Evolutionary Pressures Exerted on the Hammerhead Shark Cranium: The Advantages of Varying Cephalofoil Sizes Based on Habitat

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Abstract: *This paper addresses a new perspective on the discussion of the hammerhead shark cephalofoil. Past studies have been centered around identifying possible selective pressures that have brought on the development of this morphology and the evolutionary trade-off that hammerheads must negotiate because of its emergence. Rather than identifying all-encompassing environmental pressures that apply to all hammerhead species, recent research has prompted analysis of the varying environmental forces present in different habitats to explain the emergence and variability in the evolution of the hammerhead cephalofoil. This analysis of previously published studies concludes that pelagic (open ocean) species improve sensory capabilities at the expense of hydrodynamic efficiency through the possession of a large cephalofoil, and that coastal species have selected for improved hydrodynamics and maneuvering abilities at the expense of sensory acuity by reducing the size of the cephalofoil.*

Keywords: hammerhead shark, cephalofoil, evolution

Introduction

Among all aquatic organisms, no body form is as unique as that of the hammerhead shark. Hammerheads showcase one of the most remarkable adaptations in the animal kingdom:, a dorsoventrally compressed and laterally extended cranium that biologists have named the cephalofoil, or head wing. Unique to 9 of over 400 species of sharks, the hammerhead cephalofoil represents a significant departure from the common body form of other shark lineages. Although aspects of the cephalofoil have been studied for decades, only recently has knowledge begun to surface regarding the selective pressures that caused its formation (Mara, 2010). Because locomotor and sensory adaptations are at the forefront of evolutionary importance in aquatic organisms, previous research has defined two important factors that may have contributed to the evolution of the cephalofoil: hydrodynamic efficiency and sensory advantage. A third but less likely possibility is its use for prey handling. Studies have concluded that overall body size, cephalofoil-to-body-size ratio, and habitat have all changed with the evolution of hammerheads (Lim et al., 2010; Mara, 2010). Larger bodied and pelagic species with a larger cephalofoil relative to body size are considered closest to the ancestral build. This ancestral build has evolved to more derived species that are smaller bodied, coastally oriented, and have a smaller cephalofoil relative to their body size.

This paper contrasts the cephalofoil morphologies of hammerhead species that inhabit varying marine habitats and determines that the influences of hydrodynamics and sensory adaptations on cephalofoil evolution are likely based on this environmental context. The evidence indicates that larger cephalofoils offer a sensory advantage that is most useful in open-water environments whereas the smaller cephalofoils of coastal species offer a hydrodynamic advantage that is most useful in navigating shallow or spatially complex marine habitats. A breakthrough in knowledge regarding the selective pressures that govern this unique morphology will contribute greatly to our knowledge of shark locomotion, sensory abilities, and feeding strategies, as well as their relative importance in creating the ecologically successful group of hammerhead sharks that inhabit today's oceans. On a broader scale, this analysis serves to shed light on the evolutionary trade-off between an aquatic organism's ability to process sensory information and its energetic cost of locomotion (in this case, the amount of energy required for the shark to swim). Which, if either, of these critical functions in the organism's life is more influential in the evolution of unique morphologies? In the case of the hammerhead shark, the varying environmental pressures of different marine habitats have sculpted multiple builds, suggesting that different trade-off strategies are optimal in different environments.

The General Trend

All habitats place physical pressures on the organisms that occupy them, and these pressures are ultimately answered with the morphological and physiological adaptations that result from the evolution of the inhabitants. Occasionally, these adaptations work divergently, forming what is known as an evolutionary trade-off. These trade-offs are characterized by the formation of one adaptation that negatively affects the function of another (Mara et al., 2015). In the case of the hammerhead shark, the trade-off exists between the increase in sensory abilities through an enlargement of the cephalofoil and the additional energetic cost of movement brought on by this enlargement.

In an attempt to analyze the variation of cephalofoil size and shape that exists between hammerhead species, Lim et al. (2010) utilized mitochondrial DNA to construct a phylogenetic tree of the family Sphyrnidae and has uncovered a trend that has produced a major leap in the understanding of cephalofoil evolution. The most ancestral hammerhead species is the winghead, Eusphyra blochii, which shows the largest cephalofoil relative to its body size. The winghead is the single species in the genus Eusphyra, while the other eight hammerhead species occupy the genus Sphyrna. As the lineage progresses from ancestral to derived species, the cephalofoil has become much smaller in comparison to the rest of the body. The most derived species is the bonnethead, Sphyrna tiburo, which represents a significant change in morphology with the smallest cephalofoil-to-body-size ratio of all hammerheads (Lim et al., 2010). This reduction in cephalofoil size is believed to have been caused by the variance in the environmental pressures that are placed on different species depending on the areas that they inhabit. Interestingly, the evolution from ancestral to derived species has resulted in a trend of cephalofoil reduction as well as a shift in habitat from the pelagic to coastal environment.

