ZOOLOGY

Maneuvering in juvenile carcharhinid and sphyrnid sharks: the role of the hammerhead shark cephalofoil

Stephen M. Kajiura*, Jesica B. Forni and Adam P. Summers

Ecology and Evolutionary Biology, University of California, Irvine, USA

Summary

The peculiar head morphology of hammerhead sharks has spawned a variety of untested functional hypotheses. One of the most intuitively appealing ideas is that the anterior foil acts, as in canard-winged aircraft, to increase maneuverability. We tested this hypothesis by determining whether juveniles of two hammerhead species (*Sphyrna tiburo* and *S. lewini*) turn more sharply, more often, and with greater velocity than a juvenile carcharhinid shark (*Carcharhinus plumbeus*). Although the hammerheads were more maneuverable, further investigation revealed that they do not roll their body during turns, suggesting that the cephalofoil does not act as a steering wing. We also show that hammerhead sharks demonstrate greater lateral flexure in a turn than carcharhinids, and that this flexibility may be due to cross sectional shape rather than number of vertebrae.

Key words: elasmobranch, head morphology, canard wing, electroreception, flexibility

Introduction

The dorso-ventrally compressed and laterally expanded head of the hammerhead sharks (Elasmobranchii, Sphyrnidae) is an unmistakable distinguishing characteristic not found in any other extant vertebrate. Various hypotheses have been advanced to explain the adaptive significance of this peculiar head morphology, including a broader visual field (Tester, 1963), greater electroreceptive sampling area (Compagno, 1984; Kajiura, 2001), directional olfactory acuity (Compagno, 1984; Johnsen and Teeter, 1985) and hydrodynamic lift and maneuverability (Murphy and Nichols, 1916). However, although some of these hypotheses have existed for many years, most remain untested.

The hydrodynamic-based hypotheses propose that the cephalofoil may act as a canard wing to firstly, provide lift, and secondly, increase maneuverability (Compagno, 1984, 1988; Nakaya, 1995). In sagittal section, the sphyrnid cephalofoil resembles an airplane wing, with a broadly rounded leading edge that tapers to a thin trailing edge. Although the shape of the cephalofoil strongly suggests a hydrodynamic lift function, this possibility has never been tested (Budker, 1971). The cephalofoil also provides an ideal planing surface which could be banked and lifted to provide a significant turning force at the anterior end of the shark, where it would be most effective in causing a change in direction (Nakaya, 1995). We address the second of these proposals, namely, that the cephalofoil head morphology provides a hydrodynamic maneuvering advantage over the more usual shark head design (Murphy and Nichols, 1916).

Hammerhead sharks are a clade with worldwide distribution, with cephalofoils ranging in width from 40–50% of total length (*Eusphyra blochii*) to just 18–21% of total length (*Sphyrna tiburo*; Compagno, 1988). The variation in head morphology within the Sphyrnidae enables comparisons to be made between intermediate and extreme head morphologies. The hammerheads are nested within a group of sharks with normal, pointed heads, the requiem sharks (Carcha-

*Corresponding author: Stephen M. Kajiura, Ecology and Evolutionary Biology, University of California Irvine, 321 Steinhaus Hall, Irvine, CA 92697-2525, USA; phone: ++1-949-824 4830; fax: ++1-949-824 2181; e-mail: kajiura@uci.edu

rhinidae). Carcharhinids are also worldwide in distribution, though they appear to encompass less morphological diversity in head shape than the hammerheads (Compagno, 1988). The carcharhinids provide a useful outgroup for the analysis of hammerhead function as they occur within the same size range, occupy the same habitats and have similar (though not identical) diets.

We compared the maneuvering behavior of three shark species, two morphologically disparate hammerheads, the scalloped hammerhead (*Sphyrna lewini*) and the bonnethead (*S. tiburo*), and a carcharhinid, the sandbar shark (*Carcharhinus plumbeus*). These species possess a range of head morphologies from the broad, flattened cephalofoil of the scalloped hammerhead, to the pointed snout of the sandbar shark, with the bonnethead representing an intermediate head morphology (Compagno, 1984; Kajiura, 2001).

Our goals were to firstly, compare maneuverability (turning speed and radius) among the three species, secondly, determine whether the head of the hammerhead species is rolled in a turn to increase turning forces, and thirdly, examine other morphological features that may be important in maneuverability.

Materials and methods

Collection

Juvenile scalloped hammerhead sharks (*Sphyrna lewini*) were captured by hand line fishing in Kaneohe Bay, Oahu, Hawaii. Sharks were maintained in a large outdoor holding pen (10 x 20 m, 2.5 – 0.5 m depth) at the Hawaii Institute of Marine Biology, Coconut Island. Sandbar sharks (*Carcharhinus plumbeus*) were captured by long line fishing on the reef drop off outside Kaneohe Bay and were maintained in the same pen as the hammerheads. Bonnethead sharks (*Sphyrna tiburo*) were born in captivity and maintained in cement holding tanks (2.4 x 4.9 m, 0.6 m depth) at a tropical fish wholesale facility in the Florida Keys. The sizes of the sharks used in this study are listed in Table 1.

Table 1. Size of the sharks used to analyze maneuverability. Note that the total length (TL) of the bonnethead sharks is much smaller than for the other two species.

Species	n	Mean TL ± SD (cm)	Minimum TL (cm)	Maximum TL (cm)
C. plumbeus	20	69.2 ± 5.16	58.9	77.5
S. tiburo	20	28.1 ± 1.54	24.8	30.4
S. lewini	20	75.1 ± 18.0	47.8	96.5

Video analysis

Video footage of the sharks swimming both in a steady, forward trajectory and turning was analyzed to quantify variables of interest. A Hi8 video camera mounted on a sliding track approximately 2 m above the surface of the water was used to record the swimming behavior of the scalloped hammerhead and sandbar sharks. The swimming movements of individual sharks were recorded as they swam at a constant velocity in a horizontal, straight-line trajectory directly under the camera, as well as when they made sharp turns (defined as a change in trajectory of > 90°) to orient to a prey-simulating dipole electric field positioned on the substratum directly below the video camera (cf. Kajiura and Holland, 2002). Observations from a lateral view confirmed that when the sharks were swimming, they maintained a constant altitude above the substratum until the actual bite at the electrodes when the snout was pointed downward (cf. Wilga and Motta, 2000)

Video footage of the bonnethead sharks was collected in a similar manner except that a submersible video eye was used as the input to the video camera. The video eye was positioned just under the surface of the water over the active electric dipole and provided a clear view of the sharks without any water surface distortion.

