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Two-year migration of adult female white sharks (*Carcharodon carcharias*) reveals widely separated nursery areas and conservation concerns

Michael L Domeier* and Nicole Nasby-Lucas

Abstract

Background: Satellite tagging programs have provided detailed information about the migratory patterns of northeastern Pacific white sharks, revealing a seasonal migration between a vast offshore region and coastal aggregation sites. Although adult males undergo annual round-trip migrations, photo-identification programs have noted that sexually mature females may only visit coastal aggregation sites once every 2 years, a behavior that is presumably linked to an estimated 18-month gestation period. The whereabouts of females during their full 2-year migration were previously unknown, because of the limited battery capacity of satellite pop-up tags.

Results: Through the use of satellite-linked radio-telemetry tags with multi-year tracking capability, we describe the 2-year migratory pattern for four mature female white sharks tagged at Guadalupe Island, Mexico. The 2-year migration comprised four phases: 1) an Offshore Gestation Phase (which had an average duration of 15.5 months; 2) a Pupping Phase, which occurred along the Mexican coast between the months of April and August; 3) a Pre-Aggregation Phase (when the females were in transition between the Pupping Phase and Guadalupe Island; and 4) the Guadalupe Island Aggregation Phase, which began when the mature females arrived at Guadalupe Island between late September and early October.

Conclusions: Long-term satellite tracking of mature female white sharks highlighted the connectivity between a single presumed mating site at Guadalupe Island, and two widely separated pupping sites along the Mexican coast. The Offshore Gestation Phase provided evidence that the females remained offshore for up to 16 months during their 2-year migration cycle. The Pupping Phase along the Mexican coast coincided with the seasonal presence of young-of-the-year white sharks along the coast of North America, and with a presumed gestation period of 18 months, this placed mating between October and January, during the period when white sharks are known to be at Guadalupe Island. Tracking data during the time sharks were offshore showed that mature males and females are spatially segregated, except for their concurrent seasonal presence at Guadalupe Island. These discoveries provide important new details about the complete life history of northeastern Pacific white sharks while identifying crucial regions in which young-of-the-year, juveniles and adult females are most vulnerable.

Keywords: White shark, Mating, Pupping, Migration, Baja, Mexico, Pacific, Gestation

Background

The white shark (*Carcharodon carcharias*) is a charismatic, apex predator that routinely migrates thousands of kilometers [1-10], and yet regional population structure exists on a global scale [5,10,11]. Because there are no physical boundaries separating the white-shark populations, behavioral traits that limit mixing may be the mechanism responsible for the observed population structure. One hypothesis, based upon DNA analysis, suggests that females have restricted geographic movement patterns but males are likely far-ranging [11]. Electronic tagging studies have presented seemingly contradictory results, with both sexes found to follow wide-ranging migratory patterns [3-8], with one female tracked across the Indian Ocean [6]. The discovery of male and female seasonal site fidelity among white sharks [2,5,12,13], termed 'philopatry', provided the first evidence of a behavioral trait that could restrict gene flow. It has been suggested that

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new white shark populations are founded by straying individuals, and the tendency for philopatry is what eventually differentiates the new population from the ancestral population [5,11,14,15]. However, philopatry will only lead to unique population structure if the behavior is focused on mating and/or pupping sites. Identifying mating and pupping sites and describing the connectivity between them can be extremely challenging when studying a highly migratory fish of relatively low abundance such as the white shark, but if accomplished, the results would have significant genetic and conservation implications [16,17].

Electronic tagging of adult white sharks in the northeastern Pacific has identified a previously unknown pelagic life-history phase, with sharks spending roughly half of their time in the deep-ocean environment, sometimes traveling as far as the Hawaiian Islands before returning to the continent [3,4]. Despite this pelagic phase, photographic identification (photo-ID) programs have shown white sharks to exhibit strong seasonal philopatry to one of two aggregation sites in the northeastern Pacific [12,13,18]: one off central California, USA, and the other at Guadalupe Island (GI), Mexico. Hundreds of sharks have been tracked from these aggregation sites, but only one individual (a sub-adult female) is known to have visited both sites [9]. Males visit these aggregation sites every year whereas adult females are typically seen every other year [8,12,18,19]. This 2-year migration pattern for females is likely associated with a presumed 18-month gestation cycle [20].

