Received: 29 January 2020 | Accepted: 6 April 2020
DOI: 10.1111/jfb.14342

BRIEF COMMUNICATION

JOURNAL OF FISH BIOLOGY fsbi

Adult blacktip sharks (*Carcharhinus limbatus*) use shallow water as a refuge from great hammerheads (*Sphyrna mokarran*)

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Funding information
This work was funded by a grant from the Colgan Foundation to S.M.K.

Abstract

A refuge can be any space that keeps an organism safe from danger. Prey usually seek protection in the closest refuge available to minimize cost while maximizing survival. Aerial drone footage of blacktip sharks, *Carcharhinus limbatus*, along the coast of southeast Florida, USA, shows adult blacktips fleeing to the shallow water adjacent to the beach when confronted with or chased by a predatory great hammerhead shark, *Sphyrna mokarran*. To authors' knowledge, this is the first evidence of adult *C. limbatus* using shallow waters as a refuge.

KEYWORDS
Carcharhinidae, elasmobranch, predation, refuge, shallow water, Sphyrnidae

Numerous examples of aquatic animals seeking refuge in shallow waters to avoid predators exist (Ydenberg & Dill, 1986). Shallower waters are common refuges for smaller organisms because predator abundance typically increases with depth (Manderson *et al*., 2004). In an experimental study using Chesapeake Bay blue crabs, *Callinectes sapidus* (Rathburn, 1896), juvenile blue crabs moved to shallower waters in the presence of a larger predatory blue crab but did not use this refuge when in isolation or when in the presence of another small crab (Dittel *et al*., 1995). Juveniles of several shark species use shallow water nursery sites where the young can grow with a reduced risk of predation (Branstetter, 1990; Castro, 1993; Duncan & Holland, 2006; Heupel *et al*., 2007; Knip *et al*., 2010; Morrissey & Gruber, 1993). In fact, Heupel and Hueter (2002) suggested that predator avoidance may be a more important aspect to nurseries than prey abundance, based on their study done in Terra Ceia Bay, Florida, with juvenile blacktip sharks, *Carcharhinus limbatus* (Müller & Henle 1839). In contrast, several other studies have recorded small sharks being predated upon even when they are located in shallow waters (Ebert, 1991; Hight & Lowe, 2007; Nosal *et al*., 2013; Roemer *et al*., 2016). Unlike with juvenile or small sharks, no documentation was available to show that large adult sharks actively swim into shallower waters to avoid predation.

In the western Atlantic, *C. limbatus* overwinters in the clear, shallow, nearshore waters of southeastern Florida from about January to March. This species can form large aggregations of up to thousands of individuals within 200 m of the beach (Kajiura & Tellman, 2016). With a maximum length of ~2 m, *C. limbatus* is both an agile predator of teleost fishes, cephalopods and crustaceans (Castro, 2011; Compagno, 1984) and a prey for larger sharks, such as the great hammerhead, *Sphyrna mokarran* (Rüppell 1837) (Raoult *et al*., 2019). *Sphyrna mokarran* can reach a maximum length of ~5.5 m, although adults only occasionally exceed 4 m (Castro, 2011; Compagno, 1984). Despite their large size, they are often found in relatively shallow waters, such as tidal flats (<1.5 m), that are likely an important area for their feeding (Roemer *et al*., 2016). The prey of *S. mokarran* typically includes batoids, teleosts and other sharks (Mourier *et al*., 2013; Raoult *et al*., 2019; Roemer *et al*., 2016), so it is no surprise that *S. mokarran* have been spotted in and around the *C. limbatus* aggregations, which provide an abundance of possible prey.

On three separate occasions, an unmanned aerial vehicle (UAV, DJI Phantom 4 Pro) recorded footage of a *S. mokarran* approaching an aggregation of *C. limbatus* in the nearshore waters of Palm Beach County, Florida. The average length of *C. limbatus* caught in the area (171.8 cm total length, Kajiura, unpubl.) was used to calibrate the scale in the video footage and estimate the distance from shore for these interactions. Based on this estimate, all videos were recorded within ~50 m offshore of the beach.

On 25 February 2018, a 2:07 min video was recorded at approximately 09.00 hours. A *S. mokarran* is initially seen cruising towards a *C. limbatus* aggregation. At the 1:27 mark, the *S. mokarran* pivots sharply and begins to chase the *C. limbatus*. The burst lasts only 8 s, but the group of *C. limbatus* flee to shallower waters closer to shore. As the water becomes increasingly shallow, the *S. mokarran* makes a sharp U-turn and returns to deeper waters. The dorsal fin and upper lobe of the caudal fin of the *S. mokarran* are seen breaking the surface as it enters shallower waters, but the fins of the *C. limbatus* do not. After the *S. mokarran* terminates its initial chase and is swimming back to deeper waters, it encounters a few *C. limbatus* that turn and swim past the *S. mokarran* towards the shallows (Supplemental Video S1).