The Hi8 format video footage was digitized at 640 × 480 pixels at 30 frames per second and stored on computer. Digital movies were constructed of each shark swimming in a straight-line trajectory and also executing sharp turns to orient toward the center of the dipole. A sample frame of a shark swimming in a straight-line trajectory below the center of the video camera was captured and processed with image analysis software (Image-J). A comparison frame of the same individual turning toward the dipole was also captured and processed. Only footage in which the shark was centered in the frame was analyzed to avoid potential parallax distortion.

Turning and banking

A haphazard subsample of 45 orientations toward the dipole for both the scalloped hammerhead and sandbar sharks was examined to quantify frequency of sharp turns and frequency of body rolling. Because the first dorsal fin is stiff and rigidly inserted on the body, a clear lateral view of the fin indicates that the shark has rolled (see Fig. 1B). The results of both analyses were compared with χ^2 goodness of fit tests. Only video footage in which a single shark was in the frame was used in analysis. This eliminated the confounding effects of other individuals affecting the maneuvering of the focal shark.

Turning velocity and radius

The time it took for a shark to change its swimming trajectory by 90° as it oriented to the prey-simulating dipole electric field was quantified for the scalloped hammerhead and sandbar sharks. Turning velocity was measured in radians s^{-1}. The length of the arc described by the snout of the shark as it executed the 90° change in trajectory was also measured. Turning radius was calculated by dividing 2 times the arc length by pi and then dividing the result by the total length of the shark. Turn velocity and radius were compared with a Mann-Whitney U test. Whereas the scalloped hammerhead and sandbar sharks spanned approximately the same range of sizes, the bonnethead sharks were much smaller and were thus omitted from this analysis.

Area measurement

The digitized video footage was analyzed to quantify the dorsal surface area of the pectoral fins for all species as well as the dorsal surface area of the cephalofoil for the two hammerhead species. The dorsal sur-face area of the left and right pectoral fins was measured from the video frames for individuals swimming in a straight line (Fig. 1A, C, E). The ratio of the area of left and right fins was calculated for individuals of all three species. The area of the left and right pectoral fins was also measured for individuals that were executing a 90° turn toward the electric dipole (Fig. 1B, D, F). For individuals executing turns, the area ratio was calculated for the pectoral fin on the inside arc of the turn to the pectoral fin on the outside arc of the turn.

The area of the cephalofoil was measured for the two sphyrnid species as they swam in both straight trajectories and as they executed a turn. The area ratio of the cephalofoil was calculated for when the shark swam straight to when it was turning. If the cephalofoil was banked in a turn, the dorsal area would be smaller than when the shark swam with its head oriented horizontally.

To verify that changes in dorsal surface area of the cephalofoil would be detectable from the video footage it was necessary to measure the area of a cephalofoil rotated through a known angle. A pre-
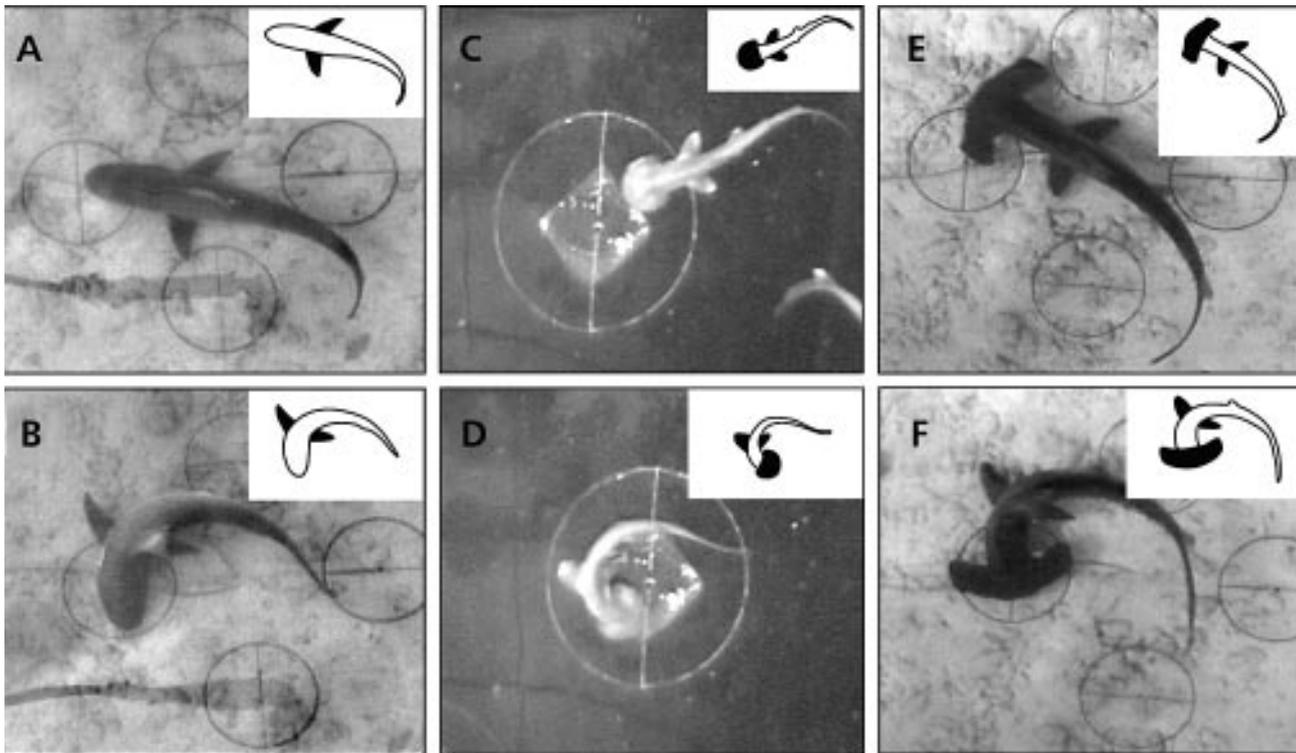

