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Radio-acoustic positioning as a tool for studying site-specific behavior of the white shark and other large marine species

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Abstract We describe a method, radio-acoustic-positioning (RAP), for continuously monitoring the movements and behavior of large marine animals. An ultrasonic transmitter on the animal can be localized with high spatial accuracy (2 to 10 m) within an area of 1 km^2, based on when the same pulse arrives at three hydrophones on sonobuoys aligned in a triangular array. Radio transceivers communicate with the base station, where the x and y coordinates of the subject are calculated using hyperbolic equations. The base station plots the individual's position and displays information from the tag's sensors in real time on a computer monitor before saving the data on a disk. The base station must be situated either on land or on a vessel within the reception range of the three buoys. We used a RAP system to monitor the movements and behavior of white sharks (*Carcharodon carcharias*) near the elephant seal rookery at Año Nuevo Island in central California. This type of system is an ideal tool to study the predatory behavior of the white shark because individuals patrol for seal prey within a zone < 1300 m from shore. We describe the operation of the system, including acoustic triangulation, range of detection and positioning, data acquisition and analysis, and positional accuracy. We illustrate the implementation of the method and its advantages and disadvantages by describing an ongoing study of white shark hunting-behavior. Sample data from this study are presented to illustrate specific points. We describe the movements of five sharks within the receiving range and their behavior relative to each other. The RAP system is compared to other complementary tracking methods. We conclude that this system has great potential for monitoring the movements and behavior of large marine animals within a relatively small zone, where feeding or reproduction takes place.

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Introduction

Our understanding of the movements and behavior of animals in the marine environment is very limited relative to the terrestrial environment. Individuals are difficult to observe in the sea because visibility at best resembles that of a moderate fog on land. Furthermore, these species live in an environment to which we are ill adapted. We usually must travel by boat to a locality to study them, enter the water with a self-contained supply of air, and can remain under water only for so long as we do not lose excess heat. Hence, there has been a strong impetus to develop methods of remotely sensing the movements and behavior of the marine species. This development has been facilitated by the advent of microelectronics and computer technology.

Various methods have been developed over the last three decades to study large marine animals. Each technique yields answers to a specific set of questions. One method is to place an electronic tag on an individual that propagates an ultrasonic signal above the species' hearing range. The animal can then be localized with a directional receiver and followed in a ship while recording information from the tag's sensors. The path of the animal is approximated by "way-points" in the course of the vessel. This technique provides tracks of fishes with a spatial error of ≤100 m during time periods of ≤10 d and over distances of ≤100 km. This methodology has often been used to describe the short-term movements of many marine fishes. Examples include the blue shark (Sciarotta and Nelson 1977; Carey and Scharold 1990), marlin (Holland et al. 1990a; Block et al. 1992; Brill et al. 1993), yellowfin tuna (Holland et al. 1990b; Block et al. 1997; Brill et al. 1999), and white shark (Carey et al. 1982; Goldman et al. 1995). Sensors on these tags have recorded directional headings (Greer Walker et al. 1978; Klimley 1993), speeds (Sciarotta and Nelson 1977), and depths (see references above).

Another tracking method is to place an "archival" tag on an individual that determines geographic positions from a property of the environment unique to the subject's present location and stores these "geolocations" in memory. These can be retrieved from the tag when the fish is captured again. These tags estimate the subject's geographical coordinates based on (1) the increase in subsurface irradiance at dawn and the decrease during dusk (Hill 1994; Klimley et al. 1994), (2) the known depth of a bottom-swimming individual at a particular time and the distribution of the depths known from tidal records for the area (Metcalfe and Arnold 1997), or (3) the latitudinal distribution of surface temperatures at the animal's longitude derived from light measurements (Smith and Goodman 1986). These archival tags also store information on the behavior of individuals. They provide a track of an animal with a higher spatial error than ultrasonic tracking (< 100 km), but record positions during longer periods (< 1 to 3 yr) and over greater distances (< 10 000 km). These are now used only to track fishes with a high rate of recapture such as southern bluefin tuna (J. Gunn personal communication), but will be applied to more species once the tags are capable of releasing from the animal at a preset time, floating to the surface, and sending their stored positions via a satellite link to a coastal receiving station (R. Hill personal communication). Archival tags have also been used extensively on pinnipeds, because these return to colonies on land where the tags can be easily retrieved and interrogated (DeLong et al. 1992; Le Boeuf et al. 1993). More accurate position-determinations can be obtained by pairing a data-storage tag with a radio beacon that can be localized by the ARGOS satellite. The accuracy of these positions is ± 1 km, but they can be obtained only during those times when the individual is both at the surface and the satellite is overhead. The latter technique has been used successfully to track seals (Fancy et al. 1988; McConnell et al. 1992; McConnell and Fedak 1996), walruses (Born and Knutsen 1997), and whales (Dietz and Heide Jorgensen 1995). However, these methods are of little use in monitoring microscale movements and behavior of animals in a limited area on the order of 1 km^2, the spatial scale of which feeding and reproductive behavior often occur in large marine animals.

