

## Space utilization and swimming depth of white sharks, *Carcharodon carcharias*, at the South Farallon Islands, central California

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### Synopsis

This paper presents information on the movements of white sharks, *Carcharodon carcharias*, at the South Farallon Islands (SFI), central California. Acoustic telemetry techniques provided preliminary data on the diurnal space utilization, movement patterns and swimming depths of four white sharks, ranging from approximately 3.7 to 4.9 m in length. Sharks swam within about 10 m of the bottom to depths of approximately 30 m, but in deeper water they tended to stray more from the bottom. Activity spaces for time periods tracked ranged from 1.84 to 9.15 km<sup>2</sup>. Indications are that an inverse relationship exists between length and activity space. During the time tracked, larger individuals swam within particular areas around the islands whereas smaller individuals did not restrict their movements in the same manner. Values of a site attachment index were inversely related to length for all sharks tracked. The site attachment indices, apparent inverse relationship between total length and activity space and observations on telemetered and other known individuals support a hypothesis that larger sharks possess site fidelity in their search for prey at SFI, within and between years. With the high frequency of predation by white sharks on juvenile northern elephant seals at SFI in the fall, the majority of the sharks' movements are probably related to their search for these pinniped prey. These data provide preliminary evidence that white sharks at SFI may search for prey by swimming in a particular area over a number of days or weeks, traversing the area in a manner which maximizes coverage, and swimming close to the bottom or at a distance far enough from the surface to remain cryptic from prey.

### Introduction

Studies of spatial and temporal patterns of space utilization can provide information on aspects of social behavior, energetics and predator–prey relationships. White sharks, *Carcharodon carcharias*, are large apex predators that exist circumglobally in cool temperate marine ecosystems (Compagno 1984). Knowledge of their feeding behavior may help to understand their potential impacts on prey. Some inferences into the predatory behavior of white sharks have come from direct

observations of feeding events, decoy experiments, and the examination of interactions with humans (Tricas & McCosker 1984, Tricas 1985, McCosker 1985, Ainley et al. 1985, Klimley et al. 1992, 1996, Strong et al. 1992, 1996, Anderson et al. 1996a,b, McCosker & Lea 1996). From these kinds of studies, hypotheses have been made regarding possible approach styles once a potential prey item has been visually located (detected). Little is discussed or known about white shark behavior before prey is sighted or after a feeding event is concluded.

The occurrence of white sharks at the South Farallon Islands, off San Francisco, during the fall months is correlated with the presence of pinniped prey (Ainley et al. 1981, 1985). Large numbers of juvenile northern elephant seals, *Mirounga angustirostris*, haul out on the islands at that time of year. These islands provide the rare opportunity to study natural white shark behavior as no baiting is necessary. Observations of white sharks at SFI have focused primarily on attacks and subsequent feeding events (Ainley et al. 1981, 1985, Klimley et al. 1992, 1996, Anderson et al. 1996a, Pyle et al. 1996). Those data are limited by the need to see the shark, and thus provide only a 'snapshot' of white shark behavior, attack and feeding. The swimming depth and movements of a single white shark at SFI reported by Goldman et al. (1996) are the only documentation of white shark behavior between feeding events at SFI. Data from that shark indicated patterns of nearshore sweeps and short distance excursions away from and back to the islands.

Since 1988, observations of seasonal predatory events and use of unbaited decoys have resulted in the identification of more than 20 individuals at SFI (Klimley & Anderson 1996, Anderson & Goldman 1996, and unpublished data). Many of the repeat visitors have been observed attacking, feeding or at decoys multiple times over many years. Known individuals (photo identified) have remained at the islands for (at least) several weeks at a time and have shown site fidelity to the islands (Klimley & Anderson 1996, Anderson & Goldman unpublished data). Two known individuals were reported feeding in the same locations in successive years indicating not only site fidelity to the islands, but to particular areas around SFI. Those re-sightings, our re-sighting of the telemetered individual from Goldman et al. (1996) at its tagging location in subsequent years, the re-sighting of telemetered sharks presented herein at their tagging locations in subsequent years, and the re-sighting of other photo identified individuals at their initial I.D. locations (Anderson & Goldman unpublished data) leads to the hypothesis of site fidelity to particular locations at SFI, along with their general site fidelity to the islands in the fall (Klimley & Anderson 1996). It also led us to inquire further about the movements of white sharks prior to, and after, feeding events.

Following the movements of individuals provides data on behavior not immediately associated with attacks and subsequent feeding events. As such, these data provide information about the manner in which

white sharks may search for prey at the islands. The purpose of this paper is to provide a preliminary description of the natural diurnal movements, space utilization and swimming depths of telemetered white sharks at SFI. From this, we describe possible white shark prey searching behavior at the islands. We also present additional evidence, to the two sharks reported by Klimley & Anderson (1996), which supports a hypothesis of area site fidelity for large (>4 m) white sharks at SFI, within and between years.

## Materials and methods

Telemetry data for this paper were collected in October of 1993, and October and November of 1994 at the South Farallon Islands, SFI (37°42' N, 123°00' W). Swimming depth and movement data were obtained from four free-swimming white sharks (three males, approximately 4.9, 3.7, and 4.6 m in length, and one female approximately 3.9 m in length) using acoustic telemetry. Sex was determined using underwater videos obtained when the transmitter was fed to the individual or when it was visually attracted to an unbaited decoy which housed a video camera (see Anderson et al. 1996b for description of decoy study). Sex of the additional known individual included in this paper were obtained by photos and underwater videos. Total lengths of individuals were estimated from repeated observations of the sharks next to the 5.4 m tracking vessel or a decoy in close proximity to the tracking vessel (by K.J. Goldman, S.D. Anderson and P. Pyle). Sharks were fed acoustic transmitters at the sites of predatory attacks on pinnipeds, which occur frequently during the fall months (Ainley et al. 1981, Klimley et al. 1992, Anderson et al. 1996a). All data are diurnal, and were gathered intermittently (when weather allowed and the shark could be located) over multi-day periods.

Transmitters were manufactured by VEMCO Ltd. (Halifax, Nova Scotia, Canada – models V4TP-8H and V4P-8H), and operated at frequencies of 30.000 and 32.768 kHz. They possessed depth sensors with a range of 0–200 m, had a life of 57–91 days, and a maximum range of 1.1 km at SFI. Swimming depth could be recorded from one-half that distance (due to signal attenuation from background noise) resulting in the accumulation of more tracking data than swimming depth data.

Each shark at SFI was fed a 3–4 kg piece of blubber from a northern elephant seal with transmitter attached,

that had been placed in the water during a feeding event resulting from a predatory attack. This procedure was followed so the shark would ingest it during the course of its natural predatory and feeding behavior. No attractants (e.g. blood or fish parts) were used to avoid altering the natural behavior of the sharks at SFI.

Immediately upon ingestion of a transmitter, sharks were monitored using a directional hydrophone (Dukane Corporation, St. Charles Illinois, model N30A5A) from a 5.4 m Boston Whaler. Swimming depth data (acoustic signals) were recorded on audio tape and later decoded by playing the tape through an analog to digital converter (Ultrasonic Telemetry Systems, Brea, California). Four data points per minute (at 0, 15, 30, and 45 s) were read manually by the lead author from the converter, and entered into a computer spreadsheet.