Fig. 1. Orientations of a sandbar shark (*Carcharhinus plumbeus*; **A**, **B**), a bonnethead shark (*Sphyrna tiburo*; **C**, **D**) and a scalloped hammerhead shark (*S. lewini*; **E**, **F**) toward a prey-simulating dipole electric field. The electrodes are in the center of the 20 cm diameter circle at which the sharks are biting in the lower panels. The dorsal surface area of the pectoral fins for all species and the cephalofoil area for the sphyrnids were measured from video frames in which the shark was swimming straight and executing a sharp turn toward the dipole. The insets represent tracings of the sharks in the video frames with the pectoral fins and cephalofoil shaded. Note that the bonnethead sharks are much smaller than the other two species, and also the clear view of the lateral surface of the dorsal fin in (**B**) as the sandbar shark rolls to its left.

served hammerhead shark head from an individual of the same size as the sharks used in the experiments was positioned from a mounted digital camera at a distance that allowed the head to fill the frame to approximately the same size as the heads in the video footage. The dorsal surface of the head was photographed while the head was in a position parallel to the imaging plane of the camera. The head was then rotated on its transverse axis to various angles (0°, 5°, 10°, 20°, 30°, 40°) from the parallel plane and rephotographed. Head area was measured from the digital photos using the same technique and image analysis software that was used for the video footage. The experiment was carried out in a single blind fashion such that the person who analyzed the images did not know what angle the head had been rotated for each photo. Head areas were compared for the different angles using an ANOVA.

Bending coefficient

The degree of flexibility demonstrated by the sharks was quantified as the bending coefficient (Aziz and Landberg, 2002). The bending coefficient was defined as the chord length from the tip of the snout to the tip of the tail during maximum lateral flexure (L1) divided by the total length of the shark (L2) and subtracted from one (Fig. 2). The bending coefficient ($1-(L1/L2)$) was computed for 20 individuals of each species. Although the bending coefficient was derived from a ratio, the data were normally distributed and homoscedastic so were compared with an ANOVA.

Second moment of area

Scalloped hammerhead and sandbar sharks across a wide range of sizes were collected from incidental mortalities in other experiments and the heads were severed in the transverse plane immediately posterior to the lower jaw. The trunk was placed on a piece of paper and the outline of the trunk was traced. The outline was scanned and used to calculate the second moment of area for the two species with the midline of the body taken as the neutral axis (MatLab). The data were analyzed with an ANCOVA with length of the shark as the covariate.
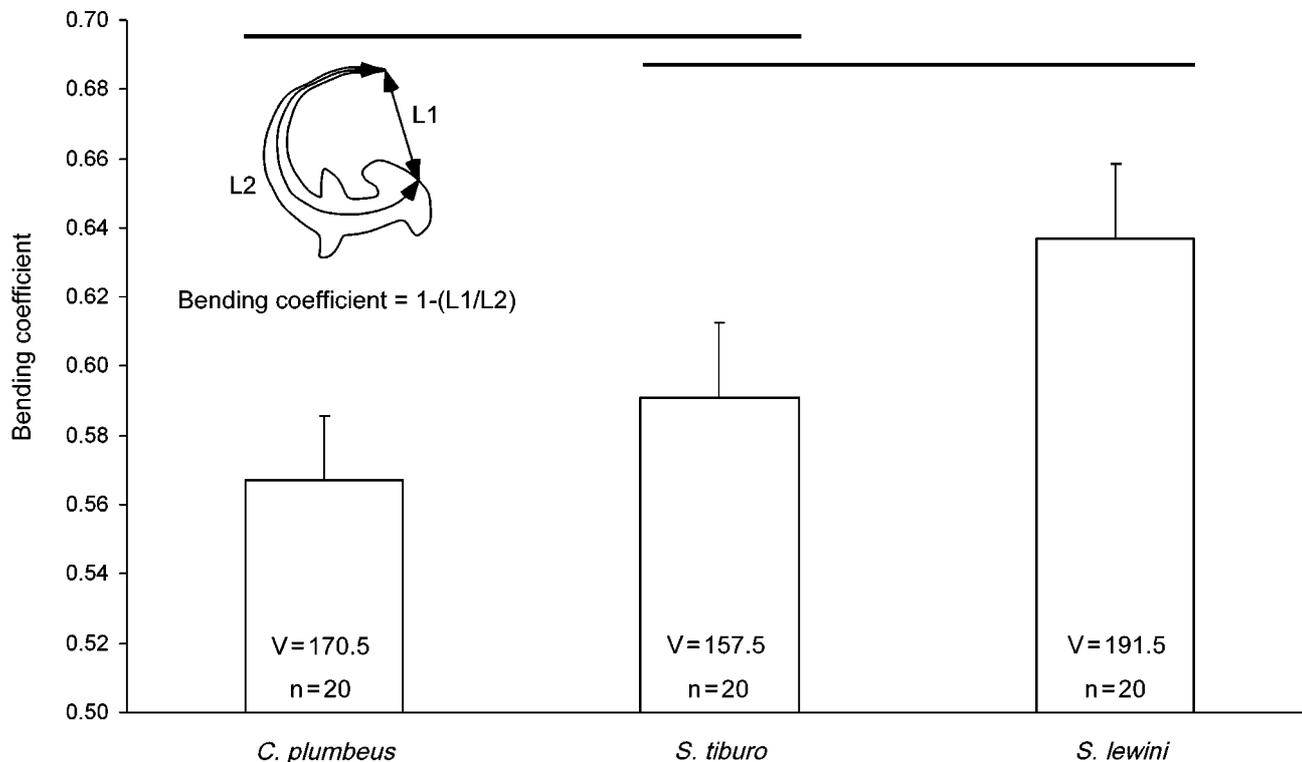

Fig. 2. Mean bending coefficient for three shark species. The bending coefficient was calculated as one minus the ratio of L1/L2. The sandbar (*C. plumbeus*) and scalloped hammerhead sharks (*S. lewini*) differed significantly in bending coefficient. The number of vertebrae for each species (mean of maximum and minimum vertebrae from Compagno, 1984) is indicated in each bar. Whereas scalloped hammerheads have the greatest number of vertebrae and the greatest bending coefficient (i.e., are most flexible), the bonnetheads have the fewest vertebrae but are not the least flexible. This indicates that flexibility is not solely a function of vertebral number. Error bars indicate standard error of the mean.

