Head morphology and electrosensory pore distribution of carcharhinid and sphyrnid sharks

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Synopsis

Selection to maximize electroreceptive search area might have driven evolution of the cephalofoil head morphology of hammerhead sharks (family Sphyrnidae). The enhanced electrosensory hypothesis predicts that the wider head of sphyrnid sharks necessitates a greater number of electrosensory pores to maintain a comparable pore density. Although gross head morphology clearly differs between sphyrnid sharks and their closest relatives the carcharhinids, a quantitative examination is lacking. Head morphology and the distribution of electrosensory pores were compared between a carcharhinid, *Carcharhinus plumbeus*, and two sphyrnid sharks, *Sphyrna lewini* and *S. tiburo*. Both sphyrnids had greater head widths than the carcharhinid, although head surface area and volume did not differ between the three species. The raked head morphology of neonatal *S. lewini* pups, presumably an adaptation to facilitate parturition, becomes orthogonal to the body axis immediately post-parturition whereas this change is much less dramatic for the other two species. The general pattern of electrosensory pore distribution on the head is conserved across species despite the differences in gross head morphology. *Sphyrna lewini* has a mean of 3067 ± 158.9 SD pores, *S. tiburo* has a mean of 2028 ± 96.6 SD pores and *C. plumbeus* has a mean of 2317 ± 126.3 SD pores and the number of pores remains constant with age. Sphyrnids have a greater number of pores on the ventral surface of the head whereas *C. plumbeus* has an even distribution on dorsal and ventral surfaces. The greater number of pores distributed on a similar surface area provides *S. lewini* pups with a higher density of electrosensory pores per unit area compared to *C. plumbeus* pups. The greater number of ampullae, the higher pore density and the larger sampling area of the head combine to provide hammerhead sharks with a morphologically enhanced electroreceptive capability compared to comparably sized carcharhinids.

Introduction

The hammerhead sharks comprise the family Sphyrnidae within the order Carcharhiniformes. They are most closely related to the family Carcharhinidae (Naylor 1992) and share many morphological similarities with carcharhinids. However, the eight species of hammerhead shark are characterized by a unique head morphology that is not found in any other extant vertebrate. The dorso-ventrally compressed and laterally expanded pre-branchial region of the head forms a cephalofoil that is an unmistakable diagnostic feature of the sphyrnid sharks (Compagno 1984).

Several hypotheses are proposed to explain the evolution of the sphyrnid cephalofoil but few have been empirically tested. It is suggested that the cephalofoil acts like a canard to provide hydrodynamic lift and increase maneuvering capabilities (Thomson & Simanek 1977, Compagno 1984). Compared to a carcharhinid, the cephalofoil provides sphyrnids greater lift and simultaneously confers a loss of hydrodynamic

stability that might aid the hammerheads in executing sharp turns (Nakaya 1995). Another hypothesis is that the cephalofoil functions in prey manipulation (Strong et al. 1990). This was suggested upon observation of a great hammerhead, *Sphyrna mokarran*, which used its cephalofoil to restrain a stingray on the sea floor while the shark bit off the pectoral fins. Other hypotheses involve potential advantages of spacing sensory structures across the surface or at the lateral ends of the cephalofoil.

The large internarial distance might provide sphyrnids with greater olfactory gradient resolution (Compagno 1984). Bonnethead sharks, *S. tiburo*, demonstrate olfactory gradient searching by differentially responding to stimuli in one nostril or the other (Johnson & Teeter 1985). However, the increased olfactory acuity hypothesis is not strongly supported upon examination of the sphyrnid head morphology. The rostral edge of the cephalofoil of several sphyrnid species is characterized by prenarial grooves that extend up to approximately a third of the head width on each side of the head (Compagno 1984). As the shark swims, water at any point along the rostral edge of the cephalofoil is channeled into the prenarial grooves and transported to the nares. These grooves serve to concentrate the olfactory stimuli at the expense of resolution as the shark will only be able to determine that an odorant was detected and not be able to determine if the source was medial or distal along the rostral edge of the cephalofoil.