Trackings were conducted by taking fixes on the shark's position. A fix consisted of theodolite positions of the tracking vessel taken from the lighthouse atop Southeast Farallon Island (for explanation of technique, see Klimley et al. 1992), or by a global satellite positioning system (GPS). The majority of fixes were taken from the lighthouse. Simultaneously, compass bearings were taken from the boat to the acoustic signal, giving a line of direction from the tracking vessel to the shark. Distances from the tracking vessel to the shark were estimated based on signal strength from range tests, thereby allowing maps showing the shark's estimated movements to be made. Accuracy of our estimates ranged from 50 to 100 m apparently due to variability in sea conditions and background noise. Fixes were taken between one and seven minutes apart to enhance the ability to map the movements of the sharks.

Each tracking session consisted of following the telemetered shark (or sharks) for as long as conditions around the islands permitted, or until dusk.

Weather permitting, attempts were made to relocate the shark the next day. This created the intermittent nature of the trackings. Searches were conducted by checking the area in which the animal was last tracked, and proceeding around the island in an inshore-offshore star pattern to maximize the chances of hearing the acoustic signal. These searches covered a radius around the island of approximately 3 km.

Observation-area curves were calculated based on the minimum convex polygon method used by Morrissey & Gruber (1993) (see also Odum & Kuenzler 1955, Winter 1977), with fixes on the shark grouped by fives. However, computation of the area utilized was not terminated at the point when there was less than a 5% increase in activity space after the addition of the next group of fixes (defined as home range by Odum & Kuenzler 1955). This was done in order to obtain the maximum amount of data on each shark due to the intermittent nature of these trackings. We feel that our data allow for an estimate of diurnal activity space to be made, but not home range at SFI as individual trackings were not lengthy enough or conducted over diel periods.

Estimates of the sharks' length were compared to the size of their respective activity spaces for times tracked (regression ANOVA). Additionally, an Index of Reuse (IOR) was calculated to examine site specificity for each individual by determining the proportion of each individual's movements that occurred in the same area (or areas) around SFI during the time tracked (Table 1). The formula used was:  $IOR = \{OV(A_1 + A_2)\} / (A_1 + A_2)$  [based on McKibben & Nelson (1986) and Morrissey & Gruber (1993)], where  $OV(A_1 + A_2)$  was the area of overlap (OV) between two daily activity spaces, and  $(A_1 + A_2)$  was the total area of both activity spaces. Activity spaces (areas) were calculated, and movements plotted, using MacDraft (Innovative Data

Table 1. Activity spaces and index of reuse (IOR) values from four white sharks at South Farallon Islands. Standard errors are given for all mean IOR values.

	Shark #1	Shark #2	Shark #3	Shark #4
Sex and approximate TL	male, 4.9 m	male, 3.7 m	male, 4.6 m	female, 3.9 m
Activity space	4.34 km <sup>2</sup>	9.15 km <sup>2</sup>	1.84 km <sup>2</sup>	4.42 km <sup>2</sup>
No. of days compared	9	7	5	4
Total no. comparisons	36	21	10	6
No. of comparisons = 0	9	17	0	4
IOR range	0.00–0.32	0.00–0.27	0.16–0.36	0.00–0.12
Mean IOR	0.10 ± 0.002	0.025 ± 0.017	0.26 ± 0.02	0.024 ± 0.019

Designs Inc. 1994). Areas used to obtain IOR values were based on the above minimum convex polygon method. This index ranges from zero (no site attachment) to one (complete congruence of daily areas).

Swimming depths were matched to bottom depths by taking a straight line between two successive mapped positions and dividing the time frame between them into one minute intervals. A detailed U.S.G.S. bathymetric map of the island area allowed bottom depth to be obtained at each one minute interval, hence the use of interpolated points. Statistical analysis (regression ANOVA) was conducted to examine the relationship between swimming depth and bottom depth. Differences between swimming depth and bottom depth were used to examine the shark's position (in the water column) relative to the bottom as bottom depth changed.

Minimum rates of movement were determined by taking a straight line between any two successive positions which were taken one minute apart (minute marks for swimming depth/bottom depth comparisons were not used), and dividing distance by time.

Attempts to locate all tagged sharks persisted throughout the fall at SFI when weather permitted. The exception being shark #2, who regurgitated his transmitter after nine days. Attempts ceased in late November, which is the time when juvenile elephant seals begin to depart SFI, shark attacks begin to become more infrequent and weather becomes an even larger factor in small vessel operations at the islands.

Observational data used in this paper are taken from an ongoing study examining shark attacks on juvenile elephant seals, individual identification and residency patterns of white sharks at SFI and along the central California coast (Anderson, Goldman & Pyle unpublished data). (See Klimley et al. 1992, Klimley & Anderson 1996, Anderson & Goldman 1996 for details on observational and photographic identification methods.) We include in this paper observational data for one additional shark, an approximately 5.5 m female called 'stumpy', who was first sighted in 1989, making this shark one of our longest known individuals. She has been extremely proficient at feeding on seals and at approaching decoys at SFI over the years allowing numerous observations on her.

## Results

Shark #1 was tracked for 11 h 40 min, and 7 h 20 min of swimming depth data were gathered on nine and

10 days (respectively) over the 17 day period of 12–28 October 1993. Fixes could not be obtained on 12 October 1993, and during some additional tracking sessions where low fog and lack of a GPS unit prevented tracking vessel positions from being taken. A total of 189 fixes were taken on shark #1, an approximately 4.9 m male. The estimated activity space of this shark during the time tracked was 4.34 km<sup>2</sup> (Figure 1). This shark's activity space extended from the northwest side of the islands around the south to the east side with most movements off the south side of SFI. The shark was never located on the north or north-east sides of the islands (Figure 2).

Shark #2 was tracked for 8 h 40 min, and 5 h 20 min of swimming depth data were gathered on seven days over the nine day period of 21–29 October 1993. A total of 141 fixes were taken on this approximately 3.7 m male. The estimated activity space of this shark during the time tracked was 9.15 km<sup>2</sup> (Figure 1). This shark's activity space covered virtually all of the waters surrounding SFI (Figure 3).

Shark #3 was tracked for 6 h 45 min, and 47 min of swimming depth data were gathered on five days over the eight day period of 25 October to 1 November 1994. A total of 116 fixes were taken on this approximately 4.6 m male. The estimated activity space of this shark during the time tracked was 1.84 km<sup>2</sup> (Figure 1). This shark's activity space was located off the west side of SFI. The shark was never located anywhere else around the islands (Figure 4).

