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# Scaling and Ecological Relationships in the Visual Ecology of Sharks

Brianna Hall

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SCALING AND ECOLOGICAL RELATIONSHIPS IN THE VISUAL ECOLOGY OF  
SHARKS

by

BRIANNA E. HALL

(Under the Direction of Christine N. Bedore)

ABSTRACT

Adaptations of visual systems, such as acuity, sensitivity, and eye size can be used to infer the relative importance of vision to an organism. The high metabolic cost of visual system development and maintenance suggests that large relative eye size (as it relates to body length) may have a significant ecological or evolutionary role. Elasmobranchs are morphologically diverse and inhabit a wide range of marine and freshwater niches. As energetic and ecological demands shift over time, several species occupy different predatory niches across their lifetime, yielding a large array of visual habitats. Additionally, eye size changes with body length allometrically, thus elasmobranchs represent an ideal group for examining scaling relationships (i.e., eye growth rate and eye size at a given body length) with respect to specific ecological lifestyle traits. Here I quantified the relationship of eye size and body length in 19 shark species and, after accounting for phylogeny, compared this scaling across species that differ in ecological traits (i.e., activity level, habitat type, habitat complexity, and diet). Relative eye size at a given size varied across species and habitat type, but not activity level, habitat complexity, or diet, all of which had a strong phylogenetic signal ( $\lambda = >0.9$ ). Deep-sea species had the largest relative eye size, followed by oceanic and coastal species which did not differ from each other. In contrast, the rate at which eye size scaled with body length was the same across all species and did not differ with ecological lifestyle trait. These results suggest that habitat type may

influence relative eye size and not the rate at which eye size scales with body length. As habitat type had the greatest influence on relative eye size, future investigations should focus on ecological lifestyle traits involving visual habitat characteristics such as light level, turbidity, and migratory patterns.

INDEX WORDS: Allometry, Visual ecology, Elasmobranchs, Eye size, Visual adaptations

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BRIANNA E. HALL

B.S., University of North Carolina Wilmington, 2013

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## CHAPTER 1

### BACKGROUND

An animal's *umwelt*, described by Jakob von Uexküll (1909), is the sum of all the information being received and transmitted by that organism's central nervous system. The *umwelt* is dependent upon the sensory modalities that an individual possesses and creates a unique sensory world that leads to differences in the way each organism interacts with its environment (Dangles et al. 2009). Interpreting environmental information is critically linked to an organism's ability to survive (i.e., locate food and suitable habitat and aid in predator avoidance) and reproduce. Understanding how sensory modalities are utilized by different species can give valuable insight into their behavior, ecology, and physiology (Phelps 2007).

Vision is a sensory modality present in nearly all animal taxa. Image forming eyes evolved from primitive eye spots and they utilize receptor cells to capture light and resolve it into images (Frentiu & Briscoe 2008). Of the ten different optical eye types found throughout the animal kingdom, vertebrates possess only one, the camera eye (Cronin et al. 2014). The modern vertebrate eye (Figure 1) contains optical components such as a lens, cornea, iris, and a mobile pupil, which collectively allow it to function in a camera-like fashion, therefore, enabling light and depth perception, image formation, and color discrimination (Lamb et al. 2007).

Visual capabilities have been of interest to scientists for decades. Well established reviews of the structure and function of eyes are found throughout the literature. One of the earliest works is on the evolution and radiation of the vertebrate eye (Walls 1942). This was the first work to describe specialized cone photoreceptors in the vertebrate eye as well as discuss the similarities of photoreceptors in vertebrate eyes. Another book compares the

structure and function of all eye types found in the animal kingdom with a focus on evolution and taxonomic distribution, and the role eye type plays in behavior and ecology (Land & Nilsson 2002). Finally, a more recent comprehensive review on vision and visual ecology comes from Cronin et al. (2014) focusing on the way eyes and photoreceptors become specialized for a variety of visual tasks such as communication, predator avoidance, mate selection, and navigation. Through these works and subsequent research, it has become widely accepted that eyes are adapted to an organism's environment and ecological lifestyle (Land & Nilsson 2002; Cronin et al. 2014).

Eye size varies considerably throughout the animal kingdom, from the 10-inch eyes of the giant squid (*Architeuthis* and *Mesonychoteuthis* spp.) (Nilsson et al. 2012), to the degenerate eyes of the blind cavefish (*Amblyopsis* spp.) (Krishnan & Rohner 2017). Eye size, both relative (as it relates to body size) and absolute, can be indicative of the importance of vision to an organism because they are metabolically costly. Therefore, an organism is not likely to waste energy developing large eyes if vision does not play a key role in the fitness of the organism (Cronin et al. 2014). Additionally, both acuity (the ability of an organism to discern spatial detail in objects) and sensitivity (the amount of light necessary for image formation) are positively correlated with eye size (Land & Nilsson 2002; Cronin et al. 2014), thus a larger eye means possibly greater sensitivity or greater acuity.

Sensitivity increases with increasing eye size because they possess a larger retina, which increases the area for photoreceptors, allowing for the production of larger images, and a larger pupil aperture, which increases the number of photons able to enter the eye (Walls 1942; Hughes 1977; Land and Nilsson 2002; Howland et al. 2004). Acuity differs greatly across species; varying by over four orders of magnitude (Land & Nilsson 2002). One factor

that dictates this variation is the angular width of the region that is viewed by each photoreceptor and is largely dictated by focal length, or the distance from the geometric center of the lens to the retina (Hueter 1980) (Figure 2). The angular width is equal to the diameter of the photoreceptor divided by the focal length of the eye (Lisney & Collin 2008). Therefore, a longer focal length, achieved with a larger eye, yields a smaller angular resolution resulting in sharper acuity (Land & Fernald 1992) (Figure 2). However, there are limitations to larger eyes. For centuries it has been understood that brain to body size allometry is considerably varied across vertebrates and is typically explained by physiological scaling and developmental constraints as it is amongst the costliest tissues in the vertebrate body (Niven & Laughlin 2008; Tsuboi et al. 2018). The retina, formed by an outpouching of the brain (Kuzawa et al. 2014), is an extension of the brain, thus eye size should also be energetically costly and follow these similar constraints (Corral-Lopez et al. 2017).

As previously mentioned, these adaptations are driven by the environment and ecological lifestyle of an organism (Cronin et al. 2014). Ecological factors that influence eye size include habitat type, where organisms that live in well illuminated environments (i.e. shallow clear water or terrestrial environments) display the evolutionary trend of possessing large eyes, both relatively and absolutely, and have higher acuity (Land & Nilsson, 2002; Warrant 2004, Caves et al. 2017). Alternatively, in light limited environments, visually oriented organisms will sacrifice acuity to increase sensitivity by either increasing the number of photoreceptors or having larger photoreceptors to capture as many photons as possible (Land & Nilsson 2002; Stöckl et al. 2017). Think of a picture with large spread out pixels (high sensitivity) versus many small, densely packed pixels in a crisp picture (high acuity). In addition to light availability, spatially complex habitats require the ability to navigate and

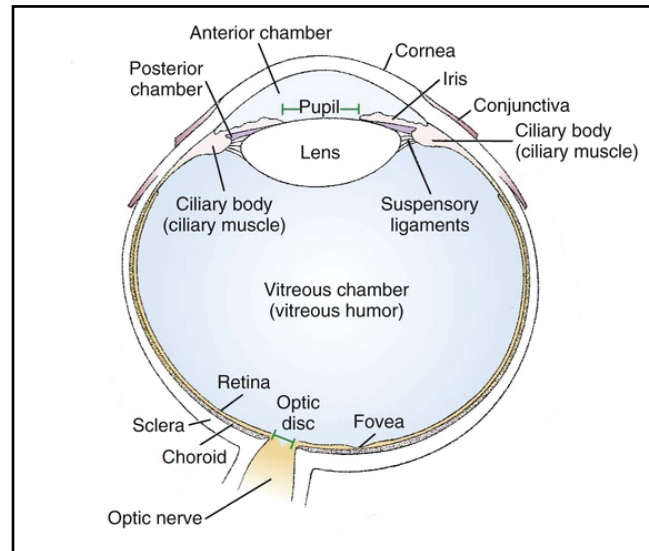
identify objects (Hughes 1977; Caves et al. 2017), therefore, it is thought that habitat complexity may also drive visual adaptations. One study found that African cichlids in rocky (more complex) substrates have greater visual acuity than cichlids living in sandy (less complex) substrates (Dobberfuhl et al. 2005). Additionally, teleosts (bony fishes) in complex environments have significantly greater acuity and eye size than those in horizon dominated habitats (Caves et al. 2017).

