



Reproductive timing and putative mating behavior of the oceanic whitetip shark *Carcharhinus longimanus* in the eastern Bahamas

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ABSTRACT: Oceanic whitetip sharks *Carcharhinus longimanus* aggregate at Columbus Point, Cat Island, The Bahamas, in at least April and May. We show that signs of putative mating activity (i.e. bite wounds) on mature females, which dominate the aggregation, are exceedingly rare at that time, but may be more common in July. Male plasma testosterone concentrations also suggest that spermatogenesis occurs in April and May and copulation is underway or has just ended by July. We support these preliminary data with direct observations of putative precopulatory behavior made at Columbus Point in July 2019. Using 25 min of video footage from the event, we identify common shark mating behaviors such as echelon or parallel swimming, following, shielding, nosing, and biting. We also describe the 'circle-back', a newly observed behavior where the male orients to the trail of the female, possibly to investigate olfactory cues. Based on these 3 parallel lines of evidence, we hypothesize that mating could occur in the eastern Bahamas as early as May, but is probably concentrated in midsummer (i.e. July), and that Columbus Point, Cat Island, may be a mating habitat for the oceanic whitetip shark.

KEY WORDS: Oceanic whitetip shark · Mating · Courtship · Pre-copulatory behavior · The Bahamas

1. INTRODUCTION

Historical accounts and catch data from the 1950s and 1960s suggest that the oceanic whitetip shark *Carcharhinus longimanus* was once relatively common in tropical and sub-tropical pelagic oceanic habitats (Young & Carlson 2020). Commercial fishing has since reduced its global population by an estimated 98%, resulting in the oceanic whitetip shark being listed as Critically Endangered on The IUCN

Red List of Threatened Species (Rigby et al. 2019) and being afforded some of the most comprehensive protections of any shark species globally (Young & Carlson 2020). An understanding of oceanic whitetip shark reproductive biology can contribute to the success of recovery efforts (Sims et al. 2000, Pratt & Carrier 2001, Young & Carlson 2020).

Most of what is known about shark reproduction comes from post-mortem examinations (Whitney et al. 2004, Pratt et al. 2005) and the study of captive

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animals (Pratt & Carrier 2001), although a growing number of recent studies have presented data on shark reproductive ecology *in situ* using non-lethal approaches (e.g. Sulikowski et al. 2016, Hammer-schlag et al. 2018). Circulating concentrations of the gonadal steroid hormone testosterone (T), for example, are often used to indicate reproductive stage and correlate well with seasonal spermatogenesis and copulation in male sharks. Generally, the highest T concentrations occur during mid- to late spermatogenesis and decline dramatically during and/or after copulation, although the exact timing of these changes can vary across species (Maruska & Gels-leichter 2011, Wyffels et al. 2020, Rangel et al. 2021). Less research has focused on shark reproductive behaviors, although an understanding of these behaviors can supplement information about reproductive traits (e.g. age at maturity, fecundity, reproductive periodicity) and inform conservation and management. Knowledge of when and where mating occurs, for example, can lead to the creation of time–area closures that protect critical habitats (e.g. Carrier & Pratt 1998).

Mating behaviors of wild, free-swimming sharks have rarely been observed (Bres 1993, Pratt & Carrier 2001, Whitney et al. 2004). Most *in situ* observations of mating behavior involve coastal species (see Pratt & Carrier 2001), including the reef-associated blacktip reef shark *C. melanopterus* (Johnson & Nelson 1978, McCauley et al. 2010), grey reef shark *C. amblyrhynchos* (Bres 1993), white-tipped reef shark *Traenodon obesus* (Johnson & Nelson 1978), and nurse shark *Ginglymostoma cirratum* (Klimley 1980, Pratt & Carrier 2001, Whitney et al. 2010), as well as the semi-oceanic scalloped hammerhead *Sphyrna lewini* (Klimley 1985, Salinas-De-León et al. 2017), silky shark *C. falciformis* (Clarke et al. 2013), and basking shark *Cetorhinus maximus* (Harvey-Clark et al. 1999, Sims et al. 2000, Wilson 2004, Gore et al. 2019). Some mating behaviors may occur universally across elasmobranch taxa. For example, courtship is thought to begin when a female releases olfactory chemical cues or exhibits behavioral cues to signal that she is receptive (Pratt et al. 2005). Males then bite or hold the fins, body, or flank of the female in order to copulate using at least 1 clasper (Carrier et al. 2004). This results in females having cuts and abrasions from the teeth of male sharks during the mating season (Pratt & Carrier 2001). For a thorough review of mating behaviors in elasmobranchs, see Pratt & Carrier (2001). Courtship and mating behaviors are largely undescribed in pelagic oceanic sharks.

Oceanic whitetip sharks exhibit site fidelity and seasonal residency at Columbus Point, southern Cat Island, The Bahamas (CI; within 20 km of 24° 07' N, 75° 17' W, Fig. 1; Howey-Jordan et al. 2013, Madigan et al. 2015). Abundant pelagic teleost prey (e.g. dolphinfish *Coryphaena hippurus*; Farrell et al. 2014) may motivate the April–May aggregation, which mostly consists of adult females, the majority of which are gravid (Howey-Jordan et al. 2013, Madigan et al. 2015). Males are less common, and juveniles are very rare (Madigan et al. 2015, V. Canabal pers. comm.), suggesting that parturition and possibly mating are unlikely to occur there in the winter (i.e. cold, dry season: November–April), although the aggregation has not been directly studied prior to April. In the summer (i.e. warm, wet season: May–October), some females leave CI and migrate to suspected mating or parturition areas in the Windward Passage, Straits of Florida, northern Lesser Antilles, or northern Bahamas (Castro 2011, Howey-Jordan et al. 2013, Ruiz-Abierno et al. 2021, M. Bond unpubl. data) and return to the eastern-central Bahamas by late summer or early winter (Howey-Jordan et al. 2013). Other adult females remain near CI for much or all of the summer (Howey-Jordan et al. 2013).

Here, we compare signs of oceanic whitetip shark mating activity and male plasma T concentrations between April–May and July in the eastern Bahamas and describe putative mating behaviors observed at CI in July. Based on these data, we evaluate whether oceanic whitetip sharks mate in the eastern Bahamas in the summer.

2. MATERIALS AND METHODS

2.1. Sampling

We conducted annual expeditions to CI for 1 to 2 wk in April–May from 2011 to 2018. A dive charter company (Epic Diving; V. and D. Canabal) also provided sightings data from regular dives at CI every spring. We attracted sharks during daylight hours by placing little tunny *Euthynnus alletteratus* in crates down-current of the vessel and baiting for 4 to 8 h daily. In July 2019, we baited for 2 d at CI and 2 d off Mayaguana (within 5 km of 22° 28' N, 73° 09' W), which is about 280 km southeast of CI (Fig. 1). Shark capture and handling procedures were described by Howey-Jordan et al. (2013). We determined sex through the presence or absence of claspers and sexual maturity based on the degree of clasper calcification and rotation for males (Clark & von Schmidt

