Enhanced visual fields in hammerhead sharks

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SUMMARY

Several factors that influence the evolution of the unusual head morphology of hammerhead sharks (family Sphyrnidae) are proposed but few are empirically tested. In this study we tested the 'enhanced binocular field' hypothesis (that proposes enhanced frontal binocularity) by comparison of the visual fields of three hammerhead species: the bonnethead shark, *Sphyrna tiburo*, the scalloped hammerhead shark, *Sphyrna lewini*, and the winghead shark, *Eusphyra blochii*, with that of two carcharhinid species: the lemon shark, *Negaprion brevirostris*, and the blacknose shark, *Carcharhinus acronotus*. Additionally, eye rotation and head yaw were quantified to determine if species compensate for large blind areas anterior to the head. The winghead shark possessed the largest anterior binocular overlap (48 deg.) and was nearly four times larger than that of the lemon (10 deg.) and blacknose (11 deg.) sharks. The binocular overlap in the scalloped hammerhead sharks (34 deg.) was greater than the bonnethead sharks (13 deg.) and carcharhinid species; however, the bonnethead shark did not differ from the carcharhinids. These results indicate that binocular overlap has increased with lateral head expansion in hammerhead sharks. The hammerhead species did not demonstrate greater eye rotation in the anterior or posterior direction. However, both the scalloped hammerhead and bonnethead sharks exhibited greater head yaw during swimming (16.9 deg. and 15.6 deg., respectively) than the lemon (15.1 deg.) and blacknose (15.0 deg.) sharks, indicating a behavioral compensation for the anterior blind area. This study illustrates the larger binocular overlap in hammerhead species relative to their carcharhinid sister taxa and is consistent with the 'enhanced binocular field' hypothesis.

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Key words: binocular vision, elasmobranch, eye, pupil dilation, Sphyrnidae, winghead shark.

INTRODUCTION

In their 400 million year evolutionary history, elasmobranch fishes (sharks, skates and rays) have evolved a rich morphological diversity (Karatajute-Talimaa, 1992; Capetta et al., 1993). One of the most unique features is the dorso-ventrally compressed and laterally expanded cephalofoil of the hammerhead sharks (Elasmobranchii, Carcharhiniformes, Sphyrnidae). This head expansion ranges from modest in the bonnethead, *Sphyrna tiburo*, to extreme in the winghead shark, *Eusphyra blochii*, in which the wing-like head has a width equal to nearly 50% of the total body length (Compagno, 1984). The head width of all of the other hammerhead species are between these two extremes (Fig. 1).

The uniqueness and peculiarity of the expanded cephalofoil has generated much speculation about its function, and several hypotheses to explain its evolution. The cephalofoil may confer advantages that include: greater lift and maneuverability (Thompson and Simanek, 1977; Compagno, 1984; Nakaya, 1995; Kajiura, 2001; Kajiura et al., 2003), enhanced prey acquisition and manipulation (Strong et al., 1990; Chapman and Gruber, 2002), greater electrosensory capability (Compagno, 1984; Kajiura, 2001) and superior olfactory gradient resolution (Compagno, 1984; Johnsen and Teeter, 1985).

Of particular relevance is how the lateral displacement of the eyes on the distal tips of the cephalofoil constrain or enhance the visual capabilities of the hammerheads in contrast to their sister shark taxa which possess a more conventional head shape. Walls stated that in hammerheads, each eye field is independent with no

possible overlap thus precluding anterior binocular vision (Walls, 1942). By contrast, Compagno argued that the widely spaced eyes on the tips of the head enhance binocular vision anteriorly and provide an increased stereoscopic visual effect (Compagno, 1984). Thus, a comparative test of binocular overlap among related species is needed (Schwab and McComb, 2007).

The visual field is the expanse of space visible to an organism without inclusion of eye movement. There are three primary measurements of the visual field: single eye (monocular), both eyes combined (cyclopean) and overlap of two monocular fields (binocular) (Collin and Shand, 2003). The point closest to the eyes at which the monocular fields overlap is termed the binocular convergence point, and the distance from this point to the central point midline of the head is the convergence distance. The shorter the convergence distance, the closer to the head the eyes support binocular vision. Binocular depth perception occurs as a result of stereoscopic vision where separate images from two eyes are combined in the brain to form a three-dimensional image. Although depth perception can be achieved with only monocular vision, it is enhanced by binocular vision (Pettigrew, 1991). In general, prey species are characterized by large monocular fields, which scan the environment for predators whereas predators demonstrate increased binocularity, which facilitates detection and localization of prey (Lythgoe, 1979).

The extent of the visual field is species-specific and dictated by factors that include head morphology, eye position, eye mobility, pupil shape, lens movement, head movement, eye socket depth and extent of eye protrusion from the body contour (Collin and Shand,
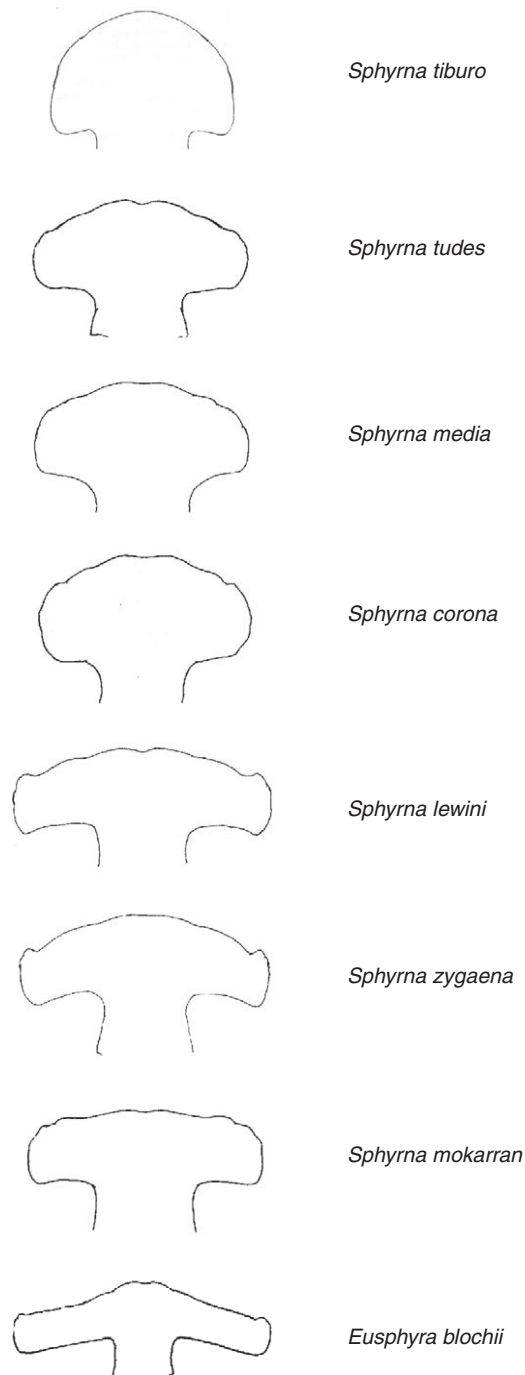
Fig. 1. Head morphology of the eight species within the family Sphyrnidae depicting the gradation in cephalofoil lateral expansion. Line drawings modified from Compagno (Compagno, 1984).

