

NOT SO STRAIGHT FORWARD: SWIMMING, MANEUVERING, AND FEEDING
KINEMATICS OF THE SCALLOPED HAMMERHEAD (*SPHYRNA LEWINI*)

by

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This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Marianne E. Porter, Department of Biological Sciences, and has been approved by all members of the supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

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Many studies on shark swimming have examined kinematic variables along straight tracks or under controlled flow speeds in flumes, but there is less known about unsteady swimming during maneuvering or feeding. Sharks may adjust their speed, undulatory kinematics, or body curvature to accommodate different actions. This study quantified variations in kinematics during straight swimming, maneuvering, and feeding in scalloped hammerhead sharks (*Sphyrna lewini*). I obtained video of three juvenile scalloped hammerheads, developed an ethogram assessing three behavioral categories, and tracked points along the body's midline. I found that velocity was lower during feeding compared to maneuvering and straight swimming, while body curvature increased during feeding turns but decreased with increasing velocity. These data will provide insight into kinematic variations in hammerhead sharks across ontogeny and among behaviors, ultimately expanding on the relationship between form and function. This also provides context for varying behaviors and trends within the movement ecology paradigm.

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CHAPTER 1: INTRODUCTION

Movement ecology is a cross-disciplinary field that studies an organism's movement during different behaviors and at a variety of scales, from individual to population-level (Hays et al., 2016; Nathan et al., 2008). At larger scales, movement ecology can describe changes over a lifespan or seasonal migration (Hays et al., 2016; Nathan et al., 2008). At the base of the movement ecology paradigm is the field of biomechanics—the study of the structure, function, and forces affecting an organism in motion (Domenici & Blake, 2000). At these smaller scales, this framework has can answer questions about movement in a particular region of the body or may assess average performance among individuals (Dakin et al., 2018; Hoffmann et al., 2017; Segre et al., 2016). Movement ecology can be broadly applied to many taxa as key questions explored in this field describe fundamental rules behind movement patterns, the impacts of prey distribution, and the influence of learning and memory (Hays et al., 2016). Here, I address some of these questions by quantifying kinematics during volitional behaviors including straight swimming, maneuvering, and feeding in the scalloped hammerhead shark (*Sphyrna lewini*). By quantifying the swimming kinematics over a range of behaviors, I will provide movement ecology data for the endangered hammerhead shark.

1.1 Undulatory swimming kinematics

During swimming, fish produce thrust by generating a wave down their midline to create a lateral displacement of the water (Biewener & Patek, 2018; Blake, 2004; Breder, 1926; Shadwick & Gemballa, 2005). Most of the propulsive force is produced through caudal fin undulations, with some contribution from body movement as well (Akanyeti et al., 2016; Liu & Jiang, 2022; Webb, 1984). Undulatory waves may be generated in the anterior region as head yaw (anterior lateral flexure of the head) or in the posterior region as tail beat (Di Santo et al., 2021; Hoffmann et al., 2017; Porter et al., 2020). The wavelength initiated in the anterior region would have a unique head yaw amplitude (HYA) and head yaw frequency (HYF), while the wavelength in the posterior region possesses a different tail beat amplitude (TBA) and tail beat frequency (TBF).

1.2 Regional wave kinematics and transitions

When a fish engages in any behavior, it may adjust the amplitude and frequency of its head yaw or tail beat. However, the timing of specific adjustments in the anterior and posterior body may be offset or in phase with each other (Akanyeti et al., 2017; Di Santo et al., 2021; Hoffmann et al., 2017; Long, 1995; Porter et al., 2020). Data from scalloped hammerhead (*Sphyrna lewini* (Griffith & Smith, 1834)), bonnethead (*Sphyrna tiburo*), and blacktip (*Carcharhinus limbatus*) sharks have demonstrated that the body does not operate as a single wave passing from head to tail (Hoffmann et al., 2017; Porter et al., 2020). Instead, the wave-motion produced in the anterior region of the body is out of phase with the posterior end (Hoffmann et al., 2017). Captive hammerhead sharks have been shown to produce a wavelength with higher anterior flexion frequency at the head ($\text{HYF} > \text{TBF}$),

and higher posterior amplitudes at the tail ($TBA > HYA$) (Hoffmann et al., 2017). This trend in regional kinematics has also been found in the wild in blacktip sharks, as well as in non-shark fish species including sturgeon, eels, and lampreys (Hoffmann et al., 2017; Long, 1995; Porter et al., 2020). Aside from wave characteristics, the timing also differs regionally. Changes in anterior motion have been found to always precede changes in the posterior body (Akanyeti et al., 2017). Thus, the wavelength decoupling initiated at the head may signal a behavioral transition from steady, straight swimming to unsteady or accelerated swimming during prey capture.

During a transition between behaviors, a fish can adjust regional wavelengths in a variety of ways. For example, to increase overall velocity (V), the fish may increase TBF while maintaining TBA (Akanyeti et al., 2017; Hoffman & Porter, 2019). This relationship between V and tail beat is not universal. Increased TBF is positively correlated with increased V in a variety of marine fish, such as the blacktip shark, European eel (*Anguilla anguilla*), and bluegill sunfish (*Lepomis macrochirus*) (Di Santo et al., 2021; Methling et al., 2011; Porter et al., 2020; Schwalbe et al., 2019; Wise et al., 2018). However, no such correlation between HYF or TBF and V was found in the Caribbean reef shark (*Carcharhinus perezi*) (Kajiura et al., 2022). Another study on juvenile scalloped hammerheads found no correlation between TBA and V when the sharks were observed in a semi-natural pond environment but found a negative correlation when observed in a flume (Lowe, 1996). Studies on wild blacktips and Caribbean reef sharks instead found a positive correlation between TBA and V (Kajiura et al., 2022; Porter et al., 2020). Variables like TBA and V may not be held constant throughout the full course of a behavior either. TBA may temporarily increase at the onset of acceleration, a trend seen across phylogeny

(e.g., bonnetheads, bamboo sharks, sunfish, bichir, and others) and ontogeny (shown in the undulatory swimming of larval fish) (Akanyeti et al., 2017; Li et al., 2021; Long et al., 2010; Schwalbe et al., 2019; Wise et al., 2018). These kinematic transitions may be indicators for behavioral transitions as well, such as transitioning between steady swimming and maneuvering or prey capture.

1.3 Body curvature, maneuverability, and the cephalofoil

Movement variation can also be seen in body curvature when maneuvering or feeding. Maneuverability refers to an animal's ability to change its speed and direction (Dudley, 2002; Fish et al., 2018; Kajiura et al., 2003; Maia & Wilga, 2013; Segre et al., 2015). This can be analyzed by measuring bending coefficient (BC) during a turn, such as when maneuvering or capturing prey. BC quantifies the curvature of the body as a relationship between total length (TL) and distance between the rostrum and tip of the tail at the tightest turn (Figure 1). Body curvature can be predicted by both the vertebral and whole-body morphologies of a shark (Azizi & Landberg, 2002; Brainerd & Patek, 1998; Porter et al., 2009, 2011). Sharks with a cephalofoil (the dorso-ventrally flattened head seen in hammerheads) are more capable of bending at acute angles (Kajiura et al., 2003). The hydrodynamics of the cephalofoil, in conjunction with the absence of rolling during turns may contribute to this increased turning capacity (Gaylord et al., 2020; Kajiura et al., 2003; Kazemi et al., 2018). This may contribute greater curvature, or larger BC, during both feeding and maneuvering turns performed by hammerhead sharks (Kajiura et al., 2003). Body curvature is also influenced by size, as smaller sharks demonstrate smaller turning radii and larger turning angles, resulting in greater body curvature and

maneuverability compared to a larger shark (Domenici, 2001; Porter et al., 2009). Natural, volitional maneuvers are impacted by many factors beyond individual morphology. This includes variables such as the presence of other individuals, risk assessment, obstacles, tank size, and other variables (Dakin et al., 2020; Maierdiyali et al., 2020; Segre et al., 2016).

1.3 Impact of respiration and feeding behavior

Swimming kinematics may also be impacted by respiratory style. Some sharks, such as those in the family Sphyrnidae (the hammerheads), are obligate ram ventilators and must swim continuously in order to constantly pass water over their gills for gas exchange (Carrier et al., 2012; Nalesso et al., 2019; Wegner et al., 2012). Alternatively, during buccal/branchial pumping a shark is able to cease active swimming and instead facilitate respiration by opening its mouth to draw water in, and then closing it to force water out over the gills (Bouyoucos et al., 2018; Kelly et al., 2020). Since obligate ram ventilators are unable to stop swimming when processing and consuming prey, they may make different adjustments to their swimming before, during, and after prey capture compared to a shark that can remain stationary. Ram ventilators may also make other changes to their movement to confer some energetic benefit. For instance, hammerhead sharks are challenged with greater drag caused by their cephalofoil, but have a dorsal fin that is longer than their pectoral fins compared to other shark species (Payne et al., 2016; Royer et al., 2020). This enables the hammerheads to swim at a 50-75° roll angle to increase the lift surface span during their continuous swimming, reducing the cost of transport by about 10% (Payne et al., 2016). One study found that scalloped hammerheads spent 48% of their

daytime and 82% of nighttime rolled at an angle (Royer et al., 2020). Both Payne et al. and Royer et al. posit that hammerheads likely develop this rolling behavior with age, due to the ontogenetic changes in buoyancy and fin aspect ratio that may shift their hydrodynamic properties (2016; 2020).