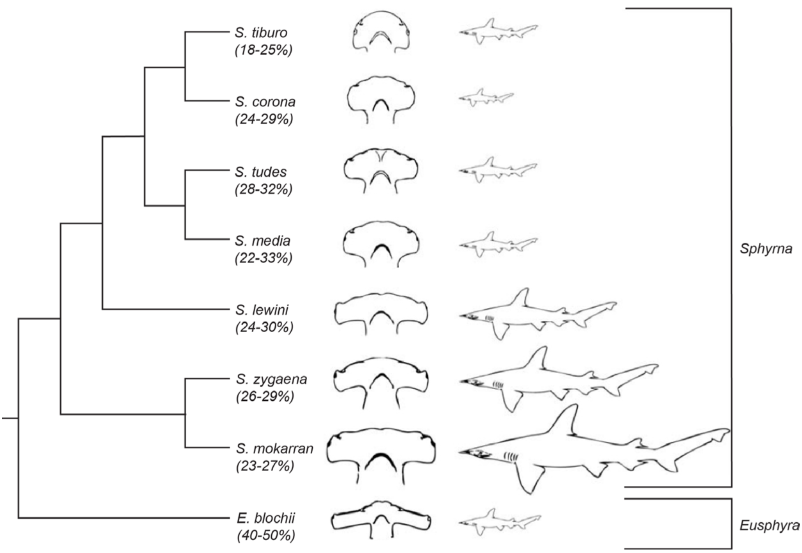

Figure 1: Phylogeny of hammerhead sharks. Parentheses show cephalofoil widths as percentage of body length (Compagno 1984; Lim et al., 2010). Modified with permission from Mara et al. (2015).

To understand why smaller cephalofoils have evolved, researchers must consider the pressures that the pelagic and coastal environments respectively place on hammerhead sharks and their roles in sculpting adaptive cephalofoil morphologies. Because swimming and processing sensory information from the environment are the two continuous actions required of hammerheads, the impact of environmental pressures on the hydrodynamics and sensory advantages of the cephalofoil are the two most important pieces of evidence to consider when discussing this evolutionary trend.

The relationship between cephalofoil size and habitat can be viewed as something of a spectrum. On one end rests the great hammerhead shark, Sphyrna mokarran, the largest and second-most-ancestral species according to Lim et al., (2010), which presents a large, rectangular-shaped cephalofoil and tends to be found in pelagic environments. The bonnethead represents the other end being the smallest, most derived species and having a smaller, shovel-shaped cephalofoil (Lim et al. 2010). Bonnetheads are also found exclusively in coastal and shallow-water habitats. The lifestyle of great hammerheads relies heavily on an ability to survey the pelagic environment with a large cephalofoil in order to find prey and potential mates in the open ocean. This enlargement, however, causes the cephalofoil to incur more drag while swimming, sacrificing hydrodynamic efficiency and increasing the shark's energetic cost of locomotion. Bonnetheads fall to the other end of the trade-off spectrum, as they can gather less sensory information from a shallow, coastal environment via a smaller cephalofoil but show a decreased cost of locomotion, and therefore conserve valuable energy. Additionally, this reduction brings a benefit of heightened maneuverability through geometrically complex coastal environments.

The Sensory Advantage

The presence of a cephalofoil has numerous benefits in the sensory context of a shark's life. The mechanoreceptive, electroreceptive, visual, and olfactory fields are all enhanced with the lateral expansion of the cranium. The mechanoreceptive functions of most aquatic vertebrates are performed by the lateral line system, which allows them to sense mechanical stimuli (e.g., sound, pressure, and movement) within the environment. This system is comprised of ciliated (hair-like) pressure-sensing cells known as neuromasts. These cells run along the length of the organism, forming "a continuous canal that is pierced periodically by epithelial pores, which link the canal lumen to the external environment" (Wonsettler & Webb, 1997, p. 195). The lateral line canal facilitates the capture of the mechanical information of the organism's own movements as well as surveying the external pressures from the environment and the movements of other organisms. The lateral expansion of the cephalofoil allows for an increase in the length of these canals across the cranium, thus enhancing the perceptual field.

