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The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony

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Abstract The degree to which white sharks, *Carcharodon carcharias*, are social while hunting is unclear. Our aim was to describe the behavior and interactions among white sharks hunting seals near a seal colony. We attached ultrasonic beacons to five adult white sharks, 4.5–5.2 m long, and recorded their movements and behavior toward each other over a 15-day period in October 1997 at Año Nuevo Island, California. This site is home to colonies of four species of seals and sea lions. Two additional sharks, females 5.5 and 4.7 m in length, were later tracked intensively during periods of 12 and 3 days during October 1998 and November 1999, respectively. We recorded stomach temperature (indicative of feeding on warm-bodied seals) and swimming depths from the 5.5-m female, swimming speed and depth from the 4.7-m female. We monitored the movements and behavior of these sharks using an array of sonobuoys moored near the island; the receptive field measured 1 km^2. Our principal findings were: (1) the sharks spent a mean time of 39.5% of each day patrolling within the receptive field; (2) no shark ever moved far out of it; (3) the sharks spent an equal amount of time and activity in the receptive field at all times of the day, daytime, twilight, and nighttime; (4) movements with respect to the island rookery were most often back and forth parallel to the shoreline, (5) tracks of three sharks, tagged at the same time and place, overlapped more often than those of the other two sharks; and (6) some sharks patrolled certain areas in the field preferentially, but there was no conclusive evidence that they defended these areas as territories. Feeding appeared to be infrequent: only two likely feeding bouts occurred during a cumulative 78-day/shark period that individuals were monitored at Año Nuevo Island. The behavior and movements of the sharks were consistent with a hunting strategy, in which individuals search for prey independently but, at the same time, remain close enough to each other to ‘‘sense’’ and exploit a kill by any one of them by joining in on the kill to feed.

Introduction

The hunting strategy of the white shark, *Carcharodon carcharias,* is uniquely adapted to the life history of seals and seal lions, which concentrate to molt and mate on shore at widely separated insular or coastal locations. Klimley et al. (1992) found that these sharks concentrated their hunting effort in a shallow zone (<37 m deep) surrounding the pinniped colonies at South Farallon Islands. The small size (<1.3 km from shore) of this high predation-risk zone made it feasible to use an array of sonobuoys to track multiple white sharks at once and monitor their behavior, swimming movements, and spatial distribution while hunting for similar prey at Año Nuevo Island (Klimley et al. 2000).

The degree to which white sharks are social when hunting is unclear. Most observations of white sharks have been of solitary individuals. For example, over a 5-year period at the South Farallon Islands a single shark was seen on 74% of 195 days when white sharks fed on pinnipeds or investigated decoys, two sharks on

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Table 1 *Carcharodon carcharias*. Estimated length and sex of sharks, date and time of tagging, and time-period during which seven white sharks were detected with a radio-acoustic positioning system at Año Nuevo Island, Central California. *Est* Estimated, *M* male, *F* female, *Interval* period between when sharks were first and last detected by array, *Presence* number of days during period in which sharks were detected by array, *Temp.-depth* telemetry transmitters providing positions and measurements of shark's stomach temperature and swimming depth, *Speed-depth* transmitters furnishing positions, swimming speed, and depth

Shark			Tagging information				
Identity	Est length (m)	Sex (M/F)	Date	Time of day (hours)	Interval (days)	Presence (days)	Transmitter type
W1	5.2	M	13 October 1997	1540	18	15	Beacon
W2	5.2	F	13 October 1997	1630	18	15	Beacon
W3	4.5		13 October 1997	1700	18	15	Beacon
W4	4.7	F	16 October 1997	1405	11	8	Beacon
W5	4.5	F	26 October 1997	1200	5	5	Beacon
W6	5.5	F	22 October 1998	0901	< 25	12	Temp.-depth
			22 October 1998	1048	28	2	Temp.-depth
W7	4.7	F	1 November 1999	1100	3	3	Speed-depth

22% of the days, and three sharks on 4% of the days (Klimley and Anderson 1996). When multiple sharks were observed, it was usually to feed on a recently killed seal. At these times, individuals often splashed water with their tails at each other (tail slap) or leapt out of the water (breach). Klimley et al. (1996b) argued that these were threat displays, indicative of competition for the prey.

Our overall objective was to describe the movements, behavior, and interactions of multiple sharks while searching for seals near a seal colony in central California. We achieved this by tagging individuals with ultrasonic transmitters, continuously tracking them, and acquiring a continuous record of their behavior with a radio acoustic positioning (RAP) system. Simultaneous tracking is certainly a formidable task. Imagine continuously monitoring five employees during an 8-h work period (33.3% per day), recording their rates of walking and separation distances as well as making inferences from their tracks on the level of social interaction. The five sharks in this study were detected over an even longer period, i.e., 9.6 h (39.5% per day), within the receptive area of array. Our ultimate aim was to describe the general hunting strategy of the sharks. We sought to determine whether these white sharks were solitary or social hunters and to establish the frequency with which they fed at a seal colony. We thus needed to record the duration of their tenure near the colony, their activity pattern by time of day, their rate of feeding success, and their degree of attraction or avoidance among themselves.

Materials and methods

We tagged five white sharks with ultrasonic beacons during October 1997, a sixth shark with temperature and depth (TD) transmitters during October 1998, and a seventh shark with a speed and depth (SD) transmitter during October 1999 (Table 1). The sharks were tagged < 800 m from shore in ≤30 m depth at Año Nuevo Island (Fig. 1a). This site is located 1,800 m from shore at the northern edge of Monterey Bay in Central California (Fig. 1b). The island and adjacent coastline is the home of a large pinniped colony of juvenile northern elephant seals, *Mirounga angustirostris*, adult California sea lions, *Zalophus californianus*, female Steller sea lions *Eumatopias jubatus*, and mixed-age harbor seals, *Phoca vitulina*, at this time of the year (B. J. Le Boeuf, personal observation).

The sharks were tracked by an array of RAP buoys (VEMCO, Halifax, Canada) moored 600 m southwest of the island (Fig. 1a). We located the array on the western side of the island beyond the surf zone where white sharks had been seen from small boats in previous years in the fall and winter. Location of the array was also influenced by observations at the South Farallon Islands of white sharks feeding on seals within a zone ≤1.3 km from shore, the "high risk" zone (Klimley et al. 1992). The buoys were moored in a triangle. The RAP buoys communicated by radio with a signal processing station situated on Año Nuevo Island. This station consisted of a radio transceiver, timing module, and laptop computer. The tracks and records of the swimming speed, depth, and stomach temperature of tagged sharks were displayed in real time on the computer monitor and stored on disk.

Two types of positional information, the frequency of detection by each sonobuoy and the location of the shark within a x, y, z coordinate system, were stored on disk for each shark as a function of time of day. The three circles*A′–C′* (Fig. 1a) depict the maximum distances at which sonobuoys A–C were capable of detecting a shark with an ultrasonic beacon above the ambient noise with seas with a wave height of 0.6 m (Klimley et al. 2000). This was the most prevalent sea-state at Año Nuevo Island during the fall. The RAP system recorded a position when the signal from the beacon on a shark was detected by all three sonobuoys. The position consisted of coordinates in an Cartesian system with its origin located in the center of the array. The positional range is indicated in Fig. 1a by the light stippling where the circular detection ranges of the three buoys overlap. Behavioral and environmental measurements (swimming speed, depth, and stomach temperature) were recorded if a tagged shark swam within the detection range of any of the sonobuoys. The operation of this specific RAP system is described in more detail elsewhere (Klimley et al. 2000).

The sharks were tagged from a small boat. Each shark was lured to the surface with a seal-shaped decoy made of plywood attached to a line on a rod and reel. Once the shark rose to the surface and began to investigate the decoy, it was reeled in slowly to the boat. The shark followed the decoy to our vessel. A seal weanling, which died naturally during the previous winter and was preserved by freezing, was placed in the water to induce the shark to approach close enough so that we could tag it from the boat.

There were two methods of tag attachment. Firstly, the transmitter was mounted on the end of a pole spear with a tether leading