It is also suggested that the eyes situated at the distal ends of the cephalofoil may enhance binocular vision anteriorly and increase the visual field whereas the large surface area of the head may increase the area sampled by the lateral line (Tester 1963, Compagno 1984). Neither of these hypotheses have been tested. Finally, by spacing the electroreceptors over a wide area, the sphyrnid head morphology may provide the sharks with a broader area of coverage and increased probability of encountering prey-generated electric fields (Compagno 1984). The various hypotheses are not mutually exclusive and it is the enhanced electrosensory hypothesis that is examined in this paper.

The enhanced electrosensory hypothesis states that the laterally expanded sphyrnid cephalofoil maximizes search area coverage to increase the probability of detecting prey. The wider head would sample a greater volume of the surrounding medium but there would need to be a corresponding increase in the number of electrosensory pores over the wider head area to maintain comparable spatial resolution of small, prey-generated electric fields. Therefore, the enhanced

electrosensory hypothesis assumes that sphyrnids have a greater head width than comparably sized carcharhinids and predicts that sphyrnids will have a greater number of pores which will yield a comparable or greater pore density.

This study compares the distribution of electrosensory pores on two sphyrnids, the scalloped hammerhead, *S. lewini*, the bonnethead, *S. tiburo*, and a representative carcharhinid, the sandbar shark, *Carcharhinus plumbeus*. Head morphology, pore number and pore density are quantified to test the assumption and predictions of the enhanced electrosensory hypothesis in hammerhead sharks.

Methods

Sharks used were incidental mortalities from other research projects and were sampled by gillnet or long line fishing. Shark precaudal length (PCL), fork length (FL), total length (TL) and most head morphometrics were measured to the nearest millimeter. Head measurements taken are illustrated in Figure 1 and include head width (HW), head length (HL), trunk width (TW), mouth width (MW), mouth length (ML), mouth to snout distance (MS), internarial distance (IN) and left and right head angle (HA). After measurement, heads were severed in the transverse plane at the posterior edge of the lower jaw and the bodies discarded. This position was chosen to standardize shark head length across species based on a skeletal feature and because no electrosensory pores are located caudal to the posterior edge of the lower jaw. Morphometric data were log transformed prior to analysis to allow utilization of linear statistical methods.

The head angle was defined as the angle described by a line from the antero-lateral edge of the incurrent naris to the opposite naris and then to the anterior edge of the center of the head (Figure 1). A high-resolution image of the ventral surface of the head was digitized on a flatbed scanner and head angles were measured with image analysis software (NIH Image v1.61). A mean head angle was obtained for each individual by averaging measurements for left and right sides.

Two methods were employed to measure surface area of the head. Each head was placed ventral surface down on a piece of paper and the head outline was traced. The outline was digitized on a flatbed scanner and image analysis software (NIH Image v1.61) was used to measure the area of the head tracing. Surface area was then estimated by doubling the traced area to
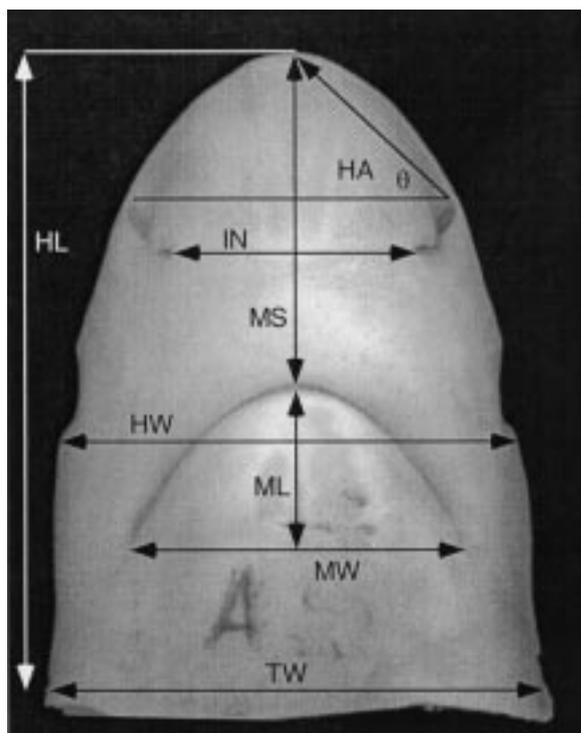
Figure 1. Photograph of the head of a sandbar shark, *C. plumbeus*, indicating head morphometrics measured on each individual. Morphometrics included head width (HW), head length (HL), trunk width (TW), mouth width (MW), mouth length (ML), mouth to snout distance (MS), internarial distance (IN) and head angle (HA). Volume and surface area of each head were also measured.

