CHAPTER 13

Connectivity among White Shark Coastal Aggregation Areas in the Northeastern Pacific

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ABSTRACT

White Sharks (*Carcharodon carcharias*) in the northeastern Pacific comprise a genetically distinct population, demographically isolated from other populations in Australia/New Zealand and South Africa. Within the northeastern Pacific, mature and subadult White Sharks show strong fidelity to aggregation sites in Central California and Guadalupe Island, Mexico, respectively.

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Individuals tagged at both sites migrate offshore to common pelagic habitats but routinely return to the coastal site where they were tagged. To date, evidence for the connectivity of these coastal sites has been lacking, raising the question whether they comprise one continuous or two distinct populations. A third coastal area, comprising the near-shore waters from Point Conception, California, and extending southward through the Southern California Bight to Sebastian Vizcaino Bay, Mexico, has been recognized as a White Shark nursery area. Although incidental catches in the Southern California Bight comprise mostly neonates and large females, little evidence exists demonstrating the movement of mature females to this purported pupping area, leaving open the possibility that parturition might occur elsewhere followed by immigration of neonates into the nursery area. We illustrate how rare events in a large tagging data set provide important information about the connectivity of aggregation areas within the northeastern Pacific. Acoustic tagging revealed the rare movement of one single female out of 140 deployments, from Central California to Guadalupe Island; the first result to demonstrate movement connecting these aggregation sites. Of 97 pop-up archival transmitting (PAT) tags deployed in Central California, only one deployment was on a large female with healing mating scars indicative of prior mating activity. This female was tracked offshore and eventually into the Southern California Bight where the tag popped up 362 d later off Santa Catalina Island. The movement of this female into the Southern California Bight coincided with the peak period for neonates in the area.

INTRODUCTION

In the past, many viewed the sea as a habitat largely free of physical barriers, a place where globally distributed species could roam unrestricted subsequently exchanging genes along the way as one very large population (Palumbi, 1994). Indeed, early genetic studies on marine fishes were consistent with this view. Most species showed little genetic divergence across very large spatial scales (Avise, 2000). However, electronic tagging studies have provided new insight into the complicated movements of highly migratory marine fish species, including the White Shark. These new data for sharks now show high levels of site fidelity and homing, setting the stage for fine-scale genetic population structure that was, until recently, unexpected.

White Sharks in the northeastern Pacific (NEP) comprise a distinct phylogenetic clade based on mitochondrial DNA markers (Jorgensen et al., 2010). To date, published genetic data collected for the NEP clade only included sharks in Central California (CC). Nonetheless, electronic tagging data indicate that the genetic isolation of NEP sharks is potentially maintained through strong site fidelity to very specific coastal and pelagic habitats (Jorgensen et al., 2010).

Tagging has shown that site fidelity also occurs at more localized scales in the NEP; White Sharks tagged near seal rookeries in CC regularly return to these same rookeries following visits to offshore locations, including Hawaii and the White Shark "Café" (Jorgensen et al., 2010). Similarly, White Sharks tagged at the Guadalupe Island (GI) Northern Elephant Seal rookery also visited the same offshore areas (also referred to as Hawaii and the Shared Offshore Foraging Area or SOFA) (Domeier and Nasby-Lucas, 2008; Chapters 11 and 12, this book) and consistently returned to GI. Although sharks from these coastal aggregation sites in the NEP overlap in a pelagic setting 1,500–4,000 km offshore, there has been no evidence of individuals moving between these coastal sites, leaving open the possibility of further population structure within the NEP. It is unknown whether the groups at these two aggregation sites comprise one continuous or two distinct populations. Understanding the degree of connectivity of these two NEP groups separated by the Mexico-U.S. border is vital for successfully determining their population status, the degree of intermixing, and management options.

Management of White Sharks in the NEP also requires information on the juvenile life stages. The Southern California Bight (SCB) has been hypothesized as a nursery area based on the concentration of neonate White Sharks occurring there in summer and fall (Klimley, 1985; Chapters 14 and 16, this book). This nursery area likely extends from Point Conception, California, southward along the coast across the Mexico-U.S. border to Sebastian Vizcaino Bay (Chapters 14, 15, and 16, this book). Recent reporting on capture records, as well as tracking data from an adult female (Chapter 16, this book), indicate that the nursery may extend further south to Cabo San Lucas and into the Gulf of California, although the smallest size classes (~150 cm; neonates) did not appear in records from the Gulf of California (Galvan-Magana et al., 2010). Neonates are either born in the SCB or are born elsewhere then immigrate into this nursery area. Klimley (1985) showed captures of White Sharks within the SCB consisted primarily of neonates and large females in summer and fall, whereas north of Point Conception captures mainly comprised males and females ≥2 m, in summer, fall, and winter. The seasonal co-occurrence of large females and neonates suggests that late-term females migrate into the nursery area for parturition. However, none of the large females caught were pregnant (five females of >4.5 m total length), and neonates were usually captured closer to shore than the mature females, raising some doubt about conclusions reached from capture data alone.

