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RESEARCH ARTICLE

Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean

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Abstract Satellite telemetry studies of 20 adult and sub-adult white sharks (360–530 cm estimated total length (TL)) in the eastern North Pacific during 1999–2005 revealed long distance seasonal migrations from the coast of California to an offshore focal area 2,500 km west of the Baja Peninsula, as well as the Hawaii Islands. Three tags were recovered allowing detailed behavioral analyses, including one shark's migration cycle from the coast to the offshore focal area and back. While near pinniped rookeries in autumn and winter, sharks avoided the surface and used water to 50 m depth, consistent with a silhouette-based hunting strategy. Offshore migrations were initiated during November–March and followed periods of decreasing pinniped abundance. Migrations were highly directed, taking 23 ± 5 days to reach the offshore focal area along similar paths among sharks and years, defining a migration corridor. Sharks exhibited a broad depth distribution (0–644 m) in the offshore focal area, and remained there for up to 167 days during spring and summer, though primary productivity and fishery data suggest that forage resources are scarcer there than in other regions of the eastern North Pacific. Archival data from one shark revealed intensive oscillatory movements while in the offshore focal area, a behavior that may be related to foraging or mating. Sharks traveling to Hawaii remained near the islands up to 122 days, potentially feeding on pelagic fishes and marine mammals that concentrate around the islands.

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Introduction

The sharks of the family Lamnidae are apex pelagic predators that range into temperate, tropical and polar oceans (Compagno 1984), and comprise the shortfin mako shark (*Isurus oxyrhincus*), the longfin mako shark (*Isurus paucus*), the white shark (*Carcharodon carcharias*), the salmon shark (*Lamna ditropis*) and the porbeagle shark (*Lamna nasus*) (Compagno 1984). The Lamnidae are unique among sharks due to the presence of counter-current heat exchangers, centralized slow-twitch muscle and elevated metabolic rates. These physiological attributes

enable lamnids to maintain warm body temperatures (Carey et al. 1982; Graham et al. 1990), which may underlie many of their ecological traits, including wide thermal tolerance, high performance swimming (Bernal et al. 2005), niche expansion into northern latitudes (Weng et al. 2005) and the ability to capture marine mammals (Ainley et al. 1985).

White sharks live in temperate and tropical waters with a distribution that spans coastal to pelagic habitats. Adult white sharks feed on fishes and marine mammals (Compagno 1984). Aggregations of white sharks near pinniped rookeries have been documented in a number of areas, including northern California (Ainley et al. 1985), southern Australia (Bruce 1992), eastern Canada (Brodie and Beck 1983) and South Africa (Ferreira and Ferreira 1996). White sharks have been observed poleward of 50° in both hemispheres and in tropical waters (Compagno 1984). Conventional tagging studies have shown movements up to 1,445 km from the point of release (Kohler and Turner 2001), while photographic identification of individual sharks has revealed movements of 700 km (Anderson and Goldman 1996). Acoustic tracking studies have shown that white sharks have average stomach temperature elevations of 10.8°C in 15–18°C waters (Goldman 1997).

Recent satellite tracking studies have rapidly expanded our knowledge of the horizontal movements and diving behaviors of white sharks. Satellite tags placed on adult white sharks in the Pacific and Indian Oceans (Boustany et al. 2002; Bonfil et al. 2005; Bruce et al. 2006) have provided new details of long-range movements and vertical habitat distribution. Boustany et al. (2002) demonstrated that white sharks tracked from the central California coast moved into an offshore region between Hawaii and Baja, as well as to the Hawaiian Islands. Bonfil et al. (2005) reported a transoceanic migration from South Africa to western Australia and back, as well as fine-scale coastal movements off the coast of South Africa and Mozambique. Bruce et al. (2006) showed that white sharks make long distance movements along the west, south and east coasts of the Australian continent, and reported one shark moving from South Australia to the North Island of New Zealand. These studies rejected the widely held belief that white sharks were coastal or neritic, and raised a number of new questions about their behaviors and life history, including the importance of nearshore versus pelagic phases, the portions of the year spent in each habitat, and the predictability of long distance movements.

In California, white sharks are known to aggregate at pinniped rookeries during northern autumn (September–November) and winter (December–February) when the abundance of immature elephant seals is at a maximum Ainley et al. (1985). However, little information existed regarding their distribution during spring (March–May) and summer (June–August). Their absence from these rookeries during the spring influx of elephant seals was thought to be a result of mature sharks moving into the Southern California Bight to mate or give birth (Klimley 1985). Parturition in the Southern California Bight is supported by the existence of young-of-the-year sharks in that region (Klimley 1985; Weng et al. 2007), but no pregnant females have ever been observed there (Francis 1996). The results of Boustany et al. (2002) were not consistent with this hypothesis, and showed offshore movments, possibly for parturition, mating, or foraging. Anderson and Pyle (2003) found that females return to the Farallones on a 2-year cycle, while males return annually, and speculated that females may travel large distances to give birth.

The discovery that top–down processes can have fundamental structural impacts on ecosystems (Hunter and Price 1992) highlights the need to understand the biology of apex predators such as the white shark. The use of new electronic tagging technologies to track pelagic animals has yielded numerous insights into the biology of species such as salmon sharks (Weng et al. 2005), bluefin tuna (*Thunnus thynnus*) (Block et al. 2005), elephant seals (*Mirounga angustirostris*) (DeLong et al. 1992) and marine birds (Weimerskirch et al. 2002). Enhanced knowledge of the long-range movements and aggregation areas of pelagic species will improve our understanding of their life history, and of their relations to the physical and biotic environment. This knowledge is essential to the management of white shark populations, which are threatened globally (Stevens et al. 2000). In this paper we investigate the seasonal movements of eastern North Pacific white sharks, compare their utilization of neritic and pelagic waters, and discuss the biological functions that they may be fulfilling in these distant habitats.

Materials and methods

Satellite telemetry

White sharks were tagged at Southeast Farallon Island (37.70°N, 123.00°W), which lies 30 km west of the entrance to San Francisco Bay, CA, USA. Pop-up archival transmitting tags (PAT tag firmware versions 2.0, 3.0 and 4.0; Wildlife Computers, Redmond, Washington, USA) were deployed on white sharks during the autumn months of 1999–2004. Each PAT tag was attached to a titanium dart with a 20 cm segment of 136 kg monofilament line (300 lb test Extra-hard Hi-catch, Momoi Manufacturing, Japan) coated with shrink-wrap. The titanium dart was custom-made, measuring 59 × 13 × 1.5 mm, with the trailing 10 mm canted at a 17° angle. The dart was inserted 17 cm into the dorsal musculature of the shark at the base of the

first dorsal fin using a 2 m aluminum pole. Sharks were not captured, but were tagged during predatory events as they swam near the 4.3 m research boat. No chum was used to attract sharks. Sizes were estimated and underwater and above water video and photos were taken to determine sex and aid in visual identification of individual sharks.

PAT tags remain attached to a study animal for a predetermined duration, and then activate an electrolytic release mechanism, floating to the surface and transmitting data to satellite-borne Argos receivers. PAT tags in this study were programmed to record depth, temperature and light measurements at 1- or 2-min intervals. If the tag was recovered it was possible to download the entire archival dataset. The archival data were compressed into bins of 12 or 24 h for transmission to Argos satellites. For each time period the tag produced a depth-temperature profile and two histograms, one of time-at-depth and one of time-at temperature. In addition, 12-light level data points were transmitted for both dawn and dusk of each day.

Data recovery

Of the 29 PAT tags deployed, 20 successfully transmitted data on the movements and habitat preferences of white sharks (Table 1), while nine did not report (Appendix 1). Three PAT tags were recovered (2-M, 17-U and 18-F) and the full archival records obtained (525 days total). Tag 2-M detached and transmitted from waters near the Farallon Islands, CA, drifted to shore and was found, yielding a 26 day archival record. Tag 17-U popped-up and transmitted from waters near Año Nuevo Island, California and was recovered at sea, yielding a 305 day archival record. Tag 18-F never transmitted, and was found near Sea Ranch, California, yielding a 194 day archival record. Subsequent analysis revealed that the battery of tag 18-F failed during the track.

For all 20 sharks, the tracking duration (the time the PAT tag remained attached to the shark) averaged 167 ± 96 days with a maximum tracking period of 367 days (Table 1). We obtained 19 satellite tag endpoint locations from Argos, and 906 geolocations based on light-based longitudes and SST-based latitudes, of which 395 were obtained from archival records. Including the known deployment locations, the total location dataset includes 945 positions. Visually estimated total lengths (TL) for the sharks in this study averaged 443 ± 49 cm. Using TL maturity thresholds of 3.8 m for males (Pratt 1996) and 4.5 m for females (Francis 1996), we estimate that 68% of the sharks we tracked were sexually mature, comprising nine males, three females and one of unknown sex larger than the female threshold. Of the remaining sharks, one was an immature male, three were immature females and two were of unknown sex (Table 1). Three of the 20 sharks in this study (1-M, 2-M and 3-M) were included in an earlier publication (Boustany et al. 2002).

