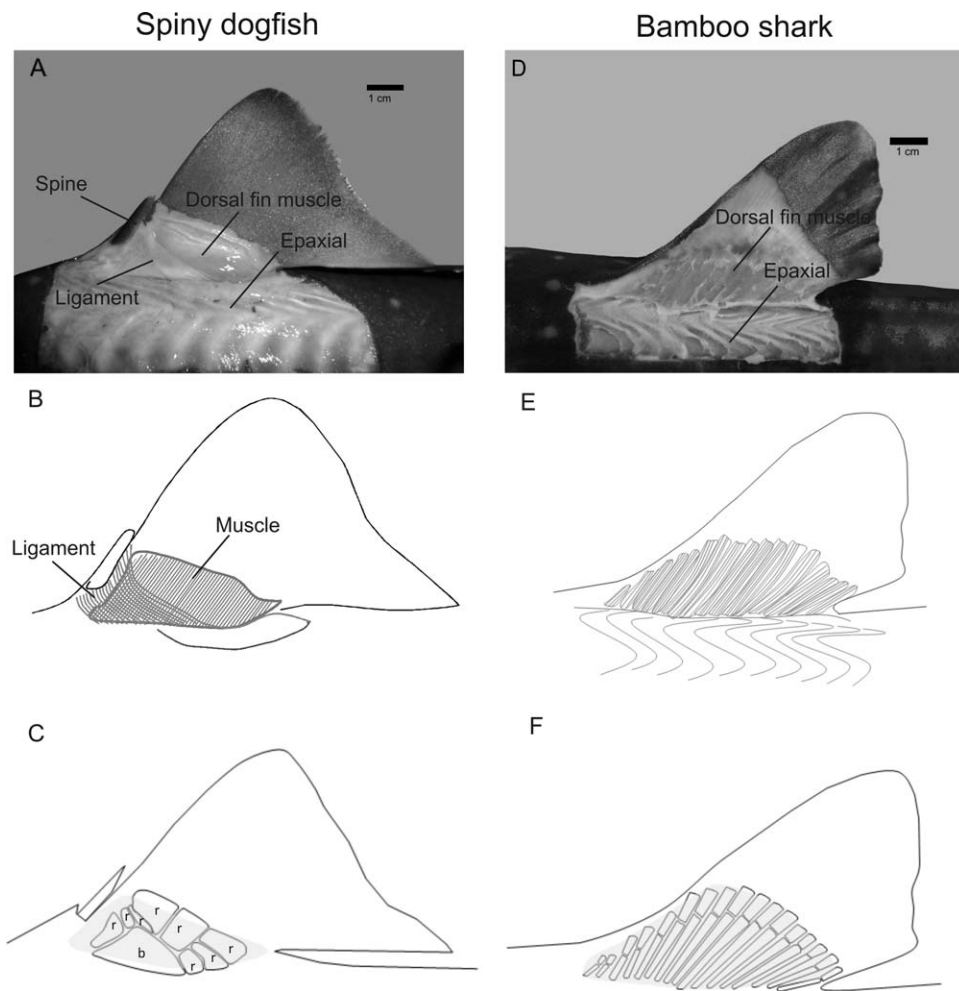


Fig. 3. Dorsal fin anatomy of two shark species, spiny dogfish on the left and bamboo shark on the right. (A) and (D)-photo of first dorsal fin with skin removed; (B) and (E)-schematic representation of the muscle mass and of the ligamentous tissues [only in (B)]; (C) and (F)-representation of the skeletal elements, r-radials, b-basals with the shaded area representing the area covered by muscle, in bamboo sharks all the skeletal elements present are radials. The second dorsal fins are slightly smaller but otherwise similar.

(Fig. 3A), but not to the dorsal fin or epaxial musculature. The dorsal fin muscle extends over the radials or basals and inserts onto the ceratotrichia overlying the distal radials, thus allowing independent movement of the skeletal structures. As previously reported, the basals and radials are not easily distinguished and vary in size and number among individuals (Fig. 3C; Benzer, 1944). However, the area occupied by basal and radials on the midline of the base of the fin is consistent among individuals. Basals articulate with supraneurals on the vertebral column.

In contrast, bamboo sharks, *C. plagiosum*, lack spines and basal elements in the dorsal fins. The dorsal fin musculature has a similar origin and insertion as in spiny dogfish. However, the muscle arrangement differs in having distinctly separated muscle bands with each band associated with and parallel to a column of radial elements with relatively thicker epimysium, the connective tissue that surrounds muscle, than in dogfish (Figs.

3D,E). The skeletal elements are composed of two rows of radials, a longer proximal row and shorter distal row that do not attach to the vertebral column. The number of radials in each row varies between 17 and 18 in the first dorsal fin and 17 and 20 in the second dorsal fin. The connection between the proximal and distal radials is made by cartilaginous pads and provides the major plane of bending. The second row of radials is partially overlapped by the ceratotrichia. In addition, each muscle spans the joints between distal and proximal radials to insert onto the proximal end of the ceratotrichia through a tendinous sheath.