The possession of a cephalofoil also beneficial for the the electroreceptive cells of the ampullae of Lorenzini, a network of gel-filled pores on the snouts of all elasmobranchs (sharks, skates, and rays) that recognize electrical impulses from the chemical reactions or muscle contractions within the bodies of other organisms. The majority of the pores are located on the ventral side of a shark's snout and, in the case of the hammerheads, serve to guide prey into the mouth as it enters the visual blind spot beneath the cephalofoil (D. Huber, personal communication, April 13, 2021). An expansion of the distribution of these pores brings two advantages: The additional pores and surface area on which they are distributed improve the shark's ability to sense direction of the recognized signals (Mara et al., 2015); the increase of volume within the cranium also allows the lengthening of the internal canals of electroreceptive cells, increasing the volume of water that is processed at any given time (McComb et al., 2009).

The visual field is also improved with the presence of the cephalofoil. The eyes of hammerhead sharks are placed at the distal ends of the cephalofoil and cause the areas of both the monocular and binocular visual fields to increase. Unlike most other sharks and some bony fishes who perceive their surroundings as two separate images through monocular visual fields with little or no overlap, hammerheads show significant overlap of the monocular fields anterior of the head, thus forming a single binocular visual field. The pelagic scalloped hammerhead, Sphyrna lewini, showcases a binocular field of 69°, which is significantly greater than in non-hammerhead species such as the blacknose shark, which shows an overlap of only 48° (McComb et al., 2009, p. 4017). There is a drawback, however, to hammerheads' widened visual field: With the lateral separation of the eyes in larger cephalofoils comes a distancing of the point of binocular overlap in the anterior direction. In other words, if the eyes are further separated laterally, a larger blind spot exists underneath the cephalofoil and in front of the mouth. Hammerhead species with large cephalofoils compensate for this with increased lateral head movement during swimming and likely utilize the improvements of the mechano/electrosensory systems to guide prey to the mouth as it enters the blind spot (McComb et al., 2009). The coastally oriented bonnethead, which has the smallest cephalofoil of hammerhead species, has a binocular overlap of 52°, showing only a slight improvement over non-hammerhead sharks (McComb et al., 2009, p. 4015). This form represents a small enhancement of visual capability over non-hammerhead species while minimizing the blind spot seen in hammerhead species with larger cephalofoils, as well as improving hydrodynamic efficiency. This morphology is indicative of one end of the spectrum that represents the cephalofoil trade-off. In the case of the bonnethead's reduced cephalofoil, hydrodynamic efficiency appears to represent a stronger evolutionary pressure relative to the importance of an improved sensory field, whereas in larger, pelagic hammerhead species, this relation is reversed. Even in bonnetheads, though it is not as conspicuous as other cephalofoil morphologies, the laterally extended structure of the head is retained and allows the species to utilize some of its sensory benefits.

The last and most widely tested portion of the cephalofoil's sensory array is olfaction. Dr. Stephen Kajiura et al. (2004) write that "there are clear olfactory advantages to the cephalofoil head morphology that could have led to its evolution, persistence, and diversification" (p. 253). The first of these advantages is an improvement in olfactory klinotaxis, or the ability to determine the direction of origin of odor stimuli. Kajiura et al. (2004) state that "the ability to resolve odors to left and right sides increases with increasing head width" due to the separation of the nostrils in either direction (p. 260). Secondly, the study states that a widening of the cephalofoil lengthens both the prenarial groove through which water enters the nostril and the olfactory rosette, which houses odor-sensing cells. These increases in size improve the shark's chance of recognizing an odor trail by allowing the shark to process more water at any given time (Kajiura et al., 2004). Hammerhead sharks also have an enlarged portion of the brain dedicated to smell compared to non-hammerhead species (Northcutt, 1977). This enlargement serves as anatomical evidence of the olfactory advantages brought on by the presence of the cephalofoil. Because the structures that recognize these odor stimuli are improved, leading to an increased volume of information that the shark must analyze, the portion of the brain that processes these stimuli therefore must also be enlarged.

Though an improvement of all four sensory aspects is clear when examining hammerhead vs. non-hammerhead species, the variation that exists between individual hammerhead species prompts further analysis. To review, an increased width of the cephalofoil, as seen in pelagic species, increases klinotaxis and the sampling area of the olfactory system and ampullae of Lorenzini. This enlargement also offers an expansion of the visual field and lateral-line system. In the case of large, pelagic species with large cephalofoils, the most influential environmental pressure on their development appears to be the need to obtain and process sensory stimuli from the environment. Pelagic species may depend on these sensory advantages for reasons that are vital to their survival and reproduction. They therefore fall towards this end of the cephalofoil-size spectrum despite an increased energetic cost of locomotion, and decreased hydrodynamic efficiency. This expansion may have occurred for two reasons. Prey may be harder to come across in the pelagic environment. The ability to lock onto and follow an odor trail or pressure signals given off by potential prey is essential for open-ocean predators. Pelagic species may also have taken this path in order to better navigate open-ocean habitats (Hoyos-Padilla et al., 2014). For example, the scalloped hammerhead, which occupies open ocean habitats during adulthood, is thought to sense and use geomagnetic fields to migrate across open ocean habitats to their spawning grounds (D. Huber, personal communication, April 13, 2021).