A third method is to localize a transmitter based on when the same pulse arrives at three stationary hydrophones aligned in a triangular array. The transducers first used in such a tracking system were mounted on the sea floor with cables leading to shore; the time delay between the arrival of the same pulse at each hydrophone pair was determined with an oscilloscope (Hawkins et al. 1974). The x and y coordinates of the codfish tracked by Hawkins et al. were then determined with a calculator using hyperbolic equations. The use of a microcomputer improved this method of tracking (Hawkins et al. 1980; McKibben and Nelson 1981). The computer performed the routine and tedious tasks of (1) timing the arrival of the pulses at the buoys, (2) establishing the delay between the arrival of the same pulse at the pairs of buoys, and (3) solving sets of hyperbolic equations to establish the coordinates of the tagged individual. Furthermore, the track of the individual could be instantaneously displayed on the computer monitor or an $X–Y$ plotter. This type of system was used to track the movements of rocky intertidal fish (Ralston and Horn 1986). The next advance in this tracking technology was the development of radio-acoustic positioning (RAP) buoys linked to a base station (O'Dor et al. 1989; Bjordal et al. 1993). Each RAP buoy consists of a hydrophone and receiver for detecting ultrasonic pulses and a radio transceiver and antenna for simultaneously sending tone bursts to the base station. This system comprises a microcomputer interfaced with a timing module and transceiver. The base station decodes the signals from the RAP buoys and plots the individual's position and displays behavioral and environmental information on a computer monitor before saving the data on a disk. The base station is situated either on land or on a vessel within the reception range of the three buoys. The size of an RAP array and its underwater detection range depends on the frequency and power of the transmitter's signal (Klimley et al. 1998).

Herein we describe a RAP system that can localize marine animals with high spatial accuracy (2 to 10 m) within an area of 1 km^2, based on when the same pulse arrives at three hydrophones on sonobuoys aligned in a triangular array. Radio transceivers communicate with the base station, where the x and y coordinates of the subject are calculated using hyperbolic equations (O'Dor et al. 1989). The base station plots the individual's position and displays information from the tag's sensors in real time on a computer monitor before saving the data on a disk. The base station is situated either on land or on a vessel within the reception range of the three buoys. We used a RAP system to monitor continuously the movements and behavior of white sharks (*Carcharodon carcharias*) near the elephant seal rookery at Año Nuevo Island in central California. The predatory behavior of the white shark is ideal for study with this type of system because the sharks search for seal prey within a predictable zone, < 1300 m from shore (Klimley et al. 1992). Specifically, we describe the operation of the system. We illustrate the implementation of the method and its advantages and disadvantages by describing an ongoing study of white shark hunting-behavior. We present sample data from this study to illustrate specific points.

