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Short Communication

Strongly directional and differential swimming behavior of an adult female white shark, *Carcharodon carcharias* (Chondrichthyes: Lamnidae) from Guadalupe Island, Mexico

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ABSTRACT. We report on an adult female white shark tracked for 288 days and 7,100 km in the NE Pacific Ocean. The shark, tagged with a real-time satellite tag off Guadalupe Island, Mexico in October 2006, remained around the island for 3.5 months but left in early February 2007 for a *ca*. 3,900 km westward migration. Heading and swimming speed data showed that: a) the arc-like route followed by this shark during oceanic travel involved strongly directional rapid movement, and b) once the shark arrived to a specific (*ca.* 680 km wide) area located 790 km north-northeast of the Hawaiian Islands, it switched into a distinct roaming behavior. The shark remained in this roaming area from late March to at least late July 2007. We show that real-time satellite tags can provide unique and valuable information about the migratory behavior of white sharks.

Keywords: *Carcharodon carcharias***,** white shark, real-time satellite tags, oceanic migration, sustained swimming speed, telemetry.

Comportamiento de nado diferencial y altamente direccional en una hembra adulta del tiburón blanco, *Carcharodon carcharias* (Chondrichthyes: Lamnidae) de Isla Guadalupe, México

RESUMEN. Se presentan datos sobre una hembra adulta de tiburón blanco rastreada por un total de 288 días y 7.100 km en el océano Pacífico nororiental. El tiburón, marcado con una marca satelital de tiempo real en la Isla Guadalupe, México, en octubre 2006, se movió durante 3,5 meses alrededor de la isla, pero la dejó a principios de febrero 2007 para migrar casi 3.900 km hacia el oeste. Los datos de velocidad y rumbo de natación mostraron que: a) la peculiar ruta en forma de arco seguido por este tiburón durante el viaje oceánico incluyó movimiento rápido fuertemente direccional de gran escala, y b) una vez que el tiburón llegó a una zona específica (aprox. 680 km de ancho) ubicada 790 km al norte-noreste de las islas de Hawai, cambió a un comportamiento distintivo de vagancia. El tiburón se mantuvo en esta área de vagancia desde fines de marzo hasta al menos fines de julio de 2007. Las marcas satelitales de tiempo real pueden proporcionar información única y valiosa sobre el comportamiento migratorio de los tiburones blancos.

Palabras clave: *Carcharodon carcharias***,** tiburón blanco, marcas satelitales de tiempo real, migraciones oceánicas, velocidad sostenida de nado, telemetría.

Satellite telemetry studies have shown that white sharks are not as coastal in nature as previously thought (Boustany *et al.*, 2002). They have seasonal oceanic migrations in the NE Pacific Ocean (Boustany *et al.*, 2002; Weng *et al.*, 2007; Domeier & Nasby-Lucas, 2008; Jorgensen *et al.*, 2010), frequent tropical migrations along the SW Pacific Ocean (Bonfil *et al.*, 2010; Duffy *et al.*, 2012), and in the Indian Ocean, the only known transoceanic return migration for a white shark (Bonfil *et al.*, 2005a).

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Notably, most of the existing information on oceanic migrations of white sharks comes from pop-up archival transmitting (PAT) tags, whose estimated tracks are prone to large position uncertainties especially in latitude (Musyl *et al.*, 2001; Itoh *et al.*, 2003). Even when Kalman filter models integrating SST satellite data are used to improve position estimates (Sibert *et al.*, 2003; Nielsen *et al.*, 2006), they typically have root mean square errors of 1.84° in latitude and 0.78° in longitude and mean great-circle errors of 213 ± 54 km between locations (Wilson *et al.*, 2007). Real time satellite tags (RTSTs) offer high-resolution data in time and space with position estimates that can be as accurate as <150 m (Bruce *et al.*, 2006), thus providing more accurate and reliable tracks. However, available information about white sharks' movements from RTSTs is limited to some data on coastal migrations in Australia and South Africa (Bonfil *et al.*, 2005a; Bruce *et al.*, 2006) and the recent oceanic tracking of eight male and four female adults in the NE Pacific (Domeier & Nasby-Lucas, 2012, 2013) and a juvenile male in Australia (Bruce & Bradford 2012).