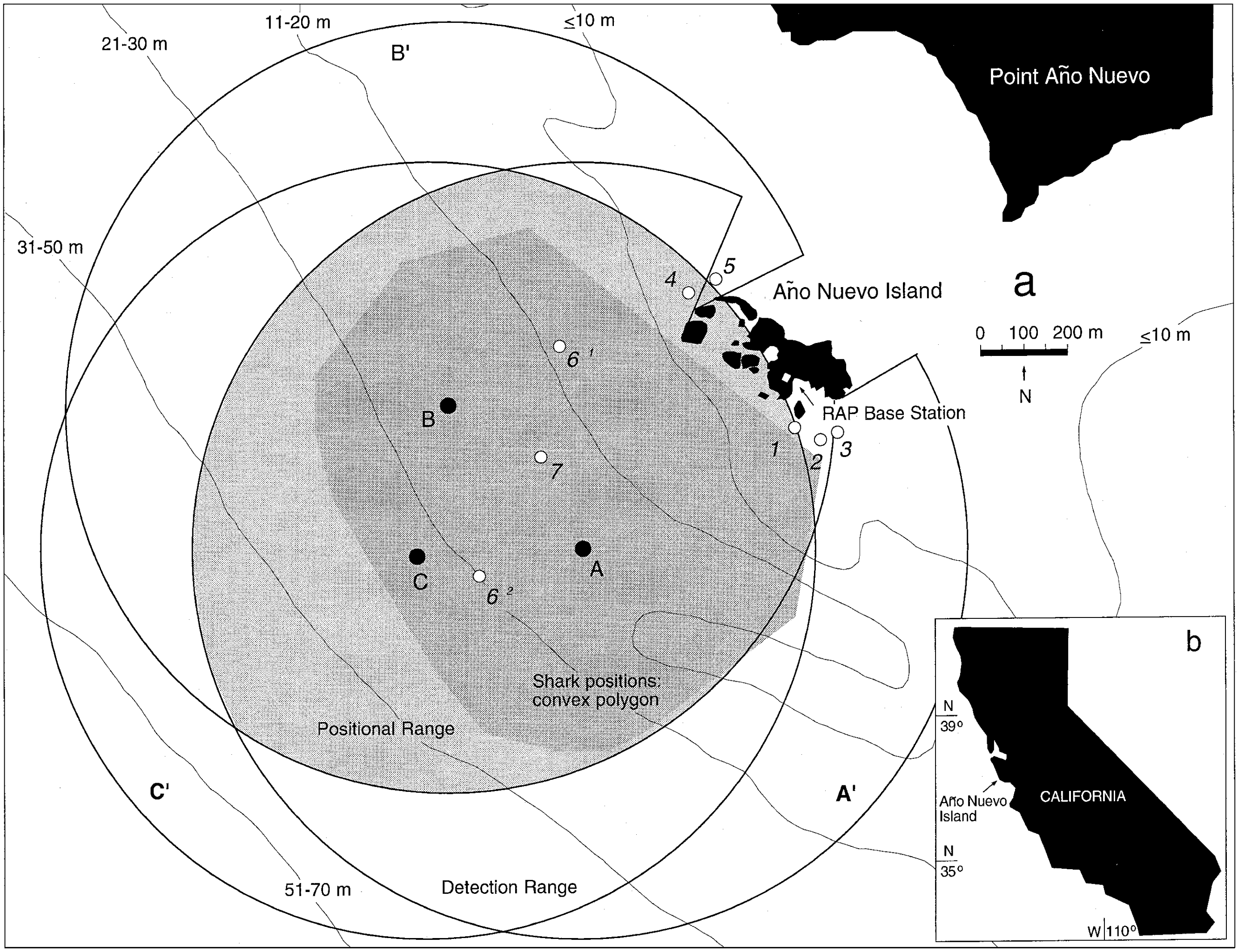


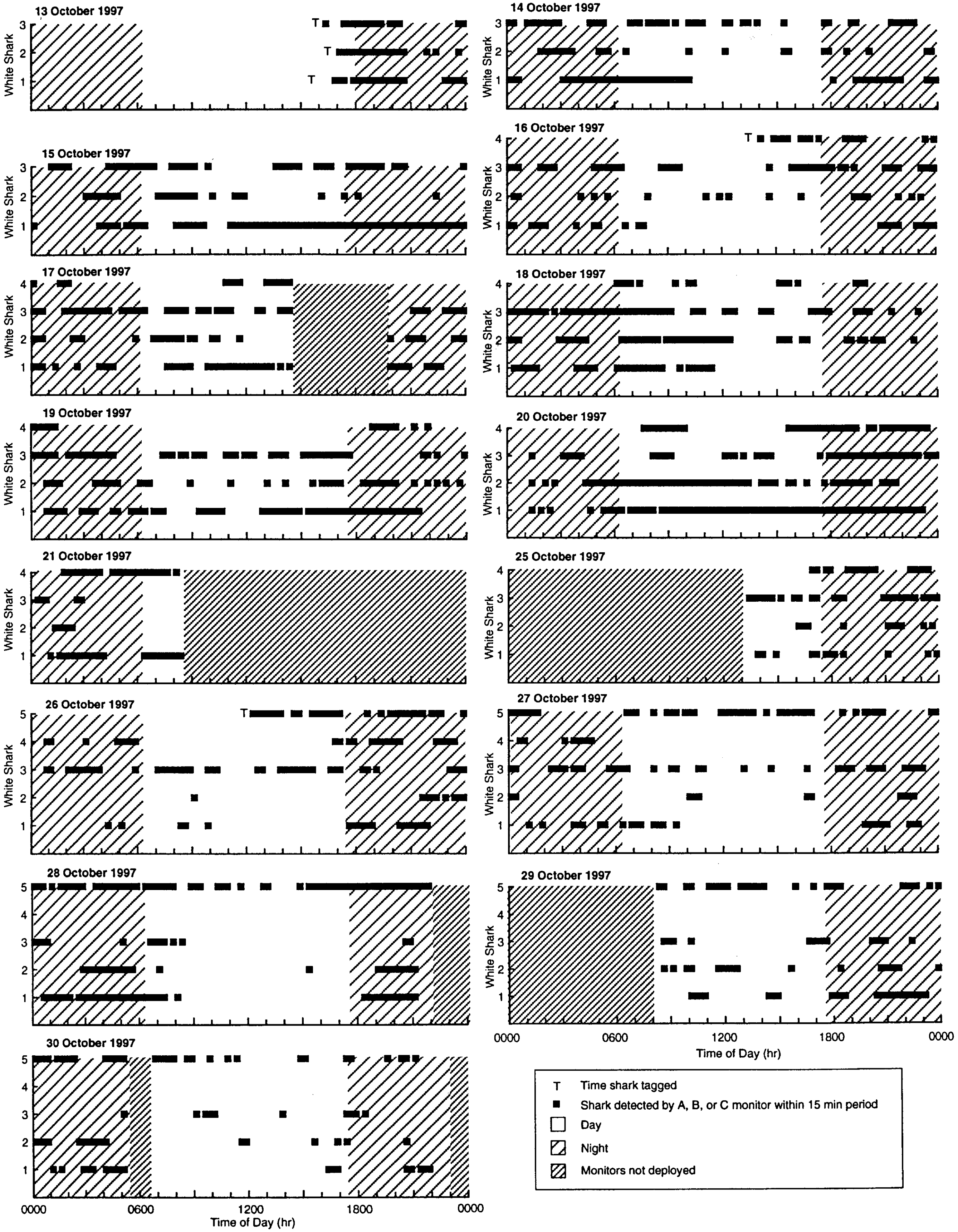
Fig. 1 Map of Año Nuevo Island, Central California with three sonobuoys and base station of radio-acoustic positioning system (*RAP*) where seven white sharks, *Carcharodon carcharias*, were tracked during 1997–1999. The beacon on the white shark emits an ultrasonic pulse that is detected by hydrophones on three sonobuoys that send information by a radio transceiver to a shore-based receiving station, where the shark's position is displayed on a computer monitor and stored on disk. ● Sonobuoys A–C; *large circles* ranges *A′–C′*; ○ locations where sharks W1–W7 were tagged; *light stippling* area in which positions could be recorded; *dark stippling* concave polygon indicating home range of seven sharks tracked in October and November 1997–1999

to a stainless steel dart held in a slot on the tip of the spear. The dart was inserted into the muscle of the shark's dorsum between the first and second dorsal fins. Five sharks were tagged with beacons using this method during 1997 and a single shark with a SD transmitter during 1999. The second method of attachment consisted of inducing the shark to swallow a piece of marine mammal meat, in which a transmitter was hidden. We used this technique to introduce a TD transmitter into the stomach of a shark in 1998.

During 1997, we simultaneously tracked five white sharks while hunting for prey. Our objective was to quantify the level of association between individuals. The beacons on the sharks provided location, from which we could calculate rate of movement and separation distance between neighboring sharks. The sharks were tracked relatively continuously from 13 to 30 October 1997 (15 days) with the exception of 21–25 October (4 days) when the tracking system malfunctioned and the equipment could not be repaired due to inclement weather.

A statistical method was used to ascertain whether tagged sharks were attracted to or avoided each other within the reception range of the array [for a more detailed explanation, see Klimley et al. (2000)]. The RAP system recorded positions using several pulses from the beacon on shark W1 with the lowest frequency, then recorded positions for the pulses from the beacon on shark W2 with the next highest frequency, and so forth, before returning to listen again for the beacon with the lowest frequency. We found the distances from each shark to the others from imaginary points on a straight line extending from last position determined for a set of pulses to the first position for the next set of pulses. As our control, we randomized the separation distances by supplanting the coordinates of each neighboring shark with the coordinates for the same shark at another time during the study. The order of these positions was randomized using values taken from a table containing random numbers.

During 1998, we tracked a single shark with a TD transmitter during 12 days from 22 October to 13 November 1998. A single shark was monitored intensively in order to identify bouts of feeding and describe the pattern of swimming associated with prey capture. We anticipated an elevation of stomach temperature when the shark swallowed a warm-bodied pinniped. In actuality, there were intermittent breaks in recording due to temporary buoy loss (1–4 days), buoy removal because of heavy seas (up to 7 days), and buoy retrieval every 8 days for recharging batteries (1–2 days). We tracked a single shark during the fall of 1999, recording measurements of swimming speed and depth. However, data could only be


13 October 1997
14 October 1997
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White Shark
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Time of Day (hr)
T Time shark tagged
■ Shark detected by A, B, or C monitor within 15 min period
☐ Day
▨ Night
▨ Monitors not deployed

◄

Fig. 2 *C. carcharias*. "Clock" diagrams showing the presence of five white sharks (W1–W5) within the detection range of either sonobuoy A, B, or C on 13–30 October 1997. Individuals are identified by ■ if detected within a 15-min period during a 24-h cycle. *White area* Daytime; *coarsely hatched area* nighttime; *finely hatched area* monitor not deployed; *T* time shark tagged

acquired at nighttime during 3 days from 30 October to 2 November because the multiplicity of radio signals emitted by cellular phones during daytime interfered with communication between the base station and the sonobuoys.

Results

Monitoring five sharks

We attached beacons to three sharks (W1–W3) during an 80-min period from 1540 to 1700 hours on 13 October 1997 while they were feeding on a sea lion (Table 1). These sharks ranged from 4.5 to 5.2 in total length (TL); one was a male, another was a female, and the sex of the third was not distinguished. We placed a fourth beacon on a 4.7-m-TL female shark (W4) 3 days later at 1405 hours on 16 October and a fifth instrument on a 4.5-m-TL female 13 days later at 1200 hours on 26 October.

The sharks visited the high predation-risk zone near Año Nuevo Island during each of the 15 days that the system was operative from 13 to 30 October 1997 (Fig. 2). We estimated the time each shark spent near the seal colony each day based on the number of 15-min periods that it was detected while the array was operating that day. These percentages for each shark are plotted below the daily operating percentages for each day of the study (Fig. 3). The amount of time spent in the receptive field was substantial. The five sharks spent a mean of 39.5% of each day within range of the array, ranging from 29.6% ($n = 15$ days) for shark W2 to 52.0% ($n = 5$ days) for shark W5. However, the sharks' visits varied considerably in length from day to day. For example, shark W1 stayed within range of the sonobuoys during 73% of the time on 15 October but only 23% of the time during the following day. The five sharks spent a median of 45 min/visit (three contiguous 15-min periods) within the reception range of the array (Fig. 4a).

We can estimate the extent to which the sharks moved away from this hunting ground based upon their median period of absence and swimming speed. The five sharks spent a median of 60 min (4 × 15 min) outside the range of the array (Fig. 4b). This median time (3,600 s) was multiplied by the median swimming speed of 1.34 m/s (25th % = 1.13 m/s; 75th % = 1.51 m/s, $n = 268$) for shark W7 to estimate the average distance of 4,824 m that sharks W1–W5 traveled along a straight line per absence. This distance must be halved (for the outward and return trip) to estimate the maximum distance of 2,412 m that the sharks moved from the colony when not searching for prey near the island. The largest estimated excursion distance using the median swimming speed was 42.5 km from Año Nuevo Island.

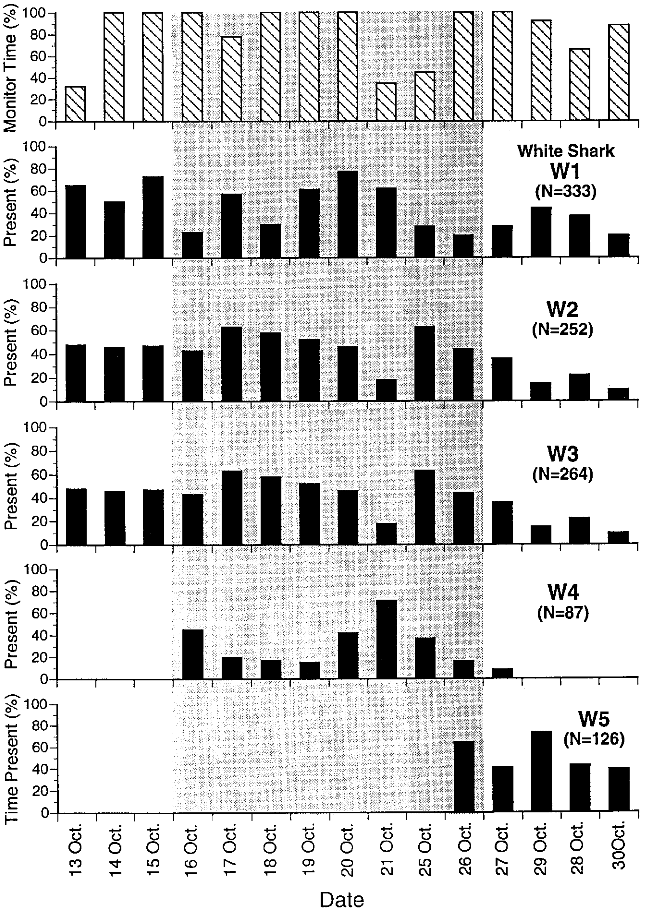


Fig. 3a–d *C. carcharias*. Percentages of 15-min periods (*hatched bars*) that sonobuoys were active during each 24-h period (**a**) and percentages of similar periods (*solid bars*) that sharks W1–W5 (**b–d**) were detected within range of sonobuoys on 13–30 October 1997. *Stippling* Days sharks W1–W4 were present