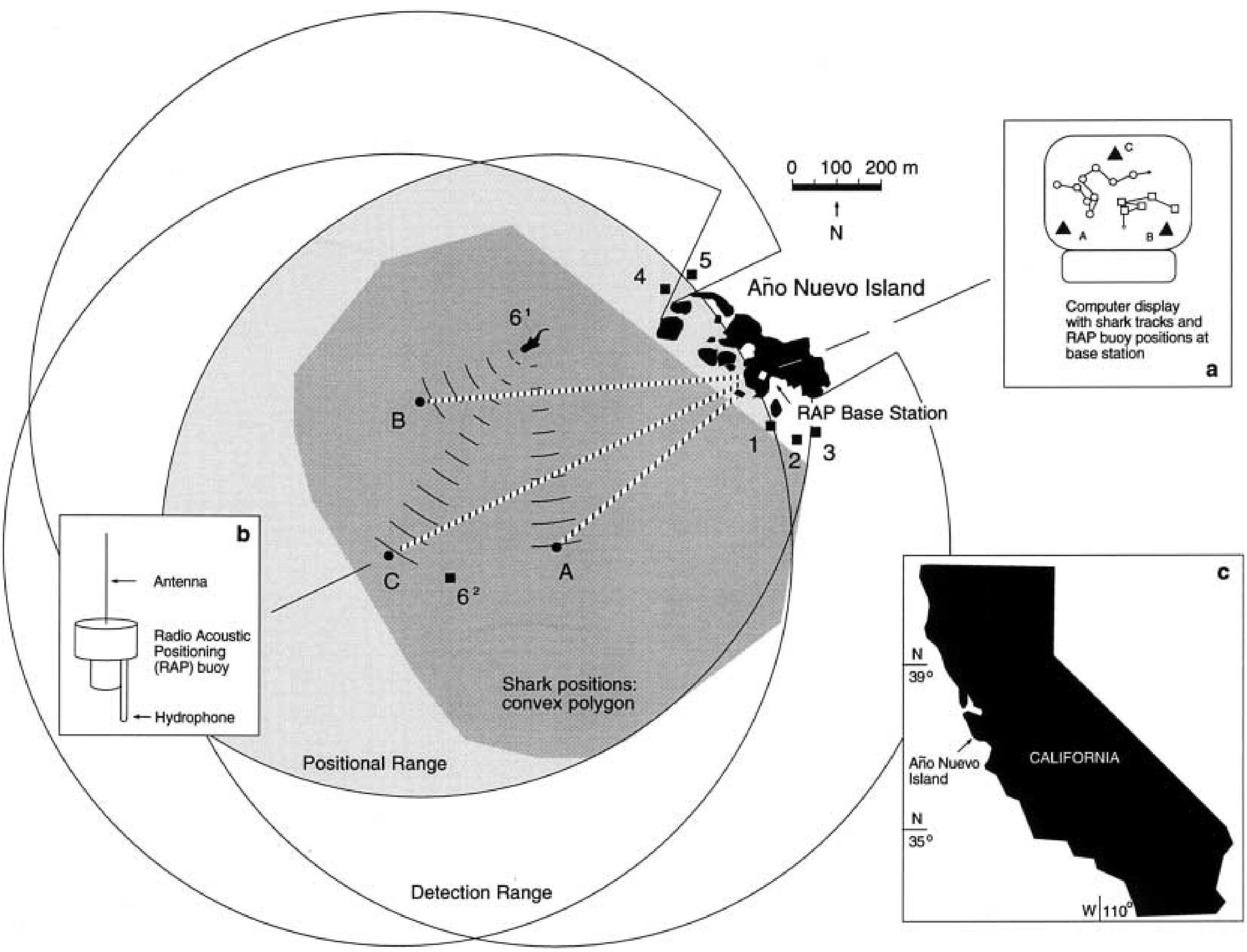


Fig. 1 Map of Año Nuevo Island, Central California (**c**), with three sonobuoys and base station of radio-acoustic positioning system (RAP). The beacon on the white shark emits an ultrasonic pulse that is detected by hydrophones on three sonobuoys (**b**) that send information by a radio transceiver to a shore–based receiving station, where the shark's position is displayed on a computer monitor (**a**) and stored on disk. (● Sonobuoys A–C; ■ locations where Sharks 1–6 were tagged; *circles* tag detection range of sonobuoys; *light stippling* area in which positions could be recorded; *dark stippling* convex polygon indicating home range of five sharks tracked during October and November 1997)