Shark #4 was tracked for three hours, and 58 min of swimming depth data were gathered on four days over the nine day period of 27 October to 4 November 1994. A total of 51 fixes were taken on this approximately 3.9 m female. The estimated activity space of this shark was 4.42 km<sup>2</sup> (Figure 1). This shark's activity space, as with shark #2, covered virtually all of the waters surrounding SFI (Figure 5)

The initial increase in activity space per number of observations (fixes) was similar for each shark up to 20 observations (Figure 1). After 25 observations, smaller sharks (#2, #4) showed up to a two-fold increase in activity space while larger sharks (#1, #3) showed little or no increase. At 35 observations, sharks #2 and #4 continued to show rapid increases in their activity spaces while sharks #1 and #3 (particularly shark #3) did not. Shark #3 maintained a small increase until reaching an asymptote at 85 observations while shark #1 did show an almost two-fold increase before reaching an asymptote at 80 observations. Shark #2

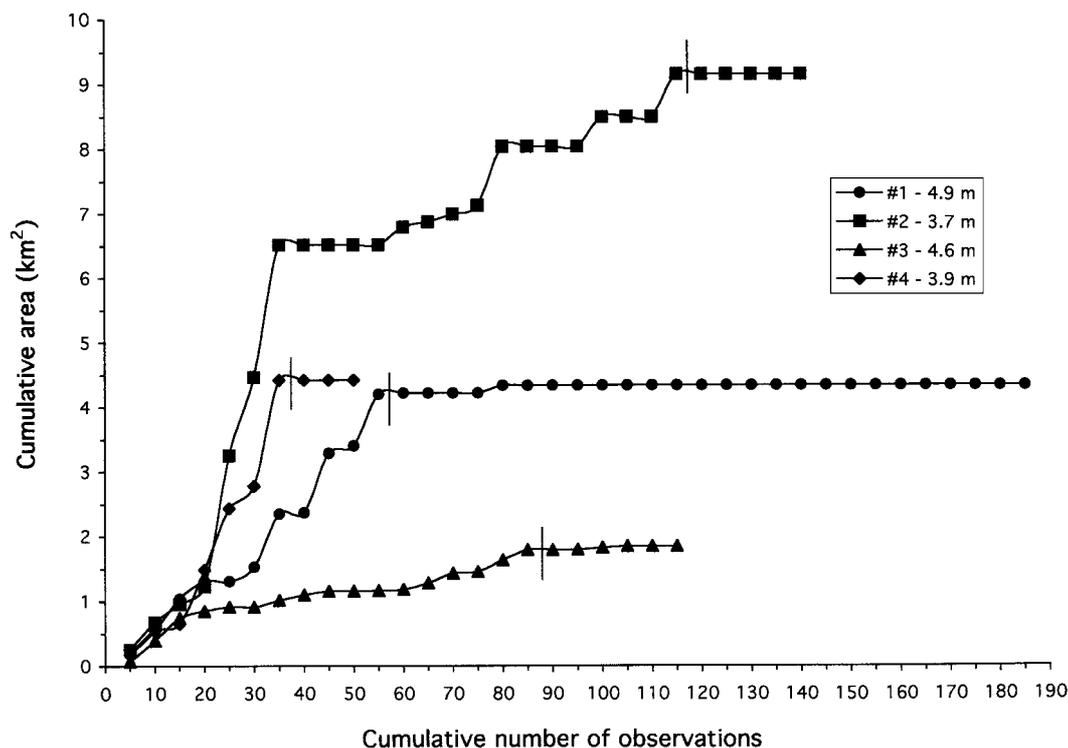


Figure 1. Observation area curves for four white sharks at South Farallon Islands. Small vertical bars indicate asymptote = number of observations to reach estimate of diurnal activity space.

continued to show an increase in activity space until reaching an asymptote at 115 observations. Shark #4 appears to have reached an asymptote at 35 observations. However, based on the shapes of the observation-area curves of the other sharks (particularly #2, the other small shark) and the number of observations it took to reach a complete asymptote for the other sharks, this may represent a false asymptote (Figure 1). Preliminary indications from the observation-area curves are that activity space is inversely related to total length (Figure 6) (regression ANOVA;  $df = 1, 3$ ;  $F = 1.86$ ;  $p = 0.31$ ).

Individual day-to-day IOR values ranged from 0.00 to 0.36 (Table 1). Values for shark #1 ranged from 0.00 to 0.32, with a mean IOR of 0.10. Day to day IOR values for shark #2 ranged from 0.00 to 0.27, with a mean IOR of 0.025. Day to day IOR values for shark #3 ranged from 0.16 to 0.36, with a mean IOR of 0.26. This shark's movements were the most restricted of the four (Figure 1) and he was the only individual to reuse the same area on each day tracked, indicated by IOR values all greater than zero (Table 1).

Values for shark #4 ranged from 0.00 to 0.12, with a mean IOR of 0.024.

Swimming depth and bottom depth were highly correlated when bottom depths were less than approximately 30 m, and non-correlated when bottom depths were greater than 30 m (Figure 7). Many horizontal movements where swimming depth and bottom depth were highly correlated were inshore-offshore movements as opposed to along-shore movements (see Figure 7a,b).

Five hours and 45 min of swimming depth data were matched to bottom depths for shark #1. Swimming depth was significantly correlated with bottom depth (regression ANOVA;  $df = 1, 348$ ;  $F = 1644.7$ ;  $p = 1.0E-133$ ). Differences between swimming and bottom depths were less than 10 m at bottom depths less than 30 m, but were larger at greater bottom depths (Figure 8a).

Four hours and 50 min of swimming depth data were matched to bottom depths for shark #2. Swimming depth was significantly correlated with bottom depth (regression ANOVA;  $df = 1, 295$ ;  $F = 5283.0$ ;