Active at daytime and nighttime

The five sharks visited the waters off the pinniped colony at all times of the day. The percentages of the day that each individual spent per hour near the island deviated little from the hourly average of 4.2% (100%/24 h), expected if the same amount of time were spent each hour of the day within the range of the array (Fig. 5). Furthermore, the frequencies, with which sharks were detected during daytime, nighttime, and twilight, differed little from the relative proportions of these periods during a 24-h day (Table 2). For example, sharks were detected in 704 of the 15-m periods between sunrise and sunset, comprising 41.0% of the total of 1,719 periods in which a shark was detected by either A

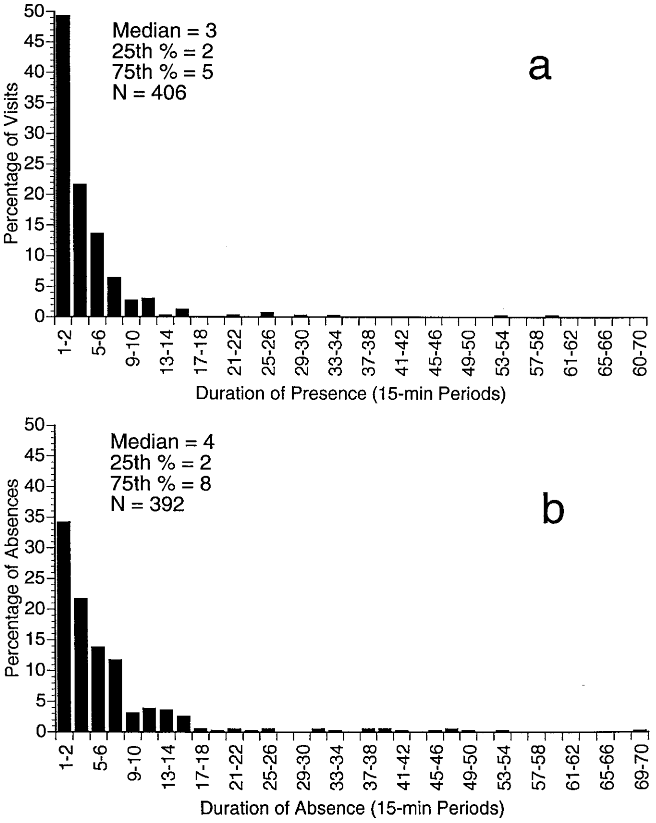


Fig. 4a, b *C. carcharias*. The percentages of visits (**a**) and absences (**b**) of increasing durations (in contiguous 15-min periods) of sharks W1–W5 to and from the reception range of the RAP system

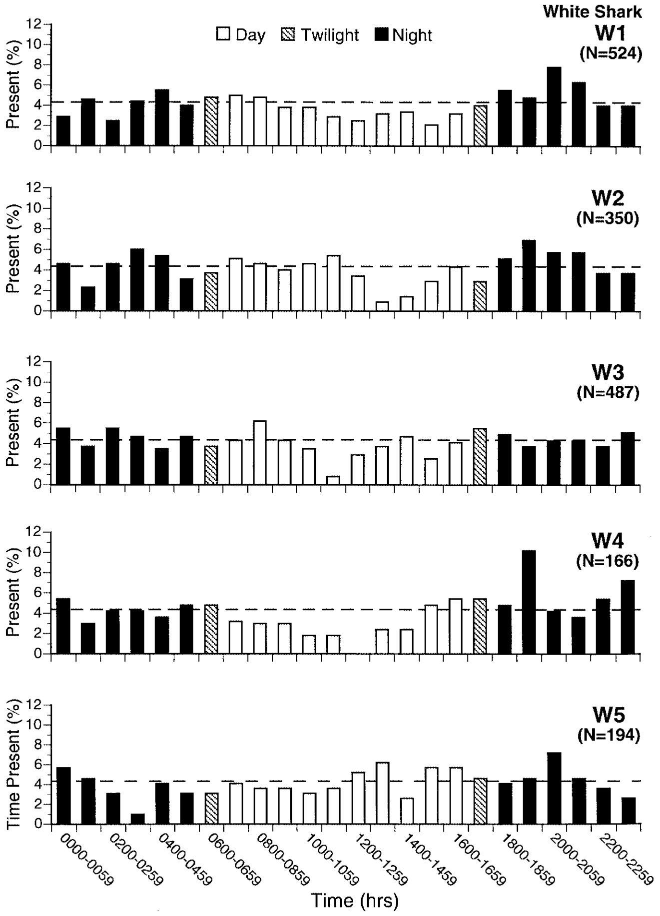


Fig. 5 *C. carcharias*. Percentage of 15-min periods when sharks W1–W5 were detected within range of sonobuoys during day (*white*), twilight (*hatched*), and night (*solid*) each hour of a 24-h cycle; *dashed line* equal amount of time spent each hour of the day

or B or C buoy. The sharks were recorded at nighttime during 55.9% and at twilight during 3.2% of these periods. It was daytime during 2,717 (44.9%) of the 6,050 periods when the array was active near the island, nighttime during 51.9% of these periods, and twilight during 3.8% of the periods. There were no significant differences between the frequency of detection and relative amount of day, night, and twilight (χ^2, test of proportions, $P > 0.684$, $n = 1710$). Neither was any statistically significant difference found between similar comparisons with other criteria such as the sharks being detected by all three sonobuoys (χ^2, $P > 0.765$, $n = 1060$) or positioned within the array (χ^2, $P > 0.376$, $n = 628$).

Patrolling close to shore

The sharks could be tracked only when within the detection range of all three sonobuoys. The extent of their movements is indicated by a concave polygon, formed by connecting the outermost points of the sharks' tracks (dark stippling in Fig. 1a). This area extended from close to shore only 700 m despite the system's ability to track the sharks at much greater distances (light stippling where ranges of the three buoys overlap). Twenty-four-hour plots of the movements of the sharks indicated that they rarely ventured far from shore, but stayed very close as illustrated by the movements of sharks W1–W4 on 14–15 and 19–20 October 1997 (Fig. 6). The tracks of the sharks were concentrated between the island and the x-axis of the array's coordinate system, 700 m offshore. The sharks at times approached to within ±2 m from shore (see solid, dotted, and dashed lines of sharks W1, W2, and W3 in Fig. 6c). This distance equaled the system's simulated positional error at that point in the receptive field (see Fig. 4 in Klimley et al. 2000). The sharks patrolled the island both during daytime (Fig. 6a, c) and nighttime (Fig. 6b, d).

Some of the sharks appeared to patrol back and forth along the shore, where they were ideally positioned to intercept seals and sea lions departing and returning to the shore-based rookeries. Thus, the distributions of headings of sharks W1 (Fig. 7a), W3 (c), W5 (e), and W6 (f) peaked along a northwest-southeast axis parallel to shore. Notice that the lines and points indicating high frequencies of headings were along the long axis of Año Nuevo Island (denoted by the stippled area on the circular diagrams in Fig. 7). Yet there were

Table 2 *C. carcharias*. Percentage of time spent at Año Nuevo by five white sharks during day, night, and crepuscular (based on Civil Twilight) periods. *RAP* Radio acoustic positioning

	Day (%)	Night (%)	Crepuscular (%)	*N*	*P*-value
RAP buoy A or B or C	41.0	55.9	3.2	1,719[a]	0.684
RAP buoy A and B and C	42.4	54.7	2.8	1060[a]	0.765
Position recorded	41.2	59.8	2.5	628[a]	0.376
Monitor time	44.9	51.9	3.8	6,050[b]	

[a] Total number of periods during which all five sharks were detected

[b] Monitor time is the number of 15-min periods for which the monitor recorded data

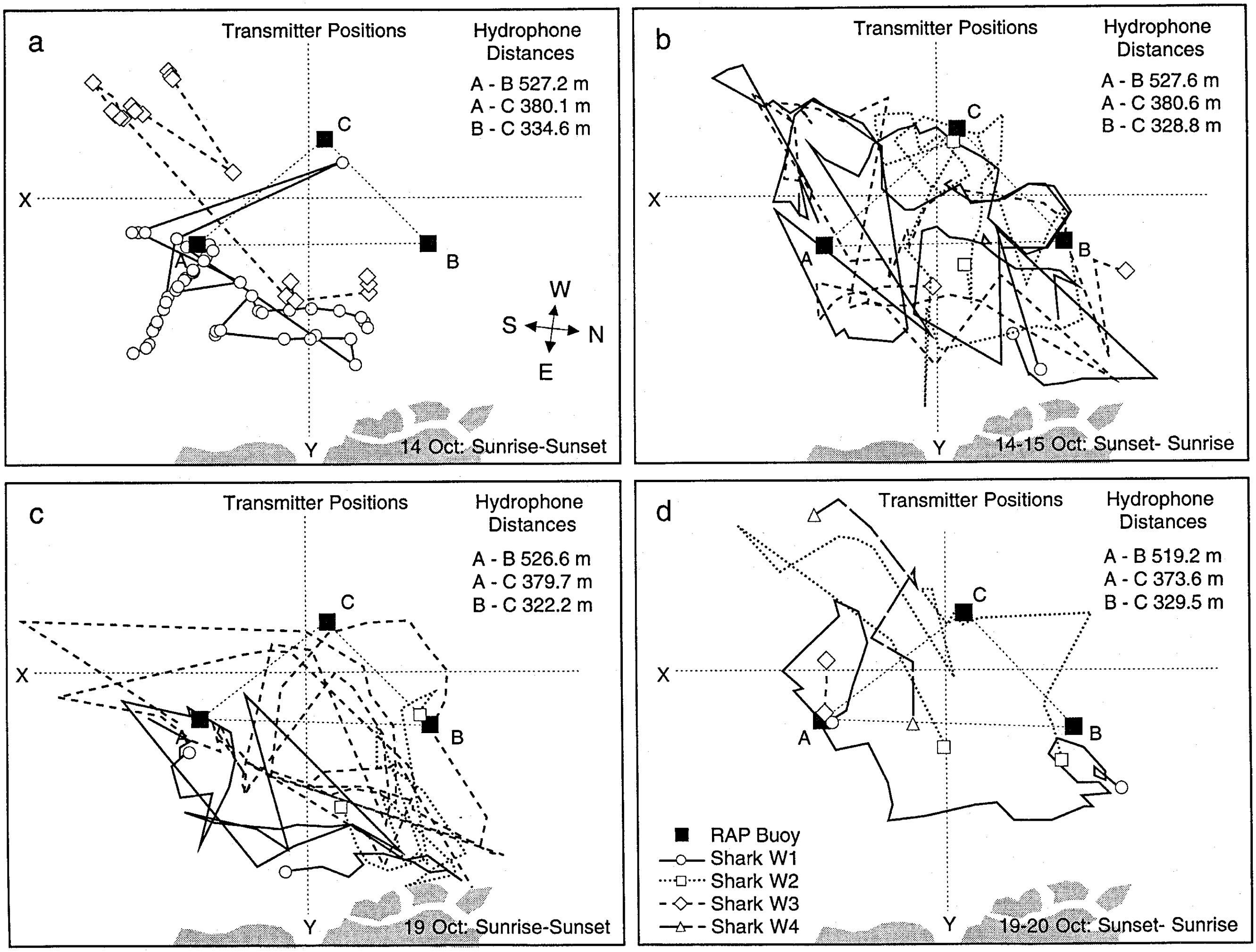


Fig. 6a–d *C. carcharias*. Paths of four sharks during daytime (**a**) and nighttime (**b**) on 17–18 October and during daytime (**c**) and nighttime (**d**) on 19–20 October 1997. Symbols given for all positions in **a**; symbols for initial and final positions in **b–d**. ■ RAP sonobuoys; ○ positions of shark W1; □ positions of W2; ◇ positions of W3; △ positions of W4

lesser peaks roughly perpendicular to the island's coastline in a southwest-northwest axis, indicative of stalking or chasing a pinniped moving to or from the island (see peak between 220° and 240° for shark W4 in Fig. 7d). These offshore excursions are evident in the plots of the movements of sharks W1–W4 on 14–15 and 19–20 October 1997 (Fig. 6). Notice the offshore movements of shark W3 during daytime and nighttime on 14–15 October 1997 and daytime during 19 October (see dashed lines in Fig. 6a–c). Shark W1 made similar excursions on the night of 14–15 October (see solid lines in Fig. 6b).