Results

Turning and banking frequencies

In a haphazard subsample of 45 orientations to an electric dipole, sandbar sharks executed turns of greater than 90° 60.0% of the time. In contrast, scalloped hammerhead sharks executed turns of greater than 90° 88.9% of the time. These turn frequencies differed significantly (χ^2 = 9.9802, p < 0.01). When the same turns were analyzed, the sandbar sharks demonstrated body rolling in 45.2% of the turns whereas the scalloped hammerheads did not demonstrate body rolling. This difference was also significant (χ^2 = 16.5789, p < 0.001). Taken together, these data indicate that scalloped hammerheads make more frequent sharp turns than sandbar sharks but do not roll as they turn.

Turning velocity and radius

The velocity of a turn (time necessary for the snout of a shark to traverse an arc of 90°) was compared between scalloped hammerhead and sandbar sharks. Although the actual arc lengths did not differ between the species (Mann-Whitney, U = 188.0, p = 0.7455), the scalloped hammerheads swept their head through an arc of 90° in less time than the sandbars. This resulted in a mean velocity of 8.2 ± 0.85SE radians s^{-1} for the scalloped hammerheads compared to 4.3 ± 0.12SE radians s^{-1} for the sandbar sharks. The data were normally distributed but were heteroscedastic, which necessitated the application of non-parametric statistics. The turning velocity was significantly greater for the scalloped hammerheads than for the sandbar sharks (Mann-Whitney, U = 30.5, p < 0.0001). The mean turning radius for the scalloped hammerheads and sandbar sharks was 13.7 and 13.4 cm respectively. When turning radius was expressed as percent of total length, the scalloped hammerheads and sandbar sharks had mean turning radii of 18.3 and 19.3% respectively. The two species did not differ in turning radius (ANOVA, $F_{1,38}$ = 1.404, p = 0.2434) which indicates that although they turned faster, the scalloped hammerheads did not turn in a tighter arc than the sandbar sharks.
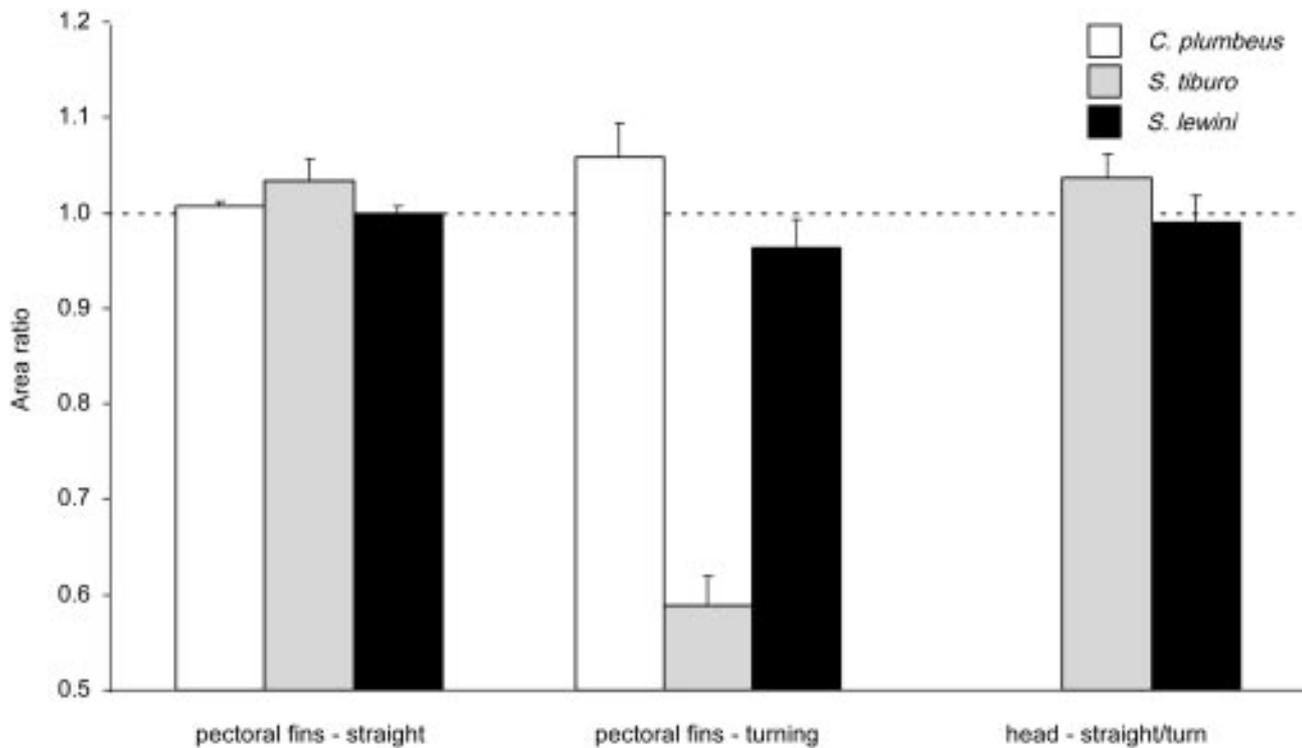

Fig. 3. Ratio of dorsal surface area of pectoral fins and cephalofoil during straight line swimming and turning in three shark species. Group 1 shows the ratio of left/right pectoral fin area in three shark species swimming in a straight line. For all three species the pectoral fin area does not differ on left and right sides (i.e., ratio is close to 1). Group 2 shows the ratio of pectoral fin area for fins on the outside and inside arc of the body during a turn. The pectoral fin area did not differ for sandbar (*C. plumbeus*) and scalloped hammerhead sharks (*S. lewini*) but was significantly different for bonnethead sharks (*S. tiburo*). Group 3 shows the ratio of the dorsal surface area of the cephalofoil as the sharks swam straight and turned. For both sphyrnid species there was no difference in cephalofoil area indicating that the cephalofoil was kept close to horizontal even while turning. Error bars indicate standard error of the mean.