Analysis

To determine the movements of each shark, we estimated longitude for each day based on threshold techniques for assessing position with ambient light levels (Hill and Braun 2001). Latitude was estimated for each day by comparing sea surface temperature measured by the tag with that measured by satellite sensors along the light-based longitude estimation (Teo et al. 2004). A speed filter of 2 m/s was used to discard points requiring movements that were not biologically feasible, based on published speeds from electronic tagging studies for white sharks of 1.2 m/s (Klimley et al. 2001) and 1.3 m/s (Bonfil et al. 2005). Teo et al. (2004) estimated the root mean square (RMS) error of light-based longitude to be within 0.89°, and the RMS error of SST-based latitude to be within 1.54°, for double tagging experiments (PAT and SPOT) on salmon sharks and blue sharks. We also directly estimated errors for white sharks in this study by comparing known deployment or endpoint locations to light/SST geolocations up to 1 day away (Table 2). For the purposes of error estimation we did not use a speed filter, so as to avoid artificially reducing errors. The straightness of tracks was calculated using the method of Batschelet (1981), in which the straightness index is the ratio of the straight distance between two points and the actual path traveled between them, such that a straight line has a value of one. Straightness was calculated only for the tracks of the two sharks with archival records that moved offshore. Sharks with transmitted records had insufficient positions to calculate straightness with confidence.

The habitat use of white sharks was quantified using the kernel density method (Silverman 1986) implemented in the animal movement extension (Hooge and Eichenlaub 1997) for ArcView 3.2 (ESRI, Inc., Redlands, CA, USA). Kernel densities were calculated for each meteorological season using a search radius equal to the mean latitude position error for our tags (1.73°). Variability in the temporal frequency of positions can bias density estimation (Aebischer et al. 1993) so we regularized our tracks to one position per day. We used the piecewise cubic hermite interpolating polynomial (Matlab, The Mathworks, Natick, MA, USA), which had the highest accuracy of available methods in a recent study (Tremblay et al. 2006). Kernel density was presented as percent of all positions, with 25, 50 and 95% contours overlaid on color-mapped data. The 25% contour was used to highlight core regions of occupancy, while 50 and 95% contours showed regions of decreasing usage.

Table 1 White sharks tracked from Southeast Farallon Island, CA, USA, 1999–2004

Shark	Tagging date	Total length (cm)[a]	Sex	Maturity	Pop-up date	Track days	Longitude (°)	Latitude (°)	Comment
1-M	19 October 1999	402	M	Mature	2 November 1999	14	–124.49	38.95	Nearshore
2-M	30 October 1999	366	M	Adolescent	25 November 1999	26[b]	–125.97	38.69	Nearshore
3-M	16 October 2000	457	M	Mature	16 April 2001	182	–156.80	20.67	To Hawaii
4-M	5 November 2001	457	M	Mature	6 May 2002	182	–141.47	26.39	To Hawaii
5-F	5 November 2001	488	F	Mature	19 July 2002	256	–133.25	21.13	Offshore focal area
6-M	5 November 2001	427	M	Mature	7 August 2002	275	–138.83	26.50	Offshore focal area
7-F	5 November 2001	442	F	Adolescent	10 December 2001	35	–123.09	37.07	Nearshore
8-M	15 November 2001	380	M	Mature	14 January 2002	60	–131.71	34.93	Initiated migration
9-M	15 November 2001	450	M	Mature	12 June 2002	209	–134.22	25.04	Offshore focal area
10-F	15 November 2002	530	F	Mature	14 February 2003	91	–134.69	26.81	Offshore focal area
11-U	24 September 2003	427	?	n/a	24 March 2004	182	–134.18	25.20	Offshore focal area
12-M	27 October 2003	396	M	Mature	23 June 2004	240	–156.39	20.97	Hawaii; pop-up position only
13-U	31 October 2003	488	?	Mature	1 November 2004	367	–147.10	24.80	Offshore focal area
14-M	5 November 2004	457	M	Mature	9 April 2005	155	–124.20	22.30	Offshore focal area
15-M	5 November 2004	457	M	Mature	10 April 2005	156	–132.29	22.67	Offshore focal area
16-M	5 November 2004	427	M	Mature	10 May 2005	186	–127.71	22.06	Offshore focal area
17-U	5 November 2004	360	?	Adolescent	06 September 2005	305[b]	–122.45	37.10	Return migration
18-F	30 November 2004	396	F	Adolescent	12 June 2005	194[b]	n/a	n/a	To Hawaii
19-F	30 November 2004	490	F	Mature	3 May 2005	154	–136.73	27.59	Offshore focal area
20-F	3 December 2004	426	F	Adolescent	8 February 2005	67	–122.87	37.77	Nearshore

[a] Total length was estimated visually

[b] Tag recovered and archival record obtained

We classified our data into six phases according to the movements of the sharks: nearshore, traveling, in the offshore focal area, near Hawaii, traveling to the south of Hawaii, and in an offshore focal area south of Hawaii. Sharks were considered to be nearshore from the date of tagging until they dove to 200 m or greater and were thus off the continental shelf, signifying departure. A dive threshold was used rather than light/SST geolocation because dive data were more temporally continuous than geoposition data. Sharks were considered to be traveling while their longitude-time trajectory showed monotonic westward motion, and to have reached their destination, either in the offshore focal area or near Hawaii, at the first inflection in this trajectory. The straight distance between the departure and arrival positions was used to determine speed, which was thus an estimate of minimum speed. Longitude was used as an indicator of migration rather than position, because we obtained far fewer latitudes than longitudes, and thus had fewer positions than longitudes. Sharks were considered to be offshore or near Hawaii until another monotonic movement eastward occurred.

Table 2 Errors in light- and SST-based geolocations determined by comparison with known deployment and pop-up locations

Known position	Shark	Longitude error (°)	Latitude error (°)
Pop-up	3-M	0.34	0.09
Deployment	9-M	0.46	1.11
Deployment	7-F	–0.68	–0.60
Deployment	20-F	–0.26	–2.17
Deployment	16-M	0.23	3.6
Pop-up	18-U	–0.77	–0.35
Deployment	19-F	–0.19	–4.17
Mean		0.42	1.73
SD		0.23	1.63

We characterized the depth and temperature preferences of the sharks using the histograms transmitted by PAT tags, which aggregated all observations into preprogrammed intervals. The mean and standard deviation for each interval were calculated from the mean value at that interval for each shark, such that error bars represent variation between individuals. Distributions were Gaussian, so comparisons are made with parametric Student's *t*-tests.

Estimates of surface mixed layer depth, Z_{ML}, were made using the temperature, T. We used pressure–temperature data collected by the tags to determine the local maximum

in the second derivative of the depth-temperature profile, C_{ZT}, (Brainerd and Gregg 1995), given by

$$C_{ZT} = \frac{d(dT/dZ)}{dZ} \quad \text{and} \quad Z_{ML} = Z \text{ at } \max\{C_{ZT}\}$$

where archival records were available we then calculated the amount of time sharks spent within the surface mixed layer and below it. Where transmitted records were available such calculations were not possible since depth and temperature occupancy data were aggregated into predetermined intervals that did not correspond to mixed layer depth.

For the three sharks with archival records (2-M, 17-U and 18-F), more detailed analyses were possible, so we assigned measurements to diel periods based on the light record (Weng et al. 2007), and characterized the depth and temperature preferences of the sharks during these periods. Vertical excursions were the greatest depths reached every one-tenth of an hour. Due to the non-Gaussian distribution of the data, we use median (first quartile–third quartile) to summarize the results, and the non-parametric Wilcoxon rank sum test for comparisons. We compared behavior across the six movement phases defined above.

The migration route was characterized in terms of factors that could potentially aid in navigation, such as bathymetry, magnetism and gravity. Bathymetry data were obtained from Smith and Sandwell (1997). Gravity data were obtained from Sandwell and Smith (1997). Magnetic declination and inclination data were obtained from Peddie (1993), while magnetic anomaly data were obtained from Bankey et al. (2002). Data were imported into ArcGIS version 9 (ESRI, Inc., Redlands, CA, USA) for comparison with shark movements.

Results

Timing of movements and focal areas

We obtained 3,336 days of observation for 20 white sharks tagged off the central California coast, revealing a seasonal pattern of nearshore residency during autumn and winter, followed by a pelagic phase during spring and summer, in which sharks move as far west as the Hawaiian archipelago (Fig. 1). The kernel density analysis (Fig. 2) shows that the migration paths of white sharks (n = 15) were consistent across individuals a single individual (17-U) was tracked from the tagging location near the Farallon Islands to an offshore focal area between the Baja Peninsula and Hawaii, and back to the coast of California, over a period of 305 days.

All 20 electronically tagged white sharks remained near the coast of California for a period of time after tagging. During this period, sharks inhabited waters ranging from 32 to 38°N and from the coast of California to 125°W. For the 15 sharks that undertook offshore migrations, the duration of the nearshore phase was 57 ± 35 days. Sharks were in nearshore waters for unknown duration prior to tagging, so these results underestimate the duration of the nearshore phase. We recorded the arrival date of shark 17-U back at the coast of California, and if we assume that it departed on the same date as the previous year, its coastal phase would be 117 days.

Offshore migrations for the 15 sharks that departed the coast began on a mean date of 2 January (earliest 19 November, latest 24 March). Female sharks (n = 4) embarked on migrations on a mean date of 15 February (earliest 25 December, latest 24 March), later than male sharks (n = 8), which departed on a mean date of 11 December (earliest 19 November, latest 23 January), but the difference was not significant (Student's t-test: t = 2.36, p = 0.07). White sharks appeared to depart the Farallones following decreases in pinniped abundance (Appendix 2).