Activity level can also influence visual adaptations. Leukart's law states that faster animals require larger eyes and consequently better visual acuity to avoid colliding with obstacles in their trajectory and track prey (Walls 1942; Hughes 1977; Brooke et al. 1999; Heard-Booth & Kirk 2012). Studies have found that avian eye size scaled positively with flight speed (Brooke et al. 1999) and that faster moving mammals have larger eyes than their smaller counterparts (Heard-Booth & Kirk 2012). Similarly, diet may affect eye size because predatory species may need higher acuity to localize swiftly moving prey such as those living in pelagic environments (Caves et al. 2017). Whereby active mammalian predators have significantly higher visual acuity than herbivores (Veilleux & Kirk 2014).

Most studies investigating eye size and ecological correlates focus primarily on mammals and birds, and to a lesser and more recent extent, reptiles and teleosts (Brooke et al. 1999; Howland et al. 2004; de Busserolles et al. 2013; Caves et al. 2017). Raptors and owls with larger bodies and eyes can resolve images from a farther distance than small bodied birds (Brooke et al. 1999). Primates and birds have the largest eyes of all vertebrates, followed by other mammals (such as rodents) and reptiles (Howland et al. 2004), however, eye size is widely variable in fishes presumably because of their variation in body morphology such as body elongation found in eels (Howland et al. 2004). However, when the eye size of species

within the Myctophidae family was investigated, all of which have a similar body shape, this variability in eye size was still present suggesting other factors of morphology or ecology are at play and more research into this variability needs to be done (de Busserolles et al. 2013).

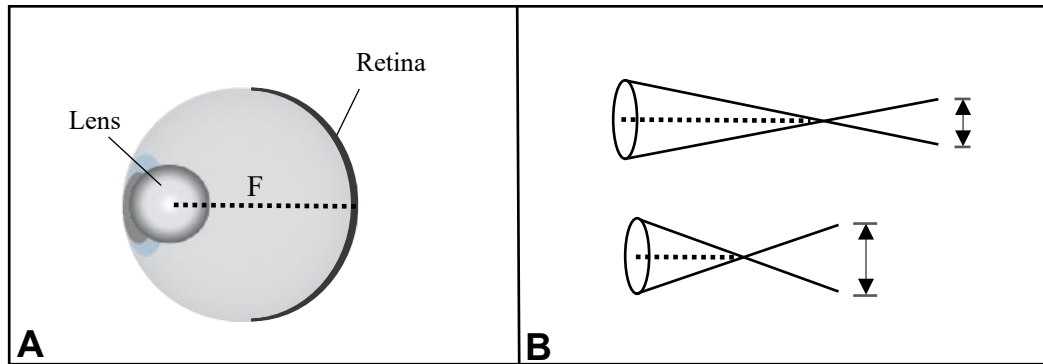
One such group that may help fill this gap are the elasmobranchs.



**Figure 1.** A schematic of a horizontal section through the vertebrate eye as viewed from above. Light passes through the cornea and enters the eye via the pupil which is expanded or contracted to regulate the number of photons entering. The light is focused by the lens, travels through the vitreous humor, and the image is received by the photoreceptors on the retina

(Walls, 1942.)





**Figure 2.** A partial schematic of the eye to demonstrate focal length (A). The focal length (F) is the distance from the geometric center of the lens to the retina (Hueter, 1980). Depicted in figure B, the longer the focal length, the smaller the angle of resolution; thus, producing a sharper image.

## CHAPTER 2

### INTRODUCTION

Elasmobranchs are a group of fishes with a long (>400 million year) evolutionary history that exhibits diverse ecological adaptations, including niche adaptations in habitats that differ widely in light level and spatial complexity (Ebert et al. 2013). To successfully occupy these diverse habitats, elasmobranchs require adaptations in eye morphology consistent with the visual parameters that define the habitat. For example, some elasmobranchs encompass the light limited deep sea, the monochromatic open ocean (pelagic) where light penetrates all around creating an ‘extended scene,’ and coastal habitats that serve as an intermediate between scotopic (dark) and photopic (bright) habitats due to light being readily available, but limited in brightness due to turbidity (suspended particles) from the close proximity to land that cause light to scatter (Warrant 2000). The aquatic environment offers unique challenges that has created a need for diversity in ecology and physiology within this group of organisms.

For example, pelagic species like the blue shark, *Prionace glauca*, live in a monochromatic and featureless habitat, and chase large, fast prey (Compagno 1999; Ebert et al. 2013). Alternatively, some benthic species, like the blacktip reef shark, *Carcharhinus melanopterus*, live in a colorful and complex reef habitat (Compagno 1999; Ebert et al. 2013). Therefore, an optical system adapted for detecting quick, silvery fish in the open ocean will be insufficient for visually discriminating conspecifics in a large school on a coral reef. No matter what the specific habitat features are, all species are challenged by optimizing visual physiologies that have opposing morphologies (Land 1981). For example, a large eye can increase both sensitivity and acuity, however physiological limitations of the photoreceptors prohibit increasing both sensitivity and acuity (Warrant 2004). For example, to increase acuity

the retina requires a greater density of photoreceptors to discern detail. However, a greater density of smaller detectors means fewer photons are absorbed by each photoreceptor. If fewer photoreceptors are receiving photons, then fewer changes in the level of light intensity can be detected; resulting in poorer contrast discrimination (i.e. less sensitivity) (Warrant 2004).

Although elasmobranchs have historically been considered to have poor vision and to rely on other senses, such as electroreception and olfaction, the discovery of a duplex retina in the lemon shark *Negaprion brevirostris* that contains both rod and cone photoreceptors suggests that vision may be more important than previously believed (Gruber et al. 1963).

However, little is known about the extent of which this sensory system is utilized by different species (Hart et al. 2006; Lisney et al. 2012). Due to their evolutionary history and diversity, elasmobranchs offer an opportunity to evaluate the pattern of eye size to body size relationship previously identified in other vertebrate phyla, such as larger eyes are found in predatory species that need to track fast moving prey or navigate complex environments (Hughes 1977; Brooke et al. 1999; Howland et al. 2004; Burton 2008). However, visual capabilities in an aquatic context are considerably lacking, primarily for large bodied predatory species such as elasmobranchs (Lisney et al. 2012).

While studies into the visual capabilities of elasmobranchs have increased in number over time, only one study thus far has attempted to compare relative eye size across elasmobranchs (Lisney & Collin 2007). In this study, larger eyes were attributed to habit and habitat such that active predators in oceanic environments tend to have the greatest relative eye size (Lisney & Collin 2007). However, these ecological correlates statistically considered. Therefore, the literature needs a more rigorous comparison of the relationship between eye size and body size in cartilaginous fishes and how it might be attributed to ecology or phylogeny under a quantitative

and statistical context. To investigate this allometric relationship, the rate at which the eye size scales with total length (slope) as well as eye size at a given total length (intercept) will be compared across species of elasmobranch. If differences are found, these coefficients will be statistically analyzed according to ecological variables.