Multi-year tracking of adult female white sharks, combined with other direct and indirect life-history observations, could identify mating and pupping sites for the tracked individuals, as well as the connectivity between these important sites. To date, satellite pop-up tags have been unable to provide data/tracks on white sharks spanning more than 1 year, but the design of a satellite-linked radio-telemetry (SLRT) tag with a multi-year battery capacity, together with the development of methods for the capture, tagging, and release of large adult white sharks, allowed for a new research approach used in this study.

Here we describe a 2-year migratory pattern for mature female white sharks, and document the connectivity between a single presumed mating site at GI and two widely separated pupping sites along the Mexican coast. This discovery is an important addition to our understanding of the life history of the white shark, a species currently listed as 'vulnerable' by the World Conservation Union (IUCN), and which is protected under the Convention on the International Trade in Endangered Wild Flora and Fauna (CITES) [21].

Results and discussion

Four mature female white sharks tagged at GI with SLRT tags (F77 and F98 in 2008; F6 and F100 in 2009; Table 1) provided multi-year tracking data. F6 and F100 completed 2-year round-trip migrations in the first 2-year period after tagging, but F77 was tracked for 3 years to capture a 2-year migration pattern, because she returned to GI the year after tagging, before embarking on a 2-year migration. The tag on F98 ceased transmitting 510 days after tagging, just before her expected return to GI; although her track is incomplete, the migratory pattern was consistent with the other tracked females, and therefore the data from F98 were included in our analyses.

Data from the GI SLRT-tagged sharks, combined with previously published life-history observations, allowed for the synthesis and description of a multi-year migratory pattern for mature, female white sharks. The 2-year migration was found to consist of four phases: 1) an offshore gestation phase (OGP), which began when the females depart GI, and ended when they migrated to coastal regions during the pupping season; 2) a pupping phase (PP), defined as the time the females remained in the coastal waters of Baja California, Mexico, during the known pupping season [8]; 3) a pre-aggregation phase (PAP), when the females were in transition between the PP and GI; and 4) the GI aggregation phase (GIAP). Although the occurrence of each of these phases was seasonal, the timing and duration of each phase varied to some degree between individuals.

Offshore gestation phase

Tagged female white sharks began the OGP by departing GI between 25 Jan and 22 Feb (median departure date 5 February) (Table 1). This phase lasted between 439 and 484 days (mean 465 days). Males also underwent an offshore phase during their 1-year migratory pattern, but it was of much shorter duration (mean 104 days) [4] and focused on a region termed the shared offshore foraging area (SOFA) [4,7], approximately halfway between the coast of Baja California, Mexico, and the Hawaiian Islands. Locations from SLRT-tagged females during the OGP were not focused on the SOFA; instead, the females used a much larger space (Figure 1) bound by a minimum convex polygon (MCP) encompassing 3,383,105 km^2. During the OGP, the SLRT data indicated that tagged females spent only 4.2% of their time within the SOFA core (defined as the 50% density contour of the offshore area utilized by adult males [7]) while the males were present, supporting a previous study which suggested strong sexual segregation for adult white sharks during the offshore phase [7].

The OGP is the longest phase of an adult white shark's migratory pattern (14-16 month duration), meaning mature females spend more time in pelagic habitats than in any other habitat type. Females experience significantly warmer SSTs by remaining offshore, perhaps facilitating optimal growth of developing embryos [7].

