



Communication Diel Vertical Habitat Use Observations of a Scalloped Hammerhead and a Bigeye Thresher in the Northern Gulf of Mexico

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Abstract: Understanding habitat use of elasmobranchs in pelagic environments is complicated due to the mobility of these large animals and their ability to move great distances in a three-dimensional environment. The Gulf of Mexico is a region where many highly migratory pelagic shark species occur, while in close proximity to coastal, anthropogenic activity including recreational and commercial fisheries. This study provides summary information on the vertical habitat use for a single male scalloped hammerhead and a single male bigeye thresher that were each caught and tagged with an archiving satellite tag. The scalloped hammerhead occupied shallow depths (<100 m) over the continental shelf during the 90 d deployment. The bigeye thresher exhibited strong patterns of diel vertical migrations by occupying depths below the thermocline (>350 m) during the day, then occupying shallower depths (50–100 m) during the night. By providing summary information, this note urges future research to provide scientific information on pelagic, highly migratory species for management efforts in the Gulf of Mexico region.

Keywords: diving behavior; time at depth; time at temperature; elasmobranch; fishery interactions

1. Introduction

Proper management of vulnerable marine predators requires a fundamental understanding of their movements, behaviors, and habitat use. Particularly in pelagic environments, elasmobranchs are often caught as bycatch in longline fisheries resulting in declining populations of species of critical conservation concern due to their life history characteristics (e.g., slow maturation, low reproductive rates) [1–5]. However, understanding habitat use of elasmobranchs in pelagic environments, especially for management purposes, is complicated due to the mobility of these large animals and their increased distribution as they often cross multiple jurisdictional boundaries [6–8]. Furthermore, large elasmobranchs in pelagic environments often display oscillatory diving behavior adding a vertical dimension to consider when quantifying habitat use [9,10].



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The Gulf of Mexico (GOM) is a region where many highly migratory pelagic shark species overlap, while in close proximity to coastal influences, such as the potential for interacting with anthropogenic activities including recreational and commercial fishing [11,12]. The scalloped hammerhead (Sphyrna lewini) and the bigeye thresher (Alopias superciliosus) are large, circumglobal species that occupy temperate, sub-tropical, and tropical areas in coastal and offshore waters such as the GOM [13,14]. Both species are of critical conservation concern, with scalloped hammerheads listed as Critically Endangered and bigeye threshers listed as Vulnerable by the International Union for Conservation of Nature (IUCN) Red List Assessment [11,15–18]. In addition to being taken as bycatch, scalloped hammerheads are targeted for the international fin trade and have some of the highest recorded at-vessel mortality rates in bottom longline fisheries due to their smaller gape sizes compared to other ram ventilating sharks [19-21]. As of 2007, thresher sharks (Family Alopiidae) including bigeye threshers in the GOM had seen a 63% decline in abundance [22]. For both scalloped hammerhead and bigeye thresher sharks, conservation actions (e.g., CITES; US Endangered Species Act) are in place, yet their populations are still exhibiting decreasing population trends, and with the difficulty of gathering information on these large, pelagic species, it is difficult to estimate the likelihood of a reduced assessment status in the future [23]. While information is available on the spatial ecology of these two species, most of the work has been done in the Pacific and Atlantic Oceans, leaving gaps in our understanding for these species in the GOM.

Scalloped hammerheads are characterized by having a late age of maturity and relatively slow growth [2,24]. Similar to other Sphyrnids, scalloped hammerheads forage along the benthos using their cephalophoil to search for teleost fishes, stingrays, and invertebrates [25–27]. Previous work on the scalloped hammerhead has shown this species to have highly directional swimming and navigation abilities [28–31], and diel oscillatory diving behavior, with the ability to do so in relatively cold and hypoxic environments [32–34]. In the GOM, Hoffmayer et al. (2013) [33] provided the first account of the vertical diving behavior of a single scalloped hammerhead, and Wells et al. (2018) [8] quantified their reduced continental shelf movements through satellite tracking. With the scalloped hammerhead's preference to find structure in pelagic environments (e.g., seamounts, petroleum platforms; [25,29]) and the large amount of anthropogenically placed structures in the GOM, the scalloped hammerhead has an especially high potential for anthropogenic interaction in this region [35].