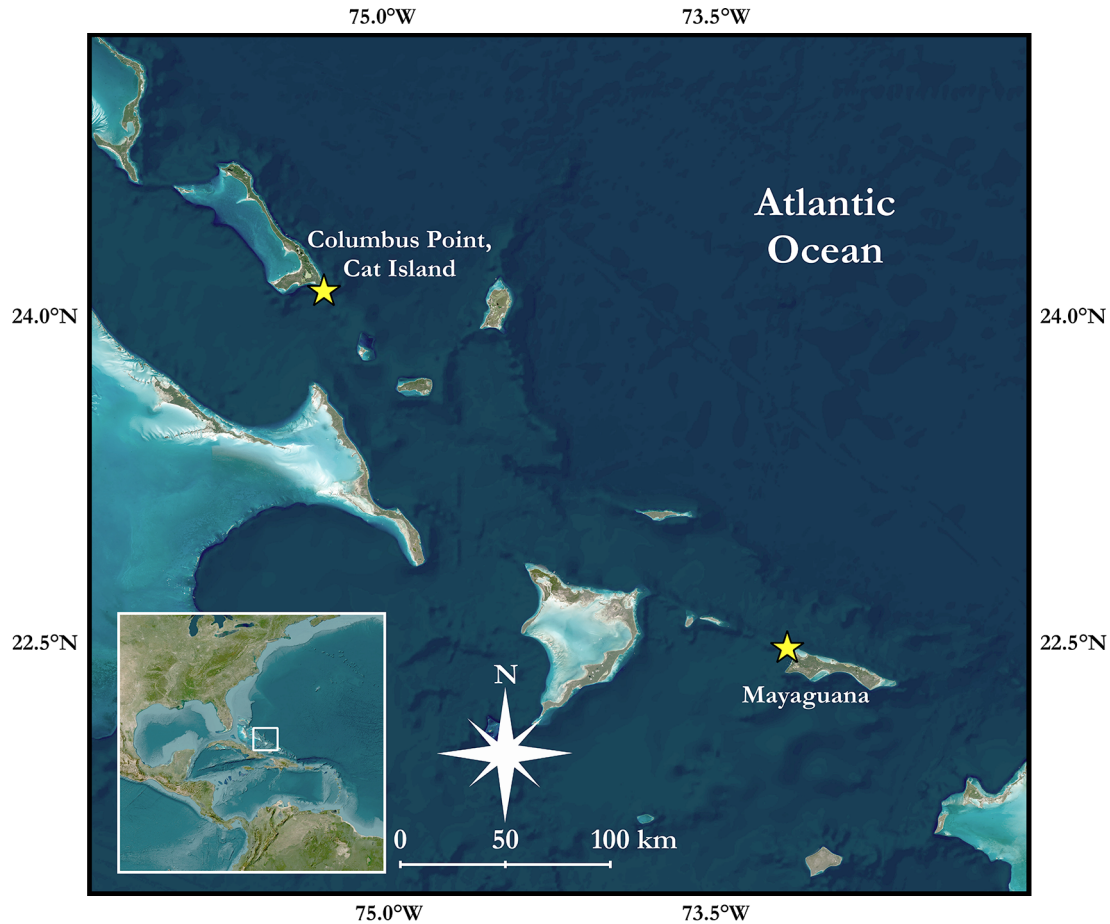


Fig. 1. Eastern Bahamas, with the inset showing map boundaries within the Greater Caribbean. Stars identify our sampling locations at Columbus Point, Cat Island, and the northeastern corner of Mayaguana

1965) and published size at maturity estimates for females (170–190 cm total length, TL; Seki et al. 1998, Lessa et al. 1999, Tambourgi et al. 2013).

As reported in past studies (e.g. Madigan et al. 2015, Gelsleichter et al. 2020), we collected various biological samples during shark workups. We drew blood via caudal venipuncture using sterile syringes and 16-gauge needles, then transferred samples to sterile vacuum tubes lined with acid citrate dextrose or lithium heparin anticoagulant before temporarily storing them on ice. We separated plasma with a centrifuge spun at $1500 \times g$ and then stored it at -20°C until hormone analysis.

2.2. Hormone analysis

We measured plasma T concentrations using commercially available AccuLite chemiluminescent immunoassay kits (Monobind) following the methods recently described for the finetooth shark *Carcharhi-*

nus isodon (Brown et al. 2020) and the bonnethead shark *Sphyrna tiburo* (Gonzalez De Acevedo et al. 2020). We measured chemiluminescence using the Synergy HT Multi-Mode Microplate Reader (BioTek Instruments) in luminescence mode. We validated each kit for use with oceanic whitetip shark plasma using parallelism to confirm that unknown analytes in serial dilutions of pooled samples (1/1 to 1/120) interacted with antibodies in a manner similar to that of assay standards. We used ‘cold spikes’ to determine percent recovery by adding a known amount of hormone standard to each pooled sample dilution and calculating recovery. We used results from validation tests to determine the ideal dilution of plasma to avoid matrix effects. Accordingly, we used a dilution factor of 1/50 for individual samples. We calculated hormone concentrations for each sample by multiplying by the dilution factor and correcting for procedural losses, which were determined by conducting ‘cold spikes’ on individual samples. Mean intra-assay variability was 4.9%. Mean inter-assay

variability was 7.8%. We grouped mature male plasma T concentrations by collection period and compared between periods using Student's *t*-test after confirming normality and homoscedasticity using the Shapiro-Wilk test and residual plots. Statistical significance was set at $\alpha = 0.05$. We conducted all analyses in R Version 3.6.3 (R Core Team 2021).

2.3. Observations of putative mating behavior

We observed 2 oceanic whitetip sharks swimming synchronously beneath the boat on 16 July 2019 at CI. D. Brake, S. Williams, and W. Pavlo entered the water to film the sharks on snorkel and recorded video footage with a Red Epic-W in a Gates Underwater Housing at 8K resolution and 2 GoPro Hero 7™ cameras in GoPro underwater housings at 2K resolution. One GoPro was attached to the Gates housing, and the other filmed separately.

One researcher analyzed 26 min 54 s of video by assigning a behavior (see Appendix of Pratt & Carrier 2001) to each animal for every second, comprising 15 min 39 s of continuous footage from one of the GoPro cameras and an additional 11 min 15 s of non-continuous, non-overlapping video shot by the other cameras. This non-continuous footage was not collected in any specific manner (i.e. we did not film select behaviors) and was choppy because snorkelers switched between cameras, cleaned lenses, and entered and exited the water. The sharks were filmed by at least 1 camera nearly the entire time they were in sight. When multiple cameras were simultaneously recording, we cross-referenced behaviors between camera angles to ensure a comprehensive review. We watched the footage using VLC media player (VideoLAN Organization, version 3.0.7.1) and saved still images using the snapshot tool. We estimated shark TL in the field and compared those estimates to measured size differences of the 2 animals swimming side by side in video stills.

3. RESULTS

3.1. Comments on the demographics and possible mating wounds of oceanic whitetip sharks in the eastern Bahamas

We captured 117 oceanic whitetip sharks at CI, most of which were females (83.8%, $n = 98$). All sharks were mature. In April, May, and July, females comprised 81% ($n = 17$), 89% ($n = 110$), and 50.0%

($n = 2$) of all oceanic whitetip captures (including recaptures), respectively. In July 2019 at Mayaguana, we captured 5 individuals ($n = 3$ mature females, 1 mature male, and 1 immature male).

We observed up to 4 female oceanic whitetip sharks with bite wounds indicative of possible mating activity at CI. One observation occurred in May, and the other 3 occurred in July. On 17 May 2013, we captured a mature, 251 cm TL female (pregnancy status unknown) with puncture wounds, slashes, and multiple jaw imprints from its gills to its flank (Fig. 2a–c). On 15 July 2019, we observed a female with bite wounds swimming near the boat, which may have been captured or re-sighted the following day, when we captured a mature, 224 cm TL, non-gravid female with jaw imprints and punctures on its right flank (Fig. 2d). While we measured and collected samples from this female, 2 males approached it repeatedly, possibly showing interest in mating. We then observed a male and a different female engaged in putative mating behaviors nearby (detailed in Section 3.3). The female had multiple bite wounds: one along the right side below the trailing edge of the first dorsal fin from the upper jaw of a shark, another located 5–10 cm above the right gill slits, and finally a row of tooth cuts ~10 cm from the base of the right pectoral fin, which had evidence of bites along its length and trailing edge (Fig. 3).

3.2. Male plasma testosterone concentrations

We collected blood samples from 10 male oceanic whitetip sharks, comprising 6 mature males captured in April–May at CI and 4 males (3 mature, 1 immature) captured in July at CI ($n = 2$) and Mayaguana ($n = 2$). The plasma T concentration of the immature male was 15.8 ng ml^{-1} . The plasma T concentrations of the mature males ranged from 28.19 to $109.25 \text{ ng ml}^{-1}$ (Table 1). Plasma T concentrations were significantly higher in mature males sampled in April–May than in those sampled in July ($t = 2.48$, $df = 7$, $p = 0.04$; Fig. 4).