Preferred prey for females in offshore waters is unknown. An expedition to the male focal area, the SOFA, found the

Table 1 Tagging and tracking data for tagged GI female white sharks

Shark number[a]	Date tagged	Total length, m	Start offshore	Arrive pupping	Depart pupping	Arrive Guadalupe	Depart Guadalupe
F98	12/9/2008	4.98	1/26/2009	4/10/2010	6/20/2010	NA	–
F77 year 1[b]	12/3/2008	5.08	2/1/2009	–	–	9/11/2009	1/25/2010
F77 year 2	–	–	1/25/2010	5/24/2011	8/4/2011	9/15/2011	12/7/2011
F6	11/19/2009	4.62	2/22/2010	5/30/2011	8/15/2011	10/6/2011	1/8/2012
F100	11/20/2009	4.62	2/15/2010	6/3/2011	7/25/2011	9/19/2011	1/13/2012

[a]Shark number corresponds to number assigned in the Guadalupe Island photographic identification database [12,19].
[b]Shark F77 returned to Guadalupe Island the year following tagging, before beginning a 2-year migration.

presence of three species of spawning squid (*Architeuthis* sp. and *Ommastrephes* sp.) and sperm whales, but no small marine mammals, and very little other epipelagic life [22]. Mature females travel east/west over a much broader area than the males, so it is possible that the preferred offshore prey differs between males and females. White sharks have never been documented to prey on healthy, large cetaceans, and are probably too small to do so; however, it cannot be overlooked that adult white-shark migrations overlap with large cetacean migrations in many parts of the world. Sperm whales and white sharks coincide within the SOFA core [22], white sharks and calving humpback whales coincide in Hawaii [3] and the south Pacific [10], and white sharks coincide with northern right whales off the east coast of the USA [23]. The growing circumstantial evidence that white sharks migrate to regions with relatively high whale density suggests a foraging link; whether the sharks are actively predating or simply scavenging upon the whales (and/or calves) is not known.

The OGP ended when the females migrated to coastal habitats along the Baja California Peninsula.

Pupping phase

Previously published analyses of fisheries data have identified seasonal pulses of young-of-the-year (YOY) white-shark pups, from April through August, within YOY hotspots along the western coast of North America [8,24,25]. The timing of SLRT-tagged females into coastal waters coincided with the identified PP. Our presumed pregnant SLRT-tagged females migrated to coastal waters

