A comparative morphological analysis of body and fin shape for eight shark species

DUNCAN J. IRSCHICK[1,2*], AMY FU[1], GEORGE LAUDER[3], CHERYL WILGA[4], CHI-YUN KUO[2] and NEIL HAMMERSCHLAG[5,6]

[1]*Department of Biology, University of Massachusetts at Amherst, 221 Morrill Science Center, Amherst, MA 01003, USA*
[2]*Organismic and Evolutionary Biology Program, University of Massachusetts Amherst, Amherst, MA 01003, USA*
[3]*Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA*
[4]*Department of Biological Sciences, University of Alaska Anchorage, 3101 Science Circle ISB, Anchorage, AK 99508, USA*
[5]*Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, USA*
[6]*Leonard and Jayne Abess Center for Ecosystem Science and Policy, University of Miami, Coral Gables, FL 33146, USA*

Sharks are diverse and ecologically important predators and are also highly varied in their biology and behaviour. Prior studies have posited basic relationships between body form and lifestyle; previous investigations of body shape in sharks, however, have been restricted to a few species, or measured dead sharks, which may show artefacts of preservation or distortion and/or require lethal sampling. Therefore, using non-lethal field methods, we examined body and fin shape in a group of eight different shark species that co-occur in coastal waters of the Western Atlantic but vary to different degrees in biology and ecology. We measured a series of 12 morphometric variables and body size (pre-caudal length) from wild individuals (*N* = 90 sharks total) belonging to the families Carcharhinidae [order: Carcharhiniformes (tiger, bull, blacktip, lemon, blacknose, Atlantic sharpnose and sandbar)] and Ginglymostomatidae [order: Orectolobiformes (nurse)]. By taking phylogeny into account using the SLOUCH method, our analysis revealed isometry of all 12 morphological variables measured relative to body length among all species, indicating that despite substantial lifestyle differences, the general body form of these carcharhiniform and orectolobiform species is overall highly conserved. Univariate analyses were consistent with this result in showing no substantial differences among species once the effects of body size were accounted for, although there was a modest difference among the species in leading edge of the caudal fin, which was also revealed by an elliptic Fourier analysis. A multivariate principal component analysis showed some differentiation among species in the height of the dorsal fin, the length of the lower lobe of the caudal fin and in overall body girth, but the lack of significant variation in the univariate analyses suggests that such differences may not be biologically substantial. Our conclusion was that these sharks are similar in gross morphology, which underscores the generality of the shark body form for different niches. Indeed, the most important variable distinguishing the species was variation in body length, which in sharks is generally linked to variation in diet type or breadth.

ADDITIONAL KEYWORDS: body form – evolution – fins – morphology – scaling – sharks – size.

INTRODUCTION

One of the most important goals of evolutionary biology is to better understand the diversity of organismal body forms that exist in nature, and how these body forms relate to the organism's ecology and life history (Wainwright & Reilly, 1994; Lauder, 1996; Biewener, 2003; Irschick & Henningsen, 2009; Losos, 2011; Irschick & Higham, 2016). Before one can make generalizations about the relationship between form and function, it is first necessary to quantify the body shapes of the species of interest. One can then start to relate variation

*Corresponding author. E-mail: irschick@bio.umass.edu

in body form to other variables (e.g. ecology, behaviour) using the comparative method (Baum & Larson, 1991; Harvey & Pagel, 1991; Nunn, 2011). Morphology is most frequently quantified through the use of standard morphometric techniques, such as obtaining simple linear measures (e.g. limb lengths) and then comparing different individuals or species, and through employing other more complex methods of shape analysis [e.g. geometric morphometrics, elliptic Fourier analysis (EFA)]. As noted by others (Baum & Larson, 1991; Larson & Losos, 1996; Losos, 2011; Nunn, 2011), analysis of body form and correlation with habitat use represents an important first step towards testing broader hypotheses regarding the process of adaptation.

Among vertebrates, sharks are one of the most diverse groups of extant predators, with more than 500 species occurring worldwide (Thomson & Simanek, 1977; Little & Bemis, 2004; Compagno *et al.*, 2005). Sharks range in size from the diminutive deep-sea bite-feeding dwarf lanternshark (*Etmopterus perryi*, total length ~15–20 cm) to the enormous epipelagic suction filter-feeding whale shark (*Rhincodon typus*, > 12 m in length), with many species falling between these extremes in body size, shape, behaviour and lifestyle (Thomson, 1976; Thomson & Simanek, 1977; Wilga & Lauder, 2004a; Irschick & Hammerschlag, 2014). For example, sharks within the family Carcharhinidae are primarily active and fast-moving sharks consuming live fish or other active prey, whereas sharks within the family Squatinidae tend to be more sedentary lie-in-wait predators that consume less active prey such as crustaceans and invertebrates (Wetherbee *et al.*, 2004; Wilga & Lauder, 2004a; Compagno *et al.*, 2005). Alongside these differences in diet and overall activity levels appear to be many differences in body shape and fin dimensions (Thomson & Simanek, 1977). For example, some sharks possess less stiff asymmetrical tails in which the upper lobe is much larger than the lower lobe (e.g. nurse sharks, *Ginglymostoma cirratum*), whereas other sharks possess a more symmetrical stiffer caudal fin [e.g. mako (*Isurus* spp.) and white sharks (*Carcharodon carcharias*); Donley *et al.*, 2004].

The exact nature of these differences and how they translate into locomotor differences is still an active topic of research, but this pattern is usually interpreted as a transition from slow-moving more manoeuvrable (nurse) to high-speed cruising (mako, white) locomotion (Thomson, 1976; Ferry & Lauder, 1996; Lauder *et al.*, 2003; Wilga & Lauder, 2004a, b; Flammang *et al.*, 2011; Maia & Wilga, 2013a, b, 2016). Comparative research shows that shark species can vary in the relative positions of fins other than caudal fins (e.g. dorsal, pectoral) along the body, with some sharks [e.g. lemon sharks (*Negaprion brevirostris*), nurse sharks] having the dorsal fins positioned closer to the caudal fin compared to others (e.g. hammerhead sharks, family Sphyrnidae)

(Thomson & Simanek, 1977). Sharks also appear to vary greatly in the relative dimensions of various fins (Thomson & Simanek, 1977; Wilga & Lauder, 2004a), although the ecological significance of these differences remains poorly understood.

Finally, sharks seem to differ in their head dimensions, with pelagic and active mobile sharks (e.g. white and mako sharks) typically exhibiting a streamlined and narrow snout, and slower-moving sharks, especially those that consume larger prey items [e.g. tiger (*Galeocerdo cuvier*) and bull sharks (*Carcharhinus leucas*)], exhibiting flattened and rounded heads (Compagno *et al.*, 2005; Fu *et al.*, 2016). These broad and flat heads, in combination with teeth suited for shearing, appear well-designed for consuming large prey such as turtles, large fish or other sharks (Cortes, 1999). In short, there appears to be remarkable variation in the shapes and relative sizes of the head, body and various fins among shark species, and there seem to be strong links to different lifestyles.

Although there have been a number of studies of overall body form within and among individual shark species (McKenzie & Tibbo, 1964; Thomson & Simanek, 1977; Hazin *et al.*, 1991; Reiss & Bonnan, 2010; Dolce & Wilga, 2013; Irschick & Hammerschlag, 2014; Fu *et al.*, 2016), we are not aware of any studies that have quantitatively measured and compared external body form and fin dimensions from live, wild, specimens from a range of different shark species in a single study. Morphological studies of single species are valuable, but comparing data among studies can be challenging. Some studies have examined differences among species in the position of fins, as well as fin and body shapes, but these studies appear to be constructed either from artist renderings, or were performed on dead sharks (Thomson & Simanek, 1977; Dolce & Wilga, 2013).

