

Pupil dilation and visual field in the piked dogfish, *Squalus acanthias*

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Abstract The relatively large eye and pupil of the Piked Dogfish, *Squalus acanthias*, is visually arresting. However, knowledge of its basic visual characteristics lags far behind other areas in this generally well studied species. This study quantifies pupil dilation in a species that is naturally exposed to a broad range of light intensities and finds that the pupil area in the dark adapted state is 35.3% of the total eye area, an increase of 12.4% from the light adapted state. The anterior and posterior extents of the horizontal visual field are assessed and compared with both morphological and electrophysiological techniques and the results are integrated with the measured head yaw to derive the anterior convergence distance and blind area. The position of the eyes and the triangular, pointed snout of *S. acanthias* provides excellent anterior vision, which likely facilitates foraging upon its mobile prey.

Keywords Shark · Elasmobranch · Squaliformes · Vision · Electroretinogram

Introduction

The Piked Dogfish, *Squalus acanthias* Linnaeus 1758, is a moderate sized squaloid shark that may be the single most abundant shark species on the planet (Compagno 1984; Compagno et al. 2005). It is distributed anterotropically in the Atlantic and Pacific basins where it seems to prefer a temperature range of 7–15°C (Compagno 1984). To remain within its preferred range in different seasons and at different latitudes, *S. acanthias* moves between shallow inshore waters and deeper offshore continental shelves and upper slopes. Although it is found from the surface to the bottom, *S. acanthias* typically remains close to the bottom even over the slopes. As a result, *S. acanthias* inhabits a large depth range from the surface to 600 m regularly and maximally to 1,460 m (Compagno et al. 2005). This maximum depth is deeper than many other shark species, including ones typically classified as deep water species, such as the etmopterid sharks (Compagno et al. 2005).

Because *S. acanthias* spans such a large depth range, it is subjected to a wide range of light intensities from bright surface waters to the aphotic zone. Consequently, its visual capabilities likely represent a compromise between these extreme environments. Unlike most fishes, elasmobranchs are characterized by mobile pupils, and pupil size is directly proportional to the amount of light entering

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the eye (Murphy and Howland 1991). Therefore, a large eye with a correspondingly large pupil would allow more light to impinge upon the retina in deep water, low light, environments (Warrant and Locket 2004; Lisney and Collin 2007). However, that same eye morphology could lead to potential visual oversaturation in the brightly lit shallow waters that this species also inhabits. It might be predicted then, that a large eye would be accompanied by a correspondingly large range of pupillary apertures to enable *S. acanthias* to function across the wide range of light intensities that it could encounter.

Squalus acanthias is a generalist predator that feeds primarily upon fishes, and some invertebrates, from midwater to the bottom (Compagno 1984; Compagno et al. 2005). This entails capturing their often fast moving and agile prey in a challenging open water environment. Their relatively large, laterally protruding eyes provide the shark with a broad visual field and anterior binocular overlap, which would facilitate prey tracking (Harris 1965). Though vision is likely an important sensory modality for predation in this species, quantitative studies are lacking. Therefore, to better understand the visual capabilities of this species, the goals of this study were to quantify i) the range of pupillary apertures ii) the extent of the static horizontal visual field and iii) the contribution of head yaw to the dynamic visual field in the Piked Dogfish, *S. acanthias*.

Methods

Sharks were maintained at the Mt. Desert Island Biological Laboratory, Salisbury Cove, Maine, in large outdoor holding tanks with flow-through seawater and were exposed to a natural photoperiod. The sharks were fed to satiation daily. All experiments were conducted at night in a lab with closed blinds to provide maximum darkness. For the pupil dilation and visual field components, a total of 6 adult female sharks were tested ranging from 79.2 to 86.5 cm total length, mean 83.9 ± 1.09 sem cm. For the head yaw component, a total of 10 adult sharks were filmed free-swimming in a large tank. Because these sharks were not handled, sizes and sexes were not determined, although the sharks were all of a similar size to the individuals used in the physiological compo-

nents and included at least some of the same individuals.