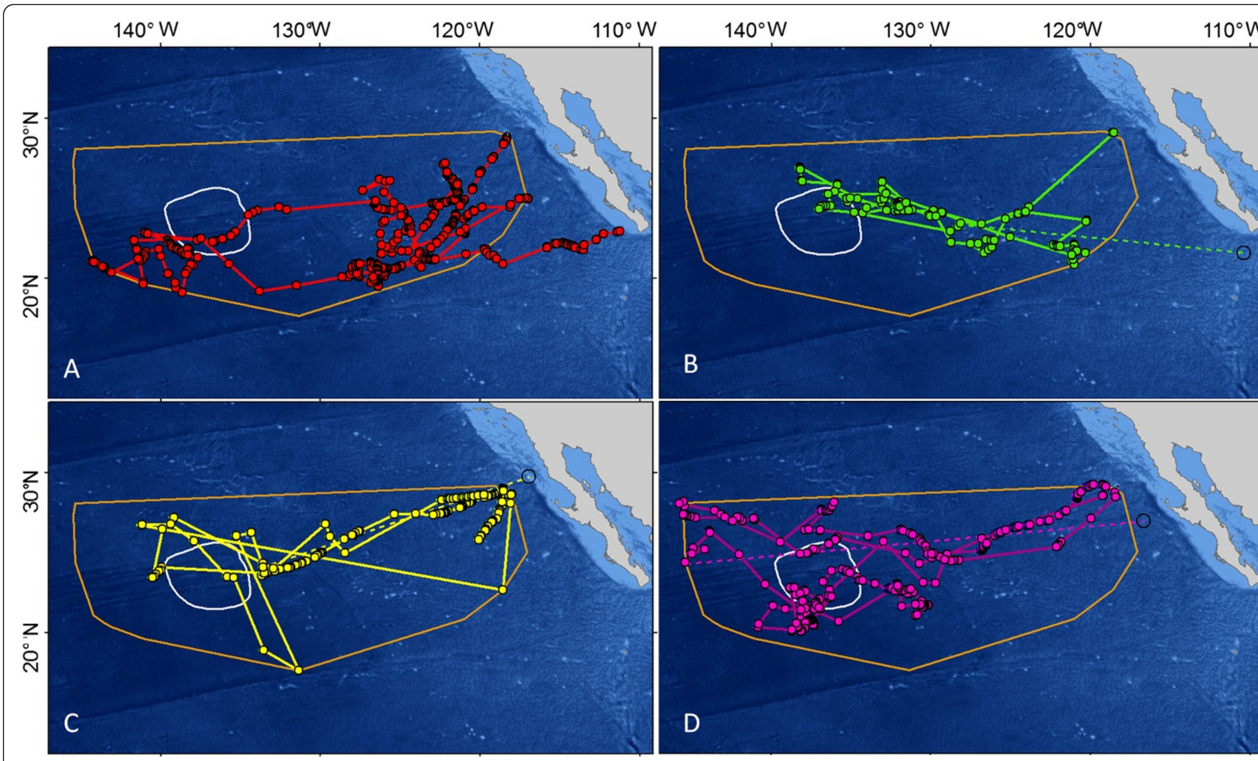

Figure 1 Location data for four satellite-linked radio-telemetry-tagged female white sharks during the Offshore Phase. The large gold contour indicates the MCP for all offshore location points for the four tagged female sharks: (**A**) F98, (**B**) F77, (**C**) F6 and (**D**) F100. The white contour indicates the 50% density contour for adult males while they were offshore [7]. The small black circles indicate the estimated end position of the offshore track as the sharks moved toward the pupping grounds.

between 10 April and 3 June (median 27 May) and departed between 20 June and 15 August (median 30 July) (Table 1). The duration of this PP varied from 52 to 77 days (mean 68 days). The approximately 2-month duration of the PP for tagged female sharks precluded precise identification of the location and timing of parturition, and it is unknown whether pups are born simultaneously or sequentially over a period.

The movement of pregnant females to coastal habitats was not simultaneous, nor restricted to a single nursery region. F77 and F98 migrated into the Sea of Cortez whereas F6 and F100 migrated to the central Pacific coast of Baja California, Mexico (Figure 2). YOY white sharks have not been collected in the Sea of Cortez [25,26], and there was no focal point of activity for F77 and F98, so it is not possible to deduce the exact location of the Sea of Cortez nursery area(s). However, both F6 and F100 remained within a relatively local region, near Sebastián Vizcaíno Bay, Mexico, a known YOY white-shark hotspot [25], suggesting that this coastal Pacific Baja California region is indeed an important pupping and nursery area for white sharks. Future directed sampling may provide more data regarding the nursery region in the Sea of Cortez. Because none of the tagged females traveled to southern California during their 2-year migration, the source of YOY California recruits remains unknown. SLRT tagging of central California females and increasing the sample size of females from GI should help resolve this remaining question.

Pre-aggregation phase

The PAP was the interval between parturition along the coast of Baja California and arrival to GI. Females left the pupping grounds between 20 June and 15 August (median 30 July) (Table 1). The SLRT on F98 ceased transmitting on 27 June 2009, 7 days after she exited the Sea of Cortez, prior to the time when she presumably would have returned to GI. The remaining three tagged females returned to GI between 15 September and 6 October (median return date 19 September), well after the return of the males to GI (average return date 22 July) [4]. The duration of the PAP varied from 42–56 days (mean 50 days) with sharks primarily located in the pelagic regions east and south of GI, but on a few occasions, they came into close proximity to GI for short periods (1 to 3 days) before returning to the open ocean (Figure 3). Photo-ID records confirmed the occasional presence of mature females at GI in early September, with numbers increasing in October and peaking in November [12,18]. It is notable that F77 returned to GI directly from the offshore waters in the first year after tagging (11 September 2009), presumably because mating was not successful in 2008. The SLRT data confirmed the photo-ID observations [18] that individual females may not reproduce every cycle. Females that skip a year between reproductive cycles exhibit a 1-year migration cycle similar to that of mature males, involving a shortened offshore phase (instead of an OGP) immediately followed by an aggregation phase (below) without undergoing the PP or PAP.