As much of the body form of shark species is a consequence of differences in girth, gathering morphological data on live sharks is especially important. Prior studies have shown that preservation can greatly impact the overall body volume of fish, and death can also greatly impact body shape, especially if specimens have been dead for many hours (Shields & Carlson, 1996). This is especially true for specimens stored in ethanol, which can become twisted and lose their original body shape (Glenn & Mathias, 1987). Moreover, given the decline of many shark populations globally, there is a need to generate data using non-lethal methods on live animals (Hammerschlag & Sulikowski, 2011). Unfortunately, obtaining sufficient samples of preserved relatively larger apex predatory shark species (e.g. tiger, bull sharks) to compare against live specimens is challenging, so we do not attempt to do that here, although future studies that addressed this point would be useful.

Our goal in this paper is to provide a morphometric analysis of eight different species of coastal

are not obligate ram ventilators, unlike the other species, and thus have relatively lower oxygen demands. Specifically, sampling occurred throughout the middle Florida Keys (USA), namely Biscayne Bay, Florida Bay and the reefs off Islamorada, Florida. Additional sampling was conducted off Grand Bahama, Bahamas. These sharks were measured between March 2013 and April 2014 for a total of 90 adult and subadult individuals from eight species (Fig. 1; Table 1). As exact sizes for sexual maturity are not definitively understood for these species, we simply provide below (Table 1) ranges of sizes sampled, as well as averages (± 1 SE). Total sample sizes are provided below. Due to the large hook size (16/0), the majority of individuals sampled were either adult or subadult. The sample sizes for the different species were as follows: tiger shark ($N = 11$), bull shark ($N = 10$), lemon shark ($N = 9$), sandbar shark ($N = 6$), blacktip shark ($N = 18$), nurse shark ($N = 17$), Atlantic sharpnose ($N = 7$), blacknose ($N = 12$). For the EFA, we sampled four of the most common shark species in Florida waters (blacktip, lemon, nurse and sandbar, all sampled in Florida). These sharks were collected from March 2013 to May 2015.

MORPHOMETRIC MEASUREMENTS

For all eight species, we measured 12 morphometric variables and pre-caudal length (PCL) following the approach of Irschick & Hammerschlag (2014). We quantified the following morphological measurements (Fig. 2) on each individual using a standard metric flexible tape (accurate to 1 mm): (1) head size (EE; distance between eyes, from the inner part of the eyes); (2) lateral span (LS): the distance spanning (i.e. around the curved dorsal 'back' of the shark) from the insertion point of the anterior edge of one pectoral fin to the same point on the other pectoral fin; (3) frontal span (FS): the distance spanning (i.e. around the curved dorsal 'back' of the shark) from the insertion point of the anterior edge of the dorsal fin to a line oriented parallel to the horizontal plane of the pectoral fin; (4) proximal span (PS): the distance spanning (i.e. around the curved dorsal 'back' of the shark) from the insertion point of the posterior edge of the dorsal fin to a line oriented parallel to the horizontal plane of the pectoral fin; (5) caudal keel circumference (CKC; total circumference at the base of the tail as measured at the caudal keel); (6) pectoral fin length (PFL; the linear distance from the insertion of the pectoral fin at the distal edge to the tip of the pectoral fin when fully extended); (7) dorsal fin 1 (DF1; distance from the anterior insertion point of the dorsal fin to the tip of the dorsal fin); (8) dorsal fin 2 (DF2; distance from the tip of the dorsal fin to the posterior insertion point of the dorsal fin); (9) dorsal fin 3 (DF3; distance horizontally across the sharks body between the anterior

and posterior insertion points of the dorsal fin); (10) caudal fin 1 (CF1; the linear distance from the dorsal insertion of the caudal fin to the dorsal tip of the caudal fin); (11) caudal fin 2 (CF2; the linear distance from the dorsal tip of the caudal fin to the ventral tip of the bottom part of the caudal fin); (12) caudal fin 3 (CF3; the linear distance from the bottom anterior edge of the caudal fin to the bottom posterior edge of the caudal fin); and (13) PCL (the linear distance from the tip of the snout to the pre-caudal pit, which is a longitudinal notch on the caudal peduncle directly on the anterior side of the caudal fin). After processing, individual sharks were released, usually within several minutes of capture.

STATISTICAL ANALYSIS OF AMONG-SPECIES (EVOLUTIONARY) SCALING

We isolated the phylogeny for the eight shark species (Fig. 3) using data from Naylor *et al.* (2012), which was taken from a larger analysis of 595 shark species based on nuclear DNA sequences. As the phylogeny from Naylor *et al.* (2012) was not ultrametric, we used the function *chronos* in the software package *ape* to adjust branch lengths such that the distance to the root was the same for all tips. We employed a method developed by Hansen *et al.* (2008), namely the stochastic linear Ornstein-Uhlenbeck model for comparative hypotheses, also known as SLOUCH. This was performed using the SLOUCH R program. We chose this method for its suitability and greater statistical power when a response variable evolves towards optima determined by one or more predictor variable along a phylogenetic tree (Hansen *et al.*, 2008). These authors showed that the regression slope between two traits can be quite different between SLOUCH and other methods where characters evolve under Brownian motion. While this method has mainly been used to study evolutionary constraints (e.g. Cooper *et al.*, 2010; Hoffmann *et al.*, 2013), it is pertinent in our case where the focus is to unravel the scaling (i.e. regression slope) between various morphometric measurements and body length, with the explicit hypothesis that the former evolves towards optima determined by the latter. SLOUCH estimates several key parameters to describe the relative importance of phylogenetic inertia in the Ornstein-Uhlenbeck mode of evolution (Hansen *et al.*, 2008). First, it estimates a phylogenetic half-life, which describes the time it takes for the trait value to move half the distance from the ancestral state to the new optimum; the lower the value, the weaker the phylogenetic inertia. Second, SLOUCH calculates an 'optimal' regression slope. This slope describes the relationship between predictor and response variable if the latter is able to evolve in sync with the former free of constraints. Lastly, SLOUCH also estimates an evolutionary slope using the standard phylogenetic

Table 1. Mean (± 1 SE) values of morphological measurements for eight shark species

