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Shallow water tidal flat use and associated specialized foraging behavior of the great hammerhead shark (*Sphyrna mokarran*)

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ABSTRACT

Evidence suggests the great hammerhead shark, *Sphyrna mokarran*, is vulnerable to a variety of anthropogenic stressors, and is an understudied species of shark due to its cryptic nature and wide-ranging movements. While recognized as both a pelagic-coastal and a highly mobile predator, minimal anecdotal evidence exist describing shallow water habitat use by this species. This report describes six cases in which a great hammerhead shark utilizes an inshore shallow water flats environment (<1.5 m in depth), five of which involve prey capture. These observations permitted identification of two novel behaviors that may allow great hammerheads to inhabit these shallow habitats: a (1) prey-capture technique termed 'grasp-turning' that involves burst swimming at tight turning angles while grasping prey and (2) a post-predation recovery period whereby the shark maintains head-first orientation into the current that may facilitate respiration and prey consumption. These behavioral observations provide insights into the natural history of this species.

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Shark; hammerhead; habitat use; behavior; predation; specializations

Understanding the habitat use and movements of large and highly mobile marine predators is inherently challenging due to their wide-ranging behaviors, the concealing nature of the environment and their increasing rarity due to human exploitation (Nelson 1977). However, these types of data can provide information for initiating effective conservation and management of threatened species (Green et al. 2009; Sims 2010, Dulvy et al. 2014).

Biotelemetry approaches are commonly employed to investigate movements and behaviors of many different shark species, with most studies designed to determine high-use areas and environmental preferences (Donaldson et al. 2008; Sims 2010; Hammerschlag et al. 2011a; Papastamatiou & Lowe 2012). While these studies can reveal new information on the habitat utilization and movements of large shark species (e.g. Bonfil et al. 2005; Skomal et al. 2009), their success is predicated on several key conditions: locating individuals,

generating a suitable sample size, tag retention and functionality, community or stakeholder acceptance, as well as ethical issues surrounding tagging impacts on animal health and survival (Hammerschlag et al. 2014). While increased use and rapid advances in aquatic biotelemetry are expanding our ability to document the behaviors of large sharks (Hussey et al. 2015), other more traditional natural history approaches to studying shark behavior (e.g. observation) can be overlooked and underutilized, possibly leading to incomplete understanding of animal biology. Natural history approaches have long been viewed as valuable for advancing the knowledge base of elasmobranch ecology and continue to provide important insights on species which are otherwise cryptic or rarely observed (e.g. Strong et al. 1990; Klimley et al. 1992; Martin et al. 2005; Fallows et al. 2013). In particular, natural history data gathered from local stakeholders or traditional ecological knowledge may provide insights that could otherwise go undetected, since these individuals spend the most time on the water and thus most likely to observe and interpret rare animal behaviors (Huntington 2000; Drew 2005; Silvano and Valbo-Jørgensen 2008).

Large hammerhead sharks (family Sphyrnidae) are among the most specialized of extant shark species, behaviorally (Gallagher et al. 2014a, 2014b), physiologically (Kajiura & Holland 2002; Mello 2009; Tricas et al. 2009; Gallagher et al. 2014a), and morphologically (Nakaya 1995; Kajiura 2001; Kajiura et al. 2003; McComb et al. 2009). Although there was a petition to list the great hammerhead on the US Endangered Species List, listing was not found to be warranted (Miller et al. 2014). On the other hand, their vulnerability to anthropogenic stressors such as fisheries bycatch (Dudley & Simpfendorfer 2006; Zeeberg et al. 2006) and reported wide-spread population declines, led to an official global listing of 'Endangered' by the IUCN Red List (Denham et al. 2007). Despite their widespread distribution, relatively little is known about their migratory patterns or habitat use across their life history. Presently, the vast majority of what is known about hammerhead shark biology and ecology is based on studies on the scalloped hammerhead shark (*Sphyrna lewini*). This is probably due to its gregarious behavior at a limited number of predictable locations worldwide (Klimley & Nelson 1981; Klimley et al. 1988; Hearn et al. 2010; Hoyos-Padilla et al. 2014; Ketchum et al. 2014). Less is known about the great hammerhead (*Sphyrna mokarran*), the largest of the hammerhead species which reaches a maximum length of over six meters.