3.3. Observations of putative mating behavior

On 16 July 2019, 2 oceanic whitetip sharks (1 male and 1 female) entered the chum slick and swam in unison under the boat at CI ($24^{\circ} 07' \text{ N}$, $75^{\circ} 19' \text{ W}$). We immediately stopped baiting and did not see the sharks feed. The Beaufort Sea State was 2, underwater visibility was excellent (~30 m), and conditions

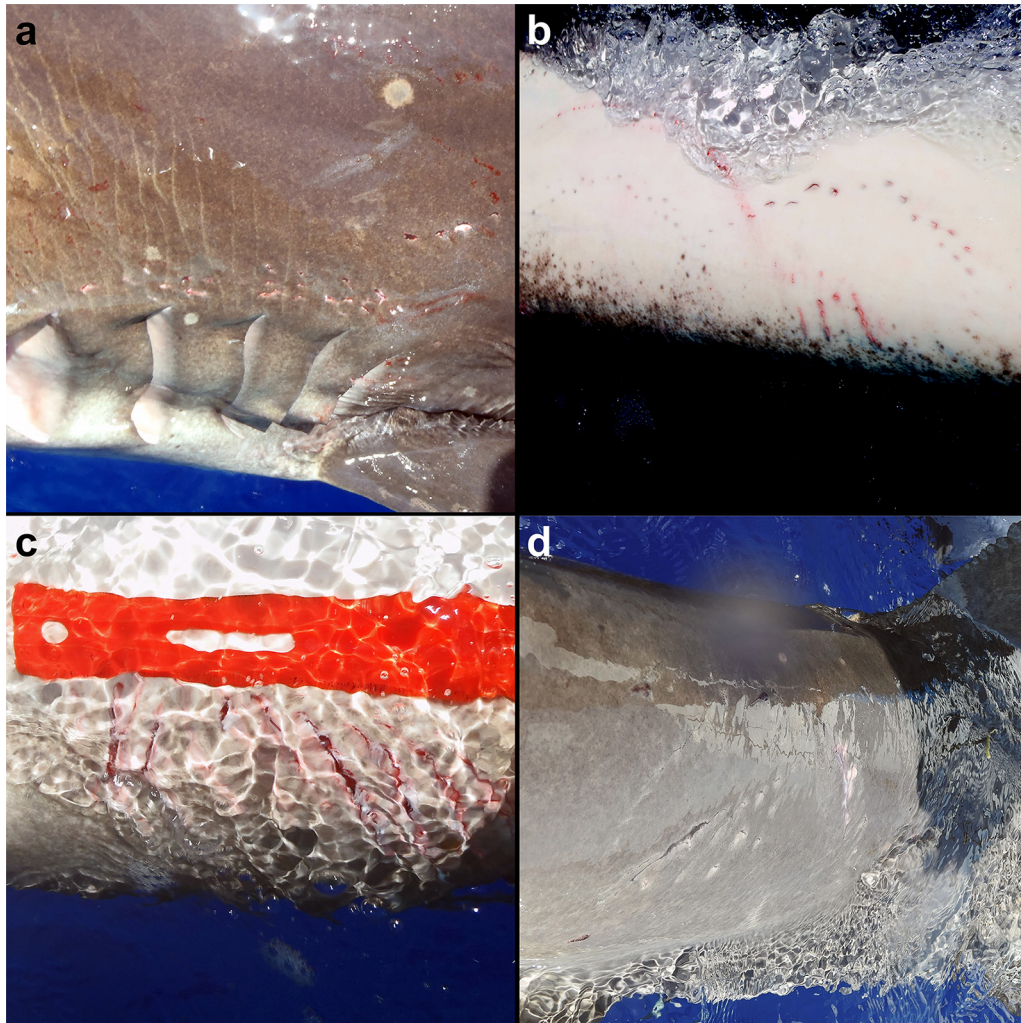


Fig. 2. Apparent mating wounds on mature female oceanic whitetip sharks *Carcharhinus longimanus* on the (a) left-side gill slits and (b,c) right ventral flank of one animal captured in May and (d) the right flank of another captured in July. In (c), the red object is a ruler with approximately 14 cm in the frame

Fig. 3. Apparent mating wounds (black rectangles) on a mature female oceanic whitetip shark *Carcharhinus longimanus* observed at Cat Island, The Bahamas, in July 2019. These wounds were acquired before we observed this female and a mature male, shown in echelon position, engage in putative precopulatory behaviors

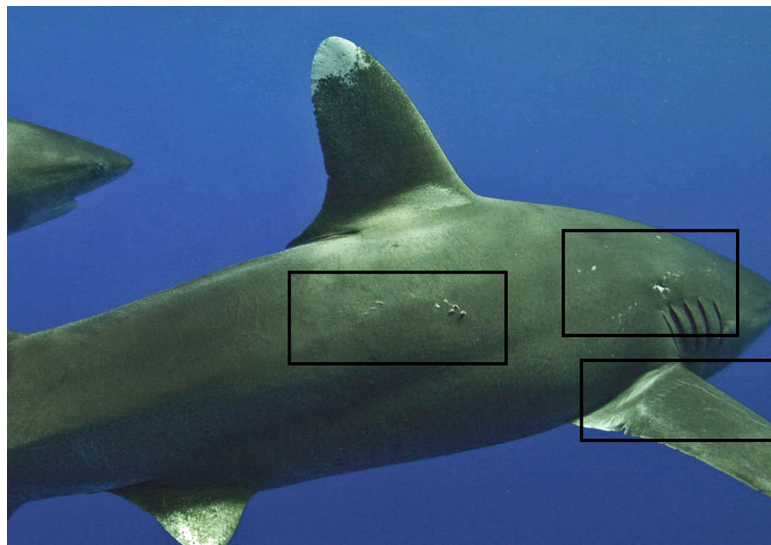


Table 1. Capture data and plasma testosterone (T) concentrations of male oceanic whitetip sharks *Carcharhinus longimanus* sampled at Columbus Point, Cat Island, The Bahamas (CI), and Mayaguana, The Bahamas. TL: total length

Capture period	Capture date	Capture location	Maturity status	TL (cm)	T (ng ml ⁻¹)
April–May	26-Apr-14	CI	Mature	252	109.25
April–May	10-May-12	CI	Mature	233	102.55
April–May	4-May-14	CI	Mature	222	92.85
April–May	3-May-14	CI	Mature	285	81.25
July	12-Jul-19	CI	Mature	244	65.05
April–May	12-May-12	CI	Mature	245	58.67
April–May	12-May-12	CI	Mature	245	58.64
July	14-Jul-19	Mayaguana	Mature	253	48.82
July	15-Jul-19	CI	Mature	241	28.19
July	13-Jul-19	Mayaguana	Immature	178	15.79

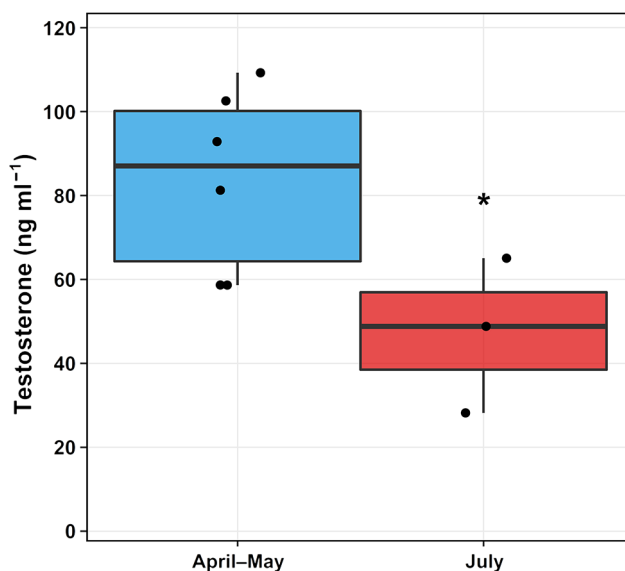


Fig. 4. Mature male oceanic whitetip shark *Carcharhinus longimanus* plasma testosterone concentrations measured in blood samples collected in April–May (blue; n = 6) and July (red; n = 3) in the eastern Bahamas, where the bold line indicates the median, upper and lower limits of the boxes correspond to the first and third quartiles, and whiskers extend to the maximum and minimum values that are not outliers. Individual plasma testosterone concentrations are shown as points. The asterisk indicates a significant difference ($p < 0.05$) in plasma testosterone concentrations between sampling periods according to Student's *t*-test

were clear and sunny. Water depth was between 700 and 1000 m, and sea surface temperature was 26.9°C.