Materials and methods

Study site

An array of radio-acoustic positioning (RAP) buoys (VEMCO Ltd., Halifax, Canada) was moored 600 m southwest of Año Nuevo Island, central California, during October and November in 1997 and 1998 (Fig. 1). This island is located 1800 m from shore at the northern edge of Monterey Bay (Fig. 1c). White shark (*Carcharodon carcharias*) predation on elephant seals of all ages at Año Nuevo has been estimated at 3 to 17 seals per year (Le Boeuf et al. 1982; Le Boeuf and Crocker 1996). The array was anchored on the western side of the island beyond the surf zone, where white sharks had been seen from small boats during fall and winter in previous years. Location of the array was also influenced by observations at the South Farallon Islands of white sharks feeding on seals within a zone ≤1300 from shore, the "high risk" zone (Klimley et al. 1992).

Electronic tags and subjects

Two types of ultrasonic tags were placed on white sharks: beacons and telemetry transmitters (Table 1). The RAP determined the positions for shark tagged with beacons. The transmitters provided positions as well as records of the shark's stomach temperature and swimming depth. The beacons (VEMCO Ltd., V22), cylindrical, 4.8 cm in diameter, and 24.0 cm in length, emitted a 10 ms pulse every 1500 ms. The transmitters (VEMCO Ltd., V22TP), cylindrical, 4.0 cm in diameter and 20.0 cm in length, produced pulses of the same duration at intervals that varied proportionally to the temperature of the stomach and swimming depth. The frequencies of the tags ranged from 40 to 52 kHz, and were separated by 2 kHz intervals in order to prevent the RAP buoys from falsely mistaking one tag's signal for that of the tag with the next nearest frequency. This "aliasing" was most likely to occur when the ambient noise level was low, receiver amplification high, and the tag with the adjacent frequency was close to the hydrophone of a particular buoy. The tags had a theoretical longevity of 230 d, with a signal strength of 153 dB re 1 μPascal at a distance of 1 m from the source.

Six white sharks were tagged with either ultrasonic beacons or transmitters during the study. Each shark was lured to the surface with a seal-shaped decoy made of plywood and 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

Table 1 *Carcharodon carcharias*. Estimatad length and sex of sharks, date and time of tagging, and time period during which 6 white sharks were detected with radio-acoustic positioning system at Año Nuevo Island, central California, USA (*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; *Depth–temp* telemetry transmitters providing positions and measurements of shark's swimming depth and stomach temperature)

Shark			Tagging information					
Identity	Est length (m)	Sex (M/F)	Date	Tim of day (hrs)	Interval (d)	Presence (d)	Transmitter type	Frequency (kHz)
W1	5.2	M	13 Oct. 1997	15:40	18	15	Beacon	40
W2	5.2	F	13 Oct. 1997	16:30	18	15	Beacon	44
W3	4.5		13 Oct. 1997	17:00	18	15	Beacon	48
W4	4.7	F	16 Oct. 1997	14:05	11	8	Beacon	52
W5	4.5	F	26 Oct. 1997	12:00	5	5	Beacon	42
W6	5.5	F	22 Oct. 1998	09:01	< 25	12	Depth–temp	40
			22 Oct. 1998	10:48	28	2	Depth–temp	44

followed the decoy to our vessel. A seal weanling, which had died naturally during the previous winter and been 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. First, the transmitter was mounted on the end of a pole spear with a tether leading 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 in 1997. 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 place a transmitter with a swimming depth and stomach temperature sensor on one shark during the fall of 1998.

The distance at which tags could be detected by a RAP buoy depended on the frequency of their signal and the level of ambient noise. Our 40 kHz beacon had a theoretical detection range of 2110 m in a Beaufort Wind Force (WF) of 1 (=0.01 m wave height), 1410 m in a WF of 3 (=0.6 m), and 990 m in a WF of 6 (=3.0 m). Our 52 kHz tag had a range of 1750 m in a WF of 1, 1220 m in a WF of 3, and 910 m in a WF of 6. The three circular changes in Fig. 1 depict the maximum distances at which Sonobuoys A–C were capable of detecting a shark with a tag emitting a signal of 40 kHz during a WF of 3. This was the most prevalent WF at Año Nuevo Island during the fall season. In contrast, the shark could be tracked only where the tag's signal was detected by all three sonobuoys (lightly stippled areas in Fig. 1 where the circular ranges of the three buoys overlap).