2003). Whereas the size of the visual field for each eye is fixed, eye mobility changes the amount of binocular overlap.

The goal of this study was to test the main prediction of the 'enhanced binocular field' hypothesis that there is greater overlap in the anterior visual fields of the hammerhead shark than in shark species with a more conventional head morphology. We experimentally compared the visual fields of three hammerhead shark species, the bonnethead (*Sphyrna tiburo* Linnaeus 1758), scalloped hammerhead

(*Sphyrna lewini* Griffith and Smith 1834) and the winghead (*Eusphyra blochii* Cuvier 1816) sharks against two carcharhinid species, the lemon shark (*Negaprion brevirostris* Poey 1868) and the blacknose shark (*Carcharhinus acronotus* Poey 1860). We also assessed other features that affect the visual fields, including pupil shape, convergence distance and blind area within the species. In addition we quantified the degree of posterior and anterior eyeball vergence and head yaw, both of which may affect anterior blind area.

MATERIALS AND METHODS
Animal collection

All experimental animals were collected with long line, hand line and gillnets from June 2006 to August 2008. Scalloped hammerhead sharks were collected in Kaneohe Bay, Oahu, HI, USA, and maintained at the Hawaii Institute of Marine Biology (HIMB) on Coconut Island, HI, USA. The bonnethead and blacknose sharks were collected near the shore of Pinellas Point within Tampa Bay, FL, USA, and New Pass, Sarasota, FL, USA, respectively, and maintained at Mote Marine Laboratory in Sarasota, FL, USA. Lemon sharks were captured near Long Key, FL, USA, and maintained at the Florida Atlantic University Marine Laboratory, Boca Raton, FL, USA. Animals were fed daily to satiation, and experiments were generally conducted within one week of capture. Despite repeated attempts to capture live specimens, only dead specimens of winghead sharks were obtained north of Darwin and processed at the Charles Darwin University, Darwin, Australia. Data on sample size and morphometrics are provided in Table 1. Experimental protocols, including care and use, were approved by the IACUC of each institution: University of Hawaii at Manoa (UHM #01-042-05), Mote Marine Laboratory (MML #07-03-SK1), Charles Darwin University (#A08002) and Florida Atlantic University (#A09-04).

Pupil dilation and shape

A single individual of each species was tested to confirm the time to maximum pupil dilation. Experiments were initiated by administration of the anesthetic, tricane methanesulphonate (MS-222) (1:15,000 w/v) (Western Chemical Inc., Ferndale, WA, USA) into a tank until the shark ceased respiration. The animal was then quickly transferred to the clear acrylic experimental tank, strapped to a stationary platform, immediately ventilated with a maintenance dose (1:20,000 w/v) of MS-222 in aerated seawater and monitored throughout the trial. The platform was positioned to minimize the distance of the shark's eye from the wall of the tank. A camera (Nikon, Melville, NY, USA) was mounted on a tripod to ensure a constant distance between the imaging plane and the eye. The eye was photographed in the light-adapted condition, and subsequently all light was extinguished. Photographs of the dark-adapting eye were taken at 0, 1, 3, 5, 10, 15, 20, 25 and 30 min briefly utilizing a dim red light for illumination. The pupil area and total eye area were quantified from the photographs using the image analysis software ImageJ (National Institutes of Health, Bethesda, MA, USA). Relative pupil area was plotted against time and the asymptote was used to determine the minimum time required for each species to become dark-adapted (ensuring maximum retinal exposure). Pupil shapes were determined from the photographs.

Visual fields – physiological

The horizontal and vertical visual fields were determined for a minimum of six individuals of each species on dark-adapted animals using the electroretinogram (ERG) technique. The experimental apparatus and protocol have been detailed previously (McComb and Kajiura, 2008) and are outlined only briefly here.

Table 1. Morphometric summary data for all shark species

Family:	Carcharhinidae	Carcharhinidae	Sphyrnidae	Sphyrnidae	Sphyrnidae
Species:	*Negaprion brevirostris*	*Carcharhinus acronotus*	*Sphyrna tiburo*	*Sphyrna lewini*	*Eusphyra blochii*
N	6	6	7	6	6
Habitat	Coastal, inshore, tropical	Coastal, tropical	Coastal, inshore	Coastal, pelagic	Benthopelagic, brackish
Eye position	Lateral	Lateral	Lateral	Anterior lateral	Anterior lateral
Pupil shape	Round	Round	Horizontal	Slight horizontal	–
Total length (cm)	73.7±1.9	104.5±1.1	81.6±1.9	56.1±1.1	108±2.5
Inter-ocular distance (cm)	8.6±0.2	11.1±0.2	12.6±0.2	14.8±0.3	44.6±1.2
Horizontal plane					
Monocular (deg.)	159.0±0.5	171.7±1.4	175.9±1.1	181.7±1.8	–
Binocular – physiological (deg.)	10.0±1.5	10.7±1.3	13.4±0.7	31.7±3.7	48.3±2.7
Binocular – morphological (deg.)	11.8±0.7	13.6±0.8	16.4±0.5	34.4±2.6	48.3±2.7
Cyclopean (deg.)	308±0.7	332.7±1.8	338.3±2.1	331.7±1.7	–
Anterior eye rotation (deg.)	9.5±0.3	10.5±1.8	11.7±0.8	9.5±1.5	–
Posterior eye rotation (deg.)	9.3±0.9	15.2±1.9	14.7±0.9	9.8±1.0	–
Vertical plane					
Monocular (deg.)	184.8±0.4	192.0±0.7	189.1±0.7	187.0±1.7	–
Binocular (deg.)	4.3±0.6	9.3±0.7	9.1±1.6	7.0±1.9	–
Cyclopean (deg.)	360±0.0	360±0.0	360±0.0	360±0.0	–

Values represent means ± s.e.m.