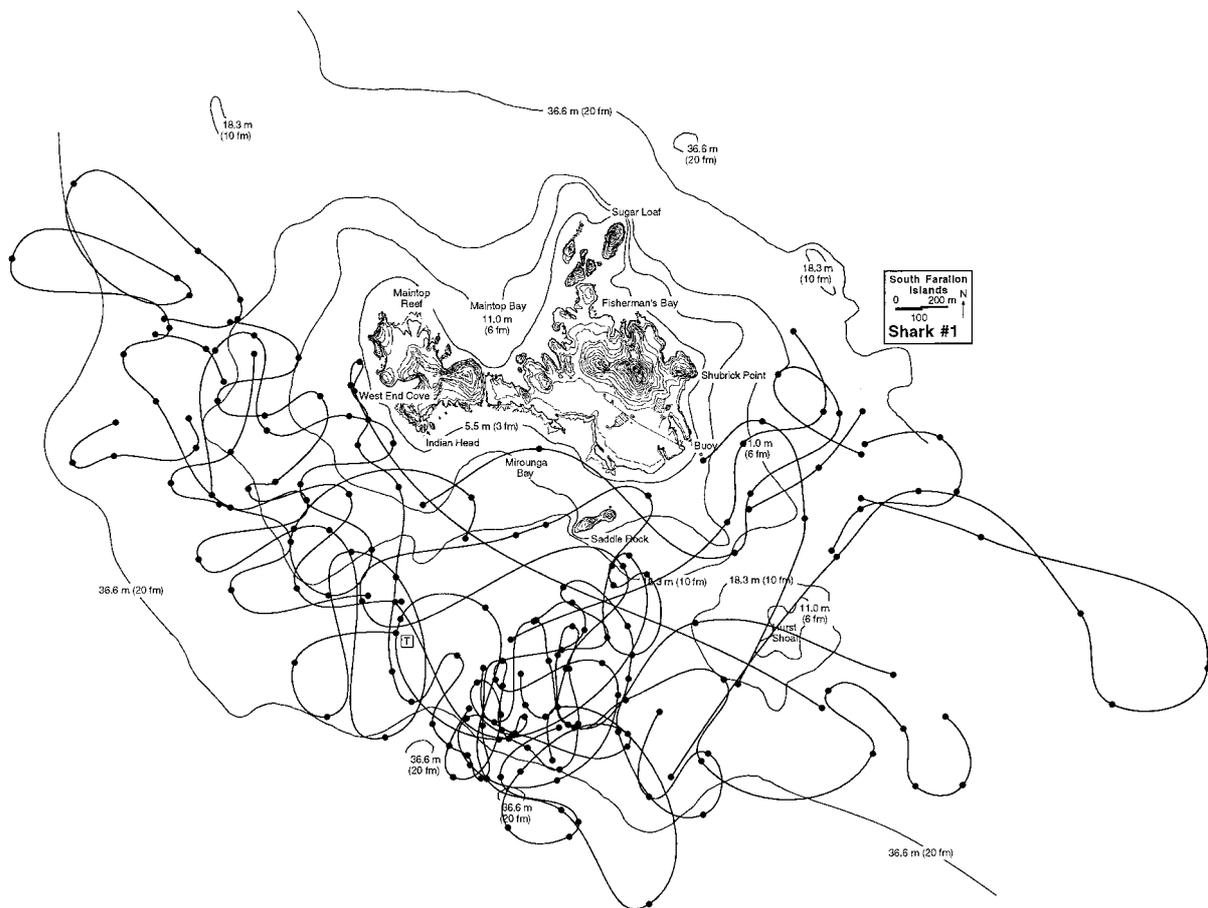


Figure 2. Intermittently recorded horizontal movements of shark #1 (12–28 October 1993). Solid circles represent fixes (on the shark) taken between one and seven minutes apart. Boxed 'T' indicates tagging location.

$p = 6.4E-190$ ). Differences between swimming and bottom depths were less than 10 m at bottom depths less than 40 m, but were larger at greater depths (Figure 8b).

All swimming depth data were matched to bottom depths at one minute intervals for shark #3. Swimming depth was significantly correlated with bottom depth (regression ANOVA;  $df = 1, 46$ ;  $F = 195.0$ ;  $p = 5.7E-18$ ). Differences between swimming and bottom depths were less than 10 m at bottom depths less than 23 m, but were larger at greater bottom depths (Figure 8c).

All swimming depth data were matched to bottom depths at one minute intervals for shark #4. Swimming depth was significantly correlated with bottom depth (regression ANOVA;  $df = 1, 57$ ;  $F = 80.49$ ;  $p = 2.0E-12$ ). Differences between swimming and bottom depths were less than 10 m at bottom depths

less than 25 m, but were larger at greater bottom depths (Figure 8d).

Klimley & Anderson (1996) reported on a male known as 'cut dorsal', and a female known as 'cut caudal' as sharks (both  $> 4$  m) which demonstrated site fidelity to a particular location at SFI over several years. We add here, observational data on an approximately 5.5 m female known as 'stumpy' who has been sighted 15 times over seven seasons (from 1989 to 1995; nine attack-feeding events and six decoy deployments) in the same area off the east southeast side of SFI, with three of the predatory events occurring in the same season. She has been sighted only twice at another location (along the southwest side of the islands) over the same time period.

Three of the four telemetered sharks from this study have been re-sighted at SFI since their initial

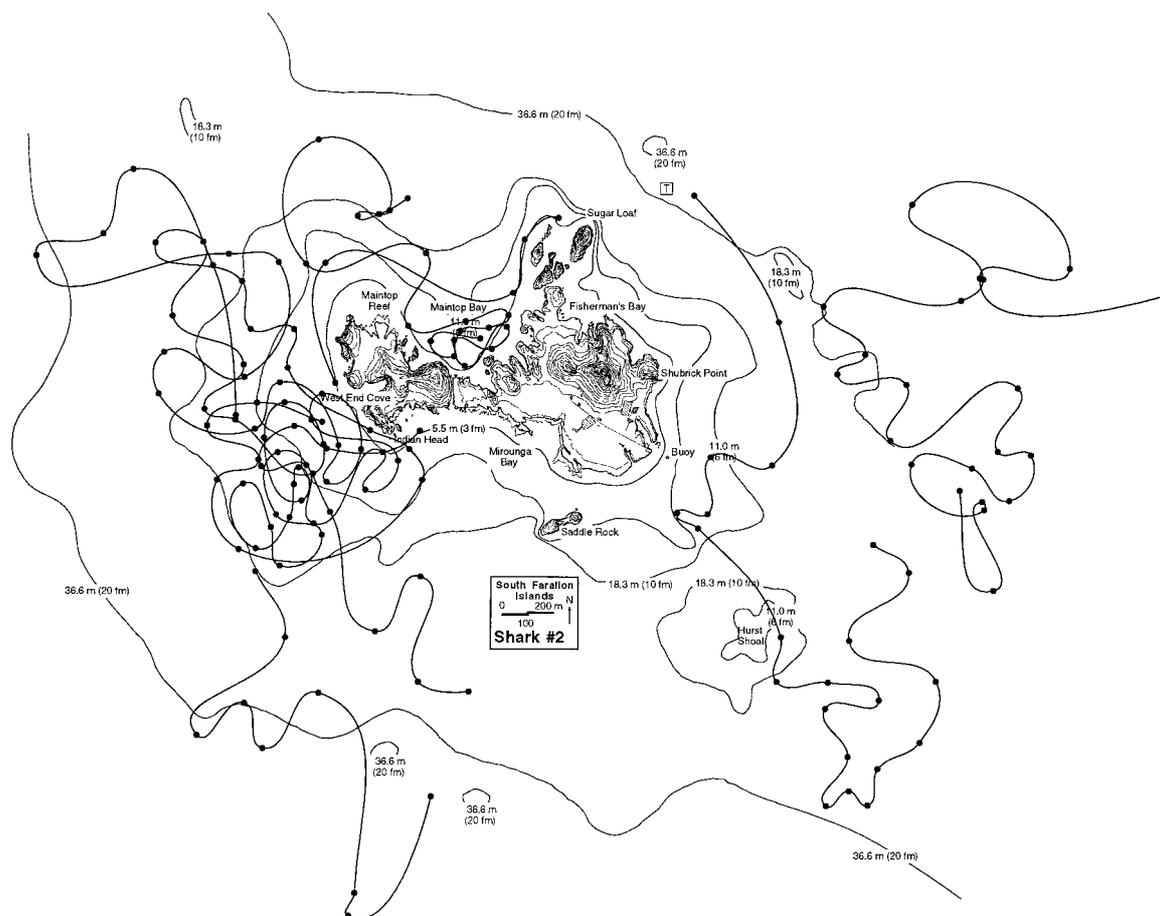


Figure 3. Intermittently recorded horizontal movements of shark #2 (21–29 October 1993). Solid circles represent fixes (on the shark) taken between one and seven minutes apart. Boxed 'T' indicates tagging location.

tagging and tracking. Shark #1 was sighted once in 1994, three times in 1996, and once in 1998. Four of those sightings were close to the initial tagging location and one (in 1996) was within its activity space (Figure 2). The smallest male from this study (shark #2) has been re-sighted 11 times; three during the 1994 season (two attack-feeding events and one decoy deployment), seven during the 1995 season (two attack-feeding events and five decoy deployments) and once in 1996 (boat investigation). The 1994 sightings were at three different locations, the sightings from 1995 were from all around SFI and the 1996 sighting was off the south side of SFI. Shark #3 has been re-sighted three times in the area it was tagged, once in 1995, once in 1996 and again in 1998 (all attack-feeding events). None of these sharks have been sighted outside the activity spaces reported for them in this paper.