Bigeye threshers are characterized by having an extremely low fecundity, slow growth, and are considered opportunistic feeders preying on a broad range of taxa including cephalopods (e.g., giant squid) and teleost fishes (e.g., Family Paralepididae) [36–39]. Like other thresher sharks, bigeye threshers are thought to use their long caudal fins to stun their prey, and the large eyes of the bigeye thresher extending onto the dorsal surface of the head suggest binocular vision, enabling foraging from below [14,36,40]. Previous work on the bigeye thresher has demonstrated that this species exhibits strong diel vertical migration behaviors by residing in deeper, colder waters during the day (i.e., below the thermocline), then moving into comparatively shallower, warmer waters during the night for reasons likely related to foraging behavior [16,36,37,40–42]. Much of the previous work on the vertical habitat use of bigeye thresher has been done with relatively small sample sizes (n < 5) with the exception of Coelho et al. (2015) [37] with a sample size of 15 bigeye threshers in the Atlantic, demonstrating the difficulty of studying this species, and the challenges of using the right tool to quantify habitat use and behavior at such depths.

While vertical habitat use patterns are emerging for these two species, collecting as much region-specific scientific data as possible is needed to provide managers updated information to predict future movements and prevent unintended capture through directed fisheries. We had the unique opportunity to provide summary information on the vertical habitat use of these two highly migratory pelagic sharks from the northern GOM. While the data presented here represent just two, mature, male individuals, these trends add to the existing vertical habitat information for these two species and highlight the need for future studies in the GOM region. Here, we present a snapshot of summary statistics of two sharks with overlapping geographical distributions in a region that heavily interacts with anthropogenic activity.

2. Materials and Methods

2.1. Scalloped Hammerhead Shark

On 5 November 2015, a mature male scalloped hammerhead was caught using hook and line gear offshore of Corpus Christi, Texas (96.375° W, 27.845° N; Figure 1A). The scalloped hammerhead was brought alongside the boat for measurements (243 cm fork length; 82 kg weight estimated) and to be fitted with a MiniPAT tag (Wildlife Computers, Inc., Redmond, WA, USA). The MiniPAT is a pop-up satellite archival transmitting tag (PSAT) that was programmed to archive water temperature (resolution = $0.05 \,^{\circ}$ C; accuracy 0.1 °C; range = -40 to 60 °C), pressure (depth; resolution = 0.5 m; accuracy: $\pm 1\%$ of reading; range = 0-1700 m), and light-level data every 5 min for up to 90 d. The MiniPat measured 12.4 cm in length, 3.8 cm in diameter, and weighed 60 g in air. The MiniPat was inserted into the dorsal musculature of the scalloped hammerhead with a titanium anchor and preprogrammed to archive data for 90 d, when it would then detach from the shark, float to the surface, and transmit data to the Argos satellite system. Data messages were then viewed, processed, and downloaded through the Wildlife Computers Data Portal and horizontal position (geo-location) estimates were processed using the manufacturer's software, Geolocation Processing Estimator 3 (GPE3; Wildlife Computers Inc., Redmond, WA, USA). Through a gridded ($0.25^{\circ} \times 0.25^{\circ}$) state-space model, GPE3 provides two maximum likelihood position estimates per day, interpolated and smoothed with a cubic spline.



Figure 1. (**A**) Satellite tagging (triangles) and pop-off (circles) locations of the MiniPat (scalloped hammerhead shark; red symbols) and the high-rate PSAT X-tag (bigeye thresher shark; yellow symbols) in the northern Gulf of Mexico. (**B**) Horizontal position estimates (red points) for the scalloped hammerhead shark from the GPE3 software (Wildlife Computers Inc., Redmond, WA, USA), paired with maximum depth information when possible (blue color scale). Tagging (red triangle) and pop-off location (large red circle) are shown for reference.