Experimental apparatus

The light source stimulus was a white-light-emitting diode that delivered a beam of light through a clear acrylic cylinder, which was beveled to terminate in a 1 mm-wide slit. The light source was mounted to a mobile track fitted on a protractor, which allowed 360 deg. rotation around the eye in precise degree increments. The center of the protractor was first positioned with a micromanipulator above the shark horizontally at the lateral margin of the cornea. The light guide was rotated around the eye and delivered a vertical beam plane that illuminated the retina from the dorsal to ventral margins. The protractor device was then adjusted to an orthogonal position for determination of the visual field in the vertical plane. A 100 μm tip glass recording electrode pierced the sclera so that the tip was within the vitreal component of the eye to detect a change in electrical potential when light impinged upon the photoreceptive layer of the retina. A reference electrode was positioned upon the skin and the output from the electrodes was differentially amplified (1000×) and filtered (low-pass 1 kHz, high-pass 0.1 Hz) with a differential amplifier (DP-304; Warner Instruments, Hamden, CT, USA). The data were acquired and digitized with a Power Lab® 16/30 data acquisition system model ML 880 (AD Instruments, Colorado Springs, CO, USA).

Experimental protocol

Experiments were initiated by administration of the anesthetic MS-222 (1:15,000 w/v) into a tank until the shark ceased ventilation. The animal was then quickly transferred to the experimental tank and immediately ventilated with a maintenance dose (1:20,000 w/v) of MS-222 in aerated seawater and monitored throughout the trial. The electrodes and light guide were positioned using micromanipulators, and the room was darkened for 45 min to allow dark-adaption and maximum pupil dilation. The trial began with a computer-controlled 2 s flash of light directed at the retina, which resulted in a clear ERG response. After a 3 min recovery period, the light guide was repositioned in 10 deg. increments under dim red light and the stimulus repeated. The increments were reduced from 10 deg. to 1 deg. for precision as the limit of the visual field was approached. The limit of the visual field was defined as the last angle to produce a detectable ERG response.

The extent of the horizontal and vertical visual field was defined by four demarcations: anterior horizontal (AH), posterior horizontal (PH), dorsal vertical (DV) and ventral vertical (VV). Using these measurements we calculated the horizontal and vertical monocular, binocular and cyclopean fields of view. Additionally, we calculated the convergence distance and blind area using the demarcations and the inter-ocular distance (IOD) of each animal.

The horizontal and vertical visual field demarcations, as well as monocular, binocular and cyclopean fields were compared using a one-way analysis of variance (ANOVA) (Systat Software, San Jose, CA, USA) with pairwise multiple comparisons by Tukey *post-hoc* tests. Any non-normal or heteroscedastic data were analyzed with a Kruskal–Wallis one-way ANOVA on ranks with multiple comparisons using Dunn's method. Due to variability in animal size, analysis of covariance (ANCOVA) was used to facilitate comparison of convergence distance and blind area. Heteroscedastic data were log-transformed for multiple comparisons by Tukey *post-hoc* tests.

Eye rotation

Visual fields were measured on anesthetized animals whose eyes were in a relaxed and static position. Therefore, to account for eye movements under muscular control, we estimated the maximum potential horizontal anterior and posterior eye rotation of six freshly dead individuals for each species (except lemon shark N=4). After careful dissection of the surrounding tissue, surgical forceps were used to fully retract the medial (providing convergence) and lateral (providing divergence) rectus muscles. A camera was mounted on a tripod dorsal to the sharks and photographs were taken in the relaxed converged and diverged positions, and the degree of rotation determined from the photographs using Image J software (Rasband, 1997). The extent of anterior and posterior eyeball angular rotation was compared among species using a one-way ANOVA with pairwise multiple comparisons by Tukey *post-hoc* tests.

Head movement

The extent of lateral head yaw was quantified by examining video of the swimming kinematics of six individuals of each species. A

digital video camera was mounted on a mobile track that extended over the experimental tank and positioned to capture a dorsal view of sharks swimming in normal non-excited conditions. To reduce the effects of parallax distortion only footage in which sharks swam in a straight line directly below the camera was used. The frames in which the shark demonstrated a central, maximum right and maximum left deflection were overlain in Photoshop (Adobe, San Jose, CA, USA). The head yaw was quantified by insertion of a reference line that bisected the eyes and another reference line that ran through the midline of the snout creating a crosshair. The extreme right and left photographs were individually overlain on the central photograph and the angle of rotation measured using Image J software (Rasband, 1997) (Fig. 2). The degree of head yaw was compared among species using a nested ANOVA (SAS statistical software, Cary, NC, USA) and multiple comparisons with Tukey's (HSD) test.

Visual fields – morphological assessment
The winghead shark was intended to be included in all physiological measurements; however, despite several attempts, only dead specimens were secured. Therefore, to provide a comparable visual field metric, the horizontal anterior binocular overlap of the winghead shark and all of the other species was measured using a morphological method. Photographs were taken of the dorsal side of each individual's head and the angle described from a reference line parallel to the longitudinal axis of the body at the lateral margin of the eye and another reference line to the medial line of sight using Image J software (Rasband, 1997). The anterior binocular overlap was calculated using a minimum of six individuals from each species. The data were normalized by log transform and compared using one-way ANOVA and pairwise comparisons with Tukey *post-hoc* tests. Paired *t*-tests were conducted on the horizontal binocular overlaps measured using morphological and physiological techniques in order to validate our methodologies.