Feeding style has an impact on swimming kinematics as well. In order to capture and consume prey, sharks must adjust their V, curvature, jaw movements, and other body kinematics depending on their approach. Ram feeding, suction, and food manipulation are examples of feeding strategies in sharks (Motta et al., 1997). Ram feeding, similar to the ventilation style, involves the shark swimming forward with its jaw open to engulf prey (Carrier et al., 2012). Suction is a hydraulic transport mechanism, which is typically followed by manipulation bites in order to reposition the prey (Motta et al., 1997). There are also other feeding mechanisms that are unique to hammerheads. One method is the “pin-and-pivot” technique, in which the hammerhead uses its laterally extended head to hold its prey down against the substrate (the pin) and rotate about the prey (the pivot) presumably to restrain and manipulate it in their jaws (Chapman & Gruber, 2002; Roemer et al., 2016; Strong et al., 1990). Another technique is “grasp turning,” where hammerheads have been observed to make several tight turns prior to successfully consuming the prey (Roemer et al., 2016). During the grasp turning technique, the hammerheads were also found to orient themselves towards an oncoming current as a strategy to aid in ventilation while keeping the prey in their jaws (Roemer et al., 2016). Electroreception is another factor that can affect feeding. Sharks can detect electrical stimuli given off by prey due to electroreceptors concentrated on the head (Freitas et al., 2006; Kajiura, 2001; Wueringer et al., 2011). Scalloped hammerhead sharks have been observed to position the edge of

their cephalofoil closest to an electrical stimulus before bending and pivoting about the perceived prey (Kajiura & Holland, 2002).

The feeding techniques utilized by hammerheads thus require a degree of maneuverability that may suggest trends in V when feeding. For instance, sailfish were observed to swim slower than expected during interactions with prey— this is likely an effect caused by the high degree of maneuverability exhibited during the prey's evasion techniques (Marras et al., 2015; Wilson et al., 2013). Thus, increased speeds would hinder a predator's maneuverability and accuracy when trying to catch the escaping prey with its bodily weapon (Marras et al., 2015; Wilson et al., 2013). Therefore, the unique feeding behaviors observed in hammerheads may highlight distinct changes in their V , body curvature, and overall body-wave kinematics when capturing prey.

1.5 Goals and hypotheses

Swimming kinematics involve a complex network of physical, behavioral, and environmental considerations. There is a breadth of information collected on steady, straight swimming in wild and captive sharks; However, there are fewer studies exploring the impact of unsteady swimming on kinematics during varying behaviors. In a movement ecology framework, these studies can inform about an animal's ability to tune its body to different conditions, especially considering species-specific limitations (such as being an obligate ram-ventilator). They can also elucidate the nuances of maneuvering during swimming compared to maneuvering during feeding. This may shed light on the learning involved in specialized feeding behaviors, even in more unique instances such as bonnethead sharks that feed on seagrass (Leigh et al., 2018). Sharks can learn behaviors as

quickly as other vertebrates, whether through conditioning, habituation, or associations (Guttridge et al., 2009). However, quantifying the changes in body movement during that process ultimately allows us to further link form and function.

I quantified scalloped hammerhead swimming at the smallest scales within the movement ecology framework by analyzing kinematics during three behaviors: straight swimming, maneuvering, and feeding. Specifically, I quantified V (all behaviors), regional kinematics (straight swimming), and BC as a proxy for turning (maneuvering and feeding) (Table 2). These variables were also assessed in the context of TL (all behaviors) and presence of neighboring sharks (feeding).

1.5.1 Velocity: all behaviors

I expected slower velocity during a feeding turn, compared to the other two behaviors. During prey encounters, animals may react by slowing down and increasing turning rate (Hays et al., 2016; Marras et al., 2015). Due to the tightness of the hammerhead's grasp turning, pin-and-pivot, or other turns for locating food, I hypothesized that this species would decrease V to effectively grasp the prey. By contrast, I expected straight swimming would have the highest V , because the shark is moving in an uninterrupted path without turns. V is also expected to be higher as the TL of the shark increases, a trend seen in previous studies (Domenici, 2001; Mu et al., 2019; Porter et al., 2009).

1.5.2 Regional kinematics: straight swimming

To examine the regional kinematics during straight swimming, I measured the head yaw amplitude (HYA; bl), head yaw frequency (HYF; Hz), tail beat amplitude (TBA; bl), and tail beat frequency (TBF; Hz). I expected the same decoupling of wavelengths in the head (anterior) and tail (posterior) regions as seen in previous studies (Hoffmann et al., 2017; Long, 1995; Porter et al., 2020). Within these wavelengths, I expect regional variations that highlight a greater TBA than HYA as the tail makes larger lateral sweeps, and a greater HYF than TBF as the head can make faster side-to-side motions due to the lower anterior amplitude (Hoffmann et al., 2017; Long, 1995; Porter et al., 2020). In general, I expect frequencies to increase as V increases. This trend has been seen in a variety of marine fish, as the increase in wavelengths generated per a unit of time enable the fish to produce greater forward thrust (Bainbridge, 1958; Di Santo et al., 2021; Methling et al., 2011; Porter et al., 2020; Schwalbe et al., 2019; Wise et al., 2018). I may also expect amplitudes to increase with increasing V , as prior studies have shown a potential to increase TBA at least temporarily at the onset of acceleration (Akanyeti et al., 2017; Li et al., 2021; Schwalbe et al., 2019; Wise et al., 2018). As TL increases, I expect amplitudes to increase. TBA has been found to remain constant at about 20% the total body length of a fish; thus, as the body gets longer, the posterior amplitude as a relative constant must increase (Saadat et al., 2017). Conversely, I expected frequencies to decrease with increasing TL. Prior studies have demonstrated this trend; for instance, one demonstrated that species specific length-at-age can be estimated by measuring TBF, and the relationship was inversely related (Bainbridge, 1958; Broell & Taggart, 2015; Gazzola et al., 2014).

1.5.3 Bending coefficient: maneuvering and feeding

During maneuvering and feeding behaviors, I expected a larger BC (where rostrum is closest to the tip of tail) during feeding compared to other maneuvers due to the tight turns made in their characteristic grasping behavior (Chapman & Gruber, 2002; Roemer et al., 2016; Strong et al., 1990). As TL increases, I expected lower BC due to the increase in cross-sectional area associated with increasing size of a shark, making it inherently less flexible (Domenici, 2001; Kajiura & Holland, 2002). I expect BC to increase (tighter turns) if there are neighboring sharks in the immediate vicinity, as prior studies have shown that hammerheads will abruptly change direction when another shark approaches (Myrberg & Gruber, 1974). In general, sharks have been shown to display more agonistic behaviors (which can manifest as dominance or submission) rather than tolerance; therefore, the presence of another shark alone may cause the other to suddenly change its path as a submissive ceding behavior (Brena et al., 2018; Myrberg & Gruber, 1974). Finally, I expect BC to decrease with increasing V. Since maneuverability has been found to decrease with increasing TL, and V increases with TL, I anticipate a lower capacity for tight turns (Domenici, 2001; Fish et al., 2003; Mu et al., 2019; Porter, 2009).

CHAPTER 2: MATERIALS AND METHODS

2.1 Filming the study animals

For this study, I filmed three juvenile scalloped hammerhead sharks (*Sphyrna lewini*; N=3) that were housed and cared for at Aquarium Encounters in Marathon, FL. The aquarium staff was responsible for all husbandry and animal care, and I have an Institutional Animal Care and Use Committee exemption to film these captive animals (A(E)20-01). Aquarium staff and collectors captured the animals near Jacksonville, FL, USA in 2020. Sharks were housed in a tank with a diameter of 12 m and depth of 1.5 m. Aquarium staff fed the sharks chunks of fish twice a day to satiation.

Filming for this project took place during October 2020 and March 2021. Sharks were recorded in 4K at 30 fps (frames per second) using a GoPro HERO7 set to a linear field of view to minimize distortion. The camera was secured above one section of the tank. I obtained a total of four hours and nineteen minutes of recordings. Using NIH Image J, I used tank structure to set a scale and measured the total length (TL, cm) for each shark (Schneider et al., 2012). I took measurements using screen captures from the video when the shark body was aligned linearly from the rostrum to the tip of the tail. TL measurements were recorded for each video clip to account for slight variations in the standardized body length (bl) resulting from swimming depth and proximity to the measured tank structure.

The average size of the sharks was 73.4 cm in October 2020 and 103.6 cm in March 2021, representing an approximate 30% increase in total length over 6 months.