Based on visual inspection the dorsal fin muscles appear to be composed of white fibers in spiny dogfish and intermediate fibers in bamboo sharks. CSA was calculated along with unilateral theoretical maximum tetanic tension (P_o) for both dorsal fins in both species and interspecific variation was noted. Theoretical maximum tetanic tension for the first dorsal fin ranged from 7.3 to 25.3

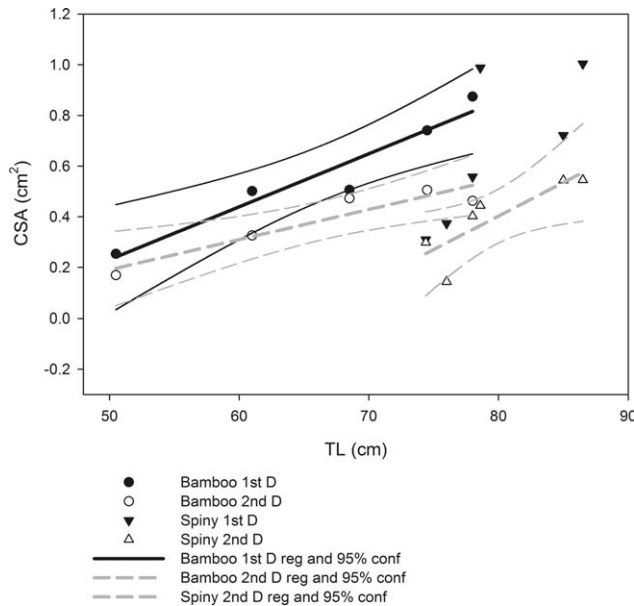


Fig. 4. CSA regressed onto shark TL for the first (black lines) and second dorsal (grey lines) fins of bamboo sharks and spiny dogfish, thicker lines represent the plot regressions and thinner lines the respective 95% confidence intervals.

N in bamboo sharks and 9.0 to 29.0 N in spiny dogfish. Maximum tetanic tension values for the second dorsal fin ranged from 4.9 to 14.6 N in bamboo sharks and 4.1 to 15.8 N in spiny dogfish. Regressions were run for CSA with total length (Fig. 4) and were significant except for the first dorsal fin of spiny dogfish.

The resultant regressions are the following:-
Bamboo shark

$$CSA_{D1} = -0.816 + (0.0209 \times TL), r^2 = 0.924,$$

$$P = 0.0097$$

$$CSA_{D2} = -0.407 + (0.0119 \times TL), r^2 = 0.887,$$

$$P = 0.017$$

Spiny dogfish

$$CSA_{D1} = -2.918 + (0.0449 \times TL), r^2 = 0.544,$$

$$N.S. (P = 0.093)$$

$$CSA_{D2} = -1.719 + (0.0265 \times TL), r^2 = 0.705,$$

$$P = 0.037$$

where, CSA_{D1} -cross sectional area of first dorsal fin, CSA_{D2} -cross sectional area of second dorsal fin, and TL-total length in cm.

Significant differences were found in the regressions between the first and second dorsal fins for bamboo sharks for the intercept (ANCOVA, $P < 0.05$) as well as for the slope (ANCOVA, $P < 0.05$). [F (3,9) = 10.23, $P < 0.05$, covariate TL, F (3,9) = 4.47, $P < 0.05$, covariate fin, F (3,9) = -2.91, $P <$

0.05 interaction, F (3,9) = 0.83, $P > 0.05$]. Differences between the first dorsal fin in the two species could not be assessed since the regression for spiny dogfish was not significant. For the second dorsal fin, the two species differed in intercept and slope [ANCOVA, intercept $P = 0.0280$, slope $P = 0.0329$, F (3,10) = 5.74, $P < 0.05$, covariate TL, F (3,10) = 3.78, $P < 0.05$, covariate species, F (3,10) = 2.57, $P < 0.05$ interaction, F (3,10) = -0.96, $P > 0.05$].

Muscle Activity

In both species, the muscles on both sides of the first and second dorsal fins and epaxial muscles below the dorsal fins were active during the majority of a cycle. Muscle activity among the three implants on a side was also similar for onset and duration variables. However, the pattern of activation of the left and right muscles differed between species.

In spiny dogfish, all muscles implanted were active during a turn. Figure 5A shows a representative trace of activity patterns of dorsal fin muscles in a spiny dogfish during a turn, while Figure 6A shows all the trials combined. The two-way ANOVA showed no differences between individuals for all the variables tested. Burst duration was similar for the same muscles in the first and second dorsal fins. However, burst duration was longer for outer (or contralateral) muscles of the first dorsal fin than for inner (or ipsilateral) muscles of the first dorsal fin relative to the turning side ($H = 17.36$, d.f. = 5, $P < 0.05$). In addition, the duration of the activity of the outer muscles in the second dorsal fin was also longer than the duration of the activation of the muscles in the inner second dorsal ($H = 17.36$, d.f. = 5, $P < 0.05$). Burst duration within muscles on the same side for each fin was similar. Although burst duration was longer, paired t-tests between inner and outer muscle pairs revealed onset to be similar.