Movements of white sharks to an offshore focal area 2,500 km west of Baja California, centered at 23°N, 134°W, and ranging from 18 to 26°N and 125 to 140°W, were undertaken by male and female, and mature and immature sharks (Table 1). Sharks arrived at the offshore focal area between 2 December and 12 April, with a mean date of arrival of 28 January. Female sharks arrived on 8 March (earliest 11 January, latest 12 April), while male sharks arrive significantly earlier on 30 December (earliest 1 December, latest 21 February) (Student's t-test: t = 3.07, p = 0.02).

All sharks that travelled to the offshore focal area except for one (17-U) were still in this region when their tags released, 109 ± 58 days later. The longest offshore residency in this area was 167 days (shark 9-M). The offshore migrations to the focal area traversed straight-line distances of 1,961 ± 406 km over 23 ± 5 days at an average minimum speed of 88 ± 14 km/day (0.23 ± 0.05 TL s^{-1}). The fastest migration (14-M) occurred at a minimum speed of 119 km/day (0.30 TL s^{-1}).

Return migration to foraging areas on the coast of California was exhibited by a single shark (17-U) that was tracked for 305 days. This shark was tagged at the Farallones on 5 November 2004, remained near the coast for 103 days, and embarked on the westward migration on 16 February 2005. Its movement to the offshore focal area covered a straight-line distance of 2,234 km, and took 27 days at an average speed of 90 km/day. It remained in the offshore focal area for 137 days before initiating its return migration to the North American coast on 31 July

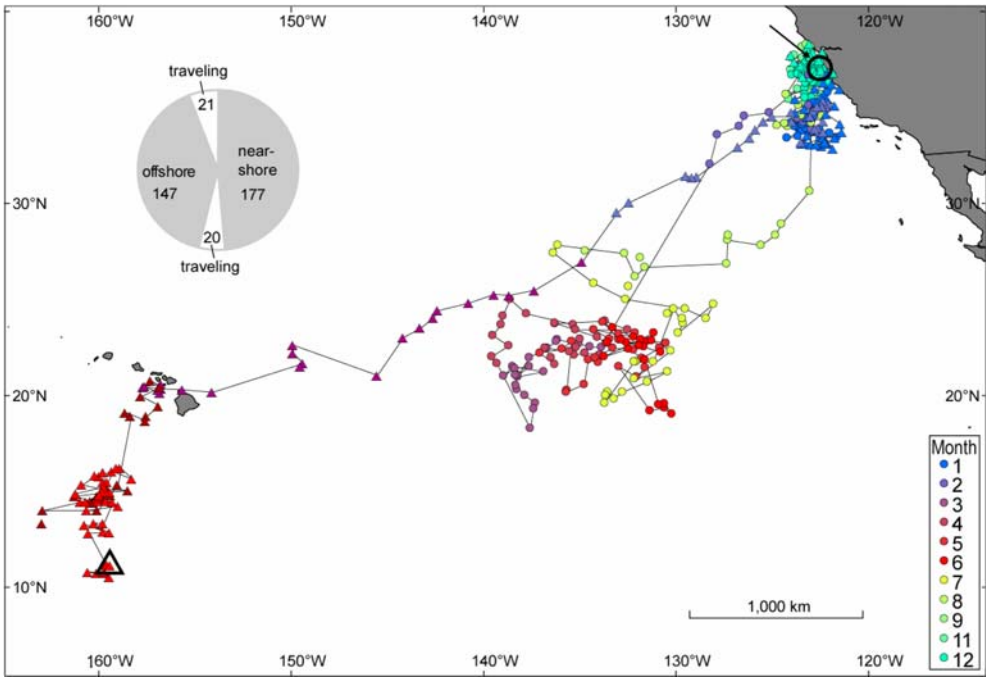

Fig. 1 Movement patterns for two out of 20 white sharks tracked from 1999 to 2005. Sharks 17-U (*small circle*) moved from the tagging location in California (*arrow*) to the offshore focal area and back to California where the tag popped up (*large circle*); white shark 18-F (*small triangle*) moved from California to Hawaii, where the tag stopped recording data (*large triangle*). Colors denote month. Pie diagram shows days of the year spent in four phases by shark 17-U

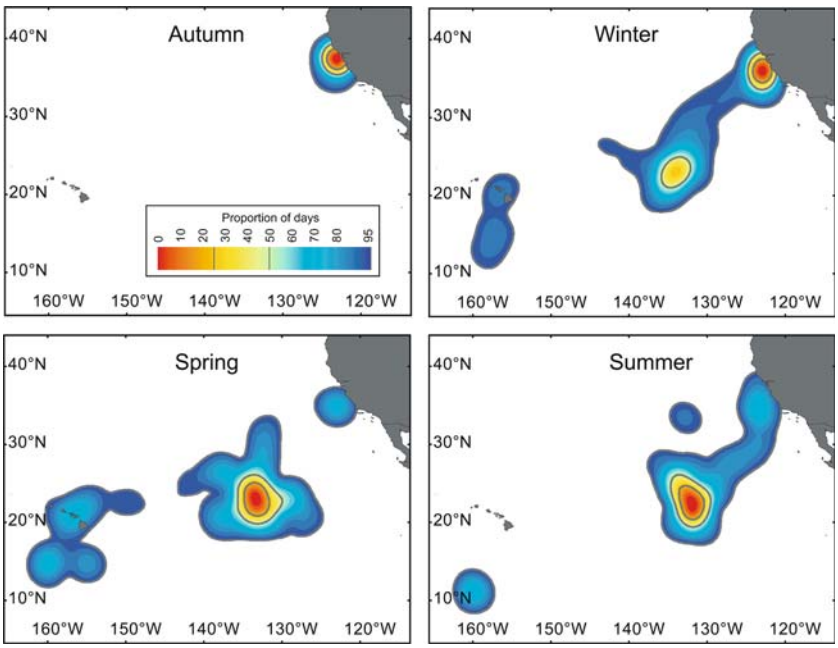

Fig. 2 Kernel density estimates for white sharks that made offshore movements (n = 15) during northern hemisphere meteorological seasons. Contours encompass 25, 50 and 95% of all positions

2005, which occurred in 22 days, at an average speed of 75 km/day. The shark inhabited shallow nearshore waters between 35 and 38°N from 21 August 2005 until the tag released and transmitted on 6 September 2005, 10 km from Año Nuevo Island.

Directed movements to waters near the Hawaiian Islands were undertaken by four white sharks, along routes that did not pass through the offshore focal area, and included male and female, mature and immature sharks (Table 1). Sharks occupied waters from 18 to 23°N and 154 to 163°W. The migration to the islands covered 3713 ± 56 km and occurred in 37 ± 2 days at 101 ± 6 km/day (0.27 ± 0.03 TL s^{-1}) (n = 3). Sharks remained near the Islands of Kauai, Maui, Lanai, Kahoolawe and Hawaii for 62 ± 50 days. One shark (3-M) inhabited these waters from 26 December 2000 until its tag released 122 days later on 16 April 2001, when it was in the Kealaikahiki Channel between Kahoolawe and Lanai (Boustany et al. 2002), 11 km from Lanai. Another shark (4-M) inhabited waters of Molokai and Maui for 61 days from 15 January

to 17 March 2002, before heading east from the islands into the offshore focal area, the only shark that visited both offshore aggregation areas. The tag on a third-shark (12-M) released and transmitted 5 km from the north shore of Maui near Paia on 23 June 2004. Shark 18-F utilized waters near Lanai and Kahoolawe for 13 days from 22 March to 4 April 2005, before moving south to a region 700 km to the south of the island of Hawaii (Fig. 1). This southern migration extended to 11°N, and the traveling period lasted for 8 days, with a speed of 87 km/day (0.26 TL s^{-1}). It was in these waters for 57 days later when the battery failed.

Focal areas were strongly differentiated from migration routes by the straightness of tracks, quantified using the straightness index (Batschelet 1981), based on the tracks for the two sharks with archival records that traveled into offshore waters. Migration phases between the central coast of California and the offshore focal area or the islands of Hawaii had straightness indices (SI) of 0.78 ± 0.12, significantly greater than the SI for the Farallones, the offshore focal area and the Hawaiian Islands of 0.16 ± 0.21 (Student's *t*-test, $t = -5.88$, $p = 0.0003$). Shark 17-U inhabited three focal areas, the Farallones, the offshore focal area, and Año Nuevo (37.11°N, 122.34°W); and undertook two migrations, one away from the coast of California to the offshore focal area, and another returning to the California coast. Shark 18-F utilized a focal area at the Farallones, another near the Main Hawaiian Islands, and a third 700 km south of Hawaii. The paths taken by white sharks during migration did not show clear relationships with magnetic features of the earth's crust (Appendix 3).

The errors in light- and SST-based geolocations were estimated by comparison to known tagging positions and satellite tag endpoint positions determined by the Argos system (Table 2). Of the 20 white shark tags that reported data, light and SST geolocation estimates were obtained within 1 day of the start and endpoints for seven of 38 possible events.

Nearshore California

In nearshore California waters, white sharks ($n = 16$) spent 99 ± 3% of their time at depths shallower than 50 m, but only 22 ± 16% of their time in 0–5 m depths (Figs. 3, 6a). Sharks spent the majority (92 ± 10 %) of their time in ambient temperatures of 10–14°C (Fig. 6b). Mixed layer depths averaged 36 ± 18 m.