The great hammerhead is considered a nomadic and migratory coastal-pelagic/semi-oceanic species (Compagno 1984; Queiroz et al. 2016). There is consequently a paucity of information on its habitat utilization and behavior. To our knowledge, there have only been three published telemetry-tracking studies focusing on the movement of this species (Hammerschlag et al. 2011b; Graham et al. 2016; Queiroz et al. 2016). Hammerschlag et al. (2011b) documented a range extension for this species in the Atlantic Ocean based on a female shark that migrated from the Florida Keys to north of the mid-Atlantic. In addition to providing data corroborating this range extension, satellite tracking of 18 great hammerheads tagged in Florida by Graham et al. (2016) revealed all of their Core Habitat Use Area (CHUA) fell within the combined waters of the Florida and US Exclusive Economic Zones (EEZ). However, Queiroz et al. (2016) found that this species makes repeated movements into the Atlantic Ocean associated with use of frontal zones where they are targeted by commercial longline fisheries. Much remains to be learned on the habitat use of this species, especially in shallow inshore environments.

While this species is primarily found over continental shelves, island terraces, and deep coral reefs (10–30 m, Compagno 1984; Compagno et al. 2005), it is known to occupy in-shore habitats

to feed on elasmobranchs such as stingrays. Strong et al. (1990) documented a natural predation by *S. mokarran* on a southern stingray (*Dasyatis americana*) in 6 m depth of water, located 12 km east of North Bimini Island, Bahamas. Similarly, Chapman and Gruber (2002) documented predation by a great hammerhead on a spotted eagle ray (*Aetobatus narinari*). This event took place within a pass between two of the northernmost islets of small cays approximately 5 km south of South Bimini Island, Bahamas. Although the pass was fringed with fire coral, creating depths of less than 1 m, the predation event was confined to the pass, which dropped steeply to a uniform depth of 3 m. Our own observations, combined with anecdotal evidence suggest that great hammerheads may enter even shallower inshore habitats (<1.5 m depth) such as tidal flats to feed, but no published data exist to substantiate these behaviors. It has been documented that it may be beneficial for elasmobranchs to forage in warm waters but return to cooler waters to rest (Bernal et al. 2012). However, to our knowledge, there are no published reports of great hammerhead predatory behavior within shallow tidal flat ecosystems. Further investigations into shallow water use by otherwise offshore species and potential mechanisms driving such behavior could augment our understanding of how species tolerate environments with potentially lower dissolved oxygen, higher temperatures, as well as persistent fishing pressure that could render sharks vulnerable to stranding, exhaustion, and capture.

In the present study, we used a combination of direct observation, discussions with fishers/stakeholders, and analysis of digital media generated by local fishers/stakeholders to describe new aspects of the natural history of the great hammerhead with a focus on foraging within inshore shallow water flat environments (i.e. seagrass flats and back reef flats, <1.5 m depth). The information adds to our knowledge of the behavioral ecology of this species and potentially provides avenues leading to future research.

Methods and results

Below, we describe six instances of inshore shallow water flat (<1.5 m) habitat use by *S. mokarran*, composed of our own personal observations, first-hand reports gathered from various stakeholders, and analysis of video obtained from local fishing guides and their clients. We used various forms of communicative instruments including social media outlets, and in-person open-ended interviews with various stakeholder groups that spend large amounts of time within tropical and sub-tropical inshore flat ecosystems. Once a case was found to be potentially pertinent to this study, we contacted the individuals who witnessed the events, subsequently conducting more interviews to obtain supplementary data on environmental parameters and details of the respective flats habitat. The data presented below was based on opportunistic observations derived from different sources. The level of detail and available information therefore varies by case. Additionally, more information was attainable *post hoc* from our analyses of video compared with still photographic images.

Case 1

On 6 May 2012 at 14:30, study author Robert Roemer (RR) observed from a ~150 m distance while wading and fishing for bonefish (*Albula vulpes*), a great hammerhead shark inside a shallow water flat on the east side of Rock Sound, Eleuthera Island, Bahamas (near Poison Point, 24°49'0.01"N -76°11'59.99"W). The single individual was identified by its distinctive sickle-shaped large dorsal fin protruding entirely out of the water column. It

had an estimated total length (TL) of 2.5 m. The water depth the shark was occupying was ~0.7 m. This location contained shallow areas such that bonefish were observed with their caudal fins and dorsal fins partially-to-fully exposed while likely feeding on benthic prey items ('tailing', Crabtree et al. 1998). RR observed the shark move sinuously forward with wide sweeps of its cephalofoil. This calm, non-erratic behavior was repeated within the flat habitat, for a total distance of roughly 15 m, and a period of 10 min until the shark was presumably alarmed and darted away, not to be seen again (a distance of ~80 m between RR and the shark). At the time of observation, the flat environment was large and relatively uniform with water depth varying from 0.2 to 0.9 m during a low incoming tide. The benthic habitat comprised various hard and soft coral species, including rose coral, *Manicina aerolata* and shallow-water starlet coral, *Siderastrea radians*. The following species of teleosts and elasmobranchs were also identified in the area both before and after the shark was observed: scrawled cowfish (*Acanthostracion quadricornis*), bonefish, yellow fin mojarra (*Gerres cinereus*), neonate and juvenile lemon sharks (*Negaprion brevirostris*), and several species of stingrays (*Dasatidae* spp.).