Figure 5B shows a representative trace of activity patterns of dorsal fin muscles in a bamboo shark during a turn, while Figure 6B shows standardized data for all the trials. The two-way ANOVA showed no differences between individuals for all the variables tested. Burst duration was similar between the first and second dorsal fins, and between the inner and outer fin muscles relative to the turning side for the first and second dorsal fins. Burst duration was also similar among muscles on the same side of each fin. Inner and outer muscle pairs revealed onset to be similar (paired t-tests).

During turning, the first and second dorsal fin muscles were active in both species, with contralateral and ipsilateral musculature showing bursts throughout the turn. Mean muscle onset and offset patterns for the two species can be compared in Figure 6. The second set of two-way ANOVA revealed that onset and burst duration were not

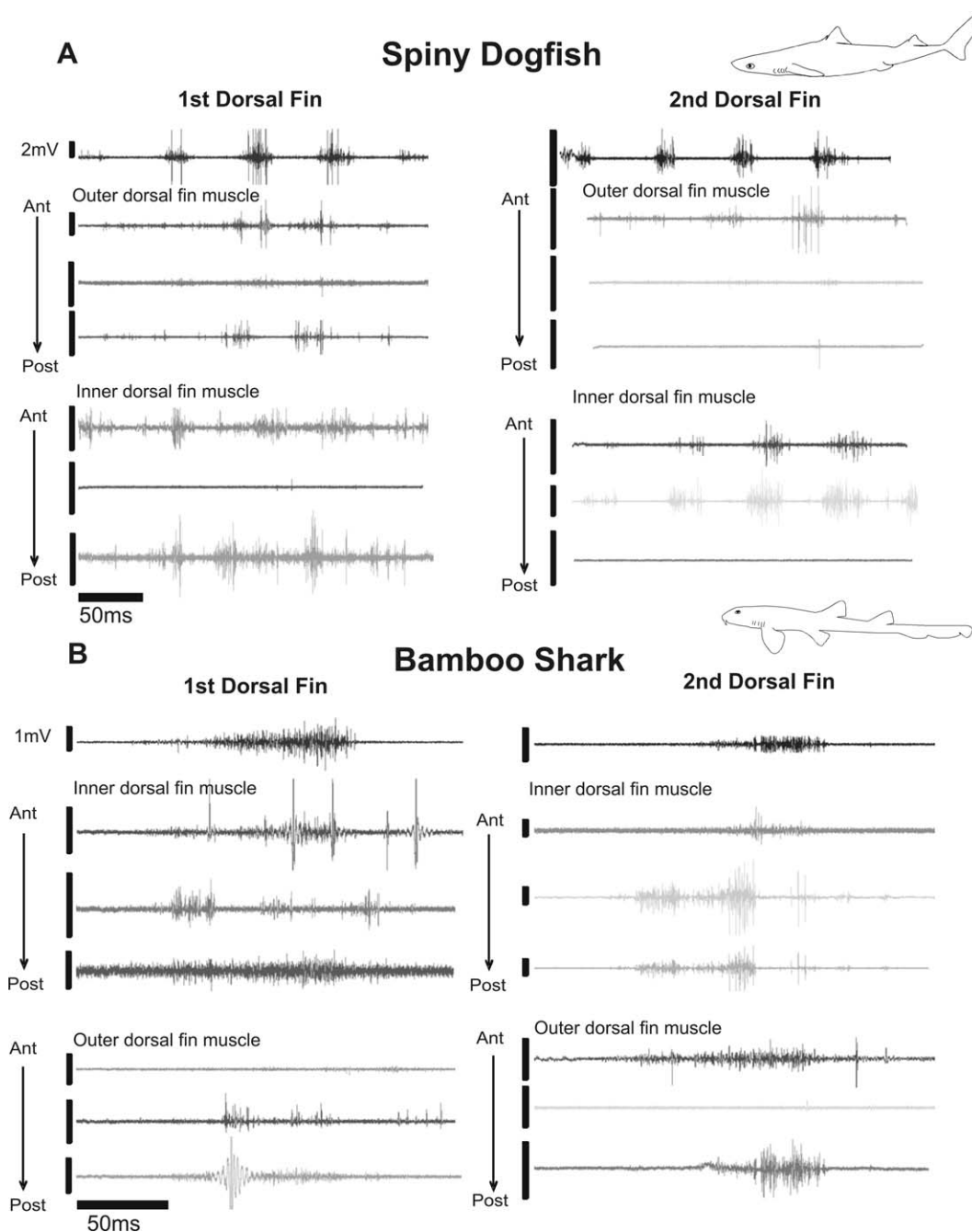


Fig. 5. Representative traces showing activity during maneuvering of spiny dogfish (A) and bamboo shark (B) dorsal fins. Note muscle activity along both fins and sides in the two species.

