

TAILS OF THE SEA: MORPHOLOGICAL SCALING AND ONTOGENY OF
SHARK CAUDAL FINs

BY

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A Thesis Submitted to the Graduate Faculty of
WAKE FOREST UNIVERSITY GRADUATE SCHOOL OF ARTS & SCIENCES
in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

Biology

May, 2019

Winston Salem, North Carolina

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ACKNOWLEDGEMENTS

To begin with, I would like to thank my advisor, Dr. Miriam Ashley-Ross for her endless support, guidance and patience in my time here. I would also like to thank my committee members, Dr. William Conner and Dr. T. Michael Anderson for their advice and ideas throughout the process. Many thanks to the various undergraduates, Abigail Whalen, Matthew Bagby and Fritz Thompson who assisted with data collection by performing many of the linear measurements on the photos. Christine Vega, Noah Bressman, Francesca Giammona and members of the Dr. James Pease lab provided me with endless support and guidance through the years and were incredible helpful.

In addition, this project would not have been possible without the support and assistance of all of the Museum Collections and companies that helped tremendously with data collection. The collections at Harvard University, Cornell University, University of Washington, University of Florida Gainesville, The Field Museum, The North Carolina Museum of Natural Sciences and The Burke Museum provided all of the preserved specimens used in this study and allowed me to visit their collections and use their materials. Companies like the Ana Banana Fishing Co and Reel Sonar provided me with the live animals used in this study and even allowed me to attend on a fishing trip. Lastly, I would like to thank my family for their support and love for the duration of my education at Wake Forest University.

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ABSTRACT

Mary Caroline Regan

Morphological Scaling and Ontogeny of Shark Caudal Fins

Thesis under the direction of
Miriam Ashley-Ross, Ph.D. Professor of Biology

Sharks are critical to ocean ecosystems and have been studied in many ecological and biomechanical capacities. One area of study that is relatively lacking is analysis of caudal fin shape with respect to ecological changes throughout ontogeny. Caudal fins are the sharks' main propulsion structures and as such can dictate a certain amount of their behavior such as what prey they go after, what habitats they occupy, and how they grow over time. Many sharks begin in a nursery environment, such as mangroves, which can protect against predation before becoming large enough to occupy their adult habitats. This study aimed to focus on how the caudal fin may be changing as the shark grows both within a species and amongst a variety of species. After analyzing nine species across five orders it was found that certain linear tail measurements are changing allometrically but many are growing isometrically. Those that are allometric may be adjusting their caudal lobe ratios to better fit their adult environments after leaving their juvenile nursery habitats. Further studies should focus on quantifying the fluid dynamics behind these shape changes to better understand the role the caudal fin is playing in their lifespan.

INTRODUCTION

Ontogeny in Organisms

As an organism grows from egg to adult, it necessarily changes in linear dimensions, areas, and volume. If proportions are maintained while size increases (as in cubes of different sizes), the growth pattern is termed *isometric*. In contrast, *allometric* growth describes a change in shape and proportions. A classic example of allometry is the enlarged claw of male fiddler crabs (Huxley & Tessier, 1936). Huxley and Tessier quantified the growth curve of the claws in relation to growth of the abdomen, and developed a principle equation to describe the phenomenon. One of their most important contributions was the notion of, and way to determine, an allometric coefficient, α , which is used as a metric for whether the body part in question is growing isometrically or allometrically (faster/slower) than expected with overall body size increase (Huxley & Tessier, 1936). Scaling relationships, or morphometrics, has matured into an active area of research that has been applied to all major groups of organisms.

Within fishes (both cartilaginous and bony), most scaling studies have focused on feeding or locomotor anatomy and performance, as those are thought to be under the most intense selective pressures. It is generally well established with carnivores, that the bigger you are, the bigger prey you eat (Brown, 1981). In a wide range of taxa, prey is roughly 20% the size of a predator, meaning as the predator grows, it begins to eat larger prey as well (Scharf et al., 2000). This effect is more significant in species that are higher in the food chain and

considered more predatory; primary consumers tend to have a smaller relative prey size, around 10% (Scharf et al., 2000). Changing size therefore often necessitates a change in prey selection; alterations in body or head/mouth shape may help fish manage transitions to different prey.

Fish Locomotion

Swimming performance is traditionally divided into multiple facets: maintained cruising speed, acceleration, and maneuverability (Supplementary Figure 1). Size and shape of the body, fins and tail (and their oscillatory or undulatory movement patterns) greatly influence performance in each category. Smaller reef fish with oscillatory short fins, such as butterflyfish, are known for being adept at maneuverability (Webb, 1984). Oscillation of short fins is not very efficient at propulsion, but enables precise turning and maneuvering among corals. In contrast, a fish that undulates its body and caudal fin, such as a tuna, is effective at high-speed cruising (Webb, 1984). Undulatory movements with high-aspect fins facilitates propulsion through the water with high hydrodynamic efficiency.

While butterflyfish and tuna are considered specialists for their respective locomotor modes, some fish are generalists, exhibiting similarities to the specialists in two or more of the three locomotion types (acceleration, cruising, and maneuvering). Sharks are often considered generalists; they are very adept at cruising while also exhibiting maneuverability and acceleration. Some species of sharks are more adept at one over the other; e.g., mako sharks are very strong at acceleration while nurse sharks excel at maneuverability. The caudal fin

plays a major role in locomotion by communicating thrust forces to the water that allows forward motion (Webb, 1984). In general, a larger caudal fin will allow for greater thrust and forward propulsion.

How the fins grow and change shape can alter the efficiency of turns, which may be crucial in environments such as mangroves but may not be as important for large predators crossing open oceans. Fu et al. (2016) showed that as tiger sharks grew, the caudal region shifted from a juvenile asymmetrical tail (larger dorsal lobe) to an adult symmetrical tail (dorsal and ventral similar in size). Disparity in caudal fin lobe size may therefore suggest some function of an enlarged dorsal lobe allowing for a tighter turning radius rather than forward thrust (Fu et al., 2016). Caudal fin shape also affects its contribution to strain energy storage, which lessens required muscular effort and thus may increase locomotor efficiency during long swims or fast escapes from predators (Lingham-Soliar, 2005). Efficiency is often estimated using tail beat frequency (TBF): how many times the fish beats its tail back and forth within a given time period. While smaller sharks can swim at relatively faster speeds, they have a higher TBF; this means that smaller sharks can move in faster bursts but use power less efficiently than larger sharks with lower TBF (Graham, Dewar, Lai, Lowell, & Arce, 1990). In contrast, the genera *Negaprion* and *Triakis* are adapted for more efficient swimming, and have a lower TBF (Graham et al., 1990).

Though caudal fin shape has been demonstrated to affect swimming performance in a few shark species, few longitudinal studies across ontogeny have been done because capture and data collection can be logistically

challenging and dangerous, and data collection often results in the death of the animal. The few studies that have been done have examined: (1) how linear measurements can help predict overall body mass in white sharks (Mollet & Cailliet, 1996); (2) how muscle anatomy and fiber arrangement in the caudal region affect swim speed (Lingham-Soliar, 2005); and (3) how the caudal fin dimensions and area in four shark species (blacktip, bull, nurse and tiger) changed with total body size (Irschick & Hammerschlag, 2015). Irschick and Hammerschlag (2015) found negative allometry of tail parameters in the two large shark species (bull and tiger), but no relationship with size in blacktip and nurse sharks (Irschick & Hammerschlag, 2015)(Irschick & Hammerschlag, 2015). By correlating anatomical measurements with life history and habitat, scaling studies hold out the promise of predicting shark movements and abilities without having to track them extensively or house them in a tank.

Habitat Differences in Sharks

Sharks occupy a variety of environments and ecosystems throughout their lifetime. In many species, juvenile sharks begin their lives in protected nurseries, such as mangroves, and can stay for up to six months (blacktip sharks; Heupel et al., 2004). Inhabiting nurseries allows sharks to grow and develop in habitats low in predation, as the prop roots of the trees make it difficult for large predators to enter and attack (Heupel et al., 2007; Heupel & Hueter, 2002). Navigating in these environments requires the ability to turn and maneuver through the roots while still maintaining speed and energy levels to feed.

Once juvenile sharks reach an appropriate size, they move into their adult environments, which present different challenges. Blacktip, hammerhead, and nurse sharks all occupy complex reef environments as adults. Bonnethead, lemon and sand sharks occupy sandy flats near reefs, feeding on small fish among the seagrass (Jhaveri et al., 2015). Dogfish and bull sharks may occupy estuaries and occasionally rivers, which are often murky and difficult to navigate by sight. Trying to avoid obstacles in these rivers may require a more similar shape in caudal fin to juveniles in mangroves. Finally, adult white sharks move out into more open waters or reef ecosystems and perform transoceanic migrations (Wetherbee et al., 2007), requiring energetic efficiency.

Diet can likewise shift drastically throughout a sharks' lifetime – from small fish and invertebrates in mangrove nurseries as juveniles to feeding on large marine mammals as adults. The speed and power required to chase and consume a sea lion (Hussey et al., 2012) prioritizes acceleration and cruising speed, quite different from the maneuverability required to navigate between prop roots and find crabs. Habitat and prey type are thus expected to place constraints on sharks' tail morphology.

By combining a variety of niche factors such as diet, migratory patterns and habitat tracking locations the species used in this study can be placed in three different adult habitat categories. Rocky reefs are occupied by species (Spiny Dogfish, Nurse Shark and Bullhead Shark) tend to feed on small benthic organisms and dwell on the seafloor. Coral reefs and sandy flats are associated with species that stay within the photic zone, feed on a range of sizes of fish –

including small sharks – and that stay within the edges of a coral reef. These complex reef habitats are occupied by Bonnethead Sharks, Blacktip Reef Sharks, Lemon Sharks and Sharpnose Sharks. The final habitat is the Open Ocean, which is occupied by the Shortfin Mako Shark and the Spinner Shark. These sharks tend to feed on much larger and faster prey or schools of fish swimming through the open ocean. They also tend to have large transoceanic migrations and do not frequent coastal waters.