This paper presents results of the RTST tracking of an adult female white shark including oceanic travel. We identify strongly directional rapid movement during the oceanic traveling phase in addition to roaming in an area away from previously-reported focal centers of white shark activity in the NE Pacific. The results are particularly important because this is only the fifth-ever and the largest adult female white shark tracked to date with a RTST.

A 5.10 m TL female white shark was fitted with a Smart Positioning and Temperature Transmitting (SPOT2) satellite tag (Wildlife Computers, Redmond, WA) off the north east coast of Guadalupe Island, Mexico (29°03'N, 118°16'W) at 10:57 a.m. on 16 October 2006. In order to maximize the number of possible fixes for the sharks the tag was set to transmit if dry at all hours, days and months, with a maximum of 500 transmissions per day. The shark was tagged using techniques described by Bonfil *et al*. (2005b). A towel was used to blindfold the shark and keep it completely calm, thus avoiding the need to use any type of anesthetic. Pressure-aerated sea water was pumped directly into the shark's mouth during the entire time it remained out of the water using a 5 cm wide industrial hose fitted at the end with a metallic pipe surrounded by 2.5 cm neoprene to protect the shark's teeth from breaking while ensuring that the shark's bite would not prevent water flow. A veterinarian took blood samples from the lateral abdominal vein and injected the shark with vitamins (E and complex B), antibiotics (Amikacin), and steroids (Prednisone) to help it recover from exhaustion and avoid shock.

The Argos system classifies location quality as class 3, 2, 1, 0, A, B, and Z with class 3 being the most accurate (error <250 m) and class 0 the least accurate (error ≥1.5 km). Positions classified as A, B or Z have no estimate of error and can be either as accurate as a quality 3 message or several hundred km in error. Our track was constructed using positions from all location classes except 0, A, B and Z class positions that fell out of the plausible range of movement of a shark given the immediate previous valid position. Positions that implied a swimming speed of a) more than double the maximum cruising speed reported in the literature for a white shark (8 km h^{-1}; Domeier & Nasby-Lucas, 2008) sustained for >10 min, or b) speeds >50 km h^{-1}, were eliminated from the track. Headings for each segment of the track were calculated using the heading tool of Google Earth on a plot of the shark's track.

Swimming speed was calculated by estimating the distance between adjacent positions using the Haversine formula for great circle distance on an R code program and dividing this by the time elapsed between both positions' time stamps. However, in order to explore possible patterns in sustained swimming speed, calculations were based on data that were filtered by keeping only one transmitted position per day. The position with the highest quality satellite class location for each day was always used; when several positions of equal quality existed for one day the location most equidistant in time to adjacent day positions was kept.

An analysis of time spent by the shark in four geographic quadrants around Guadalupe Island was performed. The four geographic quadrants were arbitrarily defined as shown in Figure 1. Data analysis included calculating the total number of days in which transmissions were received in each quadrant. When two quadrants received transmissions during the same day, parts of the day were allocated to each quadrant proportionally to the time at which transmissions were received. Days of no-transmission and positions beyond 20 km from shore were not incorporated into this analysis.

The female white shark (bearing tag 40788; thus we refer to it as 'shark 40788' hereafter) was tracked intermittently for a total of 7,100 km and 228 days, from 16 October 2006 to 31 July 2007, when transmissions ceased. The tag transmitted a total of 90 different days during this period providing 169 usable position fixes.

Satellite tracking data for shark 40788 were broken down into three distinct spatial dynamics behaviors: 1) extended usage of the coastal and nearby waters off Guadalupe Island during autumn and the first half of the winter with a preference for the NE coast, 2) a fast and strongly directional westward long-distance migration across the NE Pacific Ocean, and 3) search-like movement in a large 'roaming' area NNE of Hawaii (Fig. 2).

Transmitted data indicate that the shark remained around Guadalupe Island and its vicinity for the next 3.5 months after tagging, traversing a total minimum of 951 km during this period (Fig. 1). Data on time spent by the shark in each of four quadrants around Guadalupe Island are consistent with a preferential usage of the NE coast (17.2 days; 48%) followed by the SW (12.3 days; 34%), with considerably less time spent in the SE (4.5 days; 13%) and only marginal use of the NW coast of the island (2 days; 6%). There was no apparent seasonality in the spatial behavior around the island, with the shark making one or more brief incursions into the west coast from the eastern side of the island each month from October to February.