different among muscles or species ($P > 0.05$), mainly due to high variability. Duty cycle values showed high variation among muscles, species and trials, ranging in mean values from 20 to 48%. Asynchrony indices were not different between species or between first and second dorsal fins (mean 0.42 ± 0.21). Cycle duration was similar in the two species, although the coefficient of variation was high, especially for spiny dogfish ($CV_{\text{bamboo}} = 31.4\%$; $CV_{\text{spiny}} = 57.9\%$).

Journal of Morphology

DISCUSSION

Dorsal Fin Morphology

Based on dissections from two distantly related species, morphology of dorsal fins is diverse and complex. The two species represent two different lineages of shark evolution, Squalia and Galea, respectively, and possess very different arrangements of the musculoskeletal structures that have significant implications for fin function. In

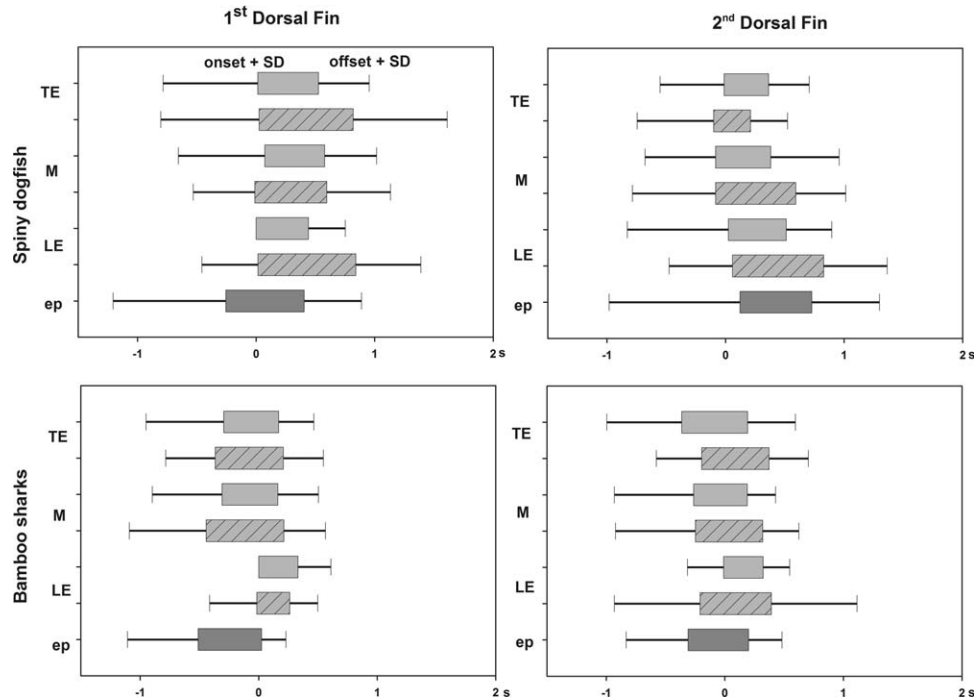


Fig. 6. Temporal variables (onset and offset) for dorsal fin muscle activation in spiny dogfish and bamboo sharks during maneuvers for all individuals ($n_i = 3$) and trials ($n_t = 4$, $n_i \times t = 12$) (Ep-red epaxial; LE-leading edge; M-middle; TE-trailing edge; striped represents outer muscle in relation to the turning side and solid represents the muscle closer to the turning side). Note how muscle activation on the two sides of both fins overlaps and how burst duration is longer on the outer side of the turn in the spiny dogfish but not in the bamboo shark.

addition, the two species inhabit different environments that require very different locomotor abilities. Based solely on external anatomy, the dorsal fins of these two species were predicted to have different internal morphology and thus function. Fin placement along the anterior–posterior body axis and fin morphometrics separated the two species in a principal component analysis. Bamboo sharks have large discrete muscle bands extending into relatively large dorsal fins coupled with more posterior placement of both fins, which suggest that these structures function for thrust production similar to accelerator specialists with posteriorly placed fins (Webb, 1984). In contrast, in spiny dogfish, a simple smaller muscle mass extending into a relatively larger first dorsal fin than second placed over the center of mass suggests a stabilizing function, similar to what is thought to occur in white sharks (Lingham-Soliar, 2005).