Pectoral fin area

The dorsal surface area of the pectoral fins was quantified for sharks as they both swam straight and executed sharp turns. Sharks of all three species swimming at a constant velocity in a straight-line trajectory had equivalent pectoral fin dorsal surface areas on left and right sides (ANOVA, *C. plumbeus* $F_{1,38} = 0.008$, p = 0.9284; *S. tiburo* $F_{1,38} = 0.427$, p = 0.5176: *S. lewini* $F_{1,38} < 0.001$, p = 0.9982) (Fig. 3). In contrast, the area of the pectoral fins during a turn differed dramatically on the inside and outside of the body arc for the bonnethead sharks but this difference was not seen in scalloped hammerhead or sandbar sharks (ANOVA, *C. plumbeus* $F_{1,38} = 0.289$, p = 0.5939; *S. tiburo* $F_{1,38} = 123.876$, p < 0.0001; *S. lewini* $F_{1,38} = 0.065$, p = 0.7998). The pectoral fin positioned on the outside of the body arc during a turn had a measurably greater dorsal surface area than the pectoral fin on the inside of the body arc for the bonnethead sharks. This was due to the pectoral fin on the inside of the arc apparently being tucked under the trunk while the pectoral fin on the outside of the arc was splayed out away from the trunk. Whether this movement was under active muscular control or was merely a function of the fins moving passively as the body flexed remains uninvestigated. This pattern of fin movements was not seen in the other two species.

Cephalofoil area

To determine the change in dorsal area of the cephalofoil as a shark banked in a turn, the dorsal surface area of the cephalofoil was measured for a head rotated at various angles with respect to the camera. There was a significant difference in area between heads with the dorsal surface parallel to the imaging plane of the camera and heads rotated from that parallel plane (ANOVA, $F_{2,15} = 6.332$, p = 0.0101). A Scheffé post-hoc test indicated that there was no detectable difference in head area for a head rotated 5° from parallel (Scheffé, p = 0.6268) but there was a significant difference in area for a head rotated by 10° (Scheffé, p = 0.0124). This indicates that a shark banking less than 10° from horizontal produces detectable differences in head area.

The dorsal surface area of the cephalofoil was quantified from the digitized video footage of the two sphyrnid species swimming straight and turning. The area did not differ for an individual swimming in a
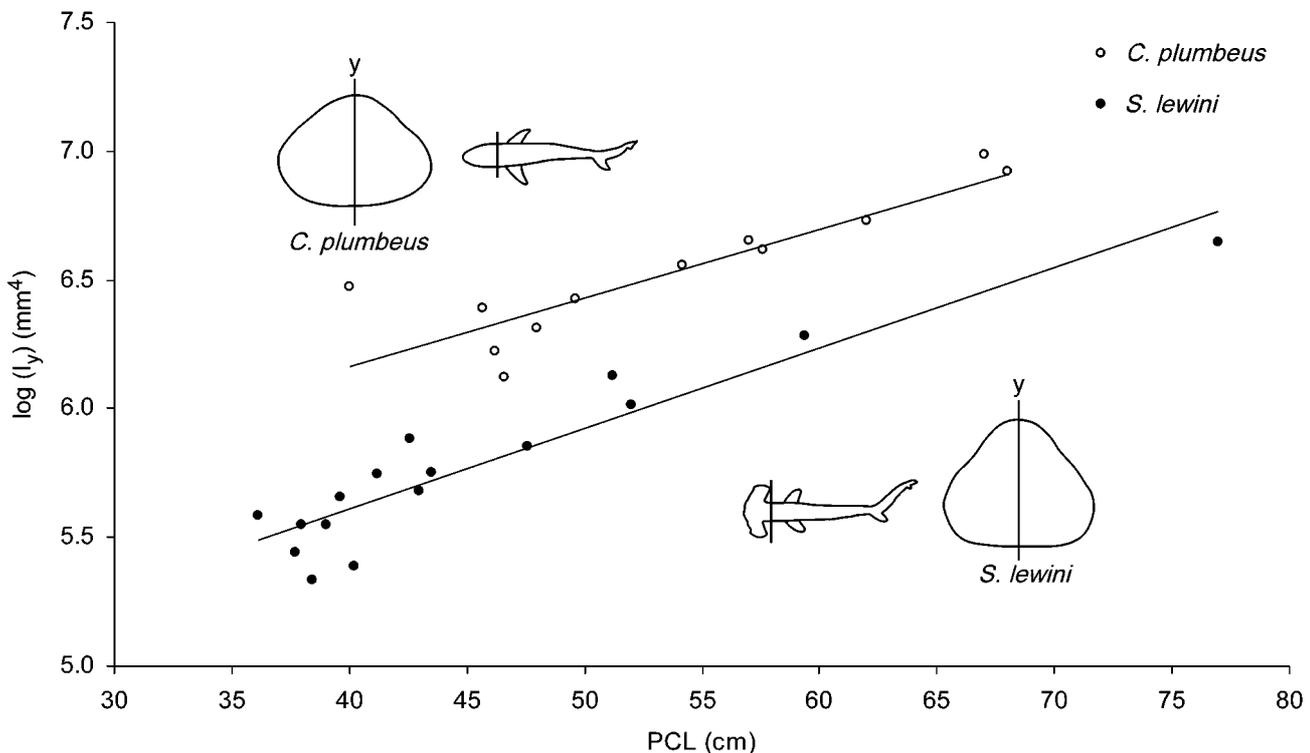