Constant rapid strongly directional movement characterized the second spatial dynamics behavior: oceanic migration (Fig. 2). Transmitted data indicate that once shark 40788 left Guadalupe Island on 3 February 2006 (110 days after tagging) it swam continuously in a parsimonious way within a narrow heading. The semi-circular track of shark 40788 was devoid of major deviations from a strikingly direct route to a large area *ca.* 790 km north northeast of the Hawaiian archipelago. This movement was characterized by strong directionality as evidenced by a track whose segments had headings restricted between 208° and 319°; only 3 out of the 67 segment headings comprising oceanic travel deviated from this range until the shark changed behavior well inside the 'roaming' area (see below). Shark 40788 took only 52 days to span the 3,903 km that separate Guadalupe Island from its westernmost location in the 'roaming' area in the central NE Pacific Ocean, and with the three exceptions noted above (all lasting less than 15 h) it never backtracked on its westward path during its oceanic migration phase.

Shark 40788 arrived to a *ca.* 252,000 km^2 and 680 km wide 'roaming' area on 20 March 2007 (45 days after leaving Guadalupe Island) and remained there until transmissions ceased. Once inside the 'roaming' area the animal's westbound directional movement continued for seven more days but was followed by the first substantial change in direction since the shark had left Guadalupe Island (Fig. 2). Our data suggest that at this point (27 March 2007) the shark switched to a third spatial dynamics behavior typified by a search-like movement pattern. The shark moved in a zigzag fashion

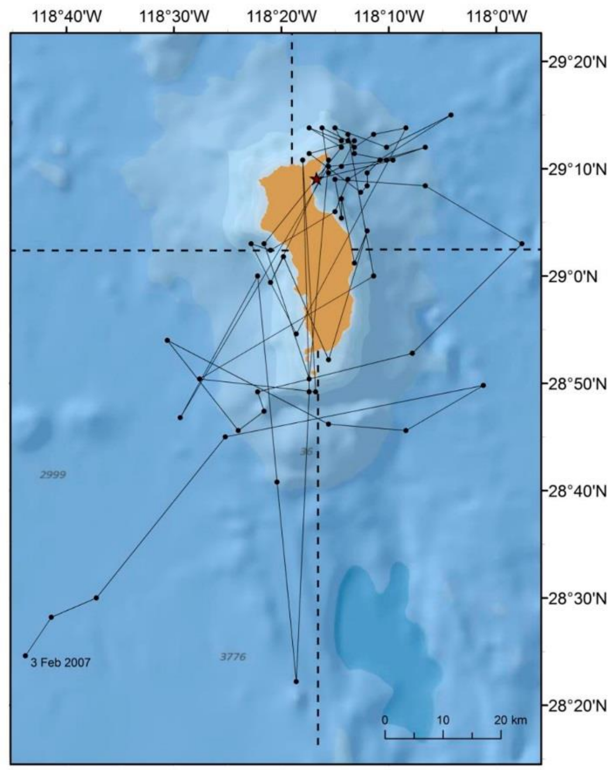

Figure 1. Usage of the marine environment off Guadalupe Island by shark 40788. Different shades of blue represent depth, darker color greater depth. Black star shows tagging site. Dashed horizontal and vertical lines arbitrarily define four quadrants. The data show the female shark's preference for waters closer to shore in the NE coast and zigzagging behavior in the south of the island before departure for oceanic migration. The shark did not necessarily follow the path depicted by the straight lines, sequentially joining each of the locations reported by the tag.

inside the roaming area for the next four months, first describing a clockwise loop that crossed its arrival track to this roaming area, then moving further back east along its approaching path for *ca.* 300 km. Northward and then southeastward movement for about 500 km followed this; finally the shark moved across the northern edge of this roaming area back west towards its westernmost position. The last position transmitted by shark 40788 was received on 31 July 2007. Shark 40788 was photographed back in Guadalupe Island in October 2008 (M. Domeier, *pers. comm.*, 31 October 2011); the SPOT tag had fallen off and the fin had healed.