There are several ways that dorsal fins can be stiffened and thus confer stability when swimming. The relatively higher density and increased number of layers of connective tissue and the arrangement of stratum compactum of the first dorsal fin of white sharks, *Carcharodon carcharias*, compared to tiger, *Galeocerdo cuvier*, and sand tiger, *Carcharias taurus*, sharks suggests increased passive stiffness and thus is thought to function as a stabilizer (Lingham-Soliar, 2005). Most groups of sharks have aplesodic dorsal fins, in which the radials do not extend to half of the

fin web (Shirai, 1996; Wilga and Lauder, 2004). However, in Lamnidae there is an intermediate condition to plesiodic fins with the radials extending halfway into the fin (Shirai, 1996). This might explain the greater passive stiffness of white sharks compared to that of tiger and sand tiger sharks, providing the conditions for a stabilizing role (Lingham-Soliar, 2005). Regional passive stiffening of fin elements has also been identified in longhorn sculpin pectoral fin rays (Taft and Taft, 2012).

However, distinct arrangement of skeletal elements, area occupied by muscle, and size of subdivisions might render the dorsal fins of spiny dogfish functionally distinct. Spiny dogfish have evolved to cope with greater requirements for stability based on activity levels and regular incursions into the water column (Compagno, 1984), and stiffness of the dorsal fins can be controlled through contraction of dorsal fin muscles. The presence of a fin spine and the surrounding thick ligamentous sling promotes fin stabilization and creates planes of bending other than the ones defined by skeletal elements. Together, the spine and muscle may provide a combination of static and dynamic stabilizing mechanisms compared to the passive only stabilization of white shark dorsal fins by increased cartilaginous support. The musculoskeletal arrangement in the dorsal fins of spiny dogfish indicates that muscle contraction

would create bulging at the base of the dorsal fin that would increase hydrostatic pressure and stiffen the ligaments making the fin stiffer and thus more stabilizing. Muscle contraction to produce active stiffness has been reported for the radialis muscle in the caudal fin of sharks (Flammang, 2010). The presence of a spine appears to be a retained ancestral condition, since spines are found in what are thought to be basal taxa: *Cladoselache*,[†] *Hydobus*,[†] and *Ctenacanthus*[†] (Schaeffer and Williams, 1977; Maisey 1984).

In contrast, bamboo sharks have an anatomical mechanism for finer control of fin shape. Mobile joints between distal and proximal radial columns determine the plane of fin bending, while the absence of a connection between the basals and supraneurals provides a greater range of movement. The absence of basals in bamboo sharks and the presence of two rows of radials with a longer first row and a shorter second row indicate highly directional mobility and resembles the arrangement of digit phalanges (Zákány and Duboule, 1999). The highly mobile synchondrosis between the proximal and distal radials described here resembles the joint between the pterygiophores and soft rays of the dorsal fins in actinopterygian fishes (Konstantinidis and Conway, 2010). Furthermore, the intercept for CSA regressions and theoretical maximum tetanic tension is higher for bamboo sharks compared to similar sized spiny dogfish, which indicates a greater forces produced by the muscles of the dorsal fins for locomotor functions. Muscle arrangement relative to force production affects efficiency (Gans and Gaunt, 1991). The greater insertional angle of the muscles into the fin of bamboo sharks indicates greater lateral force transmission for thrust production during lateral undulations of the fin.

In bamboo sharks and spiny dogfish, the dorsal fin musculature originates from the stratum compactum and inserts onto tendinous sheets of the ceratotrichia, suggesting that the fins function independently of the axial musculature, which is supported by our experimental data on muscle activation. This may be a conserved feature among shark taxa with the exception of the *Hypnosqualea* (Batoidea) group where the dorsal fin musculature originates from the vertebral centra (Shirai, 1992) and could just be a consequence of the reduced size of the dorsal fins in this group (Shirai, 1996).

Dorsal fin evolution remains to be investigated in elasmobranchs, despite the existence of genetic mechanisms known to produce changes in the placement of the two dorsal fins upon which natural selection can act (Mabee et al., 2002; Dahn et al., 2007; Hadzhiev et al., 2007). Early placement of median fins during development is related to Hox gene suppression together with Sonic hedgehog (Shh) expression (Mabee et al., 2002; Dahn et al., 2007; Hadzhiev et al., 2007). Differen-

ces in timing and spatial domains of Shh expression correlate well with morphological diversification of fin placement and shape in skates and sharks (Dahn et al., 2007). Swimming is a behavior that takes up a considerable percentage of a fish energetic budget. It is likely that given the genetic flexibility of these structures, evolution has acted upon these traits to increase fitness. A comparative study of the dorsal fin skeleton and associated musculature across a wider range of species would clarify the role of phylogenetic placement, function and ecology in dorsal fin morphology.

Dorsal Fin Function

Here, we have presented evidence that the dorsal fins of spiny dogfish and bamboo sharks are moved actively during routine turning in spiny dogfish and bamboo sharks and thus these fins have a critical role in locomotion.