2.2 Ethogram generation and use

I viewed the full-length videos to create an ethogram of shark behaviors observed (N=246 behaviors; 134 from 2020 and 112 from 2021) for analysis (Table 1). In the ethogram, I categorized the behaviors as follows: straight swimming, in which the shark swims a linear path across the frame; turning, any instance of a maneuver or curved path without engaging food pieces; and feeding, any interaction with food pieces whether successful or unsuccessful at consuming the food (Figure 2). For all behaviors, I noted whether more than one shark was in the frame. For feeding, I indicated whether the shark was successful or unsuccessful at food capture as well. I selected clips for 2D kinematic analysis based on the following criteria: in each clip, the shark must maintain level swimming; the entire body must remain in frame for the full length of the clip; and must include at least three full tail beats, with at least one before and after the maneuvering/feeding behaviors (Porter et al., 2014, 2020).

2.3 Video analysis

I used Microsoft Video Editor to save individual clips of each behavior from the full video based on the recorded “start” and “end” times of each observation. The start time for each clip began when the full body of the shark was in frame, while the end time marked the end of the behavior when the rostrum met the edge of the frame (the last frame before the shark swims off screen). I processed videos using LoggerPro (Vernier Software &

Technology, Beaverton, OR USA), in which I was able to track points along the shark's body for kinematic analysis. I labeled three anatomical landmarks along the body of the shark: (A) tip of the rostrum, (B) anterior edge of the 1st dorsal fin, and (C) tip of the tail (Hoffman et al., 2017; Porter et al., 2014; Figure 1). Due to the influence of size on swimming kinematics, I standardized the TL of the sharks as 1 bl (Di Santo et al., 2021; Hoffmann et al., 2017).

2.4 Kinematic variables

2.4.1 Velocity for all three behaviors

The kinematic variables quantified differed by behavior. A summary of the variables and abbreviations used in this study can be viewed in Table 2. I measured velocity (V ; bl/s) for all three of the behaviors. I calculated V as the average displacement of point B (see Figure 1) from frame-to-frame in each clip (Hoffman et al., 2017).

2.4.2 Regional amplitude and frequency during straight swimming

Variations between anterior and posterior swimming kinematics were collected for straight swimming videos only. For the anterior body, I measured head yaw amplitude (HYA; bl) and head yaw frequency (HYF; Hz). For the posterior body, I measured tail beat amplitude (TBA; bl) and tail beat frequency (TBF; Hz). Each amplitude was quantified as the difference between the maximum lateral peak-to-peak sweeps of the head or tail, while frequencies were calculated as the oscillations per second of the head or tail (Herskin & Steffensen, 1998; Hoffman et al., 2017; Porter et al., 2020; Sánchez-Rodríguez et al., 2020).

2.4.3 Bending coefficient for maneuvering and feeding

For maneuvering turns and feeding turns only, I quantified the sharks' body curvature as BC. This was calculated with the formula $1 - (L1/TL)$; where L1 equals the distance between the tip of the tail and tip of the rostrum when the shark is at its tightest turn, and TL is the total length of the shark (Azizi & Landberg, 2002; Brainerd & Patek, 1998; Kajiura et al., 2003; Figure 1). I measured L1 by taking the minimum length acquired in LoggerPro between points A and C. TL was collected by measuring the maximum length between A and C. When BC is equal to 0, the shark is in a straight line, and when BC is equal to 1, the head of the shark is touching the tip of the caudal fin (Figure 1).

2.5 Statistical analysis

In our statistical analysis, I used a two-way ANOVA model to examine V for the behaviors (straight swimming, maneuvering, and feeding) using behavior and TL as main effects. I used a three-way ANOVA to examine amplitudes (HYA and TBA) during straight swimming, using V, TL, and amplitude regions as main effects. I also used a three-way ANOVA to analyze frequencies (HYF and TBF) during straight swimming, using V, TL, and frequency region as main effects. Finally, I used a four-way ANOVA to examine BC for the turning behaviors (maneuvering turns and feeding turns), using behavior, V, TL, and presence of neighboring sharks as main effects.

CHAPTER 3: RESULTS

3.1 Shark sample sizes and total length

I obtained videos of three scalloped hammerhead sharks at two time points: October 2020 and March 2021. In October 2020, 134 videos satisfied the criteria for behaviors established in the ethogram, with 37 straight swimming clips, 70 maneuvering turns, and 27 feeding turns identified (Table 1). The average shark size was 73 ± 0.62 cm (mean and SEM). In March 2021, 112 videos satisfied the criteria, with 29 straight swimming clips, 52 maneuvering turns, and 31 feeding turn videos. The average shark size was 104 ± 0.68 cm, a nearly 30% increase between the two time points.

3.2 Velocity for all behaviors

A two-way ANOVA examining velocity (V; bl/s) using behavior and total length (TL; cm) as main effects was significant ($F_{5,240} = 13.03$; $p < 0.0001$). Both behavior ($F = 14.83$; $p < 0.0001$) and TL ($F = 22.98$; $p < 0.0001$) are significant main effects, while the behavior*TL interaction term was not significant. Swimming and maneuvering V (mean = 0.68 bl/s and 0.69 bl/s; respectively) were significantly greater than feeding V (0.58 bl/s) (Figure 3A). As the TL of the shark increases, V decreases significantly (Figure 3B).

While I report relative V standardized by TL, I calculated absolute velocities for comparison. Straight swimming V ranged from approximately 40-100 cm/s, maneuvering turns ranged from 30-130 cm/s, and feeding turns ranged from 35-80 cm/s. Using a linear

regression model, I find that V is positively correlated with absolute TL when each behavior is viewed individually.

3.2 Regional kinematics during straight swimming: amplitude and frequency

A three-way ANOVA examining amplitude during straight swimming was significant using region (anterior = head yaw amplitude; HYA, and posterior = tail beat amplitude; TBA), TL, and V as main effects ($F_{3,128}=13.15$; $p<0.0001$). Both amplitude region and TL were significant main effects ($F=25.94$; $p<0.0001$ and $F=13.06$; $p=0.0004$; respectively), while V was not a significant main effect ($F=3.64$; $p=0.0585$). TBA was double the HYA (0.30 and 0.15 bl; respectively), thus posterior amplitudes were greater than anterior (Figure 4A). As shark TL increases, both HYA and TBA decrease significantly (Figure 4B). Finally, although not a significant relationship, there was a close trend for amplitude to decrease ($p=0.0585$) as V increases for both regions, (Figure 4C).

A three-way ANOVA examining frequency during straight swimming was significant using frequency region (anterior = head yaw frequency; HYF, and posterior = tail beat frequency; TBF), TL, and V as main effects ($F_{3,128}=22.36$; $p<0.0001$). All main effects were significant: frequency region ($F=26.41$; $p<0.0001$), TL ($F=7.79$; $p=0.0061$), and V ($F=23.704$; $p<0.0001$). HYF (mean=1.41 Hz) was significantly greater than TBF (mean= 1.09 Hz) (Figure 5A). For both regions, TL and frequency were negatively correlated, while V and frequency were positively correlated (Figures 5B and 5C).

3.4 Bending coefficient during maneuvering and feeding

A four-way ANOVA examining bending coefficient (BC) with behavior, TL, V, and presence of neighboring sharks as main effects was significant ($F_{4,175}=118.45$; $p<0.0001$). Each main effect was significant: behavior ($F=345.74$; $p<0.0001$), TL ($F=6.35$; $p=0.0127$), V ($F=4.34$; $p<0.0386$), and neighbors ($F=7.38$; $p=0.0073$). BC among the hammerheads was significantly greater during feeding turns (mean=0.69) compared to maneuvering turns (mean=0.26). The BC was about 3X greater on average during feeding compared to maneuvering (Figure 6A). Sharks without neighbors in the video frame had a significantly higher BC (mean=0.44) compared to sharks with neighbors in frame (0.30) (Figure 6B). As TL increases, BC decreases. While TL was a significant effect when considered within the suite of variables in the model, the relationship between TL and BC had an R^2 close to zero and was not predictive. As V increases, BC decreases as well (Figure 6C).

CHAPTER 4: DISCUSSION

In this study, I quantified swimming kinematics in the context of behavior, examining straight swimming, maneuvering, and feeding turns. The feeding behaviors required significantly lower velocity (V ; bl/s) and bending coefficient (BC) compared to straight swimming or maneuvering, supporting our hypotheses. Our data expands upon prior research on regional kinematics in fish; anterior and posterior wavelengths were discrete and decoupled from each other. Tail beat amplitude (TBA; bl) was significantly greater than head yaw amplitude (HYA; bl) and tail beat frequency (TBF; Hz) was significantly lower than head yaw frequency (HYF; Hz), agreeing with previous studies (Hoffmann et al., 2017; Long, 1995; Porter et al., 2020). TBF was also positively correlated with V ; however, TBA was not correlated, supporting the variations in TBA found in other studies (Akanyeti et al., 2017; Kajiura et al., 2022; Li et al., 2021; Long et al., 2010; Lowe, 1996; Porter et al., 2020; Schwalbe et al., 2019; Wise et al., 2018). As a result, this study highlights the need for continued investigation of kinematics as the body reconfigures across behaviors, ontogeny, and evolutionary time (Long et al., 2010).