The observation occurred between approximately 10:40 and 11:05 h. The sharks remained in the top 10 m of the water column. We estimated that the male was 200–225 cm TL and the female was

225–250 cm TL. Both animals were larger than the size at maturity, and the male had large claspers. The female had apparent bite wounds at the start of our observation (detailed in Section 3.1; Fig. 3). The male had no visible wounds. Early in the observation, another oceanic whitetip shark (sex undetermined) investigated the snorkelers, but it did not interact with other sharks and moved away from the immediate area after approximately 25 s.

The 15 min 39 s continuous video sequence (see Video S1 in the Supplement at www.int-res.com/articles/suppl/n050p181_supp/ for highlights)

began with the male and female 'echelon swimming' (Table 2) for 4 s, with the male mirroring the female's movements within 1 body length of and parallel to the female and its snout lined up to the female's flank between the trailing edge of the right pectoral and second dorsal fin (similar to 'parallel swimming'; Pratt & Carrier 2001). We observed echelon swimming more than any other behavior (~38% of total time observed for both the male and female; Fig. 5).

The male bit the female twice. Early in our observations, the male circled wide to intercept the female, crossed over the female's trail at roughly 1 body length behind its caudal fin, changed direction to follow the female ('circle-back'; Table 2, Fig. 6a), and approached to within 0.5 m below and behind the female's right pelvic fin ('following'; Table 2). The male accelerated and bit the female's right flank along the midline between the right pectoral and pelvic fin ('courtship bite'; Table 2). The female avoided the male by abruptly turning its longitudinal axis 30° away, lifting towards the surface, and rapidly accelerating ('direct avoidance'; Table 2). Simultaneously, the female angled its pectoral fins ventrally and shook its entire body vigorously. We saw no new injuries on the female.

Between bites, the male approached the female from below and behind the female's right posterior and rotated its dorsoventral axis at an oblique angle to the female so that its ventral surface was directed slightly towards the female ('rotating'; Table 2, Fig. 6d). The female mirrored the male's behavior by rotating slightly away from the male, demonstrating avoidance while echelon swimming ('shielding'; Table 2, Fig. 6d). Four seconds after beginning to shield, the female slowed and hung almost motionless at a 45° angle to the surface ('stalling'; Table 2)

Table 2. Putative mating behaviors of 2 oceanic whitetip sharks *Carcharhinus longimanus* at Columbus Point, Cat Island, The Bahamas, in July 2019

Behavior	Description	Previous observations
Female avoidance		
Direct avoidance	Abruptly accelerating and rotating away from the male, most often during a male bite attempt. Can include the lowering of pectoral fins and vigorous quivering.	Pratt & Carrier (2001)
Shielding	Rotating away from the male while parallel swimming or swimming in a circle to the opposite direction of the male's position along its flank.	Gordon (1993), Whitney et al. (2004)
Female acceptance		
Stalling	Slowing noticeably and lifting its snout towards the surface. The female initiates and the male matches the female's speed.	Gordon (1993), Pratt & Carrier (2001)
Male precopulatory behavior		
Circle-back	Leaving a position alongside the female to loop behind the female, often initiated during parallel swimming. The circle-back can begin with the male turning away from the female or accelerating ahead before crossing in front of the female. The male may circle back at the same depth as the female or arch high above the female, but remains within 3 body lengths of the female. When the male crosses the female's trail, the male abruptly turns and follows the female, ultimately returning to a position that allows parallel swimming.	
Close-swimming	Swimming asynchronously in the same direction as the female and within 2 body lengths of the female.	Gore et al. (2019)
Courtship bite	Biting the female between the pectoral and pelvic fins without grasping.	Stevens (1974), Pratt (1979), Pratt & Carrier (2001)
Echelon (parallel) swimming	Swimming, often synchronously, within one body length of the female. The male positions itself parallel to the female with its snout lined up anywhere between the female's second dorsal fin and snout, but most often between the female's pelvic and pectoral fins.	Clark (1963), Klimley (1980), Carrier et al. (1994), Harvey-Clark et al. (1999), Sims et al. (2000), Gore et al. (2019)
Following	Swimming closely behind the female, often positioned slightly below and behind the female's pelvic or caudal fins.	Johnson & Nelson (1978), Gordon (1993), Carrier et al. (1994)
Nosing	Approaching the female from behind and below the female until its snout is just below the female's cloaca.	Johnson & Nelson (1978), Gordon (1993), Harvey-Clark et al. (1999), Pratt & Carrier (2001)
Rotating	Rotating its dorsoventral axis towards the female while parallel swimming.	

while slowly turning 270° away from the male. After 4 s, the female resumed swimming in a circle for 48 s, continually angling away from the male while echelon swimming ('shielding').

Shortly after, the male circled back from an echelon position and followed the female for 8 s before returning to its previous position along the female's right flank. After echelon swimming for about 1 min, during which the female shielded, the male approached the female within 0.5 m of the female's right flank. The male bit the female below its midline just anterior to the pelvic fin. The female avoided the male as on the first occasion (Fig. 7). We saw no new marks on the female.

The male also exhibited variations of the 'circle-back' behavior, which was the second most common

male behavior after echelon swimming (Fig. 5). Repeatedly, the male caught up to the female until their snouts were nearly in line, turned 45° away from the female, swam towards the surface, and circled above and then behind the female, reaching nearly 3 body lengths of separation between itself and the female in a wide, high-arching circle-back (Fig. 6c). Often, the male then resumed the following behavior for a few seconds before echelon swimming or 'close swimming', where the pair swam asynchronously in the same direction (Table 2). During half of these circle-backs, the male left the female's side without crossing in front of the female ('rear circle-back'; Fig. 6a,c). During the other half, the male swam ahead and circled around the female, crossing in front of the female before approaching from

behind and slightly below the female's caudal fin ('forward circle-back'; Fig. 6b). Circle-backs dominated the last 5 min of the continuous sequence, during which the male exhibited the behavior 10 times, including 9 high-arching circle-backs. On 7 of those 9 occasions, the male crossed in front of the female. One of the male's passes brought it directly in front of the female at the same depth. All others took place 1–3 body lengths above and in front of the female. Both animals swam out of sight at the end of this sequence.

The additional, non-continuous video footage showed similar behavior, but, notably, the male avoided the female on 3 occasions. On 1 occasion, the male crossed in front of the female until they were perpendicular, then it abruptly turned and accelerated away from the female as its right pectoral fin came in line with the female's snout. The female responded by avoiding contact. On 2 occasions, the female's flank came within 0.5 m of the male's snout while echelon swimming, and the female abruptly avoided the male by accelerating and turning away; the male did not attempt to bite in either instance and avoided the female's caudal fin as the female turned. We also observed the male briefly 'nosing' the female on one occasion (Table 2).

4. DISCUSSION

We inferred mating attempts from observations of bite wounds on adult female oceanic whitetip sharks, analyzed plasma T levels in males caught in April–May and July, and observed the first instance of putative mating behavior for this species in July. Our results suggest that some oceanic whitetip sharks mate in the summer near Columbus Point, Cat Island, The Bahamas.