Routine turning maneuvers are thought to account for most of the activity budget of a swimming fish (Liao, 2007). Pillars in an aquatic setting forced spiny dogfish and bamboo sharks to navigate around them to continue swimming, thus curvature radius was not controlled and the fish was not restricted to a horizontal plane. This is likely one of the causes for the high variability observed in turning maneuvers among and within individuals. Another study on turning maneuvers in leopard sharks has shown that turning performance is controlled by multiple variables, namely flexion at the midline and the lag time of that same flexion and that these changes in posture during turns can be related to the environment where the shark is swimming (Porter et al., 2011). In addition, routine locomotor performance operates at substantially less power than the maximal in actinopterygian fishes (Syme et al., 2008) and the same is expected in elasmobranchs. This and the fact that stereotypy is expected to be higher near maximal performances might be a second cause of the high variability reported here for muscle activation during turning.

The duration of cycles and muscle bursts were longer in turning than in steady swimming (Maia and Wilga, 2013). In contrast to steady swimming activation patterns, which are cyclical with short burst durations (Maia and Wilga, 2013), turning maneuvers are characterized by activation of all muscles in the dorsal fins with high coefficient of variation. In another similar study of bluegill performing other routine behaviors such as kick and glide, C-starts and braking, intra- and interindividual variation in cycle or burst duration in the dorsal fin muscles was low (Jayne et al., 1996). However, the bluegill study did not look at routine turns where behavioral plasticity is likely to be higher.

During turning maneuvers, the muscles in the first dorsal fin of spiny dogfish are active longer on the outer side during a turn, that is, contralateral side. This is consistent with stiffening of the fin and increasing resistance against the medium to augment drag and improve turning performance (Webb, 2006).

Overlap in the activation of contralateral and ipsilateral musculature occurs during turning maneuvers in spiny dogfish and white-spotted bamboo sharks. Simultaneous activation of the dorsal fin musculature on both sides would serve to stiffen the fin against the flow during a turn. Due to high flexibility of the fins in bamboo sharks, stiffening of the fins might not be as effective as in spiny dogfish. Instead, dorsal fin function in bamboo sharks might have a role in the later phases of the turn, by propelling the animal and decreasing the overall radius of the turn. The higher flexibility of the axial body of bamboo sharks might compensate for a reduced lateral area of the trunk and median fins to create drag during turns. Smaller CSA of the body in carcharhinid and sphyrnid sharks results in higher flexibility during turns (Kajiura et al., 2003) and the same could apply to bamboo sharks. Bamboo sharks are overall more competent at turning in small spaces compared to spiny dogfish and appear to be related to whole body flexibility (Porter et al., 2009).

Red epaxial muscle is thought to produce negative power during turning, as this behavior normally relies on white axial muscle (Johnson et al., 1994). When fish contract the white muscle, the adjacent red muscle can also be active but instead of producing force it will stretch. However, red muscle is activated during C-start maneuvers in largemouth bass, as well as during escape responses (Johnson et al., 1994). Similarly, in spiny dogfish and white-spotted bamboo sharks, the red epaxial musculature is always active with muscle bursts of comparable intensity to the dorsal fin muscles.

Maneuvering behaviors are crucial in capturing prey and escaping predators (Webb, 2006). The strategies that spiny dogfish and bamboo sharks utilize during turning maneuvers differ based on morphology and muscle patterns. Analysis of 3D-kinematics of turning events might provide insight into how fins are interacting with the flow.

This study presents evidence of differences in dorsal fin morphology, which suggests that divergent functions may exist between major shark groups, despite all the pitfalls of a two species comparative study (Garland and Adolph, 1994). There are external and internal differences in the morphology of the fins between spiny dogfish (*Squalia*) and bamboo sharks (Galea; Shirai, 1996, this paper). The skeletal arrangement differs markedly between these two species and the muscular system reflects the skeletal differences. The anatomy is likely to be the same in close related species to each of the two species studied here. Future investigations in other

taxa using phylogenetic independent contrasts will shed some light on how these distinct fin morphologies have evolved. During maneuvering, the dorsal fin muscles are bilaterally active in both species. Contralateral activation in dorsal fin muscles during turns might be necessary to stabilize the fin against hydrodynamic loads. Temporal differences in bilateral activity occur primarily during steady swimming (Maia and Wilga, 2013) rather than during maneuvering. This study is the first to investigate muscle activity of the dorsal fins in chondrichthyans and only the second in a fish species. Dorsal fins in sharks have been considered to be passive structures (Harris, 1936) and here we present data that clearly indicates an active role of dorsal fin muscles in two species during maneuvering.

ACKNOWLEDGMENTS

The authors would like to thank Ashley Stoeher and Brittany McGee for help with the experiments, as well as Jason Ramsay, Jordan Balaban, and Stacey Sakai for animal care, help with experiments and fruitful discussions. The authors would like to thank the GSO trawl crew for obtaining spiny dogfish and SeaWorld San Diego for donating bamboo sharks. Jacqueline Webb and Edward Durbin provided comments on an earlier version of this manuscript.