RESULTS
Pupil dilation and shape
Maximum pupil dilation was determined from the asymptote of pupil dilation *vs* time and occurred at 3 min for the bonnethead shark, 10 min for the scalloped hammerhead shark, 20 min for the blacknose shark and 25 min for the lemon shark. As a precaution, all species
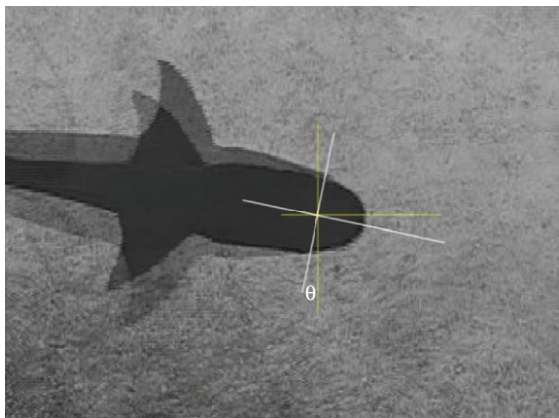

Fig. 2. Methodology used to measure head yaw. Video frames in which the shark demonstrated maximum left and right deflection were overlain on the head in the central position. Crosshairs were placed on each frame (bisecting the eyes and the center of the snout) and used to calculate the angle (θ) of head yaw.

were dark-adapted for a minimum of 45 min prior to experimentation, to ensure maximum pupil dilation of all individuals (Cohen and Gruber, 1977; Kuchnow, 1971). Pupil shape varied among species with the blacknose shark possessing a round shape, the lemon shark a vertical slit, the bonnethead shark a horizontal slit and the scalloped hammerhead shark a rounded pupil with slight horizontal elongation.

Visual fields
Comparison of the functional horizontal and vertical visual fields shows that the field demarcations in both planes differed among species (horizontal: anterior ANOVA, $P<0.001$; posterior ANOVA, $P<0.001$) (vertical: dorsal ANOVA, $P=0.022$; ventral ANOVA, $P=0.008$). The results of pairwise comparisons are provided in Fig. 3. The monocular, binocular and cyclopean visual fields were calculated from the visual field demarcation data and are summarized in Table 1. The visual fields in the horizontal and vertical planes differed among species (Fig. 4) (horizontal ANOVA, $P<0.001$; vertical ANOVA, $P=0.002$). All species possessed horizontal anterior binocular overlap. However, the overlap in the scalloped hammerhead shark (32 deg.) was larger than all other species whereas overlap for the bonnethead (13 deg.), lemon (10 deg.) and blacknose (11 deg.) sharks did not differ. All species had a 360 deg. panoramic vertical visual field around the head. All pairwise multiple comparisons are outlined in Table 2.

The horizontal convergence distance differed among species (ANCOVA, $P=0.017$). The scalloped hammerhead shark had a shorter horizontal convergence distance than the lemon shark. The vertical blind area differed among species (ANCOVA, $P=0.050$) with the blind area of the scalloped hammerhead being larger than the lemon shark. The horizontal blind area and vertical convergence distance did not differ among species.

Eye rotation
The maximum anterior and posterior eyeball rotation in the horizontal plane was measured for six individuals of each species. Rotations differed among species in the posterior direction (ANOVA, $P=0.008$) but not in the anterior direction (ANOVA, $P=0.l631$) (Fig. 5). The posterior eye rotation of the blacknose shark was greater than the lemon and scalloped hammerhead sharks. All pairwise multiple comparisons are provided in Table 2. Utilizing the degree of eyeball rotation data from each species the dynamic visual fields were constructed with the eyes in the converged (anterior) and diverged (posterior) positions.

Head movement
The maximum right and left head yaw was determined for six individuals of each species by analyzing video footage of free-swimming sharks. Maximum total (right + left) head yaw differed among species (nested ANOVA, $P<0.001$). A Tukey's (HSD) pairwise comparison revealed that the total head yaw of the two sphyrnids (scalloped hammerhead shark, 16.9±0.2 deg.; bonnethead shark, 15.6±0.3 deg.) differed from each other and from that of the two carcharhinid species (lemon shark, 15.1±0.2 deg.; blacknose shark, 15.0±0.3 deg.) (Fig. 5). The head yaw of the two carcharhinid species did not differ.

Visual fields – morphological assessment
The horizontal binocular overlaps differed among species (one-way ANOVA, $P<0.001$), with that for the winghead shark (48.3±2.6 deg.) greater than all other species (Tukey, all $P<0.001$). The binocular overlap of the scalloped hammerhead shark (34.4±2.6 deg.) was greater than that of the lemon (11.8±0.7 deg.; Tukey, $P<0.001$),
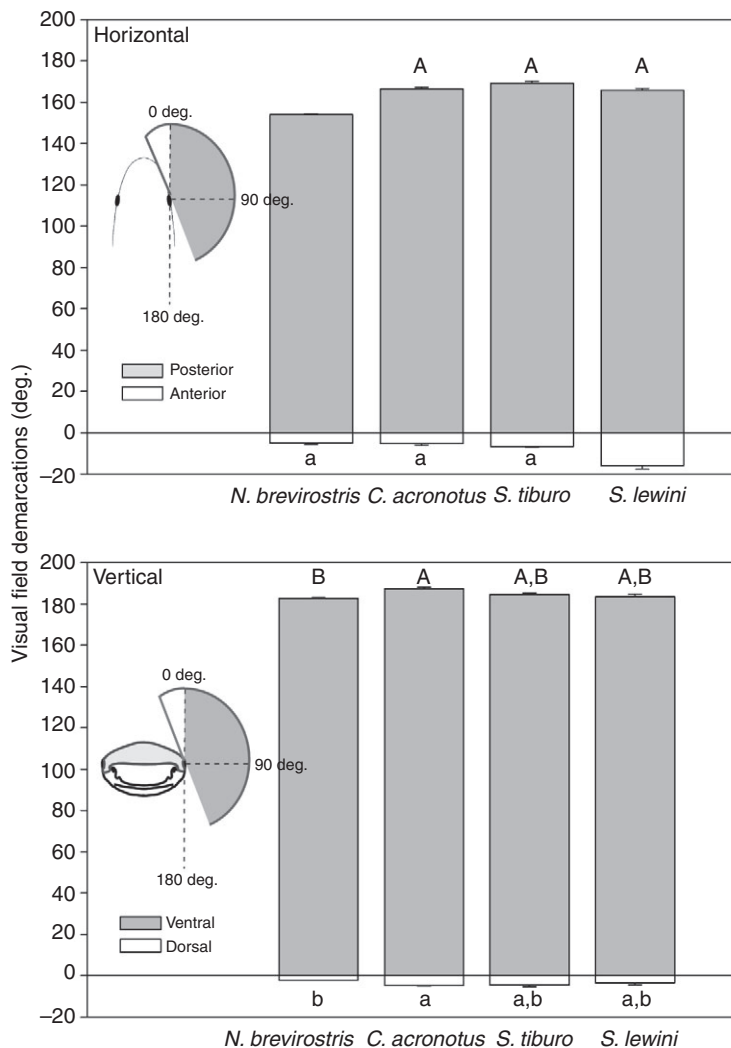
Fig. 3. The visual field demarcation limits measured for both the horizontal and vertical planes for two carcharhinid and two sphyrnid sharks (*Negaprion brevirostris*, *Carcharhinus acronotus*, *Sphyrna tiburo*, *Sphyrna lewini*). Visual field values are presented as means ± s.e.m. Bars that share the same upper or lower case letter do not differ (*P*<0.05). Line drawings modified from Compagno (Compagno, 1984).

