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Movements of electronically tagged shortfin mako sharks (*Isurus oxyrinchus*) in the eastern North Pacific Ocean

Nicole Nasby-Lucas¹ , Heidi Dewar^{1*}, Oscar Sosa-Nishizaki², Cara Wilson³, John R. Hyde¹, Russell D. Vetter¹, James Wraith¹, Barbara A. Block⁴, Michael J. Kinney¹, Tim Sippel¹, David B. Holts¹ and Suzanne Kohin¹

Abstract

Background: Most information on shortfin makos (*Isurus oxyrinchus*) in the eastern North Pacific (ENP) currently comes from fisheries data and short-term tracking studies. Although range has been inferred from catch and conventional tag data, little is known about the migration patterns and behavior in the ENP. This long-term electronic tagging study was designed to examine in detail the movement patterns and behavior of mako sharks in the ENP.

Results: In this study, a total of 105 mako sharks (104–280 cm fork length) were successfully tagged in the California Current between 2002 and 2014 with Argos satellite tags, including 93 satellite-linked radio-transmitting (SLRT) tags and 71 pop-up satellite archival tags (PSATs). This included 29 males that are in the size range of maturity, but only one mature female. Mean track durations from SLRT data were 337 days (max 1025), and PSAT tags were 136 days (max 272). Estimated minimum distance traveled in 1 year ranged from 6945 to 18,800 km/year. Habitats utilized included the entire California Current, the Sea of Cortez and offshore in the areas of the North Pacific Subtropical Gyre, North Pacific Transition Zone and North Equatorial Current. Seasonal movements within the California Current coincided with periods of higher primary productivity and chlorophyll *a*, and sea surface temperatures (SSTs) between 15 and 25 °C. SST ranged from 11 to 31 °C throughout the range, indicating a broad thermal tolerance.

Conclusions: Some of the key findings include the discovery of a high degree of variability between individuals in their vertical and horizontal movements, a strong influence of body size and season on mako shark movements, and the repetitive use of certain areas by individuals. These results expand our understanding of the distribution of mako sharks in the ENP. Although mako sharks are thought to comprise a single stock throughout the North Pacific, horizontal distribution of tagged mako sharks in this study was limited to the ENP demonstrating some spatial sub-structure. This study provides important data that can be used to identify fishery and gear vulnerabilities and inform management.

Keywords: Shortfin mako, Habitat preferences, Migration, Behavior, Pacific

Background

The development of electronic tags has revolutionized the study of highly migratory species, such as sharks, and enables collection of data on movements and behaviors over multiple years. One species in particular that has proved to be an excellent platform for fin-mounted

satellite tags that transmit when the shark is at the surface is the shortfin mako (*Isurus oxyrinchus*) (hereinafter referred to as mako shark). Mako sharks seasonally occur in coastal regions, but their movements and behaviors away from the coast have been difficult to determine. There have been numerous studies conducted around the world using satellite tags on mako sharks to provide insight into distribution, behavior, and habitat use throughout their range [1–5]. We report here on the

*Correspondence: heidi.dewar@noaa.gov

¹ Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, San Diego, CA, USA
Full list of author information is available at the end of the article



largest of these studies to date, which was conducted in the eastern North Pacific (ENP).

The mako shark is a pelagic predator with a worldwide distribution from temperate to tropical waters. With a fusiform shape (lamniform) and lunate tail, the mako shark is one of the fastest pelagic predators, with anecdotal reports of top speeds exceeding 50 km/h and individual sharks routinely traveling distances greater than 50 km/day [2, 5, 7–9]. Like its lamnid relatives, including the white shark (*Carcharodon carcharias*), the mako shark is equipped with countercurrent heat exchangers, which enable it to maintain internal temperatures several degrees above ambient water temperature [10–13]. Endothermy enhances muscle and digestive performance and provides advantages enabling mako sharks to better exploit fast-moving prey. The diet of mako sharks off California includes highly mobile pelagic prey such as jumbo squid (*Dosidicus gigas*), Pacific saury (*Cololabis saira*), Pacific sardine (*Sardinops sagax*), Pacific chub mackerel (*Scomber japonicus*), tuna (*Thunnus* spp.), other sharks, and for larger mako sharks, marine mammals [14, 15] indicative of a eurythermal shark capable of a foraging on a wide variety of prey.

Mako sharks are caught in commercial and recreational fisheries in the ENP with their high muscular performance and activity levels contributing to their popularity as a sport fish. In the US commercial high-seas longline and California large-mesh drift gillnet fishery, they are caught incidentally but are typically landed and commercially sold. In Mexican waters, mako sharks are caught by middle size and artisanal fisheries along the western coast of the Baja California Peninsula [16–18]. Globally, mako sharks make up a significant proportion of sharks in the international fin trade [19]. Similar to many shark species, mako sharks are vulnerable to overfishing due to their slow growth, late age of maturity, and low fecundity [20, 21]. The first length-based, age-structured, fully integrated model for this species in the North Pacific was completed in 2018. It indicated that makos are not being overfished and that overfishing is not occurring [22]. In contrast, in the North Atlantic the most recent assessment estimated that mako sharks are overfished and that overfishing is occurring [23]. The International Union for Conservation of Nature (IUCN) lists mako sharks as endangered worldwide [24]; however, this global listing is likely of limited use as indicated by the contrast in stock status which highlights the fact that the status of the species is variable across oceans.

Current information on the distribution, stock structure, and habitat use of mako sharks in the ENP is derived primarily from genetics, fishery, and conventional and acoustic tagging studies [7, 8, 25–29]. Genetic analyses suggest a single population across the North Pacific [25,

26]. In the ENP, the range of mako sharks has been primarily inferred from catch and conventional tag data. These data indicate that they typically occur in coastal regions seasonally, but their movements and behaviors away from the coast have been difficult to determine. Based on fisheries data, their distribution in the ENP encompasses the temperate North Pacific from the coast of southern Washington to Baja California, Mexico, and across the Pacific Ocean to Japan and Taiwan. Conventional tag data show that although the majority of makos tagged in Southern California are recaptured locally (total recaptures $n=317$, a small number have been caught elsewhere, including near Acapulco ($n=1$) to the south and in the western Pacific toward Hawaii and Japan ($n=8$) [29].

In the ENP, the Southern California Bight (SCB; the area from Point Conception to Punta Colonet, just south of the US/Mexican border, and including the area surrounding the Channel Islands) appears to be an important habitat for mako sharks across size classes. Young-of-the-year (YOY) (age-0, defined as sharks less than 100 cm fork length (FL) [29, 30]) and juvenile mako sharks comprise the majority of fisheries catch, suggesting that the SCB is a nursery area, although catch composition may also be influenced by gear selectivity. While smaller sharks dominate the catch, large individuals, including mature males and females, are also encountered [31–33].

While these datasets provide a general view of the distribution and size structure of mako sharks along the West Coast of North America, data gaps remain. The available data are limited in time and space and are primarily fisheries dependent. While acoustic telemetry studies have been performed within the SCB and provided data on short-term movements, behaviors and foraging patterns [7, 8, 27], these tracks do not provide insight into large-scale and seasonal movements and provide little information on mako shark distribution or habitat use outside the California Current. Thus, for a large portion of the year, the predominant habitat of mako sharks is unknown. An additional challenge is that the majority of data are for small or immature sharks. Conventional tags provide no information between tagging and recovery, have a low recovery rate (6.5% [28]), and provide minimal insights into large-scale migratory patterns. Without information on movements across extended timeframes, it is difficult to determine seasonal patterns, the degree to which mako sharks interact with different fisheries, the scale of movements, changes in movement pattern with ontogeny, and whether individuals return annually to specific locations. Filling these data gaps is critical for sustainable management, especially as we move toward ecosystem-based management schemes.

We report here on a long-term satellite tagging study of mako sharks in the ENP that was conducted as a part of the Tagging of Pacific Pelagics (TOPP) program [34]. The primary objectives of this long-term study were to examine (1) residency within the SCB, (2) seasonal movement patterns, (3) temperature and depth preferences, (4) long-term movements in relation to oceanographic conditions within and outside the California Current Region, and (5) movement patterns in relation to international boundaries and the distribution of fisheries. Subsets of this rich dataset have been used in previous publications [9, 34–38]. This paper is intended as a first description of this large dataset; further in-depth analyses to examine movement with respect to environmental parameters are planned for companion publications.

Results

Data recovery and track durations

A total of 105 mako sharks were successfully tagged (i.e., provided some data) between June 2002 and June 2014 including 60 males from 104 to 260 cm FL (165 ± 34 cm, mean \pm SD throughout, unless otherwise indicated), 43 females from 107 to 280 cm FL (169 ± 36 cm), and two sharks of unknown sex of 236 and 275 cm FL (Additional file 1: Table S1, Fig. 1). This included 53 small sharks (<165 cm FL; 31 males, 21 females) and 52 large sharks (>165 cm FL; 29 males, 22 females, two sex unknown) with 29 males that are in the size range of maturity, but only one mature female. All but four sharks were tagged in the SCB (Fig. 2).

Satellite-linked radio-transmitting (SLRT) tags were deployed on 93 mako sharks, of which all but four transmitted data. The 89 tags that reported included 39 small sharks (104–163 cm FL) and 50 large sharks (167–280 cm FL) (Additional file 1: Table S1). A total of 62 tracks were greater than 6 months (20 small, 42 large sharks; 30 female, 32 male sharks) and 36 were greater than 1 year (8 small, 28 large sharks; 18 female, 18 male sharks) (Additional file 1: Table S1). Mean track duration was 337 ± 243 days (max 1025), with tracks for small sharks (226 ± 176 days, max 697) significantly shorter than for large sharks (424 ± 254 days, max 1025) (Mann–Whitney rank-sum test, $U = 503.5$, $n_1 = 50$, $n_2 = 39$, $p = 0.0001$). The number of locations per day ranged from 0 to 16 with gaps from 1 to 140 days (median 2 days). After tracks were filtered to include only the high-accuracy daily position, 83% of location classes were 1, 2, or 3.

Pop-up satellite archival tags (PSATs) were deployed on 71 mako sharks, of which 16 either did not report or did not provide usable data. The remaining 55 tagged sharks included 34 small sharks (104–163 cm FL) and 21 large sharks (168–260 cm FL) (Additional file 1: Table S1). Deployment durations ranged from 3 to 272 days

(129 ± 73 days) with 37 tracks ≥ 90 days (19 small, 18 large sharks). Of the 55 PSAT tagged sharks, 39 were double-tagged providing corresponding SLRT position data. Light-based geolocation provided movement data for the other 16 sharks. Twenty-five of the tracks from double-tagged sharks were between 3 and 8 months (9 small, 16 large sharks). Ten PSATs were recovered and provided 18–224 (total 1039) days of high-resolution archival data. Depth records from 6 of the 55 sharks tagged with PSAT tags were consistent with a mortality event. One shark sank to 280 m for 3 days, 3 days after release, likely indicating a post-release mortality. Five other sharks sank after deployments of between 79 and 240 days. These five mortality events were not considered to be associated with tagging. Two double-tagged sharks provided no data from either tag, while this is suggestive of mortality, their fate could not be definitively determined.

Horizontal movement

The movements of SLRT-tagged makos covered a large portion of the ENP. The pop-off points of the PSAT-tagged sharks were also within this range. The extent of latitudinal movements along the coast (47°N to 3°N) spanned from Washington State to just south of Puerto Vallarta, Mexico, and in offshore waters from the Equatorial Counter Current to the North Pacific Transition Zone (NPTZ). Overall longitudinal range extended from the coast out toward the Hawaiian Islands (105°W to 155°W) (Fig. 3). The farthest movements to the west occurred between 12 and 20°N with large sharks extending to 155°W and small sharks reaching 142°W. Two female sharks (173 and 182 FL) traveled the farthest south to 2.8 and 4.2°N (Fig. 3). Five male sharks (147–187 FL) traveled the farthest to the northwest, moving to 142°W off the coast of Oregon and Northern California between 37 and 46°N (Fig. 3). Mean rate of movement was significantly different between small and large sharks (t test, $t = 5.0$, $df = 85$, $p < 0.0001$) with small sharks averaging 23.2 ± 17.4 km/day with a max of 109.2 km/day and large sharks averaging 31.8 ± 22.3 km/day with a max 142.4 km/day. Estimated distance traveled for sharks with tracks greater than 1 year ($n = 36$) ranged from 6945 to 18,800 km/year.