Variable	Tiger shark	Bull shark	Lemon shark	Sandbar shark	Blacktip shark	Nurse shark	Blacknose shark	Atlantic sharpnose shark
PCL	277.9 ± 3.2 (265.0–303.0)	189.2 ± 1.8 (181.0–196.0)	173.9 ± 5.3 (130.0–195.0)	160.0 ± 4.2 (123.0–186.0)	127.9 ± 1.7 (120.0–141.0)	181.2 ± 1.5 (175.0–195.0)	92.8 ± 2.0 (75.0–103.0)	71.4 ± 3.2 (53.0–82.0)
Eye-to-eye	40.5 ± 1.0 (37.0–46.0)	34.4 ± 0.9 (31.0–40.5)	22.5 ± 0.65 (18.0–25.0)	22.9 ± 0.4 (20.5–25.0)	17.3 ± 0.3 (15.0–19.5)	26.7 ± 0.3 (24.5–28.8)	14.1 ± 0.6 (10.5–20.0)	8.9 ± 0.4 (7.0–10.0)
Lateral span	87.6 ± 2.3 (70.0–97.0)	76.7 ± 2.7 (65.0–89.0)	56.9 ± 2.1 (41.0–65.5)	56.9 ± 1.5 (47.0–68.5)	48.7 ± 1.0 (44.0–58.0)	60.8 ± 1.4 (54.0–71.5)	32.6 ± 1.5 (24.1–45.0)	19.8 ± 1.0 (15.0–23.0)
Frontal span	95.1 ± 3.8 (72.0–111.0)	85.6 ± 3.7 (68.5–104.0)	57.0 ± 2.1 (41.0–68.0)	63.9 ± 2.4 (49.0–79.0)	52.1 ± 1.4 (44.3–64.5)	65.0 ± 2.1 (52.0–81.0)	35.2 ± 1.5 (27.5–43.0)	22.3 ± 1.3 (15.5–27.0)
Distal span	88.9 ± 3.2 (73.0–111.0)	69.9 ± 3.9 (56.0–91.5)	49.4 ± 2.0 (35.0–60.0)	60.2 ± 2.3 (48.0–79.0)	45.9 ± 1.5 (36.0–56.5)	38.7 ± 1.8 (28.0–58.5)	32.5 ± 1.4 (27.0–40.0)	19.3 ± 1.1 (14.0–22.5)
CKC	38.5 ± 1.0 (33.0–46.0)	31.5 ± 0.7 (28.5–35.5)	25.1 ± 0.9 (17.0–28.5)	24.8 ± 0.7 20.5–29.0)	21.8 ± 0.4 (19.5–24.0)	30.1 ± 0.6 (26.0–33.0)	14.3 ± 0.5 (11.3–18.0)	9.8 ± 0.4 (7.5–12.0)
Pectoral fin	45.9 ± 1.3 (39.0–53.0)	44.0 ± 1.5 (39.0–51.0)	37.2 ± 1.4 (25.0–43.0)	38.0 ± 0.6 (33.0–40.5)	26.8 ± 0.4 (24.0–31.3)	39.1 ± 1.5 (35.0–61.0)	16.3 ± 0.6 (12.0–20.0)	9.8 ± 0.5 (7.0–12.0)
Dorsal fin 1	38.6 ± 0.7 (35.0–44.0)	37.2 ± 1.0 (32.5–40.5)	28.3 ± 1.0 (19.0–31.0)	33.7 ± 0.8 (28.0–36.5)	23.9 ± 0.4 (21.0–27.0)	30.8 ± 0.9 (23.5–35.5)	15.1 ± 0.4 12.5–16.0)	10.1 ± 0.4 (8.5–12.0)
Dorsal fin 2	26.6 ± 0.9 (20.0–31.0)	28.7 ± 0.7 (25.0–31.0)	20.5 ± 0.9 (13.0–23.5)	27.5 ± 0.5 (23.0–29.5)	20.0 ± 0.7 (14.0–25.0)	24.1 ± 0.6 (20.5–30.5)	11.4 ± 0.3 (9.5–12.5)	7.9 ± 0.3 (6.5–9.0)
Dorsal fin 3	31.3 ± 1.0 (26.0–37.0)	32.2 ± 2.0 (25.5–41.0)	22.4 ± 0.9 (14.0–26.5)	24.3 ± 0.8 (18.0–27.0)	19.5 ± 0.7 (12.5–24.0)	24.9 ± 1.1 (20.0–38.0)	12.0 ± 0.5 (8.5–15.0)	8.7 ± 0.4 (7.0–10.0)
Caudal fin 1	81.8 ± 1.5 (74.0–90.0)	63.9 ± 1.2 (57.0–68.5)	56.6 ± 1.8 (38.0–61.0)	54.6 ± 1.3 (48.0–65.0)	44.8 ± 0.5 (42.0–49.0)	65.9 ± 2.2 (48.0–77.5)	30.0 ± 0.9 (24.5–34.0)	21.0 ± 0.6 (18.1–24.0)
Caudal fin 2	85.0 ± 1.6 76.0–96.0)	65.2 ± 1.4 (58.2–71.0)	54.1 ± 2.0 (36.0–62.0)	57.5 ± 1.6 (44.0–69.0)	47.7 ± 0.8 (43.0–54.5)	66.1 ± 1.3 (56.0–74.0)	29.1 ± 0.8 (25.0–34.0)	23.3 ± 1.0 (18.0–27.0)
Caudal fin 3	38.3 ± 0.9 (33.0–43.0)	29.6 ± 1.2 (23.0–33.0)	25.1 ± 0.7 (19.0–27.0)	21.8 ± 0.8 (17.5–27.0)	19.2 ± 0.7 (13.0–24.0)	18.5 ± 3.0 (13.0–68.5)	12.6 ± 0.5 (9.2–16.0)	8.44 ± 0.3 (7.0–10.0)

Ranges are in parentheses. Values are in cm. CKC, caudal keel circumference; PCL, pre-caudal length.
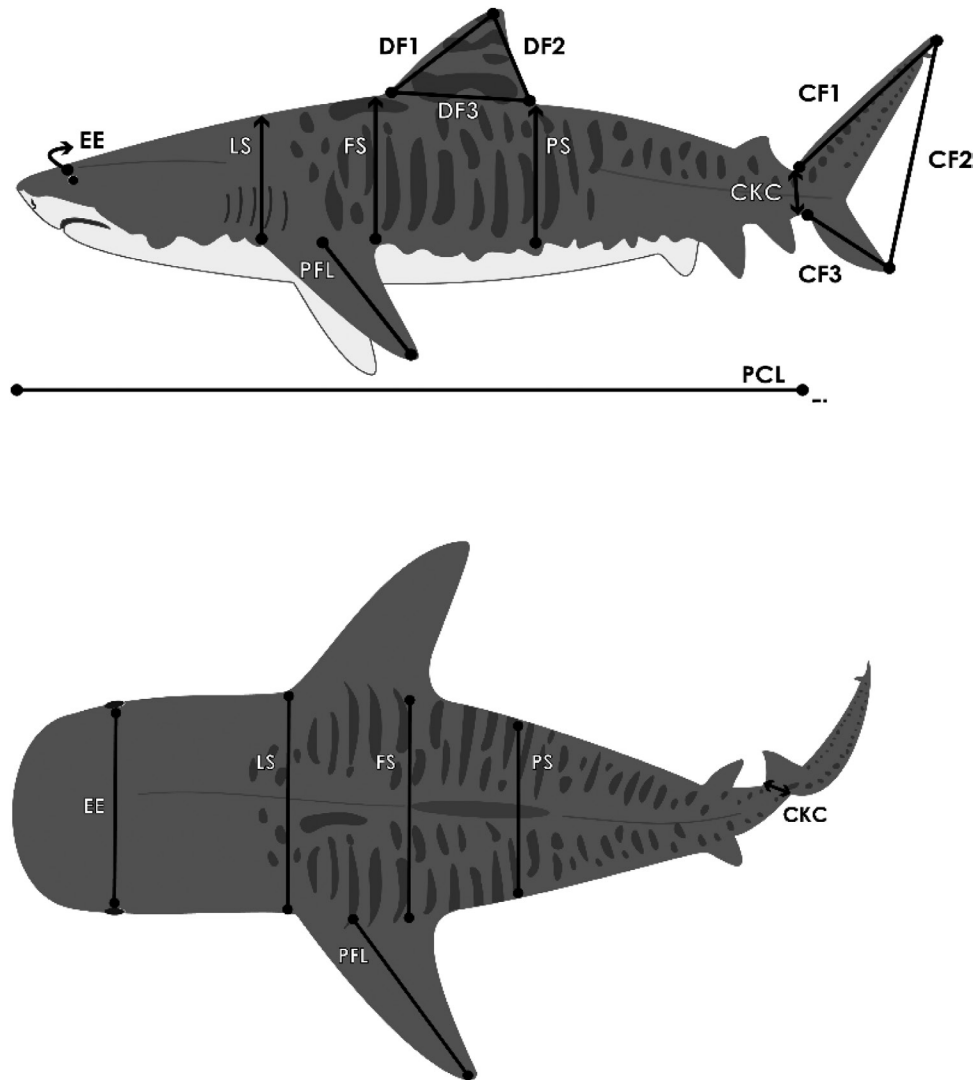
Figure 2. A diagram of a tiger shark with the morphological variables measured in this study depicted. Note that all four variables shown (LS = lateral span, FS = frontal span, PS = proximal span and CKC = caudal keel circumference) along the body axis of the shark were all measured across the body (see Materials and Methods above for more detailed descriptions of landmarks of morphological measurements).

generalized least squares. The difference between the two slopes informs us the potential influence of phylogenetic inertia on the evolutionary relationship between the predictor and the response traits. Regressions were carried out in Microsoft Excel 2013, and all variables were log10 transformed prior to scaling analyses.