blacknose (13.6±0.8 deg.; Tukey, *P*<0.001) and bonnethead (16.4±0.5 deg.; Tukey, *P*<0.001) sharks. The binocular overlaps measured morphologically compared with those measured physiologically revealed differences for the blacknose (paired *t*-test, *P*=0.041) and the bonnethead (paired *t*-test, *P*=0.002) sharks but not for the scalloped hammerhead (paired *t*-test, *P*=0.087) or the lemon (paired *t*-test, *P*=0.245) sharks. The overall difference in mean binocular overlap between methods never exceeded 3 deg. for any species and the morphological method overestimated that of the physiological method (Table 1).

DISCUSSION

This study is the first to test the predictions of the 'enhanced binocular field' hypothesis. This hypothesis proposes that the position of the eyes on the distal tips of the cephalofoil of the hammerhead sharks will confer greater anterior binocular overlaps and enhanced stereovision compared with carcharhinid sharks. These predictions were tested by comparing the visual fields of three hammerhead species (*E. blochii*, *S. tiburo*, *S. lewini*) with two carcharhinid species (*C. acronotus*, *N. brevirostris*).

Pupil dilation and shape

The blacknose shark possesses a round pupil, which is the most common pupil shape found in vertebrates (Walls, 1942). In bright conditions the round pupil can constrict to a near perfect pinhole protecting the eye from excess light (Walls, 1942). The lemon shark has a vertical slit pupil that can constrict down to a nearly closed position, serving to better protect the eye from intensity changes than the round pupil (Walls, 1942). Although the activity patterns of the blacknose shark are not well documented, it has been reported that the visual system of the lemon shark is adapted for both daylight and dim light (Gruber and Cohen, 1978). However, a heightened crepuscular and nocturnal activity pattern has been reported for the juvenile lemon shark (Sundström et al., 2001). Hueter mapped the retinal cone and ganglion cell topography of the lemon shark and discovered a prominent visual streak in the horizontal meridian and correlated this area of visual specialization to behavior and habitat (Hueter, 1991).

A horizontal visual band has also been reported in the bonnethead shark (Osmon, 2004), which possesses horizontal slit pupils. Both the lemon and bonnethead sharks possess a higher density of ganglion cells on the horizontal meridian of the retina but differ in the orientation of the slit pupil. The consequence of pupil shape upon the function of the visual streak is not well understood. In cattle, which have horizontal oval pupils, visual acuity is reduced on the horizontal but not the vertical plane. In the same experiment, simulated round pupils maintained acuity on both the horizontal and vertical planes (Rehkämper et al., 2000). In terrestrial
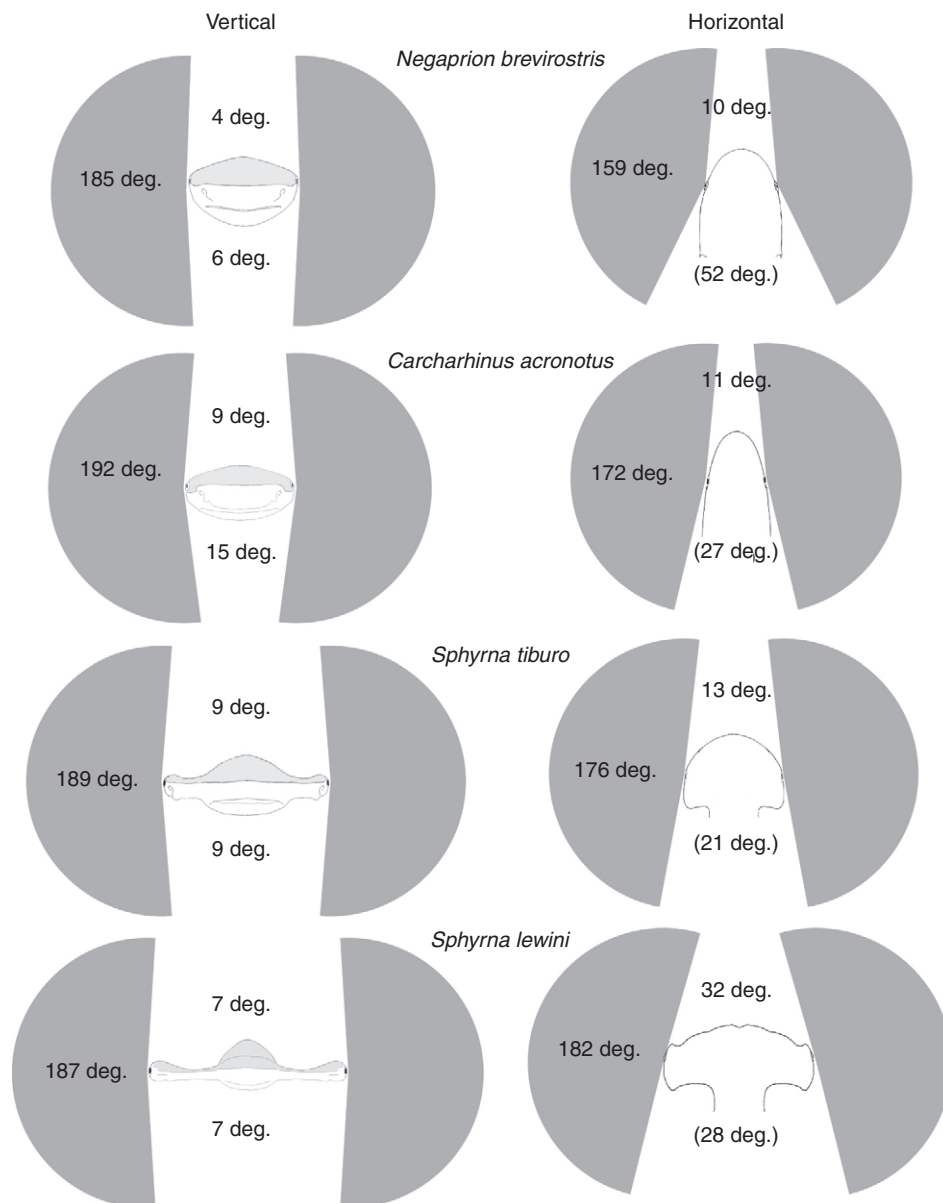
Vertical