Evolutionary Differences in Sharks

Sharks have existed for roughly 455 million years, and in that time have become some of the most efficient predators and fastest swimmers (Gardiner et al., 2012). Notable adaptations making them such efficient predators include dermal denticles for hydrodynamic efficiency and Ampullae of Lorenzini which allow for electroreception (Klimley, 2013). These features have helped sharks exist and thrive in their environments and are a common feature amongst the 503 extant species of sharks. I will focus on 9 species in this study, highlighted in Figure 1 (adapted from Velez-Zuazo and Agnarsson, 2011).

While all species share some common features, there are many distinguishing features that have evolved over time amongst the roughly 30 families of sharks. One of these differences between sharks is in caudal fin shape. Species in the Lamnidae family (white and mako shark) are generally known to have similar sized dorsal and ventral lobes of the caudal fin, while the Carcharhinidae family (blacktip and spinner shark) have drastically different size dorsal and ventral lobes. The most extreme example of lobe sizes is the

Ginglymostomatidae family (nurse sharks), which have little to no ventral lobe present in their caudal fins (Klimley, 2013). Many of these tail differences may correlate to differences in ecological niche as well. The Ginglymostomatidae are not considered large and fast predators; the nurse shark, a slow bottom dweller, represents them best. While the shape and proportions of the dorsal and ventral caudal lobes affect swimming performance, the patterns in these variables may have arisen due to two different influences. It may be that tail shape is a consequence of the evolutionary history of the particular family, and thus closely related sharks will all have similarly shaped tails. An alternative explanation is that tail shape varies according to habitat, and adult sharks occupying similar habitats will show similarity in shape, irrespective of phylogenetic relationships.

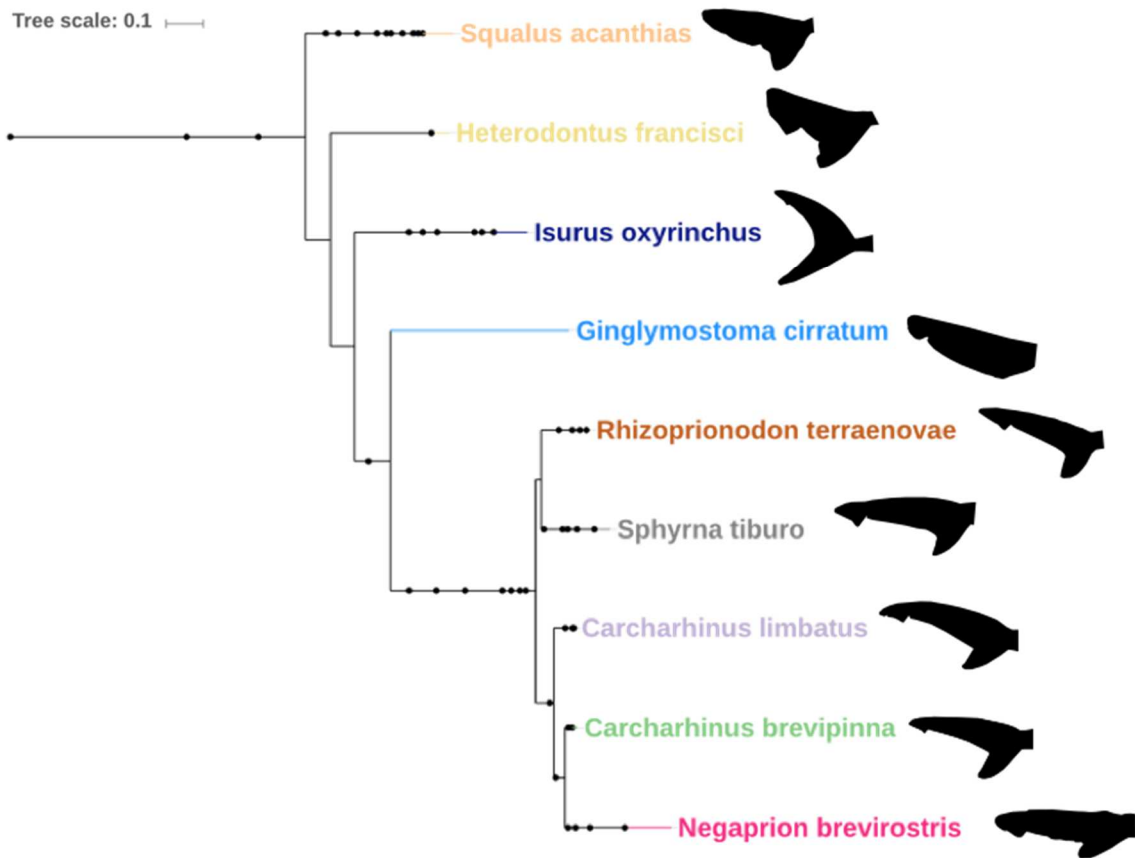


Figure 1 Phylogenetic tree of species used in this study – Bayesian consensus data used in (Vélez-zuazo & Agnarsson, 2011). Each species is highlighted according to a color pattern used in the Results section PCA with the tail silhouette accompanying each name. Tree compiled and manipulated using iTOL, an expanded version can be found in Supplementary Figure 2.

Objective

This study aims to answer the question of whether phylogeny or habitat is the principal determinant of adult shark tail shape. I will examine different species in which the juveniles all start out in mangrove and shallow reef nurseries (other than *Isurus oxyrinchus*) and then later transition into their different adult environments. Looking at differences in sharks with varying adult habitats – coral reefs / sandy flats, rocky bottom reefs, and the open ocean – will allow me to

discriminate between the alternative hypotheses. If phylogeny is the important factor, then closely related sharks will follow the same ontogenetic trajectory for tail shape, regardless of adult habitat. Conversely, if environmental demands dictate tail shape, then adult shark species occupying similar habitats will converge on similar tail shapes, even though they represent different families. I will use similar analytical methods to a study on crocodilian cranial ontogeny, which quantified how various species and sizes differed in skull shape, and determined the influence of phylogeny on the observed patterns (Watanabe & Slice, 2014). Data from that study are shown in Supplementary Figures 3 and 4 as illustrative of the types of analyses I intended to follow.

MATERIALS AND METHODS

Data Collection

Photos of specimens were taken during visits to (1) museums with research collections (Table I) and (2) purposeful ocean shark fishing trips, in which animals were brought onboard, photographed and released, with handling lasting no longer than 10 minutes. Data was acquired for 139 specimens of nine different species from six different families (Carcharhinidae, Ginglymostomidae, Lamnidae, Squalidae, Heterodontidae, and Sphyrnidae) and five orders within the class Chondrichthyes (Table II). In order to analyze changes in tail size and shape, I acquired lateral-view photos of the specimens taking care to flatten the tail when necessary. A size reference in the image allowed me to accurately scale specific measurements - three standard body length measurements, four tail specific measurements (following Irschick and Hammerschlag, 2015) and three tail area measurements (Figure 2) - using the program ImageJ (Rasband, 2015). The species selected showed a range of caudal fin shapes (Figure 3).

Table 1 / List of Museums and Collections visited for Data Collection – included are also two companies that assisted with photos of live specimens caught on fishing trips (denoted by asterisks).

Museum	Affiliation	Location
Museum of Comparative Zoology	Harvard University	Cambridge, MA
Burke Museum	University of Washington	Seattle, WA
Florida Museum of Natural History	University of Florida Gainesville	Gainesville, FL
Cornell Museum of Vertebrates	Cornell University	Ithaca, NY
Friday Harbor Laboratories	Washington University	Seattle, WA
Field Museum		Chicago, IL
NC Museum of Science and Natural History		Raleigh, NC
* Reel Sonar Inc		
* Ana Banana Fishing Co		Tampa Bay, FL

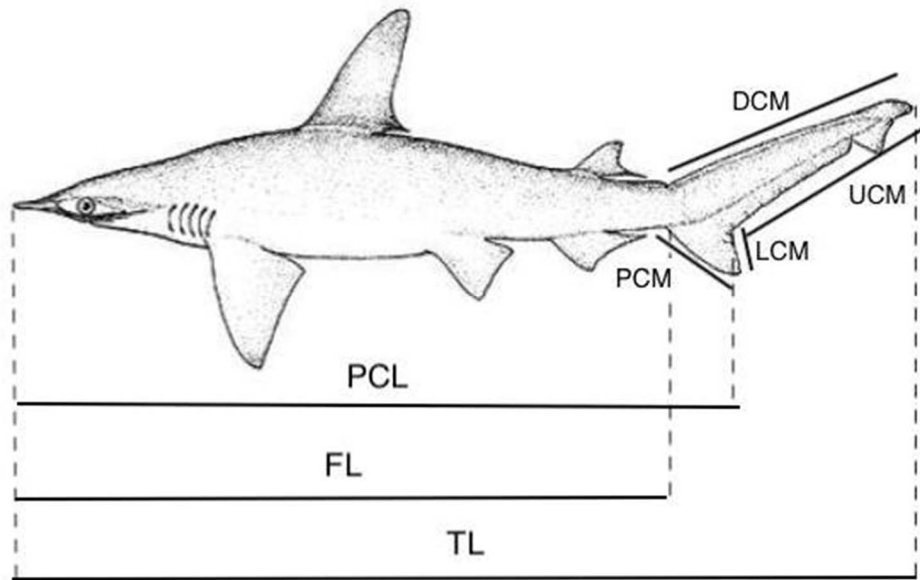


Figure 2 Measurements taken on each shark, displayed on model bonnethead shark image. Whole body measurements include Total Length (TL), Fork Length (FL), and Precaudal Length (PCL). Tail specific measurements include Dorsal Caudal Margin (DCM), Upper Caudal Margin (UCM), Lower Caudal Margin (LCM), and Preventral Caudal Margin (PCM). In addition, the Dorsal and Ventral lobe areas were measured using the Polygon tool in ImageJ; the sum of these areas equaled total caudal area.