Table 1. Mean number of electrosensory pores, standard deviation, range, sample size and range of shark sizes for scalloped hammerhead, bonnethead, sandbar and blacktip sharks.

Species	Mean pores	SD	Range	n	Shark PCL (cm)
S. lewini	3067	158.9	2796–3400	35	36.1–59.4
S. tiburo	2028	96.6	1891–2223	19	38.0–70.0
C. plumbeus	2317	126.3	1983–2585	36	53.4–116.0
C. limbatus	2224	167.9	2038–2364	3	45.2–132.0

account for both dorsal and ventral surfaces. A second technique was used to verify the estimate thus obtained. A subsample of ten heads of each species was selected to represent a wide range of sizes. Each head was coated with several coats of liquid latex, which vulcanizes at room temperature. The latex was removed from the head in quarters (left, right, dorsal, ventral) and each section was laid out, traced, digitized and analyzed as above. From this subsample, a correction factor was generated for each species to more accurately represent the true surface area from the head trace area. Corrected head area data were normalized by log transformation prior to analysis.

Head volume was measured using a seawater volume displacement technique. An acrylic box was filled with seawater to the level of the spillover spigot in the side of the box. A head was placed into the box and the volume of water displaced by the head was measured in a graduated cylinder placed immediately below the spigot. Head volume data were log transformed prior to analysis.

After measurement, heads were fixed in 10% formalin, allowed to soak in several changes of freshwater for 24–48 h, transferred through a graded alcohol series (10%, 20%, 40% isopropanol) and preserved in 40% isopropanol.

Total number of electrosensory pores was counted for 35 *S. lewini*, 19 *S. tiburo*, 3 *C. limbatus* and 36 *C. plumbeus* individuals. The size ranges included individuals from juveniles to adults for all species except *S. lewini* which included only juveniles (Table 1). Each head was divided into dorsal and ventral surfaces and all pores were counted on both left and right sides. As each pore was counted, fingernail polish was applied with a toothpick to prevent recounting. For the three main study species, *S. lewini*, *S. tiburo* and *C. plumbeus*, four dorsal and eight ventral pore fields were identified based on natural divisions of the pores on the heads (Figures 2,3). The pore fields could be recognized on all three species despite the differences in gross head morphology. The number of pores in each of the twelve pore fields was examined in a subsample of ten individuals of each species. Counts of left and right sides were summed for each pore field for each individual. A mean number of pores in each pore field was generated for the ten individuals of each species. The percentage of pores in each pore field was calculated from the mean and used to compare the relative number of pores across species.

To compare the pore distribution patterns, a representative head from each species was selected and the dermis was carefully dissected from the head. The intact dermis was cut along the frontal plane to divide the dermis into dorsal and ventral halves which were cleaned of subdermal tissue. Each dermal sample was sandwiched between panes of glass, backlit by natural sunlight and photographed with color slide film. Pores
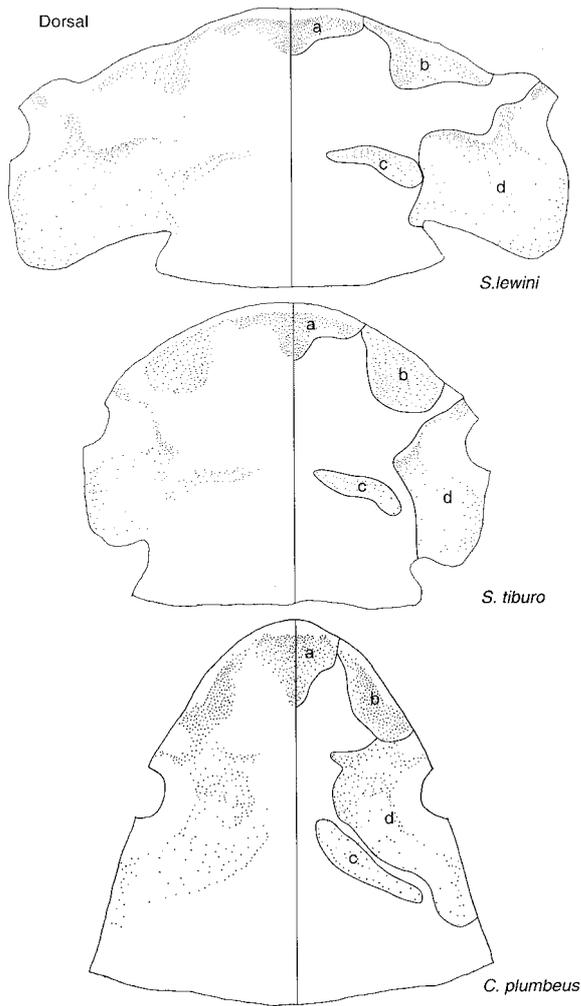
Figure 2. Distribution pattern of electroreceptor pores on the dorsal surface of the head of scalloped hammerhead, bonnethead and sandbar sharks. Pores are illustrated on the entire dorsal surface and the right side of each head is subdivided into four pore fields (a–d) which correspond across species.