We used electronic tagging data to determine connectivity within the NEP between White Sharks in CC and GI and between CC and the SCB nursery area. The specific goals of this study were to (1) track potential movement patterns between CC and GI; (2) describe the movement of a mature female from CC that moved into the White Shark nursery habitat in the summer/fall pupping season; and (3) further elucidate the life history, population structure, and connectivity of White Sharks within the NEP.

MATERIALS AND METHODS

Ninety-seven pop-up archival transmitting (PAT) tags (PAT 2.0, 3.0, and 4.0 and Mk10-PAT; Wildlife Computers, Redmond, WA) were deployed on White Sharks in CC. Deployment and position estimation methods are described in detail in Jorgensen et al. (2010). To determine the rate of travel during migration from satellite tag tracks, we calculated the net displacement distance over time between position estimates connecting the coastal area and the Café.

Additionally, we deployed 110 individually coded acoustic transmitter tags (V16-4H; Vemco, Halifax, Nova Scotia) in CC [described in detail by Jorgensen et al. (2010)] and 31 of the same tag model on White Sharks at Guadalupe Island (see Figure 13.1 for deployment date information). Six VR-3 acoustic listening stations were placed at aggregations sites in CC from October 16, 2006 through December 2, 2009. Three VR-2 acoustic receivers were actively stationed around GI from August 2008 through October 30, 2009. Acoustic data were analyzed using MATLAB® (The MathWorks, v.7.9.0.529). Total length was estimated as each shark swam alongside a research vessel of known length. Video and photography were used to help determine sex and individual identification.

RESULTS

Of the 141 acoustic tag deployments, 110 at CC and 31 at GI, a single individual was detected at both locations (Figure 13.1a). The 366-cm female, S153, was tagged on September 14, 2008 near Tomales Point in CC and remained locally during the following month until October 13, 2008. During this 29-d period the shark was detected 528 times with a mean time between detections of 28.9 min. (minimum = 1.1 min.; maximum = 5.4 d). The shark was next detected at GI, 1,000 km to the southeast, 29 d later on November 12, 2008. The minimum mean velocity the shark would have to travel from CC to GI was 34.5 km/d. S153 then remained at GI until March 7, 2009. During this 115-d period, the shark was detected 15,365 times with a mean time between detections of 11.0 min. (minimum = 1.1 min.; maximum = 7.9 d). On March 7, 2009, the shark apparently departed, coincident

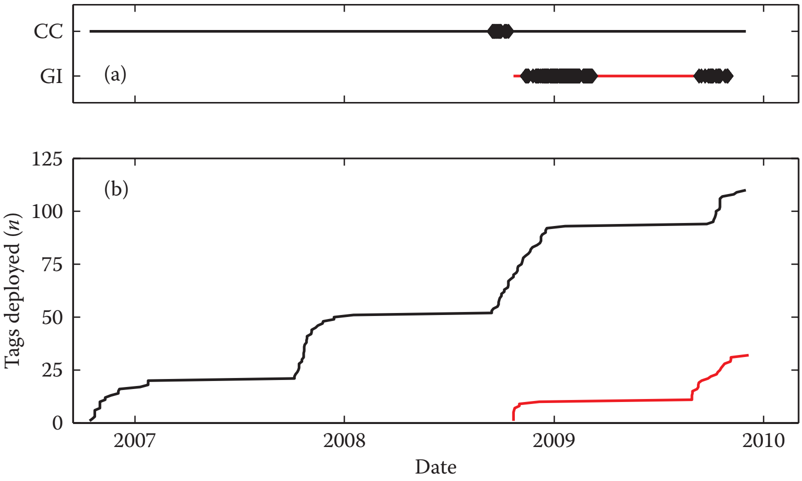

Figure 13.1 Movement of *Carcharodon carcharias* between CC and GI determined from acoustic tagging. (a) Receivers were actively deployed at CC from October 15, 2006 and December 14, 2009 (black line) and from October 22, 2008 to October 30, 2009 at Guadalupe Island (red line). White Shark S153 was tagged in Central California on October 13, 2008 and was detected (black diamonds) locally for 29 d before leaving the area. The shark was subsequently detected at GI on November 12, 2008. S153 remained near GI for 115 d until March 7, 2009. Then, after a 185-d absence, the shark returned to GI on September 10, 2009 and remained there for an additional 50 d. (b) The cumulative number of acoustic tags deployed at CC (black line) and GI (red line) over time totaled 110 in CC and 31 at GI. The movement of only a single individual suggests that such exchanges are relatively rare.