Automated tracking system

Operation

The VEMCO RAP system uses the same hyperbolic navigation principle used by ocean vessels and airplanes to determine their geographic coordinates from the delay in the reception of radio pulses emitted from stationary beacons. However, for underwater tracking, ultrasonic pulses are emitted by a transmitter attached to an animal and detected by three hydrophones and receivers on buoys moored at known locations (Figs. 1, 2):

First, the relative positions of the three sonobuoys are established within an x, y coordinate system with its origin centered within the triangular buoy array. The base station updates the buoys' clocks and instructs them to determine their relative positions. The beacon on RAP Buoy A transmits a 34.0 kHz pulse, with RAP Buoys B and C listening for the pulse. Then, Buoy B transmits and Buoys A and C receive. Finally, Buoy C transmits and Buoys A and B receive the pulse. The spacing is determined by multiplying the speed of sound underwater by the time taken for the signals to reach the other sonobuoys. The speed of sound in seawater can be determined by the following equation (Anonyme 1968): $C = 1410 + (4.21T - 0.037T^2) + 1.10S + 0.018D$, where C = speed of sound (m/s), T = temperature (°C), S = salinity (‰), and D = depth (m). The user can specify the interval between successive buoy position-determinations. These are stored along with the positions of the tracked individuals in a file on the microcomputer (Columns 2,3, and 4: Table 2).

Second, the position of a tagged individual is determined in the following manner: each pulse from the transmitter on the fish propagates through the water at a known speed, with the time of arrival at each hydrophone being dependent upon the distance between the fish and each hydrophone. The base station updates the clocks of the buoys and instructs them to record the times of pulse arrivals over a specified interval. At the end of this period, the base station receives a radio packet from each RAP buoy comprised of its identity, clock time, and the measured pulse-arrival times. All three sonobuoys must receive pulses for the base station to calculate a position. The number of pulses received at the buoys depends on the user-set duration of the period that RAP listens for each transmitter frequency. A sorting algorithm determines when the same pulses arrive at each of the three sonobuoys. This process is termed "alignment." The base station then establishes the delay between when the pulse arrives at the nearest buoy (t_0) and the two more distant buoys (t_1 and t_2). Two independent time intervals ($t_1 - t_0$, $t_2 - t_0$) are needed together with the locations of the sonobuoys and speed of sound to calculate the position of the transmitter. The locus of points for each of these intervals is a hyperbola, its foci being the locations of the two sonobuoys. The two time delays define two hyperbolic functions that intersect at the position of the individual. [See O'Dor et al. (1989) and Lagardère et al. (1990) for the algorithms used to determine the position of the sound source.]

The RAP system produces an accurate position only when the pulse propagated from the transmitter directly reaches each of the three sonobuoys. An aberrant position results when the pulse reflects off the sea floor or surface and indirectly reaches one or more of the sonobuoys. The signal is more likely to travel by multiple paths when the tagged individual swims near the surface or bottom. The longer period of time taken to travel over the greater distance increases the delay between when this pulse arrives at one buoy versus another buoy and results in a position that appears to be more distant from the two buoys. These spurious positions can be avoided by excluding sets of positions with a high spatial variance. The VEMCO radio-acoustic system calculates a standard deviation for each set of positions when tuned to the frequency of each transmitter. The field record can be played back saving only those positions with standard deviations lower than a chosen threshold value in the resulting file. A challenge to using this system effectively is to determine empirically a threshold that eliminates infrequent positions with low positional accuracy yet retains more common positions with high accuracy.