This study seeks to quantitatively assess how the relationship of eye diameter to total body length varies across species of elasmobranchs and with respect to specific ecological traits. To address my objectives, I measured eye size in 19 species of shark. Then, using a Bayesian linear model, I quantified the diversity in the allometric parameters of eye size. This allowed me to determine if the rate at which eye diameter scales with body length (slope) and the eye size at a given body length (intercept) differs across species. I then used a phylogenetic Bayesian mixed effects models to investigate the relationship between the differences in slopes and intercepts among species in the context of their visual ecology and phylogeny. Specifically, do activity level, habitat type, habitat complexity, or diet explain the variation in eye size?

Historically slopes of allometric equations have been conserved throughout vertebrate species for many physiological traits such as eye size (Howland et al. 2004) and metabolic rate (Bigman et al. 2018). Therefore, it is hypothesized that the rate at which eye size scales with body size will be consistent across species. Conversely, because relative eye size is widely variable across teleosts (Howland et al. 2004; de Busserolles et al. 2013; Caves et al. 2017) and elasmobranchs (Lisney & Collin 2007), there will be differences in eye size at a given total length across species. These differences will be attributed to either activity level, habitat type, habitat complexity, or diet. Specifically, in accordance with previous studies, it is predicted that highly active species in oceanic or deepwater habitats (Brooke et al. 1999; Lisney & Collin 2007) with high mobility and cryptic prey (Veilleux & Kirk 2014), or species in spatially complex environments (Caves et al. 2017), will have the greatest relative eye size, but the rate at

which eye diameter scales with body length will be the same across species (Howland et al. 2004). It was found that slopes are consistent, but intercepts varied across species and that habitat type best explains this variation. This study is the first quantitative analysis comparing the allometric relationship to ecological traits within this group of species.

## CHAPTER 3

### METHODS

#### *Data collection*

Specimens were either acquired through museum collections (alcohol-fixed) or opportunistic sampling from bottom trawl, gillnet, longline, and drumline fishing (fresh or frozen). Total length (cm) and eye diameter (cm) measurements were recorded for all specimens. As little shrinkage is associated with storage of specimens in alcohol, both eye diameter and body length measurements can be taken from either fresh, frozen, or fixed specimens (Hueter 1980; Lisney & Collin 2007). To measure eye diameter, photographs were taken of one eye of each specimen following the protocol from Shütz and Shulze (2014). A portrait photograph in lateral view was taken for each specimen. For calibration, a ruler was used as a scale overlay. To ensure the overlay was fixed on a firm surface and in the same plane as the eye, the ruler was placed flat against the specimen's head directly adjacent to the eye. Photographs were accepted for analysis if all areas of the exposed eye (skin to skin) were free from obstruction and the photograph and scale overlay were at the appropriate angle (parallel to the eye). The maximum diameter of the eye along the horizontal axis (Figure 3) was measured in each photograph in ImageJ (NIH Institute, Bethesda, Maryland, USA).

#### *Estimation and comparison of species-specific regression coefficients*

Slopes and intercepts were estimated from Bayesian linear models on log-transformed data. Traditional allometric regressions on a logarithmic scale estimate the intercept at 1 cm total length, which falls well outside the size range of specimens measured in this study. To estimate a more meaningful intercept, the total length data was centered on the median body length for all specimens in the study (100 cm total length) therefore, the  $\log_{10}(100)$  cm was subtracted from all

individual total lengths for each species (Quinn & Keough 2002; Bigman et al. 2018). Data can be centered on any value, and thus the intercept represents the eye diameter at a given body length and will be referred to as the relative eye size or ‘standardized intercept.’ While slopes represent the rate at which eye diameter scales with total body length. Slopes and intercepts were compared across species using 95% Bayesian Credible Intervals.

### ***Comparison of coefficients across ecological traits***

Slopes and standardized intercepts of eye diameter allometries were compared across four ecological traits (activity level, habitat type, habitat complexity, and diet). These traits were assessed based on previous research focusing on differences in eye size based on ecological factors in various species as well as data availability. Categorical ecological traits were divided into three categories that were chosen based on well-established criteria in the literature and for their repeatability for future studies. Full descriptions of the ecological categories can be found in Table 1. Habitat type was categorized into coastal, oceanic, or deepwater using distribution maps and habitat characteristics from the IUCN red list, in concert with methods by Dulvy et al. (2014) and Bigman et al (2018). Habitat complexity was categorized into three broad spatial complexity categories: featureless, horizon-dominated, and complex habitats using habitat characteristics from the IUCN red list and defined following Caves et al. (2017). Diet of all recorded food items for each species was mined from *Sharks of the World* (Ebert et al. 2013) and Cortés (1999). Species were then allocated to diet categories modified from Raschi (1986) based on prey mobility and if prey exhibited crypsis, a means of camouflage. These categories were: (1) sessile or slightly motile, no cryptic prey; (2) Moderately motile, no cryptic prey; and (3) High motility, cryptic prey species. Species-specific assignments of ecological traits are found in Table 2.

### Phylogeny:

Using a modeling framework that accounts for the shared evolutionary history between species is a common way to avoid the inflated Type I error rates and biased regression coefficient estimates that would occur if evolutionary history went unaccounted for (Freckleton 2009, Revell 2010). To incorporate evolutionary history when assessing if slopes and standardized intercepts differ with respect to ecological lifestyle traits, a phylogenetic random effect was included in all ecological and life history trait models.

### Statistical analysis:

To estimate species-specific slopes and intercepts for the relationship of eye diameter as a function of total length, a single linear model was fit in a Bayesian framework following the R-language pseudo-code, “ $\log_{10}(\text{eye diameter}) \sim \log_{10}(\text{total length}) * \text{species}$ ”. The response variable was the  $\log_{10}$ -transformed eye diameter and the explanatory variables were the  $\log_{10}$ -transformed and centered total length (i.e., centered around 100 cm), species identity, and the interaction term of  $\log_{10}$ -transformed and centered total length and species. Including this interaction allowed for an estimation of standardized intercepts and slopes for each species. This model was fit in R v..3.5.1 using the *brm* function in the *brms* package (Burkner 2017, 2018; R Core Team 2019). The assumption that errors are independent and normally distributed with a mean of zero and constant variance was met. A Bayesian framework was used in favor of a traditional frequentist approach to allow for the estimation of the entire posterior distribution of each slope and intercept, which facilitates accurate comparison across species. Following recommendations for Bayesian linear models using the *brms* package, (<https://github.com/stan-dev/stan/wiki/Prior-Choice-Recommendations>), weakly informative regularizing priors were used. The *get\_prior* function in *brms* was used to identify the best priors for the model (Burkner



2017, 2018). The prior for all species-specific slopes, standardized intercepts, and the residual error of the model, was set to a “student-t” distribution, with three degrees of freedom, a location (i.e., mean) of zero, and a scale of ten. Finally, the species-specific coefficients were considered significantly different if the 95% Bayesian Credible Intervals (BCI) did not overlap.