Data on sustained swimming speed are consistent with the three distinct spatial dynamics behaviors described above for shark 40788 (Fig. 3). Sustained swimming speed data for shark 40788 around Guadalupe Island was characterized by low spread and

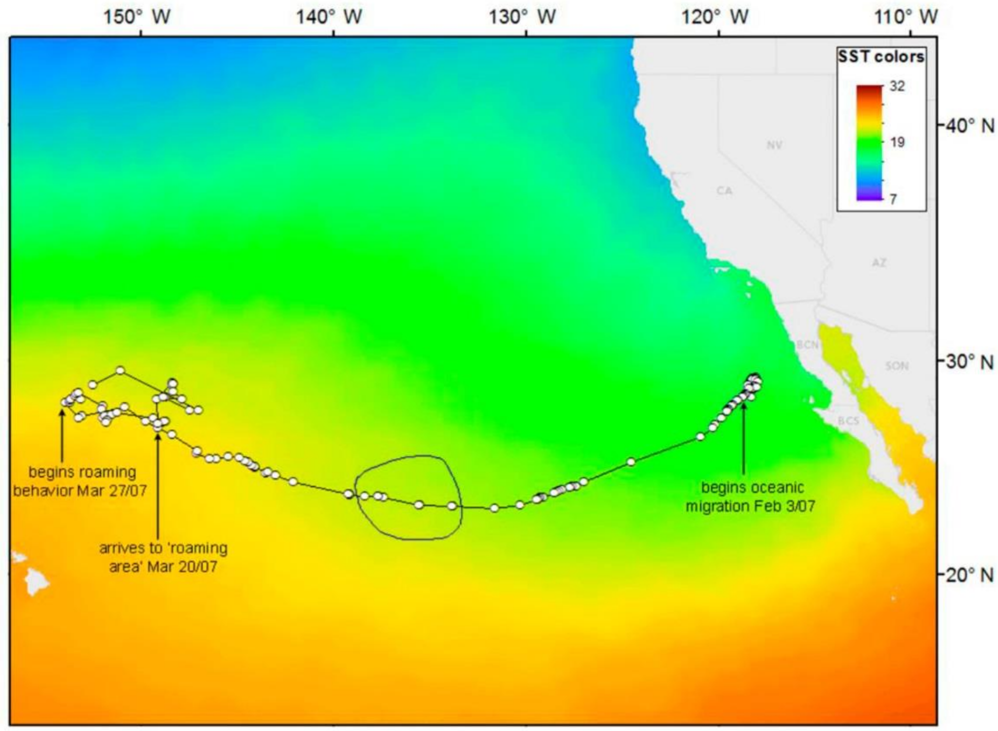

Figure 2. Complete track of SPOT-tagged shark 40788 from 16 October 2006 to 31 July 2007 overlaid on a composite SST map covering the tracking period. The shark spent 3.5 months around Guadalupe Island then migrated west for 52 days and 3,903 km following a remarkably smooth arc path to a roaming area where it engaged in search-like swimming behavior for the next four months. Arrows show notable dates along the track; the elliptical figure in the center of the map corresponds to the 50% density countor for the Shared Offshore Foraging Area as defined by Domeier & Nasby-Lucas (Domeier & Nasby-Lucas, 2012).

low values between 0.05 and 2.05 km h^{-1} (average 0.56 km h^{-1}). This pattern changed sharply as soon as the female shark left the island and embarked on its oceanic migration: sustained swimming speed increased and became more spread with values ranging between 0.88 and 5.04 km h^{-1} (average 3.12 km h^{-1}); however during this phase the data showed a downward trend. Finally, sustained swimming speed during the searching behavior inside the roaming area decreased to values ranging between 0.22 and 2.93 km h^{-1} (average 1.47 km h^{-1}). Average sustained swimming speeds between each of these three spatial dynamics behaviors were all significantly different from each other (Welch two-sample *t* test: t = -13.22, $P < 2.2\ e^{-16}$ for island *vs* migration; t = -5.11, $P = 7.10\ e^{-6}$ for migration *vs* roaming; t = 7.38, $P = 1.33\ e^{-9}$ for island *vs* roaming).