4.1. Possible mating wounds

Male sharks presumably bite females to encourage cooperation during courtship, signal intent, stimulate ovulation, or stay in close contact during copulation (Springer 1967, Stevens 1974, Tricas & Le Feuvre 1985, Maruska et al. 1996, Pratt & Carrier 2001, Carrier et al. 2004, Conrath & Musick 2012). We ob-

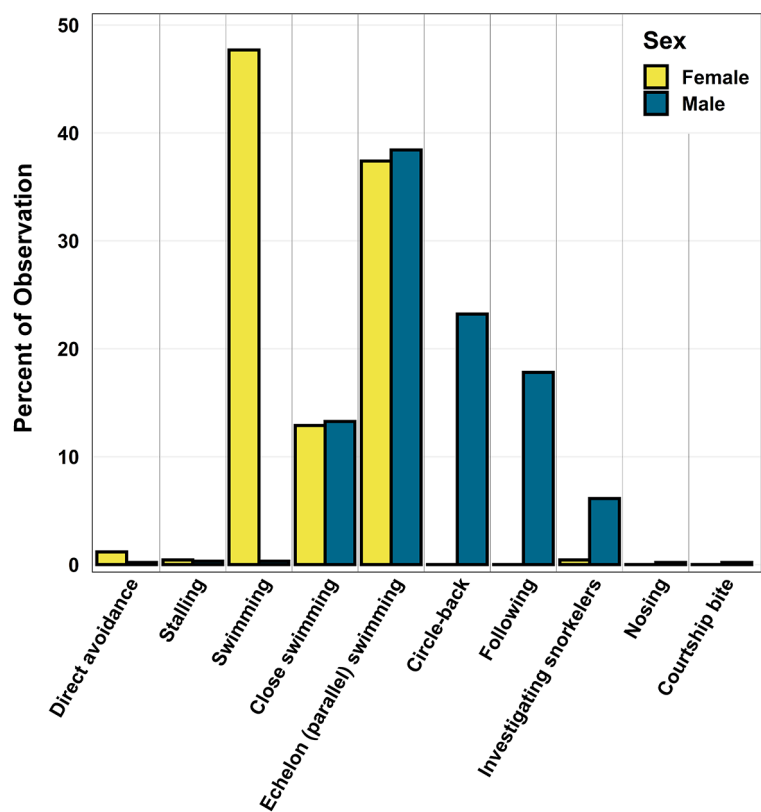


Fig. 5. Distribution of behaviors exhibited by 1 male and 1 female oceanic whitetip shark *Carcharhinus longimanus* observed during 26 min 54 s of putative precopulatory behavior at Columbus Point, Cat Island, The Bahamas, in July 2019

served apparent mating wounds on females from the gill slits to the flank, including the pectoral fin base (Pratt & Carrier 2001), where mating wounds are also seen on other species (e.g. silky shark; Whitehead et al. 2022). We saw mating wounds on most females at CI in July ($n = 2$ of 3, or 3 of 4 depending on how many unique individuals were observed), but saw mating wounds on almost no females at CI in April–May ($n = 1$ of 127), suggesting that mating behavior does not generally occur in the weeks to months prior to our annual April–May expeditions. However, we have not sampled at CI in those months; thus, although we find it unlikely, it is possible that mating occasionally occurs at CI earlier in the year.

4.2. Male plasma T concentrations

Circulating T levels in male carcharhiniform sharks increase during sexual maturation (Rasmussen & Gruber 1993, Gelsleichter et al. 2002), then

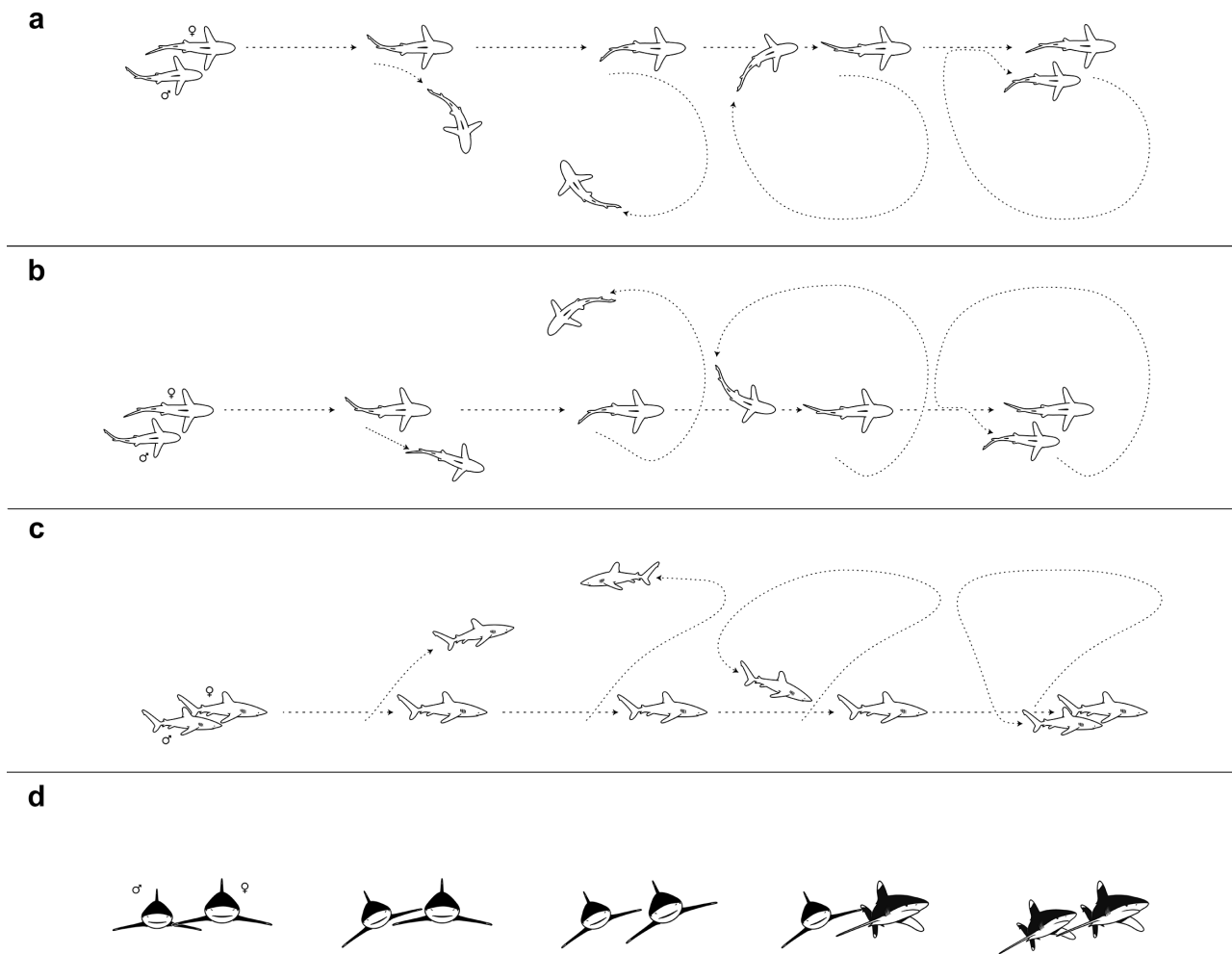


Fig. 6. Select mating behaviors exhibited by oceanic whitetip sharks *Carcharhinus longimanus* at Columbus Point, Cat Island, The Bahamas, in July 2019, including variations of the male circle-back behavior, such as (a) rear circle-back, (b) forward circle-back, and (c) high-arching circle-back, and (d) male rotating and female shielding

undergo cyclical patterns in relation to reproductive stage (Manire & Rasmussen 1997, Hoffmayer et al. 2010, Brown et al. 2020, Gonzalez De Acevedo et al. 2020). Generally, plasma T concentrations appear to be greatest in male carcharhinids and sphyrnids during mid- to late spermatogenesis, then decline precipitously during and after the copulatory period, reaching their nadir during periods of reproductive inactivity (Manire & Rasmussen 1997, Hoffmayer et al. 2010, Brown et al. 2020, Gonzalez De Acevedo et al. 2020). It is noteworthy that peak plasma T concentrations in mature male sharks actively undergoing spermatogenesis can often be 5 to 10 times the levels observed in reproductively inactive mature males (Manire & Rasmussen 1997, Gelsleichter et al. 2002, Hoffmayer et al. 2010, Brown et al. 2020, Gonzalez De Acevedo et al. 2020), which generally have

plasma T concentrations that are comparable to, if not indistinguishable from, those in immature males (Gelsleichter et al. 2002). For mature male oceanic whitetip sharks, plasma T concentrations suggest that spermatogenesis is occurring in April–May, when T concentrations are high (approximately 6-fold greater than in the immature male), and that the copulatory period is underway or has just ended in July, when T concentrations are low. This is consistent with the declines generally reported in other male carcharhinids at that point in the reproductive cycle; mature male finetooth sharks, for example, had comparable declines in plasma T concentrations when mature females in the same population exhibited fresh mating wounds and the earliest signs of pregnancy (i.e. uterine eggs bearing blastodisc-stage embryos; Brown et al. 2020). At the very least,