Additionally, the (approximately) 4.3 m telemetered shark from Goldman et al. (1996) has been sighted five times since it was tagged in 1991 (three attack-feeding events and two decoy deployments). The 1994 sighting was close to the location it was tagged (attack-feeding event), while in 1996, this shark was sighted at two predatory events and approached two decoys in locations where it was initially tracked.

## Discussion

Telemetered movements indicate that the two larger individuals restricted their movements to specific areas around SFI, whether to a small activity space (shark #3: Figure 4) or to a slightly larger activity space which included a main area and excursions within the overall

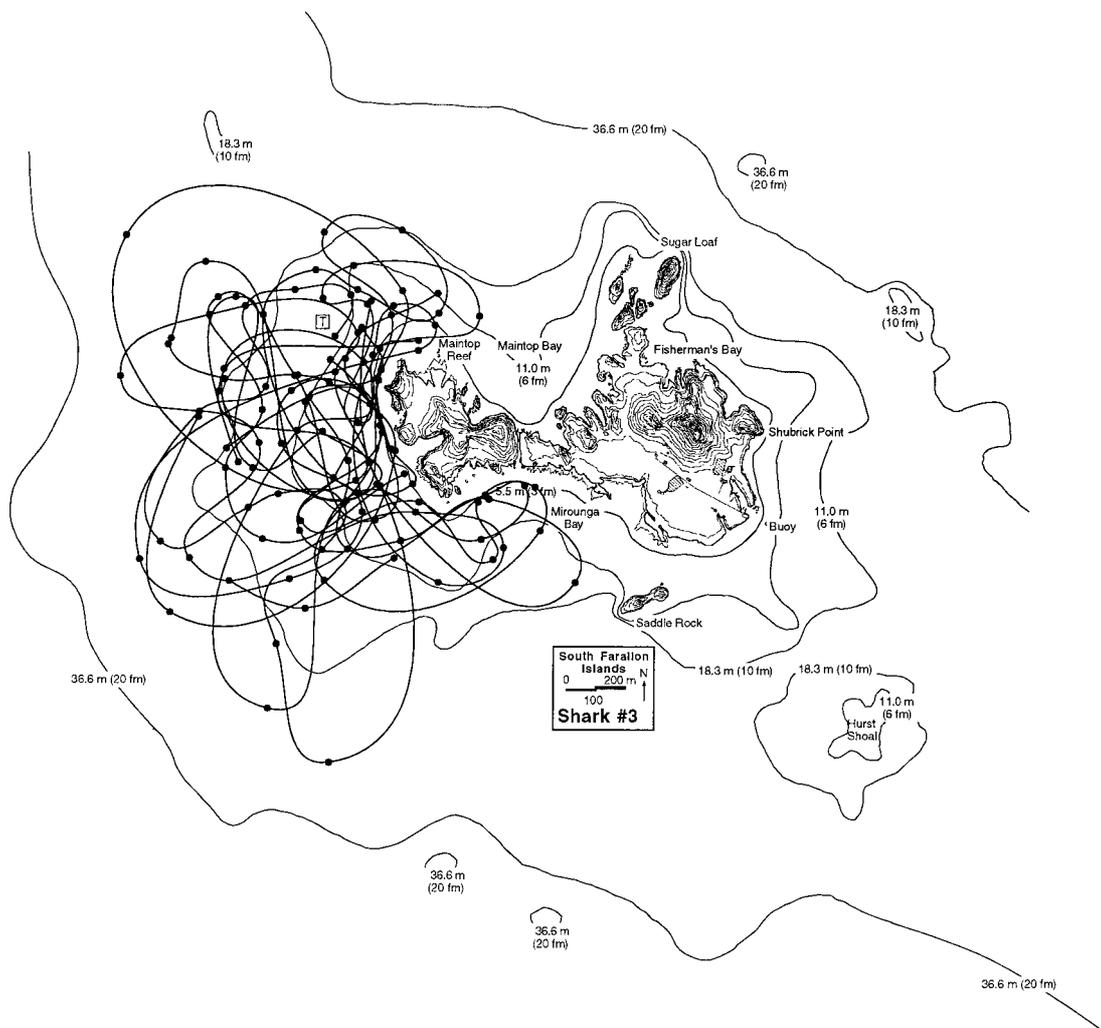


Figure 4. Intermittently recorded horizontal movements of shark #3 (25 October–1 November 1993). Solid circles represent fixes (on the shark) taken between one and seven minutes apart. Boxed 'T' indicates tagging location.

activity space (shark #1: Figure 2). The two smaller individuals did not restrict their movements in a similar manner, and their activity spaces encompassed all areas around SFI (sharks #2, #4: Figures 3, 5).

Based on our limited sample size of telemetered sharks, it appears that differences in diurnal activity spaces (space utilization) among white sharks at SFI is inversely related to the length of the individual (Figure 6). The larger white sharks (greater than approximately 4 m TL) utilized smaller activity spaces (Figures 1–6). The intermittent nature of the trackings may cause slight underestimates of activity spaces. However, we believe that two properties of our

telemetry data support them as giving accurate estimates of diurnal activity space. First, the observation-area curves for three of the four sharks reached an asymptote between 80 and 115 observations (Figure 1). Secondly, these data were obtained over several days or weeks at different times of day increasing the chances of finding the sharks in other locations if they were to move, as was seen in the two smaller (<4 m) sharks. It is possible that the trends seen in the cumulative activity space of the first three sharks would have occurred with shark #4 had more (possibly over 80) observations been obtained. We believe the estimate of activity space for shark #4 to be an