Monthly and seasonal movement patterns were apparent (Figs. 3, 4, 5). Large and small sharks were found in the SCB region most frequently during the months of July through September. In September through November, sharks began to disperse both offshore and to the north and south along the coast, ranging from Washington to near Magdalena Bay, in southern Baja California, Mexico. From December through May, sharks in the California Current moved south, occurring predominantly between

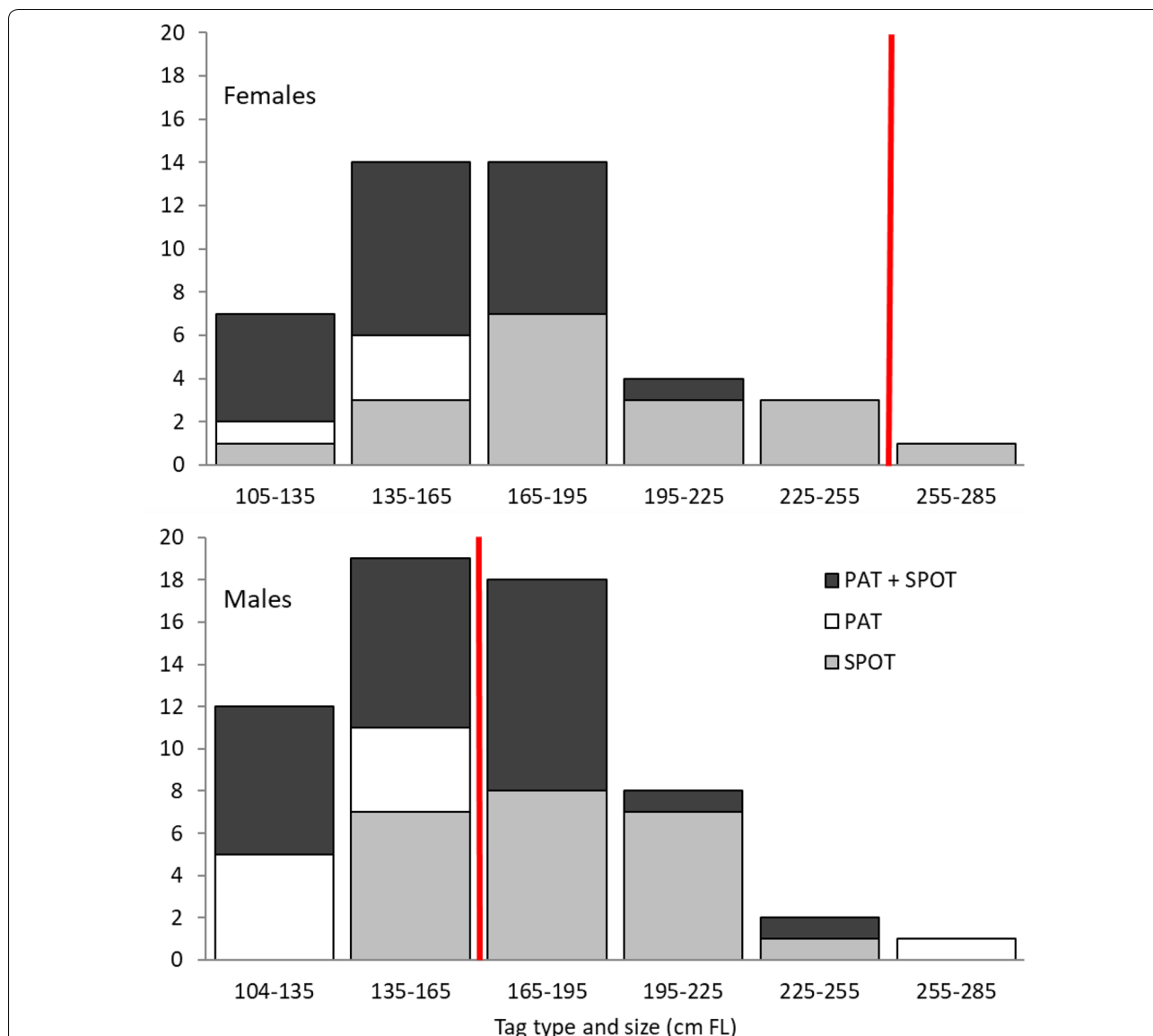


Fig. 1 Size and sex distribution of successfully tagged mako sharks indicating the type of tag(s) deployed. The red line approximates the estimated length of maturity for male and female mako sharks. There were an additional two PSAT tagged sharks of unknown sex not included in the figure (236 and 275 cm FL)

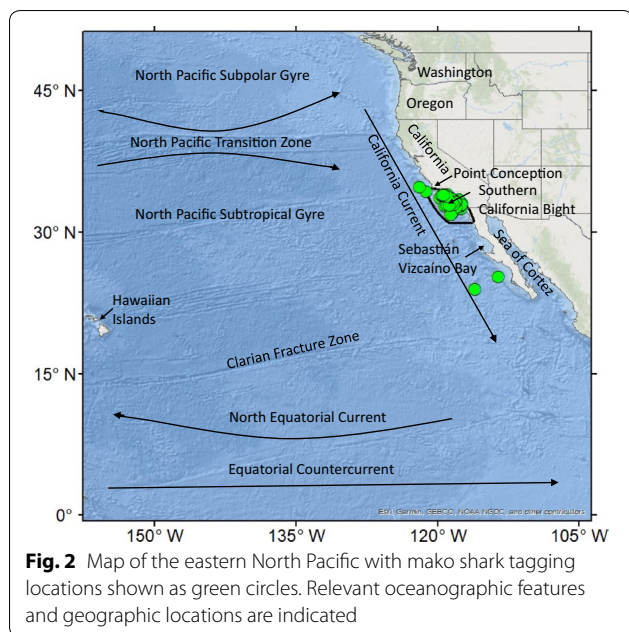
Central California and tip of the Baja Peninsula. Larger sharks ventured farther offshore. Offshore data showed areas of higher use toward the Hawaiian Islands between 12 and 20°N (Fig. 5), with an increase in presence offshore during December–June. Most sharks returned to the SCB during June–August.

Differences in movements were apparent between size classes. The overall range of movement was greater for large sharks both north–south (large: 2.8°N to 47.4°N, small: 9.9°N to 45.7°N) and west (large: 155.4°W, small: 142.0°W) (Fig. 6a, b). Mean monthly longitudes by size were significantly different (*t* test, $t=7.0$, $df=22$,

$p<0.0001$), while mean monthly latitudes were not (*t* test, $t=0.8$, $df=22$, $p=0.43$). The difference in range north–south despite the fact that they were not statistically significant is primarily due to a few outliers, with the females that travelled as far south as 3°N in the region of the Equatorial Countercurrent. This highlights the fact that even with some common patterns, the overall range of movements varies across individuals.

General habitat preferences

Depth and temperature data from the PSATs were used to characterize habitat use. Across regions, makos ranged



from the surface to depths exceeding 700 m. Mean maximum depths were 402 ± 143 m for large sharks (range 248–700 m) and 302 ± 58 m for small sharks (range 200–500 m) and were significantly different (Mann–Whitney rank-sum test, $U = 65.5$, $n_1 = 19$, $n_2 = 18$, $p = 0.001$). Maximum depths did not differ significantly by sex between large males and females and small males and females (Mann–Whitney rank-sum test, small $U = 30.5$, $n_1 = 10$, $n_2 = 9$, $p > 0.25$ and large $U = 33$, $p > 0.65$). The majority of time was spent in the top 50 m for both size classes (large sharks 88.2%: small sharks 90.2%). Ambient water temperatures recorded ranged from 5.3 to 30.2 °C. The coldest temperatures were associated with the deepest dives. Mean minimum temperatures were 7.3 ± 1.1 °C for large sharks (range 5.3–8.8 °C) and 8.5 ± 1.1 °C for small sharks (range 6.8–11.6 °C) and were significantly different (Mann–Whitney rank-sum test, $U = 164.5$, $n_1 = 19$, $n_2 = 18$, $p = 0.001$). The majority of time was spent from 14 to 22 °C for both size classes (large sharks 75.7%, small sharks 80.7%).

Using filtered SLRT positions to delineate habitat utilization, the sea-surface temperature (SST) extracted from satellite imagery indicated mako sharks utilized SSTs from 11.2 to 31.2 °C (18.9 ± 3.5 °C) (Fig. 7), with variability associated with region and time of year (see below). The highest SST values were within the Sea of Cortez (SOC) and the lowest between northern California and Washington. The mean SST experienced by SLRT-tagged sharks and PSAT-tagged sharks was similar, but the range was greater for SLRT-tagged sharks which had longer tracks and traveled over a broader

range than PSAT-tagged sharks including into the SOC. Mean primary productivity values were 6.5 ± 0.7 mg C m⁻² day⁻¹, and chlorophyll *a* (Chl-*a*) values were 0.5 ± 0.8 mg m⁻³. The highest levels of primary productivity (> 6.5 mg C m⁻² day⁻¹) and Chl-*a* (> 0.5 mg m⁻³) were found in coastal waters from Washington to mainland Mexico and into the SOC, while the lowest levels were found offshore (Fig. 7, Table 1). Hovmöller plots (latitude or longitude versus time) show movements within the California Current coastal region in relation to SST, Chl-*a*, and primary productivity (Fig. 8). Seasonal range expansions to the north in the summer and fall and the south in the winter and early spring were coincident with periods of higher productivity and Chl-*a* in these regions. Movements also corresponded with warming in the north and cooling in the south with sharks occurring primarily at SSTs between 15 and 25 °C.

Diel behavioral patterns were examined using high-resolution archival data from PSATs ($n = 10$). Data for small and large sharks were not significantly different (two-sample Kolmogorov–Smirnov test, $D = 0.3$, $p = 0.6$) and were combined for all analyses. The combined depth histograms showed that 48% and 55% of time was spent in the top 10 m during the day and night, respectively, 13% and 4% of time was spent below 50 m during the day and night, respectively, with 2% and 0.07% below 150 m during the day and night, respectively (Fig. 9a). Temperature histograms showed that 78% and 90% of time was spent between 14 and 22 °C during the day and night, respectively, with 13% and 2% of time spent in waters colder than 14 °C during the day and night, respectively (Fig. 9b). Based on the recovered time-series data, maximum depth per day was significantly deeper during the day than at night (day $125.7 \text{ m} \pm 96.6$, night 58.6 ± 55.3) (Mann–Whitney rank-sum test, $U = 708,495.5$, $n_1 = 950$, $n_2 = 949$, $p < 0.0001$). Similarly, minimum temperature per day was significantly cooler during the day than at night (day $11.9 \text{ °C} \pm 3.1$, night $14.7 \text{ °C} \pm 2.7$) (Mann–Whitney rank-sum test, $U = 209,125.5$, $n_1 = 950$, $n_2 = 949$, $p < 0.0001$). The mean mixed layer depth (MLD) for all 10 recovered tags was 18.6 m (minimum 11 m, maximum 31 m).

While general patterns among individuals were apparent, fine-scale vertical behavior for individual sharks varied within and between regions. Dive patterns for a single shark are shown in Fig. 10. Within the SCB, the shark's behavior included days when it spent the majority of the time day or night near the surface (Fig. 10a), and others when it made repetitive deep daytime dives between the surface and around 200 m (Fig. 10d). Distinct behaviors were also observed in Sebastián Vizcaíno Bay (SVB) with shallow dives below the MLD day and night and little time in warm surface waters (Fig. 10b), and just north of

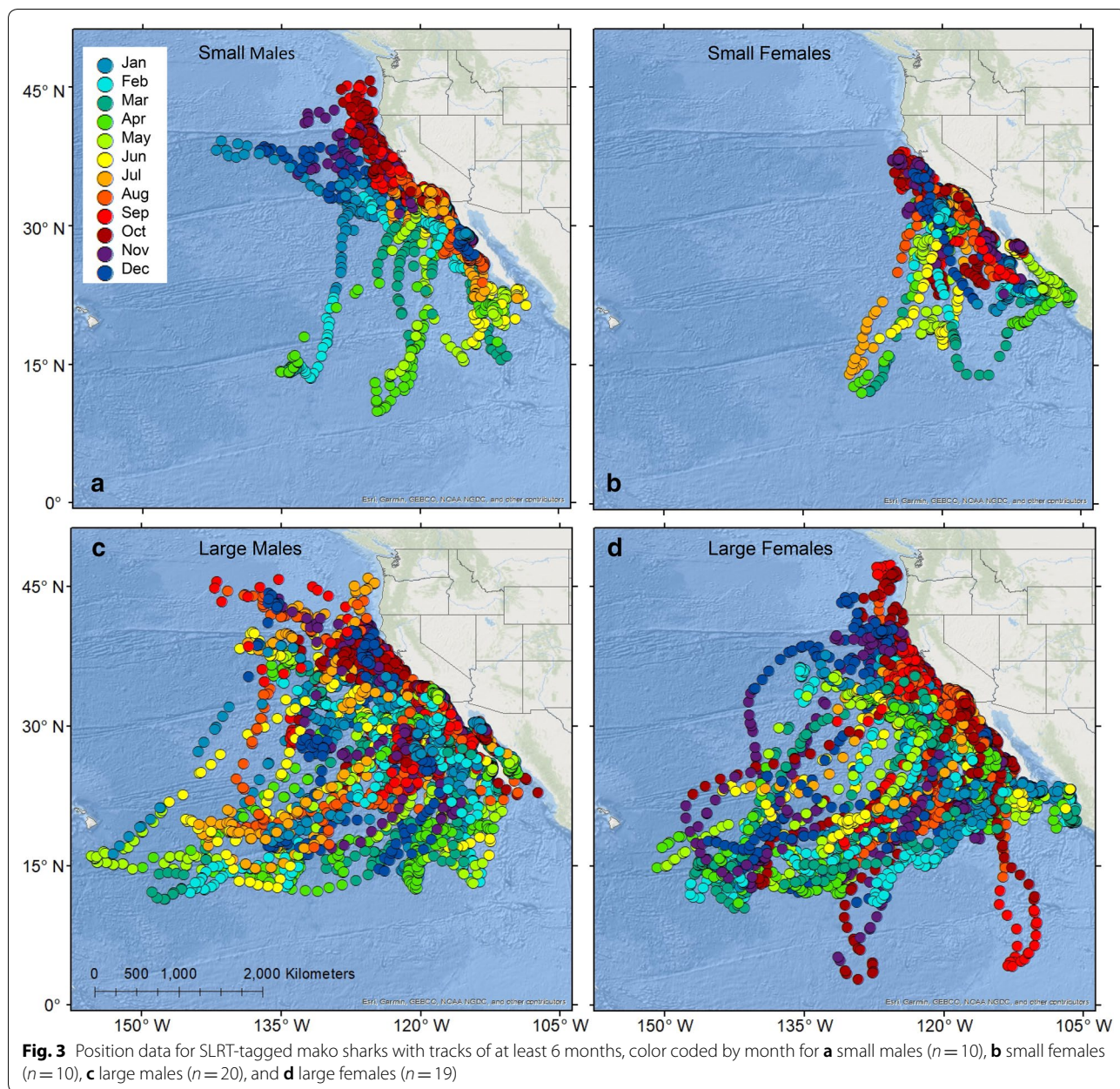


Fig. 3 Position data for SLRT-tagged mako sharks with tracks of at least 6 months, color coded by month for **a** small males ($n = 10$), **b** small females ($n = 10$), **c** large males ($n = 20$), and **d** large females ($n = 19$)

Point Conception with dives below the MLD during the day and near the surface at night (Fig. 10c).