On 28 February 2019, a 5:27 min video was recorded at approximately 08.30 hours. In this video, large orange buoys set ~50 m offshore provide a point of reference. A *S. mokarran* appears at the 0:59 mark and is tracked for the remainder of the video. The *S. mokarran* swims in a looping circular pattern, with several *C. limbatus* located between the *S. mokarran* and the shore. As the *S. mokarran* approaches the *C. limbatus*, they accelerate towards the shore. The dorsal fin and upper lobe of the caudal fin of the *S. mokarran* are seen breaking the surface when it is at its closest approach to the shore. At that point the *S. mokarran* turns and swims back out to deeper waters. This U-shaped approach to, and retreat from, the beach is repeated four times. Although the *S. mokarran* makes multiple approaches towards the *C. limbatus*, it does not initiate a chase (Supplemental Videos S2–S5).

The third video was recorded on 3 March 2019 at approximately 09.30 hours. The 3:25 min video tracks a *S. mokarran* swimming approximately parallel to the shore, between 10 and 35 m from the beach. At the 2:47 mark, the *S. mokarran* pivots sharply to pursue a single *C. limbatus*. The chase lasts 20 s (Figure 1a), with the *C. limbatus* swimming parallel to the shore, before turning towards the shore (Figure 1b). As the *C. limbatus* flees towards the shore, the *S. mokarran* executes a sharp U-turn and terminates the chase about 10 m from the shore. As the *S. mokarran* turns away from shore and back to deeper waters, the dorsal fin and upper lobe of the caudal fin are seen breaking the surface (Figure 1c). In contrast, the *C. limbatus* remains completely submerged until it reaches the swash zone. Once in the swash zone, the dorsal fin and upper lobe of the caudal fin of *C. limbatus* can also be seen breaking the surface of the water, and the shark struggles to swim until an incoming wave provides sufficient depth for efficient locomotion (Supplemental Video S6).

In all three events, *C. limbatus* use the shallow waters close to shore as a refuge from *S. mokarran*. Although refuging in shallow waters is seen in other smaller organisms, this appears to be the first evidence that adult *C. limbatus* refuge in shallow waters in the presence of a predator, *S. mokarran*. The area is characterized by a gently sloped sandy seafloor with an absence of vertical relief. As a result, there is no structure or shelter available for the *C. limbatus* to use as a refuge. The proximity to a shallow water refuge could provide an explanation for the close association of *C. limbatus* with the nearshore environment.

In two of the three videos, *S. mokarran* actively chased one or more *C. limbatus* towards the shore but was unsuccessful at capturing its prey. The chasing behaviour showed the dorsal fin and upper lobe of the caudal fin of *S. mokarran* breaking the surface of the water in every video as it neared the shore, whereas *C. limbatus* remained completely