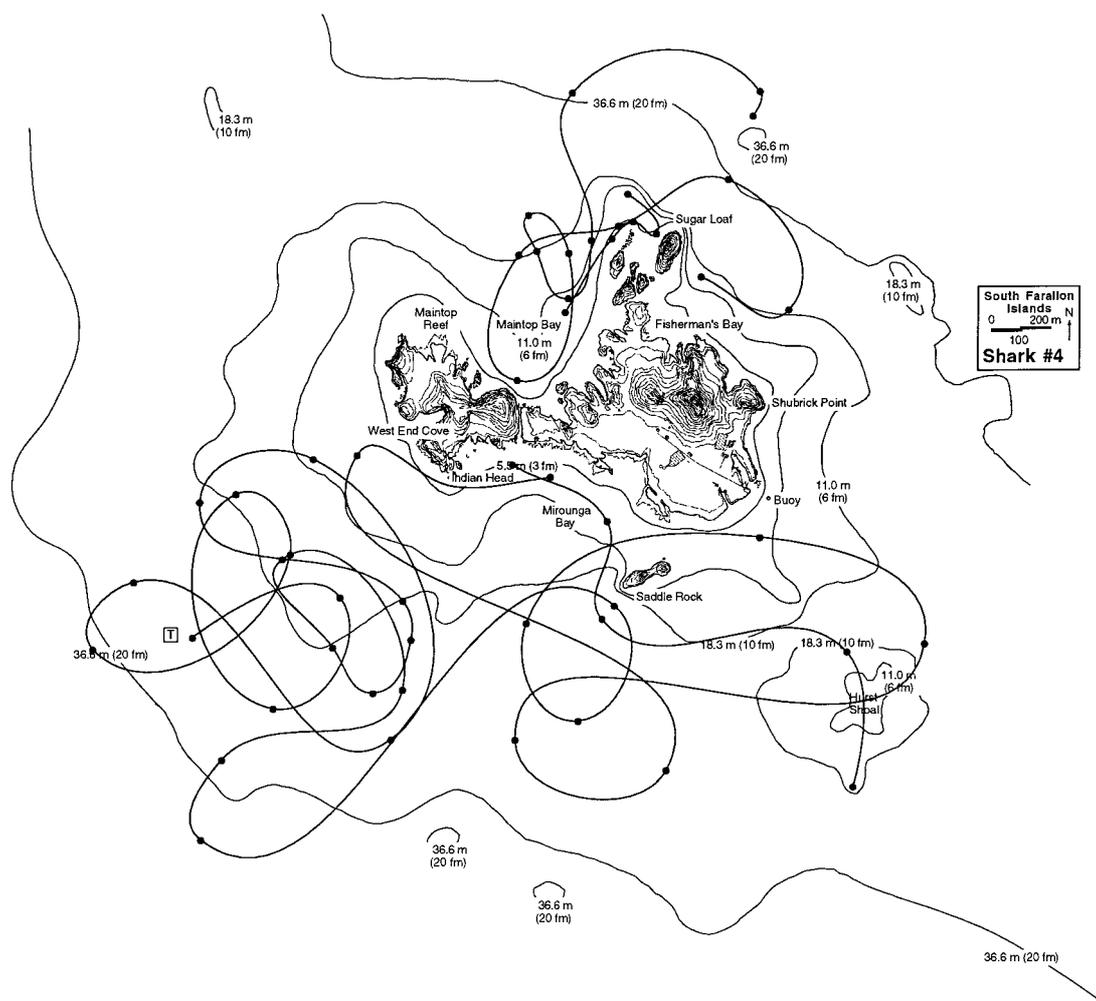


Figure 5. Intermittently recorded horizontal movements of shark #4 (27 October–4 November 1993). Solid circles represent fixes (on the shark) taken between one and seven minutes apart. Boxed 'T' indicates tagging location.

underestimate, but are uncertain as to what degree (Figure 1).

The IOR calculations also suggest that the larger sharks were more site specific than the smaller individuals (Table 1). Mean IOR values were five to 10 times higher for the two larger sharks, and the fraction of days with IOR values of zero were considerably smaller for the larger sharks indicating that they remained in the same areas more consistently. Another hypothesis could be that the IOR values are related to sex instead of length, since the small female (shark #4) had a maximum IOR of only 0.12 and the smallest male had a maximum IOR closer to those of the two larger sharks. This hypothesis seems unlikely because many known

individual sharks at SFI are large females (e.g. 'stumpy' mentioned herein) that have been site specific over a number of seasons (Anderson & Goldman unpublished data). Additionally, the smaller male (shark #2), like the small female, utilized the entire island area, and their mean IOR values are almost identical.

The IOR values from this study are comparable with previous studies describing site attachment in other sharks (McKibben & Nelson 1986, Morrissey & Gruber 1993). Strong et al. (1992, 1996) discuss site attachment of white sharks in South Australia, from re-sightings (at the same location) over periods of time ranging from days to more than one year, indicating it is probably not a regional phenomenon in this species.

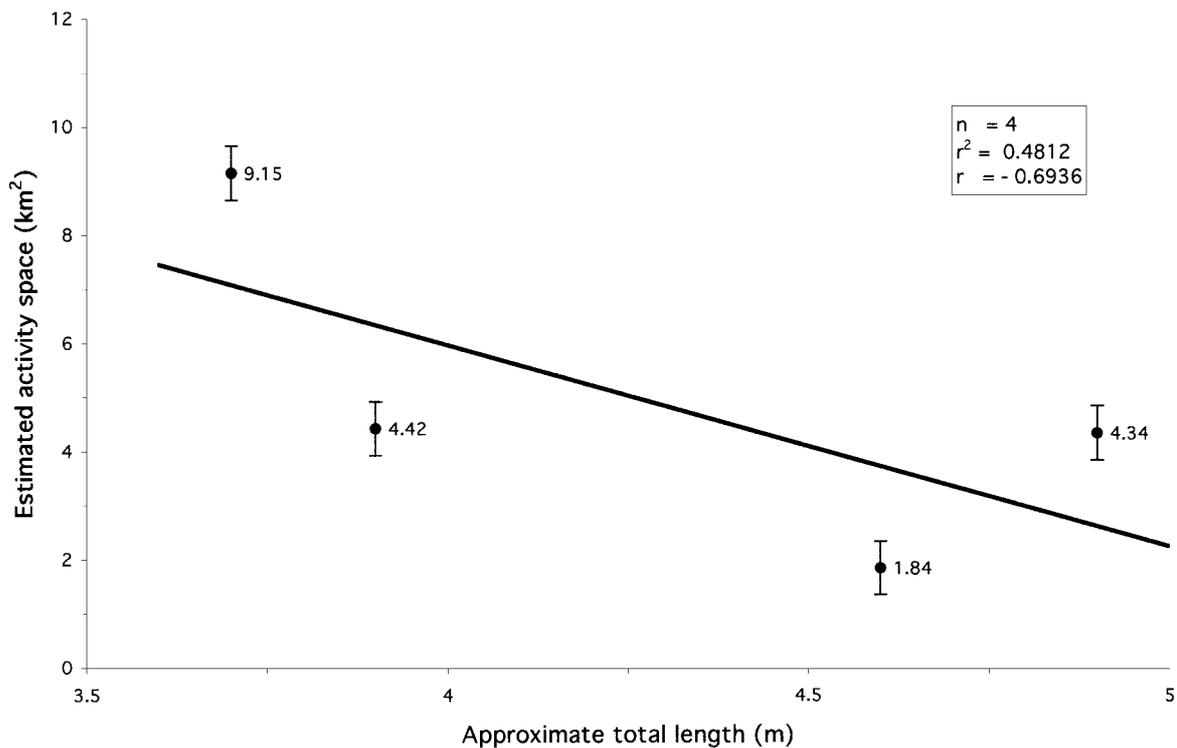


Figure 6. Estimated main activity space vs. approximate total length for four white sharks at South Farallon Islands with 95% confidence limits.

The combination of our tracking data, related observation-area curves and IOR values, observational data on telemetered and non-telemetered sharks and the two individuals from Klimley & Anderson (1996), support a hypothesis of area site fidelity in sharks larger than approximately 4 m total length, while smaller individuals (<4 m) do not appear to show site fidelity while at SFI. These observations provide further evidence of site specificity in large white sharks (>4 m) at SFI, within and between years. Another hypothesis might be that these areas are not activity spaces, but territories which would cause smaller and presumably less dominant sharks to continuously move in their search for prey at SFI. This does not seem likely, in that telemetered sharks were tracked in the same area at the same time, and several sharks are usually observed at sites of attacks and feeding events with no aggression towards each other (Anderson, Goldman & Larson unpublished data). Additionally, several other white sharks were observed at attacks and decoys in the activity spaces of the telemetered sharks during tracking sessions, indicating these activity spaces are neither exclusive nor defended.