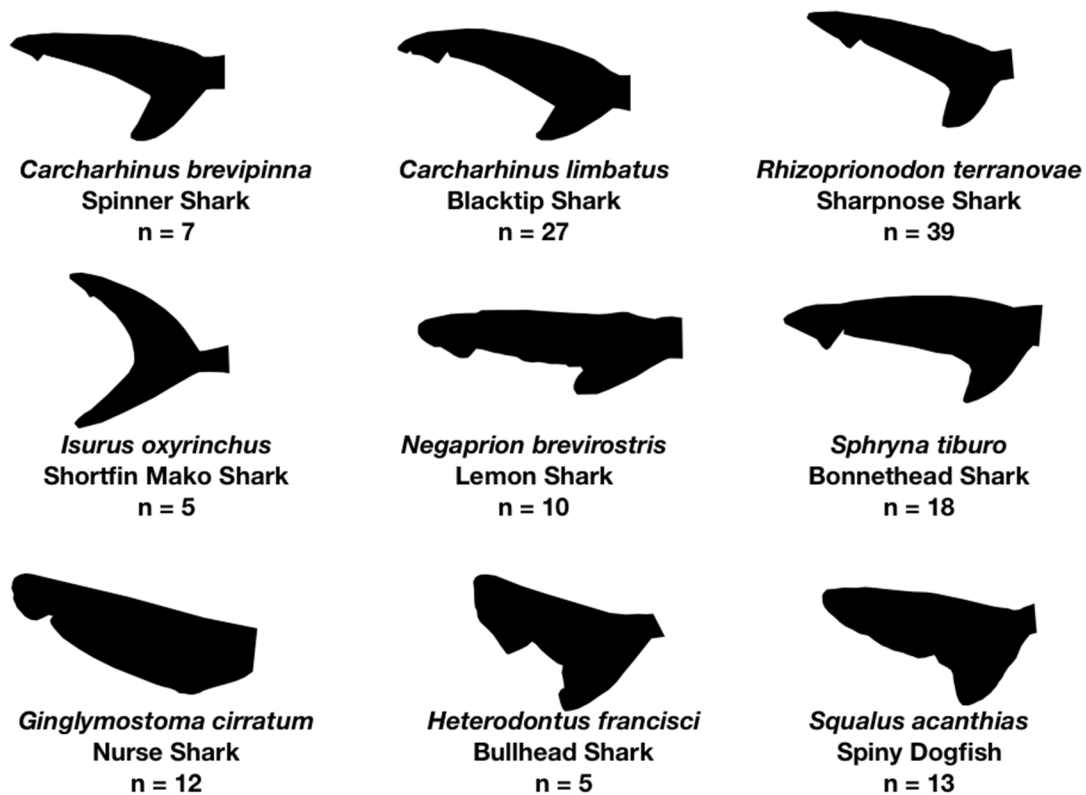


Figure 3 Silhouettes of the caudal fins of study species including sample size (n).

Data Analysis

All measurements were log transformed before being analyzed so as to fit the normal distribution. To determine significance in allometric or isometric growth each species was fit to a linear model of each tail measurement as a function of Total Length. There were no significant differences between models made using Total, Fork, or PreCaudal Length; therefore, Total Length was selected. Each species slopes of the linear measurement against Total Length was tested to determine if the slope was significantly different from 1.

The four linear tail measurements (DCM, UCM, LCM & PCM; Figure 2) were then used to create a Principal Component Analysis that highlighted any

shape patterns that emerged within a species and across different species. This was done using the R base package by running an analysis using “prcomp”.

PC2 was used in a linear model that tested the effect of both Adult Habitat and Order on PC2 to test if there were any significant differences between the groups. An ANOVA was run on the model followed by a post-hoc Tukey test to determine significant differences between Habitats or Orders.

The R packages “ape” and “picante” were used to test if phylogenetic signaling had any affect on the data (Bolker et al., 2014; Kembel et al., 2010). In order to obtain one value for each species the results of PC2 were averaged for each species and put into the analysis for comparison. Averages were compared to morphological and genetic data collected by Velez-Zuazo and Agnarsson (2011), which was also used to produce the phylogenetic tree used in this study. “Picante” uses Bloomberg’s K-Statistic in order to determine if the trait is following Brownian motion ($K = 1$) indicating a strong phylogenetic rate change or a more structured evolutionary rate change ($K = 0$) which is driven by an outside factor apart from random evolutionary change (Harmon, 2019). The package compares the trait values to the most recent common ancestor in the tree to determine any modification that is occurring.

Table II List of species analyzed. Sample size (N) and size range analyzed are listed, along with reference values for common size ranges for each species, and typical habitats at juvenile and adult stages.

Common Name	Order	Scientific	N	Size Range (cm)	Birth Size (cm)	Maturity Size (cm)	Juvenile Habitat	Adult Habitat
Spinner Shark	Carcharhiniform	<i>C. brevipinna</i>	7	65-113	70	140	Shallow Flats	Open Ocean
Blacktip Reef Shark		<i>C. limbatus</i>	27	15-130	50	100	Shallow Flats	Sandy/ Reef
Lemon Shark		<i>Negaprion brevirostris</i>	10	33-67	55	230	Mangrove	Sandy/ Reef
Sharpnose Shark		<i>Rhizoprionodon terraenovae</i>	39	5-94	32	60	Mangrove	Sandy/ Reef
Bonnethead Shark		<i>Sphyrna tiburo</i>	18	17-95	30	75	Mangrove	Sandy/ Reef
Nurse Shark	Orectolobiform	<i>G. cirratum</i>	13	27-106	30	??	Rocky Reefs	Rocky Reefs
Bullhead Shark	Heterodontiform	<i>H. francisci</i>	3	16-38	16	60	Shallow flats	Rocky Reef
Shortfin Mako Shark	Lamniform	<i>Isurus oxyrinchus</i>	5	51-118	70	200	??	Open Ocean
Spiny Dogfish	Squaliform	<i>S. acanthias</i>	13	12-96	30	70	Shallow Flats	Rocky Reef

RESULTS

Principal Component Analysis

Results of the Principal Component Analysis (Figure 4) show that PC1 explains 86% of the variation in the data, PC2 explains 11.9%, PC3 explains 1.4% and PC4 explains less than one percent of the data. The loadings of the different variables determined that all four tail measurements contributed equally to PC1 and PC2 was driven positively by LCM (0.81 rotation) and negatively by DCM (-0.36 rotation) and UCM (-0.44 rotation). PC1 is heavily correlated with Total Length (Figure 5) and thus is essentially a size axis.

PC2 is expected to capture information about shape irrespective of size. One-way ANOVAs and Tukey tests were run on PC2 scores with data coded according to Habitat and Order (phylogeny). Habitat had a significant effect on Principal Component 2 ($p < 0.001$; Figure 6A), with Rocky, Open and Sandy all significantly different from each other. Likewise, Order showed a significant effect on Principal Component 2 ($p < 0.001$; Figure 6B). A post-hoc Tukey test determined that Squaliform was not significantly different from either Carcharhiniform or Heterodontiform, but all other orders were significantly different from either other.

As seen in Figure 4, *Ginglymostoma cirratum* and *Isurus oxyrinchus* are strongly separated from the rest of the data while the remaining species grouped together around 0 for PC2. *C. brevipinna* separates out from that group within PC1, though that likely results from only large individuals of that species being available for analysis, while other species had smaller individuals. *H. francisci* seems to have an overall larger PC2 score than most of the Carcharhiniformes which may be explained by the distinct tail shape associated with their species.

A second PCA was performed using the four tail measurements and also the two tail areas calculated to determine if tail area rather than linear measures provided increased discriminatory power (Figure 7). The separation of species did not change appreciably, though several species were shifted in the area of PC-space occupied. PC1 was once again a size axis, accounting for 79% of the variance. PC2 accounted for 13% of the variance, being mainly driven positively by Dorsal Lobe Area (0.62 rotation) and Lower Caudal Margin (0.49), and driven negatively by Dorsal Caudal Margin (-0.41 rotation) and Upper Caudal Margin (-0.44).