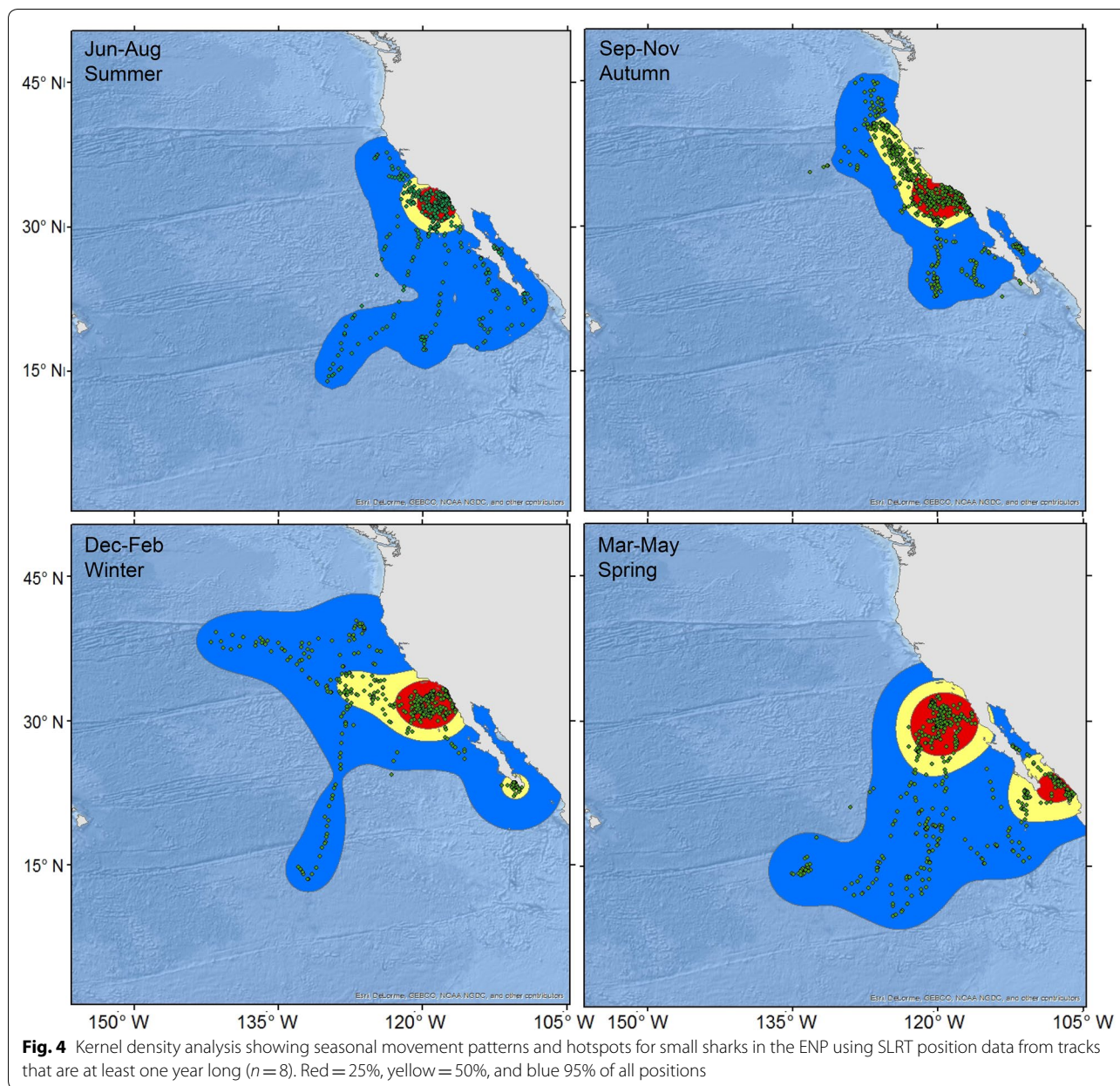
Habitat preferences and behaviors by region

Movements, behaviors and habitat characteristics of mako sharks were examined for five regional areas: (1) the SCB; (2) the coastal region north of Point Conception; (3) the west coast of Baja California; (4) SOC; and (5) offshore. Coastal was defined as being within 200 nautical miles off the coast to approximate the US and Mexico exclusive economic zones (EEZs) which includes the approximate bounds of the California Current (Figs. 11,

12). Regions were chosen based on areas of utilization, beginning with the SCB. Environmental variables for each region were extracted from SLRT tag positions. Overall, large sharks spent 38% of detection days in the US EEZ, 21% in the Mexican EEZ and 41% offshore, while small sharks spent 49% of detection days in the US EEZ, 29% in the Mexican EEZ, and 22% offshore.

Southern California Bight

All but four sharks were tagged in the SCB (Fig. 2). Three of these four moved into the SCB after tagging. Both large and small sharks had the highest occurrence in the



SCB between July and September (Fig. 11). Although some sharks were within the SCB in all months, in some cases they appeared to be passing through the region. For a summary of SST, Chl-a, primary productivity, and swimming depths in this region, see Table 1 and Fig. 12.

For sharks tagged in the SCB with more than 1 year of data, 27 sharks (77%) returned to the SCB in the following year(s), arriving between mid-April and mid-September (mean return date July 2 for small sharks and June 22 for large sharks), and stayed for as long as 158 days (83 ± 27 days for small sharks and 60 ± 46 days for large sharks). For the eight sharks that did not return, seven

were large and one was small. Of the seven large sharks, four stayed offshore or north of Point Conception and the remaining three were off the coast of Baja California from July to September. The small shark was traveling from off Baja California north toward Southern California when the tag stopped reporting in mid-July.

North of Point Conception

For sharks with more than 1 year of data, 23 traveled north of Point Conception, including 19 large sharks (68%) and 4 small sharks (50%). The highest percentage of

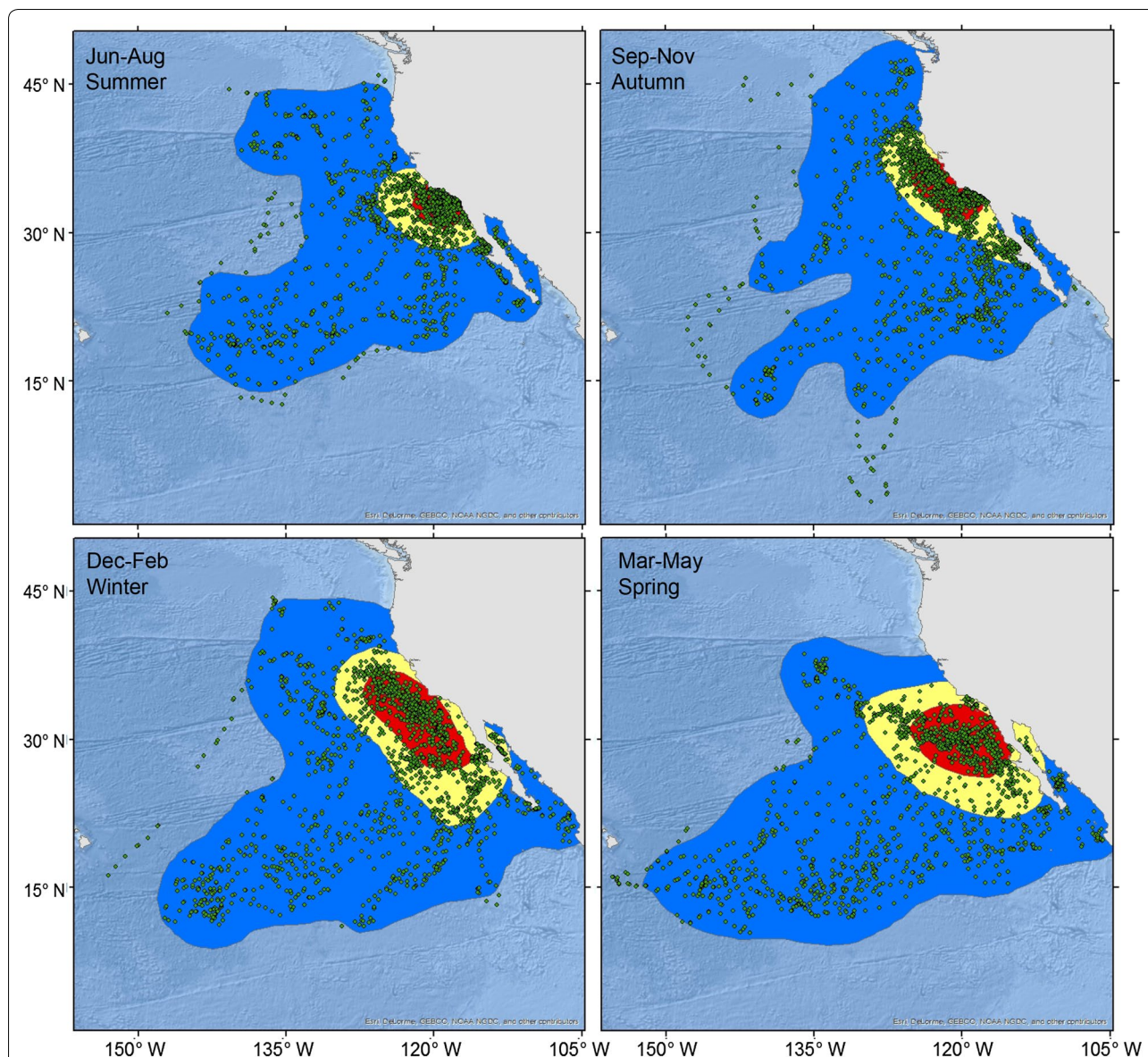


Fig. 5 Kernel density analysis showing seasonal movement patterns and hotspots for large sharks in the ENP using SLRT interpolated position data from tracks that are at least 1 year long ($n = 28$). Red = 25%, yellow = 50%, and blue 95% of all positions

occurrence in the coastal region north of Point Conception was during August–December (Fig. 11). In general, SSTs in this region were colder and the sharks tended to spend more time at the surface with fewer deep dives. For a summary of SST, Chl-a, primary productivity and swimming depths in this region, see Table 1 and Fig. 12.

West coast of Baja California

For sharks with more than 1 year of data, 31 visited the region along the west coast of Baja California including

23 large sharks (82%) and 4 small sharks (50%). Tagged mako sharks were present in this region year-round with the highest occurrence in the spring (February to June) (Fig. 11). This region was relatively warmer and sharks spent time deeper in the water column. For a summary of SST, Chl-a, primary productivity and swimming depths in this region, see Table 1 and Fig. 12.

Of all SLRT-tagged sharks (including those with tracks less than a year, $n = 89$), there were 12 sharks (119–190 cm FL) that spent more than 1 week in SVB (6 immature females, 2 immature males, and 4 mature

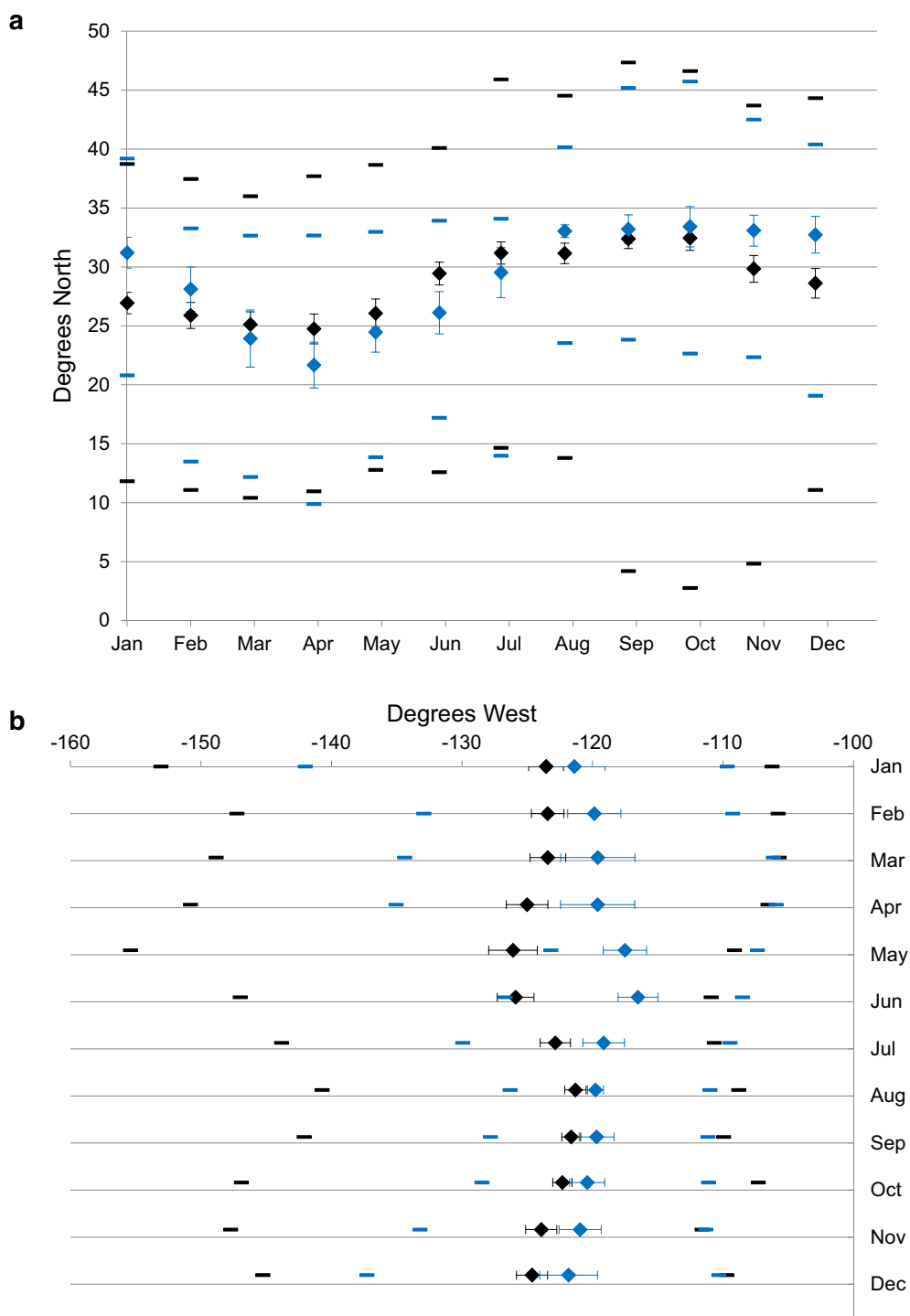


Fig. 6 Mean **a** latitude and **b** longitude with standard error by month for large (black, $n=28$) and small (blue, $n=8$) SLRT-tagged mako sharks with tracks greater than a year. Black and blue bars show the minimum and maximum latitudes and longitudes for large and small sharks during each month