STATISTICAL ANALYSES OF BODY SHAPE DIFFERENCES

Univariate ANOVAs were carried out within Minitab 17 on a PC laptop. All variables were log10 transformed prior to the ANOVAs. To tease apart the specific morphological differences among shark species, we consulted with a statistician at the University of Massachusetts at Amherst. We were informed that the simplest and likely best approach was univariate ANOVAs on each morphological variable using three terms in each model [PCL (body size), species and the interaction between PCL and species]. The key term of interest is the interaction between species and PCL, which informs us that for a given body size, there is heterogeneity among the species in the variable. We performed this analysis on all log-transformed and non-size-adjusted morphological variables other than PCL.

We did not use phylogenetic correction on this analysis after consulting with a fellow scientist steeped in phylogenetic methods (D. Moen, pers. comm.). The primary concern of not incorporating phylogeny is an overestimation of degrees of freedom (Felsenstein,
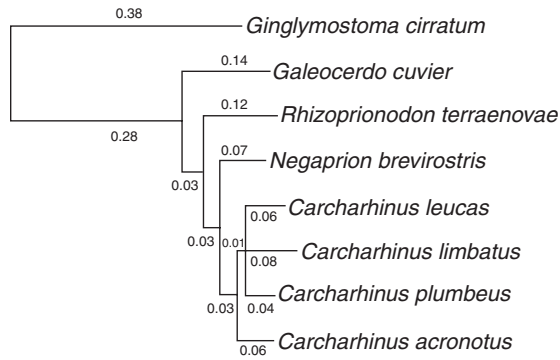
Figure 3. The estimated phylogenetic relationships including branch lengths among the eight shark species studied here based on analysis of nuclear DNA. Data were extracted from Naylor *et al.* (2012), and details on the methods of phylogenetic reconstruction are included in that paper.

1985), but in the case of an ANOVA, if there are several closely related species that are similar to one another, they will contribute little to the ANOVA that tests whether species are different. The phylogeny becomes important when one tests whether two characteristics of species are related – that is, one tests the relationship between two variables across species. Since our goal is to determine if the species differ, therefore, a standard ANOVA is the more conservative option.

We then performed a principal component analysis (PCA) using as input all 13 log-transformed variables (including PCL). The first loading consisted of approximately equal loadings from all variables and primarily reflects differences in body size among the eight shark species (Table 3). We then examined both loadings of each variable on the different PCs, as well as examined plots of various PCs against one another (e.g. PC 2 vs. PC 3) to determine groupings.

ELLIPTIC FOURIER ANALYSIS

We used EFA to describe shape variation in the pectoral, dorsal and caudal fin for the shark species for which we were able to gather images with sufficient sample sizes. All variables were log10 transformed prior to EFA analyses. We used the magnetic lasso tool and fill layer option in Adobe Photoshop CS6 on a PC to digitally isolate greyscale silhouettes of the pectoral fins, dorsal fins and caudal fins for the EFA.

EFA is commonly used to describe the shape of two-dimensional outlines that do not possess clearly defined homologous landmarks by mapping the distance from the geometric centre of the outline to each point on the contour with a polar coordinate function (e.g. Ferson *et al.*, 1985; Joshi *et al.*, 2011).

This radius function can then be expressed in terms of a Fourier series with a series of harmonics, with the number ranging from one to infinity (see Shen *et al.*, 2009 for a more detailed overview for EFA); the lower harmonics approximate the coarse-scale features of outlines, whereas the higher harmonics capture more subtle variation. That is, the more harmonics that are used in the EFA, the better it is able to capture subtle variation among the shapes (Bonhomme *et al.*, 2014). Choosing the number of harmonics is therefore a matter of balancing the ability to capture shape variation and computational economy. In this study, we determined the suitable appropriate number of harmonics based on the percentage of total harmonic power captured (Bonhomme *et al.*, 2014).

RESULTS

The tiger sharks were the longest species sampled (average PCL = 277.9 cm) with Atlantic sharpnose being the shortest (average PCL = 71.4 cm; see Table 1). At the extremes, the longest shark sampled was a tiger shark (PCL = 303 cm), and the shortest shark sampled was an Atlantic sharpnose shark (PCL = 53 cm). In general, although the slopes from the SLOUCH analyses tended to be slightly lower than the non-phylogenetic slopes (Figs 4, 5), there was no significant deviation from the expected slope of 1.0 for each of the 12 morphological values across the eight species (Table 2). This indicates that, among the eight species, changes in body and fin shape with size can be largely explained under isometric expectations. This was true for both the non-phylogenetic and the phylogenetic analyses (Table 2).

The univariate tests clearly show that the primary axis of variation among the species was body length, with PCL being significantly different for at least the $P < 0.01$ level for each of the variables. By contrast, only one variable (caudal fin 1) showed a significant result ($P < 0.05$) for both the species and species * PCL terms (Table 3). However, this term was only barely significant, and given the number of tests, was not substantial. These data indicate that, once body size is accounted for, there are no substantial significant shape differences among the species.

The PCA is consistent with this above analysis in showing some modest level of differentiation among the species (Table 4; Fig. 6). The first PC explained 92.5% of the variation, and, following other studies (e.g. Berner, 2011), can be interpreted as a general component of body size (i.e. length). The second and third PCs explained 2.7% and 1.5% of the overall variation, with the fourth and fifth PCs explaining far less variation (0.9% and 0.7% of variation, respectively). The fact that the first 'size' PC explains such a large
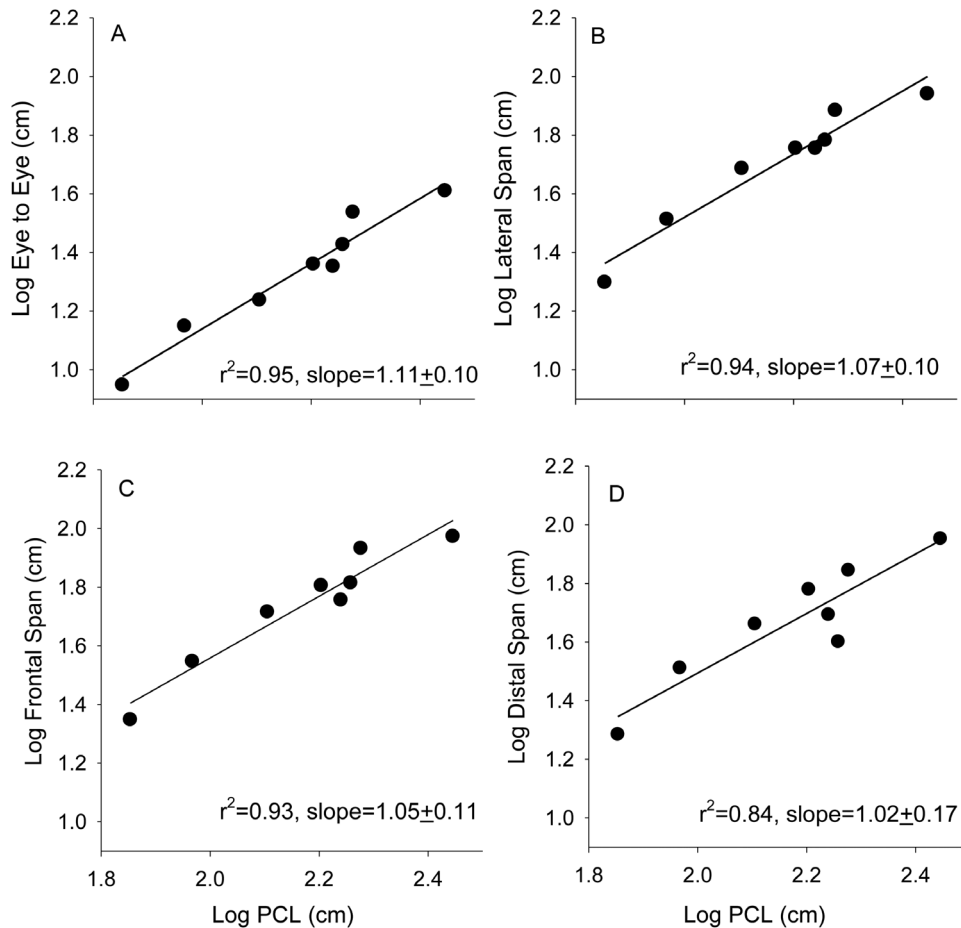
Figure 4. Scaling relationships between log-transformed values of pre-caudal length (PCL) (x-axis) and (A) eye-to-eye span, (B) lateral span, (C) frontal span and (D) proximal span based on raw data (line is from linear least squares regressions). Each point is a species mean. Regression statistics for raw data and from the SLOUCH analyses can be seen in Table 2. Included in the graphs are slope values from raw data (± 1 SE), and r^2 values.