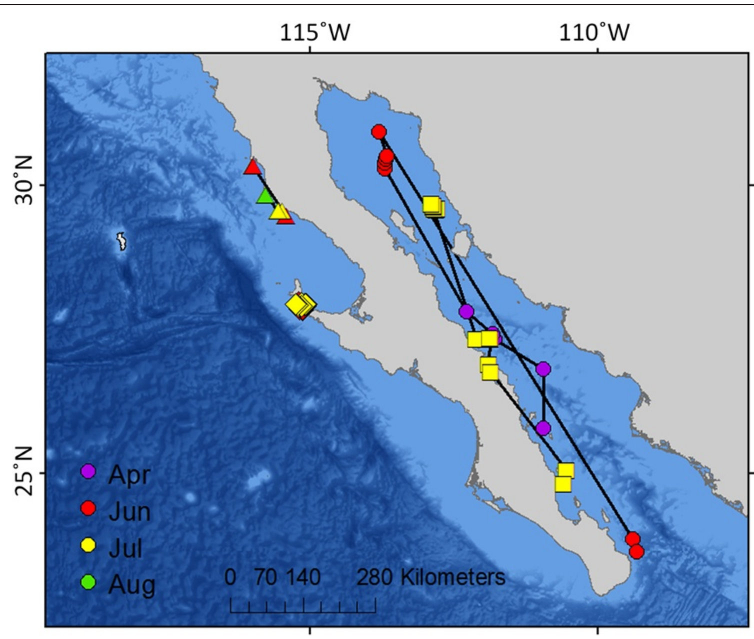

Figure 2 Location data for the four satellite-linked radio-telemetry-tagged female white sharks during the pupping phase. Location data for each shark is indicated by shape (F6 triangle, F77 square, F98 circle, and F100 diamond) and by color for each month.

The purpose of the PAP can only be speculated. The females could benefit from the pinniped populations of GI if they migrated directly to the island from the pupping grounds, but the presence of males may be a deterrent. The migratory behavior of the tagged females during the PAP supports the hypothesis that females actively avoid males until the mating season [7,8]. The PAP may be a period when the females are physiologically preparing to mate again, while avoiding the risks associated with should say inhabiting the same space as adult males.

Guadalupe Island aggregation phase

The GIAP was a period of seasonal residency at GI presumably the time and place of mating [8]. The GI arrival of three tagged females occurred over a relatively narrow temporal window between 11 September and 6 October (Table 1). The percentage of time that SLRT tag transmissions were located within 15 km of GI peaked at close to 100% during the months of October and November (8%, 55%, 98%, 97%, 74%, 52%, and 7%, for August to February, respectively). Conspecific wounds to both male and female white sharks are frequently seen at GI [8,12], confirming that the mating aggregation does involve risk of injury. Male/male aggression certainly occurs, because wounds are seen prior to the arrival of females, but whether the males are defending mating sites or prey resources is unknown.

The GIAP ended when the females departed for the open ocean between 7 December and 25 January (median 23 December) (Table 1), after 83 to 136 days at the island.