Pupil dilation

To quantify pupil dilation, a shark was removed from the large holding tank and held in an anesthetic bath of MS222 (1:10000 wt:vol) until spiracular ventilation ceased. The shark was then secured with Velcro straps to a stage in a glass aquarium and ventilated through the mouth with aerated seawater that was spiked with a low maintenance dose of MS222 (1:25000). The spiracles were plugged to ensure that the ventilatory water flowed over the gills.

A digital camera with a macro lens was mounted on a tripod, positioned near the tank and manually focused upon the eye. The eye was illuminated for 5 min with a 75 W incandescent bulb mounted on the outside of the tank as well as ambient fluorescent room lighting. The incandescent bulb was positioned approximately 10 cm dorso-laterally to the eye to mimic the direction of natural downwelling light and to provide maximum illumination of the retina and iris, both responsible for pupillary response (Kuchnow 1970). The total irradiance at the surface of the eye was approximately 690–720 mW m^{-2} . The eye was photographed under these light conditions and then the incandescent bulb and the room light were extinguished and the tank covered with a black velvet cloth to eliminate any possible stray light. Photographs were taken in the dark at 1, 2, 3, 5, 10, 20 and 30 min as the shark was dark adapting. A dim red light-emitting diode (LED) torch was used to illuminate the eye long enough to expose the photographs (<5 s) as another study revealed that sharks are generally insensitive to red light (McComb et al. 2010). After 30 min, the black cloth was removed, the incandescent bulb and the room lights were switched on and the shark was readapted to the bright light. Photographs were taken after 1, 2, 3 and 5 min of light adaptation. At the end of a trial, the shark was measured and revived by ventilating with anaesthetic-free seawater. All sharks were successfully revived and returned to the holding tank.

To quantify the pupil area, each photograph was imported into the software ImageJ where the entire visible portion of the eye was outlined and the area in pixels measured. The area was then measured for the pupil only and the pupil area was expressed as a percentage of the total eye area.

Visual field

The horizontal visual field was determined using both physiological and morphological methods. The physiological method of determining the visual field consisted of an electroretinogram technique (ERG) in which a shark was anaesthetized, secured to a stage and ventilated with aerated seawater as described above. A 20 gauge needle pierced the sclera and a 10 T chlorided silver wire was inserted into the vitreous humor. A reference electrode contacted the dorsal surface of the body and provided the inverting input to a differential amplifier.

A submersible LED slit lamp was mounted to a protractor and was able to freely rotate in the horizontal plane and project a narrow vertical slit of white light upon the pupil from different angles. The LED slit lamp produced an irradiance on the eye of approximately $7.3 \mu\text{W cm}^{-2}$. To begin an experiment, the shark was dark adapted for a minimum of 30 min and the light guide positioned directly lateral to the center of the pupil (90°). The computer-controlled LED slit lamp was activated for 1 s and the response of the retinal photoreceptors was detected by the recording electrode, amplified (100–1000x), filtered (0.1–1 kHz, with a 60 Hz notch filter), digitized (1 kHz) and recorded on the computer using the software Chart. The slit lamp was repositioned around the eye in 10° increments and the retinal response recorded. As the slit lamp approached the anterior and posterior visual field extremes, smaller $1\text{--}2^\circ$ increments were employed to achieve greater resolution. The slit lamp eventually contacted the snout and trunk at the anterior and posterior extremes preventing it from moving any farther in either direction.

To complement the ERG technique, a morphological approach was employed. A photograph was taken of the dorsal surface of each shark and opened using the software ImageJ. Lines were extended from the lateral most margin of the lens toward the snout and toward the trunk. The angles described by these lines were measured for each individual and compared to the angles achieved using the ERG technique.

Head yaw

In conjunction with the visual field measurements of anaesthetized sharks, the head yaw of free-swimming individuals was also quantified to determine the

dynamic movement of the visual field during swimming. A digital video camera was placed in a housing and positioned in the large holding tank to record a field of view looking straight down on the dorsal surface of the free swimming sharks. A total of ten individuals were filmed swimming in a straight line directly beneath the camera. The video was edited using the software Final Cut Pro and the frames containing the maximum left and right head excursions were superimposed and aligned at the origin of the first dorsal fin using the software Adobe Photoshop. The yaw angle was determined by using the software ImageJ to measure the angle described from the tip of the snout at the maximum left excursion to the origin of the first dorsal fin and then to the tip of the snout at the maximum right excursion.