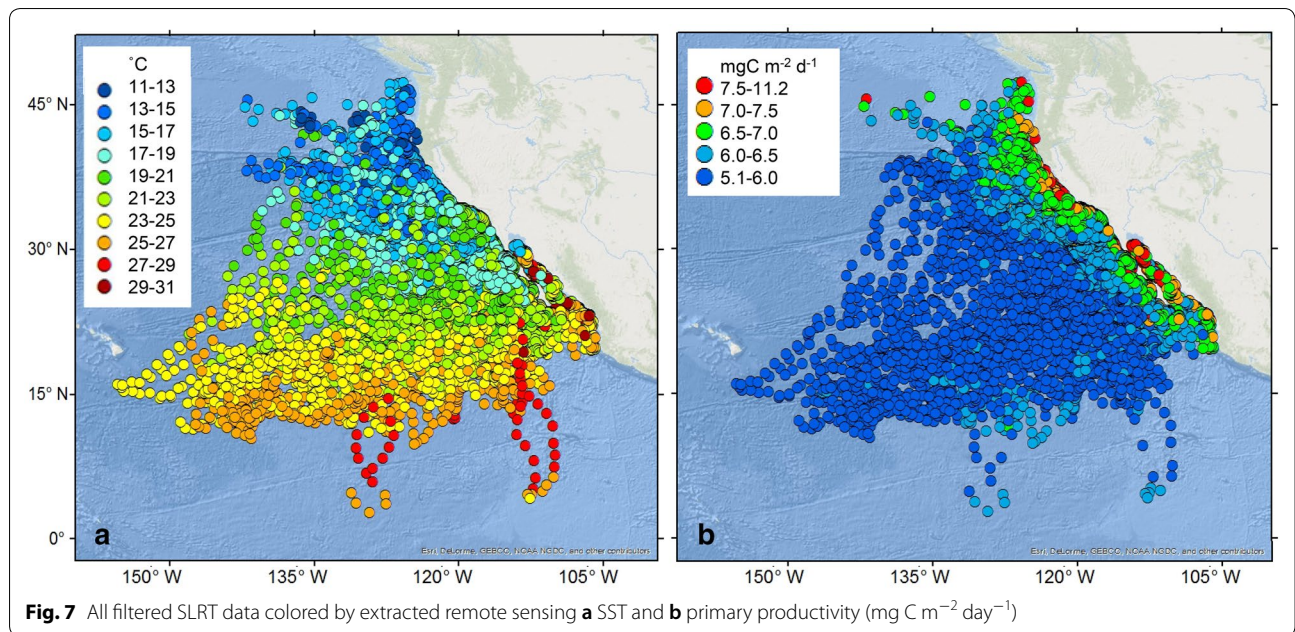


Fig. 7 All filtered SLRT data colored by extracted remote sensing **a** SST and **b** primary productivity ($\text{mg C m}^{-2} \text{ day}^{-1}$)

Table 1 Summary of environmental factors by region

	N Pt Conc	SCB	Baja	SOC	Offshore
SST min (°C)	11.3	11.9	14.1	14.4	11.3
SST mean (°C)	15.4	17.9	19.6	23.2	20.9
SST max (°C)	20.2	24.1	29.5	31.2	28.8
PP mean ($\text{mg C m}^{-2} \text{ day}^{-1}$)	6.9	6.8	6.5	7.1	5.8
Chl-a mean (mg m^{-3})	0.9	0.6	0.4	1.2	0.1
Max depth (m)	350	528	~700	NA	680
% Time at surface (<5 m)	50.2	46.7	36.7	NA	30.3
% Time <50 m	94.2	92.1	84.7	NA	70.4
% Time >150 m	0.9	1.6	1.5	NA	6.1

Summary of SST (sea surface temperature), PP (primary productivity), Chl-a (Chlorophyll a), maximum depth, percent time at the surface, percent time <50 m, and percent time >150 m for each region (SCB Southern California Bight, N Pt Conc north of Point Conception, Baja Baja California Mexico, SOC Sea of Cortez, and offshore)

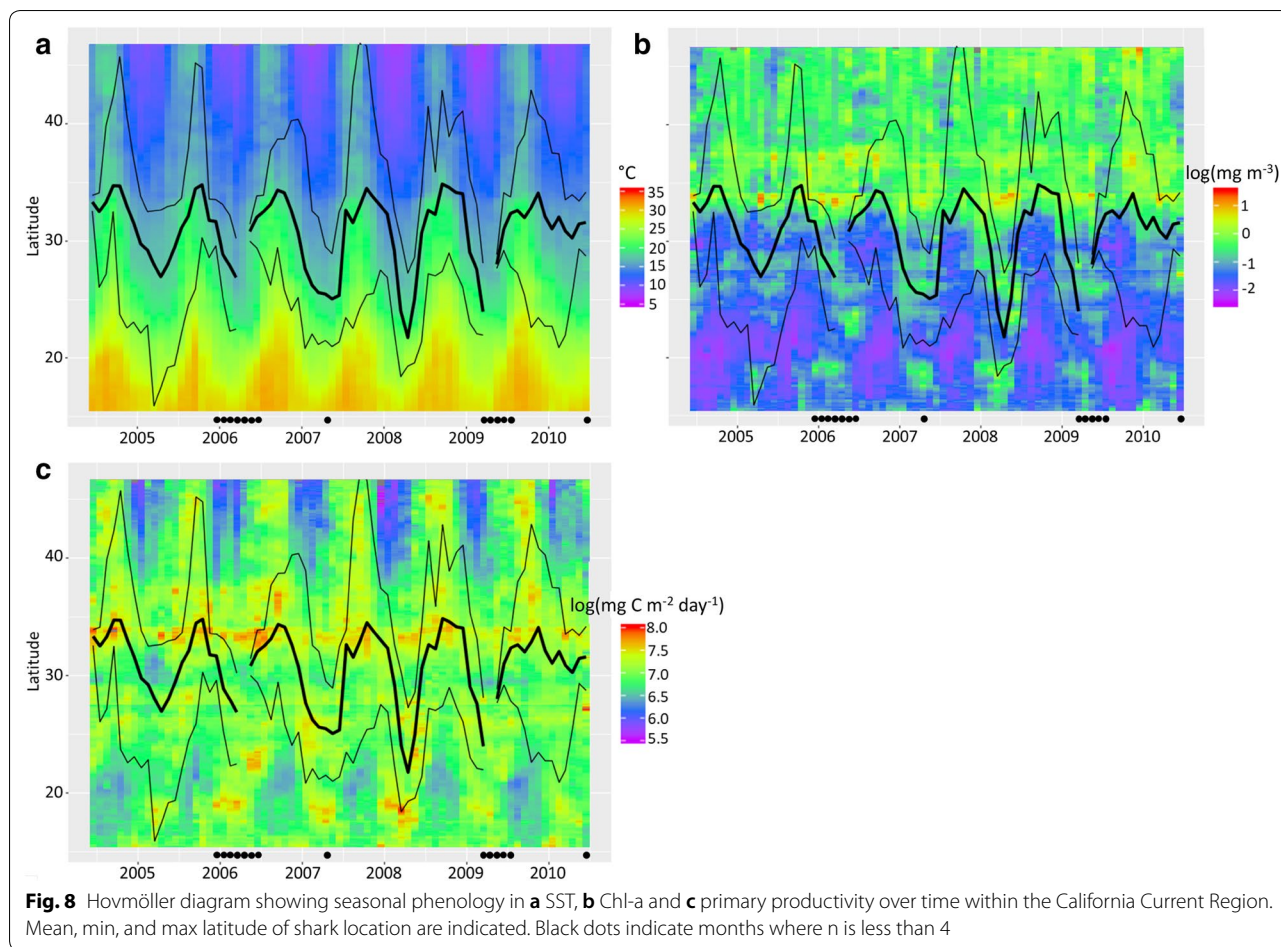
males). These sharks were present between mid-July and early February and stayed for between 10 and 131 days (44 ± 29 days). One of the large sharks (female, 173 cm FL) did not return to SCB in the year following tagging, but traveled to SVB and remained from 1 July through 9 September. There was not a significant difference between time spent in this area for small or large sharks (Mann–Whitney rank-sum test, $U = 15$, $n_1 = 8$, $n_2 = 4$, $p > 0.05$) or for male or female sharks (Mann–Whitney rank-sum test, $U = 9$, $n_1 = n_2 = 6$, $p > 0.05$), while in SVB, sharks spent a mean of 30.8% of time at the surface (<5 m) and 87.6% of time in the top 50 m with 0.2% time below 150 m (see Fig. 10b for an example).

Sea of Cortez

Three SLRT-tagged sharks with tracks ranging from 4 to 13 months traveled into the SOC with at least one shark occurring there during each month. Shark 04-13PS, tagged off Baja, moved into this region in March and was still there in November when the tag stopped reporting (poor location data July through September). Shark 07-4PS was tagged in July in the SCB and traveled into the SOC in August and was still there in November when the tag stopped reporting. The third shark (09-2S) was tagged in August in the SCB and moved into the SOC in October and remained there until the following August when it moved back along the west coast of Baja to SVB. The shark then moved into the SOC again in October and remained there for the next 16 months at which point the tag stopped transmitting. Sharks encountered a broad range of SSTs in the SOC as a consequence of visiting there in the winter and summer (Table 1). SSTs were significantly lower from December to April (21.0 ± 2.9 °C) than from May to November (25.7 ± 2.5 °C) (t test, $t = 16.5$, $df = 400$, $p < 0.0001$). Chl-a did not differ significantly between December to April and May–November (t test, $t = 1.1$, $df = 400$, $p = 0.27$). PSAT data were not available from sharks in this region. SLRT tags reported poorly during the summer months, indicating that the sharks were likely spending less time near the surface as SST increased.

Offshore

For sharks with more than 1 year of data ($n = 38$), all but two sharks utilized the offshore region. The two