Case 2

On 10 March 2014 at 10:22, a great hammerhead roughly 2.5 m TL was observed at a distance of less than ~8 m by Matthew Glaze, and was first spotted at an approximate distance of 270 m. Wave action was less than 0.3 m, on a sunny day with prevailing winds less than 5 knots and water clarity of 16 to 18 m. The lone hammerhead was occupying a shallow back-reef in the Republic of Palau, on the south side of German and Lighthouse Channels (7°17'15.7"N 134°27'46.9"E) during a low incoming tide. The approximate depth of the occurrence and back-reef habitat was between 0.8 and 1.3 m with uniform benthic contour for 450 m. The benthic substrate consists of various hard coral rubble created from constant wave action and as a result is quite barren. It has minimal flora or fauna with the exception of a fairly common presence of bubble algae, (*Valonia* spp.) and nominal reef teleosts. The shark was first sighted when a bait ball composed of sardines (genus *Sardinella* or possibly *Sardinops*) was being actively predated on by a giant trevally, *Caranx ignobilis* (Figure 1(A)–(C)). This feeding activity appeared to attract the great hammerhead from a distance of ~20 m. As it moved through the shallow reef flat habitat, it performed erratic movements, and employed rapid surges of speed in its attempts to feed on the sardine bait ball. The right flank of the shark had numerous scarring/wounds. Also present in close proximity to the bait ball were two nurse sharks (*Ginglymostoma cirratum*) and a spotted eagle ray (*Aetobatus narinari*). After a total time of 15 min, the hammerhead moved slowly into a deeper natural channel on the reef flat (Figure 1(D)) and eventually into deeper waters off the reef edge after which it was not observed again. Other teleosts present on the reef flat habitat were houndfish (*Tylosurus crocodilus*), parrotfish (*Scaridae* spp.), wrasse (*Labridae* spp.), butterflyfish (*Chaetodontidae* spp.), and angelfish (*Pomacanthidae* spp.). While the number of anthropogenic disturbances is low on the reef flat habitat, this area is subject to large, direct discharges of raw sewage from Palau's largest city, Koror. Information from this case and associated photo documentation was provided to Matthew Glaze after RR performed a search on social media for professional photographers that have recorded hammerheads in shallow water environments.

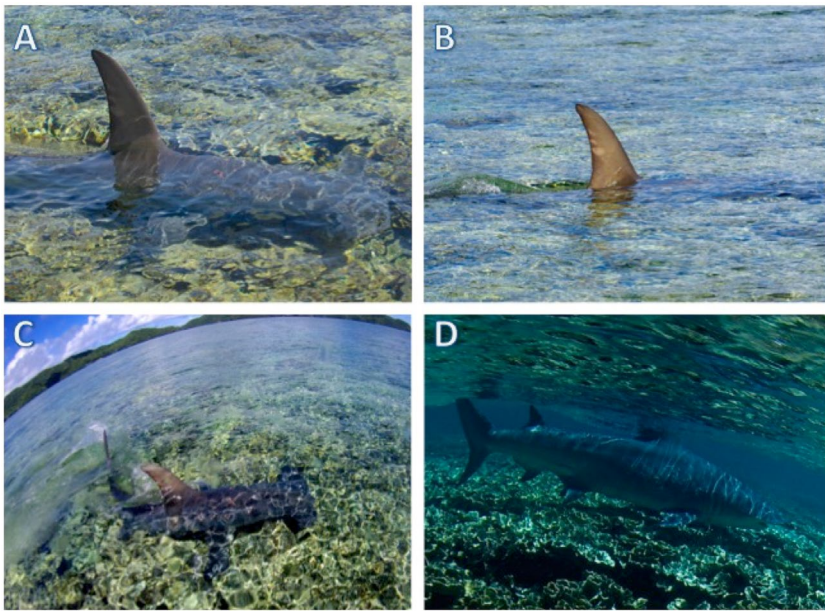


Figure 1. (Colour online) A great hammerhead in the Republic of Palau: (A) lateral view of animal skimming coral substrate; (B) dorsal fin of the same individual protruding almost entirely out of the water, fin may appear dried due to extended heat exposure; (C) top-down view of animal turning on minimal radius; (D) underwater view of animal showing ventral proximity to the back-reef habitat. Published with permission of the copyright holder, Matthew Glaze.