Fig. 4. Log of second moment of area plotted against precaudal length for scalloped hammerhead (*S. lewini*) and sandbar sharks (*C. plumbeus*). For any given size, the sandbars have a significantly greater second moment of area than the scalloped hammerhead sharks. This is due in part to the cross sectional shape of the trunk for the two species. Whereas sandbar sharks have a more dorso-ventrally compressed trunk immediately behind the head, the scalloped hammerheads have a more laterally compressed trunk which is easier to bend. The mid-sagittal plane (i.e., neutral axis, y) is indicated on the outline of the shape of the trunk in the transverse plane for each species.

steady, forward trajectory or executing a sharp turn (ANOVA, *S. lewini* $F_{1,38} = 0.029$, $p = 0.8646$; *S. tiburo* $F_{1,38} = 1.016$, $p = 0.3199$). This indicates that the cephalofoil was kept close to horizontal and was likely not used by either species to bank during a turn. Alternatively, if the cephalofoil was used to bank, it was rolled from horizontal by less than 10°.

Bending coefficient

The bending coefficient ($1-(L1/L2)$) differed significantly among the species (ANOVA, $F_{2,51} = 3.635$, $p = 0.0334$). The scalloped hammerheads had a significantly greater bending coefficient than the sandbar sharks (Scheffé, $p = 0.034$) but neither species differed significantly from the bonnetheads (Fig. 2). The scalloped hammerheads thus exhibited the greatest amount of lateral flexure whereas the sandbar sharks were the most stiff-bodied species.

Second moment of area

The second moment of area was calculated for the post-cranial trunk cross section of the scalloped hammerhead and sandbar sharks. A significant difference in second moment was found between these two species (ANCOVA, $F_{1,30} = 4.202$, $p = 0.0492$). For any given size, the sandbar sharks had a greater second moment of area than the scalloped hammerheads, which indicates a greater amount of stiffness and resistance to lateral bending for the sandbar sharks (Fig. 4).

Discussion

This study is the first to compare maneuverability in juvenile sphyrnid and carcharhinid sharks. The two hammerhead shark species we tested are more maneuverable than a typical carcharhinid shark, supporting the widely held view that hammerheads are very agile sharks. Scalloped hammerheads perform sharp turns ($> 90°$) almost 50% more often than sandbars, and they turn with about twice the speed. Although scalloped hammerheads demonstrate a greater turning ability than sandbar sharks, the cephalofoil, if it is rolled at all, is rolled by less than 10° during turns. Surprisingly, although both hammerhead species remained relatively level during turns, sandbar sharks rolled their entire body in nearly half the turns we analyzed. We propose that the cephalofoil does not function to bank the shark around turns, but rather provides hydrodynamic stability in turns.

Four advantages that come with level swimming through a turn may explain the lack of roll in the hammerheads: Firstly, juvenile sandbar sharks and hammerheads of both species typically swim with the ventral surface of the head only a few centimeters above the bottom when hunting prey (personal observations, SMK). The more conical snout of the sandbar sharks can roll without making contact with the substratum, but the expanded blades of the hammerhead cephalofoil could dig into the bottom, effectively tripping the shark. Secondly, because of the potentially large moment generated by even slight movements of the cephalofoil, the hammerheads must necessarily maintain their head level in a turn. Exaggerated banking would result in decrease stability which would likely be more detrimental than beneficial. Thirdly, when an airplane rolls to facilitate a sharp turn, there is a resultant loss of lift which is typically offset with an increase in thrust (Smith, 1985). By maintaining the cephalofoil horizontal as they turn, hammerheads do not need to produce additional thrust to offset a loss of lift. Fouthly, the cephalofoil acts as an electroreceptive organ to localize prey items, and the strength of the electrical signal decreases with the third power of distance (Kalmijn, 1982). If the head were tipped in a turn it would cause a large attenuation in the signal from a prey item perceived by ampullary organs on the 'uphill' side of the head, and a concomitant increase in signal on the 'downhill' side. This situation requires that the shark integrate information from the electroreceptive organs with data from the vestibular system to compute the real distance and direction of the prey. By keeping the head horizontal this increased level of neural processing is unnecessary.

The electrosensory system in conjunction with the high degree of maneuverability enables the hammerheads to detect and orient to benthic or pelagic prey. When they are young, all hammerhead sharks target buried, cryptic prey, though as adults many species switch from benthic to pelagic prey (Clarke, 1971; Compagno, 1984; Cortes et al., 1996; Stevens and Lyle, 1989). Capturing buried prey is a two stage process in which the shark must first detect the animal and then bite it. Detection of cryptic prey appears to be largely, if not exclusively, mediated by electroreception, a sense augmented by the expanded cephalofoil (Kajiura, 2001; Kajiura and Holland, 2002). Although the hammerheads can electrically detect prey several head lengths away, they may not be able to sufficiently localize the weak electrical signals to accurately bite the prey on the first pass. Because of their ability to turn quickly, hammerhead sharks can maintain electrical perception of a localized prey item while they reposition their mouth for capture. In contrast, less maneuverable carcharhinid sharks are not able to execute sharp turns as quickly as the hammerheads and may demonstrate a different strategy for prey capture (Kajiura and Holland, 2002).