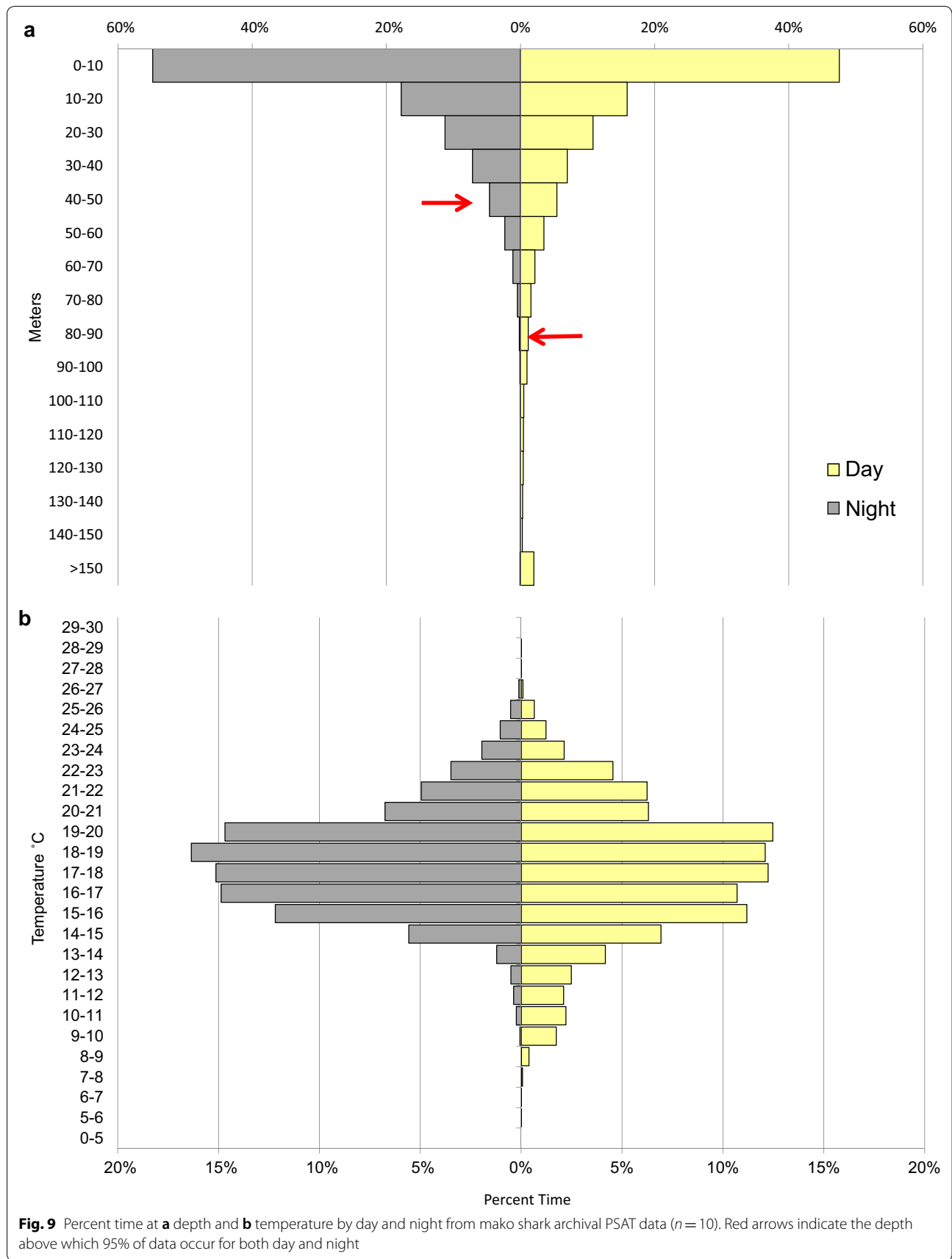


sharks that did not travel offshore (one large and one small shark) both spent significant time in the SOC (8–16 months). Mako sharks were offshore in all months, with the highest occurrence from December through June (Fig. 11b). For a summary of SST, Chl-a, primary productivity and swimming depths in this region, see Table 1 and Fig. 12. SSTs were cooler in the northern portion of the offshore region, 15.9 ± 1.8 °C for the NPTZ and area north of Point Conception and 21.5 ± 3.3 °C for the offshore area south of Point Conception toward the North Equatorial Current. Movements varied greatly among individuals, and although there was no common offshore destination, there were some notable patterns. Multiyear tracks indicated similar patterns in offshore movements over consecutive years for individual sharks. For example, shark 09-1S, a 205-cm FL immature female, traveled to the same offshore region in three consecutive years, from mid-December to mid-February the first year, mid-February to mid-March the second year, and mid-March to mid-April the third year (Fig. 13). In addition, four of the sharks large enough to be mature, including three males ≥ 223 cm FL (08-8PS, 09-3S, and 09-12PS)

and one female ≥ 280 cm FL (14-1S), moved directly from the SCB region offshore to the southwest with no north–south movements along the coast (Fig. 14). The two mature sharks with tracks greater than 1 year both moved offshore in the fall and returned to the SCB by the following summer.

Regional differences in habitat

PSAT data showed a shift in vertical habitat use between regions. Mako depth distributions from the SCB and north of Point Conception were similar although overall temperatures experienced in the north were cooler with the highest percent of time spent at 14–16 °C in comparison with 16–18 °C in the SCB (Fig. 12). Warmest temperatures and deepest vertical movements were apparent in the offshore region where overall the highest percent of time was spent between 22 and 24 °C and where the least amount of time of all regions was spent near the surface with progressively more time (compared with other regions) below 50 m (Fig. 12). Intermediate between offshore and the two US coastal regions was the Baja Peninsula region where



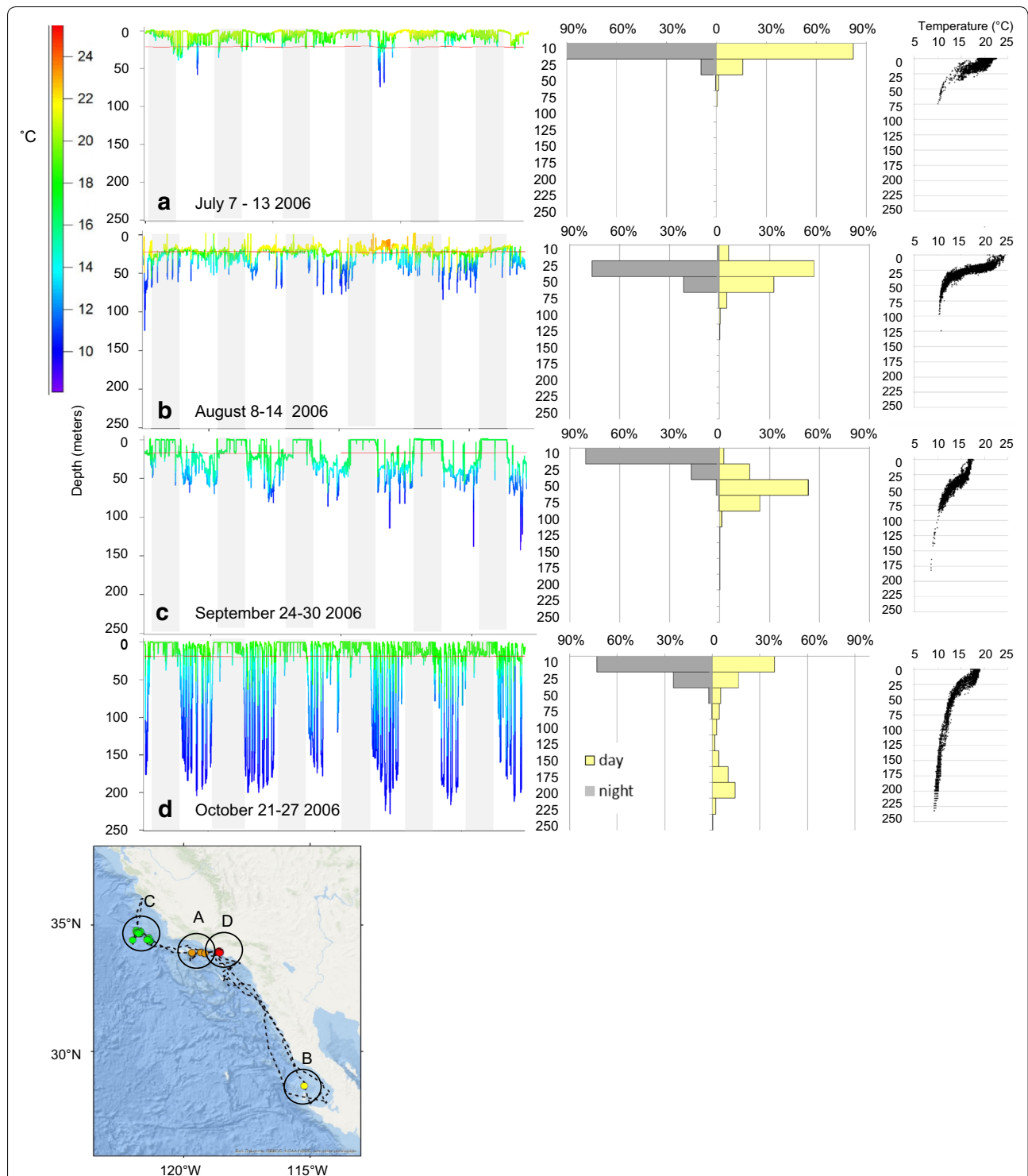
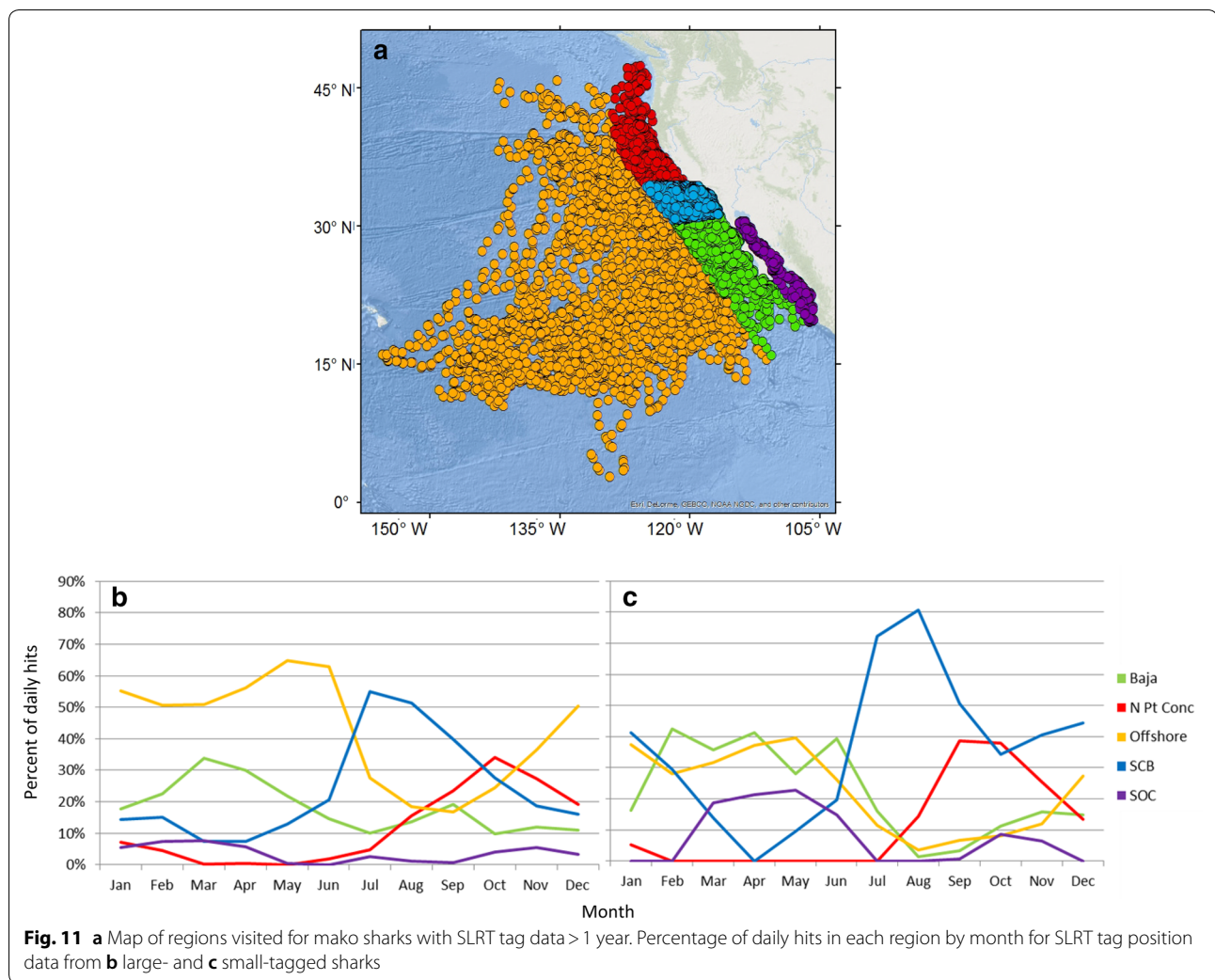


Fig. 10 Vertical patterns from recovered PSAT data from tag 06-3PS, (174 cm FL M), overlaid with color-coded temperature (shaded regions are night), indicating percent time at depth day and night, and the temperature depth profile. Each plot displays 7 days of data; **a** in SCB between Santa Cruz Island and Catalina Island, **b** in Sebastian Vizcaino Bay, Baja California, Mexico, **c** just off Point Conception, and **d** SCB in the nearshore Santa Monica Bay (locations and track indicated on map)



the highest percent of time was spent between 18 and 20 °C. Additional insight into a shift in vertical habitat use offshore comes from one of the large double-tagged sharks (08-8PS, 223 cm FL) with 241 days of PSAT data and 248 days of SLRT data. This shark made two round-trip movements offshore (Figs. 14, 15). As the shark moved offshore, time spent in the top 50 m decreased from 95.5 to 60%.

Discussion

This study presents electronic tagging data of 105 shortfin makos in the ENP over a 13-year time period, depicting the horizontal and vertical movements of both sexes across a range of sizes with tracks lasting as long as 34 months. This has resulted in a large dataset that provides insight into mako habitat use and migrations and the factors that influence their behavior and offers the first opportunity to examine the effects of size

on distribution and movement patterns of mako sharks in the ENP. Some of the key findings include the discovery of a high degree of variability between individuals in their vertical and horizontal movements, a strong influence of body size and season on mako shark movements, and the repetitive use of certain areas by individuals. These results expand our understanding of the distribution of mako sharks in the ENP and the importance of oceanographic features beyond the California Current, including the Subtropical Gyre, the NPTZ, the North Equatorial Current and the SOC.