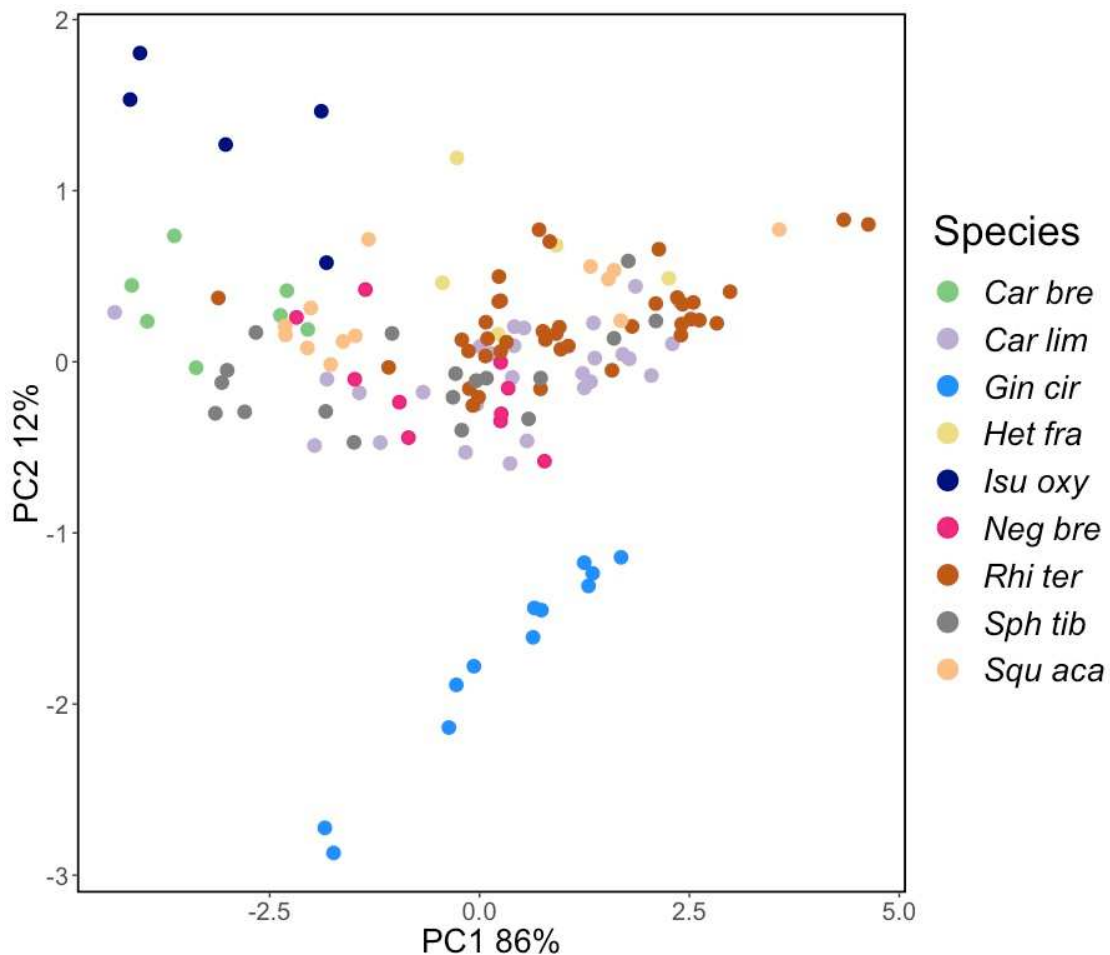


Figure 4 Principal Component Analysis of Four Linear Tail Measurements. PCA was done in R studio using the base package. PC1 accounts for 86% of the variation and is heavily correlated with TL, total length decreases as the x axis

moves positively. PC2 accounts for 12% of the variation and is positively driven by Lower Caudal Margin (LCM) and negatively by Dorsal Caudal Margin (DCM). Species are denoted by the first three letters of their genus and species.

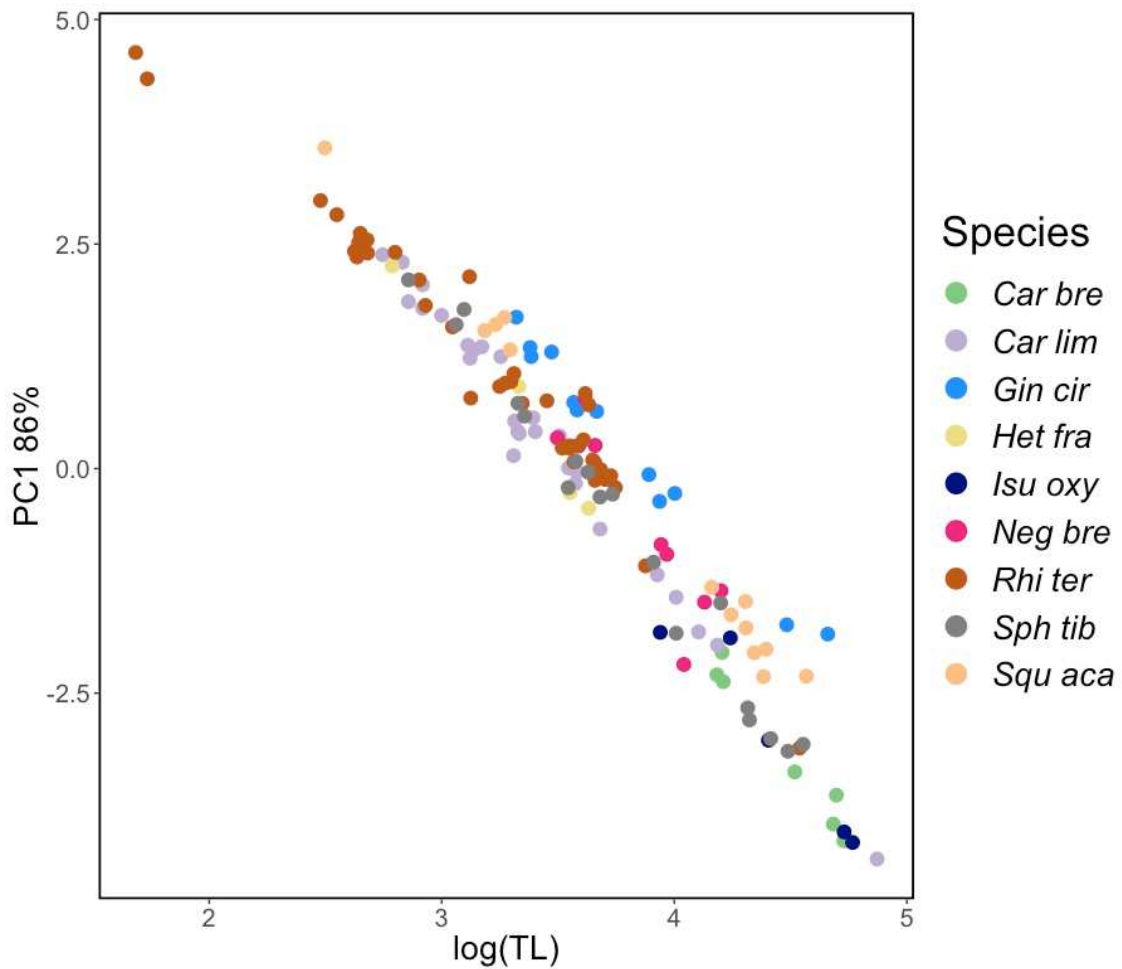


Figure 5 PC1 plotted against log transformed Total Length of all species

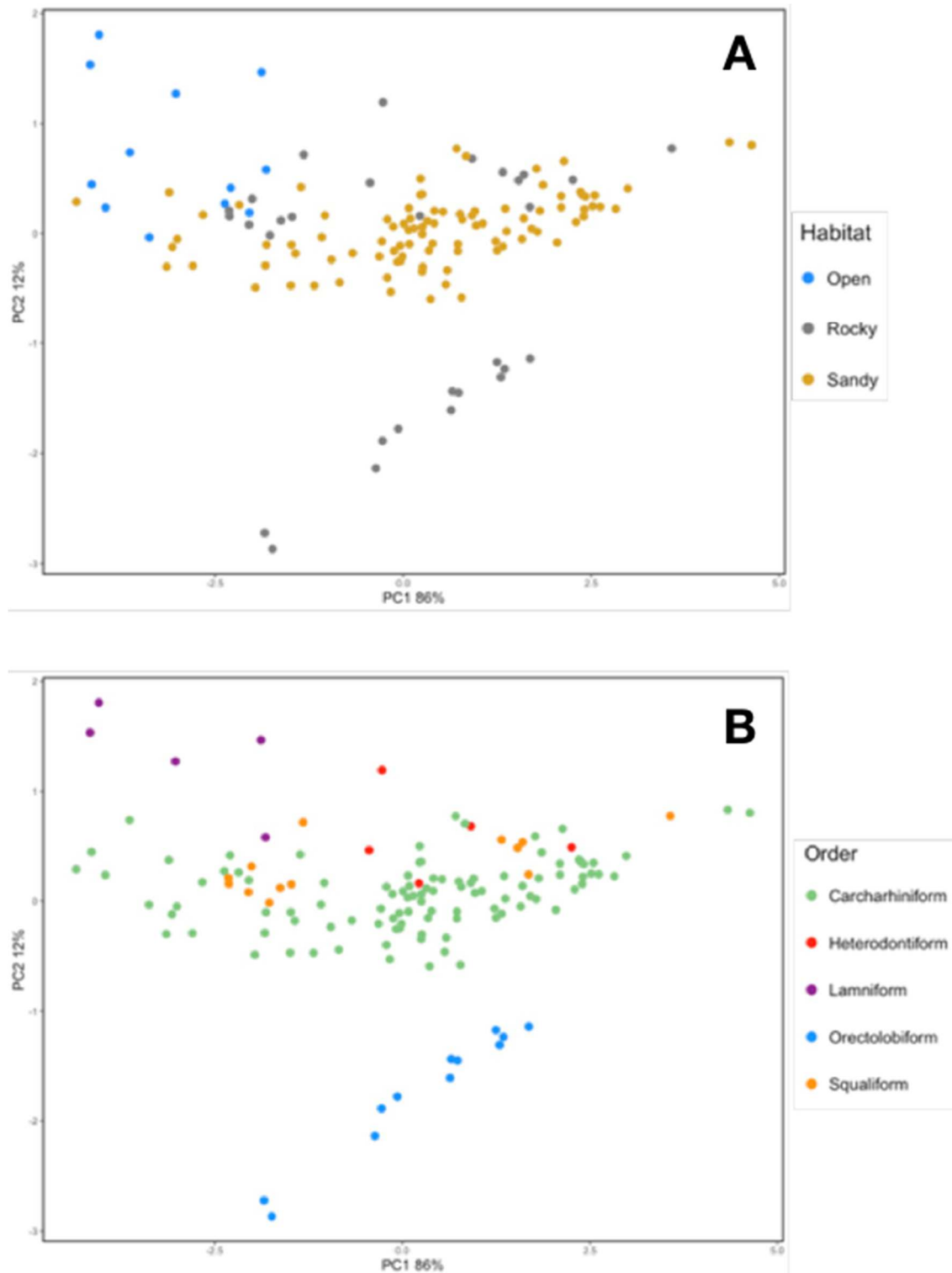


Figure 6 PCA coded by Habitat (A) and Order (B). PC2 is significantly affected by both Habitat ($p < 0.001$; all habitats different) and Order ($p < 0.001$; all orders showed significant differences except Squaliform from Heterodontiform and Carcharhiniform).