This study included only juvenile sharks. Juveniles of all three species feed primarily on benthic prey items and, when motivated by a food odor stimulus, all three
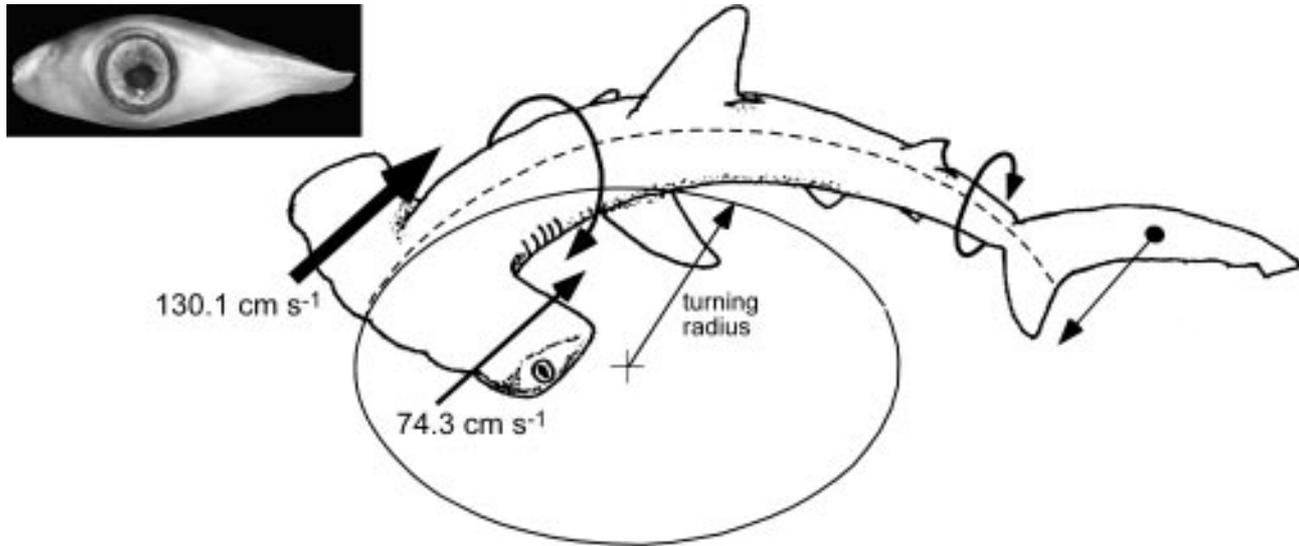
Fig. 5. As a hammerhead shark executes a turn, the outer edge of the head travels further than the inside edge. The average velocity of the midline of the head is 102 cm s^{-1}, and the head is 15 cm wide. The mean velocity of water across the inner and outer edges of the cephalofoil is illustrated. The difference in velocity across the cephalofoil should lead to increased lift on the outside edge of the head. Turning requires the heterocercal tail to generate more thrust towards the inside of the turning radius. The thrust reaction force acts on the dorsal lobe of the tail to produce a moment opposite that produced by the velocity differential across the cephalofoil. Inset shows a lateral profile of the cephalofoil of a juvenile scalloped hammerhead shark. The shape of the cephalofoil strongly suggests a hydrodynamic lift function.

species swim close to the bottom in search of prey (personal observations, SMK). Because of the natural tendency to swim close to the bottom, there is a bias against use of the cephalofoil as a planing surface. Orienting to prey items close to the bottom necessitates that the hammerheads not use their head to bank in a turn as this might cause them to 'trip' on the bottom. So, while juvenile hammerhead sharks do not use their cephalofoil as a planing surface we are reluctant to extrapolate this conclusion to adult sharks.

Adult scalloped hammerheads eat primarily pelagic prey, and in the three dimensional pelagic environment they might use their head to bank and roll in a turn. Unfortunately, filming natural or even baited feeding bouts in adult hammerheads is difficult both technically and because of the rarity of the event.

During straight-line, level swimming shark pectoral fins do not provide significant lift; however, they do play a role when changing altitude (Wilga and Lauder, 2000), but there are no studies on the contribution of the pectoral fins during turning. Wilga and Lauder (2000) found that very small changes in the angle of the fin had pronounced effects on lift generation so it is likely that changes in projected (dorsal) area of the fins during altitude changes would not be detected by our methods. However, the changes in fin angle during turning, especially a sharp turn, might be high enough to be seen from a dorsal view. Perhaps, in the absence of head or body roll the pectoral fins would be used as planing surfaces to facilitate turning. We found no difference in pectoral fin area on the inside or outside arc of the body for either the scalloped hammerheads or the sandbar sharks, which means only that if there were changes in shape (which seems likely) that they were smaller than our measurable resolution.

In contrast to the other two species, bonnethead sharks had a significant difference in pectoral fin area as they turned, indicating a gross repositioning. There is evidence that the total planing area of head and fins is constant for hammerheads, with those species possessing greatly expanded heads also having the smallest pectoral fins (Thompson and Simanek, 1977; Moss, 1984). The bonnethead, with its reduced cephalofoil, has the largest pectoral fins relative to body size among the hammerheads, and they appear to use their fins in turning whereas the relatively smaller fins of the scalloped hammerhead play a less visually obvious role. This study begs for particle image velocimetry of the fins during sharp turns, to quantify the differences in lift and drag of the two fins.