appeared as bright points of light against a dark background of skin. The photographic slides (35 mm) of each skin sample were projected onto paper, the head outline traced and each pore mapped. This produced a direct one to one correspondence map of pores on a head.

Results

The head width plotted against the length of the shark for each of the three species is shown in Figure 4.
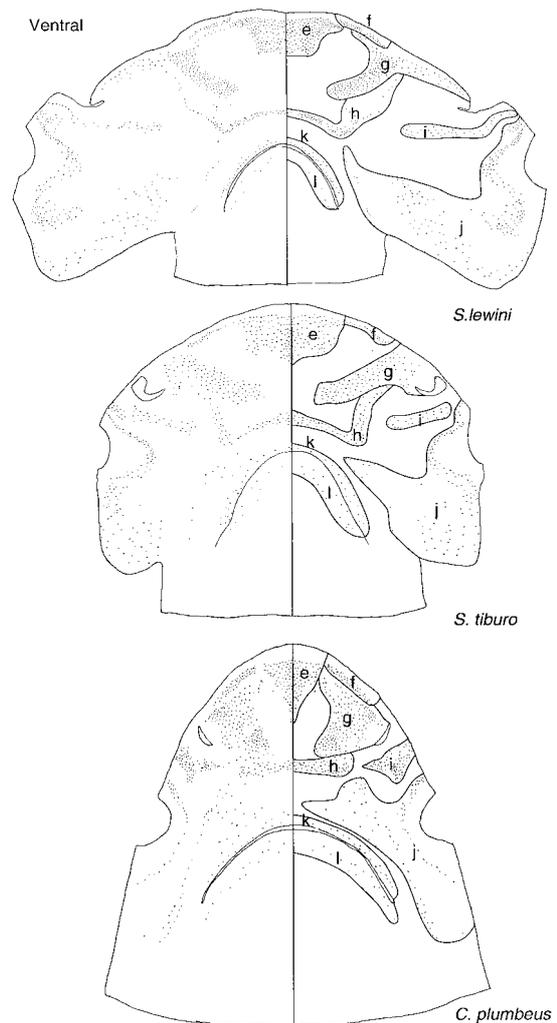

Figure 3. Distribution pattern of electroreceptor pores on the ventral surface of the head of scalloped hammerhead, bonnethead and sandbar sharks. Pores are illustrated on the entire ventral surface and the right side of each head is subdivided into eight pore fields (e–l) which correspond across species.

Not surprisingly, there are differences in head width between the three species (ANCOVA, $p < 0.0001$, df = 2). The scalloped hammerhead has the greatest head width, the sandbar has the smallest and the bonnethead is intermediate (Scheffe, $p < 0.0001$ for all species). The head width is approximately 3.01 times the trunk width for *S. lewini*, 1.67 times the trunk width for *S. tiburo* and 0.90 times the trunk width for *C. plumbeus*.