Absence of territoriality

There was little evidence of territoriality between the five sharks tracked during the fall of 1997. If the sharks favored separate areas, they might have been detected by one of the sonobuoys more often than by the other two sonobuoys. We determined whether the numbers of 15-min periods, in which sharks were detected at each of the three buoys, differed from an equal distribution during

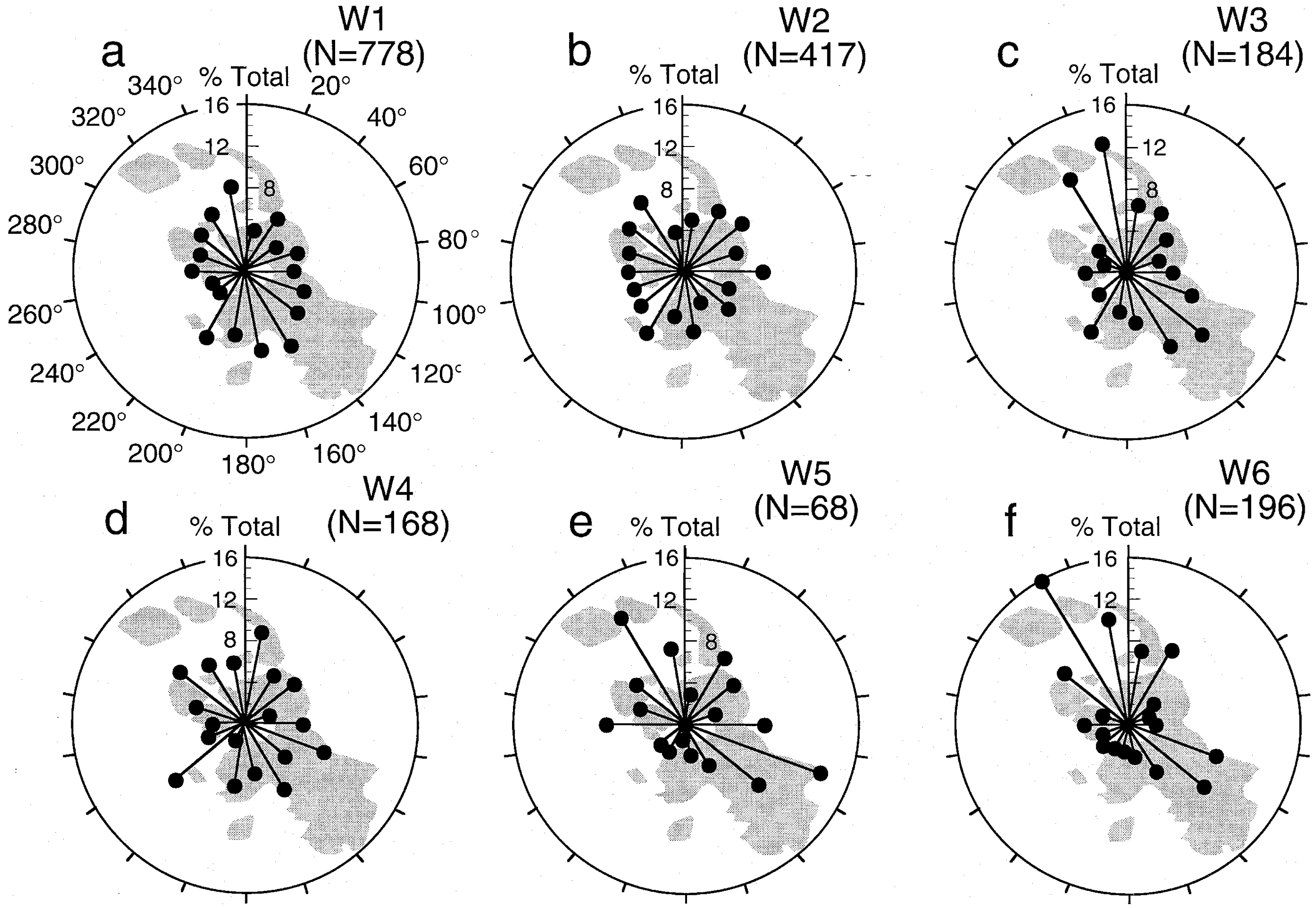


Fig. 7a–f *C. carcharias*. Percentages of headings between pairs of consecutive positions in 20-degree classes of sharks W1–W6 (**a–f**) during fall 1997 and 1998. Año Nuevo Island (*stippled area*) is superimposed upon the circular diagrams. We considered points consecutive when they were separated by no less than 1 min (eliminating less accurate positions determined over 2- to 3-s intervals) and no greater than 5 min (removing positions, between, between which sharks may have left and entered the receptive area)

the period from 13 to 30 October. For example, shark W1 was recorded 20, 16, and 17 times by sonobuoys A, B, and C on 13 October, and these were compared to equal values of 17.7 for each sonobuoy (i.e., 53 periods/3 sonobuoys) (Table 3). Similar comparisons were made for each shark for each day over this 15-day period. No statistical difference was found between the frequency of visits to the three overlapping areas near the island and an equal distribution of visits to all three areas for Sharks W1 to W5 (χ^2, test of equal proportions, $P > 0.30$–0.89).

We also examined the spatial distribution of all positions recorded for the five sharks tracked during the fall of 1997 graphically to ascertain whether they remained apart within the range of the RAP array. These positions were plotted as percentages of the total number of positions for each shark within a rectangular area 1,100 m in a northerly-southerly direction ×1,000 m in an easterly-westerly direction, roughly parallel to the coast of Año Nuevo Island (Fig. 8). These contour maps, each based upon the percentage of all positions lying within each of the 100×100-m cells, show where the five sharks distributed their time while within the array near the island. The locations of the buoys are given on the maps to give the reader a spatial reference (see *white circles*). The peak in the activity of shark W1 was east of the center of Año Nuevo Island. Sharks W2 and W3 had two overlapping peaks of activity, one off the northern end and the other off the southern end of the island. Sharks W4 and W5 had single broad overlapping areas of high activity, one with its peak east off the southern end of the island and the other with its peak east of the center of the island. These two distributions resembled that of the positions of shark W6, tracked during roughly the same period during the fall of 1998. Although each of the sharks spent more time in a slightly different location than the others, all of the sharks frequently moved over the same areas.

Social or solitary hunter?

The sharks often moved in and out of range of the array simultaneously, which is consistent with patrolling within a group, but at other times arrived and departed separately (Fig. 2). For example, sharks W1–W3 were

Table 3 *C. carcharias*. Amount of time spent by five white sharks within ranges of three RAP buoys at Año Nuevo Island during October 1997

Shark RAP buoy		W1			W2			W3			W4			W5		
		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
13 October	A[a]	20	16	17	12	15	17	10	11	11						
	E[b]	17.7	17.7	17.7	14.7	14.7	14.7	10.7	10.7	10.7						
14 October	A	44	45	46	11	20	18	38	33	36						
	E	45.0	45.0	45.0	16.3	16.3	16.3	35.7	35.7	35.7						
15 October	A	60	66	66	19	28	24	38	40	40						
	E	64.0	64.0	64.0	23.7	23.7	23.7	39.3	39.3	39.3						
16 October	A	13	22	15	7	17	12	32	37	38	16	16	18			
	E	16.7	16.7	16.7	12.0	12.0	12.0	35.7	35.7	35.7	16.7	16.7	16.7			
17 October	A	36	37	39	23	27	24	36	39	44	13	12	14			
	E	37.3	37.3	37.3	24.7	24.7	24.7	39.7	39.7	39.7	13.0	13.0	13.0			
18 October	A	25	28	29	44	45	46	46	50	51	13	7	11			
	E	27.3	27.3	27.3	45.0	45.0	45.0	49.0	49.0	49.0	10.3	10.3	10.3			
19 October	A	53	47	54	27	35	36	40	44	47	9	11	12			
	E	51.3	51.3	51.3	32.7	32.7	32.7	43.7	43.7	43.7	10.7	10.7	10.7			
20 October	A	64	58	64	56	60	60	35	29	43	25	40	33			
	E	62.0	62.0	62.0	58.7	58.7	58.7	35.7	35.7	35.7	32.7	32.7	32.7			
21 October	A	17	14	17	3	5	5	7	4	7	16	23	23			
	E	16.0	16.0	16.0	4.3	4.3	4.3	6.0	6.0	6.0	20.7	20.7	20.7			
25 October	A	9	9	8	3	7	5	19	21	22	8	15	15			
	E	8.7	8.7	8.7	5.0	5.0	5.0	20.7	20.7	20.7	12.7	12.7	12.7			
26 October	A	6	17	15	6	10	8	29	40	36	9	6	14	14	30	19
	E	21.7	12.7	12.7	8.0	8.0	8.0	35.0	35.0	35.0	9.7	9.7	9.7	21.0	21.0	21.0
27 October	A	9	25	17	6	15	11	22	22	32	4	4	8	27	29	32
	E	17.0	17.0	17.0	10.7	10.7	10.7	25.3	25.3	25.3	5.3	5.3	5.3	32.7	32.7	32.7
28 October	A	31	37	34	20	21	20	10	1	9	0	0	0	52	62	59
	E	34.0	34.0	34.0	20.3	20.3	20.3	6.7	6.7	6.7	0	0	0	57.7	57.7	57.7
29 October	A	20	17	20	10	12	13	11	3	14	0	0	0	23	23	21
	E	19.0	19.0	19.0	11.7	11.7	11.7	9.3	9.3	9.3	0	0	0	22.3	22.3	22.3
30 October	A	13	13	15	13	16	16	4	5	8	0	0	0	27	29	30
	E	13.7	13.7	13.7	15.0	15.0	15.0	5.7	5.7	5.7	0	0	0	28.7	28.7	28.7
		χ^2 analysis (*P*-value)														
		0.89				0.89			0.53			0.49			0.30	

