Evolution of the Hammerhead Cephalofoil: Shape Change, Space Utilization, and Feeding Biomechanics in Hammerhead Sharks (Sphyrnidae)

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Evolution of the Hammerhead Cephalofoil: Shape Change, Space
Utilization, and Feeding Biomechanics in Hammerhead Sharks (Sphyrnidae)

by

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A dissertation submitted in partial fulfillment of the requirements for the degree of
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DEDICATION

I dedicate this work to my parents Richard and Barbara Mara Jr. They have always supported me in all that I do and without them I could not have accomplished this feat.
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Evolution of the Hammerhead Cephalofoil: Shape Change, Space Utilization, and Feeding Biomechanics in Hammerhead Sharks (Sphyrnidae)

Kyle Reid Mara

Abstract

The relationship between form and function is often used to elucidate the biological role of a structure. Hammerhead sharks offer a unique opportunity to study form and function through phylogeny. Because sphyrnid sharks display a range of cranial morphologies this group can be used to address questions about the evolution of cranial design and investigate the effects of changes in head morphology on feeding structures and bite force. Geometric morphometrics, volumetric analyses, morphological dissections, and phylogenetic analyses of the cephalofoil were used to gain insight into changes in cranial design through evolutionary history. External morphometrics and internal volumetric analyses indicated that while the external shape of the cephalofoil and placement of the sensory structures is variable through evolutionary history, the volumes of the internal cranial elements do not change. Constructional constraints within the cephalofoil were confined to sensory structures while feeding morphology remained relatively unchanged. Analysis of the morphology and biomechanics of the feeding apparatus revealed that through phylogeny the feeding system does not change among sphyrnid species. However, size-removed bite force was lower than predicted for all sphyrnid species except Sphyrna mokarran. Despite differences in head morphology
between sphyrid and carcharhinid sharks, the feeding bauplan is conserved in sphyrid sharks with few changes to the feeding structures. Instead the chondrocranial and sensory structures are modified around the relatively static feeding core. Finally, the durophagous *S. tiburo* was found to consume hard prey in a manner that is biomechanically and morphologically different from other durophagous fishes. Furthermore, the diet of *S. tiburo* is constrained by the properties of its preferred prey.
GENERAL INTRODUCTION

Hammerhead sharks (Elasmobranchii, Carcharhiniformes, Sphyrnidae) are a unique group of cartilaginous fishes that possess a dorso-ventrally compressed and laterally expanded region of the head known as the cephalofoil. The cephalofoil is formed by lateral expansion and modification of the rostral, olfactory, and optic regions of the chondrocranium (Compagno, 1984; 1988; Haenni, 2001). The degree of lateral expansion is variable through evolutionary history. However, it generally ranges from 18% of shark total length (TL) in the bonnethead shark, Sphyrna tiburo, to 50% of TL in, the aptly named, winghead shark, Eusphyra blochii. Hammerhead fossil remains have been found in deposits dating to the Eocene (54.8 – 33.7 mya) (Gilbert, 1967). Sphyrnid sharks are circumglobal and range from sea grass flats to open ocean continental shelf habitats (Compagno, 1984; 1988). The evolution of the peculiar head shape has been studied for the last ~50 years. However, just now are the selective pressures that govern the design of the cephalofoil beginning to be understood. With the creation of a robust multigene phylogeny for sphyrid sharks (Lim et al., 2010), hammerhead sharks offer a unique opportunity for studying form and function in an historical context. Because the cephalofoil of sphyrid sharks represents such a significant morphological departure from the head morphology of their sister taxa, sphyrids can be used as a morphological extreme from which to address questions about the evolution and functional trade-offs between feeding, sensory reception and neural structures (Herrel et al., 1999). And by interpreting form and function of a closely related group of organisms such as
hammerhead sharks in an historical context we can gain a better understanding of the selective forces and constraints that govern the diversity of cranial form (Lauder and Liem, 1989; Herrel et al., 2001).

**EVOLUTIONARY HISTORY OF SPHYRNID SHARKS**

The phylogenetic relationship of hammerhead sharks indicates that the species with the most extreme lateral expansion of the cephalofoil (*Eusphyra blochii*) is the most basal while the least laterally expanded species (*Sphyrna tiburo*) is the most derived (Martin, 1993; Lim et al., 2010). Within the family Sphyrnidae there are two distinct genera (*Eusphyra* and *Sphyrna*) and eight currently recognized species (*E. blochii*, *S. mokarran*, *S. zygaena*, *S. lewini*, *S. corona*, *S. media*, *S. tudes*, and *S. tiburo*) along with the possibility of some geminate species within *S. lewini* and *S. tiburo* (Compagno, 1988; Naylor, 1992; Martin, 1993; 1995; Duncan et al., 2006; Quattro et al., 2006). Recent phylogenetic work indicates that the extreme cephalic morphology is the result of divergent selection acting on the primitive cephalofoil. Once the cephalofoil had originated, divergent evolutionary processes shaped lineages differently resulting in expansion along one lineage (*Eusphyra*) and contraction along another (*S. tiburo*). Furthermore, species of similar body size do not form monophyletic groups. The scalloped hammerhead, *S. lewini*, is more closely related to small species (*S. corona*, *S. media*, *S. tudes*, and *S. tiburo*) than it is to other large circumglobal species (*S. mokarran* and *S. zygaena*). Ancestral body size reconstructions also indicate that the common ancestor to all sphyrnid sharks was most likely a large bodied (>150 TL) shark (Lim et al., 2010).
HYPOTHESIZED FUNCTIONS OF THE CEPHALOFOIL

There has been considerable debate as to the origin and biological role of the cephalofoil (Tester, 1963; Thomson and Simanek, 1977; Compagno, 1984; Johnsen and Teeter, 1985; Strong et al., 1990; Martin, 1993; Nakaya, 1995; Kajiura, 2001; 2003; Kajiura et al., 2003). A number of hypotheses have been put forth to explain the evolution of the cephalofoil. The hydrodynamic lift hypothesis states that the cephalofoil functions similarly to a canard wing and provides hydrodynamic lift at the anterior end of the animal, thereby increasing maneuverability (Nakaya, 1995; Driver, 1997). The sphyrid cephalofoil is unique among elasmobranchs in that it has camber, possibly providing lift (Kajiura et al., 2003). Lift at the anterior end of the body is also provided by the pectoral fins (Thomson and Simanek, 1977; Wilga and Lauder, 2002). This hypothesis is supported by sphyrids with larger heads having smaller pectoral fin areas, while the total area of the cephalofoil and pectoral fins remains constant among species (Thomson and Simanek, 1977; Compagno, 1984; Kajiura et al., 2003). Furthermore, when similar sized sharks are compared, sphyrids have much smaller pectoral fins than carcharhinids which lack a cephalofoil (Nakaya, 1995; Driver, 1997).

The cephalofoil may also function in prey manipulation (Strong et al., 1990; Chapman and Gruber, 2002). This hypothesis is based on two observations of a great hammerhead *S. mokarran* using its cephalofoil to stun and pin stingrays (*Dasyatis americana*) and eagle rays (*Aetobatus narinari*) to the seafloor. After restraining the rays, the hammerhead rotated its body so that it could bite off the pectoral fins (Strong et al., 1990; Chapman and Gruber, 2002).
The remaining hypotheses concerning sphyrid cephalofoil origins are based on changes in sensory biology as a result of increased cranial surface area (Kajiura, 2003). The greater olfactory gradient resolution hypothesis is based on the greater separation distance of the nares in sphyrid sharks providing enhanced olfactory klinotaxis, increased olfactory acuity, and increased sampling area (Johnsen and Teeter, 1985). When bilateral and unilateral olfactory stimulation on live S. tiburo were performed, it was found that when a stimulus was applied to one nostril and not the other, bonnethead sharks initiated gradient searching behavior (Johnsen and Teeter, 1985). More recent work suggests that the cephalofoil can provide enhanced klinotaxis indicating that hammerheads with larger heads have an increased ability to resolve odors across the head (Kajiura et al., 2005; Gardiner and Atema, 2010). Furthermore, the cephalofoil provides for a greater sampling area than carcharhinid species (Kajiura et al., 2005). However, the olfactory epithelia surface area does not differ between sphyrid and carcharhinid sharks (Kajiura et al., 2005). A second hypothesis based on sensory biology is the enhanced binocular vision hypothesis (Tester, 1963). This hypothesis states that the placement of the eyes on the laterally expanded cephalofoil enhances binocular vision anteriorly and increases the visual field of sphyrids (Tester, 1963; Compagno, 1984; 1988). Recent work has show support for enhanced binocular overlap and a decreased blind area in the most laterally expanded species E. blochii and S. lewini (McComb et al., 2009).

The hypothesis that is most commonly proposed concerning the evolution of the sphyrid cephalofoil is the enhanced electrosensory hypothesis (Compagno, 1984; Kajiura, 2001). The basis for this hypothesis is the idea that the larger the surface area of the cephalofoil is, the greater the surface area that is devoted to electroreception,
providing the shark with increased ability to detect and spatially resolve the bioelectric fields of prey (Compagno, 1984; 1988; Kajiura, 2001; Brown, 2002; Kajiura and Holland, 2002). The laterally expanded head also enables sphyrid sharks to possess ampullary tubules that are longer than those found in carcharhinid sharks (Chu and Wen, 1979) which may confer greater sensitivity to uniform electric fields than their sister taxa (Murray, 1974; Bennett and Clusin, 1978). Previous studies have investigated and found varying degrees of support for these hypotheses individually (Nakaya, 1995; Kajiura and Holland, 2002; Kajiura et al., 2003; 2005; McComb et al., 2009). However, in order to understand the evolution and function of the hammerhead cephalofoil; sensory, neural, feeding, and morphological data must be investigated in concert.

**FUNCTIONAL MORPHOLOGY AND CONSTRAINTS**

Form and function relationships are often utilized to link an organism’s morphology with its ecological or biological role (Bock, 1980; Bock and von Wahlert, 1965). In order to truly understand how an organism’s form relates to its ecology, performance must be taken into account. Performance provides an estimate of an organism’s ability to accomplish ecologically relevant tasks such as prey consumption or the ability to escape predators (Irschick, 2002). Many such studies have drawn substantial conclusions regarding the relationship been morphology and variables such as prey type, habitat, and community structure (Herrel et al., 1996; Losos, 1992; Losos et al., 1994; Irschick and Losos, 1999; Korff and Wainwright, 2004; Toro et al., 2004).

The study of vertebrate form-function complexes, such as the cranium, is incomplete unless is incorporates the constraints imposed by its constituent elements
Functional constraints can include ecological constraints, behavioral constraints, physiological constraints, morphological constraints, and constructional constraints. Ecological constraints include environmental factors and interspecific and intraspecific interactions such as competition. When the organism’s behavior imposes limits upon the use of a structure, the term behavioral constraints is utilized. Physiological constraints involve limitations of the sensory systems and physiological processes such as nutrient processing. Morphological constraints result from constructional or architectural limitations imposed upon a given structure. Constructional constraints occur when spatial limitations are placed on a structure that has multiple biological roles (Barel, 1984; Reif et al., 1985; Motta and Kotrschal, 1992). These morphological constraints are sometimes referred to as phylogenetic constraints if the trait remains static across a range of closely related organisms (Sakamoto et al., 2010). Constructional constraints are particularly important when investigating the morphology of the spatially limited cranium. The cranium must contain all structures associated with feeding, respiration, neural integration, sensory reception, and musculoskeletal support (Barel, 1983; 1984; Motta and Kotrschal, 1992; Herrel et al., 2000; Devaere et al., 2001). However, the various components within the cranium often impose constructional constraints and trade-offs in other structures (Barel, 1983; 1984; Nijhout and Emlen, 1998; Devaere et al., 2001; Huber, 2006). Constraints have been previously demonstrated between and among sensory and feeding structures (Barel, 1983; 1984; Devaere et al., 2001; Huber, 2006).
FEEDING BIOMECHANICS

The chondrichthyan feeding mechanism is markedly different from that of bony fishes in that they lack pharyngeal jaws and have skeletal structures composed of tessellated cartilage rather than bone. Despite this pliant skeletal material, at least eight groups of chondrichthyans are durophagous, or have the ability to consume hard prey (Compagno et al., 2005; Huber et al., 2005; 2008; Ramsay and Wilga, 2007). In fishes, durophagy is often associated with enlarged jaw closing muscles, pavement-like molariform teeth, increased bite force, and fusion of the jaw symphysis (Wainwright, 1988; Turingan and Wainwright, 1993; Hernández and Motta, 1997; Clifton and Motta, 1998; Summers, 2000; Huber and Motta, 2004; Summers et al., 2004; Huber et al., 2005). These morphological modifications are often accompanied by behavioral modifications including unilateral biting, asynchronous muscle activity, tooth reorientation during biting, and specialized motor patterns (Summers, 2000; Wilga and Motta, 2000; Ramsay and Wilga, 2007).

Hammerhead sharks use a number of techniques for capturing prey. The larger species rely primarily on ram feeding and consume fish (Clarke, 1971; Compagno, 1984; 1988; Stevens and Lyle, 1989; Wilga and Motta, 2000; Motta, 2004) while the smaller species use a combination of prey capture techniques and consume a much wider array of prey species, ranging from crustaceans to fishes (Compagno, 1984; Wilga and Motta, 2000). A detailed examination of their feeding morphology, biomechanics, and prey capture behavior (kinematics) may reveal differences among species as a result of dietary and prey capture characteristics.
Despite the variation seen in feeding behavior and prey types in hammerhead sharks, feeding morphology and anatomy has been described for only one of the eight extant species (S. tiburo, Wilga and Motta, 2000). Sphyrna tiburo is the most derived species of hammerhead and also shows the greatest specialization of prey types, feeding primarily on portunid crabs in south Florida (Compagno, 1984; Cortés et al., 1996; Lessa and Almeida, 1998; Wilga and Motta, 2000; Bethea et al., 2007). Wilga and Motta (2000) found that S. tiburo exhibits very little upper jaw protrusion compared to other sharks and is the only hammerhead with molariform teeth. The feeding specialization of S. tiburo has resulted in morphological characters, such as molariform teeth, that separate it from other hammerheads. A detailed study of the cranial musculature of other hammerhead sharks is clearly needed before the evolution of cranial form in this group can be understood (Wilga and Motta 2000).

**Goals**

The goal of this study was to investigate the evolution and function of the hammerhead cephalofoil and the consequences of changes in head shape and form on feeding morphology and sensory structures and to elucidate any potential constructional constraints between or among feeding and sensory structures. For the first chapter, I utilized three-dimensional reconstructions of the internal elements within the cephalofoil along with a recently published phylogeny (Lim et al., 2010) and investigated any potential constructional constraints through evolutionary history. The specific goals for this portion of the study were to: 1) investigate the shape changes of the sphyrnid head through phylogeny; 2) examine the volumetric changes of cephalic elements through
phylogeny; and 3) investigate potential constructional constraints between and among feeding, neural and sensory structures. By interpreting form and function of a closely related group of organisms such as hammerhead sharks in an historical context a better understanding of the selective forces and constraints that govern the evolution of cranial diversity can be obtained (Lauder and Liem, 1989; Herrel et al., 2001).

In the second chapter, I investigated the functional morphology of the feeding apparatus in sphyrid sharks. A study of the feeding morphology and biomechanics of this clade may provide a window into the selective forces and constraints that govern cranial form in this unique group of very specialized fishes. Because the cephalofoil of hammerhead sharks represents such a morphological departure from the head morphology found in other carcharhiniform sharks, it can be used to address the evolution and consequences of changes in head form, and reveal functional morphological differences among species related to feeding. I utilized detailed anatomical dissections to ascertain the biomechanics of the feeding apparatus. This together with the output forces for each of the four principal jaw closing muscles was used in a three-dimensional static model of bite force (Huber et al., 2005). These data were also investigated through phylogeny using appropriate phylogenetic comparative methods (Garland et al., 2005). The specific goals for this part of the study were to: 1) describe and compare the functional morphology and biomechanics of the feeding apparatus of the hammerhead sharks; 2) investigate if changes to the feeding bauplan exist in sphyrid shark or if changes are confined to surrounding structures with conservation of the feeding apparatus; and 3) investigate the relationship between cranial design and feeding morphology within this clade.
Lastly, I investigated further the enigma of durophagy in the bonnethead shark *S. tiburo*. *Sphyra tiburo* consumes hard prey (including swimming crabs *Callinectes spp.* and small lobsters *Panulirus argus*) in south Florida (Compagno, 1984; Smith and Herrnkind, 1992; Cortés et al., 1996; Lessa and Almeida, 1998; Bethea et al., 2007). However, it does so without many of the morphological specializations typically seen in durophagous chondrichthyans (Summers, 2000; Summers et al., 2004; Huber et al., 2005; Mara et al., 2010). Little is known about how *S. tiburo* consumes hard prey without these specializations. The goals of this study were therefore to: 1) characterize the mechanical function of the feeding mechanism of *S. tiburo* through biomechanical modeling of biting and bite force measurements obtained via tetanic stimulation of jaw muscles and restraint of live animals; 2) compare the bite force of *S. tiburo* with that of other fishes; and 3) identify functional constraints on prey capture and diet by comparing the bite force of *S. tiburo* to the fracture properties of its primary prey item, blue crabs *Callinectes sapidus*.

**Literature Cited**


CHAPTER 1: CONSTRUCTIONAL CONSTRAINTS WITHIN THE HEAD OF HAMMERHEAD SHARKS (SPHYRNIDAE)

ABSTRACT

The biological role of an anatomical structure can be elucidated by investigating the relationship between form and function. The study of constructional constraints is particularly important if a structure, such as the cranium, serves multiple biological roles, and is therefore shaped by multiple selective pressures. The sphyrnid cephalofoil presents an excellent model for investigating potential trade-offs between sensory, neural, and feeding structures. In this study, hammerhead shark species were chosen to represent differences in head form through phylogeny. A combination of surface-based geometric morphometrics, computed tomography volumetric analysis, and phylogenetic analyses were utilized to investigate potential trade-offs within the head. Geometric surface landmark analyses indicate relative changes in the sensory structures through phylogeny with few changes in the feeding apparatus. The more basal winghead shark *Eusphyra blochii* has small anteriorly positioned eyes. Through phylogeny the relative size and position of the eyes changes, such that derived species have larger, more medially positioned eyes. The lateral position of the external nares is highly variable, showing no phylogenetic trend. Mouth size and position are conserved, remaining largely unchanged. Volumetric computed tomography (CT) analyses, however, reveal that there are subtle changes associated with the evolution of the cephalofoil. The volume of the
feeding muscles and jaw cartilages are positively correlated through evolutionary history. The few constraints that were found were isolated to the nasal capsule volume’s inverse correlation with braincase, chondrocranial, and total cephalofoil volume. Eye volume was also constrained by increasing head width and decreasing depth of the cephalofoil. These data indicate that much of the head is morphologically conserved through sphyrid phylogeny, particularly the jaw cartilages and their associated feeding muscles, with shape change and constructional constraints being primarily confined to the lateral wings of the cephalofoil and its associated sensory structures. Ancestral character state reconstructions agree with previous analyses that the common ancestor to all hammerhead sharks was large bodied with a relatively large laterally expanded head.

**INTRODUCTION**

The relationship between form and function can be used to reveal the biological role of a feature (Bock, 1980; Bock and von Wahlert, 1965). The study of this relationship, functional morphology, has received considerable attention with regards to understanding feeding in fishes (reviewed by Lauder, 1980). By interpreting form and function of phylogenetically closely related organisms, a better understanding of the selective forces and constraints that govern their diversity may be obtained. The study of vertebrate form-function complexes, such as the cranium, is incomplete unless it incorporates the constraints imposed by its constituent elements (Barel et al., 1989; Lauder and Liem, 1989; Herrel et al., 1999; 2000; Devaere et al., 2001; 2005).

Constructional constraints occur when spatial limitations are placed on a structure that has multiple biological roles (Barel, 1983; 1984; Reif et al., 1985; Motta and
Kotrschal, 1992). When investigating the functional morphology of the cranium, constructional constraints and spatial limitations are particularly important because a finite number of components can be contained within this morphospace. These components include structures associated with feeding, respiration, neural integration, sensory reception, and musculoskeletal support (Barel, 1983; 1984; Motta and Kotrschal, 1992; Herrel et al., 2000; Devaere et al., 2001). In anguilliform catfishes, hypertrophy of the adductor mandibulae complex results in neurocranial narrowing and the reduction of some cranial bones. This reduction is due, in part, to spatial constraints resulting in trade-offs between muscle mass and skeletal morphology (Devaere et al., 2001). Horn size of dung beetles was found to impose trade-offs on the size of nearby structures, including the eyes and wings (Nijhout and Emlen, 1998; Emlen, 2001). It should also be noted that constraints can occur in body parts that are distantly placed if these body parts rely on a common resource (Moczek and Nijhout, 2004). The co-constraints imposed between sensory and feeding structures is of particular importance when they occupy adjoining morphological space. Furthermore, head construction is primarily determined by sense organs which are affected by changes in other structures within the head (Barel, 1983; Dullemeijer, 1958; 1974). Development of the brain is constrained by the position of the nasal capsule and eyes in ray-finned fishes (Striedter and Northcutt, 2006). Developmental trade-offs have also been shown between the extrinsic eye musculature and the musculature of the feeding apparatus in developing quail embryos (von Scheven et al., 2006). Changes in size of either sensory or feeding structures may impose functional trade-offs in the other (Barel et al., 1989; Patek and Oakley, 2003; Huber, 2006). In cichlid fishes, increasing eye size results in a concomitant decrease in
suspensorium size and displacement of the adductor mandibulae (Barel et al., 1989; Liem, 1991). Other studies have found a lack of constraints between the volume of the adductor mandibulae muscle complex and the eye in cichlid fishes (Hulsey et al., 2007).

Hammerhead shark heads (Elasmobranchii, Sphyrnidae) offer a unique opportunity for studying the relationship of form and function and constraints among sensory, neural, and feeding structures. Hammerheads have a unique dorso-ventrally compressed and laterally expanded cephalofoil, dating back to their origin in the Eocene (54.8-33.7 mya) (Gilbert, 1967). The cephalofoil is formed by lateral expansion of the rostral, olfactory, and optic regions of the chondrocranium (Gilbert, 1967; Haenni, 2001). The shape of the cephalofoil ranges from extremely wide, in the case of *Eusphyra blochii* – 40-50% of total length (TL), to only moderately expanded, as seen in *Sphyrna tiburo* – 18-25% of TL (Compagno, 1984). Despite differences in lateral expansion, the volume of the head relative to TL remains unchanged within hammerheads (Kajiura, 2001).

Hammerhead sharks share a common ancestry with carcharhinid sharks (Compagno, 1988; Naylor, 1992; Martin, 1993), with the most recent molecular data indicating that the hammerhead shark with the most expanded cephalofoil, *E. blochii*, represents the most ancestral form, and the species with the least lateral expansion, *S. tiburo*, is the most derived (Figure 1.1) (Lim et al., 2010; Martin, 1993). The unique head morphology found in this group of fishes raises questions about the distribution of both sensory and feeding elements throughout evolutionary history and any concomitant trade-offs that may occur.

Numerous, non-exclusive, hypotheses concerning the evolution of the cephalofoil have been posited. Sensory hypotheses focus on the cephalofoil providing an advantage
due to the lateral expansion of the head and the resulting redistribution of the sensory structures. These hypotheses include the enhanced binocular vision hypothesis (Tester, 1963b; Compagno, 1984; 1988), the greater olfactory gradient resolution hypothesis (Tester, 1963a; Johnsen and Teeter, 1985; Compagno, 1984; 1988; Kajiura et al., 2005), and the enhanced electrosensory hypothesis (Compagno, 1984; Kajiura, 2001).

Conversely, the cephalofoil may provide hydrodynamic lift and act as an anterior lifting body as stated in the hydrodynamic lift hypothesis (Thomson and Simanek, 1977; Compagno, 1984; Nakaya, 1995; Driver, 1997; Kajiura et al., 2003). Lastly, hammerhead sharks have been observed on two separate occasions using their laterally expanded head to pin and restrain prey against the bottom leading to the final hypothesis, the prey manipulation hypothesis (Strong et al., 1990; Chapman and Gruber, 2002).

The possibility of constructional constraints within the sphyrid chondrocranium becomes paramount when considering that the relative volume of the sphyrid shark cranium does not differ from that of carcharhinid sharks (Kajiura, 2001). This indicates that the depressed cephalofoil of sphyrid sharks may result in spatial changes in the surrounding structures and thereby impose spatial constraints on the constructional morphology of the sensory and feeding structures (Herrel et al., 2000; Devaere et al., 2005). A similar situation in the depressed skull of the clariid catfish *Platyallabe tihoni* results in the gill and suprabranchial apparatuses competing for space within the head which may have lead to the loss of the suprabranchial organ (Devaere et al., 2001; 2005). Because the head of sphyrid sharks represents such a significant morphological departure from the head morphology of their sister taxa, sphyrids can be used as a morphological extreme from which to address questions about the evolution of functional
constraints between feeding and sensory reception (Nijhout and Emlen, 1998; Herrel et al., 1999; Emlen, 2001).

Geometric morphometrics indicate that ontogenetic and evolutionary changes in sphyrid head shape are not solely the result of lateral expansion of the head but involve modification of the entire cranium (Cavalcanti, 2004). However, this study only encompassed four of the eight sphyrid species and did not include the most basal hammerhead, *E. blochii*. The goals of this study were to 1) investigate the shape changes of the sphyrid head through phylogeny; 2) examine the volumetric changes of cephalic elements through phylogeny; and 3) investigate potential constructional constraints between and among feeding, neural, and sensory structures. By interpreting form and function of a closely related group of organisms, such as hammerhead sharks, in an historical context, a better understanding of the selective forces and constraints that govern the diversity of cranial design can be obtained (Lauder and Liem, 1989; Herrel et al., 2001).