portion of variation is strongly indicative that the vast majority of variation among these species resides in differences in body length. Therefore, we focused our attention on the second and third PCs, and plotted them against each other to determine how the shark species were distributed in multivariate morphospace. PC 2 had high loadings for distal span (0.42) and caudal fin 3 (0.23), and several shark species had high values for these variables, especially tiger, blacknose, blacktip and bull sharks. By contrast, nurse sharks had low values of PC 2, which is consistent with the relatively posterior location of their dorsal fin (which results in a relatively low value of distal span), and also their relatively small lobes of the lower part of the caudal fin. PC 3 had a high negative loading for dorsal fin 2 (−0.25) and a high positive loading with PCL (0.20). We interpret this high loading of PCL as indicating that sharks with high loadings of PC 3 as being relatively long ('slender') for their body length.

Sandbar and bull sharks both exhibit low values of PC 3, which indicates that they are relatively 'stocky' and have relatively tall dorsal fins, whereas nurse, Atlantic sharpnose and tiger sharks all have relatively high values, indicating that they are more 'slender' with relatively short dorsal fins. Overall, however, the fact that these variables did not differ significantly among the species once body size was accounted for suggests that the level of differentiation is modest and may not be biologically substantial.

The four species sampled for harmonics (blacktip, lemon, nurse and sandbar) did not differ significantly in the overall shape of either the pectoral fin ($F_{4,20}$ = 1.29, $P > 0.25$), or the dorsal fin ($F_{4,21}$ = 0.34, $P > 0.75$), based on harmonic analysis of the first four PC values for each fin. However, these four species did differ significantly in the shape of the caudal fin ($F_{3,20}$ = 8.11, $P < 0.001$; see Table 5 for the loadings for this PCA). We provide the loadings for the harmonics with each PC to document
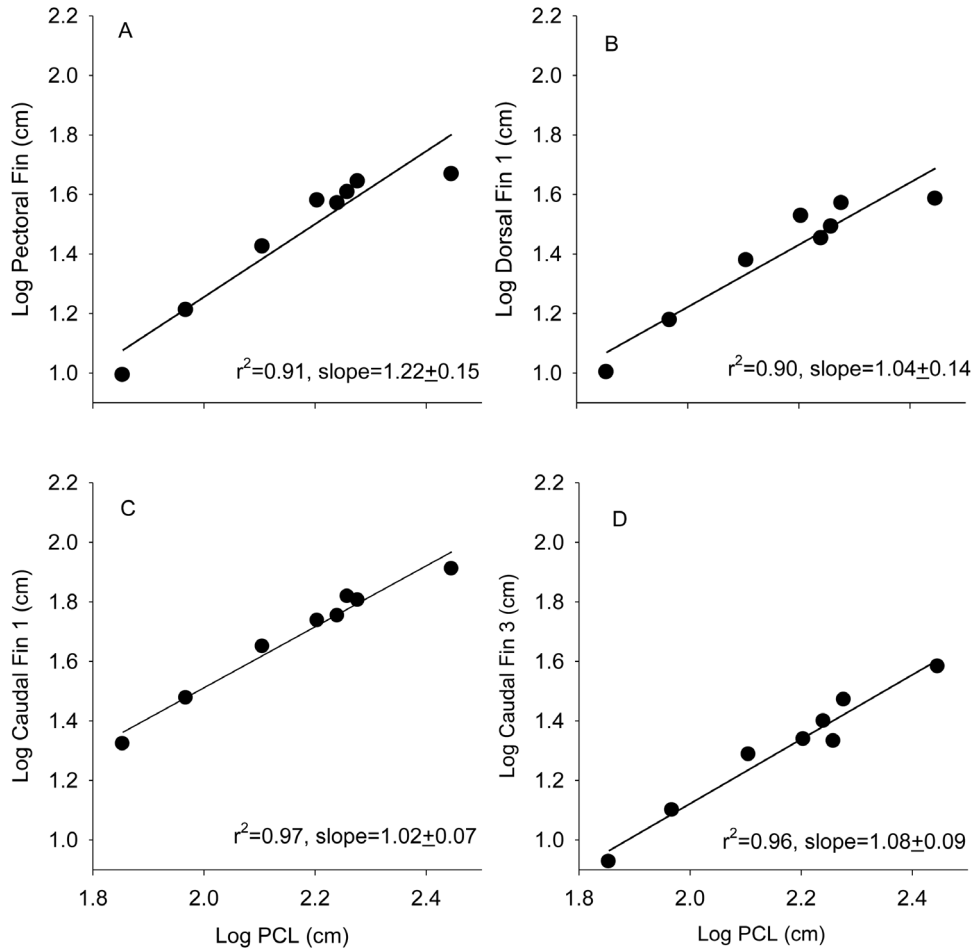
Figure 5. Scaling relationships between log-transformed values of pre-caudal length (PCL) (x-axis) and lengths of the (A) pectoral fin, (B) dorsal fin 1, (C) caudal fin 1 and (D) caudal fin 3 based on raw data (line is from linear least squares regressions). Each point is a species mean. Regression statistics for raw data and from the SLOUCH analyses can be seen in Table 2. Included in the graphs are slope values from raw data (± 1 SE), and r^2 values.

our methods, but the harmonics cannot easily be understood or compared to traditional linear morphological variables such as head length, and as noted by other authors, the best method for interpretation is through visualization, as shown in Figure 7. The primary outlier in terms of the caudal fin was the nurse shark, which displayed a larger upper lobe and a much smaller lower lobe, whereas the other three species were relatively similar in overall caudal fin shape (Fig. 7).

DISCUSSION

Our comparative analysis of body and fin shape in eight shark species reveals several findings. First, all of the 12 morphological shape variables, which describe variation in body and fin shape, scale isometrically with body size (PCL) among species, with little evidence of deviation from the expected slope of 1. These data

are consistent with the univariate ANOVAs, PCA, and EFA, which each show modest differentiation among the eight species. In other words, at least for the variables measured, one can reasonably scale up a blacknose or Atlantic sharpnose shark to the size of a tiger shark and observe relatively little difference in overall shape. That being said, it is likely that the eight species likely differ in other features we did not measure (such as more detailed features of the head), which would require further study. The lone consistent difference among species that merits further attention seems to be the leading edge of the upper lobe of the caudal fin (caudal fin 1 in our analysis), which showed some significant (albeit marginally so) differentiation among species, and which also showed some differentiation in the EFA.