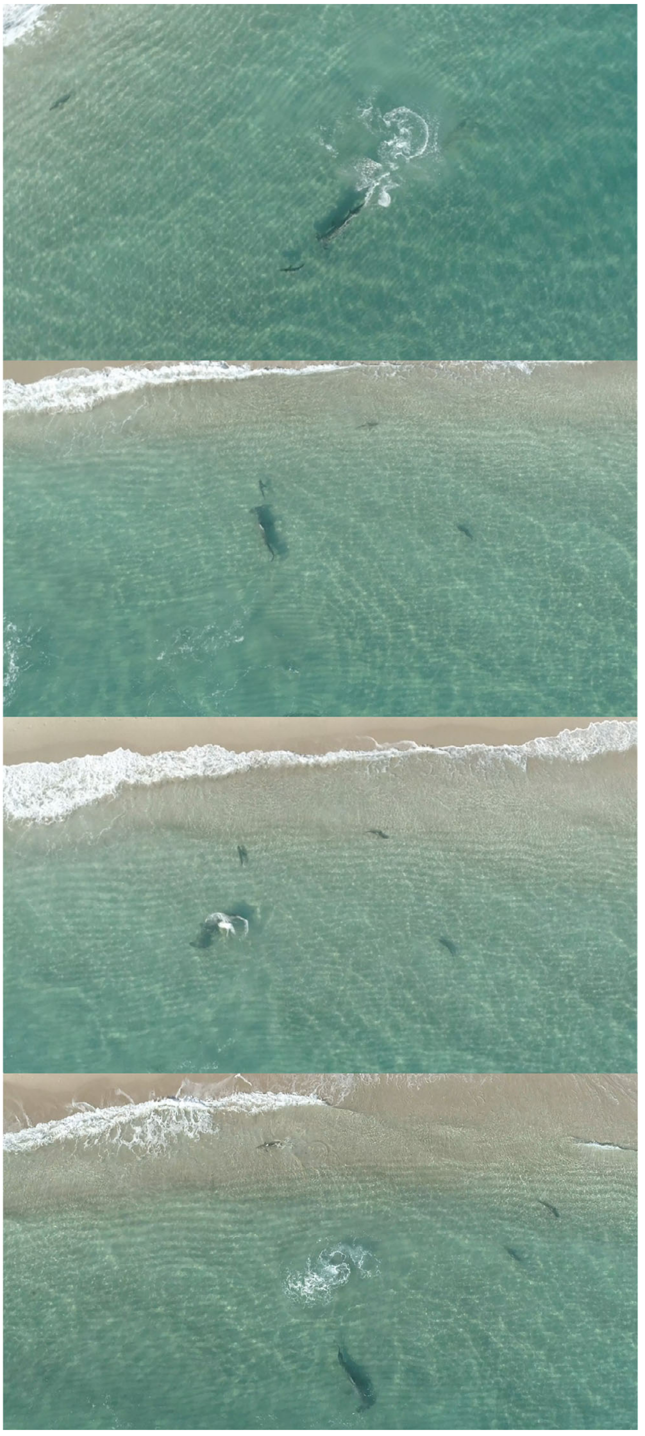

FIGURE 1 Still frames extracted from a video showing an attempted predation event filmed on 3 March 2019. (a) *Sphyrna mokarran* chasing a *Carcharhinus limbatus* parallel to the shore. Surface disturbances indicate where the dorsal fin and upper lobe of the caudal fin of *S. mokarran* had breached the surface. One other *C. limbatus* is seen close to shore in the upper left. (b) *Sphyrna mokarran* continues to chase a *C. limbatus* that swims towards the shore into shallow waters. Two other *C. limbatus* are seen to the right. (c) *S. mokarran* abandons its chase and executes a sharp turn back towards deeper waters, whereas the *C. limbatus* continues to swim towards the shore. (d) The *C. limbatus* swims parallel to the shore in the swash zone where its dorsal fin and upper lobe of the caudal fin break the surface. The video is available as Supplemental Video S6

submerged every time. The chases ended with *S. mokarran* making a sharp turn away from its intended prey and the shore, back into deeper waters. The chasing events showed *S. mokarran* struggling as it experienced difficulty following *C. limbatus* into the shallow waters.

S. mokarran are known to possess an exceptionally tall first dorsal fin, longer than their pectoral fins (Payne *et al*., 2016). Their large dorsal fin is proposed to generate lift when swimming on their side, instead of to facilitate propulsion and precise turning, as seen in every other observed shark species (Payne *et al*., 2016). The caudal fin thrusts and propels the shark forward (Maia *et al*., 2012), but both the dorsal fin and upper lobe of the caudal fin are seen breaching the surface in each video. When the dorsal and caudal fins of *S. mokarran* breach the surface, they are neither generating lift, providing thrust, nor helping to facilitate turning as efficiently as when they are completely submerged. The shallow water thus constrains the locomotion of the *S. mokarran*, which provides the *C. limbatus* with a functional refuge because their smaller size allows them to continue to swim and manoeuvre effectively away from their larger predator.

Because the *S. mokarran* initiated its approaches from deeper water, fleeing in the opposite direction would naturally lead the *C. limbatus* towards the shore. Thus, it is possible that the *C. limbatus* ended up in the nearshore environment incidentally rather than deliberately. Nonetheless, active selection for a nearshore refuge would be an adaptive behaviour and would likely be quickly propagated throughout the population.

Evidence of shallow water refuging was serendipitously documented using a UAV and should be further studied in other coastal elasmobranchs to determine its prevalence among other species. The use of UAVs permits unobtrusive observation and allows natural behaviours to be documented in the wild, providing insight into seldom-seen predator–prey interactions (Lea *et al*., 2019; Raoult *et al*., 2018). Other studies have also used aerial drone footage to document various behaviours exhibited by different shark species in the wild, including feeding, social and aggregative behaviour (Gore *et al*., 2019; Ho *et al*., 2017; Rieucau *et al*., 2018). The footage presented here can be analysed in depth to quantify swimming alignment, nearest-neighbour distances, velocity and tail beat frequency to provide a more comprehensive analysis of these parameters for both predator and prey. The predictable seasonal occurrence of large numbers of *C. limbatus* in clear, shallow waters close to the beach in Palm Beach County, Florida, provides an excellent opportunity to employ UAVs to quantitatively explore the collective behaviours and swimming kinematics of large sharks during natural predator–prey interactions. Most of the footage analysed in this study was provided by a citizen scientist, and the increasing popularity of UAVs will likely lead to additional fortuitous observations that can further inform the understanding of behaviours that are difficult to observe or have been previously undocumented.

ACKNOWLEDGEMENTS

We thank J. Jorgensen for providing some of the aerial drone footage and B. Ruddy for helping to analyse the footage. We thank the Colgan Foundation for providing funding for this study.

AUTHOR CONTRIBUTIONS

M.D.D. gathered and analysed the aerial drone footage and prepared the manuscript. S.M.K. observed the behaviours, formulated the original idea and foundation for the manuscript and reviewed the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Doan MD, Kajiura SM. Adult blacktip sharks (*Carcharhinus limbatus*) use shallow water as a refuge from great hammerheads (*Sphyrna mokarran*). *J Fish Biol*. 2020; 96:1530–1533. https://doi.org/10.1111/jfb.14342