Concomitant with the increase in head width is a dramatic decrease in head angle in neonatal *S. lewini*
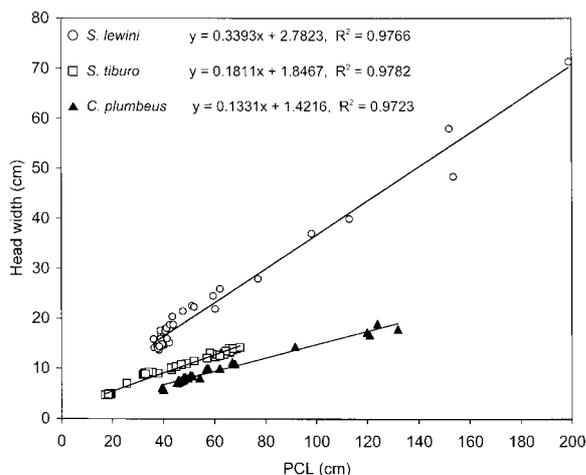
Figure 4. Head width as a function of shark precaudal length. Whereas head width increases linearly with shark size for *S. tiburo* and *C. plumbeus*, there is a dramatic increase in head width seen in immediately post-parturition *S. lewini* pups.
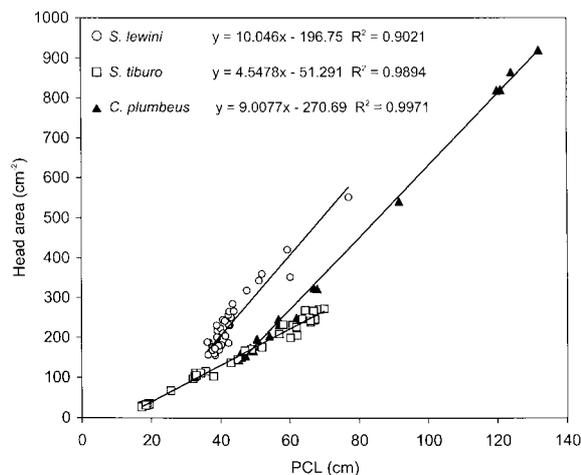

Figure 5. Anterior head angle plotted against precaudal length of sharks. Head angle decreases linearly from neonates to adults in *C. plumbeus* whereas a dramatic decrease in head angle is seen in post-parturition *S. lewini* pups. A smaller decrease in head angle is seen in *S. tiburo* neonates.

(Figure 5). The anterior head angle of *S. lewini* decreases sharply by approximately 10° as shark size increases from about 35–45 cm PCL. This sharp decrease is not seen in *C. plumbeus* where the slight decline in head angle is linear from neonates to adults. The decrease seen in *S. lewini* is apparent to a lesser

Figure 6. Surface area of the head of three shark species. For any given size, the scalloped hammerhead shark appears to have a greater head area than the other two species, the bonnethead shark and the sandbar shark. However, this difference is not significant.
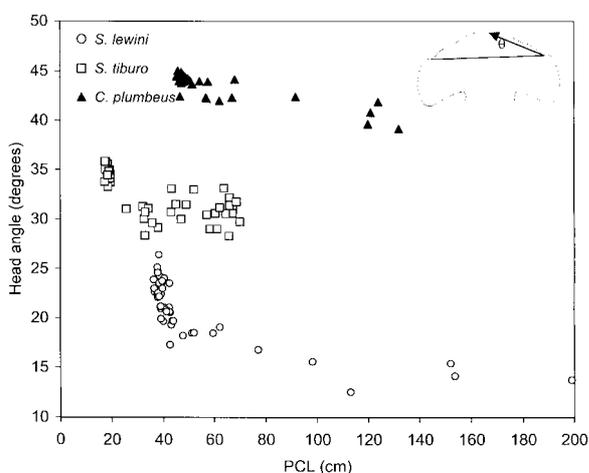
extent in *S. tiburo* where the change in head angle is approximately 5°.

Surface area of the heads was compared across the three species (Figure 6) as a precursor to calculation of the pore density (pores cm^{-2}). Surface area values estimated by doubling the traced areas were found to underestimate the true surface area of the head for all three species. Values obtained by measuring the latex skins indicate that the trace technique underestimated surface area of the hammerhead by about 1.0%, of the bonnethead by about 6.4% and of the sandbar shark by about 17.1%. Equations were generated to correct the head trace area to a better estimate of the true area based on the latex tracings. There was no significant difference in corrected head area between any of the species (ANCOVA, $p = 0.2950$, df = 2). Head volume also did not differ significantly between *S. lewini* and *C. plumbeus* (ANCOVA, $p = 0.2774$, df = 1). A significant interaction effect with *S. tiburo* precluded that species from the volume analysis.