To assess whether slopes and standardized intercepts differed with respect to ecological lifestyle traits, Bayesian mixed-effects models were performed using the *brm* function in the *brms* package (Burkner 2017, 2018). Separate models for each trait were performed using R language pseudo-code, “ $\log_{10}(\text{eye diameter}) \sim \log_{10}(\text{total length}) * \text{ecological lifestyle trait} + (\text{total length} | \text{species}) + (1 | \text{phylo})$ ”, where the response variable was the  $\log_{10}$ -transformed eye diameter and the explanatory variables were the fixed effects of  $\log_{10}$ -transformed, centered total length, the ecological lifestyle trait, and the interaction between the two (termed, ‘ecological trait models’). The random effect of “(total length | species)” allowed for a separate slope and standardized intercept to be estimated for each species. Additionally, a random effect of phylogeny, “(1|phylo),” was included to account for the shared evolutionary history between species. A phylogeny was created by pruning a larger 610 species molecular tree (Stein et al. 2018) to the desired taxon set (Figure 4). The inclusion of the phylogenetic random effect allows for the estimation of the phylogenetic signal, Pagel’s lambda, which is a measure of the correlation in traits due to their shared phylogenetic history under a Brownian model of evolution (Pagel 1999). The value of Pagel’s lambda is between zero and one, with zero meaning no phylogenetic signal in the residuals of the response variable (in this case, eye diameter), and one meaning that the residuals of the response variable perfectly match the correlation expected under Brownian motion (Pagel 1999; Freckleton et al. 2002; Caves et al. 2017). Pagel’s lambda was chosen, as opposed to other metrics to measure and test phylogenetic signal such as

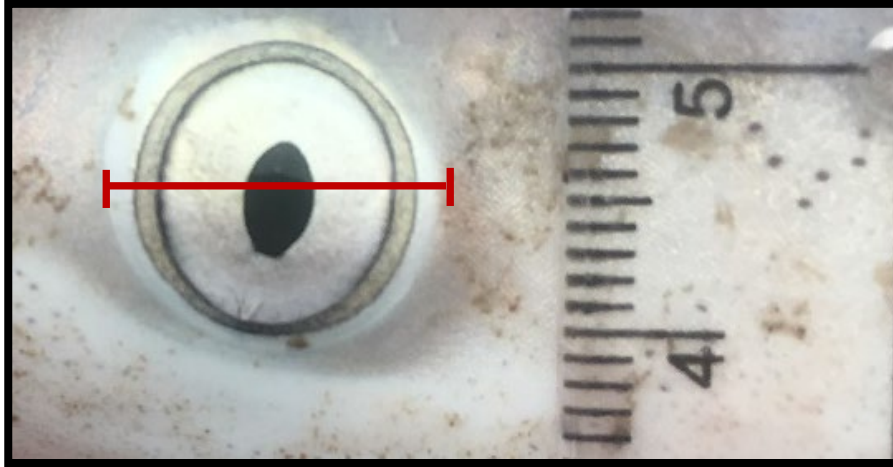
Blomberg et al.'s  $K$ , because studies have shown the strong robustness of Pagel's lambda when used in studies involving either incompletely resolved phylogenies or suboptimal branch-length information. Whereas Blomberg et al.'s  $K$  led to inflated estimates of phylogenetic signal (Molina-Venegas & Rodriguez 2017). Additionally, Brownian motion was used in favor of other models, such as the Ornstein Uhlenbeck model, because studies have shown that phylogenies containing more than 200 tips are necessary to obtain acceptable Type I error rates, which this data set does not possess (Cooper et al. 2016). Coefficients of each trait were significantly different from each other if their 95% BCI did not cross zero.

**Table 1.** Description of ecological categories used in analyses.

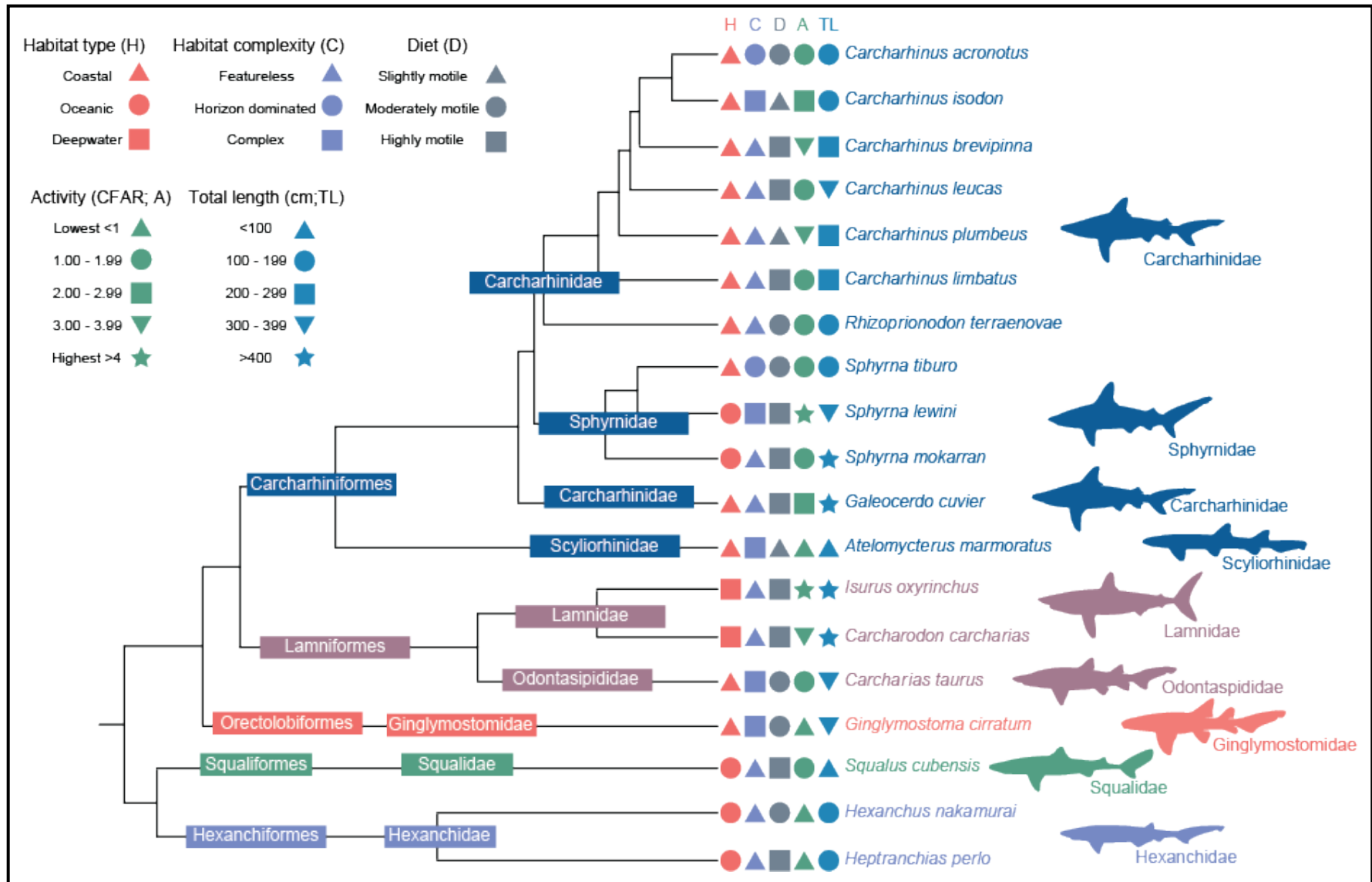
<b>Category</b>	<b>Details</b>
<b><i>Habitat Type</i></b>	
Coastal and Continental Shelf	Benthic, benthopelagic, or pelagic, found along the continental shelf from the intertidal zone to 200 m depth
Oceanic	Pelagic species that are found generally in depth less than 200 m above continental slope and plain
Deepwater	Benthic and benthopelagic species found along the continental slope at depths typically greater than 200 m
<b><i>Habitat Complexity</i></b>	
Featureless	Pelagic habitats, or any species living in the below the photic zone (> 200m depth)
Horizon-dominated	Benthic or benthopelagic within the photic zone (< 200m depth)
Complex	Reef-associated, mangroves, rocky shorelines, and crevices
<b><i>Diet Mobility</i></b>	
(1) Sessile or slightly motile	Small, low activity teleosts, crustaceans, mollusks, and bottom dwelling invertebrates
(2) Moderately motile	Active, large teleosts, rays and other small elasmobranchs
(3) Highly motile	Pelagic fish, cryptic cephalopods, and marine mammals

**Table 2.** Species-specific ecological trait categories for 19 shark species. Habitat type was categorized using distribution maps and habitat characteristics from the IUCN red list, in concert with methods by Dulvy et al. (2014) and Bigman et al (2018). Habitat complexity was categorized into three broad spatial complexity categories using habitat characteristics from the IUCN red list and defined following Caves et al. (2017). Diet of all recorded food items for each species was mined from *Sharks of the World* (Ebert et al. 2013) and Cortés (1999). Diet categories were modified from Raschi (1986) based on prey mobility and if prey exhibited crypsis.