Coastal species such as the bonnethead have a much more localized lifestyle and do not perform cross-ocean migrations, so the sensory advantages brought on by a larger cephalofoil used in large-scale movement patterns may not be prioritized in their evolution. Prey-detecting sensory capabilities may also not be as important for coastal species, which feed on much more abundant prey within seagrass and reef environments.

These coastal species also do not need an enlarged cephalofoil for sensing stimuli at large distances as open-ocean species do, as their environment is limited by shallow depths and large obstacles. Because they encounter prey sources and potential mates in a much more manageable spatial range than is present in the open ocean, coastal species may have evolved to deprioritize the improvements in sensory abilities that come with an enlarged cephalofoil in favor of the hydrodynamic advantages of a small cephalofoil discussed below.

The Hydrodynamic Toss Up

In addition to the benefits to the sensory systems, the cephalofoil brings about many changes in the hydrodynamics of hammerhead shark swimming. Because they lack the swim bladder present in bony fishes, hammerhead sharks need to continuously swim in order to refrain from sinking (Thomson & Simanek, 1997). Hammerhead sharks are also incapable of using buccal pumping: muscle contractions within the cranium that create a flow of water into the mouth and over the gills. As is the case with most sharks, the continuous arrival of oxygenated water to the gills for gas exchange and respiration is only possible through constant swimming. A lifestyle of this nature depends on a morphology that favors hydrodynamic efficiency in order to minimize energy usage and oxygen consumption during swimming.

A shark's locomotion is generated by lateral beats of its heterocercal (asymmetrical) tail. The type of locomotion that sharks employ is a drag-based undulatory system in which the caudal fin creates drag during the time that it is displaced from the sagittal plane (Ferry & Lauder, 1996). The "classic model" that describes the forces at play in shark locomotion shows the reactive-force vector pointing ventral and posterior to the shark (Ferry & Lauder, 1996). This reactive-force vector shows the displacement of water away from the body and points opposite the direction of locomotion. This reactive force created by the caudal fin is perculiar, as it creates a torque around the center of the body, pushing the shark's tail upward and its head downward. This downward pitch of the head caused by the upward rotation of the tail then "must be countered by the lift acting on the anterior portion" in order to keep the shark horizontal during swimming (Barousse, 2009, p. 8).

While most sharks generate lift solely with the pectoral fins and along the ventral surface of the body, the cephalofoil serves as an additional lift-generating structure in hammerheads. Acting as the biological equivalent of a cambered wing, the cephalofoil allows for the upward pitching of the head to maintain neutral buoyancy during swimming (Gaylord et al., 2020). An increase in surface area of the cephalofoil as observed in the winghead shark (which has the largest cephalofoil relative to body-length of all hammerheads) "creates much more lift" than the heads of other species (Barousse, 2009, p. 75). However, with this increased surface area for lift generation comes an increase in drag incurred by the cephalofoil. Gaylord et al. (2020) show a direct relationship between cephalofoil size, exerted lift, and incurred drag at varying pitch angles for 11 observed species. This is to say that a larger cephalofoil relative to body size causes an increased difficulty for locomotion at all pitch angles, and therefore an increased energy input. Swimming behaviors have been observed in some species to compensate for these issues via "active flow control" (Gaylord et al., 2020, p. 10). For example, the pelagic great hammerhead has been observed swimming at roll angles of 45° to offset the negative impacts of increased drag associated with their large cephalofoil (Payne et al., 2016). Alternatively, coastally oriented species may have evolved with a reduction in cephalofoil size to lessen the effects of this drag on energy expenditure during swimming.

Though the cephalofoil creates drag and thus costs hammerheads additional energy, it also improves maneuverability. Nakaya (1995) states that "maneuverability is optimal, when a rudder is positioned at the anterior end of the body. This may indicate that the hammerhead sharks have, in a sense, the most effective body control system among the sharks or even in all the fishes" (p. 336). This idea is supported by Kajiura et al. (2003) who found a decreased turning radius in hammerhead species when compared to non-hammerhead species. Along with sharp turning movements, quick changes in the shark's elevation in the water column are possible via small changes in pitch because of the intensity of the lift that the cephalofoil incurs when deviated from a 0° angle of attack. These quick but controlled changes in direction are beneficial in both prey capture and predator avoidance.