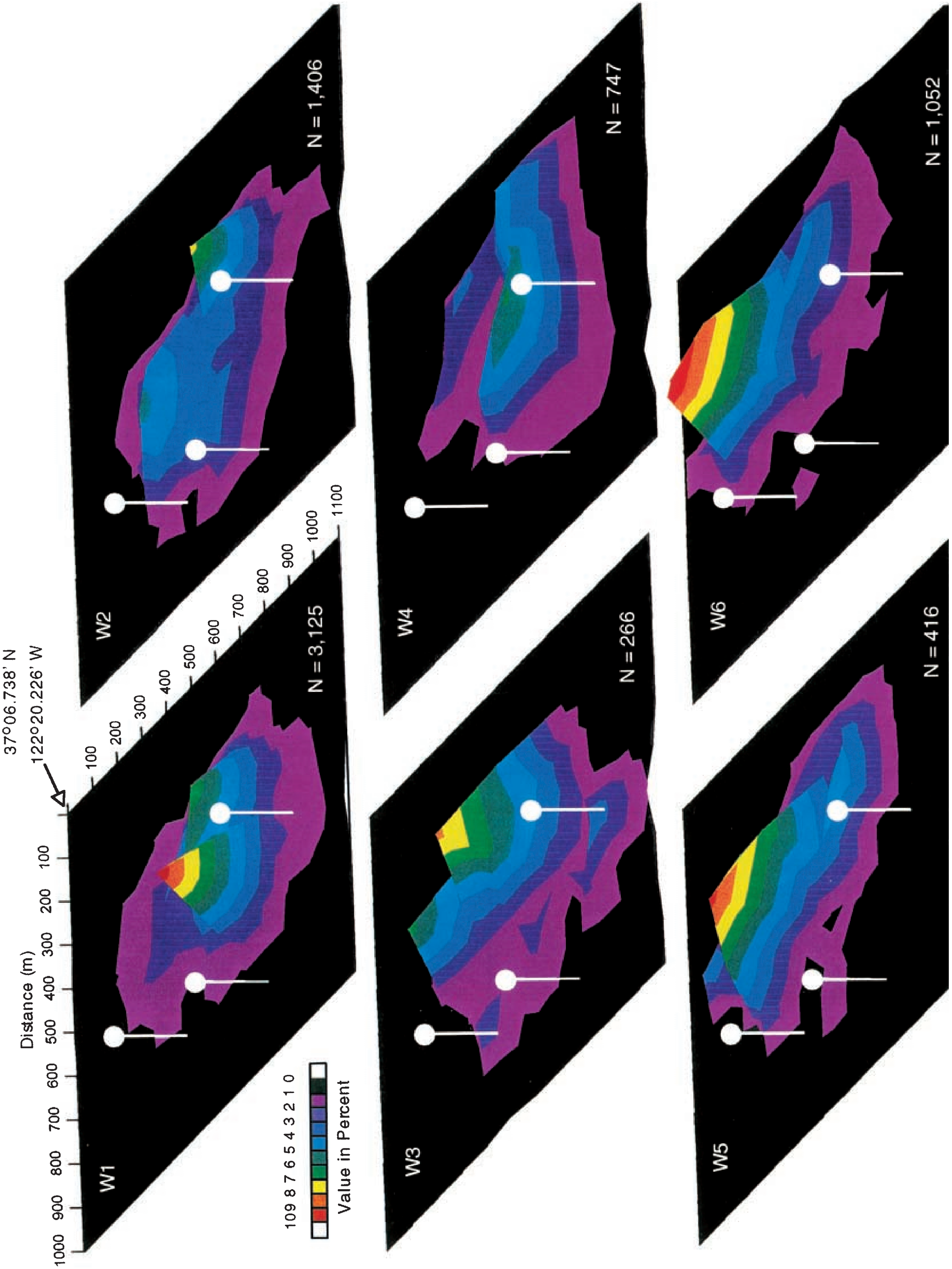
[a] *A* is number of 15-min periods in which sharks were detected by buoys *A*, *B*, *C*

[b] *E* is expected number of periods in which sharks should be detected by buoys, assuming that each shark remained an equal amount of time within the detection range of the three buoys

usually present and absent at the same time on 13 October (see *top left* record), but this pattern was not so pronounced on subsequent days. This mixture of coordinated and uncoordinated movements was evident on most days. One cannot conclude that the sharks were moving in tandem in and out of the range of the array simply from the records of their presence or absence. Furthermore, two or more sharks were often detected simultaneously by the array. The percentage of 15-min periods when more than a single tagged shark was present within the receptive range of the array ranged from 27.0% to 69.4% (mean = 54.3%) of the total number of periods that the array was active. However, the presence of more than one shark at the island is not conclusive proof of sociality.

One might ask whether the sharks tagged at the same kill were present together more often than sharks tagged on different days? The former sharks might be members of a hunting group. In order to examine this possibility, we analyzed the frequencies of detection within the ranges of the three sonobuoys (see area denoted by light stippling in Fig. 1) from 16 to 26 October 1997 (see period indicated by stippling in Fig. 3), when sharks W1–W4 were present at Año Nuevo Island. During this period, shark W1 accompanied sharks W2 and W3 for higher percentages of the time than shark W4 (see second and third bars versus fifth bar in histogram, Fig. 9). Furthermore, sharks W1–W3 were detected together a higher percentage of the time (fourth bar of histogram) than shark W1 was recorded with sharks W2 and W4 (sixth bar) or W3 and W4 (seventh bar). All four sharks were present together only 4.3% of the time (eighth bar).

There was little consistent evidence of sociality when we compared distributions of the "true" to "random" separation distances while the sharks were hunting at the pinniped colony. It is obvious that the sharks did not often swim together while near the island. The median distances separating sharks W1–W5 ranged from 80–420 m (Fig. 10). These values are evident from the lines across the clear bars above shark pairs W1-W2, W2-W3, W3-W4. One would expect shorter separation distances between sharks W1–W3, who were tagged during the same day, than between these same sharks and sharks


37°06.738' N
122°20.226' W
Distance (m)
100
200
300
400
500
600
700
800
900
1000
1100
W1
N = 3,125
W2
N = 1,406
W3
N = 266
W4
N = 747
W5
N = 416
W6
N = 1,052
10 9 8 7 6 5 4 3 2 1 0
Value in Percent

◀

Fig. 8 *C. carcharias*. 3-D contour map formed from a grid of 100 × 100-m cells with the percentages of the total number of positions of sharks W1–W6 within a 1,000 × 1,100-m area west of Año Nuevo Island. *White spheres* Sonobuoys A–C; *contours* 1%

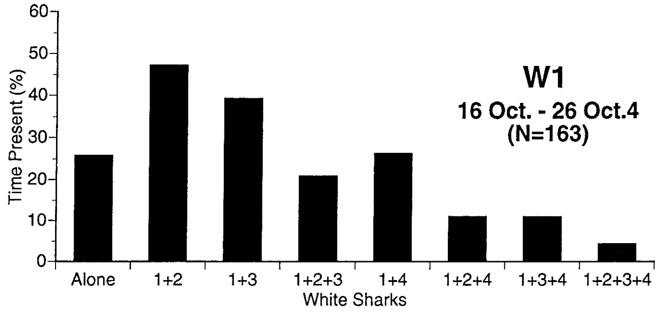


Fig. 9 *C. carcharias*. Percentage of 15-min periods when shark W1 was accompanied by sharks W2–W4 within the range of three sonobuoys from 16 to 26 October 1997

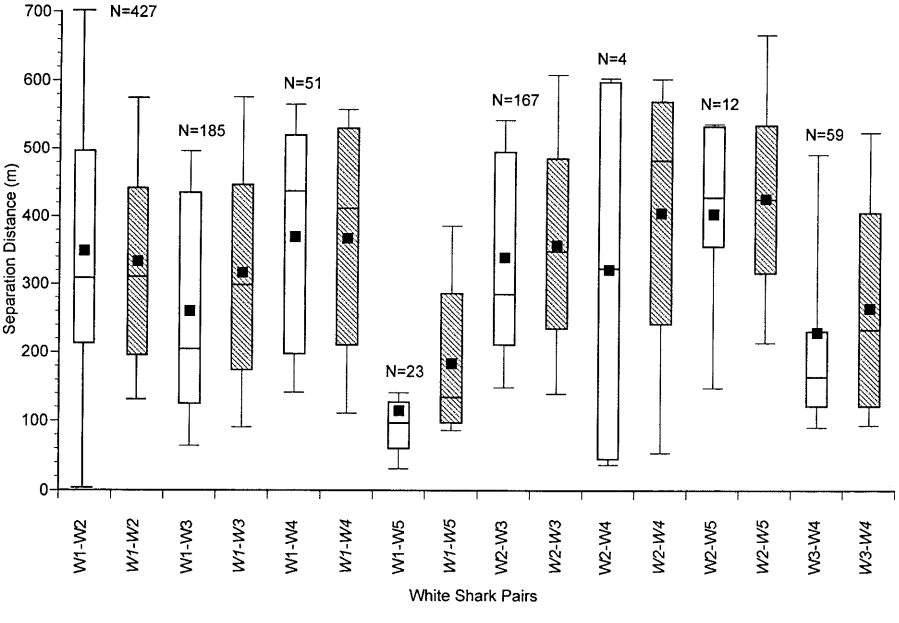
W4 and W5, who were tagged on separate days, if the former moved together as a social unit. Although the median distances between tag-mates W1-W2, W1-W3, and W2-W3 were less than the median separations between non tag-mates W1-W4, W2-W4, and W2-W5, the former tag-mate separations were greater than the median distances between non tag-mates W1-W5 and W3-W4. We can conclude that these five sharks were not hunting as a social group.

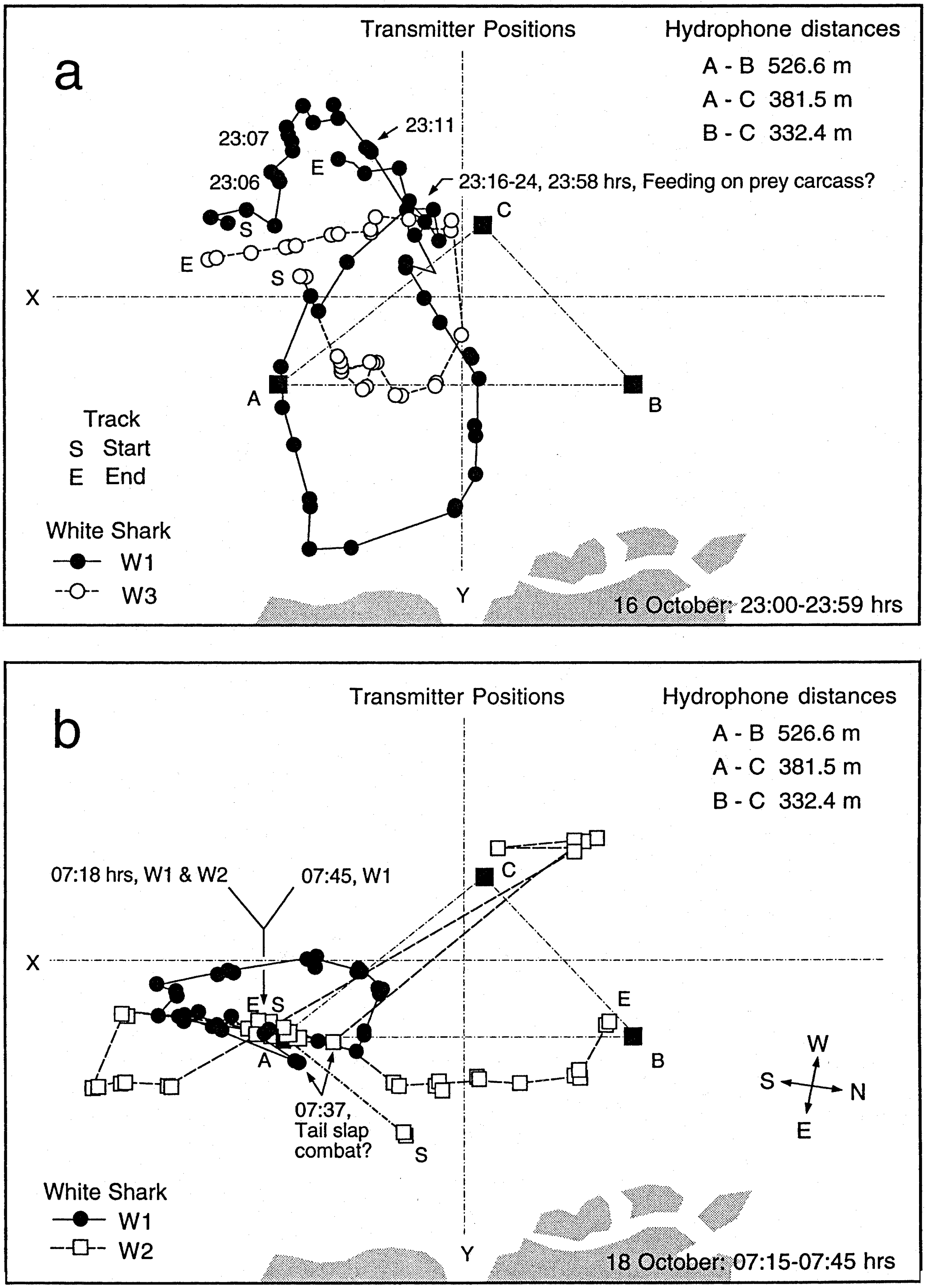
Nor was there a consistent relationship between true (clear bars) and randomized (hatched bars) separation distances between sharks (Fig. 10). If sharks were attracted to each other, the true distances between individuals should be less than the random separation distances; if avoiding each other, the true distances should be greater than the random separation distances. Little difference existed between the median true and random separations between W1-W2 (clear bar) versus *W1-W2* (hatched bar) and W2-W5 versus *W2-W5*. The median true separation distances were less than the randomized distances for W1-W3 versus *W1-W3*, W1-W5 versus *W1-W5*, W2-W3 versus *W2-W3*, W2-W4 and *W2-W4*, W3-W4 versus *W3-W4*, yet the reverse was evident for W1-W4 versus *W1-W4*. It is thus unlikely that the five sharks were either attracted to or avoiding each other during the periods spent near the seal colony. More likely the sharks were searching for prey by themselves, and the others were attracted to the site of the kill once a seal or seal lion was attacked.