**MATERIALS AND METHODS**

**Cephalofoil Shape**

The external shape of the cephalofoil and chondrocranium was investigated with landmark-based geometric morphometrics (Bookstein, 1996a; b; Adams and Rohlf, 2000; Trapani, 2003). The ventral surface of the heads from three to five mature individuals of each of six extant sphyrid species representing differences in head shape and size through phylogeny (*Eusphyra blochii* (Cuvier, 1816), *Sphyrna mokarran* (Rüppel, 1837), *S. zygaena* (Linnaeus, 1758), *S. lewini* (Griffith and Smith, 1834), *S. tudes*
(Valenciennes, 1822), S. tiburo (Linnaeus, 1758) and two fusiform carcharhinid shark outgroups (Carcharhinus acronotus (Poey, 1860), and Rhizoprionodon terraenovae (Richardson, 1836)) were digitally photographed (Canon Powershot A710, Canon USA Inc. Lake Success, NY, USA). Eusphyra blochii were obtained from local fishers in Darwin Australia, S. mokarran and S. lewini were obtained from longline sampling and local anglers from the western and eastern peninsula of S. Florida, S. zygaena were obtained from the east coast of New Zealand, the western coast of Mexico, and the east coast of S. Florida, S. tudes were collected from local fishers along the northeast coast of Trinidad, and S. tiburo, C. acronotus, and R. terraenovae were obtained from the waters of the Gulf of Mexico off Sarasota, Florida. Biologically significant points representing mouth, eye, incurrent and excurrent nares (hereafter nares) position, and overall cephalofoil shape on the left side of the ventral surface of the cephalofoil were digitized using TpsDig Software (F. J. Rohlf) (Figure 1.2). After digitization, CoordGen (H.D. Sheets, Integrated Morphometrics Package (IMP)) was used to produce Bookstein Coordinates with landmarks one and nine being used as the baseline (Bookstein, 1991, 1996a; b). Procrustes superimposition was then used to realign the coordinates so that the centroids of all the landmarks for each species overlapped, reducing variance and effectively removing size (Lele and Richtsmeier, 2001; Kassam et al., 2003).

Electrosensory Pores

The dorsal and ventral cephalofoil skin was removed from each individual anterior to the posterior margin of the jaws. The underlying connective and muscle tissues were then dissected away from the skin. The skins were then placed between two sheets of glass and backlit. Digital pictures were then taken of the electrosensory pores
and a composite image was created in Adobe Photoshop CS3 (Adobe Systems Inc. San Jose, CA, USA) by overlapping the images. The total number of pores on both the dorsal and ventral surface was counted and pore maps created using the NIH imaging software Image J v1.42.

**Internal Volumes**

Fresh frozen individuals of *R. terraenovae* (N = 3, 82.8 – 89.7 cm TL), *C. acronotus* (N = 3, 93.5 – 107.5 cm TL), *E. blochii* (N = 3, 133.8 – 165.6 cm TL), *S. mokarran* (N = 3, 210 – 249 cm TL), *S. lewini* (N = 3, 255 – 262.8 cm TL), *S. zygaena* (N = 2, 232 – 293 cm TL), *S. tudes* (N = 3, 69.3 – 102 cm TL), and *S. tiburo* (N = 3, 88.5 – 95 cm TL) were used for internal volume measurements. Each specimen was individually scanned with a 64 slice Aquilion Toshiba (Toshiba America Medical Systems Inc., Tustin, CA, USA) computed tomography (CT) scanner at a slice thickness of 0.5 – 1.0 mm. Computed tomography images for each individual were imported into AMIRA v4.1.2 software (Visage Imaging, Inc., San Diego, CA, USA) and digitally reconstructed. Internal volumes of feeding elements (hyomandibula, ceratohyal, basihyal, Meckel’s cartilage, and palatoquadrate cartilage), sensory and neural structures (eye, internal nasal capsule, internal olfactory tract, and internal braincase), and chondrocranial elements (all remaining non feeding cartilages in the head, anterior to the posterior margin of the ceratohyal) were computed. Pharyngeal cartilages were consequently not considered nor were vertebral elements. Each element was selected from the appropriate CT slices to give accurate 3D geometry in the reconstructed head. Using the posterior-most point of the ceratohyal as a landmark, the total volume of the head was also computed. Volume computations were tested for accuracy by computing
the volumes of eyes from *R. terraenovae*, *E. blochii*, *S. lewini*, and *S. tiburo*. Eye volume was digitized first from CT scans of whole heads. Eyes were then unilaterally removed from each individual and CT scanned a second time outside of the animal. Finally, the water displacement volume was determined for each eye. The different methods of eye volume measurement were then compared using a one-way ANOVA. No significant differences were found among treatments (*p = 0.08*), and all further digitized volumes were assumed to be accurate (Table 1.1). The feeding muscles involved in lower jaw adduction: quadrotomandibularis ventral (QMV), quadrotomandibularis dorsal (QMD), preorbitalis ventral (POV), and preorbitalis dorsal (POD) (Wilga and Motta, 2000), were unilaterally excised and volume determined by water displacement. The volume of bilaterally symmetrical elements was multiplied by two to account for both sides.

*Statistics*

Species geometric morphometric data were tested for significant differences with pairwise comparisons using Goodall’s F-test. Principal components analysis (PCA) of head shape differences among species was generated using PCAGen (IMP). Finally, in order to visualize the changes in shape among species, thin-plate splines were generated using IMP.

Pore counts were compared among species using three separate Kruskal-Wallis one-way ANOVAs on ranks. Dorsal and ventral pore fields were first compared within species, next dorsal and ventral pore fields were compared among species.

Raw volumes for the internal elements for all species were log transformed to account for the large size range among species and then input into a PCA to determine which variable(s) created separation among species and to reduce the number of
variables. Principal components were not considered to account for a significant amount of the variation unless their eigenvalue was greater than 1. Variables which were found to load heavily on a given principal component (loading score greater than 0.6) were retained for further analysis. Initially, volumetric and pore data were log_{10} transformed and linearly regressed against log_{10} TL. Studentized residuals were then input into a Pearson correlation analysis to investigate relationships among the size removed variables. Following this, the most recent phylogeny with branch lengths for hammerheads (Lim et al., 2010; Martin, 1993) was used to generate independent contrasts for each of the raw morphological volumes, pore data, head width (HW), and shark TL using Mesquite v2.72 (Maddison and Maddison, 2009). The method of generating independent contrasts has been previously described (Garland et al., 2005). Mesquite was used to determine if the branch lengths of the phylogeny and model of evolution adequately fit the tip taxa data. The tree used here (Lim et al., 2010) was found to adequately fit the data of the extant taxa. Positivised contrasts were then exported and independent contrasts were calculated by dividing the raw contrast for each variable by its standard deviation. The independent contrasts method transforms the original phylogenetically non-independent data set into a set of independent and equally distributed contrasts (Felsenstein, 1985). These contrasts represent rates of change along each branch of phylogeny. By utilizing this method the relatedness of taxa within a study can be removed resulting in phylogenetically removed comparisons (Garland et al., 2005).

Since the currently accepted phylogeny has only one outgroup species, C. acronotus was used as the outgroup for phylogenetic analyses. The contrasts of each
variable were then regressed through the origin against the contrast of TL to remove
the effect of size (Felsenstein, 1985). These phylogenetically corrected studentized residuals
were then input into a Pearson correlation analysis, through the origin, to investigate
relationships among the size and phylogenetically removed variables. Regressions, PCA
analysis, and ANOVAs were performed in SYSTAT v11 (SYSTAT Software Inc.,
Chicago, IL, USA), and the correlation analysis was performed in SPSS v18 (SPSS,
Chicago, IL, USA). Additionally, Mesquite was used to perform ancestral state
reconstructions using parsimony for each of the phylogenetically corrected variables to
investigate how variables change through evolutionary history. Each variable is traced
backward through evolutionary history yielding character states at each node. These
calculated character states are then used to calculate deeper nodes within the phylogeny.
All procedures followed the Institutional Animal Care and Use Committee guidelines of
Mote Marine Laboratory (08-10-RH1, 07-10-PM1) and the University of South Florida
(T3198, R3205, W3514).

RESULTS

Cephalofoil Shape

Geometric morphometric analysis revealed that all species were significantly
different from each other (p < 0.001). For ease of visualization, only shape changes on
the left side of the shark are presented. Within the carcharhinid species, *R. terraenovae*
differs from *C. acronotus* by having anteriorly positioned eyes and incurrent and
excurrent nares and anterior rostral expansion. Furthermore, the mouth is expanded and
shifted anterolaterally in *R. terraenovae* compared to *C. acronotus* (Figure 1.3).
Shape changes throughout the species are reflected by movement of the nares, eyes and cephalofoil, with relatively little repositioning of the mouth. Between carcharhinid and sphyrnid sharks the head expanded laterally, forming the cephalofoil. As a result, the eyes and nares were also carried laterally. Mouth position remained relatively constant with slight posteromedial movement (Figure 1.4). Pairwise shape comparisons within sphyrnid sharks do not necessarily reflect ancestral shape changes, only the differences between extant taxa (Figure 1.1). Furthermore, the interpretation of shape differences between tip taxa will differ slightly with changes in topology. However, overall general trends will remain unchanged. When *E. blochii* is compared to *S. mokarran*, cephalofoil expansion decreased and eye position shifted anteriomedially in *S. mokarran*. Nares position shifted anteriorly while mouth position shifted slightly posteriorly (Figure 1.5). Among *S. mokarran*, *S. zygaena*, and *S. lewini* there were few changes in overall cephalofoil shape. However, eye and nares position is first placed posterolaterally in *S. zygaena* compared to *S. mokarran* and then anteriorly in *S. lewini* compared to *S. zygaena*, and again, mouth position remained mostly invariant (Figure 1.6 and 1.7). Differences in head shape between *S. lewini* and *S. tudes* were centered around decreased lateral expansion with slight rostral anterior expansion in *S. tudes*, with almost no change in mouth position. Furthermore, both the eyes and nares are positioned anteromedially in *S. tudes* compared to *S. lewini* (Figure 1.8). Finally, *S. tiburo* displays decreased cephalofoil expansion laterally and increased expansion rostrally compared to *S. tudes*. Eye and nares position both shifted medially, while mouth position remained unchanged in *S. tiburo* (Figure 1.9). Principal components analysis of the geometric morphometric data shows separation along PC1, (78.8 % of the variation) based on
degree of lateral head expansion and PC2, (13.5% of the variation) based on placement of the nares and eyes. *Eusphyra blochii* is distinguished from the remaining species by its extreme lateral expansion, the anterior position of the eyes on the lateral tips of the cephalofoil and the medial position of the nares. Similarly, *S. mokarran*, *S. zygaena*, *S. lewini*, and *S. tudes* group together based on their moderate head expansion and laterally placed nares (Figure 1.10).

**Electrosensory Pores**

The number of dorsal pores was positively correlated with the number of ventral pores. Dorsal pore number was also correlated with increased head width. Pore numbers did not display correlated changes with any other cranial structure through evolutionary history (Table 1.2). The species with the largest number of pores was *S. lewini*, however *S. tudes*, a species with a less laterally expanded cephalofoil, had a similar number of pores (Table 1.3). Only *C. acronotus*, *S. mokarran*, and *S. lewini* had a greater number of ventral pores than dorsal (Table 1.3). The distribution of pores among the species was relatively consistent but species specific patterns are clearly recognizable (Figure 1.11). Surprisingly, *E. blochii* had few pores distributed along both the dorsal and ventral anterior edge of the cephalofoil compared to the other species.

**Internal Volumes**

In general, the spatial organization of the central core of the chondrocranium (e.g. neurocranium, rostral cartilages, and feeding system) remains constant despite the various changes in cephalofoil shape and size (light green, Figure 1.12). The position and volume of the internal sensory structures and their associated cartilages (e.g. nasal capsule, eye, and olfactory tract) are variable through phylogeny (Figure 1.12, Table 1.4).
The nasal capsule expands laterally as a result of the extreme lateral expansion seen in basal sphyrmids. The pre- and post-optic cartilages are reorganized to accommodate lateral displacement of the eyes and extrinsic eye musculature (Figure 1.13, see Compagno, 1988). The position and orientation of the jaws and suspensory cartilages remains relatively constant through phylogeny. Position and spatial organization of sensory structures displays noticeable differences through phylogeny. Eye volume is particularly striking with basal species having relatively smaller eyes (Figure 1.12).

That the number of correlations differs between the non-phylogenetically corrected and phylogenetically corrected data demonstrates that the data have a clear phylogenetic signal (Table 1.2 compared to Table 1.5). As a result of the phylogenetic signal demonstrated by this data set, only phylogenetically corrected data will be discussed further. Pearson correlation analyses revealed that changes to most elements within the head are not correlated with changes in the remaining elements (Table 1.2 p > 0.05). As the number of correlations increases, the chance of spurious correlations increases (Aldrich, 1995). Because of this, only biologically relevant correlations that occur between adjacent structures will be discussed further. However, some elements showed significant parallel patterns of change, indicating that as one structure increases in size; other structure(s) show a concomitant increase in size. This is particularly apparent in the feeding muscles (QMV, QMD, POV, and POD) and the jaw and jaw suspension cartilages (palatoquadrate cartilage, Meckel’s cartilage, hyomandibula, and ceratohyal). As the jaw cartilages increase in volume, the muscles that reside upon them also increase in volume (p < 0.025 Table 1.2). Furthermore, as one jaw closing muscle increased in volume, the remaining three muscles also increased in volume. Similarly, as
the volume of one jaw cartilage increased, the volume of the remaining jaw and the hyomandibula cartilages increased. Other positive trends dealt with increasing total volume being correlated with increased chondrocranial and braincase volume. Finally, there was a positive correlation between head width and chondrocranial volume (Table 1.2).

Negative correlations were found indicating an inverse relationship. As nasal capsule volume increases, there is a concomitant decrease in braincase, basihyal, chondrocranium, and total volume. Head width was also found to negatively affect the volume of the eye ($p < 0.039$ Table 1.2, Figure 1.12).

Ancestral state reconstructions indicate that the closest ancestor of sphyrid sharks was intermediate in length between large and small bodied hammerhead sharks (~177.49 cm TL) and similar to large bodied sharks in extent of lateral head expansion (47.45 cm or ~26.9% of TL). Meckel’s cartilage volume was found to be greater than palatoquadrate volume as is seen in all extant species (Table 1.4 and 1.6, Figures 1.1 and 1.12, Node 3). The volume of the QMV and POV was greater than the remaining feeding muscles. This trend is mirrored in extant sphyrids but not outgroups (Table 1.4). Despite the changes in volume of the various elements, electrosensory pore counts remained relatively consistent through evolutionary history (Table 1.6) as does the general spatial organization of the electrosensory system (Figure 1.11).
DISCUSSION

External Shape Differences among Sphyrnids

All species studied had significantly different head shapes. The shape of the cephalofoil has long been used to visually distinguish species of hammerhead shark (Compagno, 1984; 1988). The morphology behind these shape differences has remained largely unknown. Cavalcanti (2004) correctly concluded that the changes within the sphyrnid head are the result of modifications to almost all chondrocranial elements and not simply the result of expanding the head laterally. While the geometric morphometric analysis of the current study also reveals the underlying pattern of change in the chondrocranial elements, the placement of the eyes, nares, and mouth on the cephalofoil and how their placement changes among species is of particular interest. Eye position is variable through phylogeny (yellow lines, Figures 1.3 - 1.9). Furthermore, the eyes are not consistently laterally placed on the cephalofoil. In *E. blochii* and *S. lewini*, the eyes are positioned at the anterior edge of the distal tip of the cephalofoil, while in all other species the eye is more posteriorly placed. In order to accommodate lateral placement of the eyes, the pre- and post-orbital processes are highly modified (Compagno, 1988; Schultze, 1993) (Figure 1.12 and 1.13). The post-orbital process is particularly affected by differences in head shape. In *E. blochii*, the post orbital process is much more gracile than in the remaining species, due in part to the extreme lateral expansion seen in this species (Figure 1.13).

Given the lateral expansion seen in this group of sharks (*E. blochii*: up to ~50% of TL (Compagno, 1984)), lateral placement of the eyes has been hypothesized to result in a large blind area directly in front of the cephalofoil (Walls, 1942). However, the anterior
position of the eyes on the distal tip of the cephalofoil actually results in enhanced binocular overlap in *E. blochii* as compared to *C. acronotus*, *S. lewini*, and *S. tiburo*. *Sphyrna lewini* was also found to have a greater binocular overlap than either *S. tiburo* or *C. acronotus* (McComb et al., 2009). Furthermore, head yaw during swimming, which reduces the blind area in front of the head, was found to be greater in *S. lewini* and *S. tiburo* compared to *C. acronotus* (McComb et al., 2009). Stalk-eyed flies (Diopsidae) also display laterally displaced eyes and are conferred with improved binocular vision (Burkhardt and de la Motte, 1983). While vision is important for prey detection and tracking, it is unclear what contribution vision makes during the final stages of attack when the blind area becomes a liability. It is likely that other senses contribute to prey location in the absence of visual information when prey are close to the mouth (Gardiner and Atema, 2007). Through sphyrid evolution, it is possible that anterior placement of the eyes in *E. blochii* and *S. lewini*, was driven by selective pressures to reduce the blind area in these sphyrid sharks.

The positions of the incurrent and excurrent openings to the nasal capsule are also variable among species (red lines, Figures 1.3 - 1.9). In the more basal *E. blochii*, the nares are placed in a more medial position along the cephalofoil compared to more derived sphyrids (Figure 1.4 vs. Figures 1.5 - 1.9). It has been previously demonstrated that lateral placement of the nares, along with the evolution of the prenarial groove, has resulted in increased ability to resolve odors on opposite sides of the head (Kajiura et al., 2005). The length of the prenarial groove varies among species (Compagno, 1984; 1988). The distance between the two incurrent nares is significantly greater in hammerhead sharks than outgroup carcharhinids. Within sphyrids, *E. blochii* has the
greatest separation between incident nares, followed by *S. zygaena* and then *S. lewini*. The internarial distance (the distance between the medial margin of the prenarial groove in sphyrid or incident nares in carcharhinid shark) was significantly larger in *S. lewini* than both *E. blochii* and *C. plumbeus*, while the latter two species were not different from each other. These morphological differences in sphyrid sharks create an olfactory system that samples a larger volume of water than comparably sized carcharhinid sharks (Kajiura et al., 2005). Recent work suggests that the laterally placed nares of hammerhead sharks may confer advantage in detecting timing differences of odor arrival on opposite sides of the head. This is especially important for odor patch detection and patch following using klinotaxis (Gardiner and Atema, 2010). While these studies support parts of the enhanced olfaction hypothesis, the hypothesized increased olfactory acuity has not yet been fully investigated. However, hammerhead sharks have been shown to have greater sensitivity to single amino acids presented at the incident nares (Tricas et al., 2009). In order to truly resolve the olfactory abilities of sphyrid sharks and test the enhanced olfactory hypothesis further, a series of electrophysiological and behavioral experiments are needed to investigate the responses to combinations of amino acids (Tricas et al., 2009; Meredith and Kajiura, In Press).

Whereas eye and nares position show considerable variation through phylogeny, mouth position remains relatively constant (blue lines, Figures 1.3 - 1.9). The cephalofoil expands and contracts around the relatively static feeding structures. Mouth position may experience selective pressures to remain static based on the feeding mechanism’s role in prey capture and processing. Phylogenetic inertia could also affect mouth position, in that mouth position will remain stationary without sufficient selective pressure for
change. Furthermore, even in the presence of selective regimes that favor reorganization of the feeding elements, changes cannot occur without concomitant changes in other surrounding cranial structures to accommodate skeletal reorganization (Sakamoto et al., 2010).

The electrosensory system has long been purported as the selective pressure driving evolution of the cephalofoil (Gilbert, 1967; Compagno, 1984; 1988; Kajiura, 2001; Kajiura and Holland, 2002). Contrary to previous studies, the number of electrosensory pores on the ventral surface was not greater than that of the dorsal surface for all but three species (C. acronotus, S. mokarran, and S. lewini) (Table 1.3) (Gilbert, 1967; Kajiura, 2001; Cornett, 2006). Having a larger number of ventral pores could increase the spatial resolution of the electrosensory system and allow for more precise prey location when searching at or near the bottom (Compagno, 1984; Kajiura, 2001; Kajiura and Holland, 2002). However, the species in this study found to have a significantly greater number of electrosensory pores on the ventral surface (C. acronotus, S. mokarran, and S. lewini) are not bottom associated but coastal-pelagic species that spend much of their time in the water column (Compagno, 1984). It is possible that the increased number of ventrally located electroreceptors in these sphyrid species allows for enhanced prey localization in the water column. It should also be noted that ontogeny may play a role, as juvenile S. lewini do inhabit shallow water and feed near the bottom (Compagno, 1984; 1988). Sphyrna lewini has a larger ventral blind area than the lemon shark, Negapriion brevirostris, but does not differ significantly from C. acronotus or S. tiburo (McComb et al., 2009). Increased numbers of pores on the ventral surface may compensate for this ventrally located visual blind area.
The overall distribution of electroreceptive pores in hammerhead sharks is similar among species on both the dorsal and ventral sides of the head and located within clearly demarcated pore fields (Figure 1.11) (Gilbert, 1967; Kajiura, 2001). The pore maps reported here are consistent with those of previous studies, as is the average number of pores (Kajiura, 2001; Cornett, 2006). However, *E. blochii* lacks many of the pores along the anterior edge of the cephalofoil that are present in other hammerhead species (Figure 1.11). The reason for this difference is unknown, but is most likely related to the placement of the nares. In *E. blochii*, the nares are medially placed as compared to the lateral placement of the more derived sphyrids resulting in a medial rather than lateral position for the anterior lateral pore field (Gilbert, 1967) (Figures 1.1, 1.5, and 1.11).

Lateral expansion of the cephalofoil and the resulting greater area of electroreceptor sampling equates to a larger search area for sphyrid sharks compared to similar sized carcharhinid species (Kajiura and Holland, 2002). Juvenile *S. lewini* have comparable behavioral detection thresholds to similarly sized *C. plumbeus* (< 1 nV cm\(^{-1}\)) and similar orientation distances to prey simulating electrodes (~30 cm) (Kajiura and Holland, 2002). To date, sampling area and detection thresholds have been quantified for only two sphyrid species (*S. lewini* and *S. tiburo*), neither of which possess the extreme lateral expansion seen in *E. blochii* (Compagno, 1984). When including other sphyrid species with different degrees of lateral expansion, there would be differences expected among sphyrid sharks in both sampling area and distance prey can be detected from the midline of the body with greater lateral expansion resulting in larger sampling area and greater prey detection distance (Kajiura, 2001; Kajiura and Holland, 2002). Having electroreceptive pores spaced laterally on the head, without lateral movement of the
ampullae themselves, could result in longer ampullary tubules and greater sensitivity to uniform electric fields compared to less laterally expanded sharks (Murray, 1974; Bennett and Clusin, 1978; Chu and Wen, 1979). The physiological threshold for detection of electric fields and the behavioral threshold for reaction to electric fields have not yet been separated and could add further evidence to the enhanced electroreception hypothesis (Kajiura and Holland, 2002).

Any description of the sensory systems of an elasmobranch fish is incomplete without mention of the anterior cephalic mechanosensory lateral line. The lateral line plays a vital role in prey detection and tracking behavior (Gardiner and Atema, 2007). However, the anterior lateral line has only been described for a single species of sphyrid, *S. tiburo* (Maruska, 2001). While this study did not examine the anterior lateral line of other sphyrids, the anterior lateral line canals are laterally displaced on the cephalofoil similar to the electrosensory system (K.R. Mara, personal observation). The consequences of lateral expansion on the lateral line system of sphyrids remain enigmatic and should be the focus of a future study.

**Internal Cranial Volumes**

Correlation analyses of both non-phylogenetically corrected and phylogenetically corrected data sets show that the internal volumes display a strong phylogenetic signal (differences between non-phylogenetically corrected and phylogenetically corrected data sets) (Table 1.2 and Table 1.5 respectively). Although, the volumes of the various components in the head (hyomandibula, ceratohyal, basihyal, Meckel’s cartilage, palatoquadrate cartilage, principal jaw closing muscles, eye, internal nasal capsule, internal olfactory tract, and internal braincase) remain relatively consistent through
phylogeny, the orientation and spatial arrangement does change. The morphometric and volumetric analyses indicate that the nasal capsule and optic cartilages are variable through phylogeny. This variation reflects the differing position of the nares and eyes through phylogeny (Figures 1.4 – 1.9).

The developmental and evolutionary processes that govern the formation of the cephalofoil are not yet well understood. However, the structure and development of the vertebrate head is partially determined by \( \text{Hox} \) genes along with preoptic and postoptic neural-crest derived ectomesenchyme (Gans and Northcutt, 1983; Gans, 1993; Manzanares et al., 2000; Kuratani, 2005). There is also a possibility that hammerhead sharks with less laterally expanded cephalofoils arose as a result of changes in development, such as progenesis or neoteny (Lim et al., 2010). Furthermore, the growth rate and organization of cartilaginous elements can be influenced by environmental and developmental factors. Particularly, the growth of the brain can influence the shape of the braincase (Müller and Wagner, 1991; Herring, 1993).