4.1 Velocity by behavior and length

I found that V during feeding was significantly lower than in straight swimming and maneuvering, supporting our hypothesis. On average, V decreased by 15% during feeding, but was found to decrease by as much as 47% at minimal values (Figure 3A). The

variation among the decreased feeding V may be impacted by a variety of factors such as amount of food available, proximity of the food item to a barrier/obstacle, and prior failure or success in feeding. Although the sharks decreased V during feeding to 0.58 bl/s, a range found to be less energetically favorable in juvenile scalloped hammerheads, it may have been necessary to optimize prey capture at least for stationary or slow-moving prey (Lowe, 2001). These results support prior studies suggesting that some predators may slow down in order to increase accuracy when catching prey or to prevent the prey from detecting their presence too early (Domenici, 2001; Hays et al., 2016; Marras et al., 2015; Wilson et al., 2013). This may be particularly beneficial for obligate ram ventilators— fish whose respiratory mechanism does not allow them to stop swimming to capture and process prey (Carrier et al., 2012; Nalesso et al., 2019; Wegner et al., 2012). The decreased V during feeding may also be reflective of how the cephalofoil is used for stability in a turn. Juvenile scalloped hammerheads did not bank their heads to make a tight turn, but instead maintained a level positioning (Kajiura et al., 2003). Banking would cause a loss of lift and would require an increase in thrust to offset this; however, this could cause them to miss the prey (Kajiura et al., 2003). Therefore, if the hammerhead is not compensating for a lack of lift, it can effectively slow down to capture the prey. Additionally, one study hypothesized that predators that possess “weapons,” like billfishes, may not resort to higher speeds in predator-prey interactions (Marras et al., 2015). Although the cephalofoil of a scalloped hammerhead isn’t necessarily a “weapon,” it is a morphological structure that has been observed to aid in prey capture. For instance, the cephalofoil is used to restrain prey during their specialized grasp turning or pin-and-pivot feeding techniques (Chapman & Gruber, 2002; Kajiura et al., 2003; Roemer et al., 2016; Strong et al., 1990). More studies

would need to explore whether this negative relationship between V and feeding is true for shark species that do not utilize the same feeding behaviors or do not possess a large cranial cephalofoil. Further studies would also need to be conducted to investigate V during feeding when the shark is engaging fleeing prey. In this study, the prey was stationary in the tank and only showed minor movements due to flow in the water or from disruptions caused by the sharks. In the wild, high V movements may still be effective for a hammerhead when engaging a fleeing prey (Domenici, 2001; Strong et al., 1990). The kinematics and behavior may also change depending on ontogeny or specific type of prey. Scalloped hammerheads are generalists, feeding on a variety of prey such as crustaceans, cephalopods, and teleosts (Bush, 2003; Clarke, 1971; Compagno, 1984; Duncan, 2006). However, ontogenetic shifts in diet show a switch from primarily cryptic/buried benthic prey as juveniles to more pelagic species in adulthood (Clarke, 1971; Compagno, 1984; Kajiura et al., 2003). For instance, juvenile scalloped hammerheads have been found to consume large proportions of alpheid shrimp, gobies, and small parrotfish as well as a lesser percentage of various crabs, stomatopods, and other teleosts (Bush, 2003). The diet of adult scalloped hammerheads includes neonates and cephalopods (pelagic species) as well (Bush, 2003; Clarke, 1971). This shift is likely accompanied by altered swimming kinematics to adjust for changing food preferences.

I found that V decreased with increasing TL (Figure 3B). This refutes our hypothesis and the results of prior studies showing a positive correlation between V and TL (Domenici, 2001; Mu et al., 2019; Porter et al., 2009). One possible explanation for this incongruence is that some studies have shown the positive trend to be reversed when reporting relative (body lengths per unit time) swim speeds, as I did in this study, instead

of absolute (distance per unit time) swim speeds (Batty & Blaxter, 1992; Domenici, 2001; Videler, 1993; Wardle, 1975). For example, small fish (0.1 m) have been shown to reach speeds up to 25 bl/s, while larger fish (1 m) reached a maximum of 4 bl/s (Wardle, 1975). Since contraction time of lateral muscle increases with increasing length, smaller fish have the advantage of faster muscle contractions to supply that greater speed in terms of relative body length (Domenici, 2001; Videler, 1993; Wardle, 1975). Another possible explanation is that the amount of time to reach maximum speed increases with (non-larval) fish length (Domenici, 2001; Hale, 1996; Webb, 1976). Therefore, it may take a greater amount of time for the larger scalloped hammerheads to reach higher V compared to their smaller counterparts. Thus, it is possible that the larger sharks in our study did not reach their maximum possible V for a behavior within the short time of each clip. Another explanation for the unexpected inverse relationship between TL and V stems from the arrangement of our statistical model. All values of V are integrated, regardless of behavior. The feeding behavior, which displayed inherently lower values for V , may be negatively impacting the trend. When each trend in V is separated by behavior, I did find the expected positive correlation between TL and V .

4.2 Amplitude by region, total length, and velocity

During straight swimming, I found that body wave amplitudes (HYA and TBA) were impacted by amplitude region and TL, but not V . These results indicated that average amplitudes in the posterior region (TBA) were double the average in the anterior region (HYA) (Figure 4A). Previous studies have shown that some fish species, including scalloped hammerheads, do not generate a single continuous wave down the body, but

instead produce a unique wave from the head and from the caudal fin (Hoffmann et al., 2017; Long, 1995; Long et al., 2010; Porter et al., 2020). Amplitude has been found to increase down the body of other undulatory swimmers as the tail makes greater lateral sweeps than the head, allowing fish to swim a greater distance per tail beat (Bainbridge, 1958; Tytell & Lauder, 2004).

I found that amplitude decreased significantly with increasing TL (Figure 4B). These findings refute our hypothesis and previous research that showed that TBA is positively correlated with TL at any given speed (Bainbridge, 1958; Broell & Taggart, 2015; Hunter & Zweifel, 1971). Average amplitude is typically held at a constant proportion of 20% the total length, thus an increasing length would result in higher overall amplitudes (Hunter & Zweifel, 1971; Saadat et al., 2017). However, it is possible that the association I found is impacted by outliers. Posterior amplitude has been shown to level out around 0.2 bl at high, steady swimming speeds (Akanyeti et al., 2017). When plotting TL against amplitudes less than or equal to 0.2 bl, the positive trend is visible, but when including the unexpectedly large amplitudes, the negative relationship is present. Further research may be required to elaborate on this relationship by exploring minimal and maximal amplitude values at varying life stages.

In this study, I found that V did not significantly impact amplitude (Figure 4C). These findings are supported by prior studies that have shown that most species maintain a constant TBA associated with body length, regardless of V (Bainbridge, 1958; Gazzola et al., 2014). Jack mackerel have been shown to hold TBA constant even with changing speed (Hunter & Zweifel, 1971). However, other studies have found variations depending on the environment. For example, no correlation between TBA and V was observed in a

pond environment, a negative correlation was observed in a flume, and a positive correlation was observed in the wild (Kajiura et al., 2022; Lowe, 1996; Porter et al., 2020).

Regionally, I found that increasing V resulted in increased HYA while TBA decreased; however, this trend was not significant (Figure 4C). Results from previous studies have shown that changes in movement are initiated in the anterior region, this can explain why only the HYA increased with V (Akanyeti et al., 2017). The posterior region can also be modified at the initiation of a behavior. During maintained linear swimming, a fish's TBA has been shown to remain steady, but in the event of acceleration, the TBA may temporarily increase (Akanyeti et al., 2017; Li et al., 2021; Schwalbe et al., 2019; Wise et al., 2018). Thus, initiating a mechanism for acceleration, such as an acute increase in HYA, may indicate the onset of a behavior.

4.3 Frequency by region, total length, and velocity

I found that during straight swimming, wave frequencies were significantly influenced by region, TL, and V . Supporting our hypothesis, average anterior frequency (HYF) was significantly higher than posterior frequency (TBF) (Figure 5A). This significant difference between HYF and TBF further asserts the observation that sharks may swim using decoupled anterior and posterior wavelengths (Hoffmann et al., 2017; Long, 1995; Porter et al., 2020). The higher HYF may also be a direct result of the lower HYA generated, as the lateral distance to travel in a unit of time is shorter (Hoffmann et al., 2017; Long, 1995; Porter et al., 2020). Higher HYF can potentially increase sensory input, especially in the context of the broad cephalofoil of the scalloped hammerhead shark (Hoffman et al., 2017; McComb et al., 2009). With frequent yawing of the head, the shark

can not only expand its visual field, but can orient itself closer to signals detected by electrosensory organs (ampullae of Lorenzini) located on the anterior side of the rostrum (Hoffman et al., 2017; McComb et al., 2009; McCutcheon & Kajiura, 2013).