Horizontal movements

Regional/seasonal

Horizontal distribution of tagged makos in this study covered a broad range of the ENP including coastal and offshore habitats. The ability to make large-scale migrations has been linked to endothermy and expanded

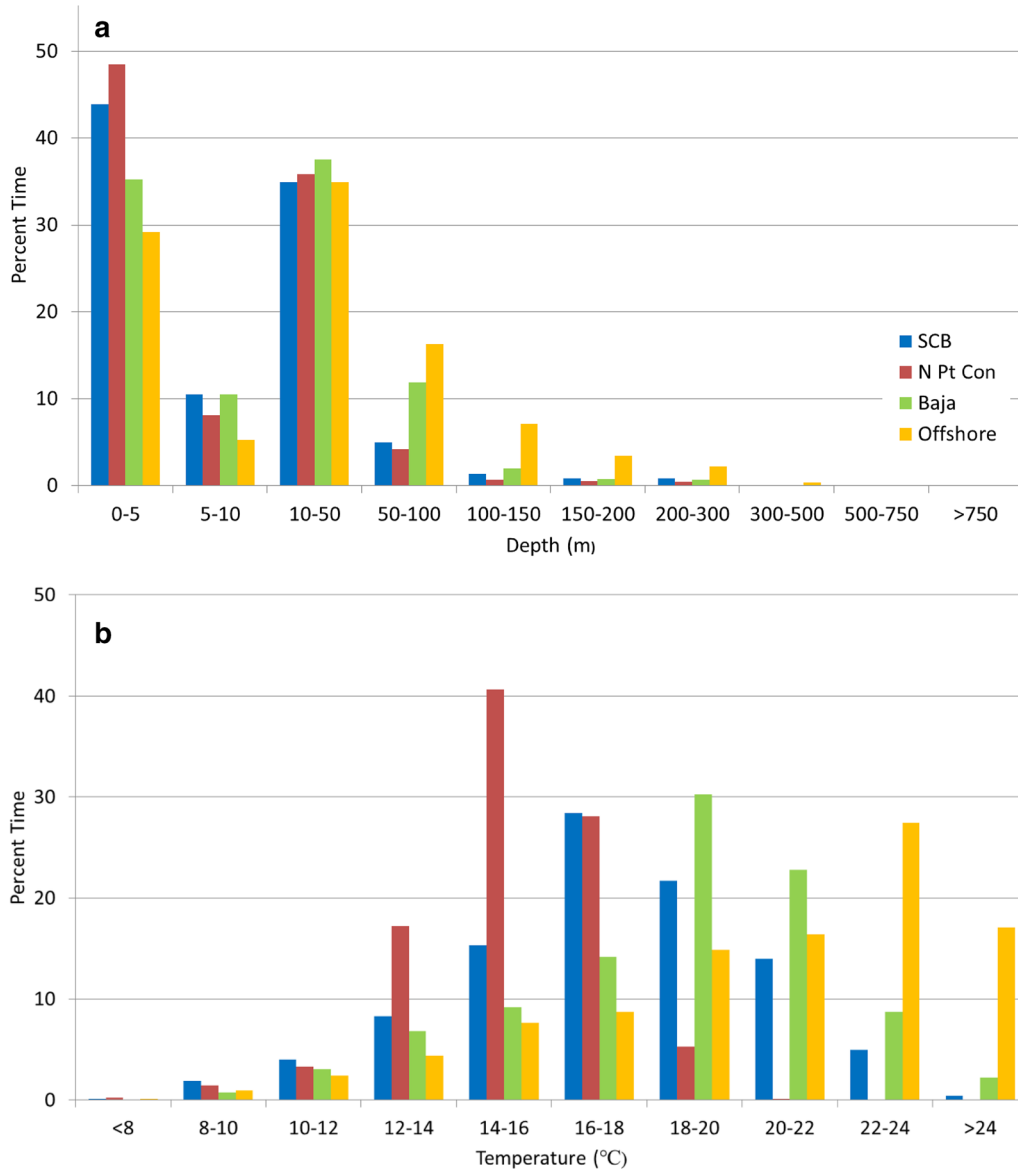
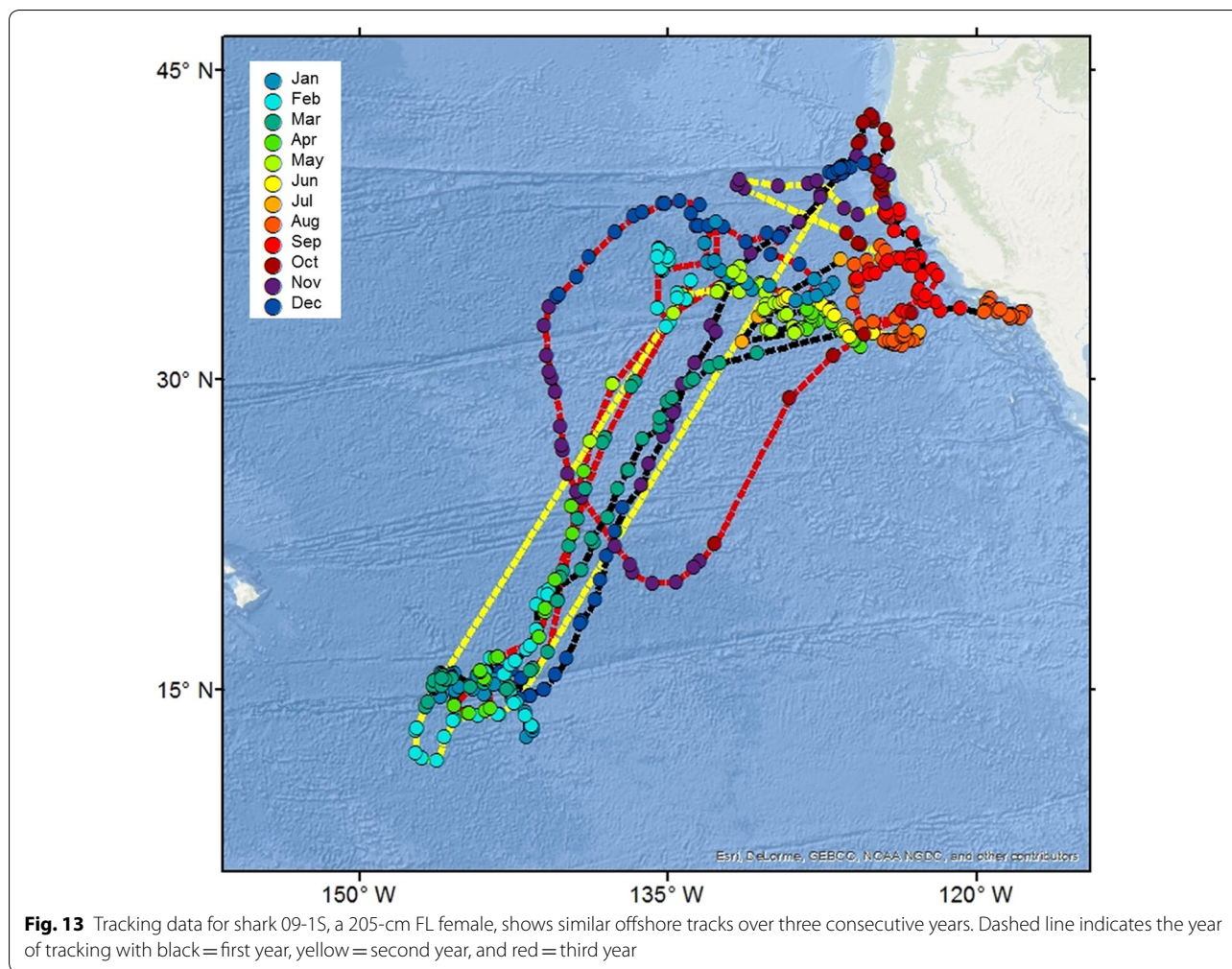


Fig. 12 Graphs showing **a** time at depth and **b** time at temperature for PSAT tag data > 3 mo within each region. Note that no PSAT data were available from the Sea of Cortez

thermal habitats and higher cruising speed [39]. The preferred habitat includes the entire extent of the California Current region off both the US and Mexican coast, as well as offshore spanning from tropical to temperate waters.

Makos demonstrated a seasonal presence in the SCB in late spring through early fall returning in consecutive years, confirming the importance of this region. Although there is a potential for tagging bias, as nearly all tags were deployed in the SCB, 77% of sharks in this study with more than 1 year of data returned to the SCB

between April and September the year(s) following tagging and stayed for as long as 158 days, demonstrating the importance of the SCB in the summer months. This confirmation of the importance of the SCB is consistent with previous tagging studies as well as catch data which identify the SCB both as a nursery area for YOY and juveniles and a foraging ground for subadults and adults [7, 8, 27]. This region is also a nursery area for other pelagic sharks including white and common thresher sharks (*Alopias vulpinus*) [40–42] and bears similarity to the Great Australian Bight where the shelf and slope



are important habitats for juvenile makos [2]. The SCB has a shallow continental shelf, offshore islands, and seamounts, which likely provide some refuge from predation for YOY and juveniles [43]. The region is also highly productive and home to a range of prey for mako sharks across size classes, from squid and fish, to marine mammals [14]. Movement into productive, coastal summer foraging grounds is also observed for mako sharks in the Atlantic and South Pacific [2, 4, 5]. In addition to mako sharks, the SCB is also a summer foraging ground for a broad range of highly migratory species including white sharks, common thresher sharks, blue sharks (*Prionace glauca*), billfish, marine mammals, turtles, and tuna [34, 44, 45].

While the SCB was important across individuals and size classes, there was no consistent movement pattern for the temporal timing of migrations away from the SCB. In the late summer and autumn, sharks either moved to the north, south, or offshore. Timing of

movements to the north corresponded to a seasonal phenology of increased SST and a period of higher productivity in the northern California Current region associated with an increase in seasonal upwelling that occurs in September through October [44, 46, 47]. The movement of sharks to the region north of Point Conception off the coasts of California, Oregon and Washington also corresponded with optimal monthly habitat predictions for sardine, which are found off Oregon and Washington from June through November and move south of Central California from December through May [48]. Mako sharks that utilized the northern region then either dispersed offshore or moved into Mexican waters during the winter when temperatures to the north drop, coastal upwelling decreases and productivity off the coast of Baja California peaks [47] (Fig. 8). This north–south migration pattern within the California current region is similar to that of other marine animals such as tunas, salmon

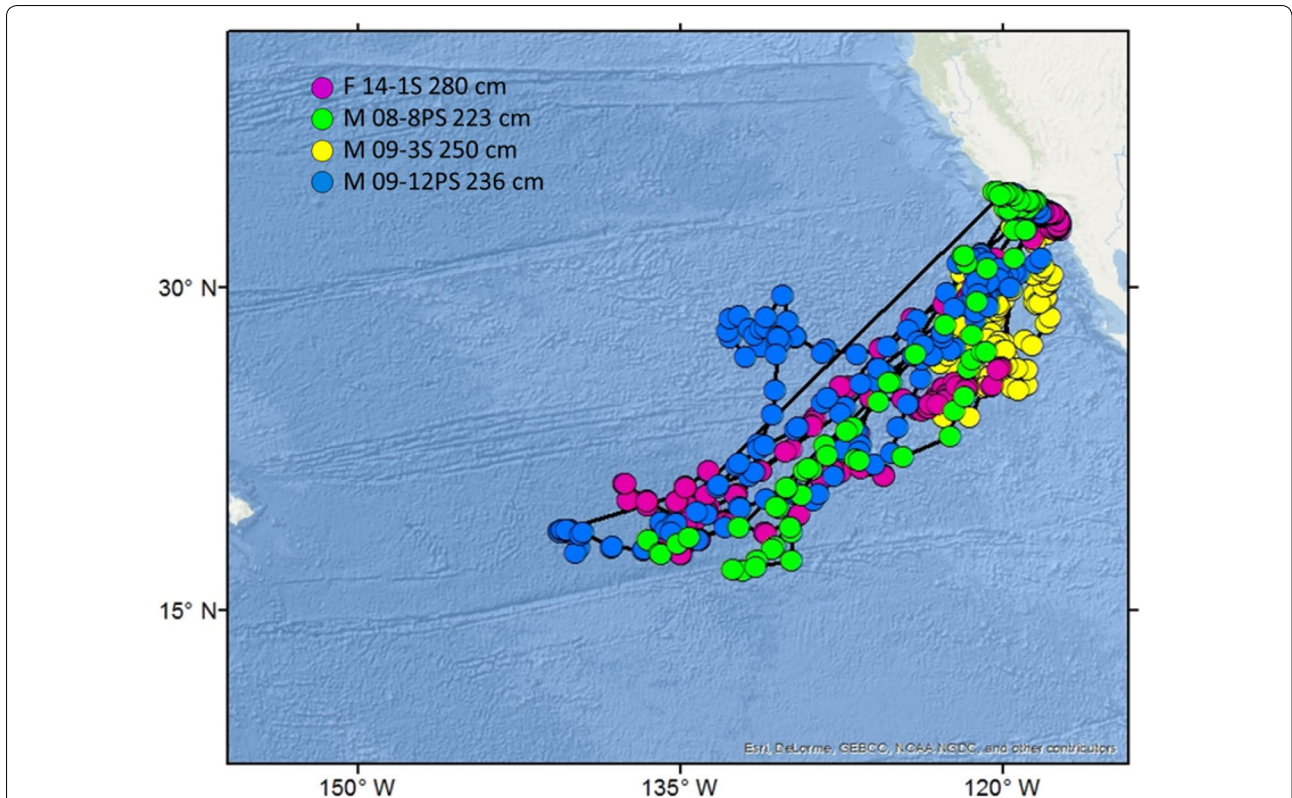


Fig. 14 Movements of four large mako sharks offshore, males ≥ 223 cm FL ($n = 3$; 248–498 days) and female ≥ 280 cm FL ($n = 1$; 456 days)

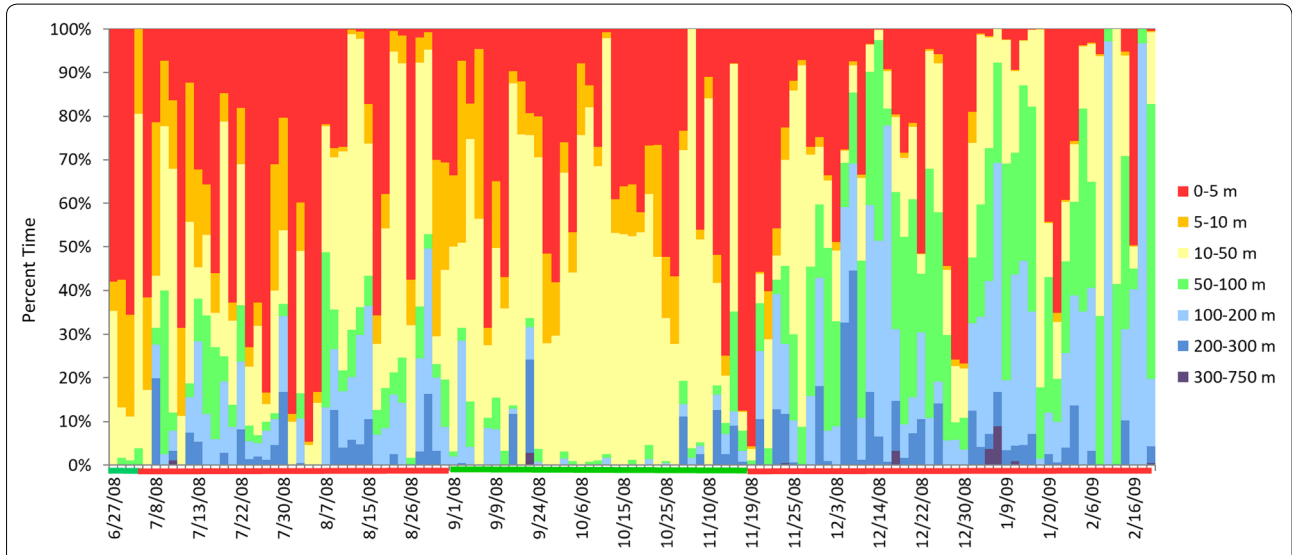


Fig. 15 Percent time at depth distribution from double-tagged shark (08-8PS; male, 223 m FL) within the SCB and offshore (SCB = green, offshore = red). See Fig. 13 for map showing offshore movement

sharks (*Lamna ditropis*), and blue whales (*Balaenoptera musculus*) [34, 44].