Results

Pupil dilation

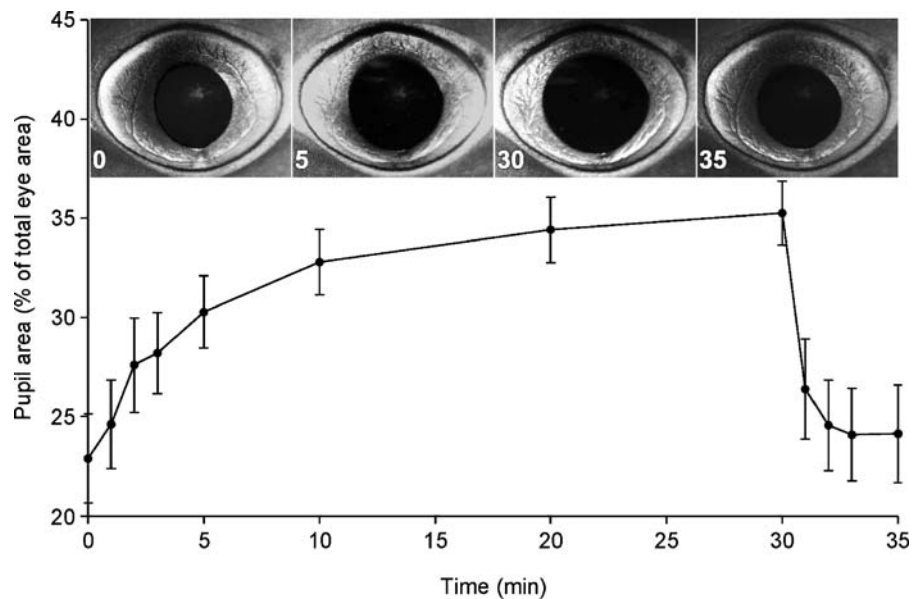
Squalus acanthias possesses a relatively large, vertically ovoid pupil in the light adapted state. As the eye becomes dark adapted, the pupil expands rostrally and caudally to a greater extent than dorsally and ventrally which results in a nearly round pupil at full dark adaption.

After exposure of the eyes to bright light for 5 min, the pupils had constricted to $22.9\% \pm 2.23$ sem of the total eye area. The pupils rapidly dilated in the dark and had expanded to $35.3\% \pm 1.61$ sem of the total eye area after 30 min. By this time the dilation rate was approaching an asymptote (Fig. 1). Upon light exposure, the dark-adapted pupils constricted dramatically within the first minute and constricted to an area of $24.1\% \pm 2.45$ sem within 5 min. After 5 min of light exposure the pupil area approached, but was still significantly greater than, the pre-dark adapted state (paired *t*-test, $p=0.003$).

Visual fields

The light from the slit lamp elicited a strong ERG waveform response which showed the classic vertebrate pattern with clear A and B wave components. As the slit lamp was rotated around the eye, it contacted the snout at a mean maximum anterior angle of $9.6^\circ \pm 0.81$ sem medial to the midline (Fig. 2).

Fig. 1 Pupil dilation in the Piked Dogfish, *Squalus acanthias*. The pupil area, expressed as a percentage of the total visible eye area, is plotted against time for dark adaption (0–30 min) and light adaption (30–35 min). Insets show photographs of the eye at time 0 (light), 5 (dark), 30 (dark), and 35 (light) min



However, a strong ERG signal was recorded from all individuals at the most anterior position indicating that the 9.6° was still within the shark's visual field. Similarly, in the posterior extreme range, the slit lamp contacted the trunk at a mean maximum posterior angle of $159.0^\circ \pm 2.34$ sem lateral to the midline, at which point an ERG response was still recorded. However, unlike for the anterior angle, the magnitude of the ERG was typically smaller near the posterior angle.

To supplement the electro-physiological method, the maximum extent of the visual field was determined using a morphological approach (Fig. 2). The maximum anterior visual field was $20.5^\circ \pm 0.33$ sem medial of the midline and the maximum posterior visual field was $168.8^\circ \pm 0.38$ sem lateral of the midline.