Case 3

On 30 January, 2015 at 16:15 during high-slack tide, Lorna Scribner (assistant lab manager of the Bimini Biological Field Station) and John Rayfield (scientific volunteer) witnessed a great hammerhead in South Bimini Island, Bahamas ($25^{\circ}41'51.4''\text{N } 79^{\circ}17'28.4''\text{W}$) within a shallow water flat environment. The backwater flat was lined with mangroves and relatively sheltered with an estimated average depth of 1.2 m and a substrate consisting mainly of turtle grass (*Thalassia testudinum*). The male shark had a TL of approximately 2.5 m and was first observed from a distance of 10 m. The shark was seen swimming erratically with its dorsal fin protruding from the water column (Figure 2 (A)–(B)). It was probably in pursuit of a spotted eagle ray, which breached out of the water column most likely to escape the shark trailing close behind. The air temperature during observation was 21.6°C and the sky was overcast. This evidence was acquired from John Rayfield after several photographs were posted and identified on his social media site. We subsequently followed up with the observer to gather information relating to this case, including photographic documentation.

Case 4

On February 11th, 2011 at 10:45, a great hammerhead (estimated 2.0 m TL) was documented in South Andros Island, Bahamas, near Leaf Cay ($23^{\circ}44'31.1''\text{N } 77^{\circ}51'10.8''\text{W}$) on the western end of the island. The observation was made by Andy Dober who was on a guided fly-fishing flats expedition for bonefish. This shark was observed in a shallow water

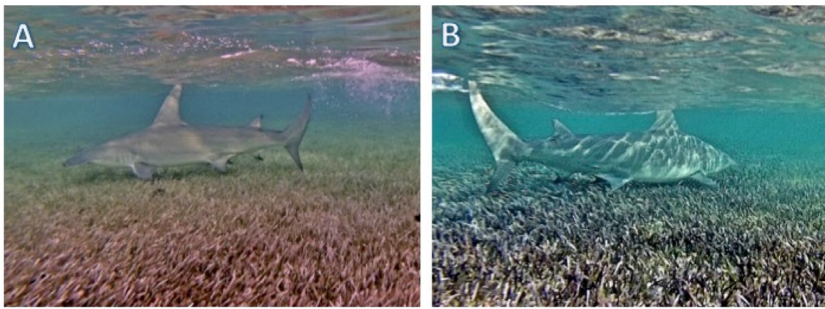


Figure 2. (Colour online) (A and B). A single great hammerhead in South Bimini, Bahamas, exploiting a mangrove lined seagrass flat environment approximately 1.2 m in depth while hunting elasmobranch species. Published with permission of the copyright holder, John Rayfield.

sand flat with an estimated depth of less than 0.9 m. The great hammerhead was initially attracted by disturbances caused by a struggling bonefish which was hooked on fly rod/reel gear (Figure 3(A)). A lemon shark was also actively pursuing the hooked bonefish. After 17-s into the video evidence, the hammerhead had isolated the lemon shark, which was still following the hooked bonefish. While in pursuit of the lemon shark, the hammerhead exhibited rapid bursts of speed while performing several successive tight turns. At the 22-s mark in the video, the great hammerhead executed a fast, straightforward motion in an attempt to close with the lemon shark (Figure 3(B)–(D)). At this point, the hammerhead made contact with the vessel, which appeared to cause it to abort its pursuit of the lemon shark and slowly move off the flat to deeper waters. Andy Dober provided video and environmental information of this event after RR interviewed several flats fishing guides in the Bahamas, then contacted AD.

Case 5

During the week of November, 25th 2014, fly-fishing guide William Benson witnessed and recorded a great hammerhead while guiding a fishing client. The hammerhead was situated on a shallow flat comprised mostly of soft sediments off the island of Key West, Florida, in close proximity to the Northwest Channel (24°35'29.8"N 81°56'17.8"W). The estimated depth of the flat was 0.9 m while the shark had an approximate TL of 2.1 m. The shark was first noticed because of the considerable amount of sediment it had disturbed during its predation on a school of permit, *Trachinotus falcatus*, which were using the shallow flat to feed (Figure 4(A)–(D)). During the observed sequence, the shark exhibited rapid burst swimming while also displaying several successive tight turns fluctuating between one-half and one-third of TL (Figure 5(E)–(H)). This was similar to the behavior observed in the great hammerhead within Case 4. These burst swimming events were first observed 07-s after initial detection of the shark and continued throughout the entire observed episode (24-s). Video evidence and environmental conditions were compiled and found to be pertinent following contact, a meeting, and an interview with William Benson.