Horizontal

Negaprion brevirostris

4 deg.

10 deg.

185 deg.

159 deg.

6 deg.

(52 deg.)

Carcharhinus acronotus

9 deg.

11 deg.

192 deg.

172 deg.

15 deg.

(27 deg.)

Sphyrna tiburo

9 deg.

13 deg.

189 deg.

176 deg.

9 deg.

(21 deg.)

Sphyrna lewini

7 deg.

32 deg.

187 deg.

182 deg.

7 deg.

(28 deg.)

Fig. 4. Static horizontal and vertical visual fields of four shark species. Values within the shaded areas represent the monocular visual field. Values shown outside of the shaded areas represent binocular overlaps, and values in parentheses indicate blind areas. All species had a horizontal anterior binocular overlap of 10 deg. or greater and blind areas posterior to the head. Both the scalloped hammerhead and the bonnethead sharks had larger horizontal monocular and binocular fields than the carcharhinid species. The vertical visual field was a full 360 deg. in all species and included both dorsal and ventral binocular overlaps. Line drawings modified from Compagno (Compagno, 1984).

vertebrates, slit pupils may be an adaptation to multifocal optical systems, which can produce a relatively shorter depth of focus and a reduction in chromatic blur upon the retina (Malström and Kröger, 2006). The ecological significance of pupil orientation among sharks with horizontal visual streaks is speculative and puzzling in this particular case, because the lemon and bonnethead sharks overlap in habitat and diet. It may be that the horizontal pupils would create a brighter, and perhaps a better focused image in the vertical meridian, because of the inverted optics of the cornea/lens system. However, to experience this increased vertical focus a vertical concentration of photoreceptors and ganglion cells must exist. At present the significance of varied pupil shape upon visual streaks and visual acuity in elasmobranchs is unresolved.

The pupil of the scalloped hammerhead shark was nearly round with a slight horizontal elongation. Although it is not as pronounced as that found in the bonnethead shark the shape of the pupil of the scalloped hammerhead shark allows tighter constriction than a round pupil and the field of view is slightly expanded on the horizontal plane.

Fast-moving species must adapt to changes in light intensity by quickly dilating or contracting their pupils. The relatively fast dilation in the bonnethead shark (3 min) indicates that it can respond rapidly to varying light conditions whereas the slower dilation response of the blacknose (20 min) and lemon (25 min) sharks may indicate adaptation to a less dynamic habitat or nocturnal activity. McComb et al. (McComb et al., 2009) report a higher temporal resolution (measured as the critical flicker fusion frequency) in the bonnethead shark than that of the blacknose shark; thus, further supporting this contention. A previous study reported a similar 25 min dilation time for the lemon shark (Kuchnow and Gilbert, 1967). It is peculiar that the pupils of the lemon shark required more time than all of the other species to dilate and there appears to be no other explanation other than the heightened crepuscular and nocturnal activity pattern reported for juvenile lemon sharks (Sundström et al., 2001). Similar to the results of this study, Kuchnow examined the pupillary responses of several elasmobranch species and found time to maximum dilation ranged from 1 to 30 min (Kuchnow, 1971). However, Gilbert et al. reported rapid dilation times in the nurse shark, *Ginglymostoma*

Table 2. *Post-hoc* pairwise comparison of visual field parameters in four shark species

| | Horizontal | | | Vertical | | |
| | Monocular | | | Monocular | | |
	N. brevirostris	C. acronotus	S. tiburo	N. brevirostris	C. acronotus	S. tiburo
C. acronotus	<0.001	–	–	<0.050	–	–
S. tiburo	<0.001	NS	–	NS	NS	–
S. lewini	<0.001	<0.001	0.021	NS	NS	NS
	Binocular			Binocular		
	N. brevirostris	C. acronotus	S. tiburo	N. brevirostris	C. acronotus	S. tiburo
C. acronotus	NS	–	–	0.033	–	–
S. tiburo	NS	NS	–	NS	NS	–
S. lewini	<0.001	<0.001	<0.001	NS	NS	NS
	Cyclopean			Cyclopean		
	N. brevirostris	C. acronotus	S. tiburo	N. brevirostris	C. acronotus	S. tiburo
C. acronotus	<0.001	–	–	NS	–	–
S. tiburo	<0.001	NS	–	NS	NS	–
S. lewini	<0.001	NS	NS	NS	NS	NS
	Convergence distance (cm)			Convergence distance (cm)		
	N. brevirostris	C. acronotus	S. tiburo	N. brevirostris	C. acronotus	S. tiburo
C. acronotus	NS	–	–	NS	–	–
S. tiburo	NS	NS	–	NS	NS	–
S. lewini	0.027	NS	NS	NS	NS	NS
	Blind area (cm^2)			Blind area (cm^2)		
	N. brevirostris	C. acronotus	S. tiburo	N. brevirostris	C. acronotus	S. tiburo
C. acronotus	NS	–	–	NS	–	–
S. tiburo	NS	NS	–	NS	NS	–
S. lewini	NS	NS	NS	0.031	NS	NS
	Anterior eye rotation (deg.)			Posterior eye rotation (deg.)		
	N. brevirostris	C. acronotus	S. tiburo	N. brevirostris	C. acronotus	S. tiburo
C. acronotus	NS	–	–	0.039	–	–
S. tiburo	NS	NS	–	NS	NS	–
S. lewini	NS	NS	NS	NS	0.037	NS