with the expected offshore migration season, and was not detected again for 185 d. On September 10, 2009, S153 returned to GI, where it was detected for another 50 d through the remainder of the data collection period, ending October 30, 2009. During these 50 d, the shark was detected 386 times with a mean period between detections of 3.1 h (minimum = 1.1 min.; maximum = 8.5 d).

A total of 68 White Sharks (23 females, 32 males, and 13 unsexed) were successfully tracked using satellite tags. The mean deployment duration was 199 d. The tagging dates, size estimates, deployment durations, and gender information are summarized in Supplemental Table S1 in Jorgensen et al. (2010). S70, a female tagged with a PAT tag on October 9, 2006 at the South East Farallon Island in CC, was tracked for 362 d, the longest deployment. Following tagging, the shark remained in the CC vicinity for more than 3 months until heading offshore near the middle of January (Figure 13.2). The shark travelled toward the Café region at a mean displacement rate of 87 km/d. Once offshore, the shark remained around the Café region until April and then made one relatively direct movement toward SCB (mean displacement rate = 60 km/d) only to return offshore (68 km/d) again. The "turnaround" occurred apparently before reaching the continental shelf, at which time the tag records showed a minimum sea-surface temperature of 13.6°C reached on April 16 and 17. In June, the shark travelled to the SCB (50 km/d), arrived at the beginning of July, and remained there until at least October 5, 2007, when the tag released according to the preprogrammed date and was first detected near Two Harbors on Santa Catalina Island (Figure 13.2). The estimated total length for S70 when tagged was 488 cm. Notably, females of >450 cm total length are believed to be reproductively mature (Francis, 1996), and S70 was the only female bearing evidence of relatively recent mating activity (Pratt and Carrier, 2001) at the time of tagging (Figure 13.3). No other females or males with satellite tags moved into the SCB during the period of tracking. Of the 23 females tagged with PAT tags, nine individuals were >450 cm (mature) and spanned a tracking period past May 16, the earliest recorded calendar date of neonate (≤150 cm) capture (Klimley, 1985). Of these nine records, two individuals returned to Central California in August [shark 50 and 59 (Supplemental Table S1 in Jorgensen et al., 2010)], and six tags popped

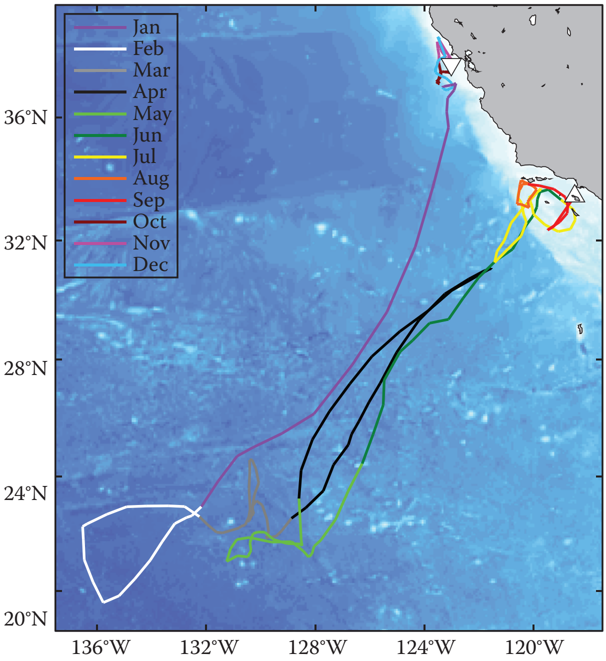

Figure 13.2 The movement of a female White Shark from Central California to the Southern California Bight. S70 was tagged on October 9, 2006 (∇) near the Farallon Islands in CC, and the tag popped off, according to schedule, October 5, 2007 (Δ) near Fisherman's Cove off the northeast side of Santa Catalina Island in the SCB. The track line describes a five-point moving average of geolocation positions, and color coincides with the month.

Figure 13.3 Shark S70 just prior to tagging on October 8, 2006, showing evidence of partially healed presumed mating-induced injury.

up in the Café region [two each in July, August, and September; sharks 8, 91, 35, 42, 46, and 137, respectively (Jorgensen et al., 2010)].