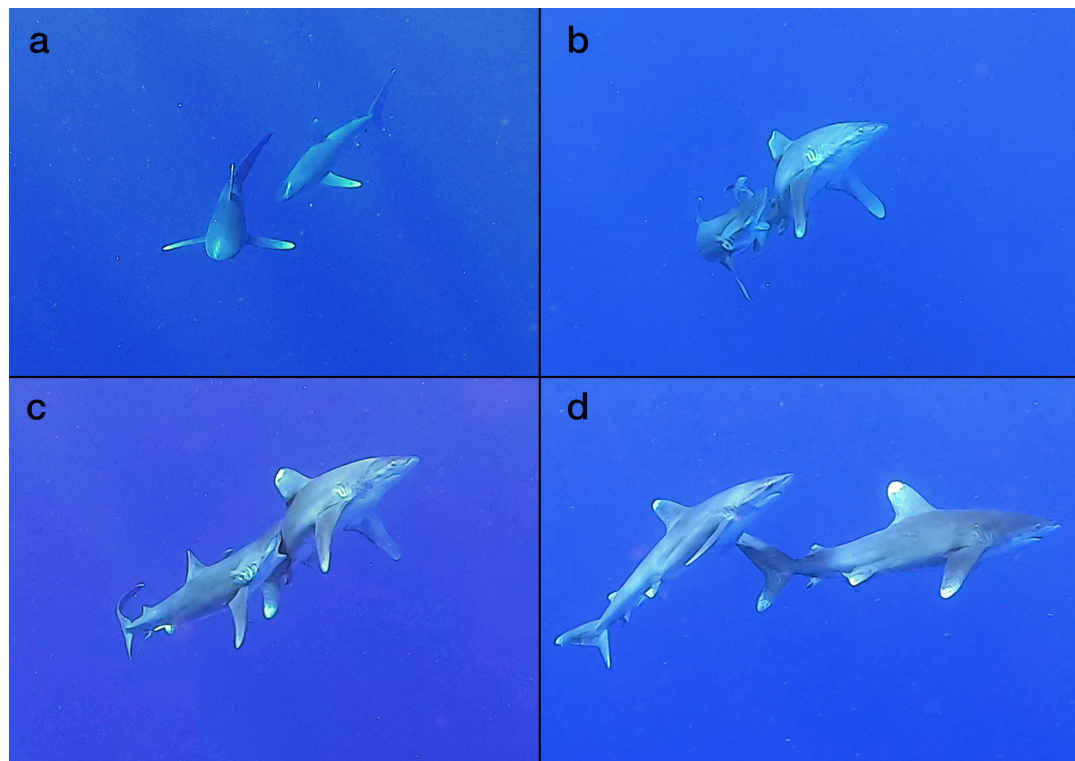


Fig. 7. Sequence of video screenshots of 2 oceanic whitetip sharks *Carcharhinus longimanus* engaged in putative mating behavior in July 2019 at Columbus Point, Cat Island, The Bahamas, showing the male's (a) approach and (b,c) courtship bite and (b–d) the female's avoidance

despite a low sample size, our data suggest that a change in reproductive activity occurs in some mature male oceanic whitetip sharks between April–May and July.

4.3. Observations of putative mating behavior

Mating behaviors are poorly described for pelagic sharks and documented for only a few obligate-swimming species, some of which have been observed copulating (e.g. white shark *Carcharodon carcharias*, blacktip reef shark, silky shark, scalloped hammerhead; Johnson & Nelson 1978, Klimley 1985, Francis 1996, McCauley et al. 2010, Clarke et al. 2013, Salinas-De-León et al. 2017). Our observations, like those for basking sharks (Harvey-Clark et al. 1999, Sims et al. 2000, Wilson 2004, Gore et al. 2019), were limited to what we interpret to be pre-copulatory, pre-courtship, or courtship behaviors (Pratt & Carrier 2001), such as close-following, nosing, avoidance, and stalling.

Courtship in sharks and rays is likely initiated by a combination of olfactory and visual behavioral cues

from receptive, mature females, although males sometimes initiate as well (Pratt et al. 2005). Females may secrete sex-attractant substances (i.e. pheromones) that signal to males a readiness to mate (Demski 1990, Kajiura et al. 2000), which could explain the 'following' and 'nosing' behaviors of the male oceanic whitetip shark (Myrberg & Gruber 1974, Johnson & Nelson 1978, Klimley 1980, Gordon 1993, Harvey-Clark et al. 1999, Pratt & Carrier 2001, Parsons et al. 2008). The male oceanic whitetip shark also engaged in variations of 'following', such as echelon swimming and close-swimming (Clark 1963, Klimley 1980, Carrier et al. 1994, Gore et al. 2019). Variations of 'following' have been observed in a mating context across multiple elasmobranch orders, including Orectolobiformes (e.g. nurse shark, Klimley 1980, Carrier et al. 1994), Carcharhiniformes (e.g. lemon shark *Negaprion brevirostris*; Clark 1963), Lamniformes (e.g. basking shark; Harvey-Clark et al. 1999, Wilson 2004, Sims et al. 2000), and Myliobatiformes (e.g. giant manta ray *Manta birostris*; Yano et al. 1999, McCallister et al. 2020). We identified a variation of following behavior where the male did a 'circle-back' to reposition himself behind the female,

possibly to reorient to the female's attractive olfactory cues. This behavior resembled a 'turn-back' described in captive bonnethead sharks, where large males selectively turned back on large females as they passed (Myrberg & Gruber 1974). It also resembled the behaviors of great hammerheads *Sphyrna mokarran* and tiger sharks *Galeocerdo cuvier* at established shark feeding sites, where animals follow a scent trail towards fish carcasses presented by a feeder. Instead of remaining in the immediate vicinity of the carcasses, they may feed and then circle back to pick up the scent trail repeatedly (S. Williams pers. obs.). At times, the male oceanic whitetip shark passed in front of the female during circle-backs, which could be related to the male signaling its intent or perhaps displaying the claspers as its only obvious secondary sexual characteristic (Parsons et al. 2008). Following behaviors may also serve a social function in same-sex groups (Myrberg & Gruber 1974, Johnson & Nelson 1978, Bres 1993, Gallagher et al. 2014) and may increase foraging efficiency for filter feeders (Gore et al. 2019).

Female sharks often avoid males, which may facilitate female choice or reflect the aggressive nature and associated energetic cost of mating that can result in serious injury or mortality (Pratt & Carrier 2001, Pratt et al. 2005, Daly-Engel et al. 2010). Female avoidance behavior can include shielding, arching, or rolling away from a male to limit access to the fins or cloaca (Pratt & Carrier 2001, Whitney et al. 2004, Conrath & Musick 2012). Here, the female avoided the male by shielding and, during male bite attempts, shaking vigorously to prevent the male from grasping its flank. The female's avoidance behaviors prevented copulation during our observations, but the presence of deeper lacerations consistent with mating wounds suggested that the female had recently been bitten with more force and possibly copulated.

Although the female regularly avoided the male, it did demonstrate some 'acceptance' behaviors, such as parallel or echelon swimming and tolerance of the male's repeated approach (Pratt & Carrier 2001). The female also appeared to 'stall', which has been interpreted in sand tiger sharks *Carcharias taurus* as signaling a readiness to mate (Gordon 1993, Parsons et al. 2008). Receptive female sharks may also raise the caudal fin while a male is 'nosing' or 'close-following', as seen in blacktip reef sharks (Johnson & Nelson 1978), or flare or cup the pelvic fins to allow the male to bite and copulate, as seen in nurse sharks (Carrier et al. 1994, Pratt & Carrier 2001), but we did not observe these behaviors.

4.4. Conclusions

Based on these 3 lines of evidence (i.e. mating wounds, male plasma T concentrations, and observed precopulatory behaviors), and because most females in April–May at CI are gravid with what appear to be late-stage embryos (Madigan et al. 2015) developed during 9–12 mo of gestation (Backus et al. 1956, Bonfil et al. 2008, Tambourgi et al. 2013), we hypothesize that mating occurs in the summer in the eastern Bahamas. Limited satellite telemetry data support this hypothesis: nearly all female oceanic whitetip sharks tagged at CI in early May ($n = 9$) remain within the eastern-central Bahamas (~500 km area) for around 30 d post-tagging (i.e. into June), with over half of all tagged animals remaining until July, and some remaining throughout the entire summer (Howey-Jordan et al. 2013). This leaves a sufficient window for oceanic whitetip sharks to mate as early as May through October, when mating may be triggered by rising sea surface temperatures in the region (Pratt & Carrier 2001, Gordon 1993). The timing of this proposed mating period aligns with previous research in the western North Atlantic Ocean (Backus et al. 1956, Ruiz-Abierno et al. 2021).