Order	Family	Species	Activity Level	Habitat Type	Habitat Complexity	Diet	Maximum Total Length (cm)	
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus acronotus</i>	1.56	coastal	horizon dominated	2	137.0	
		<i>Carcharhinus brevipinna</i>	3.00	coastal	featureless	3	278.0	
		<i>Carcharhinus isodon</i>	2.53	coastal	complex	1	194.5	
		<i>Carcharhinus leucas</i>	1.31	coastal	featureless	3	340.0	
		<i>Carcharhinus limbatus</i>	1.38	coastal	featureless	3	255.0	
		<i>Carcharhinus plumbeus</i>	3.19	coastal	featureless	1	240.0	
		<i>Galeocerdo cuvier</i>	2.05	coastal	featureless	3	550.0	
		<i>Rhizoprionodon terraenovae</i>	1.79	coastal	featureless	2	110.0	
		Scyliorhinidae	<i>Atelomycterus marmoratus</i>	0.32	coastal	complex	1	70.0
		Sphyrnidae	<i>Sphyrna lewini</i>	4.58	oceanic	complex	3	395.0
<i>Sphyrna mokarran</i>	1.52		oceanic	featureless	3	580.0		
		<i>Sphyrna tiburo</i>	1.96	coastal	horizon dominated	2	150.0	
Hexanchiformes	Hexanchidae	<i>Heptanchias perlo</i>	0.86	deepwater	featureless	3	139.0	
		<i>Hexanchus nakamurai</i>	0.84	deepwater	featureless	2	180.0	
Lamniformes	Lamnidae	<i>Carcharodon carcharias</i>	3.68	oceanic	featureless	3	600.0	
		<i>Isurus oxyrinchus</i>	4.06	oceanic	featureless	3	400.0	
		Odontaspidae	<i>Carcharias taurus</i>	1.14	coastal	complex	2	320.0
Orectolobiformes	Ginglymostomatidae	<i>Ginglymostoma cirratum</i>	0.89	coastal	complex	2	300.0	
Squaliformes	Squalidae	<i>Squalus cubensis</i>	1.87	deepwater	featureless	3	92.5	



**Figure 3.** An example photograph used for analysis. The eye is clearly visible, and the ruler is directly against the specimen vertical and adjacent to the eye. Images will be uploaded to ImageJ where eye horizontal diameter will be measured.



**Figure 4.** A phylogenetic tree of 19 shark species spanning five orders and eight families and a distribution of (H) habitat type, (C) habitat complexity, (D) diet, (A) activity, and (TL) total length (cm). The tree was pruned from a molecular tree of 610 Chondrichthyes (Stein et al. 2017).

## CHAPTER 4

## RESULTS

***Data collection***

Morphometrics, including body total length and eye diameter (cm), were collected from approximately 570 individuals. Of these, 478 individuals spanning five orders, eight families, and 19 species of shark met the minimum *a priori* requirements and were included in analyses.

***Estimation and comparison of species-specific regression coefficients***

The relationship of eye diameter (cm) to total body length (cm) varied significantly across species (Figure 5). The standardized intercepts (eye size at 100 cm total length) varied significantly and ranged from 1.008 cm in the nurse shark *Ginglymostoma cirratum* to 4.029 cm in the Cuban dogfish *Squalus cubensis*, with a mean and standard error of  $1.976 \pm 0.2$  cm (Table 3, Figure 6).

Slopes were mostly conserved across species. The slopes of eye diameter allometries ranged from 0.41 in the tiger shark *Galeocerdo cuvier* to 1.01 in the bigeye sixgill shark *Hexanchus nakamurai* with a mean and standard error of  $0.62 \pm 0.03$  (Table 3, Figure 6). Most species only differed from the two species with the shallowest and steepest slope. Consequently, these two species are the only species that have slopes that are significantly different from more than 5 other species at 13 and 14 species respectively.

***Comparison of coefficients across ecological traits***

Slopes and standardized intercepts did not vary with respect to activity level (Table 4), habitat complexity (Table 6), or diet (Table 7). For habitat type, the slopes did not differ significantly, however, the standardized intercepts of deepwater species significantly differed from coastal and oceanic species, which were not different from each other. Specifically,

deepwater species had significantly larger eyes at 100 cm total length (0.42) than oceanic and coastal species at 100 cm total length (Table 5).



**Table 3.** Estimates of intercept (a) and slope (b) of eye diameter allometric regressions for 19 shark species. The 95% Bayesian Credible Interval (BCI) is reported for intercepts (BCI a) and slopes (BCI b). Coefficients were re-estimated from log 10-transformed eye diameter and log10-transformed and centered total length data. Intercepts are back-transformed and represent eye diameter (cm) at 100 cm total length.

Order	Family	Species	N	Range TL (cm)	a	b	BCI a (95%)	BCI b (95%)
Carcharhiniformes	Carcharhinidae	<i>Carcharhinus acronotus</i>	23	39.1 - 130.8	1.6926	0.58	1.6164 - 1.7710	0.48 - 0.67
		<i>Carcharhinus brevipinna</i>	6	51.6 - 222	1.5007	0.47	1.3962 - 1.6117	0.35 - 0.58
		<i>Carcharhinus isodon</i>	45	52.8 - 143.2	1.4169	0.61	1.3681 - 1.4673	0.53 - 0.70
		<i>Carcharhinus leucas</i>	12	69.4 - 280	1.1976	0.42	1.1377 - 1.2598	0.30 - 0.54
		<i>Carcharhinus limbatus</i>	56	55.3 - 163	1.5014	0.61	1.4574 - 1.5462	0.53 - 0.69
		<i>Carcharhinus plumbeus</i>	31	53.2 - 212.5	1.6492	0.51	1.5897 - 1.7110	0.43 - 0.60
		<i>Galeocerdo cuvier</i>	24	63.4 - 384	2.3391	0.41	2.2261 - 2.4564	0.35 - 0.46
		<i>Rhizoprionodon terraenovae</i>	72	24.9 - 98.4	1.9013	0.67	1.8002 - 2.0054	0.61 - 0.73
	Scyliorhinidae	<i>Atelomycterus marmoratus</i>	14	16.5 - 48.5	2.0895	0.77	1.7528 - 2.4681	0.64 - 0.90
	Sphyrnidae	<i>Sphyrna lewini</i>	41	24 - 308	1.8440	0.61	1.7832 - 1.9066	0.57 - 0.65
<i>Sphyrna mokarran</i>		9	47.5 - 305	1.7628	0.62	1.6533 - 1.8775	0.53 - 0.71	
<i>Sphyrna tiburo</i>		49	25 - 113	1.4845	0.61	1.4356 - 1.5345	0.55 - 0.66	
Hexanchiformes	Hexanchidae	<i>Heptranchias perlo</i>	16	56.5 - 123.2	3.4564	0.68	3.2697 - 3.6520	0.47 - 0.90
		<i>Hexanchus nakamurai</i>	7	62 - 141.8	3.7205	1.01	3.4380 - 4.0195	0.75 - 1.27
Lamniformes	Lamnidae	<i>Carcharodon carcharias</i>	27	157 - 472.4	1.6397	0.59	1.4984 - 1.7903	0.51 - 0.67
		<i>Isurus oxyrinchus</i>	9	71.8 - 350.5	2.0916	0.53	1.9507 - 2.2395	0.40 - 0.66
	Odontaspidae	<i>Carcharias taurus</i>	19	43.2 - 248	1.2102	0.60	1.1614 - 1.2604	0.49 - 0.71
Orectolobiformes	Ginglymostomatidae	<i>Ginglymostoma cirratum</i>	8	47.1 - 182	1.0083	0.73	0.9470 - 1.0724	0.62 - 0.84
Squaliformes	Squalidae	<i>Squalus cubensis</i>	10	40 - 62	4.0287	0.78	3.0805 - 5.1801	0.41 - 1.15

**Table 4.** Mean coefficients and 95% Bayesian Credible Intervals (BCI) of the Bayesian mixed-effects model that assessed if the slopes or intercepts of the allometry of eye size (eye diameter) and body size (total length) differed with respect to activity level (as measured by caudal fin aspect ratio).