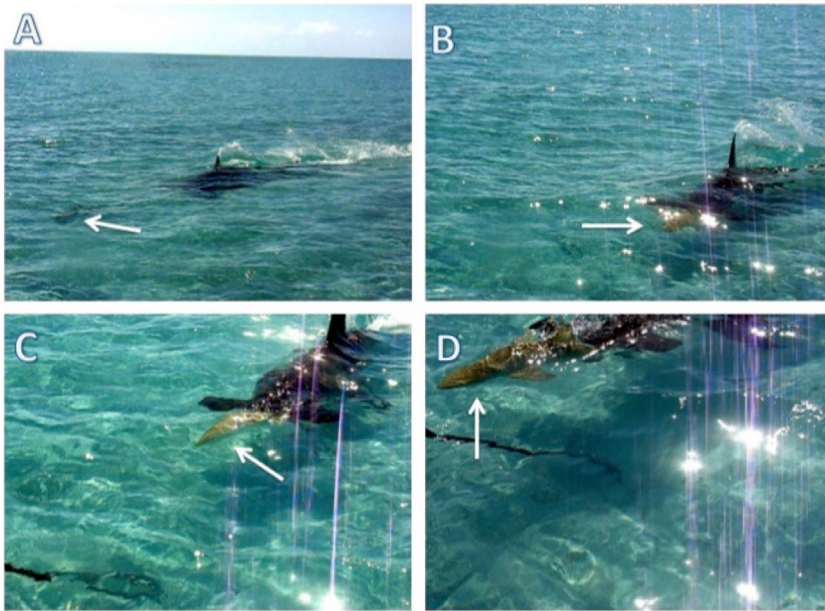


Figure 3. (Colour online) Still frames pulled from video showing a hammerhead in pursuit of a lemon shark, *Negaprion brevirostris*, in South Andros Island, Bahamas. (A) The individual great hammerhead orientates towards the lemon shark. (B-D) The great hammerhead attacks the lemon shark. Arrows illustrate the lemon shark during predation event. Published with permission of the copyright holder, Andy Dober.



Figure 4. (Colour online) Frames taken from video depicting a great hammerhead using a shallow water flat in order to prey upon a school of permit, *Trachinotus falcatus*. (A) Initial observation of hammerhead. (B) Sediment cloud in relation to individual hammerhead. Arrow details fin orientation at time of initial observation in relation to size of sediment cloud. Published with permission of the copyright holder, William Benson.

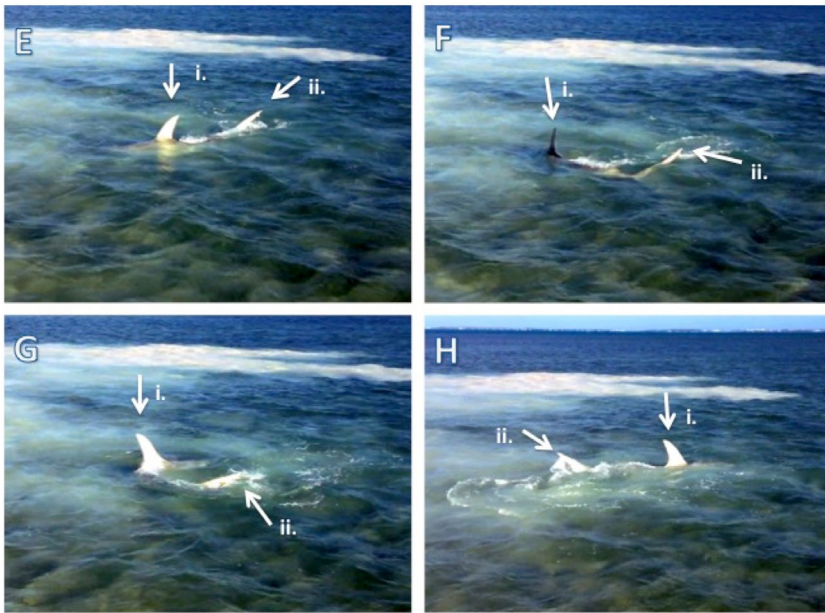


Figure 5. (Colour online) Frames (E–H) detailing example of tight turning radius exhibited by the feeding activity of the great hammerhead. Hammerhead dorsal fin labeled ‘i.’ and caudal fin labeled ‘ii.’ to help deduce orientation. Published with permission of the copyright holder, William Benson.