DISCUSSION

The predictable migratory patterns in White Sharks frequenting GI compared with those showing fidelity to seal rookeries in CC provide a compelling possibility of population structure within the NEP. Indeed, previous tagging results suggested no movement between the two aggregation sites (Domeier and Nasby-Lucas, 2008; Jorgensen et al., 2010; Chapters 11 and 16, this book). The documentation here of only one single individual moving between CC and GI despite the large number of tags suggests that such movements are relatively rare occurrences. Nonetheless, following tagging, S153 resided in CC for 1 month then moved to GI, revealing for the first time connectivity between these two NEP aggregation sites.

Given the apparent segregation between White Sharks frequenting CC and GI, the discussion of the potential genetic exchange between the groups has focused on the possibility of intermating offshore in a shared area, the White Shark Café (Jorgensen et al., 2010), or mixing in a common pool of offspring, a single nursery area in the SCB from which mixed juveniles could recruit to either GI or CC. However, this study provides the first empirical documentation of exchange through direct migration between the two groups. The continual use of acoustic receivers and tags (which have a >3-year life span), will help determine how frequently these exchanges occur, provided receivers are maintained at both locations.

Evidence of these movements might be further elucidated using individual photo-identification methods. Anderson et al. (2011) described nearly 200 individuals over 22 yrs. using dorsal fin photographs in CC. Fin morphology was shown to be conserved over long time periods (Anderson et al., 2011) and should allow comparison of sharks between CC and GI sites for years to come. At GI, 113 unique individuals were identified over 9 yrs. (Chapter 25, this book) using unique body pigmentation markers. Chapple et al. (2011) estimated the current population of mature and subadult White Sharks off CC to be 219 individuals (between 130 and 275; 95% credible intervals). At GI, an open mark-recapture framework of the 9-year photo-identification collection suggests an index of abundance near 120 adults and subadults (Chapter 26, this book); however, this may be an underestimate. Nonetheless, potentially a high percentage of adults and a fair number of subadults are currently identified in the NEP, raising the likelihood of detecting exchanges between CC and GI in the future. Acquiring body pigmentation photos in CC is problematic because of poor water clarity, whereas no limitation on acquiring dorsal fin photos exists at GI. Therefore, efforts should be made to standardize individual identification methods using fin morphology at both locations.

Further molecular testing will determine whether GI and CC adults could be genetically divergent. The answer is important for White Shark conservation, because estimates of the number of individuals in both groups is alarmingly low. If these are in fact separate gene pools, separate management measures will need to be developed. However, answering this question conclusively will be challenging. First, mitochondrial DNA has a slow mutation rate in sharks (Martin et al., 1992). Very few polymorphic sites were observed in the DNA sequence that could distinguish these putative populations from each other. In fact, over 60% of sampled CC individuals belonged to two main female lineages (Jorgensen et al., 2010), which means many more samples will be needed to test for statistical significance. Second, even low levels of mixture between CC and GI, either by gene flow or spatial overlap, can inhibit sensitivity of the genetic analyses. The use of faster evolving markers, such as microsatellite loci, may offer a better test for GI and CC adults. These markers also provide a means to genetically fingerprint individuals (Gubili et al., 2009) and quantify measures of kinship (Feldheim et al., 2004). Matching adults to their offspring in the SCB is possible given a small population size and should help discriminate between potential mixing mechanisms.

To quantify mixing between the two sites, the use of acoustic and satellite tags, photo identification and genetics are important complementary tools. The extent and patterns of mixing will be important to understand whether this population functions as a single mixed population in the NEP or as separate subpopulations with little exchange. Additionally, this will help determine to what extent management policy should be coordinated across the U.S.-Mexico boundary.