<b>Coefficient</b>	<b>Estimates (95% BCI)</b>
intercept	0.31 (0.13 – 0.50)
slope	0.71 (0.54 – 0.88)
effect of activity level on intercept	0.02 (-0.02 – 0.06)
effect of activity level on slope	-0.01 (-0.05 – 0.03)
Pagel's lambda	0.96 (0.92 - 0.98)

**Table 5.** Mean coefficients and 95% Bayesian Credible Intervals (BCI) of the Bayesian mixed-effects model that assessed if the slopes or intercepts of the allometry of eye size (eye diameter) and body size (total length) differed with respect to habitat type.

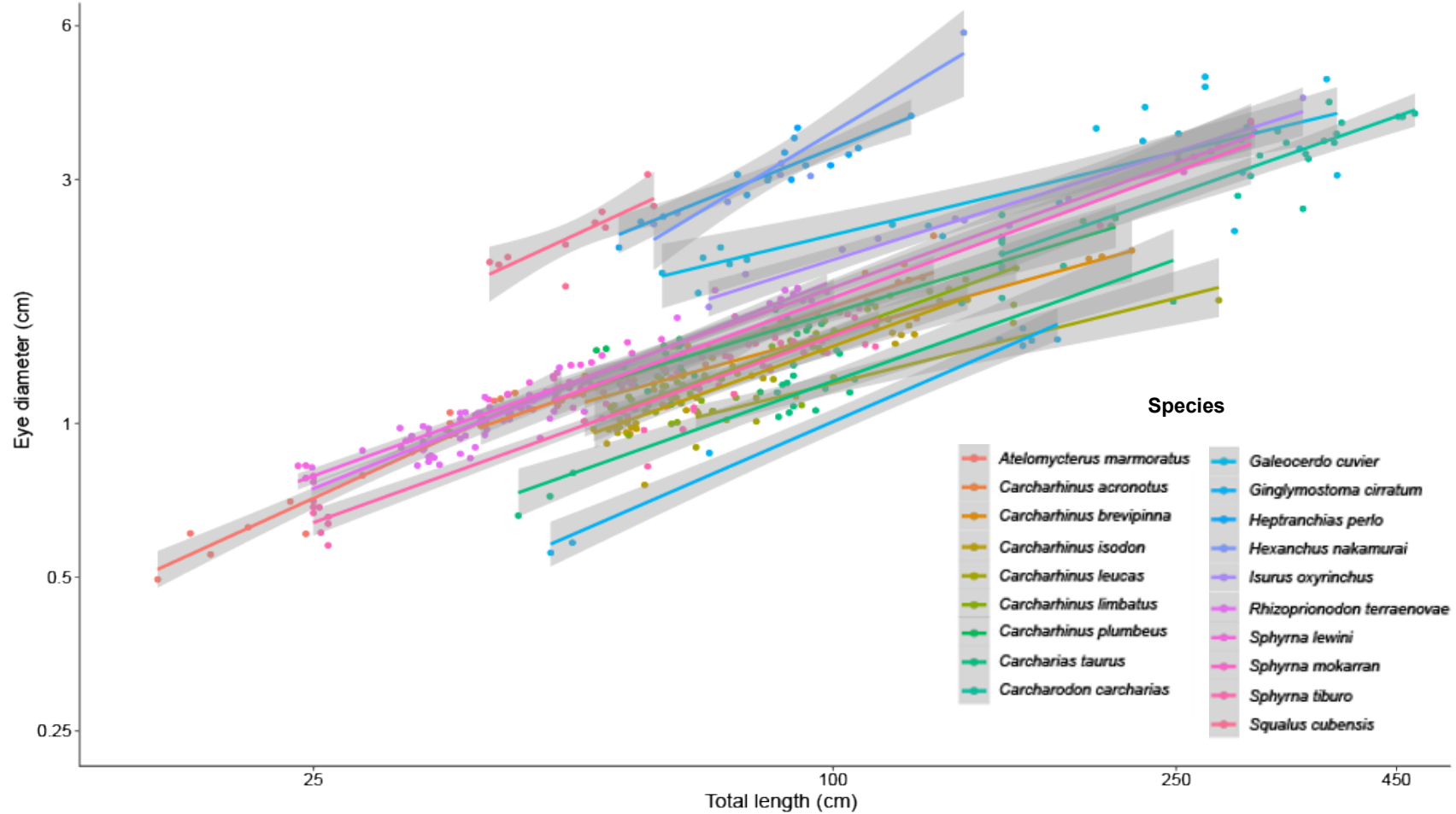
<b>Coefficient</b>	<b>Estimates (95% BCI)</b>
coastal intercept	0.15 (-0.03 – 0.34)
coastal slope	0.63 (0.44 – 0.82)
intercept difference for deepwater	<b>0.42 (0.14 – 0.70)</b>
intercept difference for oceanic	0.08 (-0.03 – 0.19)
slope difference for deepwater	0.18 (-0.14 – 0.50)
slope difference for oceanic	0.01 (-0.11 – 0.13)
Pagel's lambda	0.93 (0.88 – 0.97)

**Table 6.** Mean coefficients and 95% Bayesian Credible Intervals (BCI) of the Bayesian mixed-effects model that assessed if the slopes or intercepts of the allometry of eye size (eye diameter) and body size (total length) differed with respect to habitat complexity.