Sphyrnids have hypertrophied telencephalons occupying up to 67% of overall brain mass (Yopak et al., 2007). In sphyrids, the proportion of the brain occupied by the expanded olfactory bulb is quite large when compared to outgroup carcharhinids (7% vs. 3%) (Northcutt, 1977). Given the relatively consistent shape of the central core of the chondrocranium among sphyrid and carcharhinid species (Figure 1.12), it is likely that brain organization and development play a significant role in the shape of the central core of the chondrocranium. It is unlikely that the lateral wings of the cephalofoil are affected by changes in brain size as only the nasal capsules occupy the lateral cephalofoil.
Constructional Constraints within the Cranium

This study found few constructional constraints within the head of hammerhead sharks (Table 1.2). Morphological constraints are of particular importance when investigating the form-function relationship among various components within the head (Barel et al., 1989). Morphological constraints often result in one structure imposing constructional or architectural limitations on one or more surrounding structures (Barel, 1983; 1984; 1993; Barel et al., 1989; Motta and Kotrschal, 1992). Hypertrophy of the feeding apparatus may result in trade-offs between muscle or skeletal morphology (Barel, 1983; Devaere et al., 2001) and eye size, eye position, and overall head shape (Barel, 1993) in clariid catfishes and cichlid fishes. Constraints are imposed on the feeding apparatus, by increases in eye size (Barel et al., 1989) and extrinsic eye musculature (von Scheven et al., 2006) in cichlid fishes and chick embryos respectively. Sensory structures have also been shown to negatively affect the development of neural structures such as the telencephalon (Striedter and Northcutt, 2006). However, constructional constraints are not limited to sensory and feeding structures (Nijhout and Emlen, 1998; Emlen, 2001). Traditionally, constraints are defined as changes in one structure that result in functional or morphological trade-offs in a second, typically adjoining, structure (Barel, 1983; 1993; Barel et al., 1989; Nijhout and Emlen, 1998; Emlen, 2001). This definition has since been expanded to include trade-offs between or among structures that share a common developmental resource but may not be physically adjoining (Moczek and Nijhout, 2004). For the purposes of this study, constraints are defined as trade-offs between or among closely spaced structures.
The vertebrate cranium is a complex system that must contain structures associated with feeding, respiration, neural integration, sensory reception, and musculoskeletal support (Kohlsdorf et al., 2008). The cephalofoil of sphyrid sharks also presents a system where the currently accepted explanation for its evolution relates to enhanced sensory perception, either electrosensory or olfactory (Tester, 1963a; Johnsen and Teeter, 1985; Kajiura, 2001; Kajiura and Holland, 2002; Kajiura et al., 2005). Given the range of head expansion seen within sphyrids, they present a system in which the constraints, if any, between or among sensory, neural, and feeding structures can be elucidated. No single element imposed significant constraints on the remaining elements. The few negative correlations that were found dealt with the nasal capsule volume being negatively correlated with braincase, basihyal, chondrocranial, and total volumes (red text, Table 1.2). As the volumes of the braincase, basihyal, chondrocranium, and total volume increased the volumes of the nasal capsule decreases. The negative correlations between nasal capsule and braincase, chondrocranial, and total volume can be explained by space utilization of these adjacent structures. Given a finite amount of space within the chondrocranium and consistent cranial volume among the hammerhead sharks (Tables 1.2 and 1.4) (Kajiura 2001), if one structure increases in volume, at least one of the remaining nearby structures must show a concomitant decrease in volume. The explanation for the remaining negative correlations with nasal capsule volume remains enigmatic and these correlations may not reflect any true constraint among these structures. The only other negative correlation this analysis revealed was between head width and eye volume, where increased width of the head resulted in decreased volume of the eye. This is the result of the dorso-ventral flattening
that occurs as head width increases among the species. The most extreme case is seen in *E. blochii*, where the species with the greatest degree of lateral expansion also possesses the smallest eyes (Figures 1.4 and 1.12). As the cephalofoil is expanded laterally in basal species of sphyrnids, the depth, length, or both available for the skeletal structures surrounding the eyes and the eyes themselves is necessarily decreased. Thus, increasing lateral expansion, and the resulting dorso-ventral flattening, constrains the volume of the eye. Musculoskeletal elements affecting eye size have been previously demonstrated in other fishes (see above and Barel, 1983; 1984; Huber, 2006). However, the manner in which expansion of the cephalofoil creates constraints on the eye is unique to sphyrnid sharks as few other vertebrates or invertebrates have lateral expansions of their head as extreme as those seen in hammerhead sharks.

Feeding variables were positively correlated among species (blue text, Table 1.2). As the volume of the feeding muscles (QMV, QMD, POV, and POD) increased, the volume of the palatoquadrate and Meckel’s cartilages, along with the hyomandibula, also increased. These positive correlations suggest that the four principal jaw closing muscles do not compete for space within the head, nor do the jaws or suspensory cartilages. The lack of negative correlations related to the feeding structures indicates that not only do they not compete for space among each other; they also do not cause constraints on other elements within the head because none of the adjacent structures systematically decrease in volume. The various adductor mandibulae muscles of Lake Malawi cichlid fishes were also found to be positively correlated with each other (Hulsey et al., 2007). The strong positive correlation found among the jaw closing muscles can be explained by their common function among fishes. The positive correlations between the volumes of
the palatoquadrate, Meckel’s cartilage, and hyomandibula can also be explained by their common biological role in jaw suspension and feeding (Huber, 2006). It is possible that there are constructional constraints within the cephalofoil among elements that were not quantified in this study (e.g. connective tissue, peripheral nervous system tissue, ampullary tubules, and respiratory structures). For example, a consequence of lateral cephalofoil expansion is the lateral displacement of the electrosensory pores, which results in longer ampullary tubules within the head. While longer tubules may confer a greater sensitivity (Murray, 1974; Bennett and Clusin, 1978; Chu and Wen, 1979), they also result in a greater volume within the cranium being taken up by the tubules leaving less volume for remaining elements.

The Ancestral Sphyrid

Recent phylogenetic analyses indicate that the family Sphyrnidae is a monophyletic group within the family Carcharhinidae (Compagno, 1988; Naylor, 1992; Martin, 1995). There are two genera within the Sphyrnidae, Eusphyra and Sphyrna, and eight currently recognized species along with some possible geminate species (Martin, 1993; Duncan et al., 2006; Quattro et al., 2006; Lim et al., 2010). The most recent phylogenetic analysis of the family (Lim et al., 2010) indicates that the evolution of the cephalofoil is not as simple as was once thought (Compagno, 1988). Instead, the cephalofoil underwent divergent evolution resulting in two separate evolutionary lineages, one leading to cephalofoil expansion (Eusphyra lineage) and the second leading to cephalofoil contraction (S. tiburo lineage). Furthermore, body size does not separate species into monophyletic groups (Lim et al., 2010). Ancestral character state reconstructions indicate that the ancestral sphyrid shark was ~178 cm TL, putting it
intermediate between large and small bodied extant hammerhead sharks (Table 1.6; Figure 1.1 Node 3). This shark was similar to extant large bodied sharks in extent of lateral head expansion, ~27% of TL. Other attempts at modeling body size for ancestral sphyrid sharks have also revealed that the evolution from a large bodied shark toward smaller bodied sharks is much more plausible than the reverse (Lim et al., 2010). Further supporting these data is the first occurrence of fossilized sphyrid teeth belonging to the large bodied *S. zygaena* (Cappetta, 1987).

Ancestral state reconstructions also show that the volumes of the internal elements also displayed trends through evolutionary history. In general, the volume of the Meckel’s cartilage was greater than the volume of the palatoquadrate. This may be related to the Meckel’s cartilage having a larger area of muscle attachment than the palatoquadrate cartilage (Wilga and Motta, 2000). This analysis also found that the volumes of the QMV and the POV were greater than the remaining jaw closing muscles through evolutionary history (Table 1.6). This matches data gathered for *S. tiburo* where masses of the QMV and the POV were greater than the remaining muscles (Mara et al., 2010).

*Evolution of the Cephalofoil*

There have been numerous hypothesis put forth regarding the evolution of the hammerhead shark cephalofoil. The hydrodynamic lift hypothesis states that the cephalofoil on the anterior end of the body provides lift and increases maneuverability (Nakaya, 1995; Driver, 1997) and the cephalofoil has some camber which may result in lift generation (Kajiura et al., 2003). Furthermore, the pectoral fins of hammerhead species with larger lateral expansions of the cephalofoil are proportionally smaller with
total area of the cephalofoil and pectoral fins remaining constant across phylogeny (Thomson and Simanek, 1977; Compagno, 1984). Sphyrnid sharks were also found to be more maneuverable than similarly sized carcharhinid species. However, the cephalofoil was not found to act as a wing during turns. Instead the cephalofoil was kept relatively parallel to the substrate (Kajiura et al., 2003).

Various sensory based hypotheses have been proposed regarding the evolution of the cephalofoil. The greater olfactory gradient resolution hypothesis has received some support with the cephalofoil providing a greater sampling area and enhanced klinotactic ability (Kajiura et al., 2005; Gardiner and Atema, 2010). Furthermore, sphyrnid sharks have been shown to have slightly greater sensitivity to single amino acids (Tricas et al., 2009). However, olfactory epithelial surface area does not differ among sphyrnid and carcharhinid species (Kajiura et al., 2005). The hammerhead cephalofoil results in the eyes being laterally displaced on the head. The enhanced binocular vision hypothesis proposes that the lateral placement of the eyes results in greater binocular overlap and increased visual field. Recent work has supported this hypothesis showing that the laterally positioned eyes do result in an increased binocular overlap in basal sphyrnid species compared to derived sphyrnid and carcharhinid species (McComb et al., 2009). The hypothesis that has received the most support is the enhanced electroreception hypothesis. The cephalofoil confers a greater sampling area for electroreceptors and may provide a greater sensitivity to uniform electric fields (Kajiura, 2001; 2003; Kajiura and Holland, 2002). While other sensory modalities are important in prey tracking and localization, electroreception likely overrides these other modalities during the final stages of attack (Kalmijn, 1971; Kimber et al., 2009). Furthermore, having laterally
placed electroreceptors allows sphyrid sharks to detect prey at a much greater distance from the mid-line of the body that similar sized carcharhinid species (Kajiura and Holland, 2002).

Finally, the cephalofoil has also been hypothesized to function in prey manipulation (Strong et al., 1990; Chapman and Gruber, 2002) with the cephalofoil being used to stun and restrain prey against the seafloor. However, the data presented here show that other than a possible function in prey restraint, the feeding mechanism of sphyrid sharks is not markedly different from that of carcharhinid sharks.

The data presented in this work along with the data of others (Tester, 1963a; b; Johnsen and Teeter, 1985; Kajiura, 2001; Kajiura et al., 2003; 2005; McComb et al., 2009) indicates that sensory systems appear to have been the major evolutionary force shaping the sphyrid cephalofoil with few changes to the feeding structures. This study found little support for a feeding based hypothesis beyond prey manipulation.

Despite the sensory advantages conferred by the cephalofoil, there are potential disadvantages associated with this laterally expanded structure. While the placement of the eyes on the lateral wings enhances binocular overlap and decreases the binocular convergence distance, the absolute size of the blind area in front of the cephalofoil is increased (McComb et al., 2009). Similarly, while the cephalofoil may provide sphyrid sharks with increased maneuverability, it does so at the cost of turning ability. Sphyrid sharks are not able to roll as much as similarly sized carcharhinid species due to the risk of hitting the substrate with the cephalofoil (Kajiura et al., 2003). Finally, the risk of predation, particularly upon the lateral wings of the cephalofoil, may be increased due to increased width of the head.
CONCLUSIONS

Hammerhead sharks display a diversity of cranial shapes that vary with respect to the position of the eyes and nares, with little change in the relative position of the mouth. The eyes are first positioned at the anterior edge of the cephalofoil in basal species. Through phylogeny, eye position shifted to a more posterior position on the distal tip of the cephalofoil. External nares position is also variable through sphyrid phylogeny. Initially, in *E. blochii*, nares position is medial, similar to outgroup carcharhinids; through phylogeny, nares position shifted laterally, resulting in displacement of the incurrent and excurrent narial openings. Mouth position, however, remains relatively static through phylogeny with minor changes in position and shape. The electrosensory system of sphyrids is believed to have driven the evolution of the cephalofoil. This analysis revealed that electrosensory pore number is relatively conserved through sphyrid phylogeny, and that overall distribution of electoreceptive pores is similar among all species except *E. blochii*. This study also demonstrated that, within the cephalofoil, many of the elements do not impose constructional constraints upon each other. The few constraints that do occur are confined to the volume of the nasal capsule and eye. Nasal capsule volume was negatively correlated with braincase and total chondrocranial volume, and eye size is inversely related with head width. Consequently, as head width increases, there is a concomitant decrease in eye volume. Not only were most elements not constrained, the feeding muscles and the cartilages they rest upon showed positive correlations through phylogeny. This indicates that the feeding elements do not constrain other elements and are free to change in volume within the head.


Figure 1.1. Phylogeny of the hammerhead sharks modified from Lim et al. (2010). Based on the nuclear genes ITS2, Dlx1, and Dlx2 and the mitochondrial genes NADH dehydrogenase 2, cytochrome \textit{b}, cytochrome oxidase I, and D-loop. Differences in head shape among the species are indicated with non-scaled line drawings of the cephalofoil. Body size differences are shown among the species with a generalized body shape scaled to maximum reported size for each species. Numbers above the nodes are posterior probabilities and numbers below the node are BEST credibility values. Numbers to the right of the nodes indicate nodes for ancestral state reconstructions. Head shapes and body outlines modified from Compagno, 1984. Scale bar = 1 m.
Figure 1.2. External landmarks chosen for geometric morphometrics. Landmarks were chosen to represent the position of the mouth (10, 11, 12), eye (3, 4), incurrent and excurrent nares (5, 6), and overall cephalofoil shape (1, 2, 7, 8, 9). Landmarks were digitized on the left side of the head only, and comparisons were anchored at landmarks one and nine.
Figure 1.3. Shape differences between *C. acronotus* (gray) and *R. terraenovae* (green). Differences in shape are illustrated using vector transformations. Shape differences are assumed to be bilaterally symmetrical and are illustrated on the animal’s left side only. The head expands anteriorly (white vectors) along with the position of the nares (red) and eyes (yellow). The mouth is also expanded and shifted anterolaterally in *R. terraenovae*. 
Fig. 1.4. Shape differences between *C. acronotus* (gray) and *E. blochii* (green). Differences in shape are illustrated using vector transformations. Shape differences are assumed to be bilaterally symmetrical and are illustrated on the animal’s left side only. The cephalofoil expands laterally and the eyes (yellow) and nares (red) move laterally with the expansion. Mouth position shifts slightly posteromedially.
Figure 1.5. Shape differences between *E. blochii* (gray) and *S. mokarran* (green). Differences in shape are illustrated using vector transformations. Shape differences are assumed to be bilaterally symmetrical and are illustrated on the animal’s left side only. Cephalofoil expansion decreases while eye position shifts anteromedially. However, nares position shift anteriorly and mouth position shifts slightly posteriorly.
Figure 1.6. Shape differences between *S. mokarran* (gray) and *S. zygaena* (green). Differences in shape are illustrated using vector transformations. Shape differences are assumed to be bilaterally symmetrical and are illustrated on the animal’s left side only. Cephalofoil expansion increases slightly and the eyes (yellow) and nares (red) shift posterolaterally. Mouth position shifts slightly anterior however no other major changes are seen.
Figure 1.7. Shape differences between *S. zygaena* (gray) and *S. lewini* (green). Differences in shape are illustrated using vector transformations. Shape differences are assumed to be bilaterally symmetrical and are illustrated on the animal’s left side only. Cephalofoil shape remains largely unchanged. However, eye (yellow) and nares position (red) shift anteriorly. Mouth position also remains unchanged.
Figure 1.8. Shape differences between *S. lewini* (gray) and *S. tudes* (green). Differences in shape are illustrated using vector transformations. Shape differences are assumed to be bilaterally symmetrical and are illustrated on the animal’s left side only. Cephalofoil expansion decreases laterally and increases rostrally while eye and nares position shift anteromedially. Mouth position remains unchanged.
Figure 1.9. Shape differences between *S. tudes* (gray) and *S. tiburo* (green). Differences in shape are illustrated using vector transformations. Shape differences are assumed to be bilaterally symmetrical and are illustrated on the animal’s left side only. Eye and nares position is shifted medially while the cephalofoil decreases in lateral expansion. Mouth position, however, remains unchanged.
Figure 1.10. Principal components analysis of head shape within carcharhinid and sphyrid sharks. PC 1 explained 78.8% of the variation and indicates decreasing lateral expansion of the cephalofoil. PC 2 explained 13.5% of the variation and represents lateral placement of the nares and anterior placement of the eyes.
Figure 1.11. Electrosensory pore maps overlain onto phylogeny. Left side of each map is the dorsal surface and the right side is the ventral surface of the head. Both *S. lewini* and *C. acronotus* had a greater number of ventral pores than *R. terraenovae* and *S. tiburo* ($p < 0.001$). Phylogeny simplified from Lim et al., 2010. Numbers indicate nodes for ancestral state reconstructions.
Figure 1.12. Representative reconstructions of the internal elements of the head of hammerhead sharks overlain onto phylogeny. The chondrocranium has been removed from half of the head to illustrate other elements. Phylogeny simplified from Lim et al., 2010. Numbers indicate nodes for ancestral state reconstructions. Light green = chondrocranium, green = braincase, orange = olfactory tract, red = nasal capsule, yellow = eye, light blue = palatoquadrate, dark blue = Meckel’s cartilage, pink = hyomandibula, purple = ceratohyal, and dark green = basihyal. Scale bars = 5 cm
Table 1.1. Average volume (cm³) of the eye ± standard error measured using three different methods.

<table>
<thead>
<tr>
<th>Species</th>
<th>In Animal</th>
<th>Isolated</th>
<th>Displacement</th>
<th>Within Species</th>
<th>Pooled Species</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>R. terraenovae</em></td>
<td>5.34 ± 0.21</td>
<td>6.03 ± 0.38</td>
<td>6.33 ± 0.33</td>
<td><strong>0.13</strong></td>
<td><strong>0.464</strong></td>
</tr>
<tr>
<td><em>E. blochii</em></td>
<td>1.79 ± 0.14</td>
<td>2.1 ± 0.17</td>
<td>2.1 ± 0.21</td>
<td><strong>0.41</strong></td>
<td></td>
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<tr>
<td><em>S. lewini</em></td>
<td>28.41 ± 0.63</td>
<td>31.73 ± 0.78</td>
<td>31.33 ± 1.2</td>
<td><strong>0.08</strong></td>
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<tr>
<td><em>S. tiburo</em></td>
<td>1.84 ± 0.18</td>
<td>2.13 ± 0.03</td>
<td>2 ± 0</td>
<td><strong>0.23</strong></td>
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</tbody>
</table>

Eye volume was measured from CT scans of three individuals with the eyes intact (In Animal), from CT scans of the eyes after removal from the animal (Isolated), and via water displacement (Displacement). The different methods for measuring eye volume were not different within species (*S. tiburo* p = 0.23, *S. lewini* p=0.08, *E. blochii* p=0.41, *R. terraenovae* p=0.13) or when species are pooled (p=0.46).
Table 1.2. Correlation matrix performed on phylogenetically corrected data for sphyrnid and outgroup carcharhinid species.

<table>
<thead>
<tr>
<th>Head Width</th>
<th>QMV (cm³)</th>
<th>QMD (cm³)</th>
<th>POV (cm³)</th>
<th>POD (cm³)</th>
<th>Eye (cm³)</th>
<th>Nasal Capsule (cm³)</th>
<th>Olfactory Tract (cm³)</th>
<th>Braincase (cm³)</th>
<th>Palatoquadrate (cm³)</th>
<th>Meckel's cartilage (cm³)</th>
<th>Hyomandibula (cm³)</th>
<th>Ceratohyal (cm³)</th>
<th>Basihyal (cm³)</th>
<th>Chondrocranium (cm³)</th>
<th>Total Volume (cm³)</th>
<th>Dorsal Pore Count (#)</th>
<th>Ventral Pore Count (#)</th>
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</table>

The top line within a structure is the correlation coefficient and the bottom line is the p-value. Blue = a positive correlation between the two structures. Red = a negative correlation between the two structures.
Table 1.2 Continued. Correlation matrix performed on phylogenetically corrected data for sphyrnid and outgroup carcharhinid species.

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<th></th>
<th>Palatoquadrate</th>
<th>Meckel’s cartilage</th>
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<th>Ceratohyal</th>
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<th>Chondrocranium</th>
<th>Total Volume (cm³)</th>
<th>Dorsal Pore Count (#)</th>
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<td>.367</td>
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<td>.081</td>
<td>.160</td>
<td>.016</td>
<td>.022</td>
<td>.025</td>
<td>.188</td>
<td>.250</td>
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<tr>
<td>Olfactory Tract (cm³)</td>
<td>.712</td>
<td>.748</td>
<td>.803</td>
<td>.378</td>
<td>.138</td>
<td>.218</td>
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<td>.330</td>
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<td>Braincase (cm³)</td>
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<td>Meckel’s cartilage (cm³)</td>
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<td>.001</td>
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<td>Hyomandibula (cm³)</td>
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<td>-.139</td>
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<td>.259</td>
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<td>Ceratohyal (cm³)</td>
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<td>.201</td>
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<td>.352</td>
<td>.433</td>
<td>.415</td>
<td>.334</td>
<td>.334</td>
<td>.334</td>
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<tr>
<td>Chondrocranium (cm³)</td>
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<td>.001</td>
<td>.000</td>
<td>.446</td>
<td>.332</td>
<td>.457</td>
<td>.386</td>
<td>.252</td>
<td>.252</td>
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<td>Total Volume (cm³)</td>
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<td>.946</td>
<td>.690</td>
<td>.600</td>
<td>.096</td>
<td>.060</td>
<td>.630</td>
<td>.630</td>
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<tr>
<td>Dorsal Pore Count (#)</td>
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<td>. . .</td>
<td>.1.000</td>
<td>.946</td>
<td>.690</td>
<td>.600</td>
<td>.096</td>
<td>.060</td>
<td>.630</td>
</tr>
</tbody>
</table>

The top line within a structure is the correlation coefficient and the bottom line is the p-value. Blue = a positive correlation while red = a negative correlation.
Table 1.3. Average electrosensory pore counts ± standard error for both dorsal and ventral surfaces of the head.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Dorsal Pores</th>
<th>Number of Ventral Pores</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. acronotus</td>
<td>$898.8 \pm 22.15$ *</td>
<td>$1468.4 \pm 42.85$ *</td>
</tr>
<tr>
<td>R. terraenovae</td>
<td>$962.4 \pm 65.88$</td>
<td>$896.4 \pm 25.92$</td>
</tr>
<tr>
<td>E. blochii</td>
<td>$1270 \pm 29.24$</td>
<td>$1254 \pm 15.28$</td>
</tr>
<tr>
<td>S. mokarran</td>
<td>$917.6 \pm 30.54$ **</td>
<td>$1300 \pm 30.57$ **</td>
</tr>
<tr>
<td>S. zygaena</td>
<td>$889 \pm 41$</td>
<td>$1103 \pm 5$</td>
</tr>
<tr>
<td>S. lewini</td>
<td>$1303.2 \pm 113.75$ ***</td>
<td>$1634 \pm 140.10$ ***</td>
</tr>
<tr>
<td>S. tudes</td>
<td>$1254.8 \pm 41.48$</td>
<td>$1344.8 \pm 38.71$</td>
</tr>
<tr>
<td>S. tiburo</td>
<td>$904.8 \pm 21.49$</td>
<td>$1034 \pm 12.88$</td>
</tr>
</tbody>
</table>

The number of both dorsal and ventral electrosensory pores was not correlated with changes in any other structures within the head. *C. acronotus, S. mokarran, and S. lewini* have more pores on the ventral surface than the dorsal surface but all others are not different. *, **, *** $p < 0.001$. N = 5.
Table 1.4. Average ± standard error for volumes for each internal element of hammerhead sharks and outgroup carcharhinids.

<table>
<thead>
<tr>
<th></th>
<th>Head Width</th>
<th>TL</th>
<th>QMV</th>
<th>QMD 1&amp;2</th>
<th>POV</th>
<th>POD</th>
<th>Eye</th>
<th>Nasal Capsule</th>
<th>Olfactory Tract</th>
<th>Braincase</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>C. acronotus</strong></td>
<td>11.24 ± 0.41</td>
<td>100.67 ± 4.05</td>
<td>16.33 ± 2.96</td>
<td>10.33 ± 1.86</td>
<td>9.67 ± 1.76</td>
<td>3.33 ± 0.33</td>
<td>11.54 ± 1.01</td>
<td>12.53 ± 1.33</td>
<td>0</td>
<td>2.92</td>
</tr>
<tr>
<td><strong>R. terraenovae</strong></td>
<td>8.93 ± 0.21</td>
<td>86.20 ± 1.99</td>
<td>9.83 ± 1.36</td>
<td>4.50 ± 0.50</td>
<td>2.67 ± 0.67</td>
<td>1.67 ± 0.33</td>
<td>10.67 ± 0.42</td>
<td>9.45 ± 0.65</td>
<td>0</td>
<td>17.38 ± 0.57</td>
</tr>
<tr>
<td><strong>E. blochii</strong></td>
<td>58.00 ± 3.33</td>
<td>145.97 ± 9.91</td>
<td>13.67 ± 2.91</td>
<td>9.33 ± 2.85</td>
<td>15.00 ± 2.65</td>
<td>8.83 ± 1.59</td>
<td>3.57 ± 0.29</td>
<td>34 ± 6.30</td>
<td>0</td>
<td>13.99</td>
</tr>
<tr>
<td><strong>S. mokarran</strong></td>
<td>54.43 ± 3.31</td>
<td>234.67 ± 12.39</td>
<td>112.67 ± 17.37</td>
<td>58.67 ± 11.85</td>
<td>82.67 ± 11.62</td>
<td>50.00 ± 8.08</td>
<td>24.85 ± 1.25</td>
<td>92.83 ± 20.33</td>
<td>0</td>
<td>285.62 ± 42.85</td>
</tr>
<tr>
<td><strong>S. zygaena</strong></td>
<td>68.00 ± 8.00</td>
<td>262.50 ± 30.50</td>
<td>47.50 ± 16.50</td>
<td>25.25 ± 9.75</td>
<td>46.00 ± 17.00</td>
<td>22.00 ± 8.00</td>
<td>21.18 ± 3.29</td>
<td>62.65 ± 14.1</td>
<td>0</td>
<td>327.1 ± 73.07</td>
</tr>
<tr>
<td><strong>S. lewini</strong></td>
<td>61.53 ± 1.32</td>
<td>257.93 ± 2.45</td>
<td>49.00 ± 9.54</td>
<td>36.33 ± 6.12</td>
<td>65.67 ± 12.81</td>
<td>34.00 ± 4.73</td>
<td>47.21 ± 9.27</td>
<td>78.8 ± 16.18</td>
<td>0</td>
<td>331.83 ± 20.47</td>
</tr>
<tr>
<td><strong>S. tudes</strong></td>
<td>23.50 ± 1.74</td>
<td>81.6 ± 10.27</td>
<td>2.33 ± 0.88</td>
<td>1.63 ± 0.41</td>
<td>4.50 ± 1.32</td>
<td>2.00 ± 0.58</td>
<td>1.00 ± 0.06</td>
<td>5.41 ± 1.11</td>
<td>0</td>
<td>20.85 ± 3.98</td>
</tr>
<tr>
<td><strong>S. tiburo</strong></td>
<td>14.00 ± 0.37</td>
<td>90.83 ± 2.09</td>
<td>4.00 ± 0.00</td>
<td>3.50 ± 0.29</td>
<td>7.00 ± 0.58</td>
<td>4.17 ± 0.44</td>
<td>3.67 ± 0.35</td>
<td>11.91 ± 0.97</td>
<td>0</td>
<td>20.55 ± 1.82</td>
</tr>
</tbody>
</table>

Values in cm$^3$ unless otherwise noted.
### Table 1.4 Continued. Average ± standard error for volumes for each internal element of hammerhead sharks and outgroup carcharhinids.