As TL increased, both anterior (HYF) and posterior (TBF) wave frequencies decreased (Figure 5B). This agrees with previous studies that have shown an inverse relationship between fish size and frequency (Broell & Taggart, 2015; Cheong et al., 2006). The decreased frequencies displayed in larger fish may result from the decreased muscle contraction time with increasing size (Domenici, 2001; Videler, 1993; Wardle, 1975). However, larger fish have a greater percent of muscle relative to body mass and can produce a greater power output per contraction (Goolish, 1989). Thus, with increasing size, the fish may not need to increase the frequency as much as a smaller counterpart since it can produce greater thrust per tail beat.

Velocity was positively correlated with frequency (Figure 5C). This trend is seen across fishes, both in the wild and in captivity (Akanyeti et al., 2017; Di Santo et al., 2021; Hoffman & Porter, 2019; Porter et al., 2020; Schwalbe et al., 2019; Wardle, 1975; Wise et al., 2018). Although both amplitude and frequency can be adjusted to change swimming V , speed has been found to be consistently proportional to TBF over varying body size, geometry, and kinematics (Bainbridge, 1958; Li et al., 2021). This relationship potentially reduces the speed-specific cost of transport (Li et al., 2021). The wave generated by an undulatory swimmer produces drag, thus increasing wave amplitude to increase V would result in consequently higher drag and hydrodynamic cost (Li et al., 2021; Schultz & Webb, 2002). Therefore, fish may preferentially adjust frequency to maximize V and minimize energetic costs (Li et al., 2021).

4.4 Bending coefficient by behavior, length, neighbors, and velocity

Analyzing the impact of behavior, TL, presence of neighboring sharks, and V on BC yielded significant differences. The average BC during feeding was three times greater than the average for maneuvering turns (Figure 6A). As obligate ram ventilators, scalloped hammerhead sharks are unable to remain stationary when catching or consuming prey (Carrier et al., 2012; Nalesso et al., 2019; Wegner et al., 2012). Although the sharks were observed to occasionally approach and attempt to capture prey by simply gliding over it, they showed a strong preference for turning about the prey instead. This agrees with previous studies that explored the unique feeding behaviors shown in hammerhead sharks, such as the grasp turning and the pin-and-pivot approach (Chapman & Gruber, 2002; Roemer et al., 2016; Strong et al., 1990). The sharks may be taking advantage of their enhanced ability to bend at tighter angles along with the hydrodynamics of their cephalofoil (Gaylord et al., 2020; Kajiura et al., 2003; Kazemi et al., 2018). This may afford them the high level of flexibility required for these behaviors. Future studies could potentially explore the energetic implications of this preference to slow down and bend about the prey as well.

As the TL of the shark increased, average BC decreased. This finding is supported by prior studies that demonstrated larger turning radii and decreased maneuverability with increased size (Domenici, 2001; Porter et al., 2009). Sharks increase in girth as they grow longer, thus the increased cross-sectional area of the shark results in a greater second moment of area (Kajiura et al., 2003; Natanson et al., 2018; Porter et al., 2009). The second moment of area reflects a resistance to bending, serving as a proxy for flexural stiffness

(Kajiura et al., 2003). Although the relationship to TL resulted in a significant relationship, it was not predictive in the context of the full four-way statistical model, as evidenced by an R^2 close to zero.

BC also decreased when neighboring sharks were present (Figure 6B). I expected BC to increase due to prior studies that describe abrupt changes in direction when another shark is close by or approaching (Myrberg & Gruber, 1974). However, this difference may indicate variation in social responses. Fish have been shown to display individualized differences in feeding behavior to balance their response to hunger and fear (Mas-Muñoz et al., 2011). These differences are impacted by environmental and internal factors, thus maneuvers may vary depending on the size, speed, direction, or orientation of a nearby shark as well as the individual's own coping style (Mas-Muñoz et al., 2011). Studies have shown that sharks are less likely to simply tolerate the presence of another individual, but will instead display agonistic responses (Brena et al., 2018). It is possible that a feeding shark may not execute a complete or tight turn in order to avoid an incoming/adjacent shark. Sharks have also been observed to develop a social hierarchy mostly dependent on size where lower ranking, smaller sharks are more likely to give way to the larger ones (Guttridge, 2009; Myrberg & Gruber, 1974). There may have been an impact of social hierarchy within the tank in our study that influenced how each shark adjusted its movements. Future studies could also explore how this varies in the wild. Scalloped hammerheads have been shown to congregate offshore in the daytime, and then disperse when hunting in the night (Klimley et al., 1988). Thus, there may be differences in how the hammerheads maneuver/interact when in close proximity to each other in congregations compared to when they are out feeding.

I also found that BC decreased when V increased (Figure 6C). Although some studies on fishes have shown turning radius to be independent of V, other studies on cetaceans, pinnipeds, and yellowfin tuna have shown that increasing V is associated with larger turning radii; in other words, when animals swim faster, they make wider turns and would thus display a lower BC (Blake et al., 1995; Domenici & Blake, 1997; Fish et al., 2003; Webb, 1976). Decreased V has also been shown at the initiation of a turn and during a sustained turn in rainbow trout (Webb, 1983). The inertia of a fish, or centripetal force, will cause it to keep moving forward at a curve and would require a reduction in speed to maintain control. Therefore, as a fish begins or continues to turn, the BC increases. The fish will then decrease its V during the maneuver.

4.5 Implications of behavior

Behaviors can be influenced by many factors or may vary as part of learning (Dakin et al., 2018). Fish, in general, have been shown to have the cognitive ability for decision making and trial-and-error, but learning over ontogeny has not been fully explored in elasmobranchs (Gruber & Myrberg, 1977; Myrberg & Porcher, 2003; Newton & Kajiura, 2020). One study on learning in the yellow stingray explored its ability to learn and relearn the polarity of the geomagnetic field (Newton & Kajiura, 2020). Another study investigated object categorization in bamboo sharks over time (Schluessel & Duengen, 2014). These studies may provide context for understanding behavioral changes over size (and thus, age) in the scalloped hammerhead sharks used in this study; that is, the smaller/younger sharks may adjust their kinematics differently than the larger/older sharks as a result of learning. There were six months between filming bouts in this study, and hammerheads may have

learned the stimuli associated with feeding such as size/shape/scent of the food items, electrical signals given off by each other during feeding time, and impact of neighbor proximity. Over time, the sharks may have had to take different approaches to acquiring a piece of food, whether this be altering V and/or BC. The improvement in feeding behavior with age is apparent as the observed feeding success was approximately 7% in the younger sharks, and six months later it improved to 56%. Note that these values are estimates in the ethogram, as I considered feeding attempts to be “successful” if a food item was picked up and taken away. However, I was unable to verify that the shark consumed the food item or if it eventually dropped it off screen. Over time, the sharks may learn to adjust how/when they approach a prey item and may learn to become more efficient with age.

4.6 Limitations

The major limitation to this study is the low sample size of individuals. However, it is important to consider that scalloped hammerhead sharks (*Sphyrna lewini*) are a protected species with threatened status in the Western Atlantic and endangered in the Eastern Atlantic and Eastern Pacific (U.S. Fish & Wildlife Services). Fish trade professionals have reported that *Sphyrna lewini* is a particularly delicate species to hold in captivity, even compared to similar species such as the great hammerhead (*Sphyrna mokarran*) (Tristram et al., 2014). During capture or release, hammerheads also face greater mortality, potentially due to being obligate ram ventilators that must keep swimming to breathe (Nalesso, 2019). In the literature, sample sizes vary in biomechanics studies on endangered species and megafauna. For example, prior studies on shark kinematics have included the following sample sizes: four scalloped hammerheads,

Sphyrna lewini (Hoffman et al., 2017), three sand tiger sharks, *Carcharias taurus* (Moyer et al., 2019), three to five spiny dogfish, *Squalus acanthias* and *Squalus suckleyi* (Domenici et al., 2004; Flammang et al., 2011; Hoffman et al., 2019; Maia et al., 2017; Maia & Wilga, 2015; Porter et al., 2014), four bonnetheads, *Sphyrna tiburo* (Hoffman et al., 2017; Hoffman & Porter 2019), four bamboo sharks, *Chiloscyllium punctatum* (Maia & Wilga, 2013), five horn sharks, *Heterodontus francisci* (Edmonds et al., 2001), four leopard sharks, *Triakis semifasciata*, and five epaulette sharks, *Hemiscyllium ocellatum* (Porter et al., 2009).