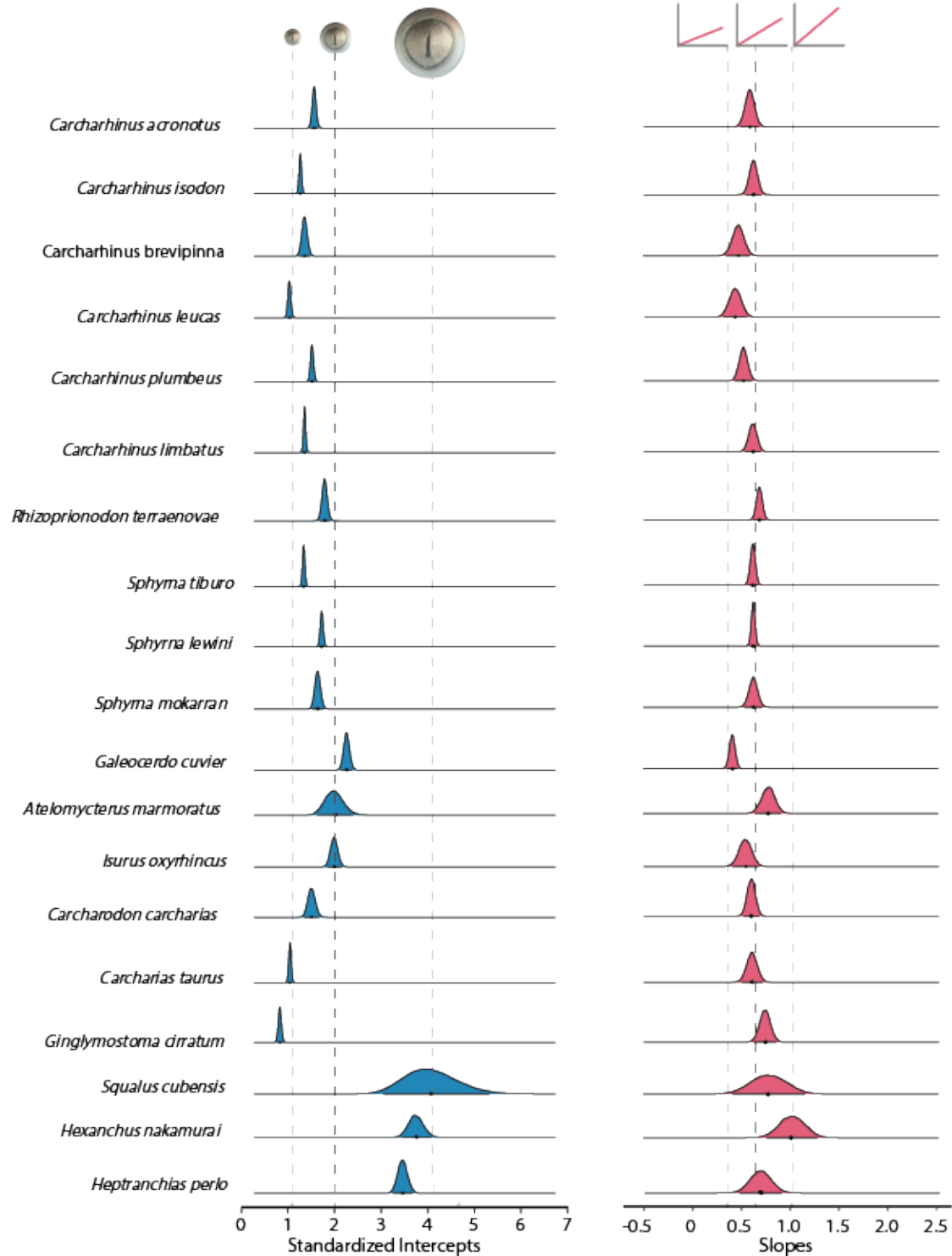
<b>Coefficient</b>	<b>Estimates (95% BCI)</b>
complex intercept	0.30 (0.11 – 0.50)
complex slope	0.73 (0.56 – 0.91)
intercept difference for featureless	0.06 (-0.06 – 0.17)
intercept difference for horizon-dominated	0.04 (-0.09 – 0.16)
slope difference for featureless	-0.07 (-0.18 – 0.03)
slope difference for horizon-dominated	-0.02 (-0.14 – 0.10)
Pagel's lambda	0.96 (0.92 – 0.98)

**Table 7.** Mean coefficients and 95% Bayesian Credible Intervals (BCI) of the Bayesian mixed-effects model that assessed if the slopes or intercepts of the allometry of eye size (eye diameter) and body size (total length) differed with respect to diet.

<b>Coefficient</b>	<b>Estimates (95% BCI)</b>
diet 1 intercept	0.33 (0.12 – 0.54)
diet 1 slope	0.72 (0.55 – 0.91)
intercept difference for diet 2	0.01 (-0.13 – 0.13)
intercept difference for diet 3	0.02 (-0.10 – 0.15)
slope difference for diet 2	0.00 (-0.12 – 0.12)
slope difference for diet 3	-0.08 (-0.20 – 0.04)
Pagel's lambda	0.96 (0.93 – 0.98)



**Figure 5.** The relationship of eye diameter (cm) and total body length (cm) for 19 species of shark. The fitted regression lines are from a linear model of log<sub>10</sub>-transformed eye diameter as a function of log<sub>10</sub>-transformed total body length for each species. The shaded grey region indicates the 95% confidence interval.



**Figure 6.** The posterior distribution of standardized intercepts and slopes for the allometry of eye diameter (cm) to total body length (cm) for 19 species of shark. Coefficients were considered variable and significantly different if the 95% Bayesian Credible Intervals did not overlap with other species. The dashed lines represent the minimum, median, and maximum standardized intercepts and slopes.

## CHAPTER 5

### DISCUSSION

#### Scaling of eye size

The quantitative assessment of how eye size varies across species and with respect to ecological and life history traits requires a thorough understanding of how eye size scales ontogenetically with body growth, or the allometry of eye diameter (Hughes 1977; Howland et al. 2004). For many species, eye size has not been examined for a broad enough size range of individuals to use an *ontogenetic* allometric approach (e.g. eye size at many size ranges within a species), therefore, a *static* allometric approach is taken (e.g. one value per species typically from the same life stage) (Lisney & Collin 2007; de Busserolles et al. 2013; Caves et al. 2017). This gives only an estimate of relative eye size compared to other species. However, for studies involving metabolic rate and gill surface area (both traits that also scale ontogenetically) that have a sufficient size range of individuals for those species, it is standard practice to estimate and report the regression equation for the ontogenetic scaling relationship (Bigman et al. 2018). As this study had a broad enough size range of individuals for each species, this ontogenetic allometric method was applied as opposed to static allometric methods. Thus, each species was plotted as their own linear regression and a species-specific intercept and slope was calculated for each species. This allows for both an understanding of the relative eye size, or eye size at a given total length, and the *rate* at which eye size scales with total body length. Thus, eye investment can be compared in not only traditional relative terms, but also in terms of investment of growth throughout the species' lifetime (Gould 1966).

For sharks in this study, relative eye size (e.g. eye diameter at 100 cm total length) was significantly different across species. As predicted, this variation in relative eye size was



explained by both ecology and phylogeny. Alternatively, the slopes of the allometric regressions, or the rate at which eye diameter scaled with total body length, were consistent across species and demonstrated hypoallometric scaling ( $<1$ ) except for the bigeye sixgill *Hexanchus nakamurai* which was isometric (slope = 1). This means that the eye diameter of all species, except for the bigeye sixgill, grew at a slower rate than predicted or that the total length is growing at a rate faster than predicted. For the bigeye sixgill, a slope of one means that the eye diameter grew at the same rate as its total body length. However, this result should be interpreted with caution because of the low sample size ( $n=7$ ) compared to other species that may have led to an overestimation of the slope and possibly intercept as can be seen in the wideness of the posterior distribution. Physiological traits exhibiting isometric slopes are typically due to environmental stressors, such as a lack of oxygen that requires a higher gill surface area for oxygen uptake (Nilsson 2010; Bigman et al. 2018). However, all deepwater species experience similar environmental stressors with respect to vision. Additionally, despite differences in environmental conditions, slopes for physiological and morphological traits have been highly conserved throughout history (Howland et al. 2004; Bigman et al. 2018).

### **Scaling of eye size with activity**

Here, species-specific standardized intercepts (relative eye size) and slopes were compared across activity level. Activity level was estimated using caudal fin aspect ratio, which has served as proxy for activity level in fishes because it has been linked to metabolic rate (Killen et al. 2016; Bigman et al. 2018), swimming speed (Sambilay 1990; Fisher & Hogan 2007), and daily ration (Palomares & Pauly 1989)- all traits that are correlated with activity. While it is recognized that this method is not without faults (e.g., as sharks are indeterminate growers, there may be modest changes in tail shape with ontogeny), caudal fin aspect ratio is a

quantitative metric that allows for a more rigorous analysis as opposed to historically assigned categories such as ‘sluggish’ and ‘moderately active’ which were traditionally allocated based on a species’ perceived activity level and may not reflect the true range of activity for the species (Bigman et al. 2018).