<table>
<thead>
<tr>
<th></th>
<th>C. acronotus</th>
<th>R. ternaenone</th>
<th>E. blochii</th>
<th>S. mokarran</th>
<th>S. zygaena</th>
<th>S. lewini</th>
<th>S. tudes</th>
<th>S. tiburo</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Palatoquadrate</strong></td>
<td>11.43 ± 1.55</td>
<td>10.73 ± 4.85</td>
<td>2.00 ± 0.18</td>
<td>3.26 ± 1.52</td>
<td>1.12 ± 0.35</td>
<td>1.22 ± 0.57</td>
<td>0.53 ± 0.34</td>
<td>0.34 ± 0.49</td>
</tr>
<tr>
<td><strong>Ceratohyal</strong></td>
<td>11.43 ± 1.55</td>
<td>14.65 ± 1.55</td>
<td>2.00 ± 0.18</td>
<td>3.26 ± 1.52</td>
<td>1.12 ± 0.35</td>
<td>1.22 ± 0.57</td>
<td>0.53 ± 0.34</td>
<td>0.34 ± 0.49</td>
</tr>
<tr>
<td><strong>Hyomandibula</strong></td>
<td>11.43 ± 1.55</td>
<td>14.65 ± 1.55</td>
<td>2.00 ± 0.18</td>
<td>3.26 ± 1.52</td>
<td>1.12 ± 0.35</td>
<td>1.22 ± 0.57</td>
<td>0.53 ± 0.34</td>
<td>0.34 ± 0.49</td>
</tr>
<tr>
<td><strong>Meckel’s cartilage</strong></td>
<td>11.43 ± 1.55</td>
<td>14.65 ± 1.55</td>
<td>2.00 ± 0.18</td>
<td>3.26 ± 1.52</td>
<td>1.12 ± 0.35</td>
<td>1.22 ± 0.57</td>
<td>0.53 ± 0.34</td>
<td>0.34 ± 0.49</td>
</tr>
<tr>
<td><strong>Chondrocranium</strong></td>
<td>11.43 ± 1.55</td>
<td>14.65 ± 1.55</td>
<td>2.00 ± 0.18</td>
<td>3.26 ± 1.52</td>
<td>1.12 ± 0.35</td>
<td>1.22 ± 0.57</td>
<td>0.53 ± 0.34</td>
<td>0.34 ± 0.49</td>
</tr>
<tr>
<td><strong>Total Volume</strong></td>
<td>11.43 ± 1.55</td>
<td>14.65 ± 1.55</td>
<td>2.00 ± 0.18</td>
<td>3.26 ± 1.52</td>
<td>1.12 ± 0.35</td>
<td>1.22 ± 0.57</td>
<td>0.53 ± 0.34</td>
<td>0.34 ± 0.49</td>
</tr>
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</table>

Values in cm$^3$ unless otherwise noted.
Table 1.5. Correlation matrix performed on raw size-removed data for sphyrid and outgroup carcharhinid species.

<table>
<thead>
<tr>
<th></th>
<th>Head Width</th>
<th>QMV (cm³)</th>
<th>QMD (cm³)</th>
<th>POV (cm³)</th>
<th>POD (cm³)</th>
<th>Eye (cm³)</th>
<th>Nasal Capsule (cm³)</th>
<th>Olfactory Tract (cm³)</th>
<th>Braincase (cm³)</th>
<th>Palatoquadrate (cm³)</th>
<th>Meckel’s cartilage (cm³)</th>
<th>Hyomandibula (cm³)</th>
<th>Ceratohyal (cm³)</th>
<th>Basihyal (cm³)</th>
<th>Chondrocranium (cm³)</th>
<th>Total Volume (cm³)</th>
<th>Dorsal Pore Count (#)</th>
<th>Ventral Pore Count (#)</th>
</tr>
</thead>
<tbody>
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<tr>
<td>QMV (cm³)</td>
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<td>POV (cm³)</td>
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<tr>
<td>POD (cm³)</td>
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</tr>
<tr>
<td>Eye (cm³)</td>
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<td></td>
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<tr>
<td>Nasal Capsule (cm³)</td>
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</tr>
<tr>
<td>Olfactory Tract (cm³)</td>
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<td>0.282</td>
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<td>0.096</td>
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<td>0.396</td>
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<td></td>
</tr>
<tr>
<td>Braincase (cm³)</td>
<td>1.000</td>
<td>0.096</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
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</tr>
</tbody>
</table>

The top line within a structure is the correlation coefficient and the bottom line is the p-value. Blue = a positive correlation between the two structures. Red = a negative correlation between the two structures.
Table 1.5 Continued. Correlation matrix performed on raw size-removed data for sphyrid and outgroup carcharhinid species.

<table>
<thead>
<tr>
<th></th>
<th>Palatoquadrate</th>
<th>Meckel's cartilage</th>
<th>Hyomandibula</th>
<th>Ceratohyal</th>
<th>Basihyal</th>
<th>Chondrocranium</th>
<th>Total Volume</th>
<th>Dorsal Pore Count</th>
<th>Ventral Pore Count</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head Width</td>
<td>-.639</td>
<td>-.625</td>
<td>-.374</td>
<td>-.651</td>
<td>-.282</td>
<td>.469</td>
<td>-.148</td>
<td>.553</td>
<td>.098</td>
</tr>
<tr>
<td>QMV (cm³)</td>
<td>.899</td>
<td>.924</td>
<td>.808</td>
<td>.878</td>
<td>.329</td>
<td>.000</td>
<td>.313</td>
<td>-485</td>
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<td>QMD (cm³)</td>
<td>.970</td>
<td>.979</td>
<td>.885</td>
<td>.900</td>
<td>.281</td>
<td>-.074</td>
<td>.324</td>
<td>-475</td>
<td>.115</td>
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<td>POV (cm³)</td>
<td>.464</td>
<td>.456</td>
<td>.638</td>
<td>.298</td>
<td>-.074</td>
<td>.020</td>
<td>.248</td>
<td>-.147</td>
<td>.415</td>
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<tr>
<td>POD (cm³)</td>
<td>.431</td>
<td>.399</td>
<td>.568</td>
<td>.154</td>
<td>-.328</td>
<td>-.177</td>
<td>.011</td>
<td>-.148</td>
<td>.196</td>
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<td>Eye (cm³)</td>
<td>.701</td>
<td>.676</td>
<td>.443</td>
<td>.682</td>
<td>.274</td>
<td>-.380</td>
<td>.155</td>
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<td>Nasal Capsule (cm³)</td>
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<td>.633</td>
<td>.696</td>
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<td>-.338</td>
<td>-.330</td>
<td>-.253</td>
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<td>.151</td>
<td>.146</td>
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<td>.244</td>
<td>.029</td>
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<td>Braincase (cm³)</td>
<td>.204</td>
<td>.226</td>
<td>.326</td>
<td>.190</td>
<td>.548</td>
<td>.659</td>
<td>.828</td>
<td>.043</td>
<td>.463</td>
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<td>.989</td>
<td>.918</td>
<td>.899</td>
<td>.238</td>
<td>-.059</td>
<td>.305</td>
<td>-.416</td>
<td>.180</td>
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<td>Meckel's cartilage (cm³)</td>
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<td>.912</td>
<td>.899</td>
<td>.282</td>
<td>-.002</td>
<td>.349</td>
<td>-.413</td>
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<tr>
<td>Hyomandibula (cm³)</td>
<td>1.000</td>
<td>.819</td>
<td>.145</td>
<td>.076</td>
<td>.314</td>
<td>-.388</td>
<td>.157</td>
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<tr>
<td>Ceratohyal (cm³)</td>
<td>1.000</td>
<td>.477</td>
<td>.101</td>
<td>.404</td>
<td>-.385</td>
<td>.237</td>
<td>.381</td>
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<tr>
<td>Basihyal (cm³)</td>
<td>1.000</td>
<td>.608</td>
<td>.859</td>
<td>-.011</td>
<td>.381</td>
<td>.480</td>
<td>.036</td>
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<tr>
<td>Chondrocranium (cm³)</td>
<td>1.000</td>
<td>.653</td>
<td>.272</td>
<td>.364</td>
<td>.104</td>
<td>.044</td>
<td>.432</td>
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<tr>
<td>Total Volume (cm³)</td>
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<td>-.006</td>
<td>.489</td>
<td>.020</td>
<td></td>
<td>.463</td>
<td>.013</td>
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</table>

The top line within a structure is the correlation coefficient and the bottom line is the p-value. Blue = a positive correlation while red = a negative correlation.
Table 1.6. Ancestral state reconstructions at each of the nodes along sphyrid phylogeny (Figure 1).

<table>
<thead>
<tr>
<th>Node</th>
<th>Basal</th>
<th>Derived</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2 3 4 7 5 6</td>
<td></td>
</tr>
<tr>
<td>Head Width (cm)</td>
<td>38.36 47.45</td>
<td>46.84 50.89</td>
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<tr>
<td>TL (cm)</td>
<td>163.21 177.49</td>
<td>181.91 199.54</td>
</tr>
<tr>
<td>QMV Volume (cm³)</td>
<td>21.03 22.09</td>
<td>23.41 30.89</td>
</tr>
<tr>
<td>QMD Volume (cm³)</td>
<td>13.32 14.00</td>
<td>14.78 18.42</td>
</tr>
<tr>
<td>POV Volume (cm³)</td>
<td>21.74 25.15</td>
<td>26.81 32.74</td>
</tr>
<tr>
<td>POD Volume (cm³)</td>
<td>10.89 13.39</td>
<td>14.16 17.20</td>
</tr>
<tr>
<td>Eye Volume (cm³)</td>
<td>9.98 9.75</td>
<td>10.85 13.34</td>
</tr>
<tr>
<td>Nasal Capsule Volume (cm³)</td>
<td>32.01 37.72</td>
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<td>Olfactory Tract Volume (cm³)</td>
<td>6.58 9.12</td>
<td>9.53 11.87</td>
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<td>Braincase Volume (cm³)</td>
<td>101.38 123.02</td>
<td>132.48 168.21</td>
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<tr>
<td>Palatoquadrate Volume (cm³)</td>
<td>17.24 18.66</td>
<td>19.78 24.52</td>
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<td>Meckel's cartilage Volume (cm³)</td>
<td>23.00 24.94</td>
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<td>Hyomandibula Volume (cm³)</td>
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<td>10.63 13.27</td>
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<td>Ceratohyal Volume (cm³)</td>
<td>7.10 7.30</td>
<td>7.65 9.38</td>
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<td>Basihyal Volume (cm³)</td>
<td>3.48 3.79</td>
<td>4.09 5.05</td>
</tr>
<tr>
<td>Chondrocranium Volume (cm³)</td>
<td>194.64 237.79</td>
<td>250.30 320.42</td>
</tr>
<tr>
<td>Total Volume (cm³)</td>
<td>1790.89 2112.35</td>
<td>2302.97 2951.16</td>
</tr>
<tr>
<td>Dorsal Pore Count (#)</td>
<td>1042.98 1070.19</td>
<td>1051.88 1005.43</td>
</tr>
<tr>
<td>Ventral Pore Count (#)</td>
<td>1286.99 1257.94</td>
<td>1257.25 1231.31</td>
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</tbody>
</table>

Indicates that at node 2, Figure 1.1, the most common ancestor between sphyrid and carcharhinid sharks was a relatively large bodied shark (163.21 cm TL) that possessed a moderately expanded cephalofoil (~23% of TL). These values place the ancestral shark intermediate between large and small bodied hammerhead sharks in length and similar to large bodied hammerhead sharks (*S. mokarran*, *S. zygaena*, and *S. lewini*) in degree of lateral head expansion (Compagno, 1984; 1988). Nodes are organized from basal on the left to more derived on the right.
CHAPTER 2: FUNCTIONAL MORPHOLOGY OF THE FEEDING APPARATUS IN
HAMMERHEAD SHARKS (SPHYRNIDAE): A PHYLOGENETIC PERSPECTIVE

ABSTRACT

Hammerhead sharks offer a unique opportunity to study form and function through phylogeny. Because sphyrid sharks possess cranial morphologies with extreme variation, they can be used to address questions about the evolution of cranial design and investigate the effects of changes in head morphology on feeding structures and ecologically relevant performance parameters such as bite force. Adult individuals of *Eusphyra blochii*, *Sphyrna mokarran*, *S. lewini*, *S. tudes*, *S. tiburo*, *Carcharhinus acronotus*, and *Rhizoprionodon terraenovae* were chosen to represent a continuum of head shape through phylogeny. The cross sectional areas of the four principal jaw adductors as well as the mechanical advantage of the jaws were used to estimate the theoretical maximum bite force. Additionally, the volume of each muscle along with the volume the palatoquadrate and Meckel’s cartilage, and hyoid arch were determined through reconstructed CT scans. Both anterior (18.2 – 642.22 N) and posterior (71.08 – 1839.43 N) absolute bite force exceeded a full order of magnitude. Within sphyrid sharks anterior and posterior mechanical advantage ranged from 0.12 – 0.26 and 0.76 – 1.01 respectively with outgroup carcharhinids having slightly greater anterior and posterior mechanical advantages. These values of anterior mechanical advantage place sphyrid sharks among other fishes classified as having low to intermediate jaw leverage.
systems. Multiple linear regression indicated that the best predictor of anterior bite force was the force produced by the preorbitalis ventral while posterior bite force was best predicted by the force produced by the preorbitalis ventral and preorbitalis dorsal along with posterior mechanical advantage. Size-removed bite force analysis indicated that *E. blochii, S. zygaena,* and *S. tiburo* all produce less force than would be predicted based on their length. Negative correlations were also found within the feeding structures. Particularly striking was the negative correlations between posterior bite force and the volumes of the POV, POD, palatoquadrate, Meckel’s cartilage, and hyomandibula. Despite these negative correlations, much of the feeding apparatus remains unchanged through evolutionary history indicating few constructional constraints within the cephalofoil. These results, along with previous data, lead to the conclusion that within sphyrid sharks the feeding bauplan has been conserved with few changes to the feeding apparatus and biomechanics. Instead, changes to the cephalofoil are confined to the chondrocranial elements and sensory structures.

**INTRODUCTION**

Diversity in cranial morphology is often associated with the occupation of novel habitats due, in part, to occupation of different feeding niches (Grant and Grant, 1995; Caldecutt and Adams, 1998; Herrel et al., 2001a; b; Adriaens et al., 2009). Furthermore, chondrichthyan fishes occupy a diverse range of feeding niches due, in part, to divergent cranial morphologies (e.g. horn sharks (Summers et al., 2004; Huber et al., 2005) and cownose rays (Summers, 2000)). In an attempt to understand this morphological and functional diversity, several studies have focused on the functional morphology of the
feeding apparatus (reviewed in Motta, 2004). Most of these studies focus on a single species (Frazzetta and Prange, 1987; Shirai and Nakaya, 1992; Wu, 1994; Motta et al., 1997; Wilga and Motta, 1998a; b; Dean and Motta, 2004a; b; Matott et al., 2005), with notable exceptions (Summers, 2000). Such performance-based comparative studies provide a window into the evolution of vertebrate design (Losos et al., 1994).

The sphyrid cephalofoil is formed by lateral expansion of the rostral, olfactory, and optic regions of the chondrocranium (Compagno, 1988; Haenni, 2001). The width of the cephalofoil is variable across species, but generally ranges from 18 to 50% of the total length (TL) of the shark (Compagno, 1984). Each species of the eight extant hammerhead sharks has a unique adult head shape (Chapter 1 this dissertation, Figure 2.1) (Gilbert, 1967; Compagno, 1984; 1988; Lim et al., 2010). Sphyrid sharks are considered to be closely related to carcharhinid sharks. Surprisingly, the species with the most expanded cephalofoil (E. blochii) represents the most ancestral form and the shark with the least lateral expansion (S. tiburo) is the most derived species (Figure 2.1) (Naylor, 1992; Martin, 1993; Martin and Palumbi, 1993; Lim et al., 2010). Furthermore, new molecular evidence suggests that ancestral hammerhead sharks were large bodied and that small body size has evolved at least two times independently (Lim et al., 2010).

Because the cephalofoil of sphyrid sharks represents such a significant morphological departure from the head morphology of their sister taxa, the hammerhead sharks (Elasmobranchii, Carcharhiniformes, Sphyrnidae) offer a unique opportunity for studying form and function in an historical context, and addressing questions about the evolution of cranial design (Lauder and Liem, 1989; Herrel et al., 2001a; b). The dorsoventrally compressed and laterally expanded pre-branchial cephalofoil has been the
subject of much speculation but little empirical testing. Reported functions include increased hydrodynamic lift, enhanced binocular vision, greater olfactory localization and resolution, enhanced electroreception, and perhaps a novel mechanism for prey capture (Tester, 1963a; b; Thomson and Simanek, 1977; Compagno, 1984; Johnsen and Teeter, 1985; Strong et al., 1990; Nakaya, 1995; Driver, 1997; Kajiura, 2001; 2003; Kajiura et al., 2003; 2005; Chapman and Gruber, 2002; McComb et al., 2009).

Hammerhead sharks use a number of techniques for capturing prey that do not differ markedly from requiem sharks. The larger species rely primarily on ram feeding and consume fish (Clarke, 1971; Compagno, 1984; 1988; Stevens and Lyle, 1989; Wilga and Motta, 2000) while the smaller species use a combination of ram and suction to consume a wide array of prey species, ranging from crustaceans to fishes (Compagno, 1984; Cortés et al., 1996; Wilga and Motta, 2000). Some smaller species (*S. media*, *S. tudes*, and *S. tiburo*) include a significant portion of crustaceans in their diet. Two anecdotal studies observed great hammerhead sharks *S. mokarran*, restraining batoid prey with their cephalofoil prior to biting off their pectoral fins (Strong et al., 1990; Chapman and Gruber, 2002). Consequently, the biological role of the cephalofoil has also been proposed as a means of prey restraint in the same manner as juvenile *Scyliorhinus canicula* use their tail and skin to restrain prey before biting (Southall and Sims, 2003). Despite the variation in cephalofoil size and shape, as well as prey types consumed by hammerhead sharks, the functional morphology of the feeding apparatus and prey capture behavior have been described for only one of the eight extant species (*S. tiburo*, Wilga and Motta, 2000; Mara et al., 2010).
The ability to capture and process food is heavily influenced by bite performance in many species. As a result, bite force, a measure of feeding performance, has been extensively studied in vertebrates, including fishes (Wainwright, 1988; Herrel et al., 2002; Korff and Wainwright, 2004; Grubich, 2005; Huber et al., 2005; 2009; Kolmann and Huber, 2009; Mara et al., 2010), lizards (Herrel et al., 2001a; Lailvaux and Irschick, 2007), crocodilians (Erickson et al., 2003), birds (van der Meij and Bout, 2000; 2006; Herrel et al., 2005a; b), and mammals (Kiltie, 1982; Aguirre et al., 2003; Herrel et al., 2008), and has been linked to the occupation of novel niches (Hernández and Motta, 1997; Berumen and Pratchett, 2008). Among the hammerhead sharks, *Sphyrna tiburo* shows the greatest dietary specialization, having a primarily durophagous diet of portunid crabs in south Florida (Compagno, 1984; Cortés et al., 1996; Lessa and Almeida, 1998; Wilga and Motta, 2000; Bethea et al., 2007). Durophagy in fishes, or the consumption of hard prey, is often associated with hypertrophy of skeletal elements and adductor muscles, larger and more molariform teeth, greater bite force, greater jaw closing mechanical advantage, and a modified biting pattern involving rapid and repeated closure on the prey (Wainwright, 1988; Turingan and Wainwright, 1993; Hernández and Motta, 1997; Clifton and Motta, 1998; Summers, 2000; Huber and Motta, 2004; Summers et al., 2004; Huber et al., 2005). *Sphyrna tiburo* exhibits few of these functional adaptations for durophagy with the exception of molariform teeth (Wilga and Motta, 2000; Mara et al., 2010).

Larger fishes, including sharks, inherently generate larger bite forces because of the larger cross-sectional areas of their jaw adductor muscles (Huber et al., 2005; 2006; Mara et al., 2010). During the evolution of hammerhead sharks, with repeated forays into
larger and smaller adult body sizes (Lim et al., 2010), this most likely resulted in differing bite performance. Whether these differences translate into differences in feeding niches or differing biological roles of the feeding apparatus remains unresolved.

Given the extreme differences in head size and shape through phylogeny, various constructional constraints are expected within the cephalofoil of hammerhead sharks (Chapter 1; Barel, 1984; Devaere et al., 2001; Hulsey et al., 2007). Through phylogeny, the internal elements become reorganized to accommodate differences in head shape (Chapter 1). Previous research has demonstrated that differences in head shape, particularly dorso-ventral flattening, can result in constraints on the position of the feeding apparatus (Devaere et al., 2005). In addition to the probable shifts in feeding performance within the sphyrid lineage, the question remains whether the sphyrid feeding bauplan has changed from that of its carcharinid ancestry as a result of the laterally expanded cephalofoil, or if the feeding structures have been conserved with morphological changes being confined to the skeletal and sensory structures of the cephalofoil.

A study of the feeding morphology and biomechanics of this clade may provide a window into the selective forces and constraints that govern cranial design in this unique group of very specialized fishes. Because the cephalofoil of hammerhead sharks represents such a morphological departure from the head morphology found in other carcharhiniform sharks, it can be used to address the evolution and consequences of changes in head design, and reveal functional morphological differences among species related to feeding. The goals of this study are to: 1) describe and compare the functional morphology and biomechanics of the feeding apparatus of the hammerhead sharks; 2)
investigate if changes to the feeding bauplan exist in sphyrid shark or if changes are confined to surrounding structures with conservation of the feeding apparatus; and 3) investigate the relationship between cranial design and feeding morphology through phylogeny in this clade.

**MATERIALS AND METHODS**

Adult individuals of *Eusphyra blochii* (Cuvier, 1816) (5, 109 – 165.6 cm TL), *Sphyra mokarran* (Rüppel, 1837) (5, 210 – 399 cm TL), *S. zygaena* (Linnaeus, 1758) (2, 232 – 293 cm TL), *S. lewini* (Griffith and Smith, 1834) (5, 246 – 265.5 cm TL), *S. tudes* (Valenciennes, 1822) (5, 73.5 – 102 cm TL), *S. tiburo* (Linnaeus, 1758) (5, 85 – 91.5 cm TL), *Carcharhinus acronotus* (Poey, 1860) (5, 93.5 – 107.5 cm TL), and *Rhizoprionodon terraenovae* (Richardson, 1836) (5, 85 – 92.6 cm TL) were chosen to represent a continuum of head shape through phylogeny and closely related carcharhinid species. *Eusphyra blochii* were collected in the waters off Darwin, Australia; *S. mokarran* and *S. lewini* were collected from various locations along the western and eastern peninsula of S. Florida; *S. zygaena* were collected from the eastern coast of S. Florida and the waters off New Zealand; *S. tudes* was collected off the northeast coast of Trinidad; and *S. tiburo*, *C. acronotus*, and *R. terraenovae* were collected from the Gulf of Mexico off Sarasota, Florida. Adult specimens were chosen to minimize the effect of ontogeny on head morphology (Haenni, 2001). All animal collection procedures followed the Institutional Animal Care and Use Committee guidelines of Mote Marine Laboratory (08-10-RH1, 07-10-PM1) and the University of South Florida (T3198, R3205, W3514).
**Volumetric Measures**

The volumetric contributions of the cartilaginous feeding elements (jaws and hyoid) were determined through digitally reconstructed computed tomography (CT) as outlined in Chapter 1 (Figure 2.2). Briefly, CT scans were performed on a 64 slice Aquilion Toshiba scanner (Toshiba America Medical Systems Inc., Tustin, CA, USA) at a 0.5 mm slice interval. Slices were then reconstructed using AMIRA 4.1.2 software (Visage Imaging Inc., San Diego, CA, USA) (Figure 2.2).

**Feeding Morphology and Bite Force Generation in Sphyrids**

The overall organization of the feeding system is similar to that of *S. tiburo* (Wilga and Motta, 2000). The jaw adducting system is composed of four principal muscles the quadratoomandibularis dorsal (QMD), quadratoomandibularis ventral (QMV), preorbitalis dorsal (POD), and preorbitalis ventral (POV). The QMD originates on the dorsal surface of the palatoquadrate and travels posteroventrally to insert on the mid-lateral raphe of the quadratoomandibularis complex. The QMV originates on the mid-lateral raphe and inserts via a broad fan-like insertion onto the Meckel’s cartilage. The POD originates on the dorsal surface of the palatoquadrate just posterior to the orbital process and inserts via a tendon onto the mid-lateral raphe. Finally, the POV originates on the posterior nasal capsule and post-orbital cartilage and travels posterolaterally to merge with the tendon of the POD to insert on the mid-lateral raphe at the corner of the Meckel’s cartilage (Figure 2.3; Wilga and Motta, 2000). For the biomechanical computations the muscles are considered to insert on the Meckel’s cartilage.

Following CT scans, the width of the head, between the distal tips of the cephalofoil, was measured and the skin was removed from both the dorsal and ventral
surfaces of the head anterior to the first gill slit. The three-dimensional coordinates of the origins and insertions of the muscles involved with jaw adduction, the QMD, QMV, POD, and POV along with the jaw joint and anterior and posterior bite points along the Meckel’s cartilage were obtained using a three-dimensional Polhemus Patriot digitizer (Polhemus, Colchester, VT, USA) with the tip of the rostrum as the center of a three-dimensional coordinate system. Each muscle was then unilaterally excised and their mass and volume determined (Figure 2.3) (Wilga and Motta, 2000). Volume was determined by water displacement in a graduated cylinder and mass on a Brainweigh B 1500 digital scale (Chapter 1). For each muscle the center of mass was determined and the superficial muscle fiber architecture was used to estimate the line of action (Huber et al., 2005). The in-lever for each muscle was calculated based on the distance between its insertion on the Meckel’s cartilage and the jaw joint. A resolved in-lever for jaw adduction was then determined from a weighted average of these individual in-levers based on the proportion of force that each muscle contributed to overall force production. Out-lever distances to the anterior and posterior bite points were determined from the coordinates of the anterior and posterior margins of the functional tooth row and the jaw joint. The weighted in-lever was then divided by the appropriate out-lever to give the gear ratio for jaw adduction at the anterior (anterior most tooth) and posterior (posterior most functional tooth) bite points (Huber et al., 2006; 2008). It is assumed that all skeletal elements act as rigid beams and mechanical advantage is equivalent to ideal mechanical advantage. The mechanical advantage of a jaw adducting system indicates the ability of the system to transfer muscle forces to prey either rapidly (low mechanical advantage) or forcefully (high mechanical advantage) (Westneat, 2003). Following
excision, each muscle was bisected perpendicular to the principal fiber direction through the center of mass and the cross sectional area was digitized with Sigma Scan Pro 4 (SYSTAT Software Inc., Point Richmond, CA, USA) (Huber et al., 2005). Maximum tetanic tension for each muscle was calculated by multiplying the cross sectional area by the specific tension of elasmobranch white muscle (28.9 N/cm², Lou et al., 2002). Forces and positions of the origins and insertions were then used to create three-dimensional force vectors for each muscle. Bilateral theoretical maximum bite force at anterior and posterior bite points was then modeled in 3D with Mathcad 13 (Mathsoft, Inc., Cambridge, MA, USA) by summation of the moments generated about the jaw joints by each muscle (Huber et al., 2005).