Assuming that the cross section of the cephalofoil is in fact a lift-producing hydrofoil, there is an interesting flow regime around the head in a turn. The cross section of the cephalfoil is similar to an airplane wing in that it has camber, that is, it is flatter on the ventral than the dorsal surface (Fig. 5). The outside edge of the expanded foil travels considerably further in a turn than the inside edge implying greater velocity over the outer edge. This should cause increased lift on the outside edge relative to the inside, establishing a moment that would tend to roll
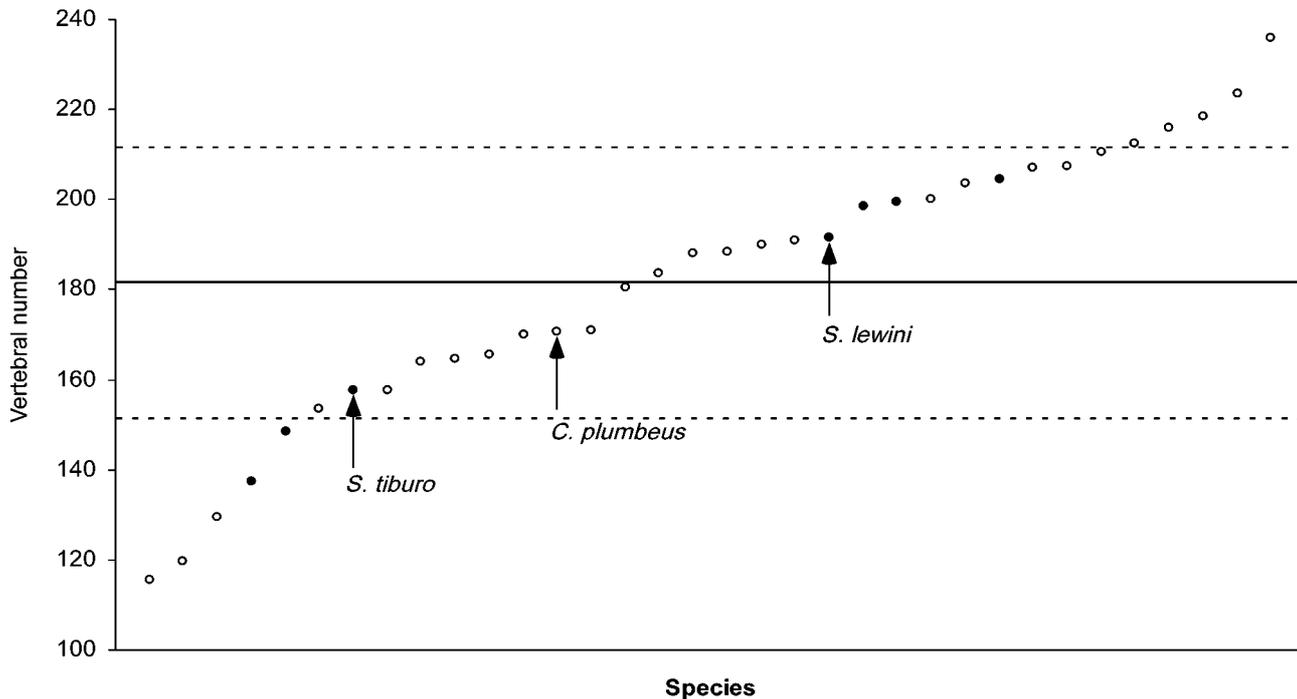
Fig. 6. The mean number of vertebrae for sphyrnid sharks (solid dots) and sharks in the genus *Carcharhinus* (hollow dots). The data were derived by taking the mean from the maximum and minimum number of vertebrae for each species from Compagno (1984). The solid horizontal line represents the mean of all species and the dashed lines represent standard deviations. The sharks used in this study all fall within one standard deviation of the mean.

the shark into the turn. The heterocercal tail, which beats towards the inside arc throughout the turn, will generate an opposite moment on the body (Fig. 5). The pectoral fins could also counteract this lift, very likely with only slight changes in attitude (Wilga and Lauder, 2000). We have not tested this hypothesis, but from a speculative point of view it is interesting that a tighter turn should involve greater asymmetry in the tail beat as well as a greater velocity gradient across the head.

Although scalloped hammerheads turn faster than sandbar sharks they do not turn in a tighter circle, a result that seems to contradict observations that sphyrnids are particularly flexible sharks (Kajiura and Holland, 2002). We will address this potential paradox by first examining flexibility, and then by showing the relationship between flexibility and turning performance. Our own experiments showed that scalloped hammerheads are able to curve their body in a tighter arc than sandbar sharks, and, in contrast to results from bony fishes (Brainerd and Patek, 1998), there is no increase in curvature with increasing vertebral number. The sharks in our study have similar vertebral counts (*C. plumbeus* 170.5; *S. tiburo* 157.5; *S. lewini* 191.5; from Compagno, 1984) and there is no relationship between the number of vertebrae and the ability to bend the body laterally (Figs. 2 and 6).

The flexural stiffness of a beam, its ability to resist bending, is defined as the product of the stiffness

(Young's modulus – E) of its material and its second moment of area (Vogel, 1988). Approximating a turning shark as a bending beam, and assuming that both scalloped hammerheads and sandbar sharks have the same material properties, we interpret second moment of area as proportional to the flexural stiffness of the shark. It is important to realize that though cross sectional area and second moment of area are related, they are not the same and can vary independently of one another. Cross sectional area is a measure of the size of a beam, whereas second moment of area is a measure of how well the material of the beam is positioned to resist bending in a particular direction. The smaller the value for the second moment of area the more easily a beam is bent. Our approach, evaluating second moment of a single cross section taken just behind the head, gives only a crude assessment of flexural stiffness.

We found that second moment of area for both species increased with body size, an unsurprising result since second moment should increase with cross section. At any particular length, a scalloped hammerhead has a significantly lower second moment than a sandbar shark, indicating that the body is more flexible, assuming that both species have the same material properties. There is no *a priori* reason to suspect that the tissue of the two species differs significantly in material properties. Over the size range we had available, the scaling

lines for second moment in the two species have the same exponent, an intriguing finding that requires the dataset be expanded to include some larger animals for further interpretation.

Flexibility could increase turning performance in two ways. Increased flexibility could decrease the turning radius, making for a faster turn at a given speed of travel by decreasing the total distance covered in making a particular turn. Alternatively, or additionally, increased flexibility could allow thrust to be oriented more obliquely to the direction of travel, increasing velocity through the turn. For scalloped hammerhead sharks flexibility implies the latter time saving device rather than the former. We found no difference in the distance traversed in a turn, but the velocity in the turn was significantly higher in scalloped hammerheads than sandbar sharks.

There is no agreed upon standard metric for assessing maneuverability; an artifact perhaps of the difficulty in measuring the parameters of intermittent locomotion (Drucker and Lauder, 2001). Scalloped hammerheads show a greater propensity for executing sharp turns, and maintain a higher speed through the turn; however, our results do not present a complete picture of biologically relevant maneuverability. For example, stopping ability, and carrying velocity through a turn are also mobility related parameters that we did not assess, though they have clear biological relevance. A finer scale study of the flow regimes around the shark's planing surfaces (as in Wilga and Lauder, 2000; Drucker and Lauder, 2001) has the potential to unravel the specific morphological features that are vital for agile swimming.

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