We propose that the smaller white sharks (<4 m total length), which would have recently prey switched from being piscivorous to feeding on pinnipeds (McCosker 1985) are still learning locations and methods to successfully feed on these new prey. New to, and unfamiliar with the area surrounding SFI they may search for prey in a more random fashion than a larger shark that has frequented the islands for a number of fall seasons and had success preying on pinnipeds. The main factors involved in this hypothesis are the number of seasons an animal has frequented SFI and its past success in locating, attacking, and feeding on prey. Successful feeding in the past may lead an individual to re-visit the same area the next time it came to SFI in search of prey. This may help explain why the two smaller telemetered sharks were tracked all around SFI, while the two larger ones along with the 4.3 m white shark tracked in 1991 (see Goldman et al. 1996) were not (Figures 3–6). It would also explain why the two individuals in Klimley & Anderson (1996), ‘stumpy’ and many other large individuals have been seen in the same areas within seasons and over many seasons (Anderson & Goldman unpublished data).

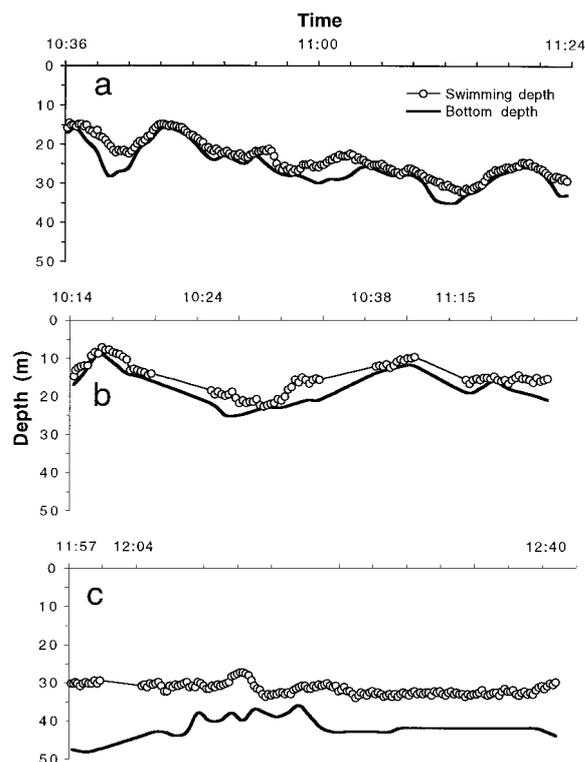


Figure 7. Examples of correlated and non-correlated swimming depth vs. bottom depth for sharks at the South Farallon Islands. Time intervals are in three minute periods. a – Swimming depth correlated to bottom depth during inshore–offshore movements (shark #1;  $r = 0.9362$ ;  $X_d < 10$  m), b – during alongshore movements (shark #1;  $r = 0.9363$ ;  $X_d < 10$  m). c – Swimming depth non-correlated with bottom depth at depths greater than approximately 30 m (from shark #2;  $r = 0.0038$ ;  $X_d > 10$  m).

Two movement patterns, nearshore sweeps and excursions away from and back to the islands, have been suggested for white sharks at SFI (Goldman et al. 1996). In general, the overall tracking records from all four telemetered sharks in this study support the suggested patterns of moving alongshore combined with on–offshore movements (Figures 2–5). When conducted within a small activity space, these types of movements provide thorough coverage of an area over both day and longer time periods (e.g. shark #3, Figure 4).

The movement patterns described (Goldman et al. 1996, and herein) are similar to the term ‘island patrolling’ used by Strong et al. (1992) to describe white shark movements near various islands in Spencer Gulf, South Australia. However, the sharks at SFI stayed at the islands for longer periods of time than

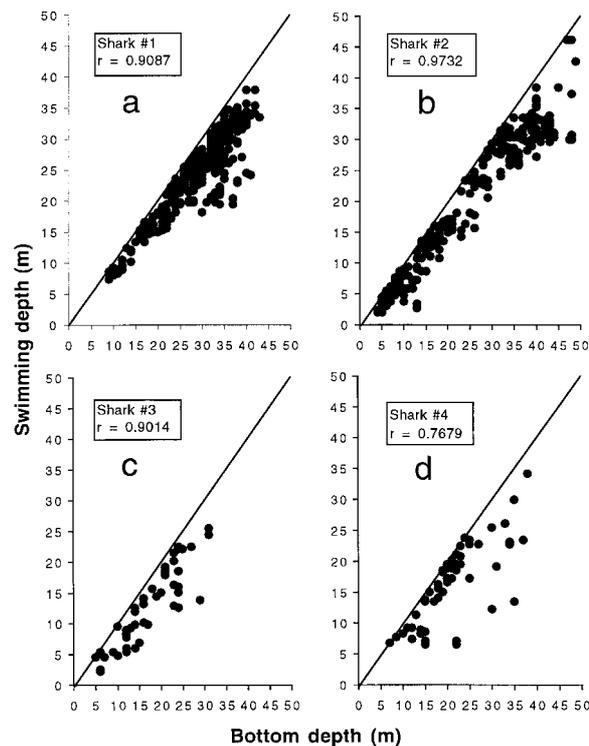


Figure 8. Swimming depth vs. bottom depth for four sharks at SFI: a – shark #1,  $n = 349$ , b – shark #2,  $n = 296$ , c – shark #3,  $n = 47$ , and d – shark #4,  $n = 58$ . Diagonal lines represents a 1 : 1 ratio of change. Correlation coefficients are given. Regression lines are not shown.

the sharks stayed at any particular island in the South Australia study. This may be due to the geographical differences and pinniped densities between the two areas, with the Farallones being the only offshore islands for hundreds of miles while numerous islands exist in Spencer Gulf. Pinniped densities per area are greater in the fall at SFI than at any of the islands in Spencer Gulf, South Australia (I. Gordon personal communication, and K.J. Goldman personal observation). With the large numbers of predatory attacks on pinnipeds at SFI in the fall months (between 35 and 73 – Klimley et al. 1992, Anderson, Pyle & Goldman unpublished data), one may presume that the longer an animal patrols in the same area, the more likely it is to be successful at either attacking a pinniped or feeding on another shark’s kill. It is interesting in that many of the sharks horizontal movements were inshore–offshore, in that the majority of initial strikes on juvenile northern elephant seals (coming to and leaving SFI) are from the front or rear, not from the side (Klimley et al. 1996).

The average minimum rate of movement, estimated from one minute intervals for the four sharks was  $2.3 \text{ km h}^{-1}$  (std. dev. = 0.6,  $n = 20$ ), which is slower than the  $3.2 \text{ km h}^{-1}$  calculated by Carey et al. (1982) and Strong et al. (1992) for sharks tracked off the east coast of the United States and in South Australia. The difference may be geographical, in that one previous tracking was linear in nature with the shark traveling many kilometers along a coastline (Carey et al. 1982) and the other trackings were from island to island (Strong et al. 1992), whereas our trackings were localized around a small group of islands.

Trackings provide a two-dimensional view of the movements and possible search behavior of white sharks at SFI. The swimming depth data and related bottom-depth information, provide a three-dimensional view. Telemetered sharks generally swam within 10 m of the bottom (Figures 7a,b), but in deeper water tended to stray further from the bottom (Figure 7c – also see Figure 8). If searching for prey, swimming near the bottom would increase crypsis from prey located at or near the surface. The combination of a shark with a dark dorsum swimming over a dark rocky bottom (Klimley 1994, Goldman et al. 1996) and light attenuation factors (Strong 1996), serve to make the shark cryptic in the water. Water clarity could affect swimming depth by forcing the shark to swim closer to the surface to visually locate prey.