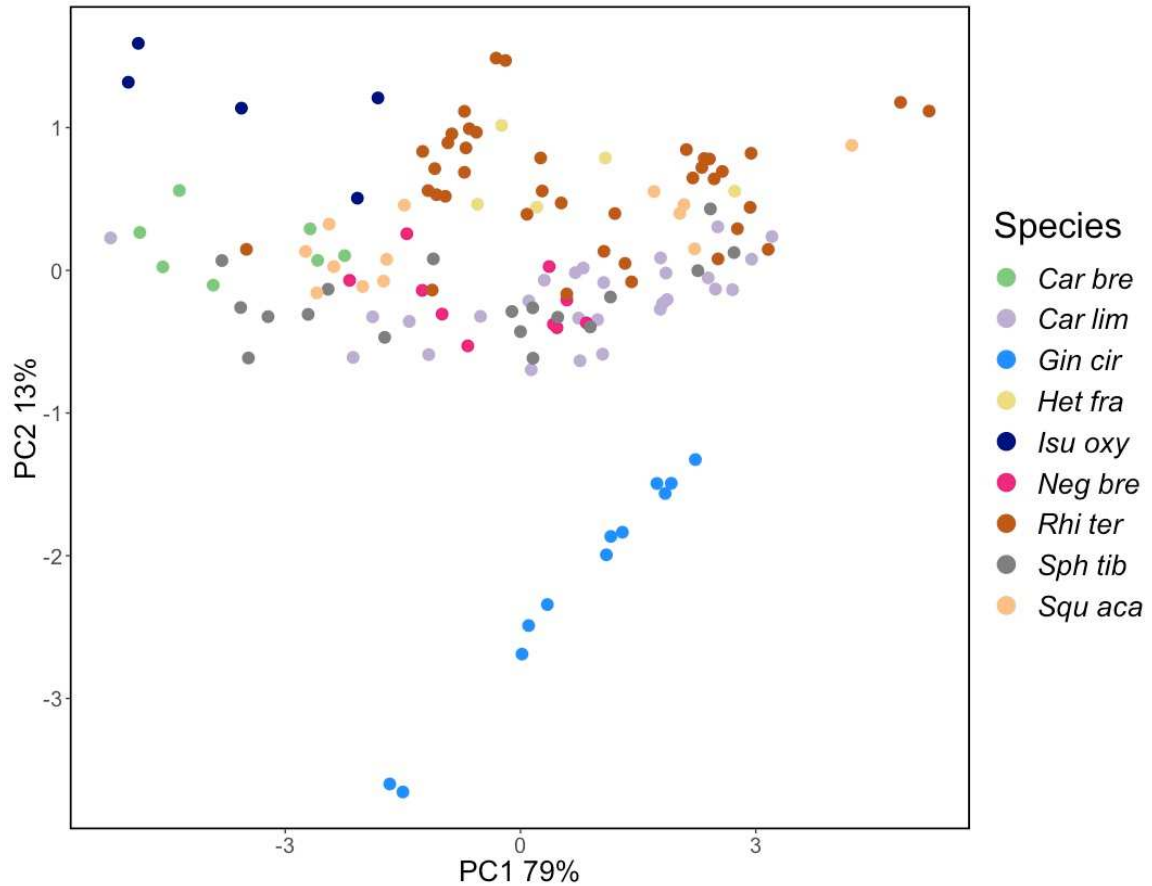


Figure 7 PCA using four linear tail measurements and two tail area measurements.

Linear Measurements

Each tail measurement (DCM, LCM, UCM and PCM) was plotted against Total Length to determine the growth patterns of each species and tail component (Figure 8). A linear model was made for each measurement of each species (Table III). While most of the slopes were not significantly different from 1, indicating isometric growth, there were 12 slopes that significantly deviated from 1, suggesting allometric growth (Table III, Figure 9). Photo comparisons

between the smallest and largest specimens can be found in Supplementary Figure 5.

Most allometric slopes occurred in the Lower Caudal Margin (LCM) of the species with *R. terraenovae*, *C. limbatus*, *S. tiburo*, *S. acanthias* growing with a slope lower than 1 (negative allometry) and *I. oxyrinchus* growing with a slope greater than 1 (positive allometry; Figure 9). Species with negative allometric growth in LCM are growing the ventral lobe at a slower rate than their dorsal lobes and total lengths. Many of those species are Sandy/Reef habitat species. In contrast, *I. oxyrinchus* grows its ventral lobe at a larger rate than the dorsal lobe (Figure 9), resulting in more equal-sized lobes of its caudal fin.

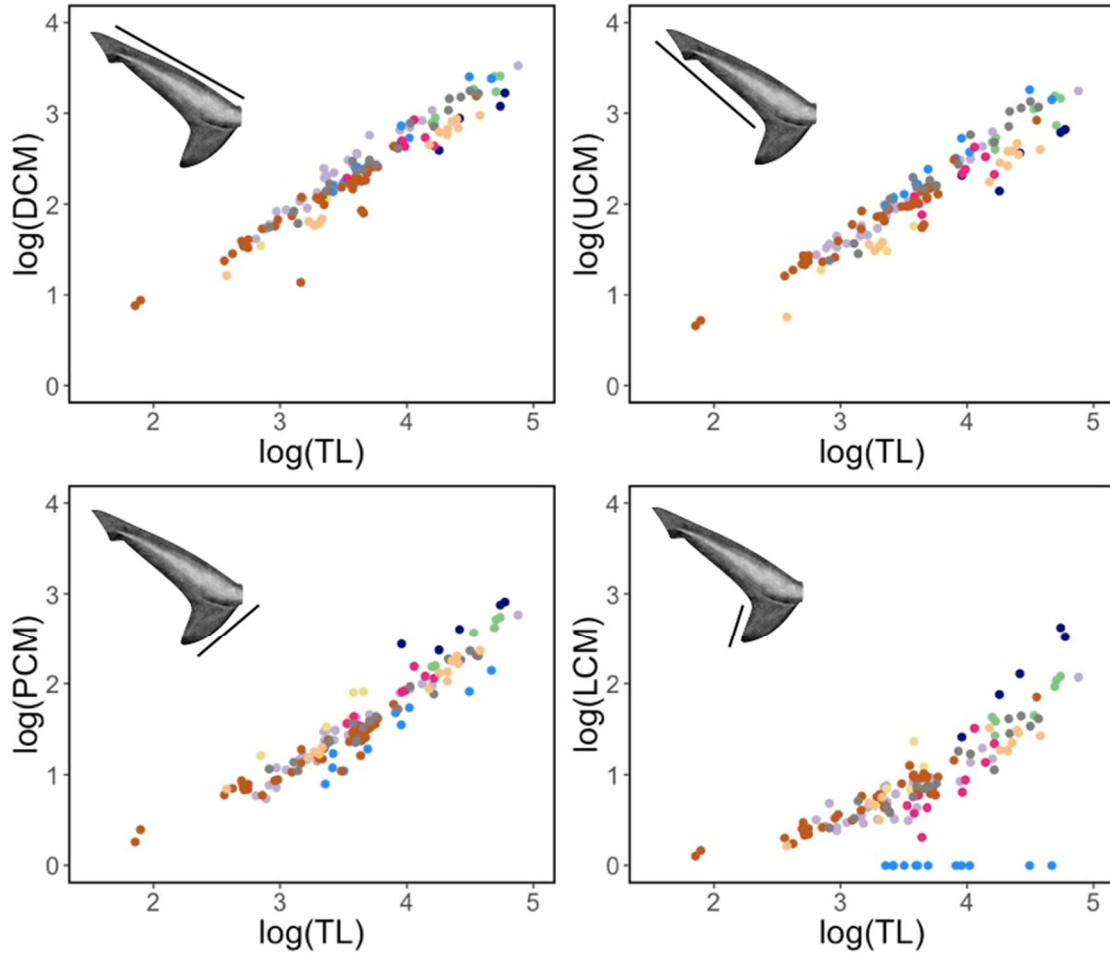


Figure 8 Log transformed Linear Tail Measurements against Total Length. Each tail measurement is highlighted on the caudal fin in the upper left corner of each panel. Slopes statistically different from 1 are highlighted in Figure 9; all slopes and intercepts are listed in Table III.