Case 6

On 22 March 2010 at 12:00, a great hammerhead shark of an estimated 3.65 m TL was observed exercising erratic burst swimming behavior on a shallow flat habitat with a mainly sand substrate (Figure 6(A)) off the northwest corner of the Marquesas Islands

(24°35′28.1″N 82°09′00.1″W). William Benson was guiding a fishing client (Gannon Dudlar) and documented the entire sequence, which was provided to RR. The flat habitat was approximately 1.2 m deep and prevailing wind speeds averaged 15 knots. The tide was outgoing, almost low-slack and the day sunny. The shark was swimming in a straight line at the time the vessel approached. It exhibited a sudden and rapid burst of speed that propelled it nearly 3.35 m (3 min into the video observation). The shark then located and attacked a nurse shark (~0.9 m in total length), situated on the benthic substrate (Figure 6(B)–(D)). During the attack, the shark exhibited 22 circular turns at high speed within a tight radius (Figure 7(A)–(B)). The great hammerhead continued to display tight rotations with limited radii, (estimated to be one-half of TL) with the nurse shark still largely protruding from its jaws (Figure 7(D)). After the nurse shark was firmly oriented within the jaws of the shark, the great hammerhead established itself so that it was facing anteriorly into the current (Figure 8(A)–(B)). The hammerhead remained facing steadily into the current with the caudal fin of the nurse shark still projecting from its jaws. The shark propelled itself minimally so as to remain stationary and did so for a span of 15 min, undisturbed by the close proximity of Benson and the vessel. After this period, the hammerhead moved slowly away from the vessel. William Benson and Gannon Dudlar provided environmental conditions and video evidence to RR and in interviews with WB and correspondence with GD.

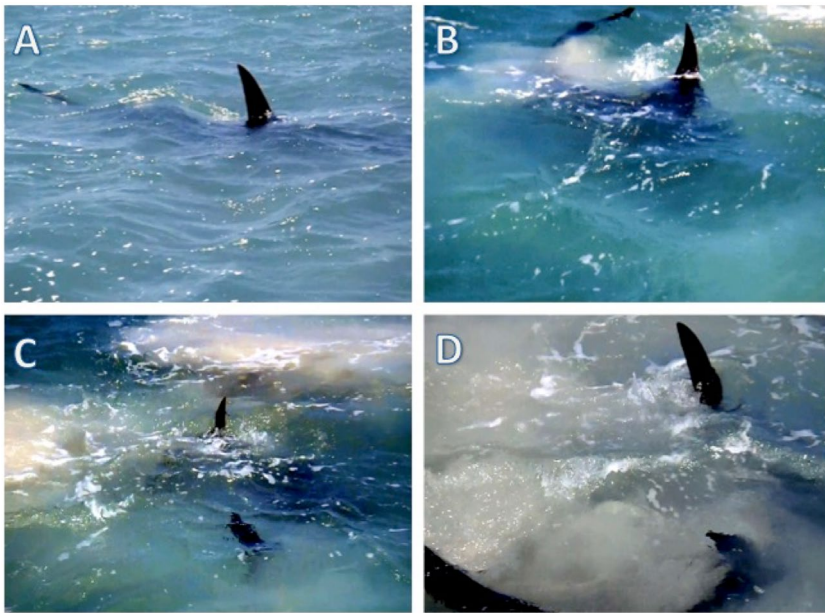


Figure 6. (Colour online) (A) The initial observation of the estimated 3.65 m great hammerhead before a predation event in Marquesas Islands. (B–D) The predation event on prey later identified as a nurse shark, *Ginglymostoma cirratum*. Published with permission of the copyright holder, William Benson.