**Statistical Analyses**

All variables were log₁₀ transformed and regressed against TL and studentized residuals input into a principal components analysis (PCA) to investigate the size-removed variables resulting in separation among species. Principal components were considered significant if their eigenvalue was greater than 1. In order to determine which variable(s) was the primary determinant of output bite force, two forward stepwise multiple linear regressions were performed with anterior and posterior bite force as dependents. In order to investigate bite force among sphyrid and closely related carcharhinid sharks, log₁₀ transformed anterior bite force values were regressed against log₁₀ shark TL to remove the effect of size. Average residual data for each species was then qualitatively compared.

To account for the phylogenetic non-independence of the data, independent contrasts for all log₁₀ transformed variables were generated using the most recent
sphyrid phylogeny which includes branch lengths (Lim et al., 2010; Martin, 1993) using Mesquite 2.72 (Maddison and Maddison, 2009). Feeding morphology data collected here were combined with volume data collected previously (Chapter 1) in the phylogenetic analysis. Because this phylogeny includes only a single outgroup, *C. acronotus* was retained as the outgroup species for phylogenetic analyses. In order to account for the large size range of the species studied here, the contrast value for each of the variables was then regressed, through the origin, against the contrast of TL. The studentized residuals were then analyzed with a Pearson correlation analysis, through the origin. Correlation analyses reveal the relationship between pairs of variables. Finally, Mesquite was used to perform ancestral state character reconstructions to investigate how feeding variables change through evolutionary history, as described in Chapter 1. Regressions and the PCA analysis were performed in SYSTAT v11 (SYSTAT Software Inc., Chicago, IL, USA) and the correlation analysis was performed in SPSS v18 (SPSS, Chicago, IL, USA).

**RESULTS**

*Feeding Morphology and Biomechanics*

Principal components analysis revealed that species separate based on a combination of mass and force of the jaw closing musculature and bite force. Two significant principal components (eigenvalue > 1) were retained for further analysis. Together these two principal components explained 78.9% of the variation in feeding morphology within hammerhead sharks. Principal component 1 explained 49.7% of the variation and represents increasing values of anterior and posterior bite force, along with
QMV and QMD mass and force. Principal component 2 explained 27.2% of the variation, and represents increasing values of POV and POD mass and force (Figure 2.4). Carcharhinid outgroups (*C. acronotus* and *R. terraenovae*) along with *S. mokarran* had among the largest size-removed bite forces or largest muscle masses and forces. Whereas *E. blochii*, *S. lewini*, and *S. tiburo* displayed among the lowest size-removed bite forces, muscle masses, and muscle forces. Similarly, *S. tudes* and *S. tiburo* displayed relatively large values for POV and POD mass and force (Figure 2.4). Principal components analysis indicated that all variables contributed significantly to separation among species, and as a result, all variables were retained for further analyses.

The raw data indicate that the masses and volumes of the feeding muscles and cartilages varied among species (Table 2.1, 2.2, Figure 2.5). The Meckel’s cartilage was consistently larger in volume than the palatoquadrate in all species (Table 2.2). Consequently, the muscles that rest upon each cartilage followed similar trends with the QMV having a greater mass than the QMD (Table 2.1). Both anterior (18.2 – 642.22 N) and posterior (71.08 – 1839.43 N) absolute bite force spanned a full order of magnitude (Table 2.1). Within sphyrnid sharks mechanical advantage ranged from 0.12 – 0.26 at the anterior bite point and from 0.76 – 1.01 at the posterior bite point. Out-groups showed similar but slightly higher anterior and posterior mechanical advantage (0.3 – 0.33 and 1.18 respectively). *Sphyrna zygaena* had the smallest (0.12) anterior mechanical advantage while *E. blochii* and *S. mokarran* had the largest (0.26) indicating a more force efficient jaw in *E. blochii* and *S. mokarran*. Posterior mechanical advantage was smallest in *S. lewini* (0.88) and largest in *S. zygaena* (1.01) (Table 2.1).
Multiple linear regression of size-removed data indicated that the best predictor of output anterior bite force for sphyrid and outgroup carcharhinid sharks was the force produced by the POV ($p = 0.029$). For posterior bite force the best predictors include POV force ($p < 0.001$), POD force ($p = 0.001$), and posterior mechanical advantage ($p < 0.001$). Furthermore, the QMV consistently produced the greatest proportion of overall muscle force in all species (Table 2.3).

Although size-removed analyses of bite force data provide little information without phylogeny being taken into account, it is sometimes instructive to qualitatively compare size-removed bite force among species, in this case within sphyrid sharks. The regression of log anterior bite force vs. log$_{10}$ shark TL indicates that species cluster relatively close together ($\log \text{ABF} = 2.144(\log \text{TL}) - 2.705$, Figure 2.6). However, species form clear groups both above and below the regression line (Figure 2.6) with the range of residual bite force falling both above and below predictions (Table 2.4). *Eusphyra blochii*, *S. zygaena*, and *S. tiburo* all have anterior bite force values that fall below predicted values with average residuals of -0.77, -1.26, and -1.22 respectively. Furthermore, the range of residual values for *E. blochii*, *S. zygaena*, and *S. tiburo* indicates that anterior bite force for all individuals sampled for these species fell well below predicted (negative residual ranges) (Table 2.4). When sphyrid sharks are compared to carcharhinid sharks, both carcharhinid sharks, *C. acronotus* and *R. terraenovae* have higher than predicted bite forces with average residuals of 1.18 and 0.66 respectively. *Sphyrna mokarran* is the only hammerhead to have consistently higher than predicted bite forces with an average residual bite force of 0.87 (Figure 2.6, Table 2.4).
Changes among Feeding and Sensory Structures

Pearson correlation analyses of the feeding morphology, bite force, and volume of the internal components of the cephalofoil indicate that much of the cephalofoil is morphologically conserved with few correlations found between elements. The feeding variables showed both positive and negative correlations. Positive correlations were particularly apparent in the volume of the feeding apparatus and muscles. Furthermore, as the palatoquadrate increased in volume the Meckel’s cartilage also increased in volume. The volume of the hyomandibula and ceratohyal also displayed this same relationship with palatoquadrate and Meckel’s cartilage volume (Table 2.5).

Similar to the internal volumes, both positive and negative correlations were concentrated in the masses of the principal jaw closing muscles (QMV, QMD, POV, and POD) with fewer correlations relating to the jaw and jaw suspension cartilages (Table 2.5). However, as the number of variables being analyzed increases, the chance of spurious correlations increases (Aldrich, 1995). Consequently, correlations such as that of the eye and ceratohyal size are most likely meaningless. Correlations will only be addressed if the elements are adjacent or nearby structures as per the definition of constraints utilized in Chapter 1. A number of both positive and negative correlations were found among volume and feeding morphology variables. Positive correlations included anterior mechanical advantage being positively correlated with POV, palatoquadrate, Meckel’s cartilage, and hyomandibula volumes, indicating more force efficient bites are correlated with increasing volumes of the POV, palatoquadrate, Meckel’s cartilage, and hyomandibula. Posterior mechanical advantage was also positively correlated with posterior bite force. The remaining positive correlations are
confined to the feeding muscles (masses and forces). Anterior bite force was positively correlated with POD mass and force and POV force. The four principal jaw closing muscles also display various positive correlations among each other. The QMV mass is positively correlated with the masses of the QMD and POV, and the force produced by the QMD. The mass of the QMD showed the same pattern as QMV with positive correlations associated with QMV and POV mass and QMD force. The masses of the POV and POD are positively correlated with POV force with POV mass also being correlated with QMD and POD force. Finally, POV and POD force are positively correlated with each other (Table 2.5). These correlations indicate that as anterior bite force increases the mass and force of the POD and the force of the POV also increase, but not the masses of the QMD and QMV. Interestingly, a positive correlation was also found between nasal capsule volume and the mass of the QMV and QMD indicating that as nasal capsule volume increased the mass of the QMV and QMD also increased. Similarly, a positive correlation between nasal capsule volume and volume of the QMD was also detected (Table 2.5).

While many variables were positively correlated, there were negative correlations among variables too. Posterior bite force was negatively correlated with the volumes of the POV, POD, palatoquadrate, Meckel’s cartilage, and hyomandibula. These negative correlations indicate, somewhat paradoxically, that as posterior bite force increases the volume of the POV, POD, palatoquadrate, Meckel’s cartilage, and hyomandibula decrease. Similarly, the volume of the basihyal was negatively correlated with the masses of the QMV, QMD and POD along with the force of the QMD. Both the chondrocranium and total volume had the same pattern of negative correlations as the
basihyal indicating that as jaw adductor muscle masses get larger the basihyal, chondrocranium, and total volume decrease in size. Lastly, the posterior mechanical advantage was negatively correlated with the force of the POD indicating that as posterior mechanical advantage increased the force produced by the POD decreased (Table 2.5).

*Ancestral State Reconstructions*

The primary ancestral node of interest is the split between the extreme lateral expansion seen in *Eusphyra* (up to 50% of TL) and the relatively moderate expansion seen in *Sphyrna* (less than ~27% of TL) (Node 3 Figure 2.1). This node represents the most common ancestor to *Eusphyra* and *Sphyrna*. This ancestor is intermediate in both TL and lateral expansion (~179.08 cm and 46.64 cm or ~26% of TL respectively) (Figure 2.1, Table 2.1 and 2.6) and is characterized by intermediate anterior and posterior bite force (Table 2.1 and 2.6).

Through evolutionary history of the sphyrnids, the general trend is for the mass of the POV to be greater than that of the remaining feeding muscles. However, the QMV consistently produces the most force despite not being a significant predictor of output bite force in extant taxa. Both anterior and posterior mechanical advantages were similar through evolutionary history and not different than extant taxa (Table 2.1 and 2.6).

**DISCUSSION**

*Feeding Morphology and Biomechanics*

When compared to closely related carcharhinid sharks, the feeding morphology of sphyrid sharks is not markedly different. Furthermore, cephalofoil width did not have a
significant effect on feeding morphology and bite force. Sphyrnid and carcharhinid sharks, both carcharhiniform sharks, have similar anatomical arrangements of the quadratomandibularis and preorbitalis muscles, have similar jaw protrusion mechanisms, and even share similar jaw motor patterns (Moss, 1977b; Compagno, 1988; Wilga and Motta, 2000; Motta et al., 1997; Huber et al., 2006). Despite changes to the chondrocranium and sensory structures as a result of evolution of the cephalofoil, the feeding bauplan remains unchanged in sphyrnid sharks compared to carcharhinid species (Table 2.1, Figure 2.5).

The mechanical advantage of the jaw closing system provides an estimation of the ability of the feeding system to transmit muscle forces to either speed efficient (mechanical advantages closer to 0) or force efficient (mechanical advantages close to and greater than 1.0) jaw closure (Westneat, 1994; 2003; Cutwa and Turingan, 2000; Wainwright and Shaw, 1999; Wainwright and Richard, 1995; Wainwright, 1999). In particular, if the mechanical advantage is greater than 1.0, the system switches from a class three to a class two lever system. Class three lever systems include those where the in-lever is less than or equal to the out-lever resulting in output forces less than or equal to the input muscle forces. However, second class lever systems are force amplifying and have an in-lever that is greater than the out-lever. In second class lever systems, the input muscle force is amplified resulting in larger output forces and a force efficient jaw closing system. This may be possible for posterior teeth where the adductor muscle inserts anterior to these teeth (Durie and Turingan, 2001; Wainwright and Richard, 1995; Turingan et al., 1995; Hernández and Motta, 1997; Huber, 2006; Huber et al., 2005; 2008; Mara et al., 2010).
Mechanical analysis of the feeding morphology indicates that sphyrid and closely related carcharhinid sharks possess both class two and class three lever systems with most sphyrid sharks having posterior mechanical advantages less than 1.0, and closely related carcharhinid sharks having posterior mechanical advantages greater than 1.0 (Table 2.1). Force amplifying systems with mechanical advantages greater than 1.0 have been previously found in both chondrichthyan oral and teleost oral and pharyngeal jaws (horn shark *Heterodontus francisci*, spotted ratfish *Hydrolagus coliei*, black drum, *Pogonia cromis*, and striped burrfish, *Chilomycterus schoepfi*) (Korff and Wainwright, 2004; Huber et al., 2005; Grubich, 2005; Huber et al., 2008). All of these fishes are durophagous; however, posterior mechanical advantages greater than one have also been found in piscivorous species such as the black tip shark, *Carcharhinus limbatus* (Huber et al., 2006). The implications of changes in mechanical advantage to jaw suspension have been described in detail (Huber, 2006). With increasing values of posterior mechanical advantage, the forces acting on the jaw joint switch from compression, which pushes the upper and lower jaws together, to tension, which attempts to pull them apart. This switch to a jaw joint in tension results in greater chance for dislocation which is resisted by robust ligamentous connections (Motta and Wilga, 1995; Huber, 2006; Huber et al., 2008).

Compared to outgroup carcharhinid sharks (anterior and posterior mechanical advantages of 0.3 – 0.33 and 1.18 respectively), sphyrid sharks had lower values for both anterior and posterior mechanical advantage. The anterior mechanical advantage for sphyrid sharks ranged from 0.12 in *S. zygaena* to 0.26 in *E. blochii* and *S. mokarran*. Posterior mechanical advantage also varied among sphyrid sharks from 0.76 in *S. lewini*
to 1.01 in *S. zygaena* (Table 2.1). Furthermore, the anterior mechanical advantage of sphyrid sharks places them with numerous teleost fishes with low to intermediate jaw leverages, including wrasses (0.13 – 0.41) and gray triggerfish (0.25 – 0.27) (Durie and Turingan, 2001; Wainwright et al., 2004; Westneat, 2004). Sphyrid shark anterior mechanical advantage is considerably smaller than that found in durophagous fish such as the horn shark (0.51), chimaera (0.68), and parrotfish (0.45 – 1.04) (Wainwright et al., 2004; Huber et al., 2005; 2008). Speed efficient jaws are often found in organisms that consume elusive prey, such as fish (Westneat, 2004). The speed efficient jaw closing system found in sphyrid sharks is not that surprising when the diet of sphyrid sharks is taken into account. Most hammerhead sharks consume primarily fish and squid (up to 82.9% and 68.9% of diet, respectively). Sphyrid sharks will also include hard prey (decapod crustaceans) in their diet, with some species, such as *S. tiburo*, consuming almost exclusively hard prey (Cortés, 1999; Cortés et al., 1996; Bethea et al., 2007). *Sphyrina tiburo* capitalizes on their hard portunid prey by mostly limiting their diet to crabs that they are capable of crushing with their posterior molariform teeth (Mara et al., 2010; Chapter 3) and by utilizing specialized motor patterns (Wilga and Motta, 2000). Despite these apparent modifications for durophagy, this species does not display many of the characteristics of other durophagous chondrichthyans, such as robust reinforced jaws, hypertrophied feeding muscles, and fused jaw symphyses (Mara et al., 2010; Wilga and Motta, 2000). In order to gain a more complete understanding of the feeding morphology of a species, mechanical advantage should not be considered alone, but as part of a larger system including muscle angles and force production in addition to lever arms (De Schepper et al., 2008).
The best predictor of output anterior bite force was the force produced by the POV. Similarly, posterior bite force was best predicted by the force produced by both the POV and the POD along with posterior mechanical advantage (Table 2.3). These results contradict previous studies that found the quadratomandibularis complex of muscles is the best predictor of output force in both *Heterodontus francisci* and *S. tiburo* (Huber et al., 2005; Mara et al., 2010). While the reason for this discrepancy remains unclear, it is possible that the lateral expansion of the nasal capsule plays a role in this difference. As the nasal capsule expands laterally, the origin of the POV on the posterior nasal capsule (Wilga and Motta, 2000) is necessarily modified and expanded resulting in a greater cross-sectional area, leading to the trend of greater force production in sphyrid sharks as compared to outgroup carcharhinids (Figure 2.5; Table 2.1). However, confounding these results is the fact that the POV has been shown to be active during jaw protrusion with activity ceasing at full jaw closure (Wilga and Motta, 2000). That the POD significantly predicts posterior bite force is surprising given the morphology of this muscle. The POD has a much broader origin on the upper jaw compared to carcharhinid species (note: during jaw protrusion this switches to the insertion for the POD) and inserts onto the mid-lateral raphe of the quadratomandibularis muscle complex at a similar shallow angle to the POV (Wilga and Motta, 2000). Static equilibrium models predict that when muscles insert at a more orthogonal angle to the lower jaw, more of the force produced by that muscle will be transmitted in the dorso-ventral plane, resulting in increased contribution to output bite force. Consequently, the quadratomandibularis complex better predicts posterior bite force in other carcharhiniform sharks (Huber et al., 2005; Mara et al., 2010).
While absolute bite force values allow for comparisons among species, size often confounds this type of analysis. Size-removed analyses allow for intraspecific comparisons of disparate taxa of varying size ranges (Herrel et al., 2004; 2007; Huber et al., 2005; Mara et al., 2010). However, size or mass specific comparisons of bite force should be interpreted cautiously. The reason for this is the method of size removal. In order to perform size-removed comparisons, bite force is linearly regressed against either length or mass of the individuals. In this type of analysis, if one or more individuals have exceptionally high or exceptionally low bite force for their length or mass, the regression line and consequently the residual data will be heavily influenced by these outliers. Furthermore, exceptionally elongated taxa (e.g. elongated caudal fin of orectolobiform or alopoid sharks) may bias the interpretation. To avoid this problem, this study investigated size-removed data from only within sphyrnid and closely related carcharhinid species (Figure 2.6, Table 2.4). Total length removed residual bite force reveals that among sphyrnid and closely related carcharhinid species, \textit{E. blochii}, \textit{S. zygaena}, and \textit{S. tiburo} all have an average residual anterior bite force that is less than predicted (-0.77, -1.26, and -1.22 respectively) (Table 2.4). While the negative average residual values are not that surprising for the piscivorous \textit{E. blochii} and \textit{S. zygaena} (Compagno, 1984), the negative residuals of \textit{S. tiburo} are surprising given the proportion of hard prey included in its diet (up to 85\% IRI) (Cortés et al., 1996). Dietary and bite performance data indicate that, at least in South Florida, \textit{S. tiburo} primarily consumes \textit{Callinectes sapidus} it is capable of crushing. Crabs falling outside the maximum crushing abilities of \textit{S. tiburo} are found in the stomachs indicating that some method of prey processing other than crushing is employed to consume crabs of this size (Mara et al., 2010; Chapter 3). Sphyrnid sharks
generally had smaller average residual bite force than outgroup carcharhinid species (Table 2.4), and both C. acronotus and R. terraenovae had higher than predicted residual anterior bite force values (1.18 and 0.66 respectively). The lone sphyrnid with comparable average residual bite force to outgroup carcharhinids was S. mokarran with an average of 0.87 (Figure 2.6, Table 2.4).

An integral part of the feeding system that is often overlooked is the morphology and biomechanics of the teeth. Biomechanical analyses reveal that S. mokarran teeth perform poorly at puncturing soft prey, but are able to be unilaterally drawn through prey with little force once puncture has occurred (Whitenack, 2008; Whitenack and Motta, 2010). The teeth of S. mokarran are typical for carcharhiniform species, with moderately long central cusps that are strongly serrated anteriorly and cuspidate posteriorly (Compagno, 1984). The teeth of S. mokarran have cusps that are slightly inclined toward the back of the jaws resulting in poor performance during puncture testing (Whitenack, 2008). Sphyrna zygaena, S. lewini, S. tudes have teeth similar to S. mokarran in appearance, however, their anterior teeth are only weakly serrated. Sphyrna tiburo has anterior teeth that lack serrations and posterior teeth that are molariform allowing for the consumption of hard prey (Compagno, 1984; Cortés et al., 1996; Wilga and Motta, 2000; Mara et al., 2010). Given the shape and performance of sphyrnid teeth (Whitenack, 2008), it is expected that large bodied sphyrnids with strongly serrated and posteriorly inclined teeth similar to S. mokarran would employ lateral head shaking to process their prey and would display relatively larger bite forces to counteract the inertia of the prey during lateral shaking. Sphyrna mokarran has been observed using lateral head shaking
to remove pieces of prey (K.R. Mara personal observation; Strong et al., 1990; Chapman and Gruber, 2002).

The evolution of jaw suspension in chondrichthyes has been thoroughly investigated (e.g. Wilga, 2002; 2005; 2010; Wilga et al., 2007; Huber, 2006). Sphyrnid and other carcharhiniform species have a hyostylic jaw suspension, which allows for extensive palatoquadrate protrusion (Wilga and Motta, 2000; Wilga, 2002; 2010). The degree of jaw protrusion is primarily determined by the length or absence of the ethmopalatine ligament; as well as the length and orientation of the cartilaginous elements of the suspensory apparatus (Wilga, 2005; 2010; Wilga et al., 2007). Furthermore, the orientation of the hyomandibula differs among elasmobranchs and can be linked to feeding style (Moss, 1977a; b), with posteriorventrally directed hyomandibulae being related to bite feeders such as carcharhiniform and lamniform sharks (Wilga, 2008; 2010). Within Sphyridae, the hyomandibulae are posteriorventrally directed (see Chapter 1 Figure 1.12, Figure 2.5), facilitating a biting method of prey capture (Wilga and Motta, 2000). Furthermore, in *S. tiburo*, there is minimal protrusion due to a relatively short ethmopalatine ligament (Wilga and Motta, 2000; Motta and Wilga, 2001). While minimal jaw protrusion may be advantageous for the durophagous *S. tiburo*, the remaining piscivorous species would be expected to have larger jaw protrusion distances. However, this remains to be tested in other sphyrid species (Wilga and Motta, 2000; Motta, 2004). A study quantifying the protrusion distance and kinematics of sphyrid sharks would help elucidate the potential consequences of lateral head expansion on feeding kinematics and jaw protrusion in sphyrid species.
Changes among Feeding and Sensory Structures

Previous research has indicated that the position and shape of the mouth is constrained within sphyrid sharks. The jaw cartilages and the muscles that rest upon them change in concert with each other through phylogeny (Chapter 1). The morphology of the feeding apparatus has been described for *S. tiburo* (Wilga and Motta, 2000; Mara et al., 2010) and is consistent within the rest of the family. Differences in tooth morphology do exist among hammerhead sharks and are apparently related to biomechanical performance and differences in diet (Compagno, 1984; 1988; Whitenack and Motta, 2010).

The volumes of the sensory, neural, and supportive structures within the cephalofoil showed both positive and negative correlations. The volumes of the palatoquadrate and Meckel’s cartilages were positively correlated with the volumes of the jaw closing musculature. Negative correlations within the cephalofoil were found between nasal capsule and braincase, chondrocranium, and total volume. Similarly, eye volume displayed a negative correlation to head width, indicating that as head width increases, eye volume decreases (Chapter 1).

Within sphyrid and closely related carcharinid species, changes in feeding morphology are independent of changes in head width. Changes in the volume of the feeding muscles are positively correlated with changes in the cartilaginous feeding elements (Table 2.5). Similarly, the masses and forces produced by the various feeding muscles also displayed positive correlations among each other. Positive correlations were detected between anterior mechanical advantage and the volumes of the POV, palatoquadrate, Meckel’s cartilage and hyomandibula (Table 2.5). This indicates that
more force efficient anterior bites are associated with increases in the volume of these correlated elements. Anterior bite force was also positively correlated with the mass of the POD and the force of the POD and POV. That anterior bite force is positively correlated with the force produced by the POV is not surprising given that this variable is the primary predictor of anterior bite force (Table 2.3). More force efficient posterior biting is correlated with increasing posterior bite force values, which is consistent with predictions of increasing mechanical advantage being related to increased force production (Durie and Turingan, 2001; Wainwright et al., 2004; Westneat, 2004).

Pearson correlation analysis revealed that there are negative correlations among feeding morphology variables through evolutionary history (Table 2.5). Particularly striking, is the negative correlation between posterior bite force and the volume of the POV, POD, palatoquadrate, Meckel’s cartilage, and hyomandibula. These negative correlations contradict predictions for the structural consequences of increasing posterior bite force (Summers, 2000; Summers et al., 2004; Huber et al., 2005), and may be related to the orientation of the muscles and their primary role in jaw protrusion (Wilga and Motta, 2000). Specifically, the POV and POD may insert at a more acute angle to facilitate palatoquadrate protrusion, consequently reducing their orthogonal component of force that contributes to jaw adductive bite force. It should also be noted that the volume of a muscle does not necessarily reflect its cross sectional area. While the volume of the muscle may decrease, muscle width may increase resulting in increased cross sectional area and consequently increased force. Supporting this, in sphyrnid and closely related carcharhinid sharks the force produced by the POV and the POD, not the volumes, are the best predictors of posterior bite force.
Sphyrnid sharks also displayed negative correlations between the volume of the basihyal and the masses of the QMV, QMD, and POD along with the force produced by the QMD (Table 2.5). Unlike the jaw closing musculature, the primary role of the basihyal is to transmit jaw abductive muscle force to the Meckel’s cartilage, such as occurs during jaw opening. Furthermore, hypertrophy of the jaw abducting musculature in specialized suction feeders (Ramsay and Wilga, 2006) could result in increased volume of the basihyal. Conversely, in biting-specialized species where the generation of suction pressure is not as important, the selective pressure for a larger basihyal could be reduced. Another negative correlation is that of the posterior mechanical advantage which is negatively correlated with the force produced by the POD. Again, this negative correlation is somewhat surprising given the POD’s function in jaw closure. Multiple linear regression indicated that the force generated by the POD was one of the best predictors of posterior bite force (Table 2.3). This negative correlation may be the result of changes to the mechanical advantage or muscle architecture among species. Either the out-lever becomes shorter or the weighted in-lever becomes longer resulting in an increase in mechanical advantage. The relationship between posterior mechanical advantage and the force produced by the POD could also be heavily influenced by *S. mokarran* which possesses a relatively large POD muscle force and among the lowest posterior mechanical advantages. *Sphyrna mokarran* may have a relatively shorter out-lever as a result of a relatively shorter palatoquadrate or a relatively longer in-lever as a result of changes in the insertion points of the adductive musculature for this species. This negative correlation could also be the result of changes to the insertion point or angle for the POV. If the POV is modified to insert at a more orthogonal angle, more of
the force it produces would be utilized for bite force. Changing the insertion angle would necessitate a change in insertion point thereby modifying the lever mechanics. Raw data point to an inverse trend between mechanical advantage and POV and POD cross sectional area (force) (Table 2.1). In sphyrid sharks, this may be due, in part, to the increased lateral cephalofoil expansion resulting in a larger origin and consequently a larger cross sectional area for the POV (Table 2.1).