2.2. Bigeye Thresher Shark

On 28 October 2019, a mature male bigeye thresher was caught using hook and line gear offshore of Venice, Louisiana (88.873° W, 28.882° N; Figure 1A). The bigeye thresher was brought alongside the boat for tagging, but measurements were not taken. The bigeye thresher was fitted with a high-rate PSAT X-tag (Microwave Telemetry Inc., Columbia, MD, USA) to measure vertical habitat use and assess post-release survival. The high-rate PSAT

X-tag measured 12.2 cm in length and 3.3 cm in diameter, weighed 46 g in air, and was inserted into the dorsal musculature of the bigeye thresher with a titanium anchor. The high-rate PSAT X-tag was programmed to archive water temperature (resolution = 0.16-0.23 °C; range = -4 to 40 °C) and pressure (depth; resolution (archived) = 0.34 m; range = 0 to 1250 m) every 2 min for up to 30 d. Due to battery limitations associated with increased resolution of temperature and depth data, the high-rate PSAT X-tag does not have the ability to collect light-based geolocation data, so horizontal movements were not estimated. The tag was preprogrammed to detach after 30 d, float to the surface, and transmit archived data to the Argos satellite system.

2.3. Data Analysis

All data analyses were done in R (R Core Team 2022 [43]; version 4.2.0). Time data were converted from Greenwich Mean Time (GMT) to Central Standard Time (CST) and separated into daytime and nighttime using the local sunrise and sunset data for each day and location using the *suncalc* package in R [44]. Depth-temperature vertical habitat use profiles were created using the MiniPat transmitted data for the scalloped hammerhead (5 min) and the transmitted PSAT data for the bigeye thresher (2 min). Due to abnormal post-release behavior of both sharks (see details below; Hoolihan, et al. [45]), the first 48 h of vertical habitat use data were removed for further analyses similar to Arostegui, et al. [46].

We created histograms of individual depth and temperature readings to examine the vertical habitat and thermal distributions of each shark. Temperature was binned every 5 °C for both sharks, while depth was binned every 10 m for the scalloped hammerhead and every 50 m for the bigeye thresher. The differences in depth bins for the two species were due to the differences in depth ranges experienced by each of the sharks. For each shark, we compared daytime and nighttime depth and temperature distributions using a two-sample Kolmogorov–Smirnov (K-S) test.

3. Results and Discussion

3.1. Scalloped Hammerhead Shark

3.1.1. PSAT Tag Summary

For the scalloped hammerhead, the MiniPAT was attached for the full preprogrammed 90 d, until it detached and transmitted information via Argos satellite on 4 February 2016. The scalloped hammerhead made the deepest dive (110 m) during the second day of deployment, likely representing abnormal post-tagging behavior (Figure 2A) [45]. Due to this abnormal behavior, the first 48 h of data were removed for following analyses, with analyzed data beginning on 7 November 2015 (88 d total). During the rest of the deployment, the scalloped hammerhead was found at depths averaging 23.8 \pm 16.6 m (mean \pm SD). During the day, the scalloped hammerhead occupied depths ranging from 0 to 91 m, averaging 27.2 \pm 18.7 m, with the most time spent in depths of 20 to 30 m (~24% of the day; Figure 3A). During the night, the scalloped hammerhead occupied depths of a similar range from 0 to 96 m but spent significantly more of the night in shallower depths averaging 21.7 \pm 14.9 m, with ~30% of the night spent in depths of 10 to 20 m (K-S test; D = 0.143, *p* < 0.001; Figure 3A).

The average water temperature experienced during deployment for the scalloped hammerhead was 22.1 \pm 2.0 °C. During the day, the scalloped hammerhead was found in temperatures ranging from 15.6 to 27.7 °C, averaging 22.0 \pm 2.1 °C, with the most time spent in temperatures of 20 to 22 °C (~39% of the day; Figure 3C). During the night, the scalloped hammerhead was found in significantly warmer temperatures ranging from 14.7 to 28.0 °C, averaging 22.2 \pm 2.0 °C, with the most time spent in temperatures of 22 to 24 °C (~38% of the night) (K-S test; D = 0.064, *p* < 0.001; Figure 3C).