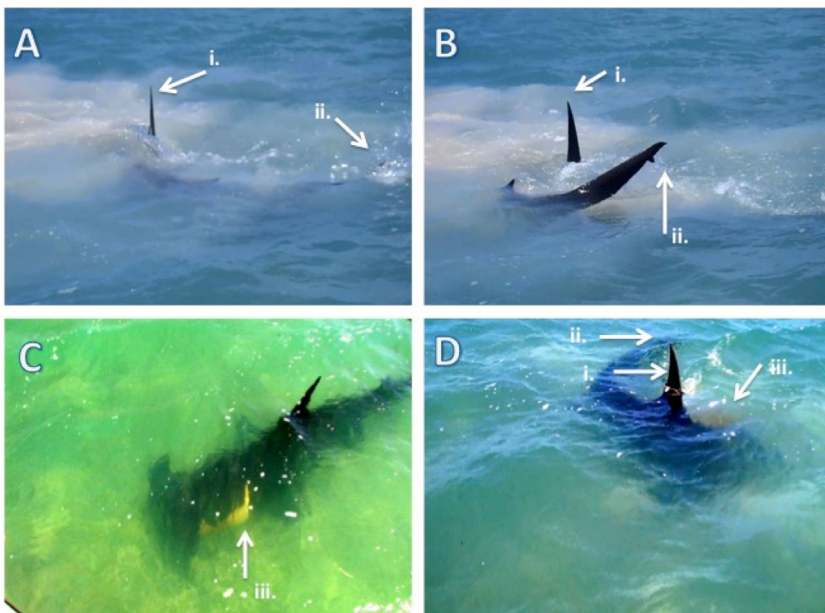


Figure 7. (Colour online) (A and B) Tight turn radius (roughly one-half of total body length) utilized by a hammerhead in order to capture prey. (C) Distinguishable caudal fin of a nurse shark, *Ginglymostoma cirratum* protruding from the jaws of the hammerhead. (D) 'Grasp-Turning' technique of hammerhead with prey still protruding from its jaws. Dorsal fin labeled 'i', caudal fin labeled 'ii', and nurse shark labeled 'iii', respectively. Published with permission of the copyright holders, Gannon Dudlar and William Benson.

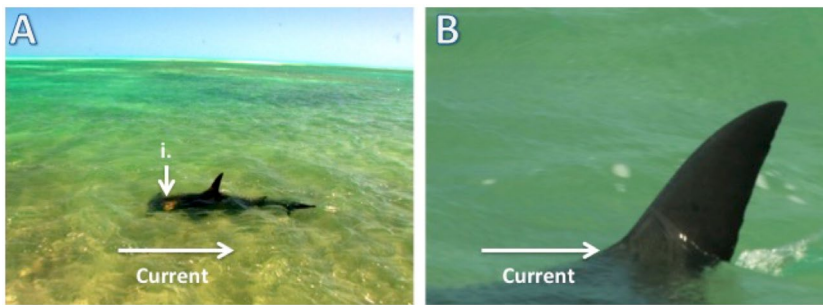


Figure 8. (Colour online) (A and B) Details the great hammerhead positioning itself, anteriorly into the current defining a possible 'recovery period' of the shark post-predation. The nurse shark is labeled 'i.' for easier perspective. Published with permission of the copyright holder, William Benson.

Discussion

Here we have documented and described six instances of inshore, shallow water (<1.5 m depth) habitat use by great hammerhead sharks. These occurred on tidal flats within various tropical and sub-tropical locations across the globe. These six cases appear to be instances of prey searching and hunting. Five of these cases involved erratic behaviors by a single individual in pursuit of elasmobranch or teleost prey. An exception to this was Case 1, where the observed hammerhead was calm, using wide sweeps of its cephalofoil. We suggest that this represents prey searching behavior before the shark had located a prey item. The observations are noteworthy for the environment in which they occurred because this species is characterized as a coastal-pelagic species, primarily occupying offshore areas (Compagno et al. 2005).

Inshore shallow water habitats in tropical and sub-tropical marine ecosystems contain high species richness and abundance and are often regarded as important to the development of numerous small and medium-sized teleost fishes and elasmobranchs (Chong et al. 1990; Blaber et al. 1995; Beck et al. 2001). Tidal flat ecosystems such as tropical and sub-tropical inshore shallow water flats are protected, provide shelter, and, are more difficult for larger predators to access. They have consequently been considered to be successful nursery grounds (Reise 2012). These ecological features can make inshore habitats valuable hunting and foraging grounds for large predatory fishes such as sharks (Hammerschlag et al. 2010). Entrance into these habitats may, however, incur several costs to predators due to tidal fluctuations that can result in temporary periodicity of low dissolved oxygen levels (Sakamaki et al. 2006) and other water-quality stressors within inshore tropical shallow waters (e.g. raw sewage effluent in Case 2). As a result, predators using these habitats may balance trade-offs between potential environmental stressors and resource abundance, thereby requiring specialized foraging or swimming techniques to exploit these environments. Two behaviors were identified during our video analyses that may be specializations permitting great hammerheads to balance these trade-offs and use shallow tidal flats in pursuit of prey. These are: (a) prey-handling behavior (Case 5, 6); and (b) a post-predation energetic recovery behavior (Case 6).