Two hammerhead (*Sphyrna tiburo* and *Sphyrna lewini*) and two carcharhinid species (*Carcharhinus acronotus* and *Negaprion brevirostris*) were compared.
 NS, not significant.

cirratum (30 s), the sandbar shark, *Carcharhinus plumbeus* (40 s), and the tiger shark, *Galeocerdo cuvieri* (45 s) (Gilbert et al., 1981). The lack of consistent methodology in both the control of light and measurement of pupil change has probably confounded the results of several studies and the ability for direct comparison among species.

Visual fields

The physiological assessment revealed that all species possessed anterior horizontal binocular overlaps of 10 deg. or greater (Fig. 4). The scalloped hammerhead shark (32 deg.) had the largest anterior binocular overlap among species. The close concordance and small margin of error (≤3 deg.) between the anterior binocular overlaps measured with the physiological and morphological methods indicate the morphological method is reliable. Measurements of the optical field (morphological) are not identical with functional retinal fields (physiological) and are slight overestimates because they are determined by examination of the angular limit from which the pupil can be seen (Martin, 1998). We determined that the winghead species exhibited the most extreme lateral head expansion, possessing a 48 deg. binocular overlap, which was greater than all species in the present study and nearly fourfold that measured in the carcharhinids. The scalloped hammerhead possessed a 34 deg.

overlap, which was larger than the bonnethead, lemon and blacknose sharks. The relatively large binocular overlaps determined for the winghead and scalloped hammerhead sharks facilitate excellent depth perception and the degree of overlap was similar to the yellow stingray, *Urobatis jamaicensis* (34 deg.) (McComb and Kajiura, 2008), and other predatory fishes such as the serranids (*Plectropoma leopardus* 36 deg., *Serranus scriba* 40 deg. and *Epinephalus fasciatus* 54 deg.) (Collin and Shand, 2003). The overlap in the bonnethead shark was greater than the lemon shark but not the blacknose shark. These findings indicate that the anterior binocular overlap has increased concomitant with the lateral expansion of the hammerheads. With head expansion the eyes of the scalloped hammerhead and winghead sharks have migrated into a more anterior position on the distal tips of the cephalofoil (Mara et al., 2009) and facilitates the enhanced binocular overlap. The eye position has not changed in the bonnethead shark (Mara et al., 2009) and this corresponds to possession of the smallest overlap measured within the hammerheads. Eye position upon the head also impacts the visual field in the carcharhinid species. The relatively small monocular field of the lemon shark (159 deg.) is due to lateral body expansion immediately posterior to the eyes, which reduces the posterior visual field compared with the other species.

A

Negaprion brevirostris

29 deg.

178 deg.

(33 deg.)

B

44 deg.

193 deg.

(18 deg.)

Carcharhinus acronotus

33 deg.

198 deg.

3 deg.

48 deg.

213 deg.

18 deg.

Sphyrna tiburo

37 deg.

203 deg.

9 deg.

52 deg.

218 deg.

24 deg.

Sphyrna lewini

52 deg.

202 deg.

(8 deg.)

69 deg.

219 deg.

9 deg.