White sharks possess good vision (Gruber & Cohen 1985), and our data may imply that white sharks can maintain visual contact with the surface to depths of at least 30 m (Figures 7, 8). Water clarity is often quite good around SFI. Secchi disc readings from a one foot diameter disc, usually taken at predatory attacks, have measured up to 15 m, and on several occasions the bottom could be seen when the depth finder on the tracking vessel read 19–20 m. Since prey are most often located at or near the surface (and the majority of attacks are surface attacks), swimming depth is probably not oriented to the bottom, but to the surface, and the shark deviates from following bottom contours at the depth where visual contact with the surface would be lost. The shark may determine its relative position above the bottom via the lateral line system, and if searching for prey the habit of following bottom contours while in shallow water may serve to create enough distance from the surface in order to maximize crypsis, which would explain the smaller differences (between swimming and bottom depths) in shallower water (Figures 7, 8).

Data presented here show that the movements of white sharks at SFI consist of patrolling type movements, combining alongshore and on-offshore movements and swimming close to the bottom until bottom depth reaches approximately 30 m. Below that depth, swimming depth tended to deviate more from bottom depth. This may allow them to remain hidden from potential prey thereby enhancing the chances of successful predation. Additionally, our telemetry and observational data along with observations from Klimley & Anderson (1996) provide support to a hypothesis of site fidelity for larger sharks (>4 m) to particular locations around SFI, both within and between years. Hence, white sharks can be included with other shark species which have been shown to possess site attachment to varying degrees (McKibben & Nelson 1986, Strong 1989, Morrissey & Gruber 1993).

Current research at SFI is working towards an updated version of Klimley & Anderson (1996), as the number of sharks exhibiting residency patterns and area site fidelity continues to slowly increase. Future research should include further testing of hypotheses presented here and examine nocturnal and crepuscular movements and swimming depths to see if diurnal activity spaces and water column orientation are maintained (and if so to what degree). This could lead to an understanding of seasonal home ranges of white sharks at SFI and a better understanding of white shark ecology and predator-prey interactions. Additionally, information regarding whether they use underwater landmarks (or other sensory modalities) to relocate a particular area may be obtained.

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## References cited

- Ainley, D.G., C.S. Strong, H.R. Huber, T.J. Lewis & S.H. Morrell. 1981. Predation by sharks on pinnipeds at the Farallon Islands. U.S. Fish. Bull. 78: 941–945.
- Ainley, D.G., R.P. Henderson, H.R. Huber, R.J. Boekelheide, S.G. Allen & T.L. McElroy. 1985. Dynamics of white shark/pinniped interactions in the Gulf of the Farallones. Mem. So. Calif. Acad. Sci. 9: 109–122.
- Anderson, S.D. & K.J. Goldman. 1996. Photographic evidence of white shark movements in California waters. California Fish and Game 82: 182–186.
- Anderson, S.D., A.P. Klimley, P. Pyle & R.P. Henderson. 1996a. Tidal height and white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. pp. 275–280. In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: Ecology and Behavior, Academic Press, San Diego.
- Anderson, S.D., R.P. Henderson, P. Pyle & D.G. Ainley. 1996b. Observations of white shark reactions to un-baited decoys. pp. 223–228. In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: Ecology and Behavior, Academic Press, San Diego.
- Carey, F.G., J.W. Kanwisher, O. Brazier, G. Gabrielson, J.G. Casey & H.L. Pratt, Jr. 1982. Temperature and activities of a white shark, *Carcharodon carcharias*. Copeia 1982: 254–260.
- Compagno, L.J.V. 1984. FAO species catalog: sharks of the world, Part 1. Food and Agriculture Organization of the United Nations 4: 237–249.
- Goldman, K.J., S.D. Anderson, J.E. McCosker & A.P. Klimley. 1996. Temperature, swimming depth, and movements of a white shark at the South Farallon Islands, California. pp. 111–120. In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: Ecology and Behavior, Academic Press, San Diego.
- Gruber, S.H. & J.L. Cohen. 1985. Visual system of the white shark, *Carcharodon carcharias*, with emphasis on retinal structure. Mem. So. Calif. Acad. Sci. 9: 61–72.
- Klimley, A.P., S.D. Anderson, P. Pyle & R.P. Henderson. 1992. Spatiotemporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. Copeia 1992: 680–690.
- Klimley, A.P. 1994. The behavior and feeding ecology of the white shark. Amer. Scientist 82: 122–133.
- Klimley, A.P., S.D. Anderson & P. Pyle. 1996. The behavior of white sharks and their pinniped prey during predatory attacks. pp. 175–192. In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: Ecology and Behavior, Academic Press, San Diego.
- Klimley, A.P. & S.D. Anderson. 1996. Residency patterns of white sharks at the South Farallon Islands, California. pp. 365–374. In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: Ecology and Behavior, Academic Press, San Diego.
- McCosker, J.E. 1985. White shark attack behavior: Observations of and speculations about predator and prey strategies. Mem. So. Calif. Acad. Sci. 9: 123–135.
- McCosker, J.E. & R.N. Lea. 1996. White shark attacks in the eastern Pacific Ocean: an update and analysis. pp. 419–434. In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: Ecology and Behavior, Academic Press, San Diego.
- McKibben J.N. & D.R. Nelson. 1986. Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. Bull. Mar. Sci. 38: 89–110.
- Morrissey, J.F. & S.H. Gruber. 1993. Home range of juvenile lemon sharks, *Negaprion brevirostris*. Copeia 1993: 425–434.
- Odum, E. & E.J. Kuenzler. 1955. Measurements of territory and home range size in birds. Auk 72: 128–137.
- Pyle, P., S.D. Anderson, A.P. Klimley & R.P. Henderson. 1996. Environmental factors affecting the occurrence and behavior of white sharks at the South Farallon Islands, California. pp. 281–292. In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: Ecology and Behavior, Academic Press, San Diego.
- Strong Jr., W.R. 1989. Behavioral ecology of horn sharks, *Heterodontus francisci*, at Santa Catalina Island, California, with emphasis on patterns of space utilization. M.Sc. Thesis, CSU, Long Beach. 252 pp.
- Strong Jr., W.R., R.C. Murphy, B.D. Bruce & D.R. Nelson. 1992. Movements and associated observations of bait-attracted white sharks, *Carcharodon carcharias*: a preliminary report. Aust. J. Mar. Freshwater Res. 43: 13–20.
- Strong Jr., W.R., B.D. Bruce, R.C. Murphy & D.R. Nelson. 1996. Population dynamics of great white sharks, *Carcharodon carcharias*, in the Spencer Gulf region, South Australia. pp. 401–414. In: A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: Ecology and Behavior, Academic Press, San Diego.
- Strong Jr., W.R. 1996. Shape discrimination and visual predatory tactics in white sharks, *Carcharodon carcharias*. pp. 229–240.

- In:* A.P. Klimley & D.G. Ainley (ed.) Great White Sharks: Ecology and Behavior, Academic Press, San Diego.
- Tricas, T.C. & J.E. McCosker. 1984. Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. Proc. Calif. Acad. Sci. 43: 221–238.
- Tricas, T.C. 1985. Feeding ethology of the white shark, *Carcharodon carcharias*. Mem. So. Calif. Acad. Sci. 9: 81–91.
- Winter, J.D. 1977. Summer home range movements and habitat use by four largemouth bass in Mary Lake, Minnesota. Trans. Amer. Fish. Soc. 106: 323–330.