Capture of prey

We identified two putative predatory attacks, one during nighttime and another during daytime, on pinnipeds during the 15-day period that the five sharks were monitored by the array during the fall of 1997. On 17 October, shark W1 made two bursts of swimming consistent with its chasing prey. These swimming accelerations are apparent in the separation between three and four points contained in clusters of positions recorded during 12-s monitoring periods at 2306 and 2307 hours (Fig. 11a). The shark then turned and swam slowly in a straight line until 2316 hours. It is possible that the shark's movement may have been slowed by the added burden of carrying the prey in its mouth. Shark W1 then appeared to feed from 2316 to 2324 hours near sonobuoy C (see *tightly clustered* positions). The shark then swam away from this site in a clockwise circular path to a distance of 600 m before returning to the prior site where it remained briefly at 2358 hours. At this time, the shark appeared to feed

Fig. 10 *C. carcharias*. Box diagrams of true (*clear*) and simulated (*hatched*) separation distances between sharks W1–W5 within the receptive field of a sonobuoy array during 13–30 October 1997. *Bottom line* Minimum, *bar bottom* 25th percentile, *within-bar horizontal line* median, *solid square* mean, *bar* top 75th percentile, *top line* maximum




a
Transmitter Positions
Hydrophone distances
A - B 526.6 m
A - C 381.5 m
B - C 332.4 m
23:07
23:11
23:06
E
23:16-24, 23:58 hrs, Feeding on prey carcass?
C
S
E
S
X
A
B
Track
S Start
E End
White Shark
W1
W3
Y
16 October: 23:00-23:59 hrs
b
Transmitter Positions
Hydrophone distances
A - B 526.6 m
A - C 381.5 m
B - C 332.4 m
07:18 hrs, W1 & W2
07:45, W1
C
X
E S
E
A
B
W
S
N
E
07:37,
Tail slap
combat?
S
White Shark
W1
W2
Y
18 October: 07:15-07:45 hrs

◄

Fig. 11a, b *C. carcharias*. Paths of sharks W1 and W3 during a putative predatory attack on a pinniped from 2302 to 0000 hours on 16–17 October 1997 **a** and sharks W1 and W2 during a predatory attack on a pinniped from 0715 to 0745 hours on 18 October 1997 **b**. ● Positions of shark W1; □ positions of shark W2; ◇ positions of shark W3; *solid line* track of shark W1; *dotted line* tracks of shark W2; *dashed line* track of shark W3; *S* start of track, *E* end of track

again (indicated by the clustered positions). An alternative explanation is that the shark took a bite out its prey and left it to become immobile before returning to feed further. This is unlikely because the attacking shark returned to the same location. A crippled pinniped would likely swim some distance from the release site before dying. Shark W3 appeared at 2349 hours at a distance of 200 m from W1, moved within 10 m from shark W1 at 2358 hours, and moved away in a westerly direction. Sharks W1 and W3 may have exchanged aggressive displays directed toward each other at this time, with shark W1, who initially killed the prey, being the loser and thus leaving the area first. It is difficult to infer from a track what actually happened during a kill without additional information such as the temperature of the shark's stomach, an elevation of which would indicate feeding on a warm-bodied seal (as suggested by McCosker 1987).

On 18 October (Fig. 11b), sharks W1 and W2 were first detected near each other at 0718 hours, possibly feeding upon prey. Shark W1 slowly swam away in a westerly direction in a wide curving trajectory before presumably returning again to feed at 0737 hours. At this time, shark W2 arrived from the northwest, turned abruptly, and moved off in a northerly direction. These two sharks may have exchanged aggressive displays at this time with shark W2 being the loser and departing from the area. Shark W1 remained in one place, possibly consuming the rest of the prey.

Monitoring a single shark

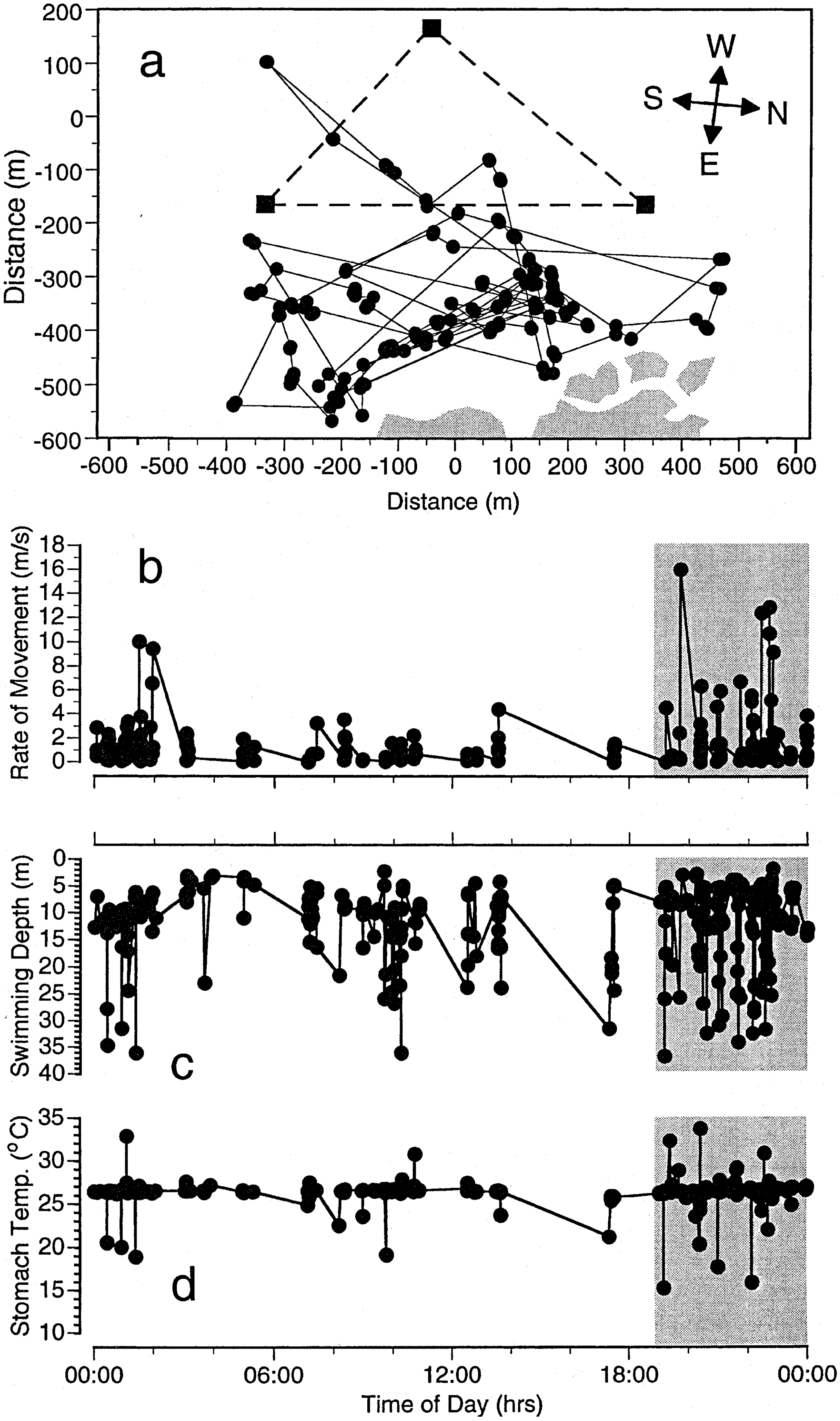
We hoped to detect feeding by shark W6 from a sustained temperature elevation recorded by a transmitter in its stomach. This shark was tracked for 12 days between 22 October and 18 November 1999. This shark was detected by one of the three buoys a mean of 21.6% of the 15-min periods in each day, ranging from 6.3% on 18 November to 55.2% on 2 November. The temperature recorded in the shark's stomach at 0901 hours after it had been fed frozen whale fatty tissue with the transmitter inside was 17.9 °C, and this rose to 24.1 °C by 1900 hours, when the shark could no longer be tracked because one of the sonobuoys broke free. When tracking resumed on 31 October, there was a mean temperature of 26.9 °C in the shark's stomach. From 31 October to 5 November (6 days), the mean daily stomach temperature stayed above 26.1 °C. The shark could not be tracked from 6 to 12 November due to the loss of another sonobuoy. On the following day, the mean stomach temperature was 17.0 °C, and the daily temperature means slowly increased over 5 days to 23.7 °C on 18 November when tracking was discontinued. The mean daily swimming depth of shark W6 was 12.2 m with the daily mean varying from 7.8 m on 5 November to 15.3 m on 3 November.

A day in the life of shark W6

How active is a white shark when patrolling off a seal colony in search of a meal? Let us examine the hunting behavior of shark W6 during a single day, 2 November 1998 (Fig. 12). Shark W6 spent a majority (55.2%) of the 24-h period searching for prey near shore in the high-predation risk zone. The shark repeatedly swam back and forth 200–300 m from shore along a north-south axis, where it was ideally positioned to intercept seals and sea lions departing and returning to the pinniped rookeries (Fig. 12a). During this day, the shark left its "picket line" and made one long excursion away from the island at 1249 hours in a southwestern direction. The shark swam rapidly along a path generally taken by pinnipeds when moving to and from Año Nuevo Island. The shark swam at a peak rate of movement of 4.0 m/s (Fig. 12b) to the surface (c) as if capturing prey, but little change occurred in stomach temperature indicative of feeding success (d).