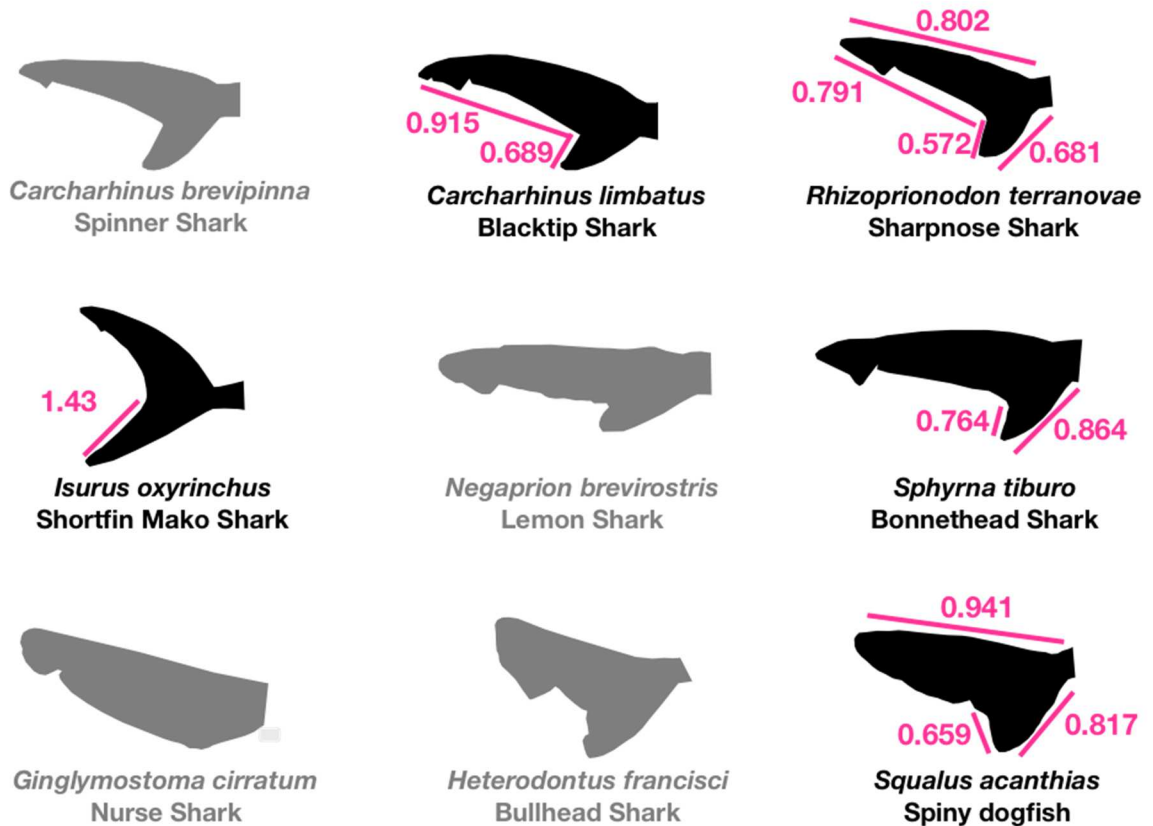


Figure 9 Adult caudal fin silhouettes with significant allometric slopes highlighted.

Phylogenetic Signaling

Two composite traits were tested for phylogenetic signal against the data used in Velez-Zuazo and Agnarsson (2011). Trait 1 was the mean PC2 value for each species and it was found that this trait significantly followed Brownian motion ($K = 0.82$, $p = 0.035$), which indicates that this trait (linear tail measurements) is not driven by a significant speciation event but rather stochastic processes. However, Trait 2, which was the ratio of Dorsal Lobe Area : Total Length averaged across the species, was found to be a structured evolutionary change ($K = 0.25$) indicating that something such as movement into different habitats may have driven the change, however it was not significant ($p =$

0.8). It is possible that this K statistic was not significant due to the low amount of species present in the test (nine), and that this pattern would become more significant if a broader species pool was tested.

Table III Summary of slopes and intercepts for each Tail Measurement against log of Total Length. Each Tail Component tested against Total Length. P values determine if each slope is significant different from a slope of 1.

Tail Comp.	Species	Slope	Error	Intercept	P Value
DCM	Car bre	0.902	0.117	-0.886	0.441
	Car lim	0.946	0.036	-0.935	0.146
	Gin cir	1.035	0.051	-1.361	0.506
	Het fra	0.940	0.040	-1.132	0.229
	Isu oxy	0.687	0.204	-0.138	0.222
	Neg bre	0.855	0.153	-0.777	0.368
	Rhi ter	0.803*	0.049	-0.646	0.000*
	Sph tib	0.952	0.037	-1.059	0.206
	Squ aca	0.941*	0.024	-1.263	0.028*
UCM	Car bre	0.824	0.212	-0.790	0.445
	Car lim	0.916*	0.028	-1.177	0.006*
	Gin cir	0.978	0.060	-1.283	0.727
	Het fra	0.894	0.252	-1.336	0.704
	Isu oxy	0.747	0.251	-0.781	0.388
	Neg bre	0.858	0.168	-1.077	0.423
	Rhi ter	0.791*	0.032	-0.793	0.000*
	Sph tib	1.074	0.050	-1.724	0.164
	Squ aca	0.945	0.037	-1.595	0.169
PCM	Car bre	1.019	0.061	-2.096	0.771
	Car lim	0.931	0.034	-1.798	0.051
	Gin cir	0.837	0.086	-1.738	0.088
	Het fra	0.828	0.193	-1.182	0.437
	Isu oxy	0.657	0.166	-0.270	0.131
	Neg bre	0.957	0.128	-1.882	0.748
	Rhi ter	0.681*	0.030	-1.013	0.000*
	Sph tib	0.864*	0.043	-1.587	0.006*
	Squ aca	0.818*	0.035	-1.397	0.000*
LCM	Car bre	0.934	0.184	-2.411	0.737
	Car lim	0.689*	0.066	-1.616	0.000*
	Gin cir	0.000*	0.000	0.000	0.000*
	Het fra	0.914	0.325	-2.199	0.807
	Isu oxy	1.430*	0.098	-4.225	0.022*
	Neg bre	1.191	0.279	-3.707	0.514
	Rhi ter	0.572*	0.037	-1.147	0.000*
	Sph tib	0.765	0.059	-1.884	0.001
	Squ aca	0.659*	0.051	-1.496	0.000*

*p < 0.05. Error = standard deviation of slope

DISCUSSION

Across the roughly 440 species of extant sharks, there is a huge variety of both habitat occupation and morphology. Sharks can be found all over the ocean and exhibit a wide diversity in morphology such as overall size, color, and caudal fin shape. Since the caudal fin is the main propulsion structure for sharks, the tails is critical to survival and its shape is known to vary among different families. The morphological differences amongst sharks may be driven by the different habitats that species occupy or by adaptations that have arisen throughout the phylogenetic history of sharks. If phylogeny were the driving force, species in the same genus, family, and even order would be expected to have similar growth patterns and tail shapes. Conversely, if adult habitat is the driving factor, species that occupied similar adult habitats would be expected to have similar growth patterns and tail shapes. A method to test these hypotheses is to sample species from a variety of families that begin in the same juvenile ecosystem but transition into different adult habitats, and quantify changes in tail shape.

With the exception of *Isurus oxyrinchus*, all species examined in this study start out in mangroves as juveniles. The mangroves provide them safety from large predators and easy access to prey. Navigating amongst the prop roots of the mangroves requires the ability to easily maneuver which is accomplished by increasing turning radius defined as an increased distance moved with a sharper angle of body (Domenici & Blake, 1991). High maneuverability is most easily achieved with a broader tail shape (Wilga & Lauder, 2002). Broader tails sacrifice

speed and power but allow for quicker and tighter turns which is beneficial for swimming through a complex environment (Wilga & Lauder, 2002). As individuals grow, they become too large to inhabit the mangrove and must move into their adult environments, which may necessitate shape changes within the caudal fin to better suit the physical features of their new adult habitats.

Species that live in Rocky Reefs often weave in and out of structures in search of a place to lie down which is very similar to swimming around the prop roots of their juvenile mangrove habitat (Castro, 2000). Thus, one would expect that species that transition from the mangroves to Rocky Reefs would not show significant changes to their tail shapes and would grow isometrically. Species in Coral Reefs and Sandy Bottoms are often found on the edges of corals, requiring similar maneuverability to the mangrove habitat. However, because their prey is typically elusive (bony fish), there is an increased demand for acceleration and speed in pursuit. The expectation is therefore an increased aspect ratio (length from the tip of the dorsal lobe to the tip of the ventral lobe divided by the chord of the caudal fin) – in other words, a slimmer and more pointed tail shape (Graham et al, 1990) – produced by positive allometric growth in the tail parameters (particularly DCM and PCM). Finally, species in the Open Ocean would be expected to maximize speed and power. They are often hunting large schools of fish through open water, which require high cruising ability (Irschick & Hammerschlag, 2015). Unlike the species of coral reefs, they do not have a need for tight turns and so would be expected to show tail shapes more similar to

those of tuna, with more symmetrical dorsal and ventral lobes produced by positive allometric growth of the ventral lobe.

Had the growth patterns of these sharks been driven strictly by phylogeny then the patterns would break down according to Order. The Carcharhiniformes all would be expected to show similar growth patterns, and adult tail shape, regardless of adult habitat. Representatives of other orders would be expected to be more divergent in growth pattern and adult tail shape due to greater time for evolutionary divergence.

The growth patterns of the nine species examined here did not fully support either hypothesis. The species that inhabit Rocky Reefs (*Ginglymostoma cirratum*, *Heterodontus francisci* and *Squalus acanthias*) were all expected to undergo isometric growth given that they occupy mangroves as juveniles and all move into Rocky Reefs as adults. While *H. francisci* and *G. cirratum* showed isometric growth as expected, *S. acanthias* varied more than expected (Figure 9). Unlike *G. cirratum* and *H. francisci* which do not tend to leave their habitat via migration, *S. acanthias* vertically migrates within the water column (P. Domenici, 2004). Vertical migration requires a different swimming mechanism that requires a more thin and elongated dorsal lobe, which is more pronounced in *S. acanthias* than in either *G. cirratum* or *H. francisci* (Wilga & Lauder, 2002). The migration behavior of *S. acanthias* may be contributing to their difference from the other species that occupy similar habitats.

The two species in the Open habitat as adults (*Isurus oxyrinchus* and *Carcharhinus brevipinna*) were expected to develop tails that had the lunate

shape associated with fast-swimming fish. Both did have high aspect ratio caudal fins, but they differed in the relative size of the dorsal and ventral lobes – *I. oxyrinchus* had symmetrical lobes whereas *C. brevipinna* had an elongated dorsal lobe (Figure 9). Thus, growth patterns were not explained fully by adult habitat.