A preference for the NE coast of Guadalupe Island by white sharks seems to be a consistent pattern when our data is considered jointly with other available observations. Domeier & Nasby-Lucas (2008) and Hoyos-Padilla (2009) reported a preference for the NE coast of the island by juvenile and adult white sharks and lesser but important usage of the SW coast of the island. Recent high-resolution data from 12 sharks tracked with RTSTs (Domeier *et al.*, 2012) shows the NE coast as the overall focal point of white shark distribution in Guadalupe Island. Other studies (Domeier & Nasby-Lucas, 2007, 2008, 2012, 2013; Nasby-Lucas *et al.*, 2009; Domeier 2012) have shown that white sharks have seasonal site fidelity to Guadalupe Island from July to May with peak numbers from September to November. Sharks generally leave for their westbound oceanic migration between December and May with mean departures dates for both sexes in February; males return to Guadalupe Island each year and females every other year (Domeier & Nasby-Lucas, 2008, 2012, 2013).

The higher location accuracy that SPOT tags provide makes the track of shark 40788 during its long-distance voyage into the Eastern Pacific Ocean of particular value. With only four comparable datasets previously reported (Domeier & Nasby-Lucas, 2012, 2013) this is only the fifth time that a long-term and high-resolution track of an adult female white shark embarking in oceanic migration is presented.

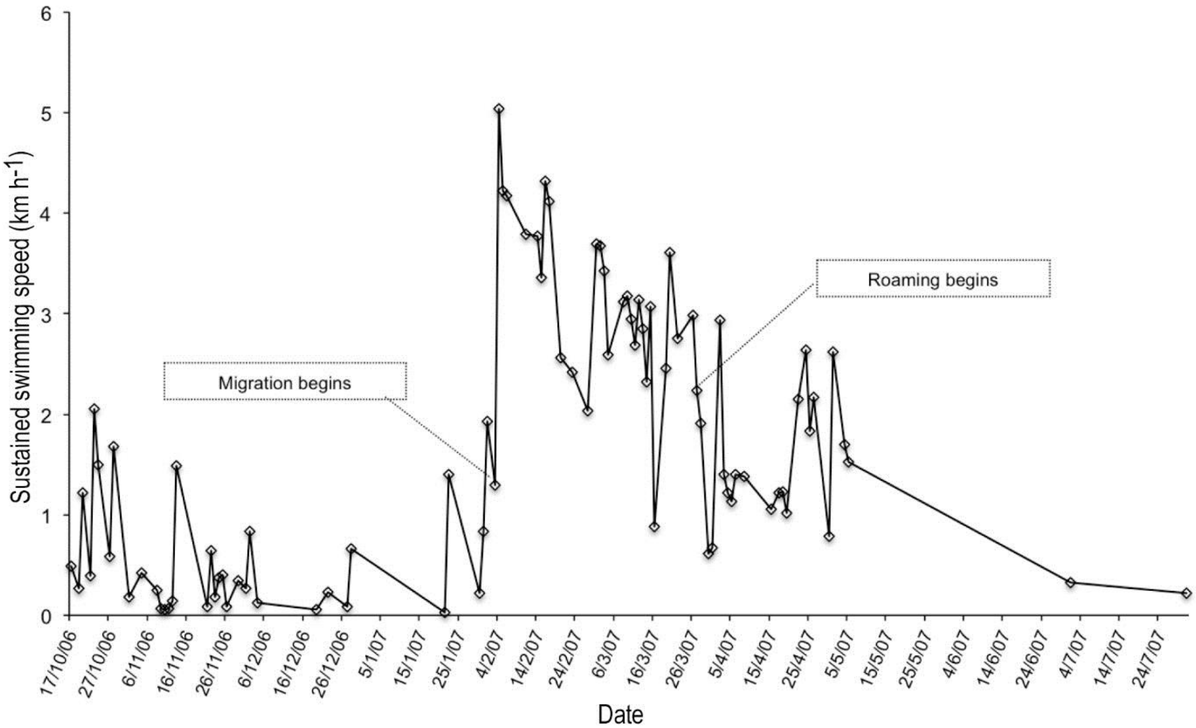

Figure 3. Estimates of the shark's sustained swimming speed from filtered positions. The data show different patterns depending on spatial dynamics behavior of the shark. As it leaves Guadalupe Island to embark on oceanic travel swimming speed increases considerably, decreasing significantly once it reaches the roaming area and begins zigzagging.