Another peak in hunting activity occurred between 1900 and 2400 hours as inferred from the variability in rate of movement, swimming depth, and stomach temperature (see stippled area in Fig. 12b–d). During this period, shark W6 displayed two bursts of speed, one at 2102 and another at 2143 hours consistent with active pursuit of prey (see dotted lines in Fig. 13b). The shark swam rapidly toward the surface with a speed of 6 m/s at 2142 hours, where it may have attempted to ambush prey (Fig. 13a). There was a temporary decrease in stomach temperature during this upward movement from a depth of 18 m to 6 m (Fig. 13c). This momentary thermal depression may have been due to cool ambient water entering the stomach and contacting the temperature sensor as the shark opened its mouth briefly. Shark W6 also accelerated with a speed of 7 m/s downward at 2143 hours with no observed change in stomach temperature indicative of feeding success.

We recorded stomach temperatures of shark W6 intermittently for 12 days from 22 October to 18 November 1997 (Fig. 14). The shark swallowed the transmitter, which was wrapped in frozen whale fatty tissue, at 0901 hours and the meat began to thaw slowly as evident from the upward slope of the curve of stomach temperatures (see uppermost left, Fig. 14). The stomach temperatures recorded from 23 October to 6 November were relatively constant, with daily medians varying from 26.9 °C on 31 October to 25.8 °C on 6 November, when monitoring ceased for a period of


a
W
S
N
E
Distance (m)
200
100
0
-100
-200
-300
-400
-500
-600
-600 -500 -400 -300 -200 -100 0 100 200 300 400 500 600
Distance (m)
b
Rate of Movement (m/s)
18
16
14
12
10
8
6
4
2
0
c
Swimming Depth (m)
0
5
10
15
20
25
30
35
40
d
Stomach Temp. (°C)
35
30
25
20
15
10
00:00
06:00
12:00
18:00
00:00
Time of Day (hrs)

◀

Fig. 12a–d *C. carcharias*. Path of shark W6 on 2 November 1998 **a** with plots showing rate of movement **b**, swimming depth **c**, and stomach temperature **d**. Rates of movement calculated for all intervals between position determinations. Intervals of 2–3 s within recording bouts of a 12-s duration often result in exaggerated rates. Note swimming movements back and forth in front of the island with a single excursion away from the island possibly to chase a pinniped. ■ RAP sonobuoys; ○ positions of shark W6

6 days due to the loss of a RAP buoy. Only rarely did the shark's stomach warm to 37.0 °C, the temperature of a freshly killed pinniped, and in these cases the warming of the stomach was temporary (one to two measurements) unlike the prolonged temperature elevation expected if the shark were to ingest a freshly killed seal or sea lion. Temporary decreases in temperature occurred, but these were also always short-lived. On 13 November, when monitoring of shark W6 was renewed, the majority of the few temperatures measured were similar to those recorded earlier except for two unusually low temperature measurements recorded at 0230 hours. In contrast, on 15 October the median temperature was 19.8 °C, well below the median daily temperatures recorded earlier for shark W6. The median increased to 20.5 °C on the next day and 23.6 °C on the following day. We do not know whether this slow increase in temperature was a response to the cooling of the stomach by feeding on cold-bodied fish or scavenging on marine mammal carrion. In conclusion, there was little strong evidence that shark W6 fed during the 12 days of intermittent monitoring by the RAP system.

Discussion

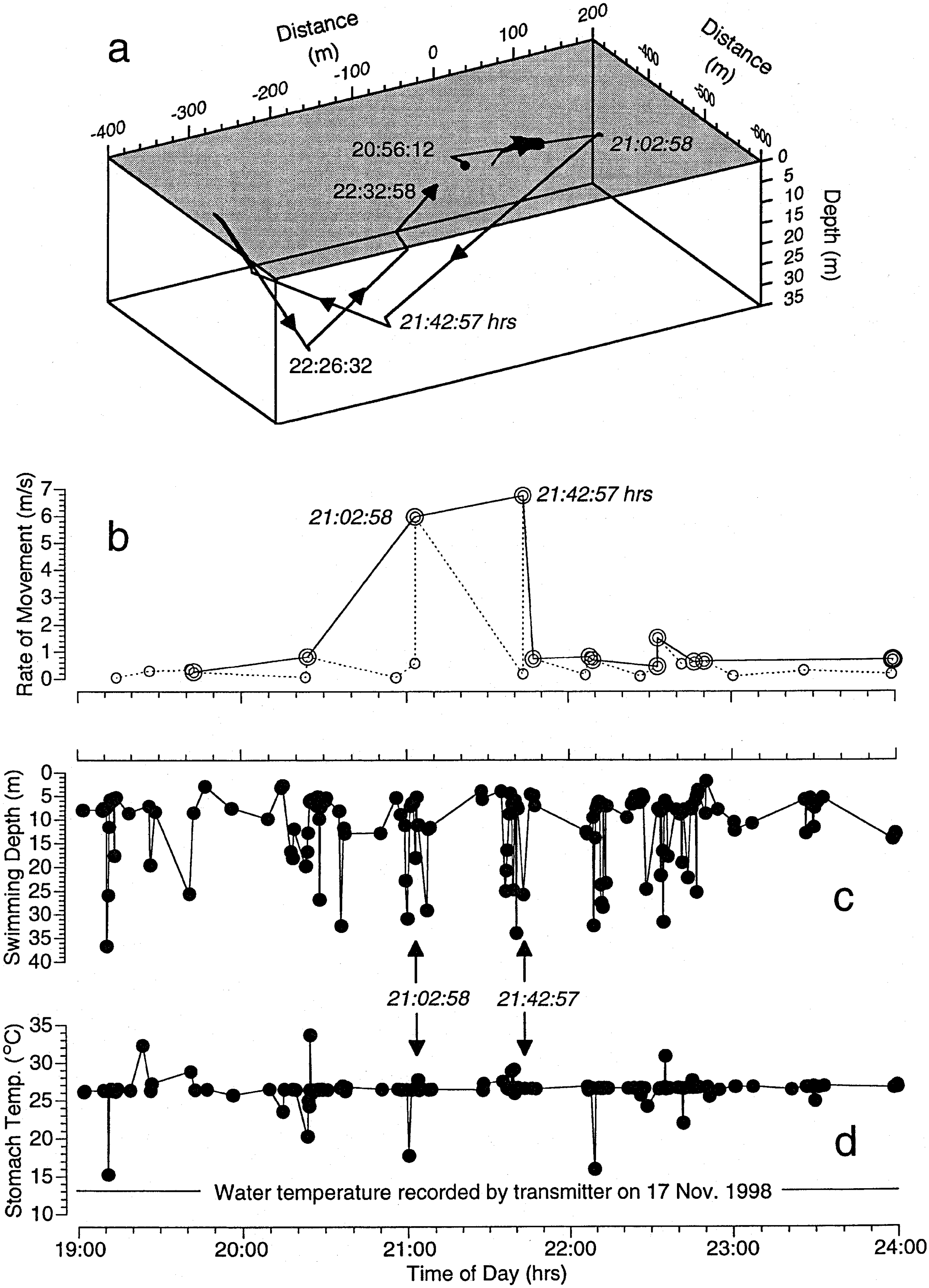
Temporal and spatial distribution

We tagged and tracked adult white sharks during the fall near the pinniped colony at Año Nuevo Island. White sharks are attracted during this season to northern elephant seal colonies in Central California. Shark-bitten seals are most commonly observed during the fall and winter at Año Nuevo Island (Le Boeuf et al. 1982; Le Boeuf and Crocker 1996). Shark kills on seals (Ainley et al. 1981; Klimley et al. 1992; Klimley et al. 1996a) and sharks attacking decoys tethered to shore (Anderson et al. 1996; Klimley and Anderson 1996) are most frequently observed in the fall at the Farallon Islands. At this time, 1- to 4-year-old elephant seals are most common at these two islands (Ainley et al. 1981; Le Boeuf and Laws 1994). Shark predation on these juveniles is evident based on the sizes of victims determined by photogrammetry after the initial strike and prior to consumption. Length of prey varied from 1.4 to 1.7 m (mean = 1.6 m) (A. P. Klimley, unpublished data) with a corresponding age of 1–2 years (Webb et al. 1998). The highest mortality rate, 54%, is for yearlings, which do not survive the first foraging trip to sea which lasts from April to September (Le Boeuf et al. 1994). Although unknown for returning young of the year, the fat content of weanling seals first going to sea is 48% of the total body weight (Kretzmann et al. 1993). These seals, presumably still high in nutritional value, are inexperienced when they first return to the island, and may behave in a manner that makes them more vulnerable to predation.

The density of these returning juvenile seals is highest in this elevated predation-risk zone where they converge on the beaches. More than 80% of the attacks documented during organized watches at the South Farallon Islands occurred in a shallow zone < 36.6 m deep extending from 25 to 450 m from shore (Klimley et al. 1992). The maximum distance at which an attack was observed was 1.3 km from the rookery. This coastal preference is characteristic of the predator: all but five of 109 white sharks caught off the western coast of North America were in waters < 80 m deep, with a median depth of 20.6 m (Klimley 1985). Within this zone, attacks are most common adjacent to beaches and rocky shores where seals and sea lions concentrate. At coastal entry and departure points, the sharks may have a greater chance of ambushing seals (Klimley et al. 1992; Klimley 1994). Attack frequency goes up during high tide when juvenile elephant seals, resting on land, are forced to enter the water (Anderson et al. 1996). The sharks tracked during this study predictably spent periods reaching 77% of the 24-h day in the receptive zone of the RAP array that extended roughly 1,000 m from shore. Here the sharks would have the greatest chance of capturing prey. The area patrolled by the sharks was similar in size to the < 1,300-m zone in which predatory attacks were observed at the South Farallon Islands (Klimley et al. 1992).

Sharks W1–W5 were detected searching for prey in this zone at Año Nuevo Island for periods ranging from 5 to 15 days during October 1997. The sharks may have stayed at the elephant seal colony longer, but the sonobuoys had to be removed on 30 October due to impending high seas. Shark W6 was detected within the reception area during 12 days over a period of 25 days during October and November 1998. These periods of residence were similar to those of white sharks tracked by boat at the South Farallon Islands (Goldman et al. 1996; Goldman 1997; Goldman and Anderson 1999).