Additionally, one study discussed the viability of sample sizes <10, which stated that lower sample sizes may be appropriate for protected species (Sequeira et al., 2019). Low sample sizes may also provide insight into the possible kinematics when sampled at high frequency (Segre et al., 2015, 2016; Sequeira et al., 2019). While I only quantified the kinematics from three sharks in this study, I filmed them at two time points six months apart and quantified the kinematics from 66 straight swimming, 122 maneuvering, and 58 feeding events. Another study showed that it was appropriate to use high sampling from a lower number of individuals since many animals tend not to express their full maximal or minimal potential when moving voluntarily (Dakin et al., 2020; Segre et al., 2015, 2016). These authors concluded that it is possible to measure average values when examining a large quantity of observations. Considering the protected status and large number of observations of the current study species, I believe that these results provide new and useful information to expand upon our understanding of undulatory swimming kinematics among behaviors.

CHAPTER 5: CONCLUSION

Within the movement ecology paradigm, many factors can influence animal behavior and biomechanics. Various movement studies on fish analyze kinematics during steady swimming or in controlled flow speeds. However, this study contributes to the exploration of unsteady swimming by measuring the voluntary movements of juvenile scalloped hammerhead sharks (*Sphyrna lewini*). I examined the impact of three behaviors: straight swimming, maneuvering, and feeding. I also aimed to investigate the impact of total length (TL) and presence of immediate neighbors on these kinematic variables. I found that relative velocity (V) was lower during feeding and in larger sharks. During straight swimming, I found that the wave generated in the anterior region (head) was decoupled from the one in the posterior region (tail). The average tail beat amplitude (TBA) was greater than head yaw amplitude (HYA), but the average head yaw frequency (HYF) was greater than tail beat frequency (TBF). Thus, wave amplitudes were maximized in the posterior body, while wave frequencies were maximized in the anterior body. The wave amplitudes and frequencies both decreased with increasing TL. I found that V was positively correlated with higher frequencies but showed no significant relationship to wave amplitudes. During maneuvering and feeding turns, bending coefficient (BC) was lower during feeding. BC decreased with increasing TL and V, and in the presence of neighboring sharks. Ultimately, these concepts can be applied to broader taxa, can provide

ontogenetic insights into a protected species, and can expand our understanding of shark behavior. In the future, studies could explore the phylogenetic differences in swimming kinematics and behavior, comparing more Sphyrnid shark species and other families of sharks as well. This might answer the still burning question of hammerhead shark biology: Why the weird head? Quantifying swimming kinematics and behavior among hammerhead species could elucidate the costs and benefits of the cephalofoil during locomotion.

TABLES

Table 1. Number of video clips per behavior and filming period

Video sample sizes in ethogram			
Behavior	October 2020	March 2021	Total
Straight swimming only, no turning or feeding	37	29	66
Maneuvering turns without feeding	70	52	122
Feeding turns	27	31	58
Total videos	134	112	246

Table 2. Kinematic variables used in this study

Kinematic variables, abbreviations, and units		
Variable	Abbreviation	Unit
Total Length	TL	bl, cm
Body Length	bl	bl
Seconds	s	s
Velocity; body lengths (bl) per second (s)	V	bl/s
Head Yaw Amplitude, scaled to TL	HYA	bl
Head Yaw Frequency	HYF	Hz
Tail Beat Amplitude, scaled to TL	TBA	bl
Tail Beat Frequency	TBF	Hz
Minimum distance from tip of the rostrum to the tip of the caudal fin during a turn	L1	bl
Bending Coefficient; $1 - (L1/TL)$	BC	No unit

FIGURES

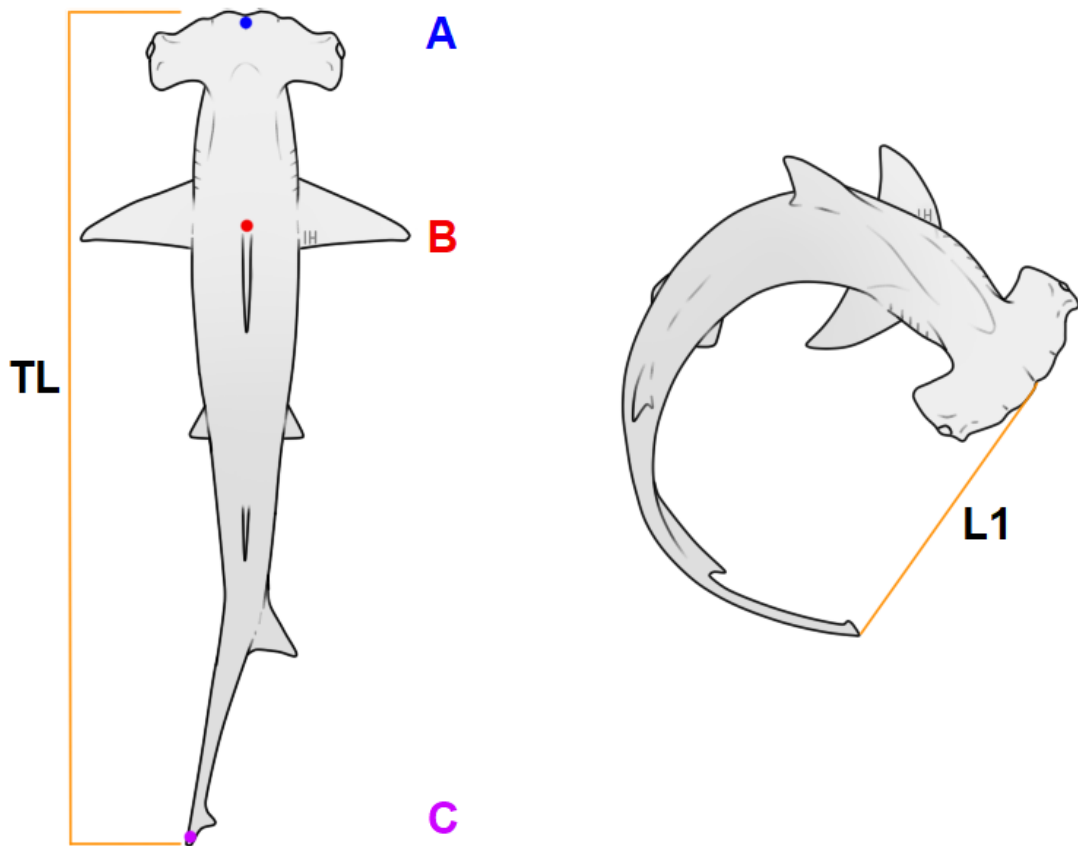


Figure 1.

Points tracked on straight swimming and turning hammerhead sharks to calculate kinematic variables (Table 2). (Left) Diagram showing the three points labeled along the midline of the scalloped hammerhead shark: (A) Tip of the rostrum. (B) Anterior insertion of first dorsal fin. (C) Tip of the caudal fin. Points were tracked using Vernier's LoggerPro. Also shown is the shark's total length, TL. (Right) During turning I calculated the bending coefficient. L1 is the shortest distance between tip of the rostrum and tip of the caudal fin indicating the tightest part of the turn. Bending coefficient is calculated as $1 - (L1/TL)$; a higher coefficient indicates a tighter turn (Illustration credit: Heerdegen, 2022).