This correlation analysis indicates that as the head of sphyrid sharks expands and contracts laterally through phylogeny, there are few constraints on the feeding apparatus imposed by the adjacent non-feeding structures. What constraints exist are among the various feeding structures. This is expected because of their common biological role in feeding and prey capture. The closest common ancestor to all sphyrid sharks was intermediate in lateral cephalofoil expansion (~26% of TL) and relatively large bodied (~179.08 cm TL) (Figure 2.1, Table 2.6 Node 3). Recent phylogenetic analyses indicate that modern sphyrid sharks are the result of divergent evolutionary process resulting in a lineage of sphyrids displaying cephalofoil expansion (Eusphyra lineage with cephalofoil expansion up to 50% of TL) and a second displaying cephalofoil contraction (Sphyrrna lineage with cephalofoil expansion up to 27% of TL) (Figure 2.1, Table 2.6 Node 3) (Lim et al., 2010). The predictions of a large bodied ancestral sphyrid presented here match those of Lim et al. (2010).

This study found that the contribution of the QMV to overall force production was similar through evolutionary history matching results from previous studies showing that this muscle consistently produces the greatest proportion of overall force (Mara et al., 2010). Finally, the reconstructed anterior and posterior mechanical advantages match
those of the extant taxa. This indicates that through much of their evolutionary history sphyrnid sharks had speed efficient jaw closing systems and their diet likely consisted largely of elusive prey.

**Conclusions**

Within sphyrnid sharks the feeding bauplan is conserved with few changes to feeding structures or feeding biomechanics. Furthermore, changes to the cephalofoil are mainly confined to the sensory structures. The mechanical advantage of the jaw closing system within sphyrnids is similar to the speed efficient jaw closing systems of fishes with low to intermediate jaw leverages. That a speed efficient jaw closing system was found among sphyrnid sharks is not surprising given the primarily elusive diet of these species. Multiple linear regression indicated that the best predictor of anterior bite force was the force produced by the POV, while posterior bite force is best predicted by the force of both the POV and POD along with the posterior mechanical advantage. Surprisingly, the lone durophagous member of the family Sphyrnidae, *S. tiburo*, had among the lowest length specific bite forces.

This analysis also revealed that changes in cephalofoil width had no effect on feeding morphology. Within sphyrnid and closely related carcharhinid sharks increasing anterior mechanical advantage is associated with increased volume of the POV, palatoquadrate, Meckel’s cartilage and hyomandibula. Similarly, increasing posterior mechanical advantage was positively correlated with increasing posterior bite force. These positive correlations are most likely related to structural modifications to the feeding structures related to increased bite force production and transmission. Posterior
bite force was negatively correlated with the volume of the POV, POD, palatoquadrate, Meckel’s cartilage, and hyomandibula, despite these structures’ role in feeding. However, posterior bite force is best predicted by the force produced by the POV and POD not the volume occupied by these muscles. Raw data also show an inverse trend between posterior mechanical advantage and the force produced by the POV and the POD, indicating that the increased expansion of the nasal capsule found in sphyrrnids sharks may result in an increased cross sectional area and increased force in the POV. Ancestral state reconstructions were found to match those predicted by other studies regarding ancestral sphyrrnid size and head width, indicating that the ancestral sphyrrnid shark was relatively large bodied with a moderately expanded cephalofoil. These data indicate that much of the sphyrrnid head is conserved through phylogeny.

LITERATURE CITED


bonnethead shark, *Sphyrna tiburo* from the eastern Gulf of Mexico. *Marine Biology* 152, 1009-1020.


Figure 2.1. Phylogeny of the hammerhead sharks modified from Lim et al. (2010). Based on the nuclear genes ITS2, Dlx1, and Dlx2 and the mitochondrial genes NADH dehydrogenase 2, cytochrome b, cytochrome oxidase I, and D-loop. Differences in head shape among the species are indicated with non-scaled line drawings of the cephalofoil. Body size differences are shown among the species with a generalized body shape scaled to maximum reported size for each species. Numbers above the nodes are posterior probabilities and numbers below the node are BEST credibility values. Numbers to the right of the nodes indicate nodes for ancestral state reconstructions. Head shapes and body outlines modified from Compagno, 1984. Scale bar = 1 m.
Figure 2.2. Dorsal (a) and lateral (b) views of the cartilaginous elements within the cephalofoil of *S. lewini*. Chondrocranium – light green, Palatoquadrate – light blue, Meckel’s cartilage – dark blue, Hyomandibula – pink, Ceratohyal – purple, and Basihyal – dark green
Figure 2.3. Morphology of the feeding apparatus shown on a reconstruction of *S. lewini*. The four principal jaw closing muscles, QMD – quadratomandibularis dorsal, QMV – quadratomandibularis ventral, POD – preorbitalis dorsal, and POV – preorbitalis ventral are overlain on the reconstruction. The left nasal capsule and optic cartilages have been trimmed to reveal the origin of POV on the nasal capsule.
Figure 2.4. PCA plot of TL removed raw feeding morphology data. PC1 explained 49.7% of the variation and indicates increasing values of anterior bite force, posterior bite force, QMV and QMD mass, and QMV and QMD force. While PC2 explained 27.2% of the variation and indicates increasing values of POV and POD mass and force. Generalized head shapes have been added to indicate where each shape lies within multivariate space (head shapes modified from Compagno, 1984).
Figure 2.5. Chondrocranium, mandibular, and hyoid arch skeletons of each species overlain onto phylogeny. Phylogeny simplified from Lim et al., 2010. Numbers represent ancestral character state reconstruction nodes. Scale bars = 5 cm.
Figure 2.6. Raw bite force among sphyrid and closely related carcharhinid species. Small bodied species (E. blochii, S. tudes, and S. tiburo) clearly group together as do large bodied species (S. mokarran, S. zygaena, and S. lewini). Furthermore, E. blochii (green dots), S. zygaena (orange dots), S. tiburo (black dots) have anterior bite force values that are lower than predicted.
Table 2.1. Average raw values ± s.e. for feeding morphology variables for sphyrnid and carcharhinid species.

<table>
<thead>
<tr>
<th>Species</th>
<th>TL (cm)</th>
<th>Head Width (cm)</th>
<th>Weighted In-Lever (cm)</th>
<th>Anterior Out-lever (cm)</th>
<th>Posterior Out-lever (cm)</th>
<th>AMA</th>
<th>PMA</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. acronotus</td>
<td>102.6 ± 2.52</td>
<td>11.43 ± 0.26</td>
<td>2.38 ± 0.089</td>
<td>7.26 ± 0.22</td>
<td>2.02 ± 0.055</td>
<td>0.33 ± 0.0037</td>
<td>1.18 ± 0.025</td>
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<tr>
<td>R. terraenovae</td>
<td>88.36 ± 1.35</td>
<td>9.14 ± 0.072</td>
<td>2.00 ± 0.089</td>
<td>6.71 ± 0.11</td>
<td>1.70 ± 0.056</td>
<td>0.30 ± 0.01</td>
<td>1.18 ± 0.045</td>
</tr>
<tr>
<td>E. blochii</td>
<td>132.18 ± 10.07</td>
<td>53.24 ± 3.52</td>
<td>2.02 ± 0.27</td>
<td>7.76 ± 0.77</td>
<td>2.15 ± 0.21</td>
<td>0.26 ± 0.015</td>
<td>0.93 ± 0.048</td>
</tr>
<tr>
<td>S. mokarran</td>
<td>286.14 ± 34.16</td>
<td>67.18 ± 9.11</td>
<td>5.33 ± 0.81</td>
<td>20.41 ± 3.38</td>
<td>6.43 ± 1.14</td>
<td>0.26 ± 0.011</td>
<td>0.84 ± 0.031</td>
</tr>
<tr>
<td>S. zygaena</td>
<td>262.50 ± 30.50</td>
<td>68.00 ± 8.00</td>
<td>3.77 ± 0.29</td>
<td>16.26 ± 1.85</td>
<td>3.79 ± 0.59</td>
<td>0.12 ± 0.098</td>
<td>1.01 ± 0.08</td>
</tr>
<tr>
<td>S. lewini</td>
<td>257.14 ± 3.34</td>
<td>60.18 ± 1.16</td>
<td>3.41 ± 0.14</td>
<td>14.56 ± 0.58</td>
<td>4.52 ± 0.32</td>
<td>0.24 ± 0.014</td>
<td>0.76 ± 0.036</td>
</tr>
<tr>
<td>S. tudes</td>
<td>92.52 ± 4.92</td>
<td>21.34 ± 3.10</td>
<td>1.41 ± 0.063</td>
<td>6.04 ± 0.34</td>
<td>1.64 ± 0.14</td>
<td>0.24 ± 0.012</td>
<td>0.88 ± 0.061</td>
</tr>
<tr>
<td>S. tiburo</td>
<td>88.10 ± 1.17</td>
<td>13.66 ± 0.23</td>
<td>1.25 ± 0.068</td>
<td>5.76 ± 0.10</td>
<td>1.51 ± 0.087</td>
<td>0.22 ± 0.013</td>
<td>0.84 ± 0.072</td>
</tr>
</tbody>
</table>

Phylogenetically corrected size-removed data showed head width had no affect on any feeding morphology variable.
Table 2.1 Continued. Average raw values ± s.e. for feeding morphology variables for sphyrnid and carcharhinid species.

<table>
<thead>
<tr>
<th>Species</th>
<th>TL (cm)</th>
<th>ABF (N)</th>
<th>PBF (N)</th>
<th>QMV Force (N)</th>
<th>QMD Force (N)</th>
<th>POV Force (N)</th>
<th>POD Force (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. acronotus</td>
<td>102.60 ± 2.52</td>
<td>67.02 ± 7.97</td>
<td>270.05 ± 33.77</td>
<td>108.55 ± 8.45</td>
<td>48.41 ± 5.36</td>
<td>37.25 ± 4.32</td>
<td>12.31 ± 1.12</td>
</tr>
<tr>
<td>R. terraenovae</td>
<td>88.36 ± 1.35</td>
<td>38.59 ± 2.57</td>
<td>157.68 ± 7.94</td>
<td>80.17 ± 3.94</td>
<td>33.49 ± 1.37</td>
<td>11.24 ± 1.21</td>
<td>8.61 ± 0.78</td>
</tr>
<tr>
<td>E. blochii</td>
<td>132.18 ± 10.07</td>
<td>52.11 ± 8.31</td>
<td>171.77 ± 30.56</td>
<td>83.49 ± 19.43</td>
<td>36.50 ± 6.84</td>
<td>52.22 ± 11.86</td>
<td>32.86 ± 7.06</td>
</tr>
<tr>
<td>S. mokarran</td>
<td>286.14 ± 34.16</td>
<td>642.22 ± 260.34</td>
<td>1839.43 ± 720.05</td>
<td>821.77 ± 268.63</td>
<td>574.42 ± 121.44</td>
<td>341.83 ± 138.51</td>
<td>234.93 ± 96.54</td>
</tr>
<tr>
<td>S. zygaena</td>
<td>262.50 ± 30.50</td>
<td>288.49 ± 47.00</td>
<td>1210.00 ± 128.00</td>
<td>372.16 ± 78.54</td>
<td>252.30 ± 34.39</td>
<td>209.60 ± 26.29</td>
<td>93.06 ± 26.73</td>
</tr>
<tr>
<td>S. lewini</td>
<td>257.14 ± 3.34</td>
<td>207.4 ± 23.20</td>
<td>623.05 ± 23.82</td>
<td>244.76 ± 17.02</td>
<td>161.58 ± 9.56</td>
<td>168.75 ± 7.50</td>
<td>100.23 ± 4.67</td>
</tr>
<tr>
<td>S. tudes</td>
<td>92.52 ± 4.92</td>
<td>38.36 ± 6.19</td>
<td>139.04 ± 21.10</td>
<td>59.85 ± 7.94</td>
<td>25.84 ± 3.88</td>
<td>40.72 ± 6.55</td>
<td>19.65 ± 3.08</td>
</tr>
<tr>
<td>S. tiburo</td>
<td>88.10 ± 1.17</td>
<td>18.2 ± 2.09</td>
<td>71.08 ± 6.05</td>
<td>36.16 ± 2.44</td>
<td>17.05 ± 1.02</td>
<td>29.54 ± 1.96</td>
<td>18.41 ± 0.95</td>
</tr>
</tbody>
</table>

Phylogenetically corrected size-removed data showed head width had no affect on any feeding morphology variable. N = Newtons
Table 2.1 Continued. Average raw values ± s.e. for feeding morphology variables for sphyrnid and carcharhinid species.

<table>
<thead>
<tr>
<th></th>
<th>TL (cm)</th>
<th>QMV Mass (g)</th>
<th>QMD Mass (g)</th>
<th>POV Mass (g)</th>
<th>POD Mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. acronotus</td>
<td>102.6 ± 2.52</td>
<td>8.88 ± 0.80</td>
<td>5.14 ± 0.51</td>
<td>5.3 ± 0.51</td>
<td>1.8 ± 0.15</td>
</tr>
<tr>
<td>R. terraenovae</td>
<td>88.36 ± 1.35</td>
<td>4.72 ± 0.30</td>
<td>2.64 ± 0.29</td>
<td>1.48 ± 0.058</td>
<td>0.74 ± 0.068</td>
</tr>
<tr>
<td>E. blochii</td>
<td>132.18 ± 10.07</td>
<td>5.11 ± 1.50</td>
<td>3.3 ± 0.94</td>
<td>5.78 ± 1.70</td>
<td>3.47 ± 1.03</td>
</tr>
<tr>
<td>S. mokarran</td>
<td>286.14 ± 34.16</td>
<td>198.22 ± 114.27</td>
<td>99.12 ± 57.76</td>
<td>141.76 ± 80.44</td>
<td>82.58 ± 47.34</td>
</tr>
<tr>
<td>S. zygaena</td>
<td>262.5 ± 30.5</td>
<td>49.80 ± 18.10</td>
<td>25.75 ± 9.75</td>
<td>48.00 ± 17.20</td>
<td>22.55 ± 8.05</td>
</tr>
<tr>
<td>S. lewini</td>
<td>257.14 ± 3.34</td>
<td>29.6 ± 1.83</td>
<td>20.73 ± 1.46</td>
<td>39.92 ± 1.69</td>
<td>20.18 ± 1.77</td>
</tr>
<tr>
<td>S. tudes</td>
<td>92.52 ± 4.92</td>
<td>2.54 ± 0.37</td>
<td>1.82 ± 0.33</td>
<td>5.12 ± 0.84</td>
<td>2.04 ± 0.35</td>
</tr>
<tr>
<td>S. tiburo</td>
<td>88.1 ± 1.17</td>
<td>1.58 ± 0.058</td>
<td>1.04 ± 0.87</td>
<td>2.64 ± 0.14</td>
<td>1.58 ± 0.11</td>
</tr>
</tbody>
</table>

Phylogenetically corrected size-removed data showed head width had no affect on any feeding morphology variable.
Table 2.2. Average raw volumes (cm³) ± s.e. for the cartilaginous elements of the feeding system of sphyrid and carcharhinid species.

<table>
<thead>
<tr>
<th>Species</th>
<th>TL (cm)</th>
<th>Palatoquadrate</th>
<th>Meckel’s Cartilage</th>
<th>Hyomandibula</th>
<th>Ceratohyal</th>
<th>Bashyal</th>
<th>Chondrocranium</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. acronotus</td>
<td>102.6 ± 2.52</td>
<td>11.15 ± 1.55</td>
<td>14.65 ± 1.84</td>
<td>4.33 ± 0.66</td>
<td>6.15 ± 0.75</td>
<td>2.19 ± 0.24</td>
<td>61.94 ± 6.70</td>
</tr>
<tr>
<td>R. terraenovae</td>
<td>88.36 ± 1.35</td>
<td>5.19 ± 0.18</td>
<td>7.05 ± 0.71</td>
<td>1.97 ± 0.10</td>
<td>2.43 ± 0.15</td>
<td>1.17 ± 0.13</td>
<td>31.80 ± 1.83</td>
</tr>
<tr>
<td>E. blochii</td>
<td>132.18 ± 10.07</td>
<td>11.43 ± 2.00</td>
<td>15.50 ± 3.15</td>
<td>6.71 ± 1.12</td>
<td>4.77 ± 0.45</td>
<td>1.91 ± 0.092</td>
<td>161.07 ± 22.47</td>
</tr>
<tr>
<td>S. mokarran</td>
<td>286.14 ± 34.16</td>
<td>73.57 ± 11.61</td>
<td>101.43 ± 17.18</td>
<td>34.69 ± 6.26</td>
<td>20.35 ± 2.98</td>
<td>7.06 ± 1.06</td>
<td>512.17 ± 81.21</td>
</tr>
<tr>
<td>S. zygaena</td>
<td>262.5 ± 30.5</td>
<td>32.56 ± 9.95</td>
<td>45.03 ± 13.28</td>
<td>19.95 ± 6.95</td>
<td>14.58 ± 5.22</td>
<td>10.00 ± 2.83</td>
<td>677.35 ± 195.70</td>
</tr>
<tr>
<td>S. lewini</td>
<td>257.14 ± 3.34</td>
<td>55.34 ± 11.25</td>
<td>69.86 ± 12.43</td>
<td>26.06 ± 6.95</td>
<td>19.88 ± 3.95</td>
<td>10.04 ± 1.61</td>
<td>571.17 ± 27.42</td>
</tr>
<tr>
<td>S. tudes</td>
<td>92.52 ± 4.92</td>
<td>2.22 ± 0.53</td>
<td>2.96 ± 0.67</td>
<td>1.34 ± 0.31</td>
<td>0.98 ± 0.23</td>
<td>1.11 ± 0.26</td>
<td>41.99 ± 7.37</td>
</tr>
<tr>
<td>S. tiburo</td>
<td>88.1 ± 1.17</td>
<td>4.45 ± 0.34</td>
<td>5.49 ± 0.45</td>
<td>2.18 ± 0.10</td>
<td>1.59 ± 0.029</td>
<td>0.61 ± 0.073</td>
<td>24.53 ± 1.77</td>
</tr>
</tbody>
</table>

The volumes of the palatoquadrate, Meckel’s cartilage, hyomandibula, and ceratohyal were all positively correlated through phylogeny (p < 0.05).
Table 2.3. Percent contribution of each muscle to total force production among sphyrid and carcharhinid species.

<table>
<thead>
<tr>
<th></th>
<th>Average TL (cm)</th>
<th>QMV</th>
<th>QMD</th>
<th>POV**</th>
<th>POD**</th>
<th>Total Force Produced by Muscles (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>C. acronotus</strong></td>
<td>102.6 ± 2.52</td>
<td>52.56</td>
<td>23.44</td>
<td>18.04</td>
<td>5.96</td>
<td>206.52</td>
</tr>
<tr>
<td><strong>R. terraenovae</strong></td>
<td>88.36 ± 1.35</td>
<td>60.05</td>
<td>25.08</td>
<td>8.42</td>
<td>6.45</td>
<td>133.51</td>
</tr>
<tr>
<td><strong>E. blochii</strong></td>
<td>132.18 ± 10.07</td>
<td>40.71</td>
<td>17.80</td>
<td>25.46</td>
<td>16.02</td>
<td>205.07</td>
</tr>
<tr>
<td><strong>S. mokarran</strong></td>
<td>286.14 ± 34.16</td>
<td>41.65</td>
<td>29.11</td>
<td>17.33</td>
<td>11.91</td>
<td>1972.95</td>
</tr>
<tr>
<td><strong>S. zygaena</strong></td>
<td>262.5 ± 30.5</td>
<td>39.82</td>
<td>26.34</td>
<td>23.35</td>
<td>10.49</td>
<td>730.45</td>
</tr>
<tr>
<td><strong>S. lewini</strong></td>
<td>257.14 ± 3.34</td>
<td>36.24</td>
<td>23.93</td>
<td>24.99</td>
<td>14.84</td>
<td>675.32</td>
</tr>
<tr>
<td><strong>S. tudes</strong></td>
<td>92.52 ± 4.92</td>
<td>40.98</td>
<td>17.69</td>
<td>27.88</td>
<td>13.45</td>
<td>146.06</td>
</tr>
<tr>
<td><strong>S. tiburo</strong></td>
<td>88.1 ± 1.17</td>
<td>35.75</td>
<td>16.85</td>
<td>29.20</td>
<td>18.20</td>
<td>101.16</td>
</tr>
</tbody>
</table>

Multiple linear regression indicated that the best predictor of anterior bite force was POV force (* p = 0.029). Similarly, the best predictor of posterior bite force was POV and POD force (** p < 0.001) along with posterior mechanical advantage. N = Newtons
Table 2.4. Bite force among sphyrid and outgroup carcharhinitid species.

<table>
<thead>
<tr>
<th>Species</th>
<th>TL (cm)</th>
<th>Anterior Bite Force (N)</th>
<th>Residual Bite Force</th>
<th>Average Residual Bite Force</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. acronotus</td>
<td>93.5 - 107.5</td>
<td>56.62 - 91.69</td>
<td>0.23 - 1.76</td>
<td>1.18</td>
</tr>
<tr>
<td>R. terraenovae</td>
<td>85 - 92.6</td>
<td>30.25 - 46.01</td>
<td>-0.0047 - 1.25</td>
<td>0.66</td>
</tr>
<tr>
<td>E. blochii</td>
<td>109 - 165.6</td>
<td>30.73 - 80.24</td>
<td>-1.22 - -0.24</td>
<td>-0.77</td>
</tr>
<tr>
<td>S. mokarran</td>
<td>210 - 399</td>
<td>193.42 - 1630</td>
<td>0.07 - 2.06</td>
<td>0.87</td>
</tr>
<tr>
<td>S. zygaena</td>
<td>246.4 - 265.5</td>
<td>154.87 - 193.83</td>
<td>-0.77 - -1.74</td>
<td>-1.26</td>
</tr>
<tr>
<td>S. lewini</td>
<td>232 - 293</td>
<td>188.18 - 335.48</td>
<td>-1.05 - 0.095</td>
<td>-0.44</td>
</tr>
<tr>
<td>S. tudes</td>
<td>73.5 - 102</td>
<td>14.67 - 51.04</td>
<td>-0.75 - 0.99</td>
<td>0.25</td>
</tr>
<tr>
<td>S. tiburo</td>
<td>85 - 91.5</td>
<td>13.41 - 25.62</td>
<td>-1.73 - -0.52</td>
<td>-1.22</td>
</tr>
</tbody>
</table>

Ranges for anterior bite force and size-removed residual bite force and overall average residual bite force for each species. Anterior bite force and shark TL were first log$_{10}$ transformed and then regressed against one another (Log ABF = 2.144(Log TL) – 2.705).
Table 2.5. Correlation matrix of feeding and head morphology data for sphyrid and carcharhinid species.

|               | AMM | PAM | BRA | RMV | BMD | WMD | CHM | MMV | QMV | QMD | POD | VOV | PBF | QMV | QMD | QMV | QMD | QMV | QMD | QMV | QMD |
|---------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Head Width (cm) | -0.11 | -0.25 | 0.46 | -0.14 | -0.21 | -0.16 | -0.10 | 0.21 | -0.47 | -0.16 | 0.36 | 0.45 | 0.42 | 0.31 | 0.18 | 0.39 | 0.34 | 0.38 | 0.43 | 0.35 | 0.18 | 0.38 | 0.24 | 0.19 |
| QMV (cm³)     | 0.63 | -0.16 | -0.19 | -0.57 | 0.45 | 0.47 | -0.18 | 0.12 | 0.68 | 0.29 | -0.32 | 0.03 | 0.09 | 0.38 | 0.36 | 0.12 | 0.19 | 0.18 | 0.36 | 0.41 | 0.07 | 0.29 | 0.27 | 0.48 |
| QMD (cm³)     | 0.69 | -0.35 | 0.02 | -0.65 | 0.56 | 0.65 | -0.02 | 0.29 | 0.60 | 0.39 | -0.16 | 0.19 | 0.07 | 0.25 | 0.48 | 0.08 | 0.12 | 0.08 | 0.49 | 0.29 | 0.11 | 0.22 | 0.38 | 0.36 |
| POV (cm³)     | 0.76 | -0.55 | -0.10 | -0.81 | 0.34 | 0.45 | 0.13 | 0.30 | 0.55 | 0.22 | -0.10 | 0.28 | 0.04 | 0.13 | 0.43 | 0.03 | 0.25 | 0.18 | 0.40 | 0.28 | 0.13 | 0.34 | 0.42 | 0.29 |
| POD (cm³)     | 0.70 | -0.61 | 0.10 | -0.77 | 0.52 | 0.60 | 0.22 | 0.52 | 0.61 | 0.42 | 0.11 | 0.49 | 0.06 | 0.10 | 0.42 | 0.04 | 0.14 | 0.10 | 0.34 | 0.15 | 0.10 | 0.20 | 0.42 | 0.16 |
| Eye (cm³)     | 0.27 | -0.21 | 0.41 | -0.15 | 0.77 | 0.88 | 0.29 | 0.43 | 0.33 | 0.66 | 0.15 | 0.21 | 0.30 | 0.35 | 0.21 | 0.39 | 0.04 | 0.01 | 0.29 | 0.20 | 0.26 | 0.08 | 0.39 | 0.35 |
| Nasal Capsule (cm³) | 0.40 | -0.39 | 0.50 | -0.42 | 0.85 | 0.85 | 0.11 | 0.71 | 0.59 | 0.77 | 0.33 | 0.63 | 0.22 | 0.23 | 0.16 | 0.20 | 0.02 | 0.02 | 0.42 | 0.06 | 0.11 | 0.04 | 0.26 | 0.09 |
| Offactory Tract (cm³) | 0.81 | -0.66 | -0.13 | -0.95 | -0.11 | 0.09 | 0.03 | 0.11 | 0.10 | -0.23 | -0.16 | 0.24 |
| Braincase (cm³) | 0.16 | 0.09 | -0.70 | -0.17 | -0.86 | -0.74 | -0.19 | -0.73 | -0.39 | -0.87 | -0.59 | 0.61 |
| Palatoquadrate (cm³) | 0.38 | 0.44 | 0.06 | 0.38 | 0.02 | 0.05 | 0.36 | 0.05 | 0.22 | 0.01 | 0.11 | 0.10 |
| Meckel's Cartilage (cm³) | 0.76 | -0.42 | -0.06 | -0.75 | 0.42 | 0.54 | -0.01 | 0.24 | 0.54 | 0.26 | -0.21 | 0.17 |
| Hyomandibula (cm³) | 0.76 | -0.44 | -0.10 | -0.78 | 0.38 | 0.47 | -0.02 | 0.24 | 0.57 | 0.23 | -0.19 | 0.21 |
| Ceratohyal (cm³) | 0.59 | -0.05 | -0.03 | -0.44 | 0.40 | 0.54 | -0.25 | -0.04 | 0.29 | 0.19 | -0.43 | 0.18 |
| Basihyal (cm³) | 0.41 | -0.47 | 0.48 | 0.19 | 0.22 | 0.14 | 0.32 | 0.47 | 0.29 | 0.36 | 0.20 | 0.37 |
| Chondrocranium (cm³) | 0.04 | 0.25 | -0.66 | -0.01 | -0.89 | -0.78 | -0.30 | -0.83 | -0.53 | -0.92 | -0.64 | 0.73 |
| Total Volume (cm³) | 0.04 | 0.21 | 0.46 | 0.04 | 0.20 | 0.13 | 0.50 | 0.33 | 0.14 | 0.31 | 0.35 | 0.37 |
| Dorsal Pore Count (#) | 0.40 | -0.32 | -0.14 | -0.48 | -0.77 | -0.50 | -0.10 | -0.39 | -0.82 | -0.81 | -0.26 | -0.16 |
| Ventral Pore Count (#) | 0.47 | 0.32 | 0.08 | 0.50 | 0.01 | 0.03 | 0.28 | 0.02 | 0.14 | 0.01 | 0.08 | 0.05 |
| AMM | 1.00 | -0.49 | -0.21 | -0.90 | -0.01 | 0.20 | -0.07 | -0.02 | 0.06 | -0.18 | -0.36 | 0.02 |
| PMA | 1.00 | -0.47 | 0.74 | -0.47 | -0.44 | -0.71 | -0.66 | 0.07 | -0.18 | -0.55 | -0.75 |
| ABF (N) | -0.50 | 0.34 | 0.07 | 0.45 | 0.00 | 0.01 | 0.24 | 0.03 | 0.14 | 0.10 | 0.10 | 0.09 |
| PBF (N) | 0.43 | 0.38 | 0.06 | 0.44 | 0.01 | 0.04 | 0.35 | 0.04 | 0.20 | 0.01 | 0.10 | 0.07 |
| QMV Mass (g) | 1.00 | 0.92 | 0.29 | 0.76 | 0.66 | 0.97 | 0.49 | 0.56 |
| QMD Mass (g) | 1.00 | 0.42 | 0.78 | 0.43 | 0.86 | 0.50 | 0.62 |
| POV Mass (g) | 1.00 | 0.70 | 0.04 | 0.41 | 0.78 | 0.65 |
| POD Mass (g) | 1.00 | 0.36 | 0.82 | 0.89 | 0.96 |
| QMV Force (N) | 1.00 | 0.66 | 0.67 | 0.21 | 0.10 | 0.64 | 0.64 |
| QMD Force (N) | 1.00 | 0.64 | 0.89 | 0.09 |
| POV Force (N) | 1.00 | 0.89 | 0.01 |

Correlation coefficients are indicated in the top line of a structure and the p-value is in the second. Blue = positive correlations while red = negative correlations. N = Newtons.
Table 2.6. Ancestral state reconstructions at each of the nodes along phylogeny (Figure 1).