Based upon the visual field angles, it is possible to calculate the anterior convergence point of the left and right visual fields. From the ERG data, the convergence point was $21.5 \text{ cm} \pm 1.95$ sem anterior to the transverse plane through the pupils and from the morphological data it was $9.2 \text{ cm} \pm 0.10$ sem. Similarly, the anterior blind area was calculated. The blind area based upon the ERG data was $76.2 \text{ cm}^2 \pm 6.82$ sem and based upon the morphological data was $33.3 \text{ cm}^2 \pm 0.62$ sem. The visual field data are summarized in Table 1.

Head yaw

As the sharks swam at a typical cruising speed, their head yawed left and right an average of $10.3^\circ \pm$

1.13 sem. The range was from 5.2 to 16.7° but the similar size of all the specimens precluded determination of whether head yaw varied with total length.

Discussion

The literature on *S. acanthias* is vast with more papers published on this species than any other elasmobranch. Despite its common use as a model organism, basic aspects of its anatomy, physiology and behavior remain unexplored. This study is the first to quantify pupil dilation and both the static and dynamic visual field in the Piked Dogfish and relate these results to the environment that it inhabits.

Vision is likely an important sensory modality for *S. acanthias* as it preys primarily upon teleosts as well as shrimp, ctenophores, and cephalopods in the water column (Castro 1983; Compagno 1984; Scott and Scott 1988). Good visual acuity and fast visual processing are required to localize and facilitate capture of their agile prey. In addition, *S. acanthias* forms large schools in which vision likely plays an important role for school cohesion and conspecific spacing. In this regard, the regular pattern of white spots along the dorsal flanks of the body may provide a signaling mechanism to conspecifics, especially in turbid water or in low light deep-sea habitats (Myrberg 1991).

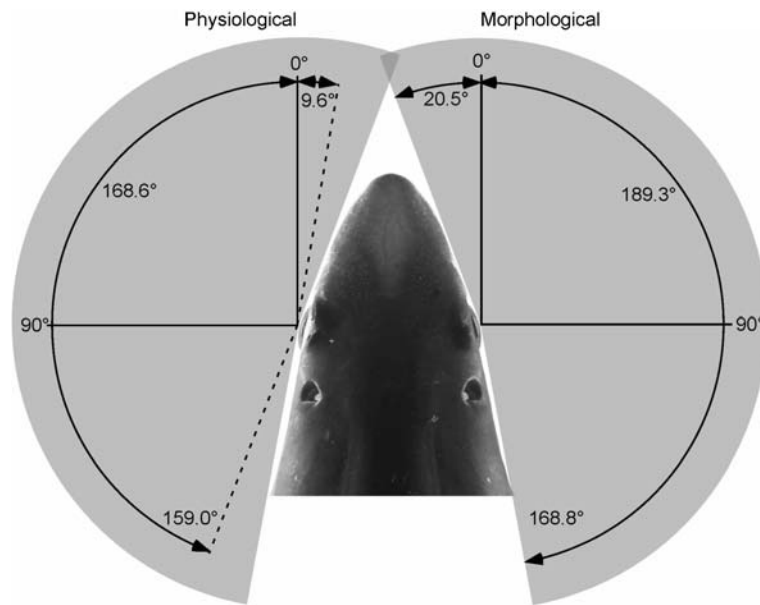


Fig. 2 Horizontal visual field determined with both morphological (*right*) and electrophysiological (*left*) methods for the Piked Dogfish, *Squalus acanthias*. The visual field extends medially by 20.5° from the midline and laterally by 168.8° from the midline to describe a visual field of 189.3° as determined based upon the eye morphology. In contrast, the

electro-retinogram technique yielded a visual field that extends medially to 9.6° and laterally to 159.0° for a total visual field of 168.6°. Shaded areas on both *left* and *right* sides represent the extent of the visual field determined by the morphological method

There is a general trend among sharks for eye size (measured as length rostral to caudal) to increase with inhabited depth (Fig. 3). The eye size of *S. acanthias* is much larger than typically shallow water species but smaller than the deep-sea species. A study of 32 shark species found that two other species in the genus *Squalus* have large eye sizes relative to body size (Lisney and Collin 2007), a feature likely characteristic of squaloid species, many of which inhabit deep-sea environments (Compagno 1984; Compagno et al. 2005).