The scalloped hammerhead, *S. lewini*, had the greatest number of pores followed by *C. plumbeus*, *C. limbatus* and *S. tiburo* (Table 1). Because of small sample size, the blacktip, *C. limbatus*, was not included in subsequent analyses. The total number of pores does not vary significantly with size (age) of the shark for any of the species (ANOVA, *C. plumbeus* $p = 0.6287$, df = 1, *S. lewini* $p = 0.8237$, df = 1, *S. tiburo* $p = 0.7126$, df = 1) and there was no significant difference
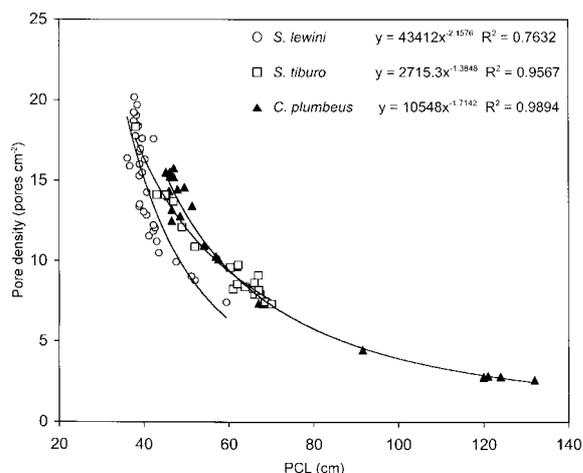
Figure 7. Electrosensory pore density (pores cm^{-2}) of scalloped hammerhead, bonnethead and sandbar sharks. Juvenile scalloped hammerheads have the greatest maximum pore density and density is inversely proportional to the size of the shark. Significant interaction effects prevented the data from being analyzed with parametric statistics.

in number of pores on left and right sides of the head for any species (paired t-test, *C. plumbeus* p = 0.1271, df = 23, *S. lewini* p = 0.9169, df = 34, *S. tiburo* p = 0.5173, df = 18). However, the total number of pores differed significantly between all three tested species (ANOVA, p = 0.0003, df = 2) with *S. lewini* having more pores than *C. plumbeus* which, in turn, had more pores than *S. tiburo* (Scheffe, p < 0.0001 for all species).

Pore density was calculated as the number of pores cm^{-2}. For all species, pore density is inversely proportional to the size of the shark because pore number remains constant whereas head area increases with shark size (Figure 7). *Sphyrna lewini* juveniles had the greatest pore density with a maximum 20.2 pores cm^{-2}. In contrast, the maximum pore density achieved by *C. plumbeus* was 15.5 pores cm^{-2}. The greater number of pores in *S. lewini* combined with the fact that it does not differ from the other species in surface area leads to the higher density of pores cm^{-2} for the scalloped hammerhead. A significant interaction effect among the species precluded statistical comparison of pore densities. Any perceived differences must be interpreted with caution because the size ranges of the species do not overlap completely; there were greater numbers of small *S. lewini* and large *C. plumbeus* individuals.

The number of pores on dorsal and ventral surfaces was also compared. The scalloped hammerhead had the greatest number of pores on the ventral surface

of the head and yielded a mean dorsal to ventral pore ratio of 0.71. The bonnethead had a mean ratio of 0.84. Although both sphyrnid species had a greater number of pores on the ventral surface of the head, *C. plumbeus* had a distribution of pores close to equal on dorsal and ventral surfaces with a ratio of 1.05. The pore distribution for *C. limbatus* was also close to uniform with a mean dorsal to ventral pore ratio of 0.94. Despite the differences in the number of pores on dorsal and ventral surfaces, the general pattern of pore field distribution on the head is conserved across the three examined species (Figures 2,3).

The pore distribution pattern on the dorsal surface of the head was divided into four pore fields (Figure 2) and the pore distribution pattern on the ventral surface of the head was divided into eight pore fields (Figure 3). The percentage of pores in each of the pore fields is mostly comparable between the species (Table 2). The notable exceptions include a greater number of pores in section b for the sandbar shark and a greater number of pores in section j for the scalloped hammerhead. In both cases the bonnethead displays an intermediate value.