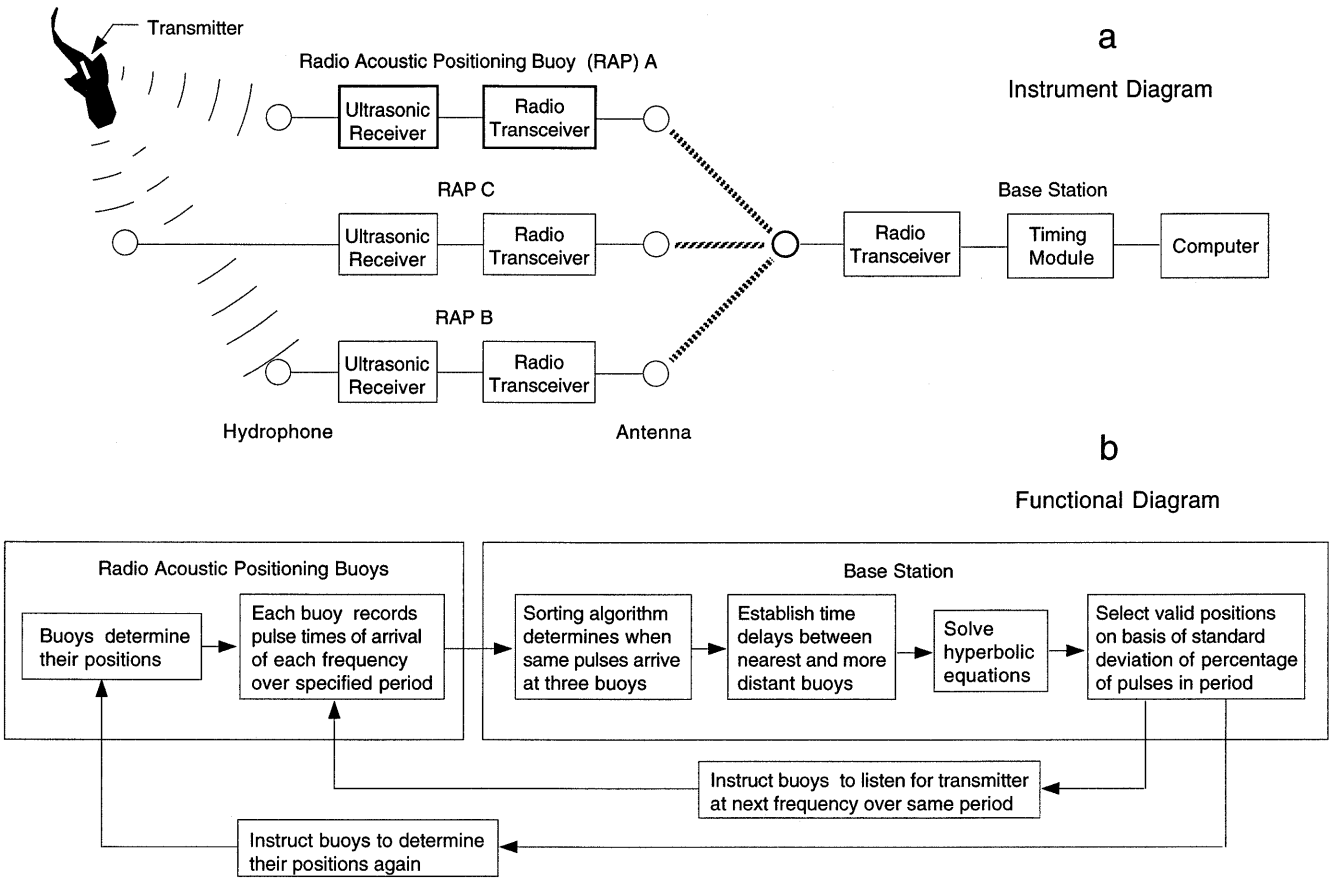


Fig. 2 Instrument (*a*) and functional diagram (*b*) of radio acoustic positioning (RAP) system used at Año Nuevo Island