The differentiation in the caudal fin is intriguing, as this feature also varies among younger and older sharks, as revealed by scaling data from larger apex

Table 2. Scaling coefficients from regressions for 12 morphological variables vs. pre-caudal length for both non-corrected (non-phylogenetic, or standard linear regression) slopes, and from SLOUCH slopes (optimal and evolutionary slopes, see Materials and Methods for more details)

Variable	Non-corrected slope ± SE	*T*-value	Optimal slope ± SE	*T*-value	Evolutionary slope ± SE	*T*-value
Eye-to-eye	1.11 ± 0.10	1.1	0.87 ± 0.19	0.7	0.86 ± 0.18	0.8
Lateral span	1.07 ± 0.10	0.7	0.89 ± 0.20	0.6	0.88 ± 0.19	2.9
Frontal span	1.05 ± 0.11	1.0	0.90 ± 0.20	0.5	0.88 ± 0.19	0.6
Distal span	1.02 ± 0.17	0.1	0.84 ± 0.19	0.8	0.83 ± 0.19	0.9
CKC	1.02 ± 0.08	0.3	0.96 ± 0.21	0.2	0.95 ± 0.20	0.3
Pectoral fin	1.22 ± 0.15	1.5	0.75 ± 0.17	1.5	0.74 ± 0.16	1.6
Dorsal fin 1	1.04 ± 0.14	0.3	0.87 ± 0.19	0.7	0.86 ± 0.19	0.7
Dorsal fin 2	0.98 ± 0.19	−0.1	0.85 ± 0.20	0.8	0.84 ± 0.19	0.8
Dorsal fin 3	1.02 ± 0.13	0.2	0.91 ± 0.20	0.5	0.89 ± 0.20	0.6
Caudal fin 1	1.02 ± 0.07	0.3	0.96 ± 0.20	0.2	0.95 ± 0.20	0.3
Caudal fin 2	0.99 ± 0.07	−0.1	0.98 ± 0.21	0.1	0.97 ± 0.21	0.1
Caudal fin 3	1.08 ± 0.09	0.9	0.90 ± 0.19	0.5	0.88 ± 0.19	0.6

These data compare different species, and not individuals within species. Slopes are provided with standard errors (SE), and we used *t*-tests to test for departures from isometric expectations (1 for all relationships). All slopes were not significantly different from 1 (*P* > 0.25 in all cases). CKC, caudal keel circumference.

Table 3. Results from univariate ANOVAs comparing different shark species for a variety of morphological variables

Variable	PCL	Species	PCL * species
Eye-to-eye	7.45**	0.95	0.96
Lateral span	24.12***	1.16	1.21
Frontal span	28.01***	1.47	1.52
Distal span	41.95***	1.33	1.39
CKC	12.99**	0.85	0.81
Pectoral fin	23.54***	1.27	1.25
Dorsal fin 1	13.21**	1.01	0.95
Dorsal fin 2	5.04*	0.46	0.48
Dorsal fin 3	5.28*	1.59	1.58
Caudal fin 1	17.33***	2.72*	2.81*
Caudal fin 2	11.29**	0.93	0.92
Caudal fin 3	4.23*	0.81	0.81

Values are *F*-values. The terms are log-transformed values of body size (PCL), species and the interaction between the two terms. *P < 0.05, **P < 0.01, ***P < 0.001. CKC, caudal keel circumference; PCL, pre-caudal length.

Table 4. Principal component (PC) loadings from an analysis of 13 morphological variables in eight shark species

	PC 1	PC 2	PC 3	PC 4	PC 5
% variation explained	92.5	2.7	1.5	0.9	0.7
Variance	12.02	0.35	0.19	0.11	0.09
PCL	0.97	−0.01	**0.20**	0.01	−0.04
Eye-to-eye	0.97	0.01	0.10	−0.07	0.12
Lateral span	0.98	0.07	−0.01	−0.10	−0.05
Frontal span	0.97	0.11	−0.05	−0.16	−0.04
Distal span	0.89	**0.42**	−0.10	0.02	−0.10
CKC	0.98	−0.08	0.10	−0.06	−0.01
Pectoral fin	0.98	−0.12	−0.04	0.03	−0.02
Dorsal fin 1	0.98	−0.12	−0.11	0.06	−0.01
Dorsal fin 2	0.94	−0.15	**−0.25**	0.11	−0.02
Dorsal fin 3	0.96	−0.02	−0.13	−0.10	0.18
Caudal fin 1	0.97	−0.16	0.13	0.04	−0.07
Caudal fin 2	0.97	−0.14	0.07	0.01	−0.05
Caudal fin 3	0.94	**0.23**	0.10	0.20	0.13

These variables include our metric of body size (PCL), and therefore, the first PC has approximately equal loadings on all variables, and can be interpreted as reflecting variation in body size. Values less than or equal to −0.2, or greater than or equal to 0.2 are bolded for PC 2 and PC 3, which explain the majority of non-size-related variation in shape. CKC, caudal keel circumference; PCL, pre-caudal length.

predatory species, such as tiger, bull and white sharks (Lingham-Soliar, 2005a, b, c; Irschick & Hammerschlag, 2014; Fu *et al.*, 2016), all of which show negative scaling of the caudal fin. By contrast, in smaller species, caudal fin measures seem to scale isometrically (Reiss & Bonnan, 2010; Irschick & Hammerschlag, 2014). While the PCA revealed variation among species in distal span (a measure of girth), the length of the lower lobe of the caudal fin (caudal fin 3), the height of the dorsal fin (dorsal fin 3) and how 'long' the pre-caudal body of the sharks are relative to size (PCL relative to

the first PC), the fact that the univariate ANOVAs did not show such differences to be statistically significant suggests that such variation may not be biologically substantial. Overall, our data indicate substantial conservatism among a group of shark species that exhibit differences in biology and ecology. Indeed, the primary axis of variation among these species is total body length, as exemplified by the very large proportion of
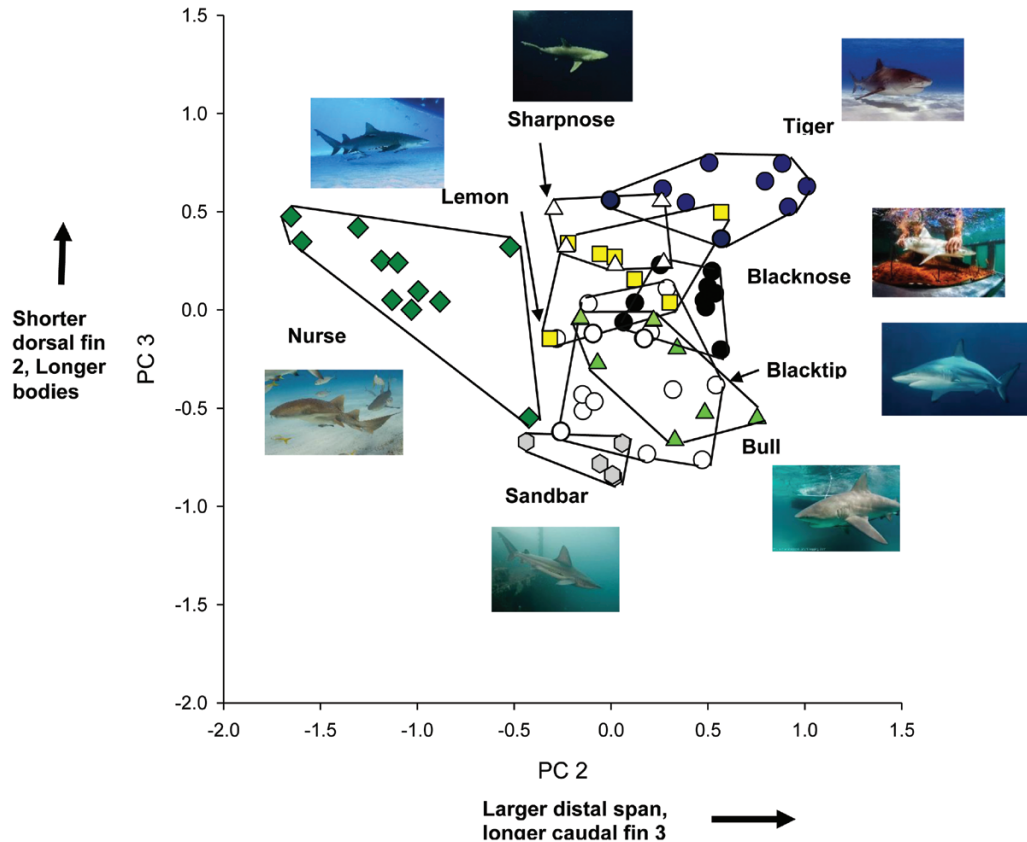
Figure 6. A plot of values for principal component 2 (x-axis) vs. principal component 3 (y-axis) for adult or subadult individuals of eight shark species. The first principal component is a metric of overall body size and was not used here for examining shape differences. The outlines bound each of the values for each species. Table 4 provides loadings for these principal components.