LITERATURE CITED

- Benzer P. 1944. Variations in the anatomy of the dorsal fins of *Squalus acanthias*. *Copeia* 3:179–180.
- Bone Q, Roberts BL. 1969. The density of elasmobranchs. *J Mar Biol Assoc UK* 49:913–937.
- Compagno LJV. 1984. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. FAO Species Catalogue for Fishery Purposes, Vol. 4. FAO, Rome.
- Compagno LJV. 1999. Endoskeleton. In: Hamlett WC, editor. *Sharks, Skates and Rays—The Biology of Elasmobranch Fishes*. Maryland: The Johns Hopkins University Press, pp. 70–92.
- Dahn RD, Davis MC, Pappano WN, Shubin NH. 2007. Sonic hedgehog function in chondrichthyan fins and the evolution of appendage patterning. *Nature* 445:311–314.
- Domenici P, Standen EM, Levine RP. 2004. Escape manoeuvres in the spiny dogfish (*Squalus acanthias*). *J Exp Biol* 207: 2339–2349.
- Donley JM, Shadwick RE. 2003. Steady swimming muscle dynamics in the leopard shark *Triakis semifasciata*. *J Exp Biol* 206:1117–1126.
- Donley JM, Shadwick RE, Sepulveda CA, Konstantinidis P, Gemballa S. 2005. Patterns of red muscle strain/activation and body kinematics during steady swimming in a lamnid shark, the shortfin mako (*Isurus oxyrinchus*). *J Exp Biol* 208: 2377–2387.
- Drucker EG, Lauder GV. 2001. Locomotor function of the dorsal fin in teleost fishes: Experimental analysis of wake forces in sunfish. *J Exp Biol* 204:2943–2958.
- Drucker EG, Lauder GV. 2005. Locomotor function of the dorsal fin in rainbow trout: Kinematic patterns and hydrodynamic forces. *J Exp Biol* 208:4479–4494.
- Flammang BE. 2010. Functional morphology of the radialis muscle in shark tails. *J Morphol* 271:340–352.