Organisms that inhabit deep-sea environments typically exhibit a number of visual system adaptations to the very low light intensity and condensed visual spectrum (Warrant 2000; Warrant and Locket 2004). Factors such as eye size, pupil size, lens diameter, visual pigment absorbance and photoreceptor and ganglion cell density are modified to accommodate vision in the deep sea (Crescitelli 1991; Bozzano 2004). However, *S. acanthias* does not possess the enormous eye size of exclusively deep-sea species and its intermediate eye size and

Table 1 Visual field parameters of the piked dogfish, *Squalus acanthias*, determined by both physiological and morphological methods. The anterior angle is measured as medial to the 0° midline and is thus recorded as negative (neg). The convergence distance is measured along the midline from the

transverse plane through the center of the eyes rostral to where the left and right visual fields overlap. The anterior blind area represents the area rostral from the transverse plane through the center of the eyes to where the left and right visual fields overlap. For all measurements, *n*=6

	Physiological (ERG)			Morphological		
	Mean	SD	Range	Mean	SD	Range
Anterior angle (°)	9.6 (neg)	1.82	7–12 (neg)	20.5 (neg)	0.82	19.6–21.7 (neg)
Posterior angle (°)	159.0	5.73	150–165	168.8	0.93	167.7–170.0
Convergence distance (cm)	21.5	4.36	17.4–28.8	9.4	0.25	9.2–9.8
Anterior blind area (cm ²)	76.2	15.25	64.4–102.1	33.3	1.53	31.3–34.7

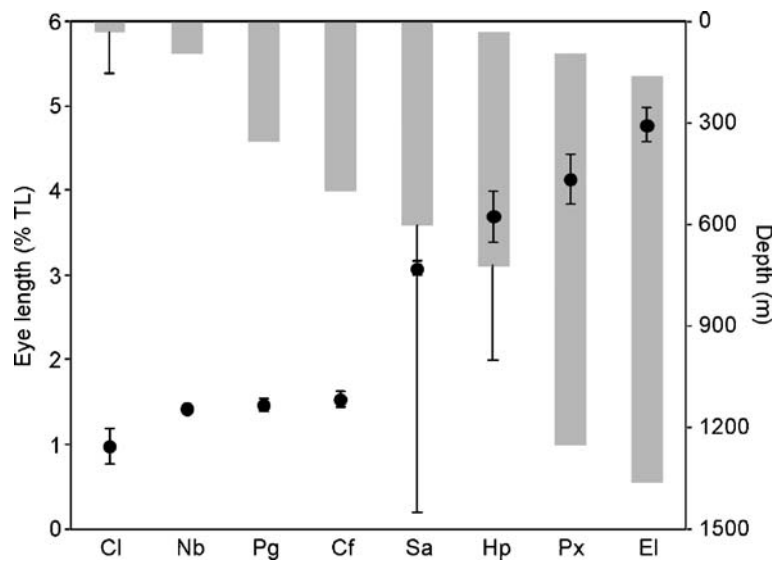


Fig. 3 Eye length (measured rostral to caudal) and inhabited depth range for 8 shark species. Mean eye length + sem (filled circles) increases with depth (bars). Maximum depths are indicated with whiskers. Cl = *Carcharhinus leucas*, $n=3$; Nb = *Negaprion brevirostris*, $n=8$; Pg = *Prionace glauca*, $n=3$; Cf =

Carcharhinus falciformis, $n=5$; Sa = *Squalus acanthias*, $n=12$; Hp = *Hepranchias perlo*, $n=5$; Px = *Parmaturus xaniurus*, $n=3$; El = *Etmopterus lucifer*, $n=3$. Eye length data from Cornett (2006) and depth data from Compagno et al. (2005)

broad depth range probably classify it as a visual generalist. Therefore, its visual adaptations may not be as dramatic as deep-sea species and may represent a compromise to its diverse habitats.