Horizontal position estimates from the GPE3 software are presented in Figure 1B. The scalloped hammerhead remained in relatively shallow waters (<200 m) on the continental shelf. When applicable, the maximum depth was paired with position estimates to provide some spatial context to the vertical habitat use over the continental shelf (Figure 1B).



Figure 2. Vertical habitat use profiles for (**A**) a scalloped hammerhead shark and (**B**) a bigeye thresher shark, satellite tagged in the northern Gulf of Mexico. Scalloped hammerhead shark depth and temperature data were archived every 5 min and transmitted from a MiniPat (Wildlife Computers, Inc.) after a 90 d deployment. Bigeye thresher shark depth and temperature data were archived every 2 min and transmitted from a high-rate PSAT X-tag (Microwave Telemetry, Inc.) after a 15 d deployment. Gray areas at the beginning of each figure denote the first 48 h of post-tagging abnormal behavior removed from analysis. Gray area at the end of the track of the bigeye thresher shark denotes when the X-tag prematurely popped off on 11 November 2019 and was removed from analysis.



Figure 3. Time-at-depth for the (A) scalloped hammerhead shark, categorized into 10 m intervals, and the (B) bigeye thresher shark, categorized into 50 m intervals. Time-at-temperature for the (C) scalloped hammerhead shark and (D) bigeye thresher shark, categorized into 5 $^{\circ}$ C intervals.

3.1.2. Scalloped Hammerhead Shark Discussion

Overall, the scalloped hammerhead spent most of its time in relatively shallow waters (<100 m) over the 90 d period. Similar behavior was observed for this species satellite tagged in the tropical eastern Pacific, where scalloped hammerheads spent most of the time near surface waters, specifically above 100 m [31]. However, it is important to note that Bessudo et al. (2011) [31] and Hoffmayer et al. (2013) [33] found scalloped hammerheads are able to make extensive dives reaching depths of approximately 1000 m, where temperatures can reach 4 °C. Most recently, Anderson et al. (2022) [47] noted a new diving record for the species in coastal-pelagic waters of Hawai'i where a scalloped hammerhead reached a depth of 1240 m. Previous research has described ways in which scalloped hammerheads increase physiological efficiency by demonstrating a "breath holding" technique that allows them to compensate and maintain a warm body while they actively pursue prey in deeper, colder depths, and by swimming on their sides to possibly help reduce the cost of transport [48,49]. However, the scalloped hammerhead described here did not seem to reach depths or temperatures that required either of these strategies. Based on the geo-location estimates, the scalloped hammerhead remained in shallow waters along the continental shelf. While deeper habitats were available nearby, the location estimates do not provide any locations within deeper habitats for the duration of this deployment. An increased sample size in the GOM region may increase our understanding of GOM-specific behavioral and physiological strategies of depth use for this species. Additionally, an increased sample size in the GOM region could aid scalloped hammerhead conservation by better understanding the diel timing of their vertical habitat use patterns to support future fishing regulations and management.

3.2. Bigeye Thresher Shark

3.2.1. High-Rate PSAT X-Tag Summary

For the bigeye thresher, the high-rate PSAT X-tag detached prematurely on 11 November 2019, which triggered the constant pressure setting to transmit the data after 15 d of deployment. Because of limitations in battery life and satellite coverage, typically only a subset of the archived data is successfully transmitted. Approximately 51% of the data recorded by the tag were transmitted via satellite for this deployment.

The bigeye thresher made the deepest dive to 775 m within the first day of deployment, again likely representing abnormal post-tagging behavior (Figure 2B) [45]. This deepest dive aligns with previous work done by Nakano et al. (2003) [50] (723 m) and Coelho et al. (2015) [37] (955 m). Similar to the scalloped hammerhead, we removed the first 48 h of transmitted data for the remaining analyses, with analyzed data beginning on 30 October 2019 for a total of 13 d. During the rest of deployment, the bigeye thresher was found at depths averaging 182.3 ± 120.1 m.