Archival records for sharks near the Farallon Islands ($n = 3$) and Año Nuevo Island ($n = 1$), California provided a detailed look at these behavioral patterns. In comparison to the other phases, the mixed layer near coastal California was thinner and cooler; white sharks spent the greatest amount of time in the mixed layer; and made the fewest excursions below this layer (Table 3). There were no strong diel patterns in behavior (Figs. 4a, 5a), and diel differences in depth (Figs. 7a, e and 8a) and temperature were not significant (Wilcoxon rank sum tests: depth, $W = 21.0$, $p = 0.47$; temperature, $W = 18.0$, $p = 1.00$; Table 4). Diel differences in the number of vertical excursions were not significant (Wilcoxon rank sum tests: depth, $W = 17.0$, $p = 0.89$; temperature, $W = 16.5$, $p = 0.77$; 5). These patterns reflected their limited vertical movements, as well as the rarity of visits to the surface.

Traveling

During migratory phases ($n = 10$) sharks spent 57 ± 7% of their time shallower than 5 m, but also undertook dives to 736 m, and spent 15 ± 10% of their time deeper than 300 m (Figs. 3 and 6c). Ambient temperatures showed a broad distribution with 20 ± 14% of the time spent at 20–22°C and 19 ± 10% spent at 6–10°C, reflecting the combination of surface swimming behavior and deep diving (Fig. 6d). During the traveling phase sharks spent significantly more time near the surface (Student's *t*-test, $t = 7.64$, $p = 0.00$) and more time deeper than 300 m (Student's *t*-test, $t = 5.25$, $p = 0.00$) than they did during the nearshore phase (Fig. 6). Mixed layer depths averaged 110 ± 28 m.

Archival records for the migratory phase away from the coast of California ($n = 2$) and the return migration back to the coast of California ($n = 1$) were consistent with transmitted PAT records reported above, and revealed that sharks had a strong preference for the surface, which was consistent through their initial westward migrations through the California current (Figs. 4b, 5b) as well as the later stages of migration in the subtropical gyre (Figs. 4c, 5c). Median depths were 2 m during both day and night (Table 4), reflecting the behavior of returning to the surface between vertical movements, and remaining there for periods up to 1.5 days (shark 17-U). Diel differences (Figs. 7b, 8b) were not significant for depth (Wilcoxon rank sum test, $W = 10.5$, $p = 1.00$) or temperature (Wilcoxon rank sum test, $W = 12.5$, $p = 0.51$). Vertical excursions were far deeper than during the nearshore phase (Table 5), and were not significantly different between day and night for depth (Wilcoxon rank sum test, $W = 13.0$, $p = 0.38$) or temperature (Wilcoxon rank sum test, $W = 6.0$, $p = 0.08$).

Offshore focal area

Sharks in the offshore focal area ($n = 9$) occupied a broad depth and temperature range (Fig. 3), spending 54 ± 18% of the time shallower than 100 m, and 46 ± 22% of the time deeper than 100 m (Fig. 6e). Sharks spent 58 ± 13%

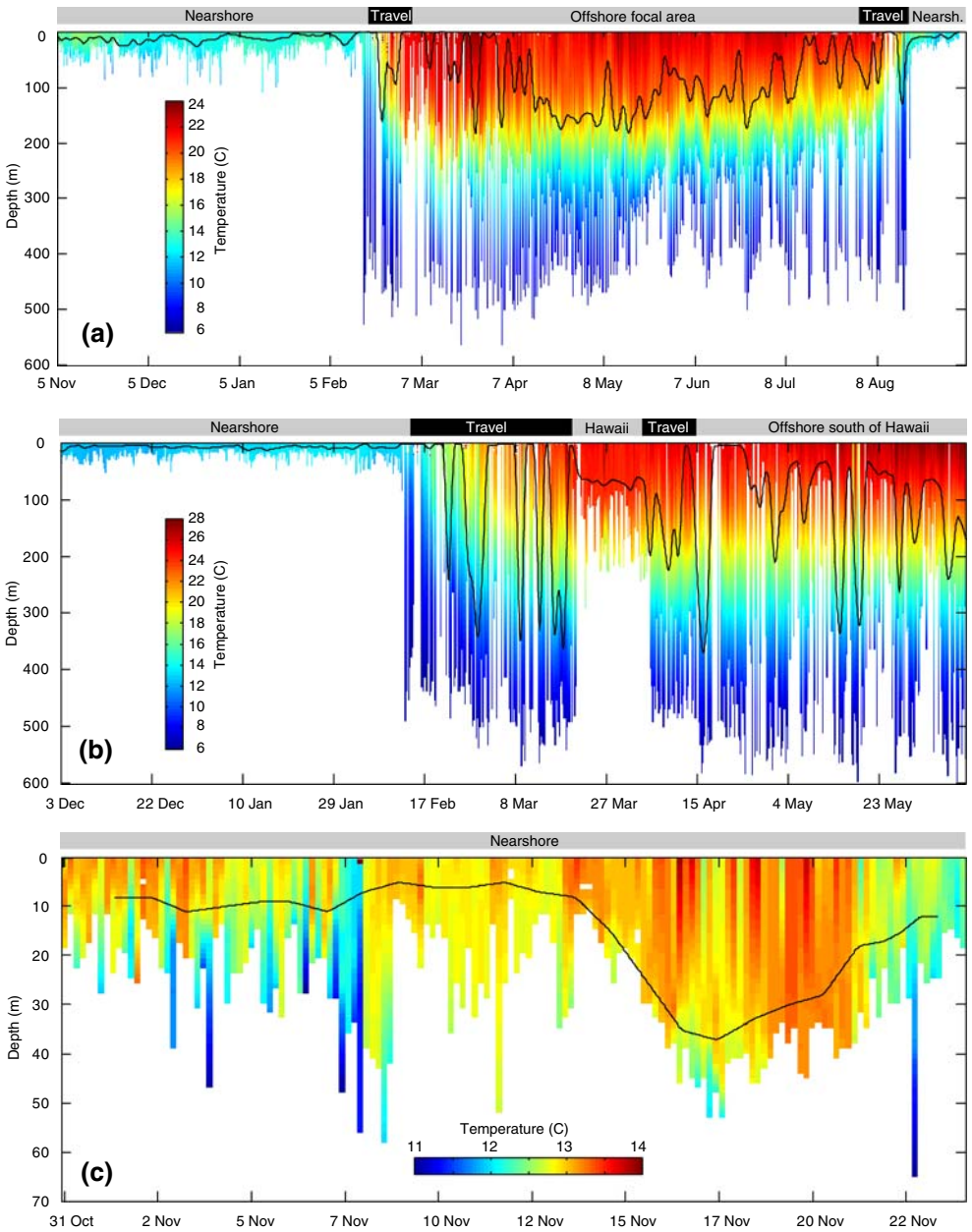

Fig. 3 Ambient temperature-depth profiles taken by **a** shark 17-U during movements from the Farallones, California to the offshore focal area and back to Año Nuevo, CA, 2004–2005; **b** shark 18-F during movements from the Farallones, California to waters near the Hawaiian Islands; and **c** shark 2-M while near the Farallones, CA. *Color* denotes ambient temperature; *black line* shows median daily depth of the shark

of the time in 20–24°C waters and 42 ± 13% of the time in 4–20°C waters (Fig. 6f). Sharks spent 29 ± 10% of the time in 0–5 m waters while in the offshore focal area, significantly more than while traveling (Student's *t*-test, $t = 7.74$, $p = 0.00$). Mixed layer depths averaged 132 ± 20 m.

The archival record of shark 17-U revealed a remarkable oscillatory behavior pattern when the shark was in the offshore area, with vertical excursions occurring throughout the diel cycle, from the surface to 644 m, ranging in temperature from 5.4 to 24.2°C (Fig. 4d). The shark moved below the surface mixed layer 30 times/day, up to a maximum of 96 times/day (Fig. 4e; Table 3), and thus had deeper median depths than during nearshore or traveling phases (Appendix 4), reflecting the continuous movements as well as the avoidance of near surface waters on some nights. Median depths during the day (60 m) were significantly shallower (Wilcoxon rank sum test, $W = 4.72$, $p = 0.00$; Table 4) than during the night (83 m), though still within the mixed layer during both diel periods. However, despite the deeper median position during night, the depth of vertical excursions was significantly deeper and cooler during day than night, and below the mixed layer during both periods (Fig. 7c; Table 5; depth: Wilcoxon rank sum test, $W = 10.2$, $p = 0.00$; temperature: Wilcoxon rank sum test, $W = 10.17$, $p = 0.00$).