Sharks traveling into the southern California Current region off of Baja California, Mexico, arrived most often either in late summer from the SCB, or late fall/early

winter after traveling north of Point Conception. Within this region, some sharks spent more time in SVB and the SOC. This included one shark (shark 09-2S; male, 174 m FL) that did not return to the SCB but traveled between the SOC and the SVB. Both of these areas are known for high productivity throughout the year and support a large biomass of sardine that are found in mako stomach contents [14, 49]. In addition, the SVB has been recognized as a nursery area for white sharks [50, 51]. The SOC is characterized by significant upwelling events in winter and early spring during which surface temperatures drop to as low as 14 °C. During the summer, surface temperatures can reach 31 °C [52]. These data showed mako sharks moving into the SOC in late summer or fall and remaining there for as long as 16 months, indicating that sharks can remain in the SOC year round despite the high SST.

The greatest insight into new habitat use for mako sharks comes from the tag data revealing extensive offshore movements which occurred predominantly in the winter and spring months. Sharks either moved directly offshore from the SCB or following movement north or south within the California Current. One important offshore region was to the south near the North Equatorial Current where fisheries data are not available. All but two sharks that moved into this area ceased southward movements at around 12–20°N and then remained in the area for some period. This region differed from the shared offshore foraging area utilized by male white sharks, which is a large area centered around approximately 23.5°N, 137°W [53, 54]. Why some sharks move into subtropical waters is not clear. It does not appear to be related to reproduction as both immature and mature mako sharks reached the same southerly latitudes and showed the same general seasonal pattern, indicating that it is more likely linked to foraging. While lower than in the California Current, productivity in this region is relatively high for oligotrophic offshore waters. Productivity is enhanced by the shoaling of the thermocline at the edge of the North Pacific Subtropical Gyre and the shear of the equatorial current, as is evidenced by an increase in nutrients, sea birds and marine mammals in this region [55]. In addition, this region also contains the Clarion Fracture, which has a large number of topographic features such as seamounts, hills, and channels. The edge between a region of vertical relief and the flat seafloor is likely associated with increased foraging opportunities [56]. Whether there is a barrier to movements further south is not clear. Beyond this point, temperatures increase and the oxygen minimum zone in the eastern tropical Pacific shoals dramatically, reaching O₂ levels of 1.5 ml/L at 200 m at ~12°N latitude [57]. Although mechanisms and cues are unclear, the movements of mako sharks are

similar to offshore migration patterns for other species that seasonally utilize the California Current, including white sharks, blue sharks, salmon sharks, Pacific bluefin tuna (*Thunnus orientalis*), and leatherback sea turtles (*Dermochelys coriacea*) [33].

The offshore movements in the northern region occurred near the boundary of the subarctic gyre and subtropical gyre in the NPTZ. In this region cool, high chlorophyll surface water sinks beneath warm, low chlorophyll water and overall productivity is enhanced [58]. Other species such as loggerhead turtles (*Caretta caretta*), albacore tuna (*Thunnus alalunga*), female elephant seals (*Mirounga angustirostris*), salmon sharks, swordfish (*Xiphias gladius*), and bluefin tuna have been shown to forage in, and travel along, this front [34, 58, 59]. Limited catch data are available for this region although mako sharks are caught in longline fisheries targeting the NPTZ farther to the west [60].

Although there was no common offshore destination across all tags, in longer tracks individuals returned to the same general offshore destination in successive years. This repeat migration behavior has been shown for other sharks such as tiger sharks (*Galeocerdo cuvier*) in the Atlantic Ocean [61] and salmon sharks in the Pacific Ocean [62] but has not been reported in studies for mako sharks, most likely due to the paucity of multi-year tracking data. This behavior differs from the offshore movements of white sharks for which mature males show repeat annual migrations that end in a specific common offshore area [54]. The ability to remember the location of foraging grounds and return to them is termed the “learned migration goal” hypothesis and has been suggested for leatherback sea turtles [63]. Such a mechanism could also be used by mako sharks to return to a location that was previously found to be favorable and could act to reduce competition for foraging in offshore habits where resources are more disperse.

Since seasonal patterns were evident, environmental factors were examined in relation to horizontal movements to assess motivations. A key factor linked to habitat use across many marine species is SST. In the California Current, sharks occurred primarily in SST ranging from 15 to 25 °C which is similar to reports from previous fisheries-dependent studies that suggested that the mako shark distribution in the Atlantic was tied to a preferred SST range of 17–22 °C [64, 65]. Over all regions, however, mako sharks in this study occurred across SST from ~11 to 31 °C indicating a much broader thermal tolerance and that overall movement is not necessarily limited by SST. Other recent electronic tagging studies in the western North Atlantic and South Pacific have also shown mako movements in areas where SST ranges from 8 to 31 °C [2, 3, 5]. The general movement

pattern of tagged mako sharks does appear to correspond with regional changes in productivity which likely coincide with prey distribution (Fig. 8) and SST does not appear to be as much of a limiting factor as previously suggested. Interpretation of environmental data is complicated by the fact that algorithms used to calculate primary productivity include temperature.

Sex and size

In addition to seasonal shifts in environmental factors, sex has been shown to influence the movements and distributions of some shark species [54, 66–68]. In general, males and females in this study used a similar geographic range with minimal north–south differences (Fig. 3). The exception was the movement of two large females that traveled south into the region of the Equatorial Countercurrent and five males that traveled up to 1400 km (to 142°W) off the coast of northern Oregon in the area of the NPTZ. Our results do not show a large degree of sexual segregation for mako sharks in the ENP; however, studies with large sample sizes based on fisheries data have shown segregation by sex in the North and South Pacific [60, 69].

Our data suggest size had a more obvious effect on the large-scale movements of mako sharks than sex. Kinney et al. [38], using a Bayesian analysis on a subset of these data, found size to be a stronger signal for spatial separation than sex, although their study was not meant to address the ecological significance of mako movement patterns. The north–south range across size classes of mako sharks in that study was similar, but larger sharks tended to make more extensive offshore movements. Larger sharks were present west of 140°W in all months and spent more time offshore and less time in the California Current. Only one small male (shark 10-4S, 147 m FL) moved west of 140°W (Fig. 3). While the range may be influenced by the smaller sample size and shorter track durations for small sharks, examples of juvenile sharks staying close to shore have also been observed for makos in the western North Atlantic and Australia [2, 4]. This is consistent with the SCB being used as a nursery for YOY and juvenile mako sharks, although further long-term tagging studies are needed to examine mako shark YOY movements. (The smallest shark in this study was 104 cm FL.) Range extension may also be influenced by swimming capabilities as smaller sharks have lower absolute swimming speeds [70].

In this study, the four largest sharks, presumed to be mature (3 males 223–250 cm FL and 1 female 280 cm), spent more time offshore in more oligotrophic waters and did not travel north or south within the highly productive coastal regions. Instead, they made repetitive

movements between the SCB and a relatively consistent offshore region (Fig. 14). This pattern of directed onshore–offshore movements with limited coastal movements indicates a potential ontogenetic shift in behavior with maturity. This shift in movement by size has been documented for other shark species such as white sharks [71]. Since the SCB is a nursery area where newborn makos are found, mature females are likely coming to the SCB for pupping, although pupping and mating have never been directly observed. The similarity in movement between the SCB and a more focused offshore region by four mature sharks may reflect that as makos mature, they are driven less by foraging and growth and more toward reproduction. Further tagging studies of mature makos in the ENP should help reveal the potential role of these repetitive offshore migrations.

Vertical habitat use

In addition to horizontal movements, the use of PSATs allowed for the analysis of vertical habitat use. Our results indicate that mako sharks exhibit high levels of variability both within and among individuals in their vertical movement patterns with sharks using different portions of the water column. Overall, both size classes spent the majority of their time in the mixed layer and thermocline, approximately the top 50 m, and most sharks made frequent vertical oscillatory dives that varied in depth. Sepulveda et al. [27] found that deep oscillatory dives in the SCB were frequently associated with successful feeding events. In addition to foraging, vertical movements are likely associated with thermoregulation with sharks returning to surface waters to thermally recharge [6, 27, 72, 73]. It has also been suggested that sharks display oscillatory diving for navigation and that they may be referencing the earth's magnetic or gravitational fields [8, 74, 75].

Variability was also apparent in diel patterns both within and among individuals. While in some areas sharks remained in the MLD day and night, in general sharks were deeper during daytime hours. This diel vertical behavior is similar to previous observations of mako sharks [1, 3, 26] as well as a range of other pelagic sharks and teleosts [45, 76–79] and is typically associated with foraging in association with the deep-scattering layer. A previous study of the offshore environment in the ENP indicated that the region north of the North Equatorial Current and east of the Hawaiian Islands was a cold spot, relatively devoid of epipelagic life, but was observed to contain an abundance of mesopelagic squid species [80]. This is consistent with analyses showing a high abundance of jumbo squid in mako shark stomachs [9, 14]. Stomachs also contained a range of epipelagic species, indicating that mako sharks are foraging throughout the

water column and that vertical habitat use may vary by region. The diversity of prey habitat is likely a key factor in the high degree of variability observed in vertical movement patterns.

In addition to foraging, oceanography can also influence vertical movement, including temperature and oxygen concentrations at depth. In this study, as sharks moved offshore the depths of their dives increased. This coincides with an increase in SST, the depth of the deep-scattering layer due to increased water clarity, and the depth of the oxygen minimum zone. In the ENP, the oxygen minimum zone is relatively close to the surface and likely constrains the vertical movements of mako sharks [9] as has been observed for other pelagic fish [45, 77, 81]. This pattern of increased depth offshore is apparent in other species in the ENP [45, 77]. More comprehensive analyses are not possible due to the limited data collected offshore. Additional insight comes from studies in the Atlantic Ocean and Gulf of Mexico. In waters with higher SST and a deep MLD, mako sharks showed a deeper depth distribution where maximum depths were 866 m and sharks spent up to 36% of their time deeper than 150 m [3] in comparison with ~700 m and 0.5 to 4.5% in this study. In more temperate waters in the Western North Atlantic, their results are more similar to findings in this study where sharks spent less time in deeper waters at cooler SST and a shallower MLD. While Vaudo et al. [3] concluded that temperature was a main driver of vertical habitat use, there may be other factors influencing depth distributions in the Pacific especially given the pronounced nearshore shoaling of the oxygen minimum zone in the ENP.

Management implications

Although efforts to incorporate electronic tagging data into stock assessments have met challenges [82–84], these data can support fishery management. While experimental design is often the greatest limitation, electronic tagging datasets have some advantages over the traditional datasets used (catch, abundance index, and conventional tag data). Beyond the initial tagging effort, they are fisheries independent and provide a more comprehensive view of distribution in time and space. Catch and conventional tagging data are only obtained when and where there is fishing activity. For mako sharks specifically, there is a large gap in catch data in tropical waters and between the US EEZ and 140°W [83] where we now have a large set of electronic tagging data. Also, electronic tagging data can reveal direct connections between regions, information that is typically only inferred from catch data. Data from electronic tags can inform a range of parameters including stock structure

and dynamics, gear vulnerability, and habitat preferences [34, 36, 44, 85–87].

Currently, for management purposes, mako sharks in the Pacific are divided into separate North and South Pacific stocks with genetic and tagging data supporting east–west mixing in the north and only minimal mixing in the south [26, 28, 88]. Consistent with the current stock structure hypothesis, tagged sharks in this study did not extend into the South Pacific. To the west, although movements in this study did not extend beyond the Hawaiian Islands, conventionally tagged sharks from the ENP have been recovered westward toward Japan [29]. Lack of movement west of Hawaii and the fidelity to the California Current confirm some substructure in the North Pacific as had been suggested [60, 89]. If there is limited exchange of mako sharks across the Pacific, there is the potential for localized depletion.

A comparison of fish and fisheries distributions both geographically and vertically provides important insights into fleet and gear vulnerability [90] and has been used for a range of species to standardize CPUE [854] as well as reduce bycatch [91, 92]. For mako sharks, the deeper distribution of larger sharks appears to translate into an increased vulnerability to deep-set longline gear targeting bigeye tuna in the subtropical gyre waters to the north and east of Hawaii. The mean size of mako sharks caught in the Hawaii Longline fisheries is larger in the deep- (mean hook depth ~250 m) versus shallow-set fishery (mean hook depth ~60 m) [93]. The fisheries-independent information on vertical movements helps distinguish between gear vulnerability and shifts in habitat use.