Additional observations and hormone data collected year-round are needed to comprehensively determine the seasonal use of CI by oceanic whitetip sharks and clarify the species' reproductive cycle. Studying the CI aggregation from June to October may provide more evidence of mating from apparent courtship scars or wounds, a shift in demographics towards more males and non-gravid females, or direct observations of copulation. Ultimately, CI may be an important foraging ground for oceanic whitetip sharks (Madigan et al. 2015), leading substantial numbers of this wide-ranging species to exhibit seasonal residency and site fidelity to this location (Howey-Jordan et al. 2013, Madigan et al. 2015). Abundant food resources may drive oceanic whitetip shark densities high enough to facilitate male–female interactions and mating, similar to dense zooplankton prey aggregating basking sharks in oceanic fronts, where courtship behaviors then occur (Sims et al. 2000). Other areas in the eastern Bahamas, such as sites where biophysical coupling (e.g. current–bathymetric interactions) leads to productivity hotspots (Hazen et al. 2013, Gove et al. 2016), may provide oceanic whitetip sharks with similar reproductive opportunities.

Management efforts at the national, regional, and global levels present a multi-pronged framework for

the recovery of the oceanic whitetip shark (Young & Carlson 2020). However, such management efforts may be compromised without an improved understanding of the species' reproductive ecology, including the timing and location of mating and parturition. We build on previous research documenting the importance of CI (Howey-Jordan et al. 2013, Madigan et al. 2015) to the oceanic whitetip shark in the western Atlantic Ocean (Camargo et al. 2016) by showing that CI may be a mating habitat in summer. This new understanding highlights the value of Bahamian shark conservation efforts, particularly the ban on longline fishing in 1993 and ban on shark fishing in 2011 (Fisheries Resources [Jurisdiction and Conservation] Act, Government of The Bahamas), in preventing shark fishing in potentially critical habitats prior to their recognition.

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LITERATURE CITED

- Backus RH, Springer S, Arnold EL Jr (1956) A contribution to the natural history of the white-tip shark, *Pterolamiops longimanus* (Poey). Deep-Sea Res 3:178–188
- Bonfil R, Clarke S, Nakano H (2008) The biology and ecology of the oceanic whitetip shark, *Carcharhinus longimanus*. In: Camhi MD, Pikitch EK, Babcock EA (eds) Sharks of the open ocean: biology, fisheries and conservation. Blackwell Publishing, Oxford, p 128–139
- Bres M (1993) The behaviour of sharks. Rev Fish Biol Fish 3: 133–159
- Brown AN, Frazier BS, Gelsleichter J (2020) Re-evaluation of reproductive cycle and fecundity of finetooth sharks *Carcharhinus isodon* (Valenciennes 1839) from the Northwest Atlantic Ocean, with new observations on ovarian cycle and reproductive endocrinology of biennially reproducing sharks. J Fish Biol 97:1780–1793
- Camargo SM, Coelho R, Chapman D, Howey-Jordan L and others (2016) Structure and genetic variability of the oceanic whitetip shark, *Carcharhinus longimanus*, determined using mitochondrial DNA. PLOS ONE 11: e0155623
- Carrier JC, Pratt HL (1998) Habitat management and closure of a nurse shark breeding and nursery ground. Fish Res 39:209–213
- Carrier JC, Pratt HL Jr, Martin LK (1994) Group reproductive behaviors in free-living nurse sharks, *Ginglymostoma cirratum*. Copeia 1994:646–656
- Carrier JC, Pratt HL Jr, Castro JI (2004) Reproductive biology of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, FL, p 269–286
- Castro JI (2011) The sharks of North America. Oxford University Press, New York, NY
- Clark E (1963) The maintenance of sharks in captivity, with a report on their instrumental conditioning. In: Gilbert P (ed) Sharks and survival. D. C. Heath and Co., Boston, MA, p 115–149
- Clark E, von Schmidt K (1965) Sharks of the central gulf coast of Florida. Bull Mar Sci 15:13–83
- Clarke CR, Lea JSE, Ormond RFG (2013) Changing relative abundance and behaviour of silky and grey reef sharks baited over 12 years on a Red Sea reef. Mar Freshw Res 64:909–919
- Coelho R, Hazin FHV, Rego M, Tambourgi M and others (2009) Notes on the reproduction of the oceanic whitetip shark, *Carcharhinus longimanus*, in the southwestern equatorial Atlantic Ocean. Collect Vol Sci Pap ICCAT 64: 1734–1740
- Conrath CL, Musick JA (2012) Reproductive biology of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives, 2nd edn. CRC Press, Boca Raton, FL, p 291–306
- Daly-Engel TS, Grubbs RD, Feldheim KA, Bowen BW, Toonen RJ (2010) Is multiple mating beneficial or unavoidable? Low multiple paternity and genetic diversity in the shortspine spurdog *Squalus mitsukurii*. Mar Ecol Prog Ser 403:255–267
- Demski LS (1990) Neuroendocrine mechanism controlling the sexual development and behavior of sharks and rays. J Aquaricult Aquat Sci 5:53–67
- Farrell ER, Boustany AM, Halpin PN, Hammond DL (2014) Dolphinfin (*Coryphaena hippurus*) distribution in relation to biophysical ocean conditions in the northwest Atlantic. Fish Res 151:177–190
- Francis MP (1996) Observations on a pregnant white shark with a review of reproductive biology. In: Klimley KP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, CA, p 157–172
- Gallagher AJ, Romeiro J, Canabal D, Canabal V, Hamerschlag N (2014) Novel social behaviors in a threatened apex marine predator, the oceanic whitetip shark *Carcharhinus longimanus*. Ethol Ecol Evol 26: 413–417
- Gelsleichter J, Rasmussen LE, Manire CA, Tyminski J, Chang B, Lombardi-Carlson L (2002) Serum steroid concentrations and development of reproductive organs during puberty in male bonnethead sharks, *Sphyrna tiburo*. Fish Physiol Biochem 26:389–401
- Gelsleichter J, Sparkman G, Howey LA, Brooks EJ, Shipley ON (2020) Elevated accumulation of the toxic metal