Alternative mating hypothesis

Jorgensen *et al.* [27] have proposed an alternative life-history hypothesis that is contradictory to the hypothesis proposed by Domeier [8]. The major difference between these hypotheses pertains to the timing and location of mating. Jorgensen *et al.* [27] speculated that white sharks are mating during their offshore phase, whereas Domeier proposed that mating occurs during seasonal, near-shore, adult aggregations. The hypothesis that white sharks are mating at coastal aggregation sites is supported by a growing body of indirect evidence: 1) the presence of mature females at GI with fresh conspecific bite wounds on the lateral surfaces of their head, pectoral fins, and flanks [8]; 2) the finding of spermatophores in the claspers of males at the GI and central California aggregation sites [8]; 3) a strong spatiotemporal overlap in the distribution of males and females at the GI and central California aggregation sites [7]; 4) strong sexual segregation during the offshore phase [7]; 5) the finding that peak presence of white sharks at GI does not correspond with the seasonal peak abundance of pinnipeds, suggesting that foraging is not the primary motivation for the aggregation [28], and 6) as presented here, a match between the estimated duration of gestation and the time between coastal aggregations and the known pupping season. By contrast, the hypothesis that mating is occurring offshore was not supported by any substantiating evidence, except for the speculative interpretation of diving patterns derived from electronic tags.

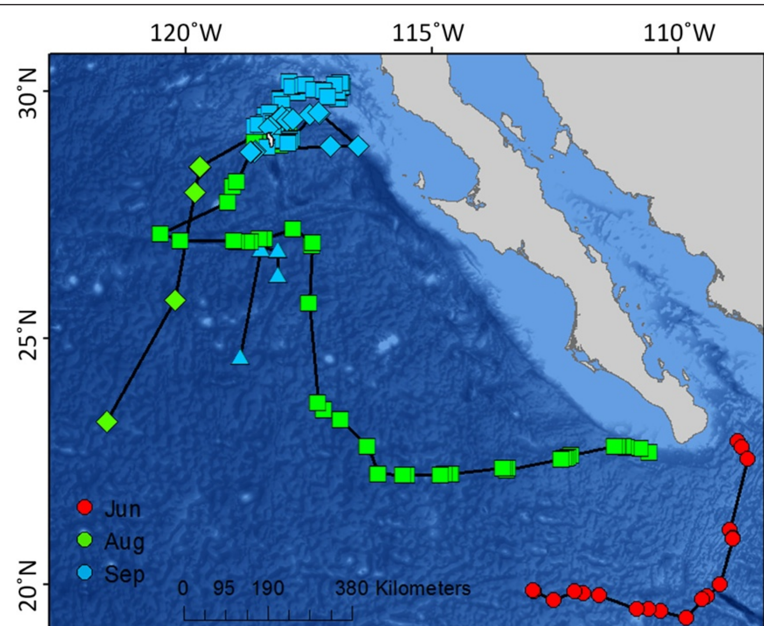

Figure 3 Location data for the four satellite-linked radio-telemetry-tagged female white sharks during the pre-aggregation phase. Location data for each shark is indicated by shape (F6 triangle, F77 square, F98 circle, and F100 diamond) and by color for each month.

The offshore-mating hypothesis is based upon the conjecture that a described vertical-diving pattern (rapid oscillatory diving (ROD)) is a result of a lek-like mating behavior in the core of the SOFA [27]. This interpretation is problematic from several perspectives. Lek-like mating systems involve the gathering of males at a traditional site for the purpose of ritualized courtship display. The males compete for the attention of females, and in turn, the females select a specific male for mating. Although the peak in ROD behavior, and thus presumed offshore mating, occurs during June/July in a period when the distribution of males temporarily constricts, even the constricted offshore space is vast (estimated to be about 64,000 km^2 [7]). Lek-like mating would require the males to be in a very small space to allow females to observe the courtship of several males at once. No electronic-tag data have ever indicated that sharks are densely populating a small, traditional offshore site. Lek-like mating systems have been described for some species of fish [29], but leks have never been seen among elasmobranchs. Females that mate in lek systems select a single male deemed superior to other males, thus the fact that white-shark pups from a single litter tested positive for multiple paternity [14] argues against lek-like mating for this species.