Fig. 5. Maximum dynamic visual field of four shark species. (A) The maximum horizontal visual fields when the eyes are in the fully converged and diverged states. (B) The maximum horizontal visual field including the eyes in the fully converged and diverged states and the maximum lateral head yaw. Values within the shaded areas represent the monocular field. Values outside of the shaded areas represent binocular overlaps, and values in parentheses indicate blind areas. Line drawings modified from Compagno (Compagno, 1984).
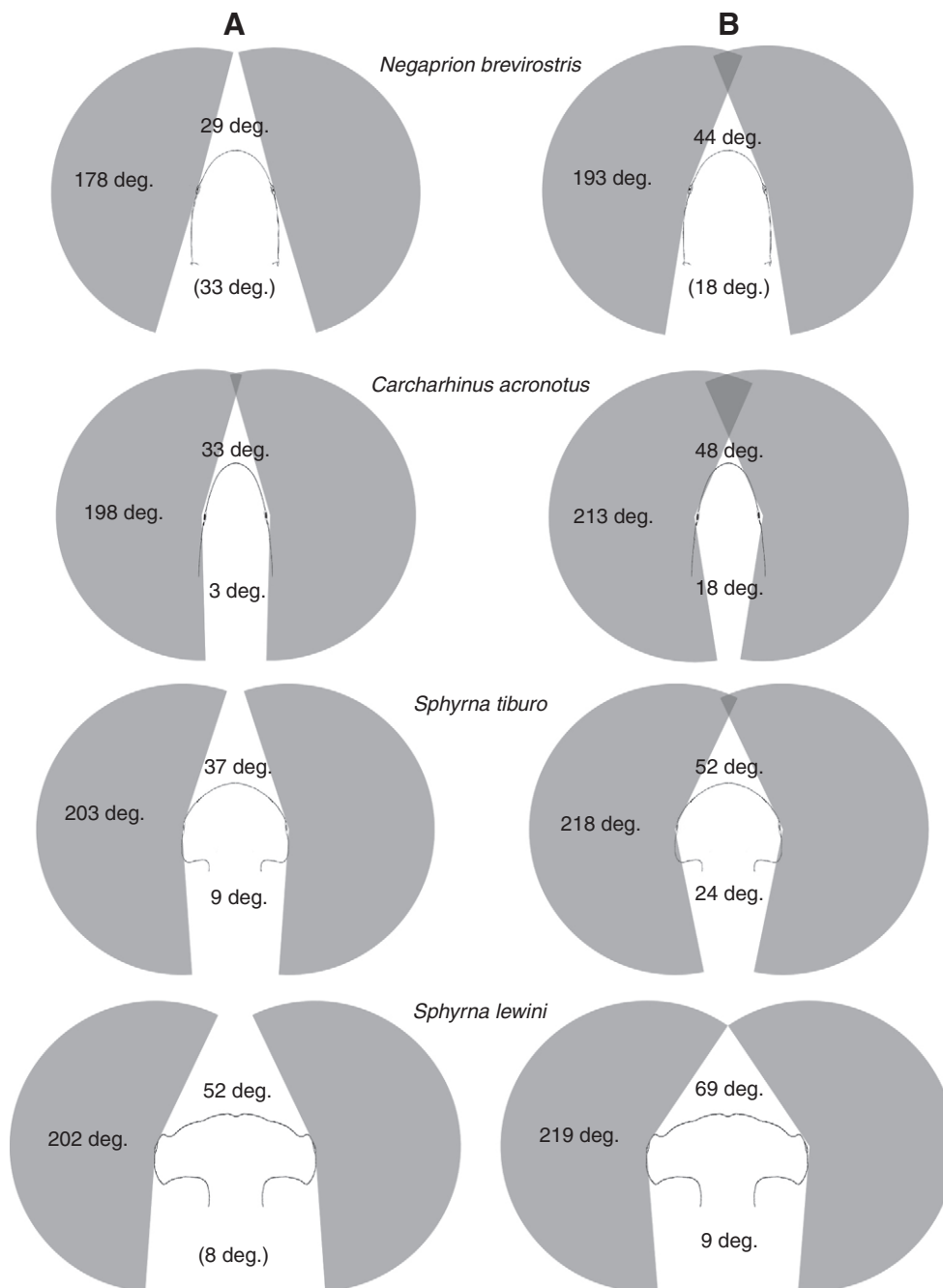
The visual field in the vertical plane overlapped dorsally and ventrally in all species providing a full 360 deg. cyclopean coverage. The dorsal and ventral overlaps in all species were generally similar in size, except in the blacknose shark where the ventral overlap was much greater. The blacknose shark forages upon fast-moving teleost prey (Cortés, 1999) and the expansive ventral visual field may facilitate prey tracking. The reduced dorsal overlap of the lemon shark is a result of a protrusion of skin above the eye. The convergence distance on the horizontal plane was smaller in the scalloped hammerhead shark than in the lemon shark and is likely to be due to the forward canting of the hammerheads eyes. The vertical blind area of the scalloped hammerhead shark was larger than the lemon shark and is a function of the widely spaced eyes forming a large base for the triangular blind area. The large dorsal blind area may have biological significance as there have been

anecdotal accounts of small fish swimming within this area around the hammerheads, perhaps eluding capture.

Head movement and eye rotation

We also tested whether species exhibit a behavioral compensation for anterior blind areas by yawing the head. During swimming the head yaws left and right thus expanding the viewable space in both the anterior and posterior directions (see Movie 1 in supplementary material). Both hammerhead species exhibit greater head yaw in the horizontal plane than the carcharhinids and the amount of yaw increased proportionately with head width. There exists then the potential for spatial information provided by the left and right eyes to be temporally integrated to generate a composite visual field that exceeds the dimensions of the static visual field. The cumulative effect of maximum eye rotation and maximum head movement reduces blind

areas and thereby enlarges the extent of the visual field. Head yaw was calculated on sharks in non-excited conditions, which probably under-represent the degree of yaw exhibited while actively searching for prey. An exaggerated head yaw requires a proportionately greater reflex eye movement, in the direction opposite to head movement, to preserve the image on the center of the visual field (vestibulo-ocular reflex).

During smooth head rotation most animals demonstrate a pattern of fixed gaze followed by fast saccades and counter rotations that shift the gaze (Fritsches and Marshall, 2002; Land, 1999). The purpose of stabilizing the gaze is to avoid retinal slip that occurs with head motion and the lag in response time of the photoreceptors (Land, 1999). While in motion, sharks stabilize their gaze through compensatory eye movements, which avoids the contamination of the translational flow-field in which they judge the distance of objects and their own heading (Land, 1999; Montgomery, 1983; Harris, 1965). It was predicted that sphyrnids would demonstrate a greater eye rotation in the horizontal plane to compensate for the exaggerated head yaw. To determine the degree of eye rotation the ocular musculature was manipulated post mortem and, therefore, the possibility of overestimation cannot be discounted. However, no differences among species were observed. When the eyes were in the maximum converged position the degree of binocular overlap increased in each species (Fig. 5). Although unlikely to occur naturally, if the scalloped hammerhead shark could maximally diverge both eyes, anterior binocular overlap would be preserved. In a previous study, scanning eye movements of *S. acanthias* reduced the extent of a posterior blind area by nearly 10 deg. (Harris, 1965). The posterior eye movements of the bonnethead, lemon and blacknose sharks would shift the field of view but only to the limit of the head and trunk of the body (Fig. 4); thereby, still retaining posterior blind areas. However, the posterior eye rotation of two species of batoids, *Raja eglanteria* and *Urobatis jamaicensis*, eliminates posterior blind areas (McComb and Kajiura, 2008) as the eyes are periscopic and the body poses no physical barrier to posterior vision.

In summary, we have tested several predictions derived from the 'enhanced binocular field' hypothesis by quantifying the visual fields of hammerhead species in contrast to carcharhinid species. The binocular overlaps in the hammerhead species increased with the expansion of the head. The findings of this study are consistent with the 'enhanced binocular field' hypothesis, and the role of enhanced vision may have influenced the evolution of the hammerhead cephalofoil.

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