Specialized prey handling behavior of a great hammerhead was first described in detail by Strong et al. (1990). During this observation, a great hammerhead (~3.0 m TL) utilized its

cephalofoil to pin a southern stingray, *Dasyatis americana* to the substrate (termed 'pin and pivot'). A similar behavior was observed by Chapman and Gruber (2002) of a single great hammerhead (~3.6 m) capturing and consuming a spotted eagle ray. While both predation events occurred in deeper water than reported in our study, they support the interpretation that our sequences represent examples of specialized foraging behavior.

We documented five cases where a great hammerhead grasped or attempted to grasp teleost and/or elasmobranch prey in its jaws. In three of the documented cases, the hammerhead made multiple (up to 22) tight turns before the prey was consumed. We term this behavior 'grasp-turning.' This may be a technique that allows hammerheads to use the force exerted by the surrounding water to help keep prey within their mouths and maneuver prey within their jaws to facilitate consumption (i.e. head down swallow). Performance of 'grasp-turning' behavior presumably provides the predatory shark with a tactical advantage over the prey within the vertically restricted space of a tidal flat.

The use of shallow water and performance of grasp-turning behaviors incur metabolic and homeostatic costs for a large-bodied elasmobranch. Previous research has demonstrated a rapid onset of anaerobic acidosis in exercise-stressed (fisheries capture) great hammerhead sharks (Gallagher et al. 2014c). While these behaviors may also be occurring in deeper waters, metabolic costs and challenges to respiration from increased activity are likely higher in shallow inshore waters that are often warmer, more saline, and possess lower dissolved oxygen concentrations (Belding 1929; Kitheka 1997; Meyer-Reil and Köster, 2000; Diaz 2001; Ridd & Stieglitz 2002; Hodoki & Murakami 2006). Our observations suggest, however, a potential mechanism for recovery from exercise stress in a sub-tropical inshore flat environment. The great hammerhead from the Marquesas (Case 6) re-positioned itself into a strong, incoming current while propelling itself at a minimal rate to remain stationary for 15 min. This likely maximizes oxygen uptake in the gills and promotes recovery from energy expenditure and anaerobic acidosis during prey pursuit (Figure 8(A)–(B)). This action may also help to further facilitate consumption: the high velocity water current keeping the nurse shark situated within the jaws of the great hammerhead while consumption continues.

During exercise in teleosts, increased water flow over the gills is proportional to oxygen uptake, even increasing in low-oxygen environments such as those of shallow tropical and sub-tropical inshore waters (Randall 1982). After exercise, gill ventilation and water flow interactions with the gills have effects on the blood respiratory and blood acid–base status (Perry & Wood 1989). Teleosts remaining in low oxygen, elevated temperature environments (like those of inshore tidal flat ecosystems) are hindered from the respiratory gill ventilator method and exhibit impaired recovery of tissue ATP and plasma glucose (Suski et al. 2006; Shultz et al. 2011). They would therefore experience more acute need for recovery from exercise. Benthic tropical elasmobranchs capable of stationary buccal pumping (i.e. epaulette shark, *H. ocellatum*) can tolerate mild hypoxic environments and have a well-developed capacity for anaerobic metabolism (Wise et al. 1998). Bonnethead sharks (*Sphyrna tiburo*) and blacknose sharks (*C. acronotus*) increase mouth gape, swim speed, and oxygen consumption rates during hypoxic conditions (Carlson & Parsons 2001, 2003). The hammerhead behavior described in Case 6 may have served a similar function as those found by Carlson and Parsons (2001, 2003). Although water quality parameters were not collected in Case 6, it is likely great hammerheads occupying warm shallow waters will encounter relatively lower dissolved oxygen by comparison with colder offshore waters. An animal's behavior is directly driven by its physiology (Ricklefs & Wikelski 2002), which is in turn

driven by its environment. Based on the metabolic responses of great hammerheads during exercise as well as water quality characteristics typical of shallow tropical and sub-tropical tidal ecosystems, the observed great hammerhead behavior that we attributed to post-predation recovery is perhaps predictable.

Hammerhead sharks are a functionally, physiologically, and behaviorally specialized group of species (Gallagher et al. 2014b). Here we provide a series of detailed opportunistic observational accounts that provide insights into the habitat use and foraging behavior of this species. We speculate that use of shallow tidal flats by great hammerhead sharks is likely common and an important aspect of their overall feeding ecology. We also describe several behaviors that we suggest are specializations that allow them to compensate for the costs of foraging in shallow environments. This study also highlights the value of utilizing natural history, social media, observational science, and local knowledge as a means for advancing our understanding of a species that is difficult to study.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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