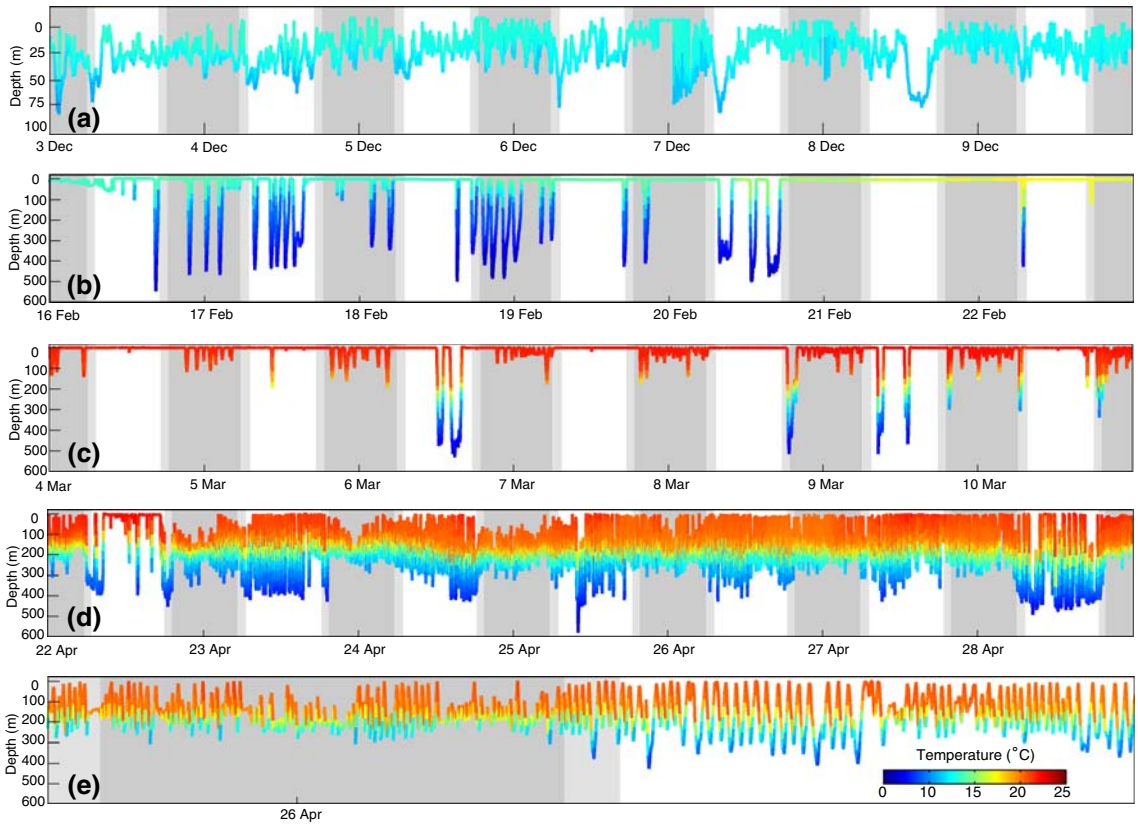

Fig. 4 One week time series of depth (*line*) and temperature (*color*) for white shark 17-U, 2004–2005: **a** Nearshore, of the Farallon Islands, California, **b** traveling west through the California Current, **c** traveling through the subtropical gyre, **d** in the offshore focal area, and **e** a single day in the offshore area. *Dark grey* denotes nighttime, *light grey* denotes twilight

Hawaii

Depth and temperature data were obtained for three of the four sharks that moved to the Hawaiian Islands. These sharks showed a broad depth distribution, spending 48 ± 27% of the time shallower than 100 m and 52 ± 27% of the time deeper than 100 m, but avoided the surface, spending only 7 ± 1% of the time in 0–5 m waters (Fig. 6g). Surface mixed layer depths averaged 113 ± 17 m, suggesting that equal division of time above and below the pre-programmed 100 m histogram threshold corresponded approximately to time in and below the mixed layer. The time in 0–5 m waters in Hawaii (n = 3), where temperatures were 24.8 ± 0.1°C, was significantly lower than during the nearshore California phase (7 vs. 22%; Student's t-test, t = 3.60, p = 0.00); and time deeper than 50 m was significantly higher (79 vs. 1%; Student's t-test, t = –27.8, p = 0.00). Temperature distribution was broad, with 36 ± 31% of the time spent in waters warmer than 24°C, and 5 ± 8% of the time in waters cooler than 14°C (Fig. 6h).

A single archival record was obtained (18-F) for the Hawaiian focal area (Figs. 3b, 5d). Median depths were within the surface mixed layer during both diel periods (Fig. 5d), and were significantly shallower (Wilcoxon rank sum test, W = 41.9, p = 0.00) and warmer (Wilcoxon rank sum test, W = 38.4, p = 0.00) during daytime (Fig. 8c; Table 4). During the nighttime, vertical excursions were significantly deeper (Wilcoxon rank sum test, W = 6.8, p = 0.00), and cooler (Wilcoxon rank sum test, W = 7.0, p = 0.00), than during the daytime (Table 5). This diel pattern was the opposite of that observed during all other phases (Fig. 5d, Appendix 5).

Travel south of Hawaii

During movement from waters near Maui to the focal area 700 km to the south (centered at 11.20°N, 159.88°W), shark 18-F used waters from the surface to 708 m, and from 5.9 to 25.8°C (Figs. 3b, 5e). The shark had a significantly deeper and cooler median position during nighttime than daytime (Fig. 8d; Table 4; depth: Wilcoxon rank sum test, W = 10.3, p = 0.00; temperature: Wilcoxon rank sum test, W = 2.3, p = 0.02), which was within the mixed layer during both diel periods. During the daytime, vertical excursions were significantly deeper (Wilcoxon rank sum

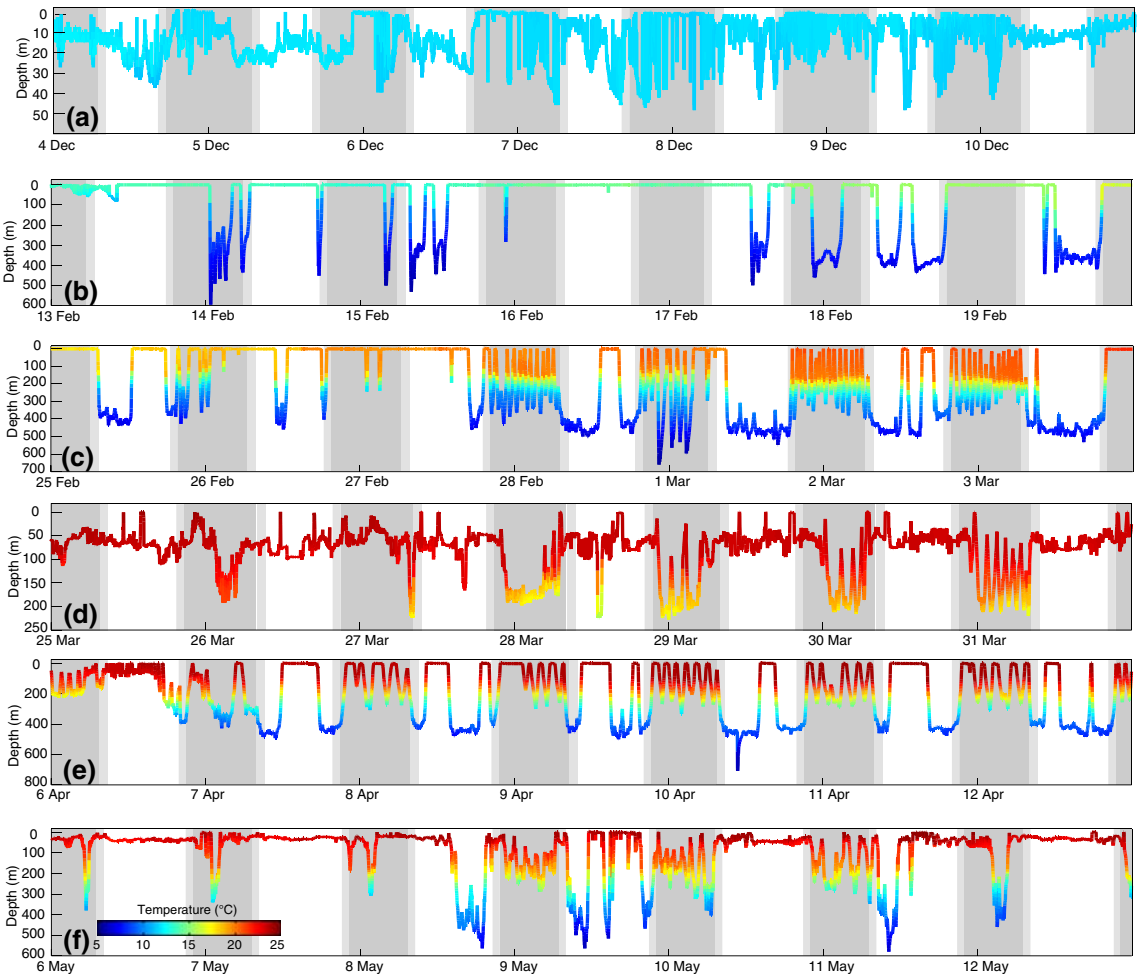

Fig. 5 One week time series of depth (*line*) and temperature (*color*) for white shark 18-F, 2004–2005 **a** nearshore, off the Farallon Islands, California, **b** traveling west through the California Current, **c** traveling west through the subtropical gyre, **d** near the Main Hawaiian Islands, **e** traveling south from Hawaii, and **f** at a focal area between Hawaii and Kiribati. *Dark grey* denotes nighttime, *light grey* denotes twilight