The smooth arc followed by shark 40788 between Guadalupe Island and the roaming area (Fig. 2) is indicative of strong directionality in the shark's migratory route and suggests a remarkable navigation capability for this shark. This movement pattern differs with previous reports of white sharks during oceanic migration tagged with PAT tags off California and Guadalupe Island (Weng *et al.*, 2007; Domeier & Nasby-Lucas, 2008; Nasby-Lucas *et al.*, 2009; Jorgensen *et al.*, 2010). Previous tracks show less directional movements typified by relatively large changes in heading that vary in frequency for each track. Whether these differences in movement pattern are true behavioral differences or are largely due to the effect of the inherent noise of the PAT-derived tracks and their comparable lower location resolution remains to be found. Further research double-tagging individual white sharks with PAT and SPOT tags should be carried out to answer this question and gain a better understanding of the finer scale details of migratory routes followed by white sharks.

Recent studies provide details of individual tracks for SPOT-tagged adult white sharks embarking in oceanic travel in the NE Pacific (Domeier, 2012; Domeier & Nasby-Lucas, 2012, 2013). However, none of these reported long-distance strongly directional movement at the scale demonstrated here (nearly 4,000 km) for an adult white shark. Tracks for four females and three males tagged off Guadalupe Island show most sharks, while in oceanic waters, display meandering tracks with relatively frequent strong changes in direction sometimes interspersed with much shorter periods of directional travel (Domeier, 2012; Domeier & Nasby-Lucas, 2012, 2013). This makes ours the first report of an adult white shark traveling in a fast and strongly directional way to a long-distance area during oceanic travel. A juvenile male white shark tracked with a RTST in Australia is the only available report of similar strongly directional movement. This male moved for about 3,000 km between Port Stephens in Australia and the west coast of the South Island of New Zealand describing a strongly arched track (Bruce & Bradford, 2012). While that track is shorter and more narrowly arched than the one followed by shark 40788 it is also indicative of strongly directional long-distance movement and further supports the remarkable navigational abilities of white sharks. Why only some individuals show this type of swimming behavior whilst others of the same populations display much less directional travel remains unknown and opens further opportunities for interesting research.

An important finding of the present study is that speed analysis allowed us to validate the different movement phases of this shark in the marine environment of the NE Pacific. In particular, the data show that the shark significantly increased its swimming speed from an average of 0.56 km h^{-1} to an average of 3.12 km h^{-1} when it switched from roaming around Guadalupe Island to its oceanic migration, and that its sustained swimming speed decreased to an average of 1.47 km h^{-1} once the shark began its search-like movements in the roaming area.

There are no other reports with detailed analyses of data from either RTSTs or PAT tags comparing sustained swimming speeds for white sharks during the different movement stages of their migratory cycle. However, Boustany *et al.* (2002) also report on a white shark traveling at considerable speed during oceanic movement (2.96 km h^{-1}) and Bruce & Bradford (2012) using a different approach to analyze RTST data were able to identify conspicuous movement changes differentiating oceanic travel from resident behavior. Future studies with RTSTs will be necessary to confirm if our findings are common to other ocean-migrating white sharks.

This contribution constitutes an important addition to the small amount of high-resolution baseline information on the spatial dynamics of white sharks and particularly that of adult females. More specifically, our results provide evidence of strongly directional and rapid movement over a vast distance that highlights the remarkable navigational capabilities of white sharks. In addition our study quantitatively demonstrates different swimming behaviors during the migratory cycle of the species and suggests extended usage of the oceanic habitat by female white sharks during their offshore migration in the Eastern Pacific Ocean.

These findings also highlight the importance of using RTSTs in addition to PAT tags for the study of marine megafauna. It follows that studies of spatial dynamics of marine species that spend considerable time at the surface should ideally be made with a combination of PAT and RTSTs whenever possible (Bonfil *et al.*, 2005a; Domeier, 2012; Domeier & Nasby-Lucas, 2012). Such an approach would be a cost effective way to increase the chances of obtaining a more complete understanding of the full collection of behaviors shown by marine fauna across their home ranges.

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