<table>
<thead>
<tr>
<th>Node</th>
<th>Basal</th>
<th>3</th>
<th>4</th>
<th>7</th>
<th>5</th>
<th>6</th>
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</thead>
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<tr>
<td>Head Width (cm)</td>
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<td>185.79</td>
<td>206.20</td>
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<td>23.41</td>
<td>30.89</td>
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<td>5.32</td>
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<tr>
<td>QMD Volume (cm³)</td>
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<td>14.78</td>
<td>18.42</td>
<td>10.89</td>
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<tr>
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<td>17.20</td>
<td>10.99</td>
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<tr>
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<td>17.24</td>
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<td>19.78</td>
<td>24.52</td>
<td>14.87</td>
<td>5.47</td>
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<td>26.43</td>
<td>33.08</td>
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<td>0.17</td>
<td>0.15</td>
<td>0.20</td>
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</tr>
<tr>
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<tr>
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<td>9.86</td>
<td>13.37</td>
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<tr>
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<td>157.69</td>
<td>168.56</td>
<td>184.32</td>
<td>238.91</td>
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<tr>
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<td>94.87</td>
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<td>75.66</td>
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<td>54.85</td>
<td>59.10</td>
<td>71.19</td>
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</table>

Reconstructions indicate that the closest relative between sphyrnid and carcharhinid sharks was a relatively large bodied (163.21 cm TL), with a moderately expanded cephalofoil (~23% of TL), numbers of both dorsal and ventral pores consistent with extant sphyrns, anterior and posterior bite force values of 108.1 N and 387.6 N respectively, with the QMV contributing ~ 43% of the total force produced by the feeding muscles. N = Newtons
CHAPTER 3: BITE FORCE AND PERFORMANCE IN THE DUROPHAGOUS BONNETHEAD SHARK, *Sphyra tiburo*

*Abstract*

Bite force, a measure of performance, can be used to link anatomical form and function. Prior studies have shown bite force to have a significant influence on dietary constraints and ontogenetic shifts in resource utilization. The bonnethead shark, *Sphyra tiburo*, is a durophagous member of the family Sphyrnidae. Its diet in south Florida waters consists almost entirely of blue crabs, which are crushed or ingested whole. This abundant coastal predator’s feeding mechanism is specialized for the consumption of hard prey, including a modified biting pattern and molariform teeth. The goals of this research were to: 1) characterize the mechanical function of the feeding mechanism of *S. tiburo* through biomechanical modeling of biting and *in vivo* bite force measurements; 2) compare the bite force of *S. tiburo* with those of other fishes; and 3) identify functional constraints on prey capture by comparing the bite force of *S. tiburo* to the fracture properties of its primary prey item, blue crabs. Maximum theoretical bite force ranged from 25.7 N anteriorly to 107.9 N posteriorly. *Sphyra tiburo* has the second lowest mass specific bite force for any fish studied to date, and its posterior mechanical advantage of 0.88 is lower than other durophagous chondrichthyans, indicating that this independent evolutionary acquisition of durophagy was not accompanied by the associated morphological changes found in other durophagous cartilaginous fishes. Blue
crab fracture forces (30.0-490.0 N) range well above the maximum bite force of *S. tiburo*, suggesting that prey material properties functionally constrain dietary ecology to some degree.

**INTRODUCTION**

While the relationship between form and function is often times apparent, a key component to understanding the relationship between these parameters and ecology is performance, the ability of an organism to accomplish ecologically relevant tasks (Arnold, 1983; Irschick, 2002). More so, to draw substantive conclusions regarding such relationships both within and among species, these data must be investigated in light of the functional constraints imposed by ecological tasks. Doing so has elucidated numerous correlations between morphology and variables such as prey type, habitat, and community structure (Herrel et al., 1996; Irschick and Losos, 1999; Korff and Wainwright, 2004; Toro et al., 2004). Bite force influences the ability to acquire food resources, and has thus been an extensively studied performance measure in vertebrates (fish (Wainwright, 1988; Herrel et al., 2002a; Korff and Wainwright, 2004; Grubich, 2005; Huber et al., 2005; 2009; Kolmann and Huber, 2009), lizards (Herrel et al., 2001a; Lailvaux and Irschick, 2007), crocodilians (Erickson et al., 2003), birds (van der Meij and Bout, 2000; 2006; Herrel et al., 2005a; b), and mammals (Kiltie, 1982; Aguirre et al., 2003; Herrel et al., 2008)).

Although bite forces are informative regarding the relative and absolute abilities of animals to capture and process prey, ecological conclusions drawn from these data are suspect without specific attention paid to the functional constraints imposed by these prey.
items. For durophagous species (consumers of hard prey), bite force is particularly influential in shaping diet because the exoskeletal armaments of their prey are among the most durable biological materials found in the aquatic environment (Wainwright et al., 1976; Summers and Long Jr., 2006). Despite the diversity of bite force studies, few have related bite force to prey characteristics in fish (Wainwright, 1988; Hernández and Motta, 1997; Korff and Wainwright, 2004; Grubich, 2005), with only a single study investigating this in cartilaginous fishes (Kolmann and Huber, 2009).

The feeding mechanisms of chondrichthyans are remarkably different from those of bony fishes. They lack pharyngeal jaws to further process prey and have skeletons composed of prismatic calcified cartilage. Despite having jaws primarily composed of a pliant skeletal material, durophagy has convergently evolved at least eight times in groups such as the heterodontids, orectolobids, triakids, sphyrids, and chimaeroids (Compagno et al., 2005; Huber et al., 2005; Ramsay and Wilga, 2007; Huber et al., 2008). Durophagy in chondrichthyan fishes is often associated with hypertrophy of their jaws and adductor muscles, molariform teeth, high bite force, and fused jaw symphyses in some cases (Summers, 2000; Summers et al., 2004; Huber et al., 2005). Behavioral and functional modifications associated with hard prey consumption also include unilateral biting and asynchronous muscle activity (Summers, 2000), tooth reorientation during biting (Ramsay and Wilga, 2007), and specialized motor patterns (Summers, 2000; Wilga and Motta, 2000). Collectively these characteristics are often related to dietary specialization (Rhinoptera bonasus Summers, 2000; Sasko et al., 2006; Heterodontus francisci Huber et al., 2005; Sphyra tiburo Cortés et al., 1996).
The bonnethead shark, *Sphyrna tiburo*, (Elasmobranchii, Sphyrnidae) is purportedly the most derived hammerhead species (Martin, 1993; Martin and Palumbi, 1993), specializing almost exclusively on crustacean prey, particularly swimming crabs (*Callinectes* sp.) in south Florida (Compagno, 1984; Cortés et al., 1996; Lessa and Almeida, 1998; Bethea et al., 2007). Compared to other sharks, the bonnethead shark exhibits less upper jaw protrusion, prolonged jaw adductor activity patterns, enlarged maximum gape, and is the only hammerhead shark with posterior molariform teeth (Wilga and Motta, 2000; Motta and Wilga, 2001). However, durophagy in *S. tiburo* is enigmatic in that it is accomplished with some, but not all, of the characteristics associated with durophagy in other chondrichthians. In particular, they lack robust jaws, hypertrophied feeding muscles, and fused jaw symphyses (Wilga and Motta, 2000). However, relatively little is known about how feeding morphology contributes to force generation and shapes not only diet but also feeding ecology in *S. tiburo*. The goals of this study were therefore to: 1) characterize the mechanical function of the feeding mechanism of *S. tiburo* through biomechanical modeling of biting and bite force measurements obtained via tetanic stimulation of jaw muscles and restraint of live animals; 2) compare the bite force of *S. tiburo* with that of other fishes; and 3) identify functional constraints on prey capture and diet by comparing the bite force of *S. tiburo* to the fracture properties of its primary prey item, blue crabs.
MATERIALS AND METHODS

Experimental Animals

Ten *Sphyrna tiburo* (55.2 - 68.7 cm precaudal length (PCL), 73.0 - 91.5 cm total length (TL), 1644 - 3420 g) were collected from the Gulf of Mexico off Sarasota, Florida using a combination of long-line and gill net fishing. Sharks were chosen within a narrow size range to remove the effect of ontogeny. For ease of comparison to dietary data (Cortés et al., 1996) shark PCL is used throughout. Individuals were housed in a 9.1 x 16.8 x 1.8 m., 22.7 kl oval tank located at Mote Marine Laboratory in Sarasota, Florida. Animals were fed bi-weekly with a diet of threadfin herring (*Opisthonema oglinum*) and white shrimp (*Penaeus setiferus*) as attempts to feed *S. tiburo* blue crabs in captivity were unsuccessful. However, cranial muscle plasticity data for elasmobranchs is lacking, therefore the potential effects of diet on muscle atrophy are unknown. In south Florida, the index of relative importance (IRI) (Pinkas et al., 1971) indicates that the diet of *S. tiburo* is dominated by blue crab, *Callinectes sapidus* (85%). Within the size range of shark studied here, the occurrence of *C. sapidus* in the diet increases to 90% with the remaining diet being seagrass, most likely incidentally ingested (Cortés et al., 1996). Upon completion of *in vivo* force measurements all animals were euthanized with an overdose of tricaine methanesulphonate (MS-222 0.1 g/L). All experimental procedures followed the Institutional Animal Care and Use Committee guidelines of Mote Marine Laboratory (08-10-RH1, 07-10-PM1) and the University of South Florida (T3198, R3205, W3514).
Theoretical Bite Force

The three-dimensional coordinates of the origins and insertions for the four principal muscles involved in jaw adduction (preorbitalis dorsal (POD), preorbitalis ventral (POV), quadratomandibularis dorsal (QMD), and quadratomandibularis ventral (QMV)) (Wilga and Motta, 2000) (Figure 3.1), the jaw joint, and anterior and posterior bite points along the lower jaw were obtained using a three-dimensional Patriot digitizer (Polhemus, Colchester, VT, USA) with the tip of the rostrum as the center of a three-dimensional coordinate system. Following Huber et al. (2005), each muscle was unilaterally excised and the center of mass was determined. Center of mass and the superficial muscle fiber architecture were then used to estimate the line of action of each muscle, from which muscle origins and insertions were determined. The in-lever for each muscle was calculated based on the coordinates of its insertion on the lower jaw and the jaw joint. A resolved in-lever for jaw adduction was then determined from a weighted average of these individual in-levers based on the proportion of force that each muscle contributed to overall force production. Out-lever distances to the anterior and posterior bite points were determined from the coordinates of the anterior and posterior margins of the functional tooth row and the jaw joint. Mechanical advantage for jaw adduction at the anterior and posterior bite points was then calculated by dividing the weighted in-lever by the respective out-lever (Huber et al., 2006; 2008). It is assumed that all skeletal elements act as rigid beams and mechanical advantage is equivalent to ideal mechanical advantage in this system. The mechanical advantage of a jaw adducting system indicates the ability of the system to transfer muscle forces to prey either rapidly (low mechanical advantage) or forcefully (high mechanical advantage) (Westneat, 2003).
Following excision, each muscle was bisected perpendicular to the principal fiber direction through the center of mass and the cross sectional area was digitized with Sigma Scan Pro 4 (SYSTAT Software Inc., Point Richmond, CA, USA) (Huber et al., 2005). Maximum tetanic tension for each muscle was calculated by multiplying the cross sectional area by the specific tension of elasmobranch white muscle (28.9 N/cm², Lou et al., 2002). Forces and positions were then used to create three-dimensional force vectors for each muscle.

Bilateral theoretical maximum bite force at anterior and posterior bite points was modeled in 3D with Mathcad 13 (Mathsoft, Inc., Cambridge, MA, USA) by summation of the moments generated about the jaw joints by each muscle (Huber et al., 2005). The static equilibrium model for lower jaw adduction is:

\[ \sum F_{LJ} = F_{PD} + F_{PV} + F_{QD} + F_{QV} + F_{JR} + F_{B} = 0, \]

where \( F_{PD} \) is the force contributed by the preorbitalis dorsal, \( F_{PV} \) is the force contributed by the preorbitalis ventral, \( F_{QD} \) is the force contributed by the quadratomandibularis dorsal, \( F_{QV} \) is the force contributed by the quadratomandibularis ventral, \( F_{JR} \) is the joint reaction force, and \( F_{B} \) is the reaction force from the prey.

**Restrained Bite Force**

Previous studies have demonstrated that theoretical modeling of bite force in chondrichthysans is a good proxy for *in vivo* maximum biting performance (Huber et al., 2005). However, no study has investigated the predictive power of theoretical bite force calculations in a species with morphological divergence in head shape. The collection of *in vivo* data allows for verification of the theoretical model. All *in vivo* bite force measurements were collected with a modified single-point load cell (AmCells Corp.,
Vista, CA, USA) which was calibrated using a digital scale (Siltec Scales, Santa Clara, CA, USA). The transducer was connected to a P-3500 strain indicator (Vishay Measurements Group, Raleigh, NC, USA). Data were sent to a 6020E data acquisition board and imported into LabVIEW 6.0 software (National Instruments Corp., Austin, TX, USA). Individual animals were removed from the holding tank and restrained on a foam padded platform such that their head hung over the edge of the platform. The tip of the rostrum was elevated and the metal arms of the transducer were placed between the anterior tips of the jaws eliciting a bite. The anterior placement of the force transducer was chosen because it cannot be placed farther back due to gape constraints. This procedure was repeated 3-5 times for each individual and the largest of the 3-5 values was recorded as the maximum bite force for that individual. The procedure took no longer than 5 minutes per individual.

**Tetanic Bite Force**

Following restrained bite force measurements, the sharks were anesthetized with a re-circulating, aerated solution of MS-222 (0.133\( \text{g l}^{-1} \)) and seawater. Once fully anesthetized, the sharks were placed ventral side up in a holding apparatus and the preorbitalis ventral, quadratomandibularis dorsal, and quadratomandibularis ventral muscles were implanted with bipolar electrodes connected to a SD9 stimulator (Grass Instruments, Quincy, MA, USA.). The preorbitalis dorsal was not stimulated because its small size and location made it difficult to implant. The jaw muscles were tetanically stimulated with the bite force transducer placed between the anterior tips of the jaws (20 V, 100Hz, 0.02 ms delay, 3ms pulse duration). Each individual was stimulated 3-4 times with a minimum of 1-2 minutes between successive stimulation events, during which
their gills were perfused with the aerated anesthetic solution. The maximum force value for each individual was recorded. Posterior forces for all in vivo tests were calculated by multiplying the anterior force by the ratio of anterior to posterior out-levers.

**Performance Testing of Prey**

Eighteen live inter-molt *C. sapidus* (23.3 - 68.4 mm carapace length (CL)) representing the crabs greater than or equal to the size range consumed by the sample of sharks from this study (Cortés et al., 1996) were purchased from local bait shops or collected by beach seine. The carapace width (spine to spine), length, depth, and mass were recorded for all *C. sapidus* prior to material testing.

Upper and lower jaws were removed from an adult 78.4 cm PCL *S. tiburo* and dried in 95% ethanol for 12 hours in order to bond them to steel plates such that the occlusal surfaces of the teeth were aligned. The jaws of this individual are comparable to those of sharks from our sample size both in size and shape. The plates were mounted in a Mini Bionix II Material Testing System (MTS, Eden Prairie, MN, USA) with an in-line 5 kN load cell. Live crabs were immobilized with a combination of MS-222, ~0.1g/L, and tonic immobility (Fedotov et al., 2006), and placed between the mounted jaws. Live crabs are required for this type of experiment because the mechanical properties of biomaterials can change postmortem (LaBarbera and Merz, 1992). Crabs were crushed at a displacement rate of ~370 mm/s, which is the average velocity of lower jaw elevation in *S. tiburo* (Mara and Motta unpublished data). In order to ensure mechanical failure of the carapace, the displacement distance was adjusted to 33% carapace depth for each crab. A successful crushing event was defined as a large crack produced in the carapace, with peak force occurring immediately prior to carapace failure.
Statistical Analyses

All bite force variables, muscle masses, muscle forces, and mechanical advantages were log\textsubscript{10} transformed and linearly regressed against shark total length to examine the effect of size on bite force. Given the small size range of \textit{S. tiburo} in this study, regressions showed no size effects, therefore, log\textsubscript{10} transformed (non-residual) values were used for the remaining statistical tests. Paired t-tests were used to identify differences among bite forces measured from theoretical, \textit{in vivo} restrained, and \textit{in vivo} stimulated treatments. A forward stepwise multiple linear regression was also performed to examine which morphological traits best explained variation in anterior theoretical bite force.

To gain an understanding of how the bite force of \textit{S. tiburo} compares to that of other fishes, particularly durophagous ones, maximum bite forces and body masses were compiled from the literature for eighteen species (Hernández and Motta, 1997; Clifton and Motta, 1998; Huber and Motta, 2004; Korff and Wainwright, 2004; Huber et al., 2005; 2006; 2008; 2009; Huber and Mara unpublished). Bite forces and body masses for all species were log\textsubscript{10} transformed and linearly regressed to determine mass-specific bite force, which was compared among species.

Failure forces obtained during performance testing of prey were log\textsubscript{10} transformed and linearly regressed against crab carapace width, length, depth, and mass to examine the scaling of prey properties. The slopes of the scaling relationships were compared to an isometric slope of 2 with respect to crab width, length, and depth, and 0.67 with respect to mass using a two-tailed t-test. All regressions and paired t-tests were
performed in SigmaStat 3.1 (SYSTAT Software Inc., Point Richmond, CA, USA) and t-tests of scaling relationships were performed manually.

**RESULTS**

Feeding Biomechanics and Bite Force

Of the jaw adducting muscles, the largest force was produced by the QMV (33.2 ± 2 SE N), which represented approximately 35% of the adductive force, followed by POV (27.7 ± 1.4 SE N), POD (17.9 ± 1 SE N), and QMD (17.4 ± 0.8 SE N) (Table 3.1, Figure 3.2). Mechanical advantage ranged from 0.24 – (±0.02 SE) – 0.88 (±0.04 SE) between the anterior and posterior bite points. Based upon these adductive forces and leverage of the feeding mechanism, the range of theoretical bite force was (13.4 – 25.7 N) and (50.3 – 107.9 N) for anterior and posterior bite points respectively. Forward stepwise multiple linear regression performed on all biomechanical variables with respect to bite force retained only the force generated by the QMD as a significant predictor of theoretical bite force (p=0.025). All other variables had no predictive power due to their non-significant relationship to theoretical bite force.

Theoretical mean maximum bite force for anterior (20.0 ± 1.4 SE N) and posterior (77.4 ± 5 SE N) biting were greater than restrained anterior (14.2 ± 1.2 SE N, p=0.017) and posterior (53.1 ± 5.2 SE N, p=0.014) bite force. Anterior (17.3 ± 2.1 SE N) and posterior (64.6 ± 8.3 SE N) stimulated bite force were not different from either theoretical or restrained bite forces (Table 3.2)

Size-removed bite force comparison among fishes indicated that *S. tiburo* has the second lowest mass-specific bite force of any fish studied to date irrespective of diet.
Only *Etmopterus lucifer* (-1.18) and *Etmopterus spinax* (-2.47) have a lower mass-specific bite force than *S. tiburo* (-1.16). Furthermore, the absolute bite force of *S. tiburo* is among the lowest of any durophagous fish (Table 3.3).

*Performance Testing of Prey*

Carapace fracture trials of *C. sapidus* typically exhibited a steady increase in force until crack propagation began, followed by material failure (Figure 3.3). Failure forces ranged from 30.0 – 490.0 N and exhibited linear relationships with all crab morphometrics (carapace length, width, depth, and crab mass) (Figure 3.4). Failure force scaled isometrically relative to carapace width and length, and with positive allometry relative to carapace depth and crab mass (Table 3.4). Deeper heavier crabs require disproportionally more force to fracture than thinner lighter crabs.

For ease of comparison to dietary data, the scaling relationship of CL to failure force will be discussed further. The non log transformed linear relationship between CL and failure force \( y=11.08x–308.08, \ p < 0.01, \ R^2=0.95 \) was used to estimate the range of *C. sapidus* that sharks in this study are capable of crushing. Based upon the range of maximum posterior bite force from the experimental analyses (50.3 N, 62.5 cm PCL-107.9 N, 60.0 cm PCL), the largest blue crab that *S. tiburo* of 55.2-68.7 cm PCL are capable of crushing range between 32.3 mm CL (62.8 mm CW) and 37.5 mm CL (73.9 mm CW) (Figure 3.5)
DISCUSSION

Feeding Biomechanics and Bite Force

The bonnethead shark *Sphyrna tiburo* differs from other durophagous chondrichthyan and teleost fishes by having relatively low bite force and a lack of: robust jaws, hypertrophied feeding muscles, and fused jaw symphysis (Summers, 2000; Summers et al., 2004; Huber et al., 2005). During closing, the lower jaw of *Sphyrna tiburo* acts as a third class lever system with relatively high force efficiency at the back of the jaws (posterior mechanical advantage = 0.88). However, the mechanical advantage of the bonnethead shark is not particularly large as force amplifying second class lever systems, with mechanical advantages greater than 1.0, have been found in other durophagous fishes, including chondrichthyan (*H. francisci* and *H. colliei*) and teleost oral and pharyngeal jaws (black drum, *Pogonia cromis* and striped burrfish, *Chilomycterus schoepfi*) (Korff and Wainwright, 2004; Huber et al., 2005; Grubich, 2005; Huber et al., 2008). In fact, even non-durophagous fishes, such as the euryphagous blacktip shark, *Carcharhinus limbatus* (post. MA=1.09), have jaw adducting mechanisms with posterior mechanical advantage exceeding 1.0 (Huber et al., 2006). It should be noted that second class lever systems cause joint reaction forces to switch from compression to tension at the jaw joint resulting in greater chance for dislocation (Huber et al., 2008). The anterior mechanical advantage of *S. tiburo* (0.24) is comparable to those of numerous teleosts possessing low to intermediate jaw leverage (wrasses (0.13-0.41) gray triggerfish *Balistes capriscus* (0.25-0.27)), and considerably lower than those of other durophagous fishes (horn (0.51), chimaera (0.68), parrotfish (0.45-1.04), etc.) (Durie and Turingan, 2001; Wainwright et al., 2004; Westneat, 2004). Furthermore,
when only durophagous chondrichthyans are considered, *S. tiburo* has lower anterior and posterior mechanical advantages (Figure 3.6).