An obvious visual adaptation in elasmobranchs is the mobile pupil. A study of the pupillary response of various elasmobranch species from the genera *Mustelus*, *Scyliorhinus*, and *Carcharhinus*, found that diurnal species dilate their pupils in 1–30 min and constrict them maximally in 2–5 min (Franz 1931; Young 1933; Kuchnow 1971). Drawing upon these results, the dark adaptation period for this study was set at 30 min and the light adaptation period was set at 5 min. At the end of 30 min, the pupil of *S. acanthias* had expanded dramatically and the dilation rate was approaching an asymptote (Fig. 1). However, there was still an increase in pupil area from 20 to 30 min and a longer period of dark adaptation would have likely yielded a slightly greater maximum pupil area. Longer dilation times are necessary for some species; for example, the Lemon Shark, *Negaprion brevirostris*, achieves maximum dilation only after 60 min (Gruber 1967).

Although diurnal species typically achieve maximum pupillary constriction in 2–5 min (Franz 1931; Young 1933), a deep-water squaloid species, *Squalus blainvillei*, does not achieve maximum constriction

for 60 min (Kuchnow 1971). For this study, the pupil constricted to close to its bright adapted state after 4–5 min (Fig. 1) and a longer light exposure time would have enabled it to completely revert to its light adapted size. Other studies have expressed pupil size in different ways (Kuchnow 1970, 1971), which confounds direct comparison and precludes determination of whether the 12.4% increase in dark adapted pupil area differs from exclusively shallow water elasmobranch species.

A potential concern in these experiments is the use of the drug MS-222 to anaesthetize the fish. MS-222 added to aquarium water produces relaxation of the accommodative musculature in the Winter Flounder (*Pseudopleuronectes americanus*) demonstrating that this drug can affect the ocular system (Sivak 1982). However, in this study, a clear pupillary response (both constriction and dilation) was observed while the shark was anaesthetized which indicates that the iris continued to function and respond to light. The observed response time was similar to other shark species that were tested without anaesthesia (Kuchnow 1971). Therefore, it is unlikely that the anaesthetic dramatically affected the response. In addition, other studies have also successfully recorded ERG responses in fish similarly anaesthetized with MS-222 (van Roessel et al. 1999; Mora-Ferrer and Behrend 2004). Finally, the

shark was maintained at an anaesthetic dosage that was just sufficient to keep it from moving. Tiny movements of the upper lobe of the caudal fin indicated that the shark was barely anaesthetized.

The horizontal visual field was determined using both morphological and electrophysiological methods. By recording retinal activity in an intact animal, the ERG technique provides an accurate assessment of the extent of the shark's visual field (McComb and Kajiura 2008). However, the barrel of the submersible LED slit lamp actually contacted the snout and trunk of the shark while still eliciting an ERG response. Therefore, the maximum anterior and posterior visual field values likely underestimated the true extent of the visual field. Along the snout, the ERG magnitude showed no signs of declining. However, along the trunk, the ERG response at the maximum angle was sometimes of a smaller amplitude than at a smaller angle. This indicates that the posterior visual field limit may be close to the value determined using the ERG technique.

There is a potential concern that the light from the slit lamp may be scattered within the eye itself and thus stimulate photoreceptors outside the narrow focal beam (Binns and Margrain 2006). This is particularly relevant because the sharks were tested under scotopic conditions and rods lack the directional sensitivity of cones (Pirenne 1962) so could be stimulated by stray light. This may account for the inability to determine the posterior margin of the horizontal visual field. However, in eight other elasmobranch species (including 1 skate, 3 rays, 4 sharks) clear demarcations of the visual field have been measured using this same technique (McComb and Kajiura 2008; McComb et al. 2009). Therefore, the broad visual field determined for *S. acanthias* is likely a reasonably accurate assessment and not due to limitations in the ERG technique.

The visual field was also determined by extending lines from the lateral margin of the lens along the snout and along the trunk. The shark cornea shares the same refractive index as the seawater, so the total refractive power of the eye is provided by the lens (Hueter 1991). The angles determined with this technique would yield the absolute greatest possible angle at which light could impinge upon the lens and be focused upon the retina. As such, these values likely overestimate the functional extent of the visual field. However, at least for the anterior angle, the

morphological measure is likely a close proxy to the actual extent of the visual field. For the posterior angle, a value between the morphological and physiological assessments most likely represents the actual extent of the visual field.