variation (92.5%) explained by the first 'size' PC. It is therefore possible that variation in body size among these species is a key factor driving their ecological and behavioural differences.

Among-species scaling often provides a window into the broader ecological and mechanistic constraints that animals face as they age (Calder, 1984; Schmidt-Nielsen, 1984; LaBarbera, 1989; Carrier, 1996; Tyler-Bonner & Horn, 2000; Dolce & Wilga, 2013). We stress that our study focuses only on scaling among species, and thus has more relevance for broader evolutionary comparisons than for examining ontogenetic changes. In some species, extreme positive allometry, either among or within species, allows individuals or species to exhibit new behaviours or occupy new niches as they grow. For example, in lizards, positive allometry of head length and width may have evolved to allow larger lizards to employ biting as a strategy during territorial encounters (Meyers *et al.*, 2002). Other work with jackrabbits (Carrier, 1996) shows how positive allometry of the limb allows juveniles to enjoy a locomotor advantage, which may be

important given their vulnerability to predators. Gill slit morphology among shark species corresponds to four character complexes that differ by habitat and swimming style (Dolce & Wilga, 2013). Among the species we sampled, we found conservatism of overall body form as shown through our scaling analyses. At first glance, two possible exceptions are the length of the pectoral fin (non-phylogenetic slope = 1.22), and eye-to-eye distance (1.11), although neither was statistically different from 1.0. However, once the values from the SLOUCH analyses were included, it becomes apparent that these trends were largely the result of a phylogenetic effect (Table 2). Our limited number of species lends less overall robustness to the phylogenetic analysis, although there is no evidence of strong positive or negative allometry from the raw data. We also note that seven of the eight species represent five genera, but are within one family (Carcharhinidae), and represent only a small slice of the vast diversity of shark body forms, which include disparate species such as Lamnidae (e.g. white sharks), Hexanchidae (cow sharks) and Squatinidae (angel sharks), among

Table 5. Results from principal component analysis (PCA) of seven harmonics from elliptic Fourier analysis (EFA) that described tail shape among four shark species

	PC 1	PC 2	PC 3	PC 4
Eigenvalue	0.01	0.002	0.0007	0.0004
% variation explained	75	13	4	2
A1	< 0.0001	< 0.0001	< 0.0001	< 0.0001
A2	0.3506	−0.0960	−0.3692	−0.5082
A3	0.1291	0.0309	−0.1386	0.0363
A4	0.0364	0.1816	−0.1262	−0.2517
A5	−0.0462	0.0762	−0.0466	−0.0924
A6	−0.0135	0.0715	−0.0146	0.0671
A7	−0.0166	−0.0585	0.0157	−0.0302
B1	< 0.0001	< 0.0001	< 0.0001	< 0.0001
B2	0.1607	−0.3799	−0.1859	0.3727
B3	0.1823	−0.3710	−0.1342	−0.1262
B4	0.0798	−0.1987	−0.2907	0.4302
B5	−0.0084	−0.0342	−0.1223	−0.2198
B6	−0.0554	0.0128	−0.1329	0.1594
B7	−0.0553	0.0813	0.0581	−0.1244
C1	< 0.0001	< 0.0001	< 0.0001	< 0.0001
C2	−0.7878	−0.3012	−0.4287	−0.1750
C3	−0.1031	−0.5433	0.5634	−0.1273
C4	−0.0116	−0.2348	0.1125	−0.0093
C5	0.1089	−0.1126	0.0669	−0.2318
C6	0.0451	0.1228	−0.1363	0.1076
C7	0.0342	0.1421	−0.0502	−0.1128
D1	−0.2137	0.1521	−0.1014	−0.0294
D2	−0.2538	0.2389	0.1474	0.2100
D3	−0.1248	0.0319	0.2173	−0.1871
D4	−0.0279	0.0014	0.0989	0.1005
D5	0.0769	−0.1160	0.0249	−0.0211
D6	0.0571	−0.1635	−0.1023	0.0349
D7	0.0519	−0.0521	−0.1151	0.1314

Because each EFA harmonic had four coefficients (A, B, C and D), there were 28 variables in the PCA.

Figure 7. A plot of principal component 1 vs. 2 from the elliptic Fourier analysis (EFA) from the harmonics based on the caudal fin for four shark species (lemon, blacktip, nurse and sandbar). Each point is an individual shark. Different colours represent different species, and the digital images are taken from actual caudal fins. Table 5 provides the loadings for this principal component analysis (PCA).

axis driving ecological and behavioural variation, as larger shark species, such as tiger and bull sharks will consume larger and harder prey regardless of a similar body shape to the other shark species examined here. However, the eight species investigated here still co-occur in parts of their coastal range as compared to more disparate species that do not co-occur in any parts of their range (e.g. deep sea vs. pelagic sharks). Thus, morphological investigations including additional species from more disparate habitats may reveal less similarity in body form.

One of the most important questions in any study of morphology is whether such variation, either among or within species, displays a clear link to function (Hildebrand *et al.*, 1985; Ricklefs & Miles, 1994; Lauder, 1996; Biewener, 2003; Irschick & Henningsen, 2009). As noted by other authors, one must interpret morphological variation cautiously, as many factors can influence structure (Gould & Lewontin, 1979; Wainwright & Reilly, 1994; Lauder, 1996). In the case of shark species, a great deal of functional work has revealed how various fins (e.g. caudal, pectoral, dorsal) are used under controlled laboratory trials, albeit typically with smaller sharks, such as bamboo (*Chiloscyllium plagiosum*, order Orectolobiformes), spiny dogfish (*Squalus acanthias*, Squaliformes) and leopard sharks (*Triakis semifasciata*, Carcharhiniformes) (Ferry & Lauder,

others. Nonetheless, the eight species both occupy a range of habitats, from shallow coastal habitats (nurse) to more pelagic ones (tiger), and also consume a variety of prey items. Further, while quantitative data are needed, the eight species appear to have different movement patterns, with tiger sharks moving vast distances (> 2000 km), while nurse, blacknose, bull and Atlantic sharpnose sharks occupy smaller home ranges (Simpfendorfer *et al.*, 2001; Heupel *et al.*, 2004; Compagno *et al.*, 2005; Hammerschlag et al., 2012a, b). The fact that these shark species can perform this wide range of ecological functions with the same basic body shape is a testimony to the evolutionary success of sharks across vast stretches of time (Compagno *et al.*, 2005). We note that size variation among these species appears to be the most important