It is challenging to ascribe any behavior to vertical movement data in the absence of visual observations. The seasonal constriction of the SOFA and the ROD-type diving pattern could be due to the pursuit of a seasonally available prey. An expedition to this region during the constriction identified the presence of three species of spawning squid and sperm whales [22], but again, the absence of behavioral observations deems it impractical to assign any cause to the ROD diving pattern. Diving patterns and mating systems aside, there are other strong arguments against the hypothesis that white sharks are mating during the offshore phase of their migratory pattern. First, electronic-tag data indicate that males and females are largely segregated during the offshore period [7], and second, the proposed mating during June/July [27] would equate to December/January pupping (accepting the 18-month gestation estimate [20]). Females arrive at adult aggregation sites approximately in September, and depart in December to end of February. No YOY have been seen at the adult aggregation sites, no obviously pregnant females have been sighted at GI, and pupping is known to occur approximately April through July.

Conservation concerns

The revelation that GI supports two Mexican coastal-nursery areas separated by 1000 to 2000 km gives rise to major conservation implications. In some coastal-shark species, females have been shown to be philopatric to specific nursery regions [30-33]. Longer-term tracking could provide confirmation of such behavior in white sharks, and explain the presence of persistent YOY hotspots [8,24,25,34] and the genetic indication that females do not disperse [11]. Females may be returning to their place of birth to pup; this phenomenon, called 'natal homing', has been suggested for sharks [35], but not yet documented. The existence of natal homing in white sharks would explain the genetic indication that dispersion of this species is sex-biased. Furthermore, natal homing creates population vulnerability; the removal of females that support a specific pupping region would cause a loss of genetic diversity and the collapse of that nursery.

The return of gravid females to coastal regions where active commercial fisheries take place presents the most vulnerable life-history stage for adult females, a threat confirmed by documented mortalities in the Sea of Cortez in 1996 [26], 2004 [36], and 2012 (reported in popular media: http://www.petethomasoutdoors.com/2012/04/great-white-shark-catches-appear-on-the-rise-sea-of-cortez-.html). The SLRT-tagged shark F98 had been reporting regular position data but ceased sending messages soon after exiting the Sea of Cortez, and she has not been subsequently resighted at GI; fishery-related mortality is a reasonable explanation. The 1-year offshore migratory pattern of adult males exposes them to far less commercial fishery pressure than females, because they rarely stray towards the coast of Mexico.

In addition to the threat to gravid females along the coast, there is also a threat to YOY and juvenile white sharks, which are found along the continental shelf in the near-shore regions. Adult white sharks are capable of breaking through most commercial fishing gear to escape, but YOY and juvenile white sharks do not have the mass and strength to do the same, therefore juveniles represent the most vulnerable stage for this species. Care must be taken to protect both the adult females and juveniles and their nursery habitats.

Conclusion

This is the first long term, continuous tracking study of individual adult female white sharks. Our results not only confirmed a 2-year migratory pattern for adult females, they also provide unifying support for the natural history hypothesis proposed by Domeier [8]. This hypothesis proposed that Guadalupe Island serves as a mating site for adult white sharks, and that this site is visited every year by adult males, but only once every two years by reproductively active females. The migratory pattern described here also supports the previously published estimate of gestation period (18 months [20]); a time that we found adult females to spend entirely in the open ocean. Our tracking has highlighted a previously unknown period of vulnerability for adult females: the period of time they are exposed to coastal fisheries when they migrate to the coast of North America to give birth. Adult males from GI, however, do not share this period of vulnerability, since they do not travel to the coast of North America once they reach sexual maturity [8].

Although the exact location of parturition cannot be determined from our tracking, it is clear that females that mate at GI support recruitment of YOY to two widely separated nursery areas; one on the Pacific side of the Baja California Peninsula and the other in the Sea of Cortez. If further tracking reveals that females are philopatric to very specific pupping grounds, the preservation of genetic diversity will depend upon the proper management of both the adult females and pups that support specific nursery area.