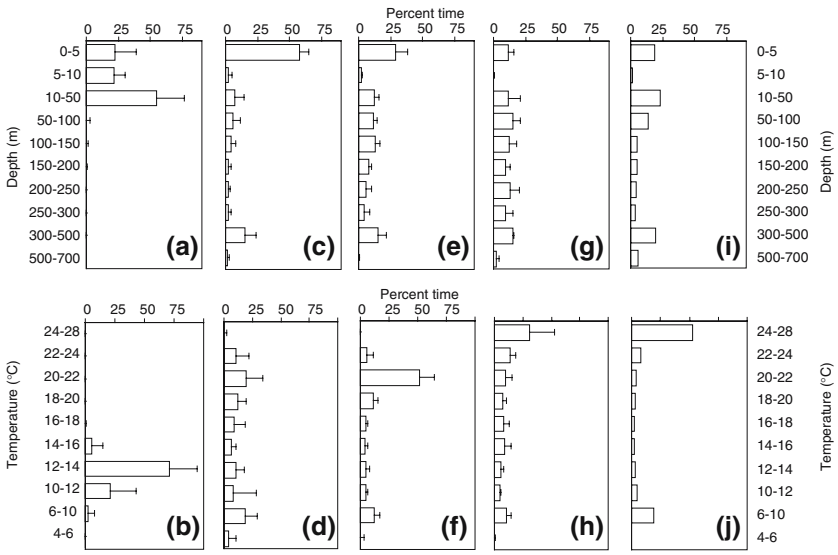

Fig. 6 Depth and temperature distribution for white sharks while nearshore (n = 16) (**a**, **b**), traveling (n = 10) (**c**, **d**), in the offshore focal area (n = 9) (**e**, **f**), and near the Main Hawaiian Islands (n = 3) (**g**, **h**), and south of the Hawaiian Islands (n = 1) (**i**, **j**). *Bars* show mean, *lines* show standard deviation

Table 3 Mixed layer properties for sharks with archival records

Phase	Mixed layer (m)	Mixed layer (°C)	Time in ML (%)	Time below ML (%)	Movements below ML day^{-1}	Max movements below ML day^{-1}
Nearshore	26 ± 16	13.3 ± 0.2	82 ± 28	12.7 ± 0.4	2.9 ± 2.9	7.7 ± 6.7
Traveling	112 ± 37	18.9 ± 1.2	71 ± 5	10.8 ± 1.6	8.0 ± 3.9	23.7 ± 12.0
Offshore focal area	104	21.5 ± 1	55	14.3 ± 4.3	30.3 ± 19.2	96
Hawaii	100	24.4 ± 0.3	55	21.0 ± 2.1	3.5 ± 2.9	12
Travel south of Hawaii	120	25.0 ± 0.5	47	12.9 ± 4.9	6.2 ± 2.0	8
Offshore focal area south of Hawaii	131	25.0 ± 0.9	60	12.4 ± 5.1	3.8 ± 2.5	11

test, $W = 10.7$, $p = 0.00$), and cooler (Wilcoxon rank sum test, $W = 10.6$, $p = 0.00$), than during the nighttime (Table 5); all excursions went beneath the mixed layer during both diel periods. The behavior of shark 18-F during this travel phase was similar to the traveling periods from California, as it returned to and remained at the surface after vertical excursions, but surface periods were shorter and median depth was much deeper than during migrations from California during both day and night (Table 4).

Offshore focal area south of Hawaii

At the focal area centered 700 km south of Kauai, shark 18-F inhabited the warmest surface waters recorded in this study, 27.2°C (Figs. 3b, 5f, 6i, j). The median daytime distribution was significantly shallower (Wilcoxon rank sum test, $W = 6.8$, $p = 0.00$) and warmer (Wilcoxon rank sum test, $W = 21.4$, $p = 0.00$) than the median nighttime distribution (Fig. 8e). During the daytime, vertical excursions were significantly deeper (Wilcoxon rank sum test, $W = 10.3$, $p = 0.00$), and cooler (Wilcoxon rank sum test, $W = 10.4$, $p = 0.00$), than during the nighttime (Table 5). On 24 April the shark made one movement deeper than the limit of the depth sensor (980 m), where the temperature was 4.5°C. This pattern of having a shallower median position but deeper vertical excursions during the day, was similar to that observed for shark 17-U in the offshore focal area between California and Hawaii.

Discussion

White sharks electronically tagged in the waters off central California, USA made long distance offshore movements on a seasonal cycle, aggregating in the coastal waters of central California during autumn and winter, and undertook offshore migrations into oceanic waters during winter and spring. Our results indicate that white sharks in the eastern North Pacific occupy neritic zones for about half the year and pelagic habitats for the remaining period. Between the two phases we identify a migration of approximately 3 weeks that links the two habitats. The offshore focal area used by white sharks is an area of low productivity and may be a region used for foraging, mating or parturition. We observed similar migration routes and destinations in males and females, as well as mature and sub-adult sharks, though there were sex-specific differences in migration timing. The neritic-pelagic migration cycle observed in this study differs from seasonal movement patterns of Australian sharks. Bruce et al. (2006) reported that white sharks spent the majority of time near the coast, but reported a single pelagic movement from Australia to New Zealand. White sharks occupied the Great Australian Bight during the southern spring and summer, made northward movements during the southern autumn and winter along the east coast through New South Wales and Queensland, and returned to the southern region by early summer. Bonfil et al. (2005) reported the movement of a white shark between South Africa and Australia but further research is needed before we will know if this is a rare movement or a seasonal pattern.

Nearshore habitat

The coastal habitat of adult and sub-adult white sharks appears to be important for foraging. The relationship between white shark movements to the Farallones and the existence of pinniped rookeries is well known (Ainley et al. 1985), and individually identified sharks return in subsequent years to this location (Anderson and Pyle 2003) as well as to pinniped rookeries at Guadalupe Island, Mexico (Domeier and Nasby-Lucas 2007) and Seal Island in South Africa (Martin et al. 2005). White sharks begin to aggregate at the Farallones in late August (Pyle et al. 1996) so the duration of this phase is likely to be substantially longer than the mean duration of 57 days in this study, since sharks were at the Farallones for unknown duration prior to tagging. The nearshore vertical behaviors of white sharks observed in this study are consistent with a strategy for hunting pinnipeds. The sharks rarely visit the surface waters, reflecting the behavior of looking for silhouettes from below and attacking by surprise (Goldman and Anderson

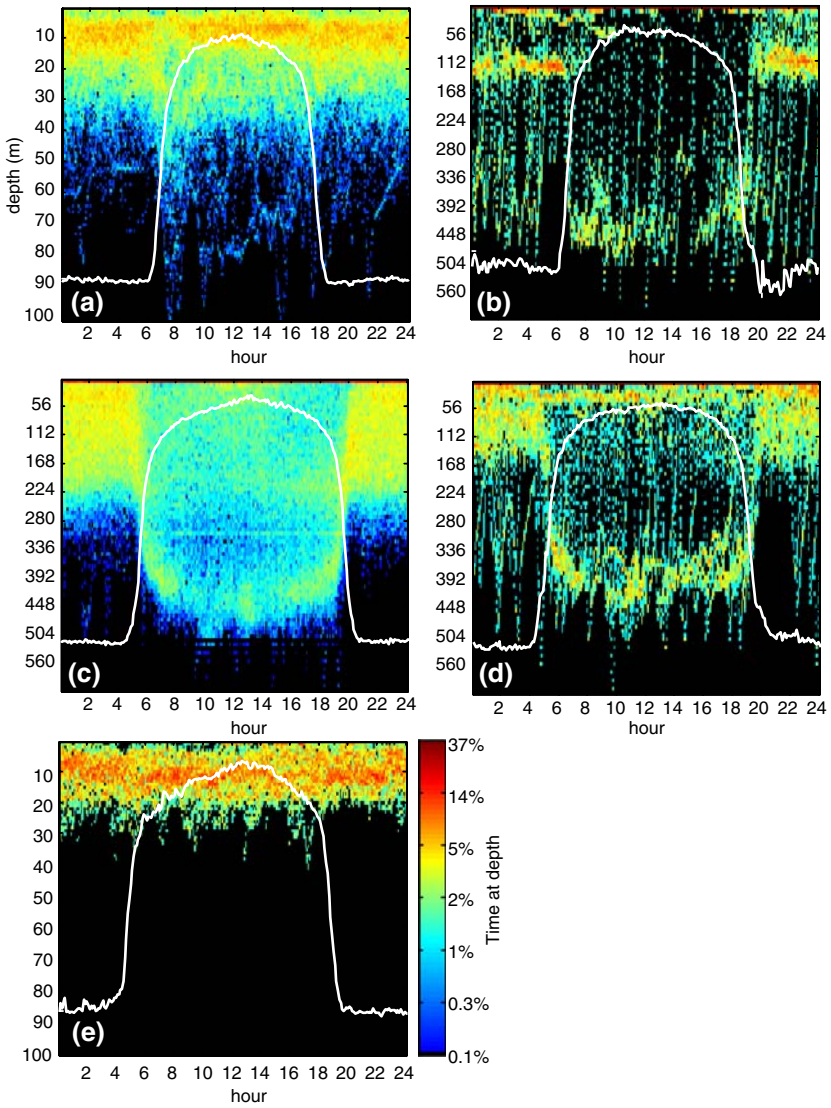

Fig. 7 Diel distribution of shark 17-U, 2004–2005 **a** near the California coast, **b** traveling west from California, **c** in the offshore focal area, **d** traveling east back to California, and **e** near the California coast. *Color* denotes percentage of time spent at each depth (log scale). *White line* shows the diel cycle of light intensity in arbitrary units

1999). Bruce et al. (2006) reported that white sharks foraging on teleosts and elasmobranchs in shallow regions also swam along the bottom with few visits to the surface.

Sharks returning to the continental margin may forage on harbor seals and sea lions prior to their arrival at elephant seal rookeries. We recorded a white shark returning to the California coast from the offshore focal area (17-U) during August, and inhabiting waters between Bodega Bay, CA and Big Sur, CA before the pop-up satellite tag transmitted near Año Nuevo Island, California. Long et al. (1996) showed a peak in predation on harbor seals and sea lions in August, which occurred in coastal areas away from elephant seal rookeries.