Discussion

This paper is the first to quantitatively test the predictions of the enhanced electrosensory hypothesis based upon head morphology and electroreceptor pore distribution of carcharhinid and sphyrnid sharks. It is hypothesized that one of the factors that might have driven evolution of the sphyrnid head morphology was an increase in electroreceptive search area (Compagno 1984). If the sphyrnid head morphology was selected to enhance electrosensory prey detection it is assumed that the sphyrnids will possess a laterally expanded head morphology compared to a similar sized carcharhinid. Given a wider head, it is predicted that the sphyrnids will have a greater number of electrosensory pores to maintain a comparable or higher pore density than a carcharhinid. These predictions are supported by the data.

The assumption of the enhanced electrosensory hypothesis is that the hammerheads have their electroreceptors extended over a greater lateral distance than the carcharhinids. This is obviously true based on the head morphology of the species. Both sphyrnid species have a greater head width than the sandbar shark (Figure 4) with electrosensory pores distributed across the entire surface of the head for all species

Table 2. Percentage of mean number of pores in each dorsal and ventral pore field (Figures 2,3) for the scalloped hammerhead, bonnethead and sandbar sharks. The percentage of pores in each pore field is comparable across species even though the total number of pores differs.

Species	Dorsal pore fields				Ventral pore fields							
	a	b	c	d	e	f	g	h	i	j	k	l
S. lewini	12.4	10.2	3.3	15.2	10.9	3.6	11.7	8.4	2.3	19.6	1.7	0.7
S. tiburo	11.8	14.5	4.0	15.1	9.7	3.7	12.1	6.4	3.0	16.2	1.8	1.7
C. plumbeus	12.3	18.8	2.8	16.5	6.8	5.3	14.5	5.0	4.2	10.5	1.8	1.4

(Figures 2,3). Thus, the electroreceptors are distributed over a greater lateral distance in the sphyrnid sharks. One of the factors which drove evolution of the cephalofoil might have been selection for a head in which the electroreceptors were spaced further apart to increase the amount of lateral area sampled by the head. This would increase foraging efficiency by allowing the shark to search a larger area of the benthos. A 1 m PCL sandbar shark has a head width equivalent to a hammerhead of only 37 cm PCL. Thus, a small hammerhead is able to search the same lateral area as a sandbar shark that is 2.7 times as long.

There is, however, a cost associated with the increased head width of sphyrnid sharks. The broad head, oriented orthogonal to the body axis, makes it potentially difficult for the hammerhead pups to be born. To minimize the trauma of birth, the head of sphyrnid neonates is curved back along the side of the body to reduce the amount of frontal area that has to pass through the cloaca of the mother (see Gilbert 1967, Castro 1983). This functional reduction in head width is beneficial whether the shark is born head first or tail first. Immediately post-parturition the head angle decreases (Figure 5) which reflects the reorientation of the head to a position orthogonal to the body axis. Among the three species examined, this change in head shape is most conspicuous in the scalloped hammerhead where the head width is greatest. It is also present to a lesser extent in the bonnethead, although the smaller head width does not necessitate as dramatic a change in morphology.

Despite the fact that the sphyrnids represent the most obvious morphological extreme within the order Carcharhiniformes, the pore distribution patterns on the heads remain recognizable across all three species examined (Figures 2, 3). In addition to the conservation of pore patterns, the percentage of pores in each of the pore fields is mostly similar across species (Table 2). This suggests that the basic pore distribution pattern is conserved across the two genera while still allowing for some flexibility based on the ecology of individual species. Both sphyrnids had a greater number of pores on the ventral surface of the head whereas the two carcharhinid species had a more even distribution of pores over dorsal and ventral surfaces of the head. This difference in pore distribution might relate to the feeding ecology of the species. Juvenile scalloped hammerhead sharks feed primarily on benthic prey such as burrowing crustaceans and their associated goby symbiont (Clarke 1971). Bonnethead sharks also feed almost exclusively on benthic crustaceans, such as the blue crab, *Callinectes sapidus* (Cortes et al. 1996), whereas juvenile sandbar sharks feed on benthic crustaceans as well as small fishes in the water column (Medved et al. 1985). Therefore, it would be advantageous for sandbar shark pups to be able to detect potential prey items around the entire head whereas sphyrnids have the highest concentration of electroreceptors on the ventral surface of the head for detection of benthic prey.