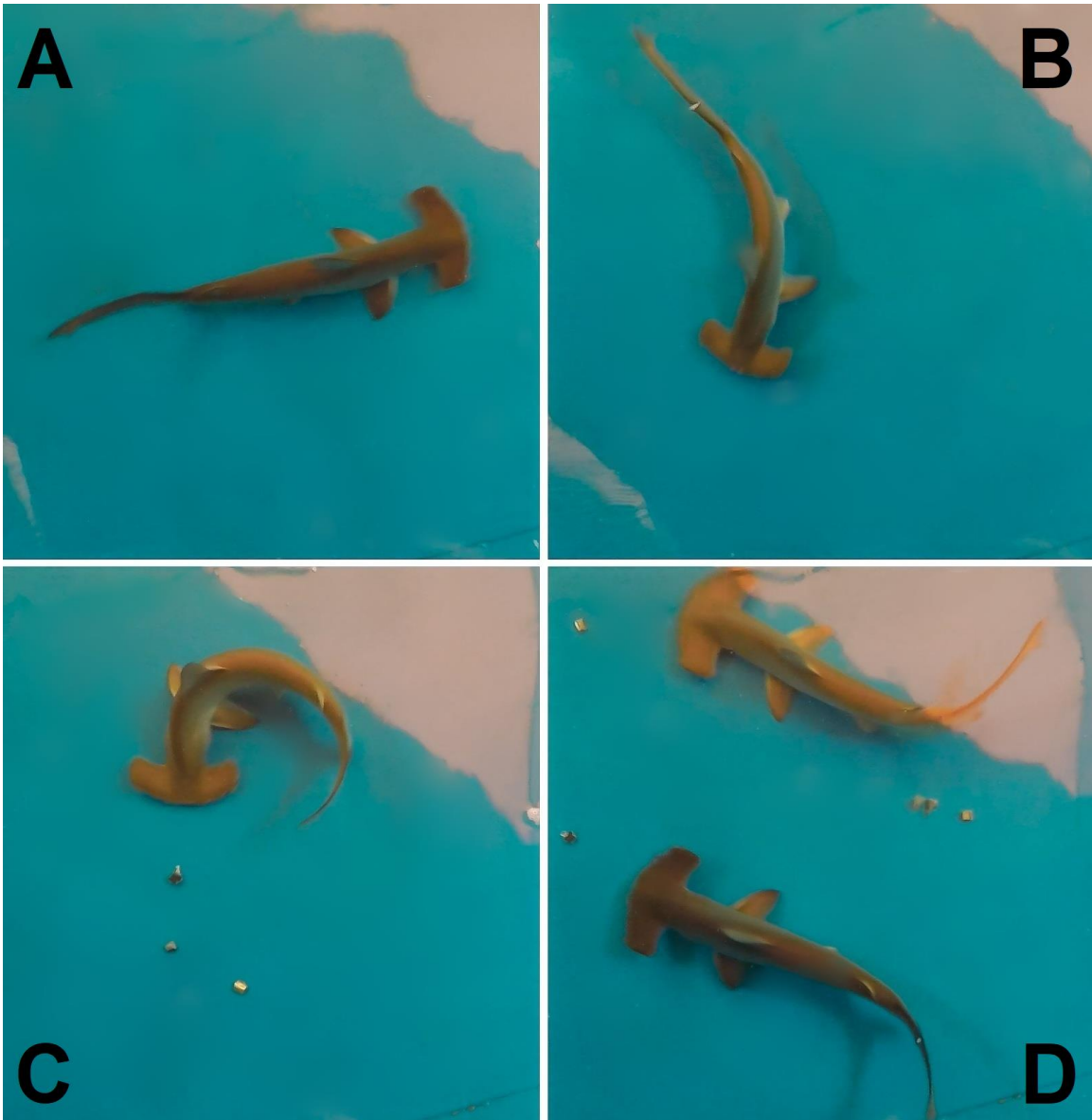


Figure 2.

Examples of logged behaviors and presence of neighboring sharks. (A) Straight swimming (when the shark swims a linear path). (B) Maneuvering turn (any turn in which the shark was not engaging with food). (C) Feeding turn (any turn during a feeding attempt). (D) Neighboring sharks (when more than one shark was present in the video clip frame).

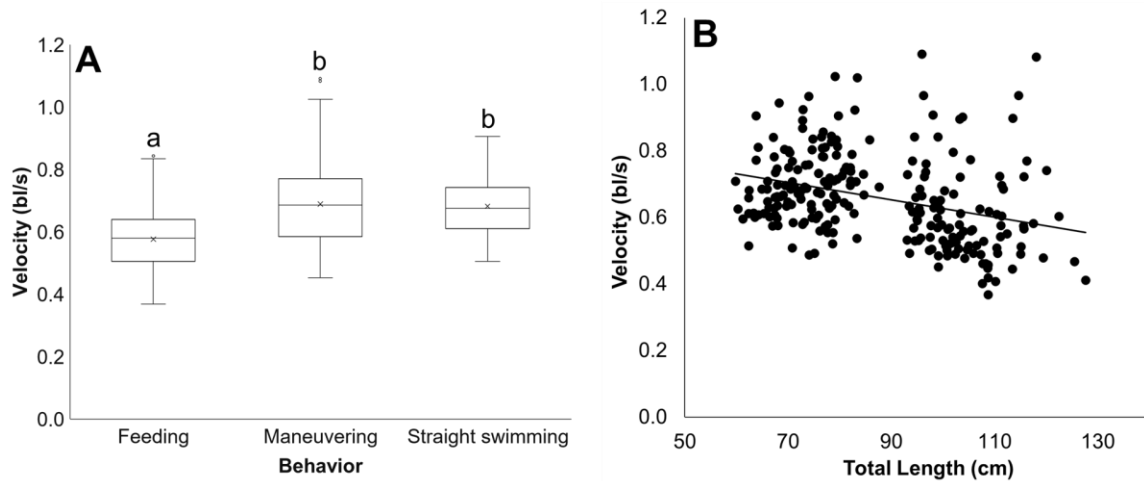


Figure 3.

The relationship between velocity, behavior, and total length was significant ($p < 0.001$). (A) Velocity varied significantly with behavior ($p < 0.0001$). The average velocity of a scalloped hammerhead shark when feeding is significantly lower (0.58 bl/s) compared to maneuvering turns (0.69 bl/s) or straight swimming (0.68 bl/s). The box and whisker plot shows the mean value as an “x” and the median as a line through the box. The lower edge of the box depicts the median of the first quartile, and the upper edge shows the median of the third quartile. The whiskers extend to the minimum and maximum values, with any outliers shown beyond them as an open point. (B) I found a negative relationship between total length and velocity ($p < 0.0001$). The distinct clusters of points show the size difference between the two time points for filming (in October 2020, the average total length was 73.37 ± 0.62 cm; in March 2021, the average was 103.61 ± 0.68 , showing an approximate 30% increase in size).

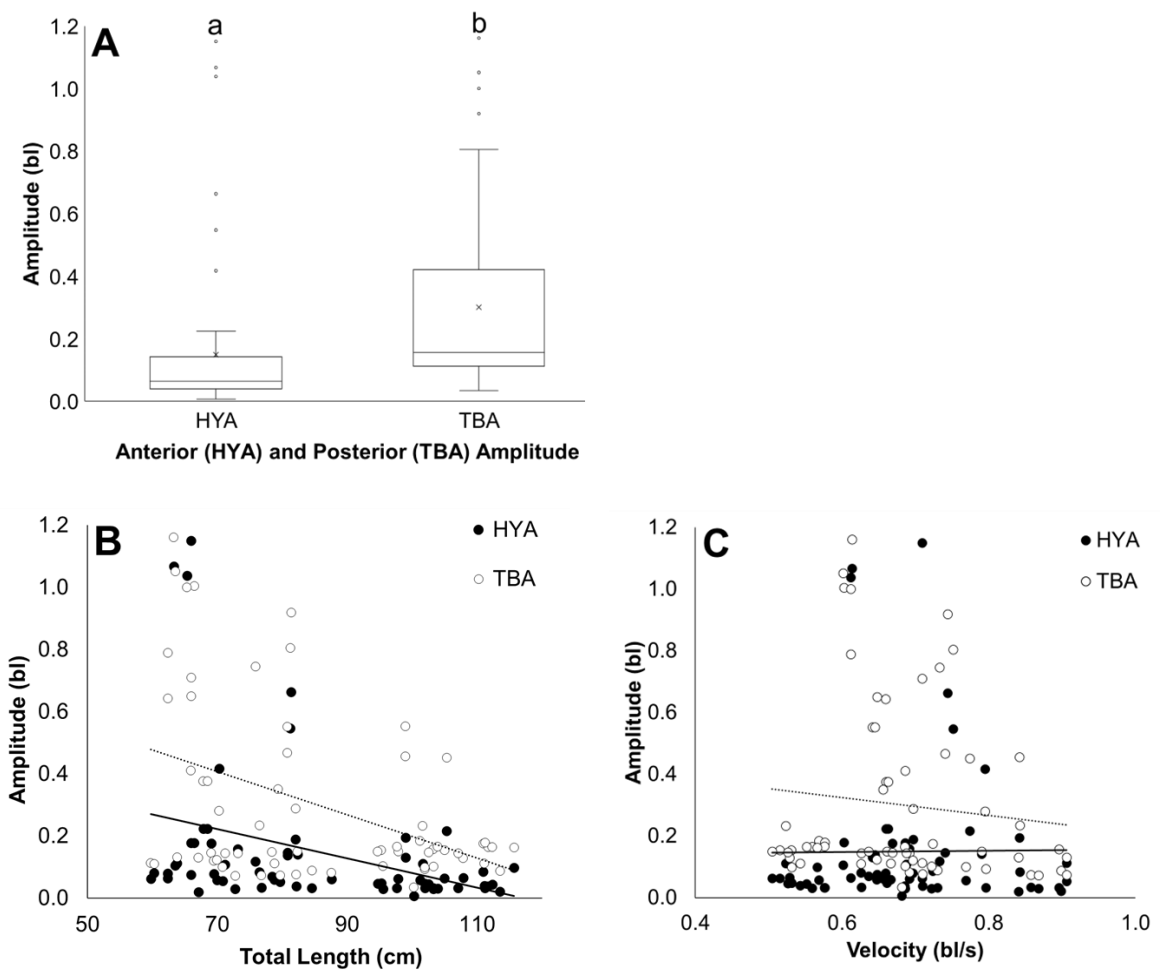


Figure 4.

During straight swimming, the average amplitude varies significantly with swimming velocity, animal length, and body region (head yaw or tail beat; $p < 0.0001$). (A) The average amplitude produced in the posterior region as the tail beat is double that of the anterior region as the head yaw. The average head yaw amplitude (anterior region; HYA) was 0.15 bl, and the average tail beat amplitude (posterior region; TBA) was 0.30 bl. The box and whisker plot shows the mean value as an “x” and the median as a line through the box. The lower edge of the box depicts the median of the first quartile, and the upper edge shows the median of the third quartile. The whiskers extend to the minimum and maximum values, with any outliers shown beyond them as an open point. (B) There was a negative relationship between total length and amplitude of the wave for both the anterior (HYA) and posterior (TBA) regions. (C) There was not a significant relationship between velocity and amplitude ($p = 0.0585$).