In general, the bigeye thresher exhibited strong patterns of diel vertical migration by occupying shallower, warmer waters during the night, compared to much deeper, cooler waters during the day (Figure 2B). During the night, the bigeye thresher occupied depths ranging from 25.5 to 420.9 m, averaging 101.7 \pm 72.6 m, with the most time spent in depths of 50 to 100 m (~64% of the night; Figure 3B). During the day, the bigeye thresher occupied significantly deeper waters ranging from 47.1 to 441.1 m, averaging 279.5 \pm 90.3 m, with the most time spent at depths of 300 to 350 m (32% of the day; K-S test; D = 0.738, *p* < 0.001; Figure 3B). The average water temperature experienced during deployment was 18.6 \pm 6.0 °C. During the night, the bigeye thresher was found in waters ranging from 9.9 to 28.2 °C, averaging 22.5 \pm 4.5 °C, with the most time spent in temperatures of 24 to 26 °C (31% of the night; Figure 3D). During the day, the bigeye thresher occupied significantly cooler temperatures of 10 to 12 °C (39% of the day; K-S test; D = 0.727, *p* < 0.001; Figure 3D).

3.2.2. Bigeye Thresher Shark Discussion

The bigeye thresher presented here aligns with the vertical habitat use expected for this species by exhibiting strong diel vertical migration patterns. These findings are similar to those for a bigeye thresher tagged previously in the Gulf of Mexico and one tagged in Hawai'i [40], and to those tagged in the northeast Atlantic [37], where bigeye threshers exhibit clear diel diving patterns with deeper dives during the day. Bigeye threshers have a rete mirabile that allows them to conserve warmth around their brain and eye region, providing physiological benefits during time spent at deeper, colder depths likely for reasons due to feeding [36,37,41,51]. The bigeye thresher shark described here may have been exhibiting diel vertical migrations for feeding purposes, similar to previous studies; however, a larger sample size would be beneficial in describing GOM region-specific behavioral and physiological strategies for this species. Additionally, Coelho et al. (2015) [37] reported ontogenetic shifts in vertical habitat use and found juvenile bigeye threshers potentially have a higher overlap with the shallow pelagic longline fishery in the Atlantic, highlighting the importance of gathering as much data as possible for a vulnerable species, specifically across maturity stages.

3.3. Potential for Fishery Interactions

Although our sample size does not permit any statistical comparisons between the two species, it is important to discuss these species together for purposes of regional management of pelagic, highly migratory species in the northern GOM. With the bigeye thresher (from our own study and others) consistently occupying comparatively shallower waters at night, and the scalloped hammerhead in similar depth ranges, both of these species are at risk of overlapping with nighttime operating tuna and swordfish commercial fisheries in the GOM [35,52,53]. In addition, there is a growing recreational and commercial industry of daytime deepdrop swordfish fisheries [54] that can heavily interact with bigeye threshers as they remain in deeper waters during the day. These fisheries routinely alter gear characteristics, location, fishing depth, and time of day of deployment to maximize catch rates of their target species; however, these adjustments can then alter the composition (e.g., species, sex, maturity) and magnitude of bycatch [52,53]. Therefore, variable diel partitioning of the pelagic environment by these species of conservation concern (and others in the region) should be evaluated further for best management practices.

4. Conclusions

This note provides summary information on the vertical habitat use of a scalloped hammerhead and a bigeye thresher in the northern GOM. While it is difficult to make direct comparisons between the two sharks used in this study, this note presents this information together as a call to future work to advance scientific investigations of pelagic, highly migratory species for management efforts in the GOM region. While it is clear how challenging studying large pelagic sharks can be, we urge researchers to continue to increase sample sizes and pair high-resolution vertical and horizontal movement information to provide the most robust data to managers. The observations presented in this note provide information on vulnerable species in a region where information has been relatively limited compared to the Pacific and Atlantic.

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