The anterior and posterior margins of the visual field were assessed using an ERG technique, which reflects the summed evoked potentials of the stimulated photoreceptors. However, the distribution of photoreceptors and ganglion cells is not uniform across the retina, resulting in areas of greater or lesser visual acuity. Numerous studies have documented areas of greater photoreceptor and ganglion cell density, typically along the equatorial plane, which form a high acuity horizontal visual streak (Hueter 1991; Bozzano 2004; Litherland and Collin 2008). This results in areas of greater visual acuity on the retina. For example, in the deep-water Portuguese Dogfish, *Centroscymnus coelolepis*, the greatest visual acuity is along the visual axis which is 32–44° anterior from the geometric center of the retina (optic axis) (Bozzano 2004). Because the slit lamp in the current study was oriented vertically and extended across the entire height of the pupil, the ERG response would be the summed response of all retinal cells in the vertical plane, not just the photoreceptors and ganglion cells that comprise the horizontal visual streak. Therefore, a smaller magnitude ERG response, like that seen near the periphery, might indicate a decreased density of photoreceptors on the corresponding portion of the retina. A detailed study of retinal anatomy is required to determine the acuity axis in *S. acanthias*, however, based upon the position of the eyes within the head, a visual axis offset, similar to *C. coelolepis*, is likely.

The pointed snout of *S. acanthias* allows the eyes to be canted forward, which provides binocular overlap of the left and right visual fields at some distance anterior to the transverse plane through the eyes (Table 1). The actual convergence point lies somewhere between the physiological (21.5 cm) and morphological (9.4 cm) values, likely closer to the morphological results. The anterior binocular overlap of the left and right visual fields is calculated by doubling the anterior angle (Table 1). This yields a binocular overlap of between 19.2° (physiological) to 41° (morphological). The true overlap is likely closer to the morphological value, which is remarkably similar to the 45° value for *S. acanthias* estimated

by Harris (1965). The large binocular overlap contrasts with shark species that possess a more blunt snout, like the Lemon Shark, *Negaprion brevirostris*, which has only a small amount of binocular overlap (Hueter and Gruber 1982). The close anterior binocular overlap also provides *S. acanthias* with good anterior vision, which facilitates predation upon its mobile teleost and cephalopod prey in the water column (Compagno 1984). In addition, prey moving out of the visual field and into the anterior blind area could be localized with the electrosensory system, which has an effective range of tens of cm around the head (Kajiura and Holland 2002; Kajiura 2003).

Because these sharks are constantly swimming, measuring the static visual field for a shark does not fully reveal how the shark perceives its environment. The static visual field data must be integrated with the shark's swimming kinematics since the left and right yawing of the head while swimming dictates what parts of the environment the shark actually sees (Harris 1965). The analogy would be to a flashlight beam illuminating a dark room. The width of the flashlight beam is fixed, like the field of view of an eye. However, as the flashlight is moved back and forth, more of the room is illuminated, in much the same way as the shark increases its total effective field of view by yawing its head, although the actual field of view of the eye remains constant. As the head yaws left and right, each eye in turn sees a greater extent of the environment anterior to the shark and there is the potential for this information to be temporally integrated to develop a composite view of the area ahead. This left and right yawing motion effectively decreases the binocular convergence distance and anterior blind area and increases the total effective visual field.

The laterally bulging eyes of *S. acanthias* contribute not only to the large horizontal visual field, they also likely provide the shark with good coverage in the vertical plane as well. However, the extent of the vertical visual field remains to be tested using an ERG technique with the slit lamp oriented in the vertical plane. In addition, these experiments were conducted on similar sized adult sharks, but there may be ontogenetic differences in visual fields and head yaw which remain unexplored. Ontogenetic differences in eye structure are documented for other shark species (Bozzano et al. 2001) and neonatal sharks have been

described to exhibit different swimming kinematics than adults (Kajiura 2003). Although the fine structure of the photoreceptors has been examined in *S. acanthias* (Stell 1972), the retinal topography of this important species is still undescribed. Therefore, many fundamental research questions remain to be explored even in this well studied species.

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