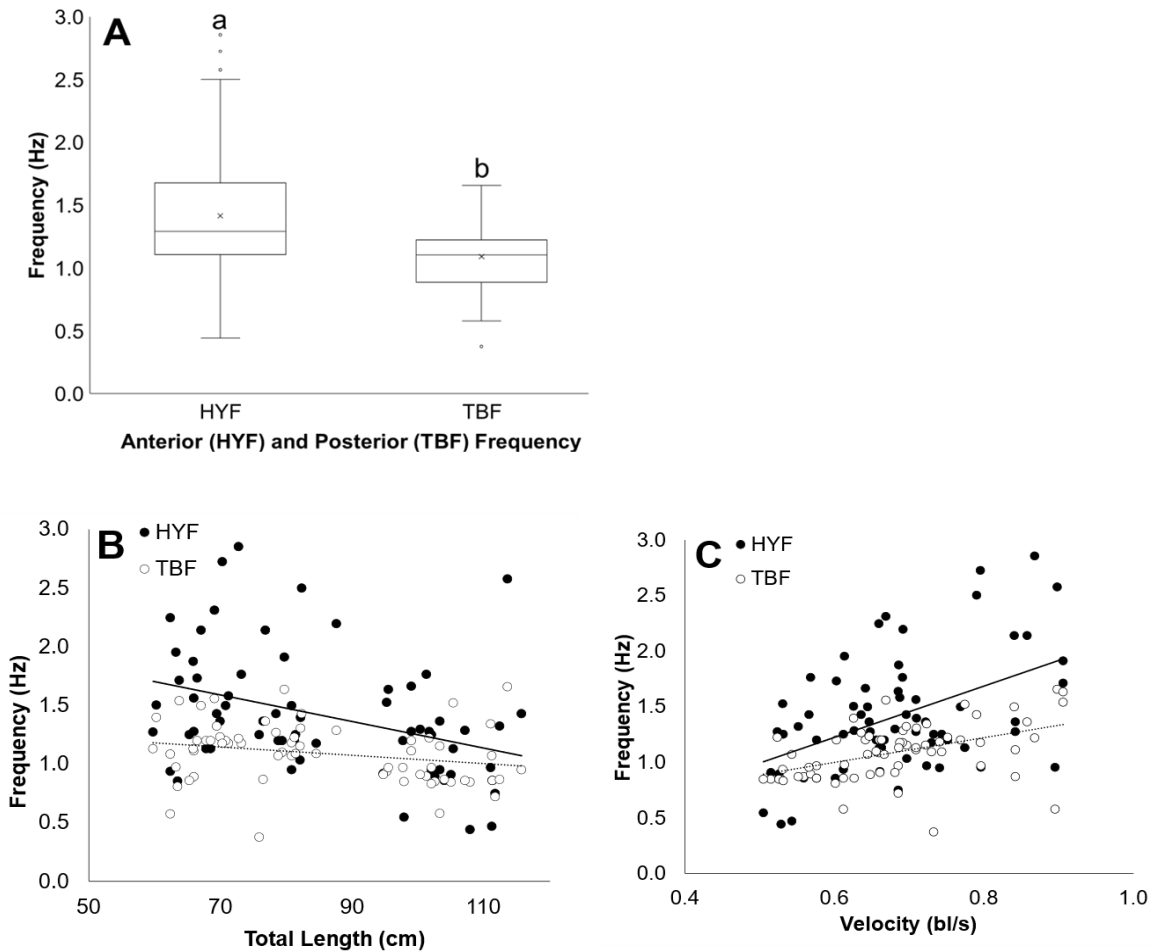


Figure 5.

During straight swimming, I found a significant relationship between frequency, velocity, total length, and body region. (A) The average frequency produced in the anterior region as head yaw frequency (HYF; 1.41 Hz) was greater than frequencies produced in the posterior region as tail beat frequency (TBF; 1.09 Hz). The box and whisker plot shows the mean value as an “x” and the median as a line through the box. The lower edge of the box depicts the median of the first quartile, and the upper edge shows the median of the third quartile. The whiskers extend to the minimum and maximum values, with any outliers shown beyond them as an open point. (B) I found a negative relationship between total length and frequency. (C) I found a positive relationship between velocity and frequency, with HYF also showing a greater rate of change as size increases.

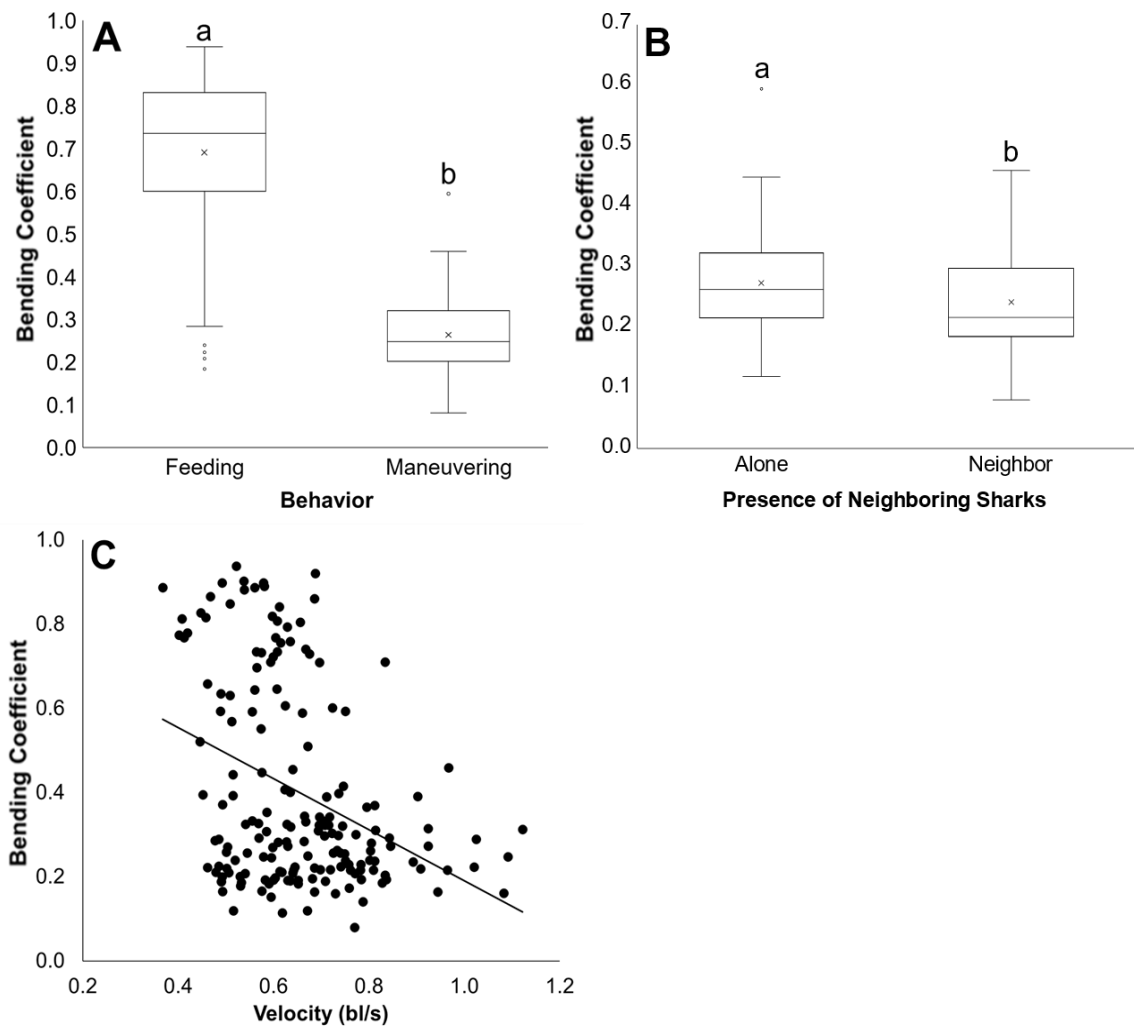


Figure 6.

During turning maneuvers, I found a significant relationship between bending coefficient, behavior, total length, velocity, and presence of closely neighboring sharks in the tank ($p < 0.0001$). (A) I found that the average bending coefficient during feeding behaviors (0.69) was about 3X greater than during maneuvering behaviors (0.26). (B) The bending coefficients were lower on average when immediate neighboring sharks were present (0.30) compared to when there were no neighbors observed (0.44). The box and whisker plots show the mean value as an “x” and the median as a line through the box. The lower edge of the box depicts the median of the first quartile, and the upper edge shows the median of the third quartile. The whiskers extend to the minimum and maximum values, with any outliers shown beyond them as an open point. (C) I found a negative impact of increased velocity on the bending coefficient

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