- Flammang BE, Lauder GV, Troolin DR, Strand T. 2011. Volumetric imaging of shark tail hydrodynamics reveals a three-dimensional dual-ring vortex wake structure. *Proc R Soc B* 278:3670–3678.
- Gans C, Gaunt AS. 1991. Muscle architecture in relation to function. *J Biomech* 24:53–65.
- Garland T, Adolph SC. 1994. Why not to do two-species comparative studies: Limitations on inferring adaptation. *Physiol Zool* 67:797–828.
- Geerlink PJ, Videler JJ. 1987. The relation between structure and bending properties of teleost fin rays. *Neth J Zool* 37:59–80.
- Gerry SP, Ramsay JB, Dean MN, Wilga CD. 2008. Evolution of asynchronous motor activity in paired muscles: Effects of ecology, morphology and phylogeny. *Integr Comp Biol* 48:272–282.
- Goodrich ES. 1904. On the dermal din-rays of fishes—living and extinct. *Quart J Microsc Sci* 47:465–522.
- Hadzhiev Y, Lele Z, Schindler S, Wilson SW, Ahlberg P, Strähle U, Müller F. 2007. Hedgehog signaling patterns the outgrowth of unpaired skeletal appendages in zebrafish. *BMC Dev Biol* 7:75.
- Harris JE. 1936. The role of the fins in the equilibrium of the swimming fish. I. Wind tunnel tests on a model of *Mustelus canis* (Mitchell). *J Exp Biol* 13:476–493.
- Jayne BC, Lozada AF, Lauder GV. 1996. Function of the dorsal fin in Bluegill Sunfish: Motor patterns during four distinct locomotor behaviors. *J Morphol* 228:307–326.
- Johnson TP, Syme DA, Jayne BC, Lauder GV, Bennett AF. 1994. Modeling red muscle power output during steady and unsteady swimming in largemouth bass. *Am J Physiol* 267(2 Pt 2):R481–R488.
- Kajiura SM, Fonri JB, Summers AP. 2003. Maneuvering in juvenile carcharhinid and sphyrnid sharks: The role of the hammerhead shark cephalofoil. *Zoology* 106:19–28.
- Konstantinidis P, Conway KW. 2010. The median-fin skeleton of the eastern atlantic and mediterranean Clingfishes *Lepadogaster lepadogaster* (Bonnaterre) and *Gouania wildenowi* (Risso) (Teleostei: Gobiessocidae). *J Morphol* 271:215–224.
- Lauder GV. 2006. Locomotion. In: Evans DH, Claiborne JB. *The Physiology of Fishes*, 3rd ed. pp. 3–46, Academic Press, San Diego.
- Liao JC. 2007. A review of fish swimming mechanics and behaviour in altered flows. *Philos Trans R Soc London* 362: 1973–1993.
- Lingham-Soliar T. 2005. Dorsal fin in the white shark, *Carcharodon carcharias*: A dynamic stabilizer for fast swimming. *J Morphol* 263:1–11.
- Lou F, Curtin NA, Woledge RC. 2002. Isometric and isovelocity contractile performance of red muscle fibers from the dogfish *Scyliorhinus canicula*. *J Exp Biol* 205:1585–1595.
- Mabee PM, Crotwell PL, Bird NC, Burke AC. 2002. Evolution of median fin modules in the axial skeleton of fishes. *J Exp Zool* 294:77–90.
- Maia A, Wilga CD. 2013. Function of dorsal fins in bamboo shark during steady swimming. *Zoology*, Available online 9 June 2013, ISSN 0944-2006, <http://dx.doi.org/10.1016/j.zool.2013.05.001>
- Maisey JG. 1984. Chondrichthyan phylogeny: A look at the evidence. *J Vert Paleontol* 4:359–371.
- Porter M, Roque CM, Long JH Jr. 2009. Turning maneuvers in sharks: Predicting body curvature from morphology. *J Morphol* 270:954–965.
- Porter ME, Rogue CM, Long JH Jr. 2011. Swimming fundamentals: Turning performance of leopard sharks (*Triakis semifasciata*) is predicted by body shape and postural reconfiguration. *Zoology* 114:348–359.
- Powell PL, Roy RR, Kanim P, Bello MA, Edgerton VR. 1984. Predictability of skeletal muscle tension from architectural determinations in guinea pig hindlimbs. *J Appl Physiol* 57: 1715–1721.
- Rasband WS. 1997–2012. ImageJ. Bethesda, MA: US National Institutes of Health. Available at imagej.nih.gov/ij/, last accessed on 07/07/2013.
- Roberts TJ, Higginson BK, Nelson FE, Gabaldón AM. 2007. Muscle strain is modulated more with running slope than speed in wild turkey knee and hip extensors. *J Exp Biol* 210: 2510–2517.
- Schaeffer B, Williams M. 1977. Relationships of fossil and living elasmobranchs. *Am Zool* 17:293–302.
- Shirai S. 1992. Phylogenetic relationships of the Angel sharks, with comments on elasmobranch phylogeny (Chondrichthyes, Squatinidae). *Copeia* 2:505–518.
- Shirai S. 1996. Phylogenetic interrelationships of Neoselachians (Chondrichthyes: Euselachii). In: Stiassny MLJ, Parenti LR, Johnson GD, editors. *Interrelationships of Fishes*. California: Academic Press. pp. 9–34.
- Standen EM, Lauder GV. 2007. Hydrodynamic function of dorsal and anal fins in brook trout (*Salvelinus fontinalis*). *J Exp Biol* 210:340–356.
- Syme DA, Gollock M, Freeman MJ, Gamperl AK. 2008. Power isn't everything: Muscle function and energetic costs during steady swimming in Atlantic cod (*Gadus morhua*). *Physiol Biochem Zool* 81:320–335.
- Taft NK. 2011. Functional implications of variation in pectoral fin ray morphology between fishes with different patterns of pectoral fin use. *J Morphol* 272:1144–1152.
- Taft NK, Taft BN. 2012. Functional implications of morphological specializations among the pectoral fin rays of the benthic longhorn sculpin. *J Exp Biol* 215:2703–2710.
- Taft NK, Lauder GV, Madden PGA. 2008. Functional regionalization of the pectoral fin of the benthic longhorn sculpin during station holding and swimming. *J Zool* 276:159–167.
- Webb PW. 1984. Body form, locomotion, and foraging in aquatic vertebrates. *Am Zool* 24:107–120.
- Webb PW. 2006. Stability and maneuverability. In: Shadwick RB, Lauder GV, editors. *Fish Biomechanics*. San Diego: Academic Press. pp. 281–332.
- Wilga CD, Lauder GV. 2000. Three-dimensional kinematics and wake structure of the pectoral fins during locomotion in the leopard shark, *Triakis semifasciata*. *J Exp Biol* 203:2261–2278.
- Wilga CD, Lauder GV. 2001. Fluid dynamics and pectoral fin function in the bamboo shark, *Chiloscyllium plagiosum*. *J Morphol* 249:195–209.
- Wilga CD, Lauder GV. 2002. Function of the heterocercal tail in sharks: Quantitative wake dynamics during steady horizontal swimming and vertical maneuvering. *J Exp Biol* 205:2365–2374.
- Wilga CD, Lauder GV. 2004. Biomechanics: Hydrodynamic function of the shark's tail. *Nature* 430:850.
- Zákány J, Duboule D. 1999. Hox genes in digit development and evolution. *Cell Tissue Res* 296:19–25.
- Zar JH. 2009. *Biostatistical Analysis*, 5th ed. New Jersey: Prentice Hall.