Departure

The timing of departure of white sharks from the Farallones may be related to the decline in abundance of pinnipeds. In this study, electronically-tagged white sharks departed the California coast on a mean date of 2 January, shortly after the peak in abundance of young-of-the-year elephant seals that use the islands for their first haul-out period and then depart as adult male seals arrive to establish mating territories (Le Boeuf and Laws 1994). Sharks left after periods of decreasing pinniped abundance that may have resulted in decreased hunting success. In years where multiple shark departures were recorded, we did not see a coordinated departure of sharks following a single decline in abundance.

Female sharks departed the Farallones later than males, consistent with a higher energy demand for females and potentially a need to remain in the Farallones for additional caloric benefit, given that the oligotrophic offshore focal area may offer reduced foraging opportunities. Without knowledge of arrival dates we do not know if females stay near the Farallones longer, or are shifted later with respect to males. Anderson and Pyle (2003) noted a biannual

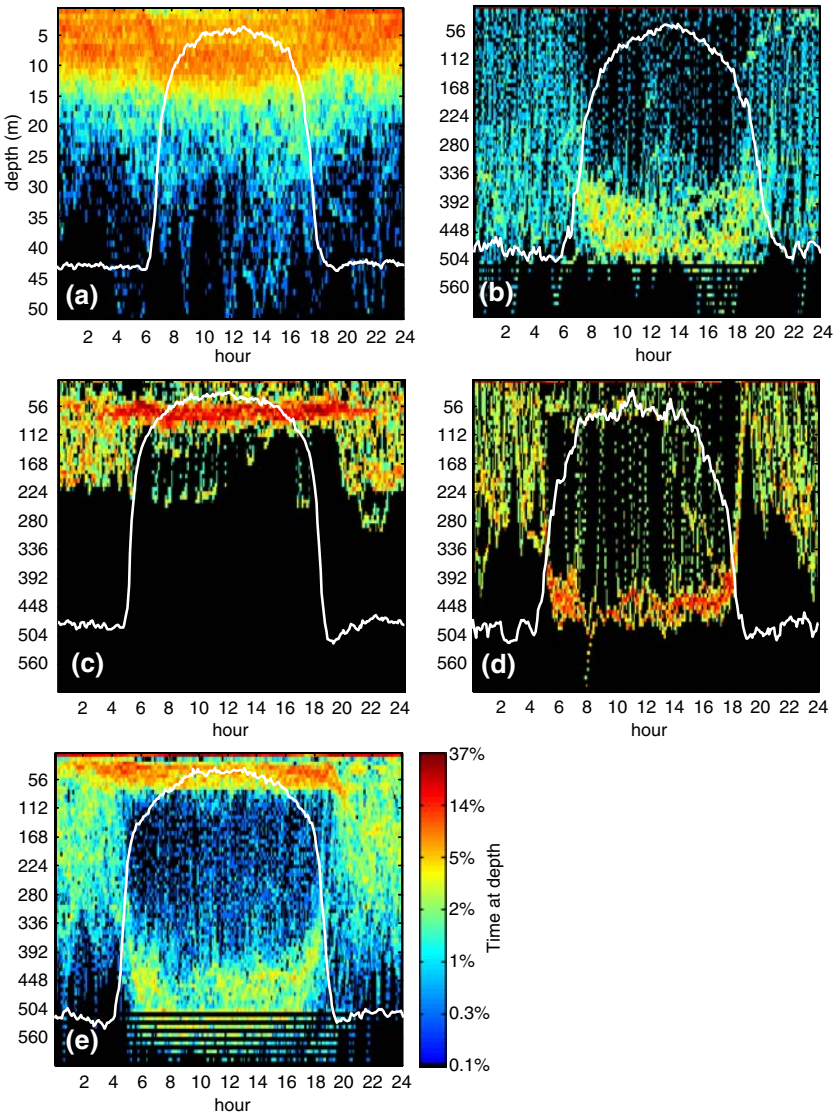

Fig. 8 Diel distribution of shark 18-F, 2004–2005 **a** near the California coast, **b** traveling west from California, **c** near the Main Hawaiian Islands, **d** traveling south from Hawaii, and **e** at a focal area between Hawaii and Kiribati. *Color* denotes percentage of time spent at each depth (log scale). *White line* shows the diel cycle of light intensity in arbitrary units

Table 4 Depth and temperature preferences for sharks with archival records

Phase	Median day (m)	Median night (m)	Median day (°C)	Median night (°C)
Nearshore	11 (10–12)	10 (8–10)	13.1 (12.9–13.2)	13.1 (12.9–13.2)
Traveling	2 (2–3)	2 (1–15)	18.5 (18.2–19.4)	18.0 (17.3–18.3)
Offshore focal area	60 (2–220)	83 (23–154)	20.7 (13.1–21.8)	20.6 (18.5–21.6)
Hawaii	63 (49–76)	94 (57–162)	24.5 (24.3–24.6)	24.0 (21.2–24.5)
Travel south of Hawaii	46 (1–428)	91 (2–212)	24.5 (9.2–25.2)	24.5 (18.6–25.1)
Offshore focal area south of Hawaii	48 (16–404)	104 (21–212)	24.8 (9.5–25.5)	23.3 (18.5–24.9)

visitation of individually identified females to the Farallones, suggesting a 2-year reproductive cycle, while Domeier and Nasby-Lucas (2007) recorded smaller female sharks visiting in consecutive years and larger visiting at multi-year intervals.

Occasionally, the departure of white sharks from the Farallones may be governed not by availability of forage or the need to move to a breeding or parturition area, but by predator avoidance. After an orca (*Orcinus orca*) killed a large prey item believed to be a white shark on 19

Table 5 Vertical excursions for sharks with archival records

Phase	Excursion day (m)	Excursion night (m)	Excursion day (°C)	Excursion night (°C)
Nearshore	38 (33–48)	46 (38–51)	11.6 (11.4–11.8)	11.7 (11.4–12.0)
Traveling	460 (450–480)	408 (370–442)	6.7 (6.6–7.1)	7.2 (6.9–9.0)
Offshore focal area	500 (492–516)	348 (316–380)	6.8 (6.5–6–9)	9.8 (8.9–10.1)
Hawaii	126 (101–213)	208 (200–228)	22.8 (18.3–22.7)	17.9 (17.3–18.3)
Travel south of Hawaii	468 (460–476)	288 (253–340)	8.1 (8.0–8.3)	13.4 (10.7–15.6)
Offshore focal area south of Hawaii	580 (564–612)	456 (420–500)	6.2 (6.0–6.5)	8.5 (7.7–9.3)

November 2000, no white sharks, attacks on pinnipeds, or interactions with decoys were observed again until 10 December 2000 (Pyle and Anderson, unpublished). The data for shark 3-M tagged on 16 October 2000 shows depths shallower than 77 m until the day of the orca attack, when a dive to 484 m occurred, indicating the shark had left shelf waters close to the Farallones. Geolocation data indicated that the shark (3-M) traveled to the west until it reached the main Hawaiian Islands. These data are consistent with the findings of (Pyle et al. 1999), who observed an orca kill a white shark at the Farallones on 4 October 1997, and subsequently saw only two white sharks through the duration of observations on 1 December 1997.

Traveling

Geolocation and speed data for 15 white sharks provide evidence for a distinct migration corridor in the eastern North Pacific that connects the coastal and pelagic aggregation areas. Straightness and minimum velocity estimates for the migratory phases of white sharks indicate directed movements from coastal to offshore focal areas in the eastern pacific and Hawaii, rather than sinuous or nomadic movements. Straightness index for sharks that visited the offshore focal area (17-U) and the main Hawaiian Islands (18-F) were typical of directed migration while the sharks were traveling between coastal and offshore focal areas, compared to residency in focal areas. For comparison, Atlantic bluefin tuna had SI of 0.84 ± 0.07 and 0.57 ± 0.13 during migration to, and breeding activity within, the Gulf of Mexico, respectively (Teo et al. 2006). Wandering albatrosses (*Diomedea exulans*) had SI of 0.65 ± 0.09 and 0.29 ± 0.08 while moving between and within foraging regions, respectively (Weimerskirch et al. 2002). Bruce et al. (2006) noted that white sharks in Australian waters spend extended periods at a foraging area then switch to a directed swimming behavior and use 'common highways' for travel to the next foraging area.

Estimates of minimum speed during the migratory phase also indicate that movements were directed rather than sinuous. To avoid bias caused by differences in shark size, comparisons are made using relative speed in TL per second. Our minimum speed estimates for the migration to the offshore focal area and Hawaii are similar to speed estimates from published acoustic and satellite tracking studies. While following acoustically-tagged adult white sharks, Carey et al. (1982) measured a speed of 0.19 TL s^{-1} (77 km/day), while Strong et al. (1992) obtained speeds of 0.21–0.25 TL s^{-1} (78 ± 41 km/day). Klimley et al. (2001) used a radio-acoustic positioning array to measure swimming speeds of 0.22 TL s^{-1} (104 km/day). Using a PAT tag, Bonfil et al. (2005) measured a transoceanic migration with a minimum speed of 0.34 TL s^{-1} (113 km/day), a higher relative speed, but a lower absolute speed, than the fastest migration in our study of 0.30 TL s^{-1} (119 km/day; shark 14-M). Bruce et al. (2006) used fin-mounted satellite transmitters on four white sharks with a mean traveling speed of 0.31 TL s^{-1} (74 km/day). If the sharks in our study had taken sinuous migration routes, their actual speeds would have been considerably higher than our estimates, and considerably higher than the published values for white shark swimming speeds.