Both size classes spent more than half their time, in the US or Mexican EEZ where the Mexican longline, California, drift gillnet and recreational fishers in California catch mako sharks. Estimated landings in the US EEZ are relatively low with a mean from 2007 to 2016 of 11 mt from the recreational fleet and 25 mt from the California drift gillnet fishery [21 and NMFS Observer data]. Mean landings in Mexico's EEZ are higher (~870 mt per year over the same period [94]) and make up a relatively large fraction of total mean North Pacific-wide landings which are estimated at ~2600 mt per year for the same period [22]. Mexican longliners typically catch juvenile size classes [95, 96]. While both size classes occurred outside the US and Mexican EEZs, larger sharks spent more time outside the EEZs and are thus more vulnerable to high-seas fleets, both in the NPTZ where they are incidentally caught in the US shallow-set longline fishery for swordfish, as well as in the tropics. As information on additional international fleets becomes available, tracking data will provide insight into vulnerability of ENP mako sharks to these fisheries. To better resolve questions

about stock structure and dynamics in the North Pacific, additional tracking data are needed for large females and ideally for sharks in the Central and Western Pacific.

Conclusions

These analyses are based on the largest satellite tagging dataset for shortfin mako sharks to date and provide detailed insight into the horizontal and vertical movements in the ENP. The scope of the project, with data from 105 sharks, tracks as long as 34 months spanning 13 years, and including both sexes across a range of sizes provides the opportunity to examine habitat use and migrations and factors that influence them. Some of the key findings include the discovery of a high degree of variability between individuals in their vertical and horizontal movements, a strong influence of size and season on mako shark movement, and the repetitive use of certain areas by individuals. These results expand our understanding of the distribution of mako sharks in the ENP and the importance of oceanographic features beyond the California Current, including the North Pacific Transition Zone, North Equatorial Current, and the SOC. Although mako sharks are thought to comprise a single stock throughout the North Pacific, horizontal distribution of tagged mako sharks in this study was limited to the ENP demonstrating some spatial substructure. This study provides important data that can be used to identify fishery and gear vulnerabilities and inform management.

Methods

A total of 113 mako sharks were tagged between 2002 and 2014 with several types of Argos satellite tags. All but four sharks were tagged in the SCB in the months of June–August. Two sharks were tagged off the coast of Baja California, Mexico, in October and January, and two were tagged north of Point Conception in November (Fig. 2, Additional file 1: Table S1). Sharks were tagged using pop-up satellite archival tags (PSATs; Model types: PAT2, PAT3, PAT4, MK10-PAT, and MiniPAT, Wildlife Computers, Redmond, WA) and/or near real-time satellite-linked radio-transmitting tags (SLRT tags; SPOT2, SPOT3, SPOT4 and SPOT5, Wildlife Computers, Redmond, WA) (Additional file 1: Table S1). In the years 2003–2009, 61% of sharks were double-tagged with both a PSAT and SLRT.

The majority of sharks were captured during the NOAA Southwest Fisheries Science Center's annual juvenile shark surveys [97]. The sharks were caught using stainless-steel longline gear with "J" hooks baited with Pacific chub mackerel or Pacific sardine. Two miles of gear with 200 hooks was deployed with a mean soak time of 4 h. Sharks were pulled onto a

cradle that was either secured to the fantail of the vessel or hoisted onto the deck. The shark's eyes were covered with a soft wet cloth, the hook removed, and the gills irrigated with seawater. A DNA sample was taken from each shark, and sex and length [either total length (TL) or FL] were recorded. If only TL was measured, it was converted to FL using the following equation [29] where lengths are in cm:

$$FL = 0.913 \times (TL) - 0.397.$$

PSATs were anchored into the dorsal musculature below the first dorsal fin using a titanium or medical-grade plastic darts. A plastic cable tie was inserted subcutaneously behind the tag insertion site and wrapped loosely around the satellite tag to reduce its movement and increase retention. SLRT tags were mounted on the dorsal fin using three nylon or stainless-steel bolts inserted through holes drilled through the fin. In most cases, a conventional tag was also inserted in the dorsal musculature below the first dorsal fin. Total time out of water was typically less than 10 min. The two sharks tagged off Mexico were caught on a commercial longline vessel and handled using similar methods. Four of the larger sharks were tagged with a PSAT using a long tagging pole at the side of the vessel.

PSATs were programmed to record pressure (which was converted to depth), temperature, and light levels every 1 or 2 min and to release after durations of 2–9 months. Transmitted data in the form of time-at-temperature and time-at-depth histograms, and temperature/depth profiles (PDT) were summarized for either 1-, 2-, 4-, 6- or 12-h periods. Because depth and temperature bins differed over the 13 years of this study, individual bins were combined to create new bins common to all tags. The resulting depth and temperature bins were 0–5, 5–10, 10–50, 50–100, 100–150, 150–200, 200–300, 300–500, 500–700 and 700–1000 m and < 8, 8–10, 10–12, 12–14, 14–16, 16–18, 18–20, 20–22, 22–24 and > 24 °C, respectively. Data from the first day after tagging and the last day before tag detachment were excluded to reduce potential influences caused by tagging effects and ensure that only data when the tag was on the shark were used [45]. In the analyses of depth and temperature preferences, data from tags recording more than 3 months were used. In most cases, maximum depth and minimum temperature were determined using the PDT data. When maximum depth and minimum temperature were determined from binned data, the depth was recorded as the minimum depth for the deepest bin and temperature as the maximum temperature for the coldest bin.

For sharks that were tagged with both a PSAT and SLRT, data from both tags were combined and the higher accuracy location data from SLRT tags were used when

available. In the absence of double-tag data, location data from PSATs were derived from light data using Wildlife Computers geolocation processing software GPE3 [98] for MK10-PAT tags, and with UKFSST [99] for PAT2, PAT3 and PAT4 tags. GPE3 implements a gridded hidden Markov model based on the methods of Pedersen et al. [100] and Basson et al. [101] using dawn and dusk light readings, surface temperature, and maximum depth as observational data, and a random walk movement model, to estimate likelihood profiles across a state space of 0.25×0.25 degree grids [Wildlife Computers, pers comm]. These types of models have been shown to produce position estimates from archival tag data with root-mean-square-error (RMSE) values of less than 0.52 and 2.4 degrees in longitude and latitude, respectively, when compared to known positions. UKFSST uses approximate longitude and latitude estimates derived from time of noon and day length based on light threshold algorithms, and SST, along with a random walk movement model in an unscented Kalman filter [99]. Lam et al. [99] found that RMSEs in UKFSST estimates of latitude and longitude for a mako shark double-tagged with a PSAT and SLRT were 0.5 and 1.2 degrees, respectively.

Archived records were obtained from recovered PSATs that provided high-resolution datasets of ambient temperature, depth, and relative light level. Tags were recovered from recaptured sharks, on beaches or using a vessel and a signal direction finder to triangulate the position of the free-floating PSAT tag. To compare nighttime and daytime activity, only archival data from recovered PSATs were used. In the transmitted data, due to the range in histogram bin intervals over the years, day- and nighttime bins were not consistent. Determination of day, night, and crepuscular periods was assigned using AstroCalc4R [102], which calculates solar zenith angles, time at sunrise, local noon, and sunset using a given location. Crepuscular periods included nautical twilight and were defined as 25 min before sunset and 75 min after, and 75 min before sunrise and 25 min after and were excluded from analyses.

SLRT tags were programmed to transmit from 200 to 500 transmissions every day, every other day, or every third day (Additional file 1: Table S1). SLRT data were filtered first by removing obviously erroneous data that showed locations well off the tracks, then by selecting a daily position with the highest location class. These daily filtered points were used to calculate distance traveled, rate of movements between points, and home range used for kernel analyses (see below). To calculate total distance traveled, the great circle distance between daily points was calculated and the total across all days was summed. Mean speed in km per day was calculated from the rates of movement between points using periods when gaps

were no greater than 5 days. Location data were visualized using ArcGIS software (Environmental Systems Research Institute, Redlands, CA).

To examine whether shark size influenced movement behavior, data were separated into two size classes consisting of small (< 165 cm FL) and large (≥ 165 cm FL) mako sharks based on the size at maturity for males. The large-size category (> 165 cm FL) consisted of mostly mature and some large immature males (males mature at 164–191 cm FL [103, 104]), large immature females, and one mature female (females mature at 253–280 cm FL [104, 105]). Kernel density analysis [106] by meteorological season was performed to examine areas of high use for both large and small sharks using the Home Range Tools [107] for ArcGIS 10.1 and 10.2 on tracks lasting at least 1 year. Note that in the later years of the study efforts shifted to tagging larger sharks.

Oceanographic characteristics examined for tracks greater than 1 year in length included depth of the MLD, and satellite-derived SST, primary productivity, and Chl-a concentrations. Mixed layer depth was calculated for recovered PSAT tags using Wildlife Computer's software (WC-DAP). SST, primary productivity ($\text{mg C m}^{-2} \text{ day}^{-1}$), and Chl-a were extracted for filtered SLRT locations using the R function "xtracto" (package: xtractomatic) [108] and the satellite data in the ERD-DAP server at the Environmental Research Division of National Marine Fisheries Service, Southwest Fisheries Science Center [109]. Data were extracted from a region encompassed by an envelope defined by the X and Y errors of the location class position estimate error [110], thus matching the scales of the position estimate errors with those of SST, primary productivity, and Chl-a. Data used were monthly composites of MODIS Chl-a, MODIS primary productivity and daily Multi-scale Ultra-high Resolution (MUR) SST.

To compare seasonal migrations of the mako sharks with the seasonal variability of the environmental conditions within the California Current, Hovmöller plots of monthly composites of MODIS SST, MODIS primary productivity and MODIS Chl-a were plotted [111]. The R function "rextractogon" (package: rerdapXtractomatic) [112] was used to extract satellite data from a region between the North America coastline and 3.85° west of the coastline (approximately 200 nmi), between 15 and 47°N . The data were averaged along longitude to show changing seasonal and annual conditions by latitude within the California Current.

Regional analyses using SLRT tag and PSAT data were performed for five main regions: three regions encompassing the California Current including (1) the SCB; (2) the coastal region north of Point Conception which includes waters off the coasts of northern California,

Oregon, and Washington; (3) and the west coast of Baja California; (4) and two additional regions including the SOC, which includes the area inside of the SOC and just south along the coast of mainland Mexico; and (5) the offshore region including areas of the North Pacific Subtropical Gyre, NPTZ, and North Equatorial Current. Seasonal utilization, oceanographic conditions, and vertical behavior were analyzed for each of the five regions.

Additional file

Additional file 1: Table S1. Deployment information. Shark identification (ID), sex (M = male, F = female, U = unknown), FL (fork length) (* = estimated length), deployment location, deployment date, PSAT (pop-up satellite archival tag) pop-update, SLRT (satellite-linked radio-transmitting tags), final date, days at liberty (DAL) PSAT (NR = no report, R = recovered tag), DAL SLRT, average sea surface temperature (SST) (°C), maximum SST (°C), minimum SST (°C), maximum depth (m), minimum overall temperature (°C).

Abbreviations

Chl-a: chlorophyll *a*; EEZ: exclusive economic zones; ENP: eastern North Pacific; FL: fork length; IUCN: International Union for Conservation of Nature; MLD: mixed layer depth; MUR: Multi-scale Ultra-high Resolution; NPTZ: North Pacific Transition Zone; PDT: profile of depth and temperature; PSAT: pop-up satellite archival tag; RMSE: Root-mean square error; SCB: Southern California Bight; SLRT: satellite-linked radio-transmitting; SOC: Sea of Cortez; SST: sea surface temperatures; TL: total length; TOPP: Tagging of Pacific Pelagics; YOY: Young-of-the-year.

Acknowledgements

We thank many colleagues, field assistants, and volunteers from the Southwest Fisheries Science Center, in particular Rand Rasmussen, Darlene Ramon, and Susan Smith who were involved at the conception of the study. We thank the crews of the R/V David Starr Jordan, F/V Ventura II, and F/V Southern Horizon. Numerous students and colleagues from CICESE, and volunteers from Moss Landing Marine Labs, California State University Fullerton, California State University Long Beach, Monterey Bay Aquarium, Scripps Institution of Oceanography and other institutions assisted during tagging cruises. Keith Poe and Steve Quinlan tagged three large makos for the study. The TOPP Program supplied many tags and maintained data on their server.

Authors' contributions

This study was initiated and designed by BAB, HD, DBH, SK, and RDV. Electronic tags were deployed on sharks by HD, JRH, MJK, SK, TS, OS, RDV, and JW. Tags were supplied by BAB, DBH, and SK. Data management was performed by HD, SK, NN, and JW. Analyses were conducted and figures were created by HD, MJK, SK, NN, TS, CW, and JW. The manuscript was drafted by NN with the help of HD and SK. All authors read and approved the final manuscript.

Funding

Funding for this study was provided by National Marine Fisheries Service, the TOPP Program and the NOAA National Cooperative Research Program.

Availability of data and materials

The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

All mako shark tagging was done in accordance with protocols approved by the Southwest Fisheries Science Center, Institutional Animal Care and Use Committee.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

¹ Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, San Diego, CA, USA. ² Laboratorio de Ecología Pesquera, Departamento de Ecología, CICESE, Ensenada, Baja California, Mexico. ³ Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Monterey, CA, USA. ⁴ Hopkins Marine Station, Stanford University, Pacific Grove, CA, USA.

Received: 30 November 2018 Accepted: 27 June 2019

Published online: 15 July 2019

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