Results for the Carcharinids were partially confounded because that family contributed all of the inhabitants of Sandy Flats/Coral Reefs. The outlier in the group is *C. brevipinna*, which occupies the Open Ocean as an adult (see above). Two of the five Carcharinid species showed isometric growth of the tail lobes, while the other three showed varying patterns of allometry in some or all of the tail measurements. Where allometric growth was seen, it was always negatively allometric – the tail is growing more slowly than expected, based on total length. Further, the ventral lobe grows more slowly than the dorsal lobe, leading to a relatively more elongate dorsal lobe. This pattern is pronounced in three of the four Carcharhinids that inhabit Sandy Flats and Coral Reefs as adults. However, the Lemon shark, also an inhabitant of Sandy Flats, grows isometrically (Figure 9). Future studies should refine the present results by examining a larger range of species with increased representation of differing habitats within each order and family and expanding their knowledge of how caudal fin shape may be related with swimming performance.

Current methods of determining hydrodynamics and swimming efficiency are measured using both flow tank estimates and musculature analysis. Since caudal fins are the main propulsion force for sharks it is important to look at how

the varying shapes contribute to the overall hydrodynamics of the sharks. Flow tank data can provide information such as critical swimming velocity, tail beat frequency and oxygen consumption. All three play a significant role in determining the hydrodynamic efficiency of a sharks swimming abilities. Studies have been done using this approach on Rocky Reef occupying leopard sharks, *Triakis semifasciata*; Coral Reef sharks like the lemon shark, *Negaprion brevirostris*; and the shortfin mako, *Isurus oxyrinchus* which occupies the Open Ocean (Graham et al, 1990). Findings from studies such as these have been able to tell us that critical speed is highly dependent on tail beat frequency. In order to increase critical speed, the species should minimize tail beat frequency, which can also result in reduced oxygen consumption. By increasing speed without drastically increasing oxygen consumption it means that the shark is able to more efficiently move through the water without expending too much energy. Expanding this study to include lab tested data of these species in a large water tunnel could help illustrate how each caudal fin shape may contribute to tail beat frequency and critical speed. Increased critical speed would be expected in caudal shapes similar to *I. oxyrinchus* given the high aspect ratio and symmetrical shape. Species with caudal fins similar to *C. limbatus* would have slightly slower speeds and species with tail shapes similar to *G. cirratum* would have significantly slower speeds than either *C. limbatus* or *I. oxyrinchus*. In addition to flow tank data, having video of these sharks moving through their respective environments and how they utilize it, which may provide more detail

on turn angles. This could elucidate some of the requirements associated with more complex ecosystems in comparison to open ocean ecosystems.

Conclusions

In this experiment I was able to determine that there are growth patterns emerging among the different species studied. There was both isometric and allometric (both negative and positive) growth seen across the nine species. Across the five Orders and three adult habitats there were patterns that indicate both phylogeny and adult habitat play a role in the growth of the species. As they grow and migrate out of their juvenile habitat (most often mangroves), their tails begin to change in order to better suit their adult environs.

This study has been one of the first that has looked extensively at growth patterns across a range of species. It has been able to provide more insight into how these sharks are growing and how their caudal fins may be changing as they age. Understanding the shape changes may provide insight into how they interact with their environment. This is critical for us to learn because protecting their environments allows them to survive and maintain the health of the ocean. It has recently been discovered that Great White sharks are beginning to venture into giant kelp forests for hunting purposes. Their prey has become limited in their natural environment due to overfishing, so they have started seeking out the prey in a habitat that they are not necessarily well suited for (Jewell, 2019). Based on their caudal fin shape, which is similar to the Shortfin Mako tail, the Great White is expected to occupy open ocean environments, chase fast prey,

and use immense power to leap out of the water and catch seals. These behaviors are all very unsuited for kelp forests, which require weaving and maneuverability to not get caught in the kelp. Understanding how caudal fin shape affects habitat use may allow fisheries and conservation managers to predict how shark populations may be impacted by human activities.

Caudal fin shape may also help to predict where some of the more cryptic species of sharks grow up, such as the Mako shark. Shortfin Makos do not live in mangroves as juveniles and given their juvenile tail shape (which is similar to the adult shape of the Carcharhiniformes) they may be expected to occupy reef edges instead. Learning more specifically about where some of these elusive species spend most of their time may help narrow search efforts and indicate unstudied habitats that are important to protect to keep those species alive.

In addition, determining the ratio of caudal fin to total length could also be an indicator of age in some species. If they grow their tails allometrically, determining a caudal fin to total length ratio could indicate what age class they are in. Previously, ageing of sharks has required studying vertebrae, which requires killing the shark first. Determining a noninvasive way to age the sharks could help protect the age classes that are more vulnerable to fishing such as juveniles.

To extend this work further, studies should observe these sharks in the wild to learn more how they utilize their habitats. This may help us to gain more understanding of how their caudal fins help in that process and how the shape may prevent them from succeeding in a more novel environment. Expanding this

study out by increasing species and size range will provide even more data to work with and analyze. This may help answer the question more confidently about what the driving force is that controls these caudal fin shape changes.

It is also important to begin to expand our knowledge beyond just the caudal fin shape, as focusing on one trait alone may distract from understanding how the organism as a whole works within its environment. Understanding how caudal fin shape changes in concurrence with head shape, body shape, muscle arrangement, etc., may broaden our understanding of shark habitat use as a whole.

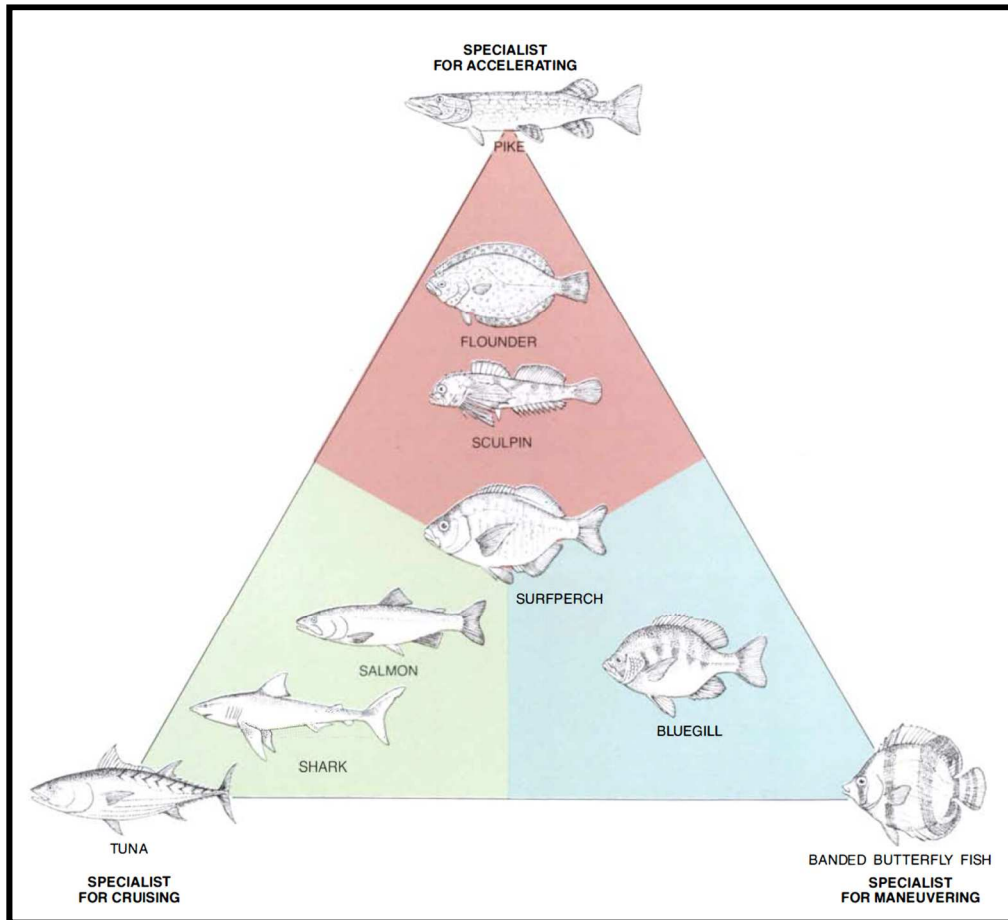
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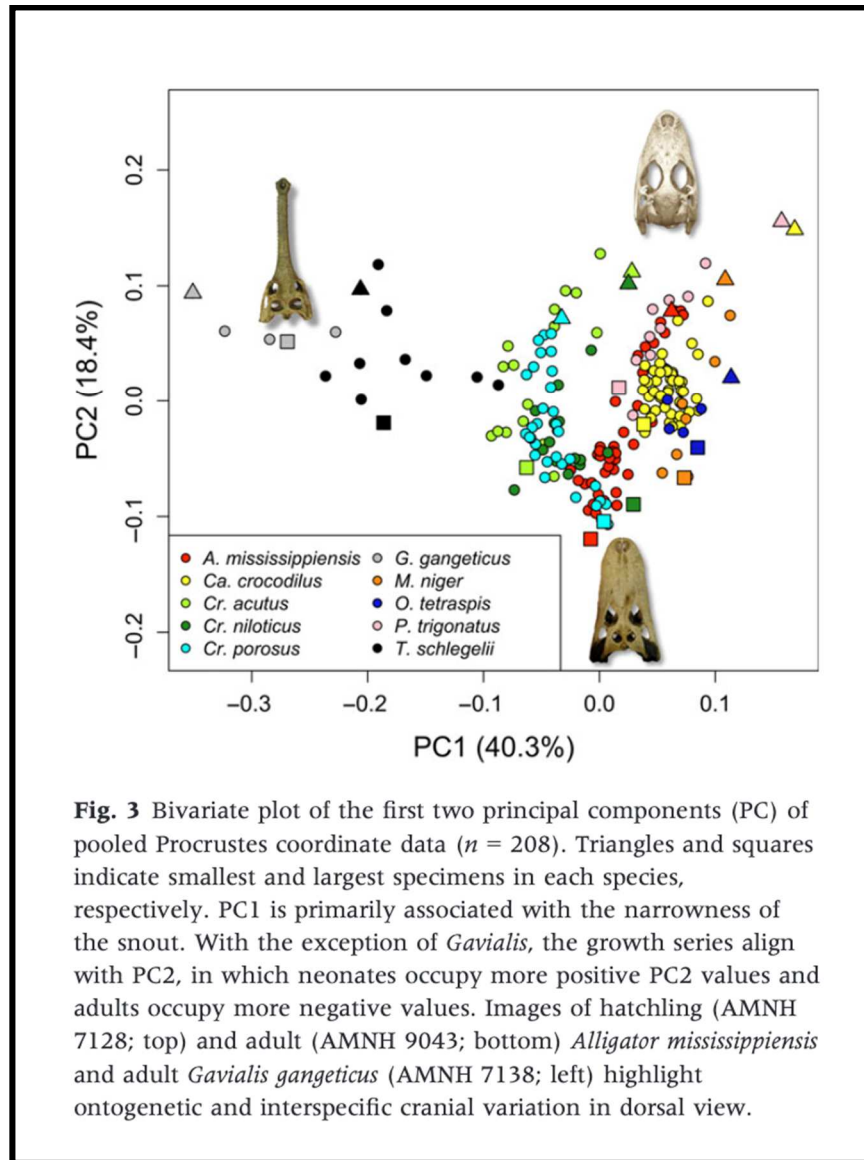
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APPENDIX