During offshore migrations, sharks passed from California Current waters into transition zone waters, and through the subtropical front (Roden 1991) and the transition zone chlorophyll front (Polovina et al. 2001). Synoptic ocean color measurements in this area show very low surface chlorophyll concentration, but the region maintains moderate productivity due to the sub duction of nutrient rich waters from the north (Seki et al. 2002). Once white sharks moved south of the south subtropical front they entered the subtropical gyre, where they remained for the duration of their offshore periods. In this region the mixed layer deepens and as a result, there is a very low rate of vertical advection of nutrients into the euphotic zone (Seki et al. 2002). The subsurface chlorophyll peak weakens and deepens considerably and primary production is extremely low (Polovina et al. 2001). The lack of minor focal areas during the migration phase suggests that white sharks did not feed extensively en route.

During all traveling phases undertaken by the two sharks with archival records, the sharks returned to and remained directly at the surface after each vertical movement, in contrast with their behaviors at neritic and pelagic focal

areas. The frequent and long periods of time spent at the surface could allow a shark to use celestial cues for navigation (Able and Able 1990) and a similar behavior for a migrating white shark was observed by Bonfil et al. (2005). While returns to shallow, warm water following dives may serve a thermoregulatory purpose (Brill and Bushnell 2001), such warming phases require only a return to the mixed layer, not a return to the surface. No clear indication of the use of geological features for navigation was evident.

Offshore focal area

The purpose of the migration to the offshore focal area is unknown, and may be foraging, mating or parturition. Direct evidence for any of these hypotheses is lacking, such as observations of mating or parturition, and data on stomach contents, or stomach temperature records. However, the behavioral data in our study contrast this region strongly from all other regions, and suggest either a foraging strategy targeting a different prey or a non-foraging purpose.

The offshore migrations of white sharks took them from the productive waters of the California current system into the oligotrophic subtropical gyre, where food resources appear to be sparse and pinnipeds are absent. The offshore focal area is south of the pelagic regions used by elephant seals, which feed in productive transition zone waters to the north (Le Boeuf and Laws 1994). The area is west of the migration routes of humpback whales between Hawaiian breeding/calving grounds and sub-Arctic Pacific feeding grounds (Mate et al. 1998). The area is south of a trans-Pacific bluefin tuna migration corridor (Perle et al. unpublished data).

Large pelagic fishes occur in this area, but at much lower concentrations than in other parts of the eastern North Pacific (Okamoto and Bayliff 2003). The dominant large pelagic fishes in the area are albacore (*Thunnus alalunga*), yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) tuna and swordfish (*Xiphius gladius*), with lower levels of other billfishes and sharks (Okamoto and Bayliff 2003). The abundances of tunas and swordfish peak in the winter and spring when the white sharks are there, whereas the abundance of billfish (*Istiophorus, Makaira, Tetrapturus spp.*) peaks in summer and fall (Okamoto and Bayliff 2003). Sharks include blue (*Prionace glauca*), silky (*Carcharhinus falciformis*), oceanic whitetip (*Carcharhinus longimanus*), shortfin mako, longfin mako, salmon shark, bigeye thresher (*Alopias superciliosus*) and pelagic thresher (*Alopias pelagicus*), with abundance peaking in the winter and spring (Okamoto and Bayliff 2003). Recent long-line data suggests that bigeye tuna fishermen have increased effort in these regions (IATTC, 2006).

The area is southwest of the subtropical summer blooms noted by Wilson (2003), and a developing food chain in such a productivity center would not be advected into the area, given the westerly currents in the region (Roden 1991). The region of temporally stable negative wind stress curl where floating debris accumulates, and which may concentrate whale carcasses, lies directly to the north of the offshore focal area but does not overlap with it.

The oscillatory pattern of shark 17-U is consistent with a searching pattern in which olfactory cues that disperse along horizontal shear layers would be encountered with the highest probability (Klimley et al. 2002). However, the deep nocturnal diving differs from behaviors observed for other upper trophic-level pelagic fishes. Whereas shark 17-U made oscillatory movements at night, many large pelagic fishes cease diving at night, remaining in shallow waters. Such a pattern has been documented in tunas (Holland et al. 1992); billfishes (Carey and Robison 1981); and a variety of other shark species (Weng and Block 2004). The shallow nighttime distributions of most of these fishes are thought to be the result of the shallow distribution of prey species associated with the deep scattering layer, which approach the surface at night (Josse et al. 1998). The pattern of white shark 17-U suggests either a different foraging strategy necessitated by a prey that does not ascend to the surface at night, or a function other than foraging for the oscillatory movements. If additional archival records of white shark behavior in the offshore focal area are obtained, they will help to determine if the single individual reported here is a representative of this population of white sharks.

The offshore focal area may be used for parturition, mating or both. The rapid oscillatory dives of shark 17-U could be a courtship activity. Bluefin tuna show distinct oscillatory diving while on their breeding grounds in the Gulf of Mexico (Teo et al. 2006). The fact that both males and females are in the focal area is not consistent with it being solely a parturition area. In some shark species females mate shortly after giving birth, such that the same region is used for both functions (Carrier et al. 2004). The possibility of mating or parturition during annual visits to the offshore focal area would be consistent with a 1-year reproductive cycle; however, female sharks appear to visit the Farallones biannually, providing evidence for a 2-year cycle (Anderson and Pyle 2003). Based on the seasonality of parturition, Francis (1996) hypothesized that the gestation period was more than 1 year; Mollet et al. (2000) hypothesized an 18-month gestation cycle. The visitation of the offshore focal area by sub-adult sharks is not consistent with a purely reproductive function for the migration.

Hawaii and vicinity

The visitation of white sharks to the waters surrounding the islands of Kauai, Maui, Lanai, Kahoolawe and Hawaii indicates these areas may be used for foraging. While in

this region, shark 18-F showed significantly deeper diving during nighttime than daytime, in contrast to diel patterns observed during other phases. The diel pattern of vertical movements near Hawaii contrasts with most patterns observed for a wide variety of pelagic sharks and fishes, in which sharks make deeper movements during day than night (Weng and Block 2004).

The pattern of shark 18-F is consistent with foraging in nearshore waters during day, and moving away from land at night. The pattern of aggregating during the day and dispersing at night has been observed in tunas at fish aggregating devices (Holland et al. 1990) and seamounts (Klimley et al. 2003). However, due to the inherent limitations in light- and SST-based geolocation, we do not know the precise locations of the shark during daytime and nighttime.Shark 18-F rarely visited the surface, which is consistent with a silhouette-based hunting strategy, but the median positions during day (63 m) and night (94 m) are likely too deep to see silhouettes of animals at the surface. White sharks have been observed near aggregation sites for spinner dolphins (*Stenella longirostris*) on the west side of Oahu, as well as near Hawaiian monk seal (*Monachus schauinslandi*) colonies on Niihau, and their presence in Hawaii corresponds to the timing of birth for humpback whales (*Megaptera novaeangliae*), allowing for the possibility of feeding on placentas (John Naughton, personal communication). Sharks may also forage on fishes, sharks and squids while near the Islands. Teleost and elasmobranch fishes are important food sources for white sharks in Australian waters (Malcolm et al. 2001), and may also be important in waters around Guadalupe Island, Mexico (Domeier and Nasby-Lucas 2007). Bruce et al. (2006) reported a similar pattern of shallow daytime and deep nighttime swimming while a white shark was near the Neptune Islands, where pinniped colonies occur.

While in the focal area south of Hawaii, shark 18-F showed far less diving than shark 17-U in the offshore focal area between Hawaii and Baja. In addition, the shape of dives differed between the two regions. South of Hawaii shark 18-F showed dive profiles with long basal periods, consistent with a dive to a target depth followed by a period of searching for prey (Josse et al. 1998), whereas shark 17-U initiated ascent immediately upon reaching the maximum depth of a dive.

Population structure

Genetic studies comparing the southwest Pacific and southwest Indian Oceans have shown separate populations of white sharks based on mitochondrial markers, but a lack of differentiation based on nuclear markers, leading to the hypothesis of greater trans-oceanic movement by males than females (Pardini et al. 2001). Satellite telemetry showed a trans-oceanic movement between these white shark populations by a female (Bonfil et al. 2005), raising the possibility that long-distance transfer of male gametes could occur through the movements of adult females. The population structure of white sharks in the Pacific Ocean is unknown, and no genetic studies have been published for this ocean basin. The present study and others based in Mexico (Domeier and Nasby-Lucas 2006) and the Southern California Bight (Weng et al. 2007) have recorded movements via satellite telemetry. Adult and sub-adult white sharks tracked from both Central California and Guadalupe Island, Mexico have visited the offshore focal area highlighted in this study, raising the possibility of connections between these two groups. Juvenile white sharks tracked from Los Angeles, CA have moved along the coast northward to Point Reyes, CA, and southward to Sebastian-Vizcaino Bay, BC, Mexico. The movements of western Pacific white sharks are unknown, so it remains possible that they make long-range movements into habitats shared by eastern Pacific white sharks. Further research into both the genetics and movements of white sharks is required to elucidate the evolutionary and ecological relationships of white sharks globally and within the Pacific basin, and to determine the role of the unusual movements to the offshore focal area highlighted in this study.

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