Despite the existence of pore pattern illustrations for several elasmobranch species (Daniels 1967, Gilbert 1967, Raschi 1978, 1984, Chu & Wen 1979), no quantitative comparisons have been performed to determine if sphyrnids have a greater number or density of electrosensory pores compared to carcharhinids. The first prediction of the enhanced electrosensory hypothesis is that sphyrnids should have a greater number of pores compared to carcharhinids to maintain a comparable pore density over the greater head width. The scalloped hammerhead had a greater number of pores than either of the carcharhinid species. In contrast, the bonnethead had fewer pores. Although the bonnethead had fewer pores than *C. plumbeus* and *C. limbatus*, it had more than *C. obscurus* (mean number of pores = 1896.8, n = 9) (Raschi 1984) and *C. amblyrhynchos* (number of pores = 1440, n = 1) (Daniels 1967). To determine whether the number of pores on *S. tiburo*

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is atypical of sphyrnid sharks, pore counts must be performed on other sphyrnid species. Thus, the prediction of greater pore numbers in sphyrnid sharks is validated for the scalloped hammerhead but not for the bonnethead shark.

The second prediction of the enhanced electrosensory hypothesis is that the sphyrnids should have a comparable, if not greater, density of pores compared to the carcharhinids. A higher pore density implies finer spatial resolution that enables the shark to determine the location of an electrical stimulus near the body surface (Raschi 1978). Although the scalloped hammerhead pups appear to have a greater pore density than the sandbar sharks this is likely an artifact of the size difference of the sampled sharks. Unfortunately, the sample does not include large scalloped hammerheads. As the sharks increase in size, the head area and volume increase but the number of pores remains the same. Therefore, the pore density will decrease with size (age) of the shark. The decrease in density and attendant resolution might not be a detriment to larger scalloped hammerhead sharks because they inhabit clear oceanic water where vision can play a more important role in prey detection (Compagno 1984). As juveniles, scalloped hammerhead pups inhabit turbid bays where vision is limited and where they might need to rely on other senses for prey detection (Clarke 1971, Compagno 1984). Therefore, it is advantageous for the pups to have the highest density of pores when they are most needed.

Although *S. lewini* had a greater head width (Figure 4), it did not significantly differ in head volume compared to *C. plumbeus* or surface area (Figure 6) compared to both *C. plumbeus* and *S. tiburo*. This is ascribed to the large, flat, wing-like cephalofoil of *S. lewini* that serves to maximize area with minimal volume. The apparently high pore density found in *S. lewini* pups is attributed to the greater number of pores over a surface area that does not differ from *C. plumbeus*. It is hypothesized that this high density of pores will provide *S. lewini* pups with superior electrosensory acuity but this remains to be tested.

The decrease in pore density and resolution with increasing size (age) of the sharks might be compensated for by an increase in sensitivity. Sensitivity to electric stimuli is a function of the population of receptor cells within the ampulla proper (Raschi 1986) and length of the ampullary canal (Murray 1974). A larger ampulla will provide for a greater population of receptor cells which will enhance sensitivity and signal to noise ratio (Raschi 1986). Also, longer canals

are more sensitive to weak electric stimuli than are short canals (Obara & Bennett 1972). Therefore, along with the increase in shark size, the size of the ampullae and length of the ampullary canals will increase thus increasing the sensitivity of the electroreceptors. The decrease in resolution might be offset by an increase in sensitivity resulting from canal elongation thus resulting in no overall change in electroreceptive capacity.

This study provides evidence that the head morphology of sphyrnid sharks is concordant with the assumption and predictions of the enhanced electrosensory hypothesis. The greater number of receptors with an equivalent or higher packing density distributed over a laterally expanded head morphology indicates that the sphyrnid cephalofoil demonstrates the characteristics expected of a head that is optimized for electroreception. Although the sphyrnid head morphology supports the predictions of the enhanced electrosensory hypothesis, behavioral tests are needed to examine whether sphyrnids are able to utilize their unique cephalofoil to detect and resolve electric stimuli to a greater extent than similar sized carcharhinids.

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