As with mixing between CC and GI, evidence that female sharks move from CC to the purported nursery grounds is rare. S70 is the first tagging record showing an adult White Shark traveling from the CC aggregation site into the vicinity of the SCB nursery area. The only other published record is from a White Shark that was photographed at the South Farallon Islands on November 7, 1988, and then photographed again 6 yrs. later on October 18, 1994, halfway between Santa Catalina Island and Newport Beach, California in the SCB (Anderson and Goldman, 1996). Interestingly, the location where this shark was subsequently photographed in the SCB was less than 30 km from where S70's tag popped up. Of the nine mature females with records extending past May 16, S70 was the only tagging record to show this movement pattern; however, this was also the only female with evidence of prior mating activity to be tagged. Two of the nine sharks returned to Central California within 1 yr. of tagging. However, the possibility that any of the remaining six individuals moved to the SCB during the parturition period after the tags popped up (in the Café region) could not be ruled out because the tags popped up between July and September. Observations of female White Sharks with relatively recent mating marks are rare in CC. During fieldwork conducted in CC over the past two decades, 395 encounters with White Sharks were photographically documented (Anderson et al., 2011), yet only five instances of apparent mating-induced trauma occurred, and of these only S70 was tagged. All of the cases were similar in that the wounds were partially healed. That mating marks are infrequently observed on White Sharks in CC suggests either that mating events are rare or that females generally remain offshore following mating during the period when such marks would be healing. Also, the absence of observations of fresh mating marks, despite such extensive observation, is inconsistent with the hypothesis that mating occurs with any regularity at coastal foraging sites in CC. Healing rates are high in White Sharks (Chapter 6, this book). Nonetheless, the possibility that the wounds on S70 occurred offshore at the Café prior to arriving at the Farallones cannot be ruled out. Despite where mating may actually occur, the presence of the partially healed scars and the subsequent movement of S70 into the SCB support the hypothesis that gravid females from the CC group migrate to the SCB to birth (Klimley, 1985).

The gestation period for White Sharks is thought to be between 12 and 18 months (Francis, 1996). Assuming this is accurate, and given the mean calendar date of neonate (≤150 cm; Francis, 1996) captures in the SCB is in August (Klimley, 1985), fertilization should occur between February and August of the previous year. If the mating wounds on S70 occurred approximately >45 d prior to the date photographed (Figure 13.3; October 9), then this observation would fit the prediction. However, the precise gestation period for White Sharks remains unknown, and the possibility of sperm storage also has not been determined for the species.

CONCLUSION

Previously, extensive, satellite tagging data sets had suggested isolation between the CC and GI aggregation sites within the NEP. White Sharks showed strong fidelity to these sites with no indication of movement between them, despite habitat overlap and seasonal mixing at offshore areas. Additionally, electronic tracking data had yet to confirm the movement of females (or males) from adult sites to the SCB. Through satellite and acoustic tagging, photo identification, and data sharing between CC and GI study sites, we revealed rare but important observations illustrating the connectivity of these three coastal areas vital to the understanding and management of NEP White Shark population. Internationally, White Sharks (*Carcharodon carcharias*) have been categorized as vulnerable to extinction on the World Conservation Union "red list" (IUCN 2010-04-27, Category VU A2cd+2cd) and are listed under Appendix II of the Convention on International Trade in Endangered Species. This study provides an update to the spatial dynamics of the NEP White Shark population offering a better understanding of a complex species by providing further information on the reproductive and migratory ecology of the species and underscoring the importance of U.S.-Mexico collaboration in research and management.

ACKNOWLEDGMENTS

This project was funded by the Sloan, Moore and Packard Foundations as a part of the Tagging of Pacific Pelagics program of the Census of Marine Life. The Monterey Bay Aquarium Foundation, Shark Diver, The Guadalupe Island Conservation Fund, Pfleger Institute of Environmental Research, Instituto Politecnico Nacional (COFAA, EDI), Iemanya Oceanica, International Community Foundation, WWF-Telcel Alliance, and Grupo Bursatil Mexicano also provided financial support. We thank J. P. Kanive, J. Barlow, C. Logan, R. Elliot, J. Cornelius, T. O'Leary, P. Douglas, G. Grivetto, K. Neff, B. Cornapple, J. Schaeffer, J. Fitzgerald, B. Becker, R. Theiss, C. Farwell, A. Carlisle, S. McAfee, J. O'Sullivan, M. Castleton, J. Ganong, L. Rodriguez, and A. Swithenbank for assistance with field work, lab work, data processing, and editing. We thank CICIMAR, the Mexican Navy, Comision de Areas Naturals Protegidas, Island Conservation, and local fishermen from Guadalupe Island for assistance. We are grateful to SeaLife Conservation, R. Repass, E. Homer and the crew of the *R.S.V. Derek M. Bayliss*, Horizon Charters, Islander Charters, *Nautilus Explorer*, *Sea Escape*, *Solmar V*, and *M/V Andrea Lynn* for vessel support. The project was conducted with U.S. permits from CDFG, MBNMS, GFNMS, NMFS, NPS, and under Stanford University animal subjects Protocol 10765. In Mexico, work was conducted with permits from Secretaria del Medio Ambiente y Recursos Naturales (SGPA/DGVS/04053/07), Comisión Natural de Áreas Naturales Protegidas (F00.RNO.RBIG.-154/07 and F00.RNO.RBIG-166/07), and Secretaria de Gobernación con Oficio (DICOPPU/211/1827/07).

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