Data acquisition and analysis

The station instructs the sonobuoys to listen over a user-set period for pulses of the signal from the transmitter with the lowest frequency, then it listens for pulses of the next highest frequency, and so forth, before returning to listen for pulses of the first frequency. An understanding of the system requires a familiarity with how the data are stored in files. Table 1 presents a sample from the computer record of five white sharks tracked simultaneously for ≤15 d during October 1997. The sample includes information for four of these sharks recorded over a period of 77 s starting at 23:27:06 h on 16 October 1997 (top data set A, B, C in Table 2). The first four columns of Table 2 give the identities and x, y, z coordinates of the three sonobuoys; date and time when the system detected a particular shark and shark's identity (1 to 6) are shown in the next three columns. The following three columns contain the coordinates of the shark within the array. For example, Shark "W1" with a beacon of 40 kHz (see Table 1) had the following coordinates, $x = -190.4$ m, $y = -44.5$ m, and $z = 0.2$ m at 23:27:06 hrs. We used a constant value of 0.2 m for the z coordinate for Sharks W1 to W5, which were tagged with beacons during the fall of 1997, because the RAP system did not record their swimming depths. The confounding effect of diving behavior on the 2-D path of the shark was minimal because the depth range in the recording area (<20 m) was small relative to the $\sim 1200 \times 1000$ m range of movement by the sharks within the array (see dark stippling in Fig. 1). We tagged a sixth shark during the following year with two transmitters, each with depth and temperature sensors (Table 1). The depth measurements for this shark served as the z coordinate in 3-D position-determinations. Shark W6′s swimming depth and temperature were 4.4 m and 24.8 °C, respectively, at 17:10:15 h on 22 October 1998 (middle data set, C, in Table 2). Note that the first two rows of the middle sample contain information from a beacon placed on the bottom with a pulse interval of 1850 ms that can be used to eliminate any error in shark positions resulting from buoy movement. The next two columns of the transmitter's record contain the number of pulses aligned by the three sonobuoys and the standard deviation to the arrival times expressed in clock cycles. The rest of the record is devoted to information specific to each sonobuoy such as: (1) the frequency of transmitter pulse detections or "hits", (2) level of underwater noise, (3) amount of amplification needed to detect pulses, and (4) voltage level of the battery in each RAP buoy.

Two types of positional information can be extracted from a RAP record. The first is the shark's position within a spatial coordinate system centered in the sonobuoy array; the second is the presence of the shark within the reception ranges of the buoys. A tagged shark can be tracked where the signal from its transmitter is detected by all three sonobuoys (light stippling in Fig. 1). The shark can be detected when it is within the reception range of any one of the sonobuoys (circles ranges in Fig. 1). The range of detection by the three buoys (combined area of all circles in Fig. 1) thus exceeds greatly the area of position determination (area delimited by the three overlapping circles in Fig. 1). For example, the base station could not determine the x, y coordinates of Shark W2 at 23:27:40 h on 17 October 1997 because the shark's signal was not detected by Buoy A despite being identified four times by Buoy B and thrice by Buoy C (see Table 2). The relative number of "hits" per buoy can provide a rough estimate of the location of the tagged individual. For example, Shark W2 was probably northwest of the island, nearer to Buoys B and C than to Buoy A.

With positional coordinates, one can calculate each shark's rate of movement and distance between the shark and its

Table 2 *Corcharodon carcharias*. Excerpts from three files produced by radio-acoustic positioning system at Año Nuevo Island. First record shows positional information for White Sharks 1 to 4 with ultrasonic beacons; second record indicates positions, swimming depths, and stomach temperatures for Shark 6 with Transmitters a and b in its stomach together with positions for stationary beacon moored close to sea floor; third record shows data from same two transmitters in Shark 6. Transmitter **a** retained within stomach of shark and Transmitter **b** having been passed by shark and fallen to bottom. Data at 17:07:16–18hrs from beacon moored at fixed location to identify spatial error in shark positions due to buoy movement, which is apparent as movement of this stationary beacon (*Buoy iden* buoy identity; *Shk no.* shark number; *PI* pulse interval; *P no.* pulse number; *Dev* deviation in timing; *Hits* detections per buoy receiver; *Noise* ambient noise; *Gain* receiver amplification; *Bat* battery)