1996; Lauder, 2000; Wilga & Lauder, 2000, 2001, 2002, 2004a, b; Flammang *et al.*, 2011; Maia & Wilga, 2013a, b, 2016). Among the eight species, the nurse shark (the one species from a different order and family) stands apart in its elongated upper lobe of the caudal fin, and its greatly diminished lower lobe, whereas the other seven species appear far more conserved. This conservatism in overall caudal fin shape can be seen in the ratios of caudal fin 1 (Fig. 2) divided by caudal fin 3, which is 3.56 for nurse sharks, but varies from 2.14 to 2.50 among the other seven species (see Table 1). Whereas the other seven shark species will hunt elusive or large prey, ranging from fish to turtles, or even other sharks (tiger and bull sharks), nurse sharks forage around coral reefs and rely on suction to capture relatively less mobile fishes and non-elusive crustaceans and shellfish from crevices in the ocean floor, and therefore rely less on rapid bursts of locomotion to capture prey (Castro, 2000; Wetherbee *et al.*, 2004).

Although it has not been tested quantitatively, nurse sharks also appear to have less rigid tails compared to these other seven species, and their caudal fins therefore appear to act as slower-moving flexible paddles when nurse sharks cruise the bottom for food (Wilga & Lauder, 2004a). Of all fish species whose locomotion has been studied experimentally in the laboratory, the caudal fin of nurse sharks is most similar to the flexibility and shape of the tail in the closely related whitespotted bamboo sharks (*C. plagiosum*, Orectolobidae, order Orectolobiformes). The dorsal lobe leads the ventral lobe during the tail beat and is oriented downward to push water posteroventrally in bamboo (*C. plagiosum*), leopard (*T. semifasciata*, Carcharhiniformes) and spiny dogfish (*S. acanthias*, Squaliformes) (Ferry & Lauder, 1996; Maia *et al.*, 2012). However, bamboo sharks have a relatively lower heterocercal tail angle (163°, longer more horizontal upper lobe) and a higher jet angle (−44.5°), compared to leopard (156°, −38.6°, respectively) and spiny dogfish (141°, −35°, respectively), which have shorter more vertical upper lobes (Wilga & Lauder, 2002, 2004). The tails of nurse sharks should function similar to those of bamboo sharks. If this trend is real, then sharks with higher heterocercal tail angles (i.e. more symmetrical lobes) may direct water more horizontally, which is in keeping with their more pelagic locomotor habits. By contrast, the white sturgeon (*Acipenser transmontanus*) possesses a highly flexible heterocercal tail with a small ventral lobe and a highly flexible dorsal lobe (Lauder, 2000; Liao & Lauder, 2000). As the tail moves from side to side during steady swimming, the caudal peduncle leads while the dorsal lobe trails behind. At a number of points in the tail beat cycle, the dorsal and ventral lobes are moving in opposite directions. This is a very different movement pattern than seen for shark tails (Ferry & Lauder, 1996; Lauder, 2000). The sturgeon tail behaves mechanically as a flexible sheet-like paddle with flexible dorsal and ventral lobes following the stiffer central tail region for much of the tail beat.

Tail flexibility and shape has a number of implications for the hydrodynamics of caudal fin function, and comparison between data on experimental flow visualization in sturgeon (Liao & Lauder, 2000), bamboo and leopard sharks (Wilga & Lauder, 2002, 2004b) illustrates the differences that may be seen interspecifically in shark species studied here when functional studies are conducted in the future. Liao & Lauder (2000) demonstrated that a highly flexible heterocercal tail like that present in sturgeon was capable of changing the orientation of the vortex wake and altering the angle of the momentum jet shed into the wake. This permits the animal to vector thrust and assist in body reorientation during vertical manoeuvring by directing the thrust reaction force above and below the centre of mass as appropriate. In contrast, shark species with a more typical heterocercal tail shape and stiffness (leopard, bamboo) were not able to reorient the vortex wake (Wilga & Lauder, 2002). This is also likely to be the pattern for some of the species, studied here, such as the lemon, bull and Atlantic sharpnose sharks. The implication of this finding is that the pectoral fins, while generally similar in shape across the shark species studied, play a significant role in generating manoeuvring torques (Wilga & Lauder, 1999, 2000a, b, 2001), while the tail does not appear to adjust the direction of thrust for more open water pelagic species, the relatively benthic nurse shark may use its flexible tail to manoeuvre and alter body pitch in search of prey near the bottom. However, other than the caudal fin, nurse sharks are similar to the other sharks examined here for most other traits, such as the shape of the dorsal and pectoral fin [however, see Thomson & Simanek (1977) for a discussion of how relative fin position is variable among shark species]. The pronounced dorsal fin is perhaps the most distinctive feature of most sharks (Maia & Wilga, 2013a, b).

Variation among shark species in dorsal fin height and shape has been noted anecdotally, but our study shows that the eight species, once body size is accounted for, do not differ significantly in dorsal fin size. Shark dorsal fins possess intrinsic musculature that allows active control of stiffness that varies by the type of musculoskeletal support in the fin. Control of stiffness in the first dorsal fin of spiny dogfish during steady swimming, especially at higher speeds, assists in maintaining stability, much like the keel of a boat (Maia & Wilga, 2013a, 2016). In contrast, undulation of the first dorsal fin in bamboo sharks while manoeuvring, which typically takes place at slower speeds, generates thrust to move in complex environments (Maia & Wilga, 2013a, b). The second dorsal fin appears to contribute to locomotor thrust generation

by active oscillation during steady swimming in both species (Maia & Wilga, 2013b, 2016). Our finding that interspecific dorsal fin traits scale isometrically among suggests that while the function of the first dorsal fin can differ markedly in function among shark species, that function also appears to be isometric with body length in the species investigated here. Furthermore, additional thrust provided by the second dorsal fin may primarily play a role in slow speed swimming by all species. Dorsal fin morphology scales isometrically, but forces induced by increased swimming speed would be expected to increase with velocity squared (Vogel, 1994), which suggests additional consequences for larger sharks with fins proportionally sized as larger sharks. Since we did not observe positive allometry of dorsal fin traits, but absolute maximum swimming speeds have been found to increase with body length, we predict that the contribution of the dorsal fin to locomotor thrust will be restricted to slow swimming speeds for all species investigated here. Prior laboratory-based research on small swimming sharks has shown that, contrary to the view that features such as pectoral fins play a role in stabilizing sharks during locomotion, their primary role may be during active turning and changing depth within the water column (Wilga & Lauder, 2004a). Our study showed a general conservatism of pectoral fin shape and relative size. Because of the importance of pectoral fins for manoeuvring, examining a wider range of sharks would be useful, especially including species from different habitats.

Our work reveals substantial conservatism in overall body form for a range of shark species, although more detailed studies on a wider range of morphological variables would be welcome. On a cautionary note, our sampling did include fully adult and subadult individuals, and therefore it would be useful to confirm our findings with only large adults, although this would be challenging with live sharks. While ontogenetic differences in body shape do exist in some shark species (Irschick & Hammerschlag, 2014), the most obvious differences occur between the smallest and largest sizes, and we excluded small juveniles. Further, we sampled a mixture of female and male sharks. Female and male sharks are known to differ in body size but there is no evidence that they differ in body shape, although more data on this point would be useful. In conclusion, the ability of the study species to consume a variety of prey items and occur in a wide range of areas in ocean environments with the same basic body shape indicates the broad functional generality of the shark body form. Our work also reveals the value of studying morphology of live animals in the field, especially for species that are challenging to obtain in museum collections.

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