Although a larger cephalofoil may provide the ability for a more intense turning or vertical movement, this may not be stable or spatially possible in a geometrically complex or spatially limited shallow-water habitat such as an oyster bed or coral reef. A sudden drastic change in elevation may prove to be damaging when navigating a complex habitat made up of sharp surfaces or substrates. This evidence indicates that the smaller, coastal oriented hammerhead species fall to the other side of the trade-off, selecting for less incurred drag along with fine-scale and smooth maneuverability, despite their reduction of sensory organs compared to the ancestral and larger-headed species.

Prey Handling

While not as prominent in the discussion of cephalofoil function, the use of the cephalofoil as a prey handling structure is worthy of mention. Great hammerhead sharks have been observed pinning southern stingrays to the sea floor with their cephalofoil. The sharks are then able to maneuver themselves into a position where they can immobilize the rays by biting off a portion of their wings. Observers witnessed a great hammerhead shark chase down a southern ray from behind, pin it to the sea floor with its cephalofoil, pivot to the front of the ray while maintaining contact, and remove the front of each of the wings (Strong et al., 1990). This hunting strategy serves as an example of hammerhead sharks utilizing their very capable and unique muscular anatomy to use their head as a multi-functioning tool. One study observes that scalloped hammerheads possess a hypaxial musculature that extends anterior to the gill slits, whereas a non-hammerhead species showed hypaxial muscles that only extended to the front of the pectoral fins (Nakaya, 1995). This forward extension of the musculature allows hammerhead sharks to have a much larger range of motion of the head, enabling this unique pinning behavior.

Though this behavior represents a noteworthy hunting tactic, it does not warrant arguments that the cephalofoil evolved for the purpose of prey manipulation. The great hammerhead is the only shark species that has been observed performing this behavior, but it is clearly not the only shark with a cephalofoil. Because this behavior has only been documented for one species, it is not realistic to claim that this behavior is a response to a significant environmental pressure placed upon the organism. In evolutionary theory, this is referred to as an exaptation. Biological structures are deemed exaptations when they function in a way that is different from the function for which natural selection originally formed them. The extension of the cranial hypaxial musculature has likely evolved for the purpose of enhanced stability and control of the cephalofoil during swimming rather than to facilitate this pinning ability. It is also known that great hammerhead sharks are "not bottom oriented" but a "species that spend much of their time in the water column" (Mara et al., 2015, p. 535). Additionally, southern rays are a preferred prey item for these sharks but are not their only food source. Because their prey ranges from bottom-dwelling rays to other free-swimming fish of similar lifestyles to their own, it is likely that this is a learned behavior resulting from years of hunting one of many prey items rather than an ability that carries the potential for a drastic change in cranial morphology.

Conclusion and Importance

Evidence indicates that both large and small cephalofoils sacrifice some aspect of biological importance to favor another, and that habitat is indicative of strategy within the trade-off between sensory and hydrodynamic benefits. As has been stated, smaller coastal species that require the ability to move through shallow water and complex habitats favor a smaller cephalofoil for increased ease of locomotion and maneuverability at the expense of enhanced sensory capabilities. Larger hammerhead species that roam the open ocean in search of scarce prey favor a larger cephalofoil that offers significant sensory advantages despite the impediment to their hydrodynamic efficiency. These claims have been supported by Dr. Daniel Huber: "In the context of the coastal environment, I think the evidence indicates that hydrodynamics wins out over sensory. In the context of the pelagic environment, I think the evidence indicates that sensory wins out over hydrodynamics" (personal communication, 4/13/21).

This body shape, variable as it may be within the hammerhead family, is not present in any other organism on the planet. Knowledge of the environmental pressures that have caused this type of evolution to occur and be confined to only one group of organisms may prove useful in understanding how physical traits are developed and propagated between lineages. Future comparative studies that explore sensory capabilities across hammerhead species may lend to the discovery of new foraging behaviors and anatomical variance across the phylogeny. Future studies within the area of hydrodynamics should include analysis of the proportions and growth rates of the rest of the organism's fins, and how they individually and collectively contribute to the complex mechanics of hammerhead locomotion. Additional research on the cephalofoil should attempt to determine the morphometric changes that occur with development and should explore the growth of the cephalofoil in species that utilize multiple habitats, coastal and pelagic, over their lifetime.

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