Methods

Satellite-linked radio-telemetry tagging

Four mature female white sharks were tagged (SPOT5 SLRT tags; SPOT-257A, Inline Finmount, 4 holes, 7 × 7; Wildlife Computers, Redmond WA, USA) at GI, Mexico in 2008 and 2009 (Table 1) as described previously by Domeier and Nasby-Lucas [7]. In summary, sharks were attracted to the research vessel by baiting a custom-made circle hook (Mustad, Gjövik, Norway) with a tuna or salvaged marine-mammal carcass. The baited hook was suspended behind the vessel via a plastic float. Four to six large plastic floats (22 kg flotation each) were evenly spaced along the line to keep the shark near the surface while providing drag. Once a shark was hooked, a smaller boat was used to follow the shark, bring the animal to the surface by shortening the distance between the floats and the shark, and guide the shark onto a large submerged platform that was attached to the larger research vessel. Once on the platform, the shark was hydraulically raised above the waterline. An irrigation hose was immediately placed in the mouth of the shark to flush seawater over the gills, the hook was removed, and a wet towel was placed over the head to protect the eyes and calm the animal. The time taken to capture the four female sharks ranged from 45 to 162 minutes (mean 77 minutes), and tagging time ranged from 14 to 17 minutes (mean 16 minutes). Each shark was measured and sex recorded prior to release. Determination of sexual maturity for female white sharks was based on a total length of at least 4.5 m [37].

SLRT tags were attached to the apex of the shark's first dorsal fin by drilling four small holes through the fin, and securing the tag with plastic bolts. Each time a tagged shark's dorsal fin was out of the water, a wet/dry switch activated the transmitter. Tags were programmed to transmit a maximum of 250 messages per day. If the tag remained out of the water long enough for an Argos satellite to receive four consecutive transmissions, the Doppler-shift-induced frequency change allowed calculation of the tag's location [38] with associated location error. All messages, even those that did not provide location, gave a status message that included the SST recorded at the location of the tagged shark.

Argos position processing

All transmitted location positions were processed using a Kalman filter and reprocessed by Argos with a smoothing algorithm. The Kalman filter [39] computes the platform location and an error estimate, based on the Argos Doppler frequency measurements obtained up to the date of the location. The smoother is based on the Rauch-Tung-Striebel formulae [40], which combines, in a backward-time recursive process, some quantities produced by the Kalman filter. The Rauch-Tung-Striebel smoother computes the location and the error conditioned on all the measurements recorded (that is, past, present, and future available measurements). Location data were further selected with a speed filter between consecutive points, using the maximum estimated sustained speed of 192 km/day [4].

Data analysis

Date of the start and end of the PP were determined either directly by date of location data when available to indicate movement from the OGP to the PP, or by examining SST associated with transmitted status messages, and matching these to moderate resolution imaging spectroradiometer (MODIS) weekly SST data from the National Aeronautics and Space Administration (NASA) Aqua satellite. The date of the end of GIAP was determined by examining the first point away from GI and calculating the date of departure back in time, based on published average speed during travel (77 km/day [4]). All location points during the offshore phase for all four sharks were used to determine a MCP for the region used while offshore. MCP was determined using the minimum bounding geometry tool in ArcGIS. The percentage of location data from August to February within 15 km of GI was calculated by using a frequency of 1 location per day, and using all data from the four tagged female sharks during those months.

Abbreviations

GI: Guadalupe Island, Mexico; GIAP: Guadalupe Island aggregation phase; MCP: Minimum convex polygon; OGP: Offshore gestation phase; photo-ID: Photographic identification; PAP: Pre-aggregation phase; PP: Pupping phase; ROD: Rapid oscillatory diving; SLRT: Satellite-linked radio telemetry; SST: Sea surface temperature; SOFA: Shared offshore foraging area; YOY: young-of-the-year.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

MLD initiated the study, designed the experiments and deployed the electronic tags on the sharks. NN performed data management and analyses, and created the figures. MLD drafted and NN edited the manuscript. Both authors read and approved the final manuscript.

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