With respect to activity level, there were no significant differences between species-specific standardized intercepts. This does not fit with the initial hypothesis and prediction that species with higher activity levels would have larger relative eye size, which was thought to be the case for species needing larger eyes for increased acuity to capture quickly moving prey or help with navigation (Brooke et al 1999; Veilleux & Kirk 2014). For example, species in the order Lamniformes tend to be high activity sharks like the white shark *Carcharodon carcharias* and the shortfin mako *Isurus oxyrinchus* of the family Lamnidae. These species had relative eye sizes of (mean 1.6 and 2.1cm, respectively), which were significantly larger than another Lamniform, the sand tiger shark *Carcharias taurus* in the family Odontaspidae (mean relative eye size 1.2cm). The sand tiger shark exhibits relatively low activity level and smaller eyes compared to both the white shark and shortfin mako. However, phylogeny explained most of the variation in eye size (Pagel’s  $\lambda = 0.96$ ).

### **Scaling of eye size with habitat type**

Standardized intercepts were significantly different with respect to habitat whereby deepwater species had larger eyes at 100 cm total length than coastal and oceanic species which did not differ from each other. I found that deepwater species had on average, approximately 2.2 times greater relative eye diameter than coastal and oceanic species. Upon closer inspection, it is not surprising that the only significant difference has been found to correlate with habitat.

Habitat, mostly associated with light availability, has often been correlated with eye morphology in many invertebrates and vertebrates (Land and Nilsson 2002; Cronin et al. 2014).

The species in this study with the largest eyes were all deepwater species that occur in the mesopelagic zone and to a lesser extent, the bathypelagic zone. Proximity to land and depth are both factors that cause considerable variation in the spectral composition of aquatic environments (Jerlov 1976). While short and long wavelengths are rapidly absorbed with depth, oceanic environments past the continental shelf tend to have some of the clearest aquatic habitats, allowing for light to penetrate to depths up to 1000 m (Jerlov 1976). Organisms in the mesopelagic zone typically have large eyes (Fritsches et al. 2003; Warrant and Locket, 2004; Lisney & Collin 2007), suggesting that vision is an important sense in this light-limited habitat. The adaptation towards large eyes within the mesopelagic zone is largely to improve sensitivity (Warrant 2000; Land and Nilsson 2002). Mesopelagic teleost fishes often have large numbers of rod photoreceptors and a reflective tapetum lucidum to aid in vision under dim light conditions (Locket 1977). While elasmobranchs are considerably less studied than teleosts in this regard, these adaptations have also been reported in elasmobranch eyes (Hart et al. 2006). Thus, it is not unexpected for elasmobranchs within this environment to also have relatively large eyes. It is important to note that there was a very strong phylogenetic signal ( $\lambda = 0.93$ ) within the category as well, so some of the variation being shown is partially explained by phylogenetic relatedness.

### **Scaling of eye size with habitat complexity**

Species were categorized into one of three habitat complexities (Table 2) and it was hypothesized that species living in a complex environment would have larger relative eye size due to increased needs for higher acuity for navigation tasks and object recognition (Hughes

1977; Caves et al. 2017). However, relative eye size and slopes did not differ across species with respect to habitat complexity. This result could be stemming from another visual characteristic of the habitat such as light availability. Pelagic environments that have light penetrating from all directions, is monochromatic (Warrant 2004), and is within the same featureless category as the mesopelagic deepwater species that are in a light limited environment with a ‘semi-extended’ scene (Warrant 2004) where the primary source of light is from downwelling light. Additionally, the high lambda value of 0.96 (Table 6) suggests that this is due to the phylogenetic relatedness of species. Interestingly, and conversely to this study, Caves et al. (2017) found that teleost species with greater acuity (and larger relative eye size) inhabited either complex or pelagic environments. This was attributed to pelagic species having absolutely larger bodies and eyes while species in complex environments had smaller absolute body size but had eyes that were relatively large. However, species in complex environments had acuity higher than expected lending support to the ‘terrain theory’ (Hughes 1977) where species in complex environments require higher acuity for navigation purposes. Perhaps this trend was not seen within this study because most elasmobranchs are generally larger bodied than their bony fish counterparts living within the same habitat complexity.

### **Scaling of eye size with diet**

Species were placed in one of three diet categories based on diet mobility and to a lesser extent, prey exhibiting crypsis. It was hypothesized that species with highly active or cryptic prey would have relatively larger eyes than species with lower motility or sessile prey while slopes remain consistent. This prediction was based on previous studies that have found predators with motile prey to have finer acuity and relatively larger eyes in mammals (Veilleux & Kirk 2014), insects (Land & Nilsson 2002) and elasmobranchs (Lisney & Collin 2007;

Litherland & Collin 2008). However, much like Caves et al. (2017) there was no significant difference between relative eye size and slopes according to diet. A lambda value of 0.96, again leads to the conclusion that phylogenetic relatedness is the cause for no variation. Alternatively, this may be because the diet categories were too broad and need more refinement for accurate comparison. Elasmobranch diets consist of a wide variety of foods (Cortes 1999) and some species have been known to have ontogenetic dietary shifts not accounted for in this study (Ebert et al. 2013). Another consideration that could explain the difference between these two studies is the use of alternative sensory systems found within elasmobranchs that ray-finned fishes do not have. Electroreception, a sensory system used to detect electric fields produced by other organisms, is found within the elasmobranch lineage (Carrier et al. 2004). Perhaps these species that eat cryptic prey are utilizing this sensory system more than vision and thus have relatively smaller eyes. Additionally, it is difficult to account for generalist or opportunist predators when utilizing these broad categories.

## **Conclusions**

This is the first examination to date that has studied the scaling relationship of eye size in elasmobranchs and that has quantitatively linked this relationship to ecological factors. There were significant differences among species for both relative eye size (the intercept of the allometry that represents the horizontal diameter of the exposed eye at 100 cm total length) and, to a lesser extent, allometric slopes (the rate at which the horizontal eye diameter increased with an increase in length). Furthermore, species with larger relative eye size were correlated with habitat in that deepwater species had eyes that were larger than oceanic or coastal species. This is unsurprising as previous work suggested that oceanic sharks that undergo diel vertical migrations and deep-sea sharks in the mesopelagic and, to a lesser extent, bathypelagic have relatively large

eyes (Lisney & Collin 2007) which partially aligns with the findings of this study. Additionally, this suggests that the slope of eye size to body size is conserved following the trend in previous studies of eye size to body size in vertebrates (Howland et al. 2004) and gill surface area and body size (Bigman et al. 2018). Variance for all other traits was better explained by phylogeny rather than ecology as most models were non-significant once phylogeny was corrected for.

Elasmobranchs demonstrate considerable variation in the interspecific organization and function of visual systems including relative eye size (Lisney & Collin 2007), pupillary shape and movement (Hart et al. 2006; Kajiura 2010; Lisney et al. 2012), retinal ganglion cell distribution (Peterson & Rowe, 1980; Lisney & Collin 2008), and rod-to-cone photoreceptor ratios (Hart et al. 2006). Despite the variation noted in previous literature, this study concludes that less variation exists in eye size than previously reported (Lisney & Collin 2007). Previous studies did not compare these ecological traits in a statistical nature and simply made broad comparisons of ecological factors.

Although many other ecological traits are associated with vision, like migratory pattern, turbidity, and light level (Cronin et al. 2014), they are not independent of each other, or the variables in this study, primarily habitat type and complexity. For example, deepwater species are light limited therefore 'light availability' is autocorrelated (Jerlov 1976). A future data set that has a larger sample size for each of these properties could look at which variables within the habitat best explain differences in eye size.

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