The white sharks patrolled the pinniped colony at Año Nuevo Islands all hours of the 24-h cycle. The possession of an area centralis in the retina with cone photorecepters indicates that the species has color vision (Gruber and Cohen 1985), consistent with a habit of daytime predation. Thus, white sharks were observed to feed upon seals and sea lions during daylight at the South Farallon Islands (Ainley et al. 1981; Klimley et al. 1992). However, there was little chance of detecting nocturnal feeding during these studies due to the absence of a nighttime watch. The RAP system was able


a
Distance (m)
-400
-300
-200
-100
0
100
200
Distance (m)
-400
-500
-600
Depth (m)
0
5
10
15
20
25
30
35
20:56:12
21:02:58
22:32:58
21:42:57 hrs
22:26:32
b
Rate of Movement (m/s)
0
1
2
3
4
5
6
7
21:02:58
21:42:57 hrs
c
Swimming Depth (m)
0
5
10
15
20
25
30
35
40
21:02:58
21:42:57
d
Stomach Temp. (°C)
10
15
20
25
30
35
Water temperature recorded by transmitter on 17 Nov. 1998
19:00
20:00
21:00
22:00
23:00
24:00
Time of Day (hrs)

◄

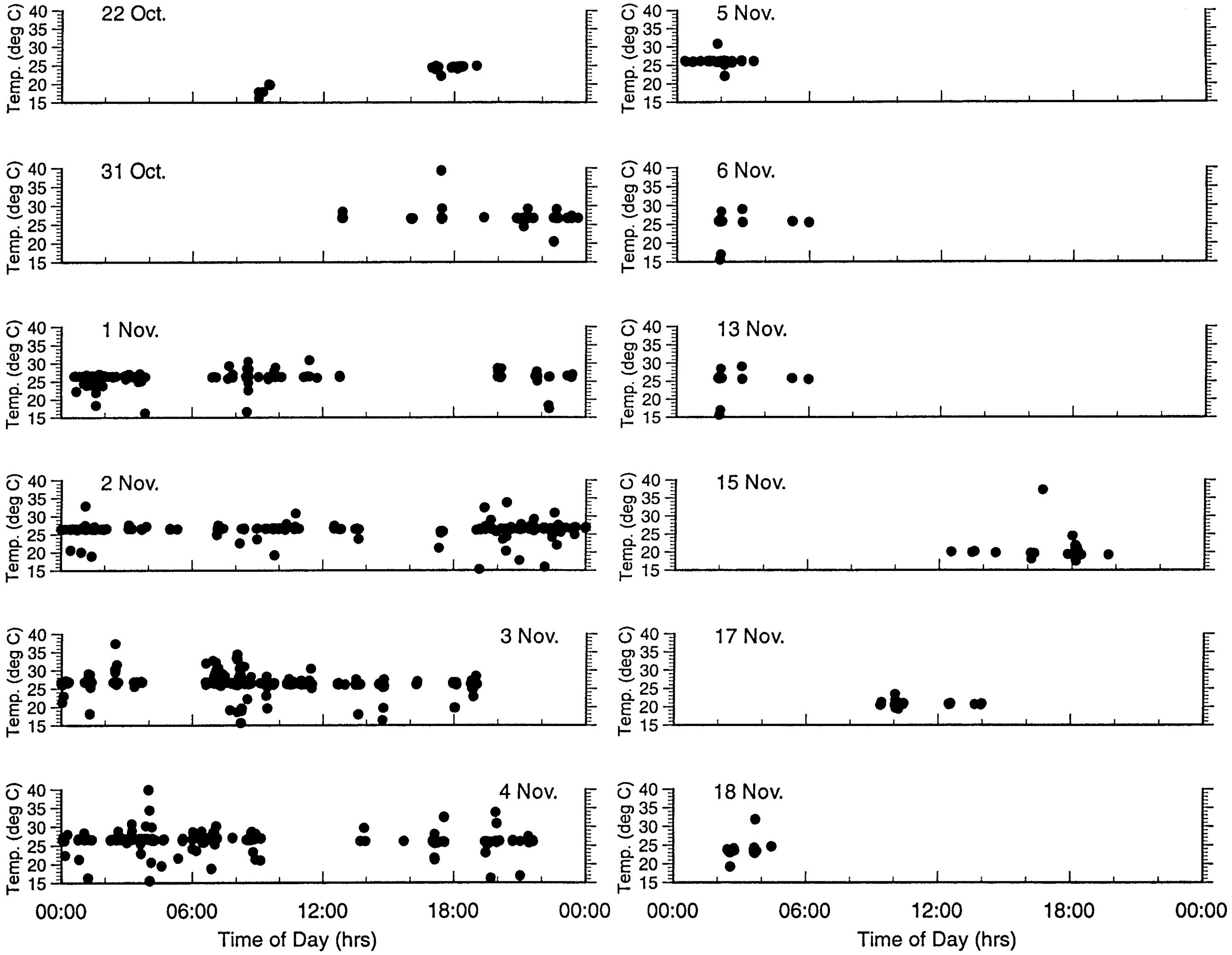
Fig. 13a–d *C. carcharias.* 3-D track **a** of shark W6 on 2 November 1998 showing rise to the surface at 21: 02: 58 hours and a dive to the bottom at 21: 42: 57 hours. Rates of movement **b**, swimming depths **c**, and stomach temperatures **d** of W6 from 1900 to 0000 hours. *Solid lines* in **b** denote "filtered" rates of movement with intervals ≥1 min (primary filter-criterion); *dotted lines* in **b** indicate rates of movement with intervals ≥1 min and ≤5 min (secondary filter-criterion); for discussion of two sampling schemes, see Fig. 7 and Klimley et al. (2000)

to detect sharks when they swam near the island during both day and night. The five white sharks tracked during the fall of 1997 and one shark tracked during the fall of 1998 remained near the island equal amounts of time during day and night. We also detected a pattern of movement indicative of a predatory attack during nighttime on 16 October 1997. This indirect evidence of nocturnal feeding is in contradiction with the lower rate of white shark attraction observed at night when chumming near sea lion colonies in South Australia (Strong et al. 1992).

Absence of social affiliation

We did not find that the five sharks traveled as a group near the island. Sharks W1–W5 were infrequently < 100 m from each other. Only rarely did the sharks actually approach each other. This occurred only during what were interpreted as predatory attacks based upon prior observations of the behavior of both predator and prey during such attacks (Klimley et al. 1996a). Shark W1 appeared to chase a pinniped at 2306 to 2307 hours, move it to a position near sonobuoy C at 2311 hours, and feed on the carcass at 2316–2400 hours and 1358 hours on 16 October 1997. Shark W3 briefly moved near the apparent site of the carcass before quickly departing as shark W1 returned to feed at 2358 hours. Sharks W1 and W2 were first detected at 0718 hours on 18 October lingering near each other at

Fig. 14 *C. carcharias.* Stomach temperatures of shark W6 during a 12-day period from 22 October to 18 November 1998. Note the absence of prolonged elevations or drops in thermal record, indicative of swallowing a warm-bodied pinniped or cold-bodied fish



sonobuoy A where they may have been feeding on the same carcass. Both sharks then left the location of the carcass, with shark W1 returning before shark W3. The latter shark then returned, but suddenly reversed its direction and hastily departed as though discouraged from further feeding by shark W1. The behavior of these sharks during these putative predatory attacks was more consistent with a second shark being attracted to the carcass of a seal after its being captured, killed, and partially eaten by the first shark. The rapid departure of shark W1 from W3 (Fig. 11a) and shark W2 from W1 (Fig. 11b) at the site of the kill was consistent with withdrawal in response to a tail slap display (see Klimley et al. 1996b).

The avoidance behavior recorded during putative kills on seals was consistent with the behavior of white sharks at whale carcasses. No more than two white sharks were ever seen at the same time near a dead fin whale during a 30-h period on 28–29 June 1997 off Long Island, New York when the whale was intermittently visited by as many as nine white sharks (Pratt et al. 1982). On one occasion, a 3- to 4-m-TL white shark with a tooth slash over the gills approached the whale, quickly changed direction, and left without feeding. This may have been an evasive action because a few seconds later, a much larger shark, 5–6 m TL, appeared in the same place and began to feed on the same part of the fin whale. Many of the sharks that visited this whale had either fresh or healed tooth slashes on their flanks, between the gills and the caudal peduncle. These scars were not the result of mating as reported for other sharks (Stevens 1974; Pratt 1979; Klimley 1980) because they occurred on males and immature females. These wounds were most likely inflicted by other white sharks while competing for the same prey. Two white sharks of similar size (3–4 m TL), tagged with ultrasonic beacons at the Neptune Islands in South Australia, were repeatedly attracted over a period of 12 h using ground fish and blood to a boat with an attached listening device (A. P. Klimley, unpublished data). Competition was evident among the two sharks as only one approached the boat at a time and was detected by the listening device.

We found no obvious association existed between the five adult white sharks that were continuously tracked close to Año Nuevo Island during the 18-day period of the study. The propensity for juveniles of the species to be rarely captured, but when captured, in large numbers at once, is consistent with their associating in schools. Seven white sharks ranging from 163 to 200 cm TL were caught close to shore near La Jolla, California, during a 14-day period between 30 October and 12 November 1955 (Klimley 1985). Three of these sharks were identical in size, 163 cm TL, and this is consistent with their being from the same year class. Individuals of this size would be 9 months old [see Von Bertalanffy growth curve, $n = 20$ sharks, Cailliet et al. (1985)]. The size at birth of white sharks ranges 120–150 cm TL (Francis 1996); the maximum litter size is 14 (Francis 1996). The similarity in the size of captured individuals, the short period over which they were caught, and the similarity of the catch to litter sizes leads one to wonder whether juveniles related by birth might school together. This might explain why ten juveniles of two size classes were caught on a single long line of 32 hooks set 1 km off Sandy Hook, New Jersey in August 1964 (Casey and Pratt 1985). If this were so, it would be worthwhile to determine the age at which sharks stop schooling and become solitary individuals.

Predatory strategy

Although sharks W1–W7 were often within the high-risk zone, we recorded a paucity of evidence of feeding, suggesting that individuals exert much effort searching before they succeed in catching prey. During the 58 days of shark monitoring (i.e., 15 days for W1, 15 for W2, etc.) during the fall of 1997, only sharks W1 and W3 appeared to feed during nighttime on 16 October 1997 and shark W1 during daytime on 18 October 1997. We recorded no elevations in stomach temperature indicative of feeding by shark W6 during the 12 days that it was monitored during the fall of 1998. No evidence of burst swimming indicative of chasing prey was found during the three nighttime periods that shark W7 was monitored during the fall of 1999. It appears that individuals must expend much time and energy patrolling near shore at a pinniped colony in order to catch prey.

If it is so difficult to capture prey, one potential feeding strategy would be to remain relatively close to each other so that, if one shark catches prey, the others can scavenge on it. Carey et al. (1982) suggested that a 4.6-m-TL white shark could survive 1.5 months between successive meals. He estimated the shark's metabolic demand during this period based on the change in muscle temperature as the shark passed through water masses of different temperatures and its metabolic supply from the energetic value of a 30-kg portion of whale fat found in the stomach of a captured shark. Each juvenile elephant seal actually contains more energy than required for short-term sustenance of a single shark. For example, a 1.4-year-old, 1.6-m-long elephant seal juvenile (of the size measured by A. P. Klimley during predatory attacks) would have a body mass of ~140 kg (Webb et al. 1998). Given a fat content of 48%, the individual would have 67.2 kg of fatty tissue, which would provide twice the energy necessary to sustain a white shark for 1.5 months according to the metabolic model. A single seal could provide a second shark with sufficient food for it to last 1.5 months before feeding again. Thus, it is not surprising that the sharks tracked during this study did not remain far from each other. Their close proximity would permit them to compete for a share of the carcass after capture by another shark.

In conclusion, during the period when five white sharks were simultaneously tracked off of Año Nuevo Island, there were only two instances of apparent feeding. In each of these cases, one shark was observed behaving in a manner highly suggestive of a successful predation (repeatedly returning to and lingering in one specific location at surface). Also, in both cases, additional tagged sharks were observed to orient towards, and approach to within 10 m of, the feeding shark before eventually yielding and leaving the scene. Additionally, Klimley et al. (1996b) reported that in 16 out of 129 visually monitored feeding bouts, other sharks approached the successful hunter, which responded with vigorous tail-slapping displays. The repeated, timely appearance of other sharks shortly after a successful predation suggests that these animals are "eavesdropping."

White sharks appear to be solitary hunters and not to exhibit a cooperative feeding strategy. However, like most shark species, they possess sensory receptors that enable them to detect ("eavesdrop"), either by mechanoreception or chemoreception, when another shark has made a successful kill. They can thus exploit this infrequent, but important occurrence by competing with the successful hunter for the rest of the prey, thus increasing their feeding rate relative to that when foraging away from other sharks.

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