Mass-specific bite force measurements are an indicator of the relative feeding performance of vertebrates. Durophagous taxa, such as the striped burrfish, *Chilomycterus schoepfi* (1.92, Table 3.3), typically have high mass-specific bite forces owing to relatively hypertrophied jaw adductors and high mechanical advantage of the feeding mechanism (Korff and Wainwright, 2004). Although *S. tiburo* has an almost exclusively durophagous diet, it surprisingly has the third lowest mass-specific bite force (-1.16) of any fish that has been studied. This includes soft prey specialists such as the spiny dogfish *Squalus acanthias* and non durophagous piscivores such as the lemon shark *Negaprion brevirostris* and blacktip shark *Carcharhinus limbatus* (Table 3.3) (Huber and Motta, 2004; Huber et al., 2005; 2008). The mass-specific bite force for *S. tiburo* places it above *Etmopterus lucifer* and *E. spinax*, both of which are deepwater lantern sharks whose diet consists of small fishes, squid, and some crustaceans (Compagno et al., 2005).

While mass-specific bite force allows for comparison of relative ability among species, comparison of absolute bite force permits ecological predictions to be made about diet. Forces required to crush prey must be generated independent of predator mass, and absolute bite force values determine the ability to consume a particular prey item (Huber et al., 2008). When comparing among species of similar size, the absolute bite force of *S. tiburo* is comparable to soft prey specialists such as *S. acanthias*, and an order of magnitude smaller than other durophagous species such as *H. francisci* (Table 3.3).
Although *S. tiburo* consumes hard shelled prey, it does so in a manner that is biomechanically different than previously described in chondrichthians. Animals that specialize on fast, agile, and elusive prey have speed-efficient jaw closing systems with low mechanical advantages (Turingan et al., 1995). Previous studies have shown a tradeoff between bite force and the ability to capture elusive prey (Herrel et al., 2002b). The bonnethead shark feeding mechanism appears to be a compromise between adductive speed and force. Furthermore, the jaw adducting musculature in *S. tiburo* can be active in a cyclical manner which could aid in fracturing prey exoskeletons (Wilga and Motta, 2000). This shark captures small, elusive blue crabs by ram feeding with a wide gape and fast jaw closure (Wilga and Motta, 2000) yet is constrained to smaller crabs by its limited bite force (see below).

*Model Verification*

Numerous methods for measuring bite force have been employed (Anderson et al., 2008), although few have been quantitatively compared (Huber and Motta, 2004; Huber et al., 2005). Previous studies have shown some methods of recording bite force are accurate predictors of maximum tetanic bite force, whereas others are less so (Huber et al., 2005; Herrel et al., 2008). In previous studies of elasmobranch bite force, it has been shown that, in some cases, theoretically determined bite force accurately predicts those produced during *in vivo* voluntary testing (Huber et al., 2005). Furthermore, in bats theoretical morphological models of bite force accurately predict bite force capacity (Herrel et al., 2008). However, other factors not accounted for in our model (e.g., inertial fluid forces, resistance of body tissues) may influence the accuracy of our theoretical predictions (see Van Wassenbergh et al., 2005).
These data show that 55.2-68.7 cm PCL bonnethead sharks are capable of producing a maximum bite force of 107.9 N at the posterior molariform teeth (Table 3.2). In bonnethead sharks no differences were found between restrained and stimulated or stimulated and theoretical testing conditions. However, both anterior and posterior theoretical bite forces (20.0N and 77.4 N respectively) were greater than restrained bite force (14.2 N and 53.1 N respectively). Both theoretical and stimulated testing conditions remove behavioral motivation as a potential variable. However, during restrained biting the animal can choose to perform less than maximally. Behavioral motivation, or lack thereof, can result in less than maximal performance (Irschick, 2002). During testing it was noted that restrained testing conditions elicited a reluctant bite from *S. tiburo*; the animal’s teeth had to be prodded numerous times to elicit a bite. Furthermore, *S. tiburo* did not voluntarily bite the force transducer even when presented with food. These results are contrary to that of the horn shark, *H. francisci*, where the sharks vigorously bit the offered force gauge, and restrained bite force was the largest among the three testing conditions (Huber et al., 2005). In the bonnethead shark, theoretical and stimulated bite force appear to be good indicators of performance, whereas voluntary bite force, under the conditions utilized here, is under representative of its biting capabilities.

*Ecological Performance*

Although high bite force may facilitate a larger range of potential prey, it is often associated with dietary specialization because increased performance allows exploitation of prey resources unavailable to other species or available to only a small number of species (Hernández and Motta, 1997; Berumen and Pratchett, 2008). Thus, access to
durophagous prey via high bite force has been shown to potentially reduce interspecific competition in fishes (Wainwright, 1988; Grubich, 2005), lizards (Herrel et al., 2001b), and mammals (Christiansen and Wroe, 2007).

That bite force can determine diet is well known (Herrel et al., 2001b; Aguirre et al., 2003; Korff and Wainwright, 2004; Grubich, 2005). However, few studies relate bite force to characteristics of known prey species (Herrel et al., 2001b; Aguirre et al., 2003; Kolmann and Huber, 2009). In south Florida the diet of S. tiburo consists of almost exclusively blue crabs and may represent specialization on prey that is unavailable to other non-durophagous species. However, maximum bite force imposes limits on the size of its preferred prey with the maximum size blue crab consumed by bonnethead sharks in the size range studied here to ~60.2 mm CL (Cortés et al., 1996). Blue crabs reportedly reach a maximum size of 88.0 mm CL, leaving the upper 32% of the blue crab population unutilized by S. tiburo of this size range (Atar and Seçer, 2003). When dietary data are compared to maximum bite force, 57/72 crabs (~79%) consumed by bonnethead sharks in the size range sampled here are able to be crushed indicating that the majority of crabs consumed by S. tiburo fall well below their performance limits (Figure 3.5). Therefore, these data indicate that S. tiburo may be selecting blue crabs, in part based on some metric of size that relates to their ability to crush and consume them. Crabs falling outside of their performance limits would require dismemberment prior to consumption by lateral head shaking or other manipulation (Wilga and Motta, 2000; Matott et al., 2005). This is supported by many blue crabs found in the stomachs of S. tiburo being dismembered (E. Cortés personal communication; K.R. Mara personal observation). Behavior and prey properties could also help explain the discrepancy
between performance and diet. Electromyography data suggests that *S. tiburo* is capable of cyclical activity in the jaw adducting musculature which could aid in fracturing the carapace (Wilga and Motta, 2000). However, no study has quantitatively investigated this cyclical activity. Furthermore, individual variation in failure force could partially explain the 21% of crabs in the diet falling above the crushing ability of *S. tiburo*. Our results provide an upper estimate of the force *S. tiburo* must produce to crush blue crabs and further data is required to address the roles behavioral and variation in prey properties play in durophagy in *S. tiburo*.

Durophagy is often assumed to relate directly to mechanical function, however an animal can maintain a durophagous diet without extensive modification of the feeding apparatus. It is known that the gastric pH of elasmobranchs can reach values as low as 0.4 (Papastamiou and Lowe, 2005; Papastamiou et al., 2007). Furthermore, chitinolytic enzyme activity has been previously demonstrated in elasmobranchs (Lindsay, 1984). If bonnethead sharks have similar gastric pH values or chitinolytic enzymes, the hard shell of their prey can be broken down chemically by the stomach rather than mechanically by the feeding apparatus. In this instance durophagy is established through the means of physiological modifications rather than morphological modifications.

The apparent correlation between bite force and diet could also be explained by gape and processing time limitations. Independent of bite force, larger items may not be consumed because of the physical dimensions of the gape or because of the adductor muscles being stretched beyond their optimal range (Kiltie, 1982; De Schepper et al., 2008). Furthermore, many studies have demonstrated an increase in processing time with
increased prey size (Verwaijen et al., 2002). The increased processing times required to consume very large crabs could make these crabs less cost effective to consume than smaller crabs with lower processing times. In addition large blue crabs may generate large crushing forces relative to other crabs which could result in serious injury to the cephalofoil, leading *S. tiburo* to avoid potentially dangerous large blue crabs (Schenk and Wainwright, 2001). However, the ability of *S. tiburo* to process large prey remains to be tested.

**CONCLUSIONS**

*Sphyrna tiburo* is unlike other durophagous chondrichthyan species. It has relatively low bite force and lacks hypertrophy of the feeding muscles and jaws. Furthermore, its posterior mechanical advantage is considerably lower than other species. In fact, the manner in which *S. tiburo* consumes hard prey is biomechanically different than previously described in chondrichthyan species. When the bonnethead shark is compared to a broad range of chondrichthyan and teleost species, its mass specific bite force is the second lowest of any species studied to date in spite of its predominately durophagous diet. Bite force modeling is an accurate predictor of maximum biting capacities in *S. tiburo*. However, behavioral motivation was found to play a large role in *in vivo* bite force measurements. The bite force of *S. tiburo* constrains the size of its preferred prey, blue crabs that it can consume. However, crabs that are larger than the maximum crushable size are consumed by *S. tiburo*. This independent evolution of durophagy without the morphological modifications seen in other durophagous taxa, indicates that
durophagy can be accomplished in the absence of high mechanical advantage and high bite force.

**LITERATURE CITED**


Figure 3.1. Feeding musculature of *Sphyrna tiburo*. QMV = quadratomandibularis ventral, QMD = quadratomandibularis dorsal, POV = preorbitalis ventral, POD = preorbitalis dorsal. Redrawn and modified from Wilga and Motta, 2000.

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Figure 3.2. Percent contribution of each feeding muscle to bite force. Average ± standard error. Multiple linear regression showed that the only variable that predicted theoretical bite force was QMD (p = 0.025). All other muscles had no predictive power due to their non-linear relationship to theoretical bite force.

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Figure 3.3. Typical crushing force curve for a 40.5 mm CL, 67.5 g *C. sapidus* crushed at a loading rate of ~370 mm/s using jaws removed from a 78.4 cm PCL *S. tiburo*. Force increases to a maximum where failure occurs (black arrow). N = Newtons

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Figure 3.4. Blue crab, *C. sapidus*, crushing results from fracture experiments on live crabs. Failure forces ranged from 30.0 to 490.0 N and exhibited a linear relationship to carapace length (CL) \( y = 11.07x - 308 \), \( R^2 = 0.87 \). Scaling analyses indicated that failure force scaled isometrically with carapace width and length. However, failure force scaled with positive allometry with carapace depth and mass. N = Newtons

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Figure 3.5. Occurrence of blue crabs, *C. sapidus*, in the stomachs of *S. tiburo* from Cortés et al. (1996). Highlighted box (dashed blue vertical lines) indicates the size range of sharks used in this study. Red solid line is the range of maximum size crab *S. tiburo* of 55.2-68.7 cm PCL is capable of crushing (32.3 – 37.5 mm CL, dashed red lines) based upon the maximum and minimum bite force. The majority of *C. sapidus* ingested by sharks can be crushed. However, crabs consumed that fall above the solid red line (~21%, green points) cannot theoretically be crushed by sharks of this size range and would require other processing methods.

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Figure 3.6. Anterior and posterior mechanical advantages for durophagous chondrichthyans studied to date. Dark line at mechanical advantage = 1 is the point where the lever system switches from a third class lever system to force amplifying a second class lever system. *Sphyrna tiburo* consumes hard prey without the advantage of a second class lever system.

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Table 3.1. Average force and mass ± standard error of the four principal jaw adducting muscles in *S. tiburo*.

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Force (N)</th>
<th>Mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quadratomandibularis Ventral</td>
<td>33.2 ± 2</td>
<td>1.37 ± 0.1</td>
</tr>
<tr>
<td>Quadratomandibularis Dorsal</td>
<td>17.4 ± 0.8*</td>
<td>0.96 ± 0.1</td>
</tr>
<tr>
<td>Preorbitalis Ventral</td>
<td>27.7 ± 1.4</td>
<td>2.43 ± 0.1</td>
</tr>
<tr>
<td>Preorbitalis Dorsal</td>
<td>17.8 ± 1</td>
<td>1.35 ± 0.1</td>
</tr>
</tbody>
</table>

Data represent raw muscle values from 10 *S. tiburo* (x̄ mass = 2440 g). Changes in the quadratomandibularis dorsal unresolved force was positively related to bite force (* p=0.025). No other muscle force or mass was related to output bite force. N=Newtons

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Table 3.2. Average maximum bite force (N) ± standard error for *Sphyrna tiburo* in each testing condition.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Restrained</th>
<th>Stimulated</th>
<th>Theoretical</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anterior BF</td>
<td>14.2 ± 1.2*</td>
<td>17.3 ± 2.1</td>
<td>20.0 ± 1.4*</td>
</tr>
<tr>
<td>Posterior BF</td>
<td>53.1 ± 5.2**</td>
<td>64.6 ± 8.3</td>
<td>77.4 ± 5**</td>
</tr>
<tr>
<td>Max Anterior BF</td>
<td>20.3</td>
<td>25.3</td>
<td>25.7</td>
</tr>
<tr>
<td>Max Posterior BF</td>
<td>79.2</td>
<td>91.1</td>
<td>107.9</td>
</tr>
</tbody>
</table>

Theoretical bite force was greater than restrained bite force for anterior (* p=0.017) and posterior (** p=0.014). Maximum bite forces are the single largest force for any of the sharks.

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Table 3.3. Comparison of absolute bite force and size-removed bite force residuals among fishes.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Mass (g)</th>
<th>Anterior Bite Force (N)</th>
<th>Residual Bite Force</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chilomycterus schoepfi(^1)</td>
<td>striped burrfish</td>
<td>180</td>
<td>380</td>
<td>1.92</td>
</tr>
<tr>
<td>Lachnolaimus maximus(^2)</td>
<td>hogfish</td>
<td>209</td>
<td>290</td>
<td>1.65</td>
</tr>
<tr>
<td>Archosargus probatocephalus(^1)</td>
<td>sheepshead</td>
<td>581</td>
<td>186</td>
<td>0.89</td>
</tr>
<tr>
<td>Heptranchias perlo(^8)</td>
<td>sharpnose sevengill</td>
<td>1614</td>
<td>245</td>
<td>0.68</td>
</tr>
<tr>
<td>Carcharhinus limbatus(^6,8)</td>
<td>blacktip shark</td>
<td>9833</td>
<td>423</td>
<td>0.35</td>
</tr>
<tr>
<td>Heterodontus francisci(^5,8)</td>
<td>horn shark</td>
<td>2948</td>
<td>206</td>
<td>0.30</td>
</tr>
<tr>
<td>Hydrolagus coliei(^7)</td>
<td>spotted ratfish</td>
<td>870</td>
<td>106</td>
<td>0.30</td>
</tr>
<tr>
<td>Halichoeres bivittatus(^2)</td>
<td>slippery dick</td>
<td>19</td>
<td>11</td>
<td>0.19</td>
</tr>
<tr>
<td>Chiloscyllium plagiosum(^7)</td>
<td>white-spotted bamboo shark</td>
<td>870</td>
<td>106</td>
<td>0.07</td>
</tr>
<tr>
<td>Halichoeres garnoti(^2)</td>
<td>yellowhead wrasse</td>
<td>21</td>
<td>10</td>
<td>0.07</td>
</tr>
<tr>
<td>Thalassoma bifasciatum(^3)</td>
<td>bluehead wrasse</td>
<td>7</td>
<td>5</td>
<td>0.00</td>
</tr>
<tr>
<td>Sphyrna mokarran(^9)</td>
<td>great hammerhead</td>
<td>580598</td>
<td>2432</td>
<td>-0.04</td>
</tr>
<tr>
<td>Negaprion brevirostris(^7)</td>
<td>lemon shark</td>
<td>1219</td>
<td>79</td>
<td>-0.06</td>
</tr>
<tr>
<td>Carcharhinus leucas(^9)</td>
<td>bull shark</td>
<td>140341</td>
<td>1023</td>
<td>-0.11</td>
</tr>
<tr>
<td>Halichoeres maculipinna(^2)</td>
<td>clown wrasse</td>
<td>18</td>
<td>5</td>
<td>-0.41</td>
</tr>
<tr>
<td>Squalus acantbias(^3)</td>
<td>spiny dogfish</td>
<td>1065</td>
<td>19.6</td>
<td>-1.05</td>
</tr>
<tr>
<td>Sphyrna tiburo</td>
<td>bonnethead shark</td>
<td>2240</td>
<td>25.7</td>
<td>-1.16</td>
</tr>
<tr>
<td>Etmopterus lucifer(^8)</td>
<td>black belly lanternshark</td>
<td>48</td>
<td>3.1</td>
<td>-1.18</td>
</tr>
<tr>
<td>Etmopterus spinax(^8)</td>
<td>velvet belly lanternshark</td>
<td>349.1</td>
<td>1.6</td>
<td>-2.47</td>
</tr>
</tbody>
</table>

Highlighted species have a predominately durophagous diet. Compiled from \(^1\)Hernández and Motta, 1997; \(^2\)Clifton and Motta, 1998; \(^3\)Huber and Motta, 2004; \(^4\)Korff and Wainwright, 2004; \(^5\)Huber et al., 2005; \(^6\)2006; \(^7\)2008; \(^8\)2009; \(^9\)Huber and Mara, unpublished data.

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Table 3.4. Scaling of crab carapace properties with respect to length, width, depth, and mass.

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>Independent Variable</th>
<th>Isometric Slope</th>
<th>Slope</th>
<th>y-intercept</th>
<th>r^2</th>
<th>t _critical _{0.05(2),16}</th>
<th>t _critical</th>
</tr>
</thead>
<tbody>
<tr>
<td>Failure Force (N)</td>
<td>Carapace Width</td>
<td>2</td>
<td>2.38</td>
<td>-2.28</td>
<td>0.87</td>
<td>1.63</td>
<td>2.12</td>
</tr>
<tr>
<td></td>
<td>Carapace Length</td>
<td>2</td>
<td>2.51</td>
<td>-1.95</td>
<td>0.86</td>
<td>2.03</td>
<td>2.12</td>
</tr>
<tr>
<td></td>
<td>Carapace Depth *</td>
<td>2</td>
<td>2.63</td>
<td>-1.48</td>
<td>0.83</td>
<td>2.12</td>
<td>2.12</td>
</tr>
<tr>
<td></td>
<td>Crab Mass *</td>
<td>0.67</td>
<td>0.87</td>
<td>0.71</td>
<td>0.85</td>
<td>2.22</td>
<td>2.12</td>
</tr>
</tbody>
</table>

Failure force scaled with positive allometry to carapace depth and crab mass (*, p \leq 0.05).

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OVERALL CONCLUSIONS

The overall goal of this study was to investigate the evolution and function of the hammerhead cephalofoil and the consequences of changes in head shape and form on the feeding morphology and sensory structures, and any resulting constructional constraints within the cephalofoil. For the first part of this study, I investigated the changes in external morphology through phylogeny along with the potential constructional constraints within the cranium. The goals of the first part of this were to 1) investigate the shape changes of the sphyrid head through phylogeny; 2) examine the volumetric changes of cephalic elements through phylogeny; and 3) investigate potential constructional constraints between and among feeding, neural, and sensory structures.

Through phylogeny the position of the eye and nares is variable; however, there are few changes to the relative position of the mouth. The position of the eye shifted laterally through phylogeny and to a more posterior position on the distal tip of the cephalic wing. The external nares are medially placed in basal species and through phylogeny shifted first laterally and then medially again. Despite changes to cephalic morphology the electrosensory system is relatively conserved within sphyrid and closely related carcharhinid species with all species except (C. acronotus, S. mokarran, and S. lewini) having the same number of dorsal and ventral pores. Carcharhinus acronotus, S. mokarran, and S. lewini all had a significantly greater number of pores on the ventral surface of the cephalofoil. Despite E. blochii not differing markedly from other sphyrid sharks in pore distribution, it lacks pores along the anterior surface of the ventral
cephalofoil. This is most likely related to the position of the nares and their affect on the anterior lateral pore field. In light of the external morphometric changes to the cephalofoil through phylogeny, changes to the internal cranial volumes were also expected. This portion of the study also determined that, through evolutionary history, there are few constructional constraints among the various elements within the cranium. The few constraints were isolated to sensory structures. Nasal capsule volume was negatively correlated with braincase, basihyal, chondrocranial, and total volumes. As the volumes of these cranial structures increases the volume of the nasal capsule is decreased. The other constraint of note is the negative correlation between eye size and cephalofoil width. As width of the head increases its depth decreases to keep the volume constant, consequently the volume of the eye is constrained to be smaller. Within the cephalofoil there were also elements that were positively correlated through phylogeny. Positive correlations were particularly apparent among the volumes of the feeding muscles and jaw cartilages. For these biting sharks, the volume of the jaws and supportive cartilages increase in size as the adductive muscle that are attached to them increase in size. These findings also indicate that although the head has changed in form through evolutionary history, there have been no major changes to the internal cranial volumes.

These data indicate that much of the head is morphologically conserved through sphyrid phylogeny, particularly the jaw cartilages and their associated feeding muscles, with shape change and constructional constraints being primarily confined to the lateral wings of the cephalofoil and its associated sensory structures. Ancestral character state reconstructions agree with previous analyses that the common ancestor to all hammerhead sharks was large bodied with a relatively large head.
The second portion of this study was focused on describing the functional morphology of the feeding apparatus of hammerhead sharks. While feeding morphology has been described for a single species of hammerhead shark, *S. tiburo*, a detailed study of the feeding apparatus through phylogeny is required to answer questions about the effects of changes in head morphology on feeding structures. The goals of the second part of this study were to: 1) describe and compare the functional morphology and biomechanics of the feeding apparatus of the hammerhead sharks; 2) investigate if changes to the feeding bauplan exist in sphyrid sharks or if changes are confined to surrounding structures with conservation of the feeding apparatus; and 3) investigate the relationship between cranial design and feeding morphology through phylogeny in this clade.

Through phylogeny changes to the cephalofoil are mainly confined to the sensory structures and chondrocranium. Furthermore, the feeding bauplan is conserved within sphyrid sharks compared to closely related carcharhinid sharks with few changes to the feeding structures and feeding biomechanics. Sphyrids as a group have relatively low anterior mechanical advantages that are similar to low to intermediate jaw leverage systems in teleosts. Within elasmobranchs the anterior mechanical advantage is somewhat lower than that of other piscivorous elasmobranchs. Anterior bite force is best predicted by the force produced by the preorbitalis ventral muscle while posterior bite force is best predicted by not only the force produced by the preorbitalis ventral but also the force produced by the preorbitalis dorsal and the posterior mechanical advantage. Size-removed bite force analysis indicated that in general sphyrid sharks have lower bite forces for their body size than closely related carcharhinid sharks. Furthermore, the lone
durophagous sphyrid, *S. tiburo*, had among the lowest average residual bite force. Surprisingly, this analysis also revealed that the width of the cephalofoil had no effect on feeding morphology. However, positive correlations were found between the anterior mechanical advantage and the volumes of the POV, palatoquadrate, Meckel’s cartilage, and hyomandibula. Paradoxically, this study also revealed that posterior bite force was negatively correlated with the volume of the POV, POD, palatoquadrate, Meckel’s cartilage, and hyomandibula despite these structures’ role in force production and transmission. The reasons for these surprising negative correlations remain elusive but may be related to changes in lever mechanics, particularly changes to the weighted in-lever through phylogeny. Furthermore, although volume is an accurate measure of muscle size, it does not necessarily reflect the cross sectional area of the muscle. Cross sectional area determines the force produced by the muscle, and it is the force produced by the POV and POD that were best predictive of posterior bite force not the volume.

The final portion of this study investigated bite force and feeding performance in the durophagous hammerhead, *S. tiburo*. Durophagy in *Sphyrna tiburo* is an ecomorphological conundrum as they consume hard prey but lack many of the characteristics associated with durophagy in other chondrichthyans. The goals of this third portion were to: 1) characterize the mechanical function of the feeding mechanism of *S. tiburo* through biomechanical modeling of biting and bite force measurements obtained via tetanic stimulation of jaw muscles and restraint of live animals; 2) compare the bite force of *S. tiburo* with those of other fishes; and 3) identify functional constraints on prey capture and diet by comparing the bite force of *S. tiburo* to the fracture properties of its primary prey item, blue crabs *Callinectes sapidus*. 
The manner in which *S. tiburo* consumes hard prey is biomechanically different than has been described previously in chondrichthyans. It has relatively low bite force and lacks the hypertrophied jaw adducting musculature and jaws found in other durophagous taxa. Furthermore, when posterior mechanical advantage is compared among durophagous species, *S. tiburo* is considerably lower. Mass specific bite force analysis indicates that *S. tiburo* has among the lowest size-removed bite forces of any fish species measured to date. When the bite performance of *S. tiburo* is compared to the mechanical properties of its known prey, it was discovered that *S. tiburo* consumes crabs that it is biomechanically incapable of crushing. Instead, various methods of prey manipulation and processing are likely utilized to consume large un-crushable crabs. Durophagy in the bonnethead indicates that durophagy can be accomplished without the morphological modifications seen in other durophagous taxa.

While I described the morphometric changes to cephalofoil, the internal volumetric differences among species, the constructional constraints among internal elements, and the functional morphology of the feeding apparatus; there are clearly some areas that deserve further attention. Of particular interest are the biomechanical consequences of the expanded cephalofoil on the structural and material properties of the chondrocranium in sphyrint sharks. Furthermore, the morphology and biomechanics of shark teeth have been shown to differ among shark species. Within sphyrint sharks, tooth morphology ranges from large serrated teeth to pavement-like teeth. An investigation of the functional morphology of sphyrint teeth could elucidate differences in tooth morphology related to diet. I also did not sample every species of hammerhead (six out of eight). Although it is unlikely that the overall patterns will change
considerably, it is possible that upon inclusion of the remaining sphyrid species further constraints among internal elements will arise. Furthermore, while the sensory systems of this group of sharks have been investigated previously, more detailed work is needed on adult specimens, especially of the basal species, to truly understand the evolutionary pressures that resulted in the expanded cephalofoil. My study’s findings of few constructional constraints within the cephalofoil and lack of change to the feeding structures, along with the data of others, points strongly toward sensory systems as the selective pressure resulting in the evolution of the cephalofoil. However, this research cannot rule out the potential hydrodynamic role of the cephalofoil.
ABOUT THE AUTHOR

Kyle R. Mara was born in Kennett, MO on 11 – February, 1980 and spent much of his younger years on Minot Air Force Base, ND. Here he gained an appreciation for nature and began to nurture his interest in elasmobranchs. Upon graduating from Senath – Hornersville High School in 1999, Kyle went to Southeast Missouri State University and received his B.S. in Biology. Kyle then moved to Tampa, FL to begin his doctorate at the University of South Florida under the guidance of Dr. Philip J. Motta on the evolution and functional morphology of the hammerhead cephalofoil. He has taught many courses from general biology to comparative vertebrate anatomy, and received a certificate of appreciation for outstanding graduate teaching assistant. Upon completion of his degree, Kyle has authored five papers.