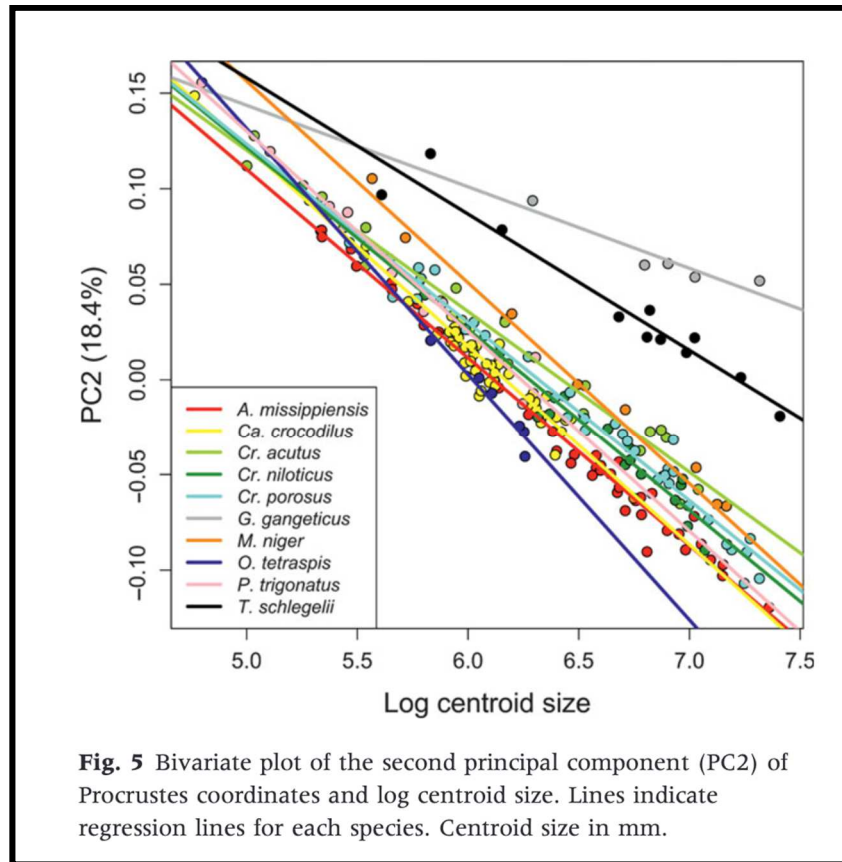
*Supplementary Figure 1. Functional-Morphology Plane of a variety of Fishes. Tradeoffs that can occur in the morphology of different fishes displaying some that have a specialist body and others that take a generalist approach to three locomotion types. Specialists cluster toward the three points of the triangle while generalists are closer to the center of the triangle. Reprinted from Webb, P. (1984). Form and Function in Fish Swimming. *Scientific American*, 251(1), 72-83.*

Supplementary Figure 2. Phylogenetic tree of families of sharks – Bayesian consensus data used in (Vélez-Zuazo and Agnarsson, 2011). Species highlighted in blue will be used in this study for morphometric and phylogenetic analysis. Tree compiled and manipulated using FigTree v1.4.3.



Supplementary Figure 3. Taken from (Watanabe & Slice, 2014) detailing the phylogenetic analysis this study aims to recreate. PCA analysis utilized two traits among the skulls and was able to isolate differences amongst phylogenetic groups to determine significant differences. They were able to determine how different taxa underwent ontogeny in the cranium by comparing shape changes from neonates to adults within each species. Neonates tended to have more positive PC2 values whereas adults had more negative. PC1 values varied more between the taxa, with more molecularly similar taxa grouping together – G.

gangeticus and *T. schlegelii* are closely related, but are not as closely related to another crocodilian grouping of *Cr. porosus*, *Cr. niloticus*, and *Cr. acutus*.



Supplementary Figure 4. Taken from (Watanabe & Slice, 2014) detailing the size analysis this study aims to recreate. One of the PCA traits of the skulls plotted against an overall size metric of each animal to determine significance in growth patterns amongst the species. Based on the similarity of slopes among the taxa the authors determined that ontogeny was less of a contributor to morphological differences and rather it was phylogenetic components that drove the variation from the PCA analysis. They were also able to draw the conclusion that while juvenile skull shape varied between taxa, as adults the shapes were more similar.



Ginglymostoma cirratum



Heterodontus francisci



Isurus oxyrinchus



Negaprion brevirostris



Rhizoprionodon terraenovae



Sphyrna tiburo



Squalus acanthias

Supplementary Figure 5. Images of smallest and largest specimen for each of the nine species. Total length is denoted in the bottom left corner of each image.

CIRRICULUM VITAE

Mary Caroline Regan

Education

Wake Forest University, Winston-Salem, NC, May 2019

Master of Science in Biology

Thesis Topic: Tails of the Sea: Morphological Scaling and Ontogeny of Shark Caudal Fins

Wake Forest University, Winston-Salem, NC, May 2017

Bachelor of Science in Biology, Minor in Chemistry

Research Interests

- Biomechanics of shark tails and corresponding migration patterns
- Evaluating reef health based on shark population and presence
- Ecological importance of shark habitats and threats to those habitats

Research Experience

Masters Thesis Research, Department of Biology, Wake Forest University, Fall 2017 – Present

Research Advisor: Dr. Miriam Ashley-Ross

Graduate Summer Research, Friday Harbor Labs, University of Washington, Summer 2018

Research Advisors: Dr. Adam Summers and Dr. Alice Gibb

- Participated in the Fish Biomechanics course
- Compiled and analyzed data on flatfish skin resistance to tearing

Student Researcher, Department of Biology, Wake Forest University, Fall 2015 – May 2017

Research Advisor: Dr. T. Michael Anderson

- Assisted PhD students in data collection of soil sample analysis
- Compiled data on soil samples for NutNet international data collection project

Student Researcher, Marine Research Facility, Woods Hole Oceanographic Institute, Fall 2016

Research Advisor: Dr. Simon Thorrold

- Performed Stable Isotope Analysis of samples collected in Northeast and Northwest Atlantic Ocean
- Analyzed similarities and differences between isotopic values of samples to create population estimates of benthic marine fish

Field Experience

Friday Harbor, WA – Participated in Fish Biomechanics course, which requires several trawls, seines and miscellaneous fishing trips

Belize - Two weeks diving and snorkeling on reefs performing fish and coral surveys

Tampa Bay - Competed and won a fishing species tournament, collected shark tail data

Cape Cod, MA - Spent a day on WHOI research vessel R/V Tioga collecting chemical and biological ocean data

Australia - Visited the various ecosystems in Australia including the Great Barrier Reef

Teaching Experience

Teaching Assistant, Department of Biology, Wake Forest University, Fall 2017 – Spring 2019

- Teach 30 students each semester in Bio 114 Comparative Physiology laboratory exercises
- Prepare weekly lectures of basic comparative physiology topics
- Lead students through experiments
- Grade lab reports, quizzes, and presentations students give several times during the semester

Undergraduate Teaching Assistant, Department of Biology, Wake Forest University, Spring 2017

- Assist main teaching professor with weekly class preparation and grading of Ecology and Conservation Biology of Coral Reefs
- Traveled with and assisted students during week long lab component to Lighthouse Reef, Belize

Presentations

- *Comparison of shear forces in flatfish skin of the Pacific Northwest* Research In Progress Seminar, Wake Forest University 2018
- *Comparison of shear forces in flatfish skin of the Pacific Northwest* Poster Presentation, Society for Integrative and Comparative Biology, 2019

Funding Awards

Vecellio Grant – Wake Forest University, 2018 & 2019

- \$1500 grant to support travel costs for research

Friday Harbor Labs Funding – FHL University of Washington, 2018

- \$2000 toward supporting cost of the 2018 Fish Biomechanics Summer course

Cocke Travel Fund – Wake Forest University, 2019

- \$500 toward traveling to Society for Integrative and Comparative Biology conference

Societies

Society for Integrative and Comparative Biology, 2019