- mercury in the Critically Endangered oceanic whitetip shark *Carcharhinus longimanus* from the northwestern Atlantic Ocean. *Endang Species Res* 43:267–279
- ✦ Gonzalez De Acevedo M, Frazier BS, Belcher C, Gelsleichter J (2020) Reproductive cycle and fecundity of the bonnethead *Sphyrna tiburo* L. from the northwest Atlantic Ocean. *J Fish Biol* 97:1733–1747
- ✦ Gordon I (1993) Pre-copulatory behavior of captive sand tiger sharks, *Carcharias taurus*. *Environ Biol Fishes* 38: 159–164
- ✦ Gore M, Abels L, Wasik S, Saddler L, Ormond R (2019) Are close-following and breaching behaviours by basking sharks at aggregation sites related to courtship? *J Mar Biol Assoc UK* 99:681–693
- ✦ Gove JM, McManus MA, Neuheimer AB, Polovina JJ and others (2016) Near-island biological hotspots in barren ocean basins. *Nat Commun* 7:10581
- ✦ Hammerschlag N, Skubel RA, Sulikowski J, Irschick DJ, Gallagher AJ (2018) A comparison of reproductive and energetic states in a marine apex predator (the tiger shark, *Galeocerdo cuvier*). *Physiol Biochem Zool* 91: 933–942
- ✦ Harvey-Clark ACJ, Stobo WT, Helle E, Mattson M (1999) Putative mating behavior in basking sharks off the Nova Scotia coast. *Copeia* 1999:780–782
- ✦ Hazen EL, Suryan RM, Santora JA, Bograd SJ, Watanuki Y, Wilson RP (2013) Scales and mechanisms of marine hotspot formation. *Mar Ecol Prog Ser* 487:177–183
- ✦ Hoffmayer ER, Sulikowski JA, Hendon JM, Parsons GR (2010) Plasma steroid concentrations of adult male Atlantic sharpnose sharks, *Rhizoprionodon terraenovae*, in the northern Gulf of Mexico, with notes on potential long term shifts in reproductive timing. *Environ Biol Fishes* 88:1–7
- ✦ Howey-Jordan LA, Brooks EJ, Abercrombie DL, Jordan LKB and others (2013) Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the oceanic whitetip (*Carcharhinus longimanus*) in the Western North Atlantic. *PLOS ONE* 8:e56588
- ✦ Johnson RH, Nelson DR (1978) Copulation and possible olfaction-mediated pair formation in two species of carcharhinid sharks. *Copeia* 1978:539–542
- ✦ Kajiura SM, Sebastian AP, Tricas TC (2000) Dermal bite wounds as indicators of reproductive seasonality and behaviour in the Atlantic stingray, *Dasyatis sabina*. *Environ Biol Fishes* 58:23–31
- ✦ Klimley AP (1980) Observations of courtship and copulation in the nurse shark, *Ginglymostoma cirratum*. *Copeia* 1980:878–882
- ✦ Klimley AP (1985) Schooling in *Sphyrna lewini*, a species with low risk of predation: a non-egalitarian state. *Z Tierpsychol* 70:297–319
- ✦ Lessa R, Santana FM, Paglerani R (1999) Age, growth and stock structure of the oceanic whitetip shark, *Carcharhinus longimanus*, from the southwestern equatorial Atlantic. *Fish Res* 42:21–30
- ✦ Madigan DJ, Brooks EJ, Bond ME, Gelsleichter J and others (2015) Diet shift and site-fidelity of oceanic whitetip sharks *Carcharhinus longimanus* along the Great Bahama Bank. *Mar Ecol Prog Ser* 529:185–197
- ✦ Manire CA, Rasmussen LE (1997) Serum concentrations of steroid hormones in the mature male bonnethead shark, *Sphyrna tiburo*. *Gen Comp Endocrinol* 107:414–420
- ✦ Maruska KP, Gelsleichter J (2011) Hormones and reproduction in chondrichthyan fishes. In: Norris DO, Lopez KH (eds) *Hormones and reproduction in vertebrates*. Academic Press, San Diego, CA, p 209–237
- ✦ Maruska KP, Cowie EG, Tricas TC (1996) Periodic gonadal activity and protracted mating in elasmobranch fishes. *J Exp Zool* 276:219–232
- ✦ McCallister M, Mandelman J, Bonfil R, Danylchuk A, Sales M, Ajemian M (2020) First observation of mating behavior in three species of pelagic myliobatiform rays in the wild. *Environ Biol Fishes* 103:163–173
- ✦ McCauley DJ, Papastamatiou YP, Young HS (2010) An observation of mating in free-ranging blacktip reef sharks, *Carcharhinus melanopterus*. *Pac Sci* 64:349–352
- ✦ Myrberg AA, Gruber SH (1974) The behavior of the bonnethead shark, *Sphyrna tiburo*. *Copeia* 1974:358–374
- ✦ Parsons GR, Hoffmayer ER, Hendon JM, Bet-Sayad WV (2008) A review of shark reproductive ecology: life history and evolutionary implications. In: Rocha MA, Arukwe A, Kapoor BG (eds) *Fish reproduction*. Science Publishers, Enfield, NH, p 435–469
- ✦ Pratt HL (1979) Reproduction in the blue shark, *Prionace glauca*. *Fish Bull* 77:445–470
- ✦ Pratt HL, Carrier JC (2001) A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. *Environ Biol Fishes* 60: 157–188
- ✦ Pratt HL, Carrier JC, Hamlett WC (2005) Elasmobranch courtship and mating behavior. In: Hamlett WC (ed) *Reproductive biology and phylogeny of Chondrichthyes: sharks, batoids and chimaeras*. Science Publishers, Enfield, NH, p 129–169
- ✦ Rangel BS, Hammerschlag N, Sulikowski JA, Moreira RG (2021) Physiological markers suggest energetic and nutritional adjustments in male sharks linked to reproduction. *Oecologia* 196:989–1004
- ✦ Rasmussen LEL, Gruber SH (1993) Serum concentrations of reproductively-related circulating steroid hormones in the free-ranging lemon shark, *Negaprion brevirostris*. *Environ Biol Fishes* 38:167–174
- ✦ R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org
- ✦ Rigby CL, Barreto R, Carlson J, Fernando D and others (2019) Oceanic whitetip shark *Carcharhinus longimanus*. The IUCN Red List of Threatened Species 2019: e.T39374A2911619
- ✦ Ruiz-Abierno A, Márquez-Farías JF, Miller V, Angulo-Valdés JA, Hueter RE (2021) Seasonal abundance and size structure of sharks taken in the pelagic longline fishery off northwestern Cuba. *Mar Coast Fish* 13:275–291
- ✦ Salinas-De-León P, Hoyos-Padilla EM, Pochet F (2017) First observation on the mating behaviour of the endangered scalloped hammerhead shark *Sphyrna lewini* in the Tropical Eastern Pacific. *Environ Biol Fishes* 100: 1603–1608
- ✦ Seki T, Taniuchi T, Nakano H, Shimizu M (1998) Age, growth and reproduction of the oceanic whitetip shark from the Pacific Ocean. *Fish Sci* 64:14–20
- ✦ Sims DW, Southall EJ, Quayle VA, Fox AM (2000) Annual social behaviour of basking sharks associated with coastal front areas. *Proc R Soc B* 267:1897–1904
- ✦ Springer S (1967) Social organization of shark populations. In: Gilbert PW, Mathewson RF, Rall DP (eds) *Sharks, skates, and rays*. Johns Hopkins Press, Baltimore, MD, p 149–174
- ✦ Stevens JD (1974) The occurrence and significance of tooth

- cuts on the blue shark (*Prionace glauca* L.) from British waters. J Mar Biol Assoc UK 54:373–378
- ✦ Sulikowski JA, Wheeler CR, Gallagher AJ, Prohaska BK, Langan JA, Hammerschlag N (2016) Seasonal and life-stage variation in the reproductive ecology of a marine apex predator, the tiger shark *Galeocerdo cuvier*, at a protected female-dominated site. Aquat Biol 24:175–184
- Tambourgi MRdS, Hazin FHV, Oliveira PGV, Coelho R, Burgess G, Roque PCG (2013) Reproductive aspects of the oceanic whitetip shark, *Carcharhinus longimanus* (Elasmobranchii: Carcharhinidae), in the equatorial and southwestern Atlantic Ocean. Braz J Oceanogr 61: 161–168
- ✦ Tricas TC, Le Feuvre EM (1985) Mating in the reef white-tip shark *Triaenodon obesus*. Mar Biol 84:233–237
- ✦ Whitehead D, Gayford JH, Hoyos EM, Shorter NM, Galván-Magaña F, Ketchum JT (2022) First description of a sex segregated aggregation of silky sharks (*Carcharhinus falciformis*) and the frequency and distribution of mating wounds off the tip of the Baja California Peninsula. Environ Biol Fishes 105:953–960
- ✦ Whitney NM, Pratt HL, Carrier JC (2004) Group courtship, mating behaviour and siphon sac function in the white-tip reef shark, *Triaenodon obesus*. Anim Behav 68: 1435–1442
- ✦ Whitney NM, Pratt HL Jr, Pratt TC, Carrier JC (2010) Identifying shark mating behaviour using three-dimensional acceleration loggers. Endang Species Res 10:71–82
- ✦ Wilson SG (2004) Basking sharks (*Cetorhinus maximus*) schooling in the southern Gulf of Maine. Fish Oceanogr 13:283–286
- ✦ Wyffels JT, George R, Adams L, Adams C and others (2020) Testosterone and semen seasonality for the sand tiger shark *Carcharias taurus*. Biol Reprod 102: 876–887
- ✦ Yano K, Sato F, Takahashi T (1999) Observations of mating behavior of the manta ray, *Manta birostris*, at the Ogasawara Islands, Japan. Ichthyol Res 46:289–296
- ✦ Young CN, Carlson JK (2020) The biology and conservation status of the oceanic whitetip shark (*Carcharhinus longimanus*) and future directions for recovery. Rev Fish Biol Fish 30:293–312

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