Buoy spatial coordinates				Date	Time of day (hrs)	Shark spatial coordinates				Transmitter					Buoy A				Buoy B				Buoy C			
Buoy iden.	x (m)	y (m)	z (m)			Shk. No.	x (m)	y (m)	z (m)	PI (msec)	Depth (m)	T (°C)	P no.	Dev. (cycles)	Hits	Noise (dB)	Gain (dB)	Bat (V)	Hits	Noise (dB)	Gain (dB)	Bat (V)	Hits	Noise (dB)	Gain (dB)	Bat (V)
A	−264.8	−118.7	0.2	16.10.97	23:27:06	1	−190.4	−44.5	0.2	1501			8	126384	9	12	24	11.3	10	15	33	11.4	9	9	21	11.2
B	264.0	−118.7	0.2	16.10.97	23:27:08	1	−184.7	35.0	0.2	1501			8	126384	9	12	24	11.3	10	15	33	11.4	9	9	21	11.2
C	32.8	118.7	0.2	16.10.97	23:27:09	1	−192.4	41.0	0.2	1501			8	126384	9	12	24	11.3	10	15	33	11.4	9	9	21	11.2
				16.10.97	23:27:11	1	−192.6	39.3	0.2	1501			8	126384	9	12	24	11.3	10	15	33	11.4	9	9	21	11.2
				16.10.97	23:27:12	1	−194.2	38.1	0.2	1501			8	126384	9	12	24	11.3	10	15	33	11.4	9	9	21	11.2
				16.10.97	23:27:40	2				4428					0	30	24	11.3	4	26	45	11.3	3	27	21	11.2
				16.10.97	23:27:46	3	−319.4	261.7	0.2	2998			4	42741	7	12	27	11.4	4	27	48	11.3	7	15	36	11.2
				16.10.97	23:27:49	3	−308.6	252.0	0.2	2998			4	42741	7	12	27	11.4	4	27	48	11.3	7	15	36	11.2
				16.10.97	23:28:04	4	232.7	−314.6	0.2	1500			3	270193	4	26	45	11.3	8	6	18	11.3	10	9	27	11.2
				16.10.97	23:28:05	4	236.4	−315.3	0.2	1500			3	270193	4	26	45	11.3	8	6	18	11.3	10	9	27	11.2
				16.10.97	23:28:21	1	−221.1	−16.0	0.2	1501			8	903	9	9	18	11.3	9	9	27	11.3	10	9	15	11.2
				16.10.97	23:28:23	1	−230.6	−2.5	0.2	1501			8	903	9	9	18	11.3	9	9	27	11.3	10	9	15	11.2
A	−258.1	−127.1	1.0	22.10.98	17:07:16		−52.4	−47.0	20.0	1850			4	33	5	9	27	11.2	6	6	24	11.3	6	6	15	11.2
B	258.1	−127.1	1.0	22.10.98	17:07:18		−53.3	−46.7	20.0	1850			4	33	5	9	27	11.2	6	6	24	11.3	6	6	15	11.2
C	−55.8	127.1	1.0	22.10.98	17:10:15	6[a]	−141.1	−140.6	4.4		4.4	24.8	9	6861	10	9	15	11.2	12	14	33	11.3	12	12	33	11.2
				22.10.98	17:10:18	6[a]	−141.1	−141.3	4.4		4.4	24.8	9	6861	10	9	15	11.2	12	14	33	11.3	12	12	33	11.2
				22.10.98	17:10:21	6[a]	−142.6	−140.0	4.4		4.4	24.8	9	6861	10	9	15	11.2	12	14	33	11.3	12	12	33	11.2
				22.10.98	17:10:24	6[a]	−140.6	−146.0	4.4		4.4	24.8	9	6861	10	9	15	11.2	12	14	33	11.3	12	12	33	11.2
				22.10.98	17:10:27	6[a]	−140.8	−146.0	4.4		4.4	24.8	9	6861	10	9	15	11.2	12	14	33	11.3	12	12	33	11.2
				22.10.98	17:10:37	6[b]	−138.8	−155.6	6.2		6.2	24.6	5	2345	9	9	18	11.2	11	9	30	11.3	11	24	48	11.1
				22.10.98	17:10:40	6[b]	−140.3	−159.1	6.2		6.2	24.6	5	2345	9	9	18	11.2	11	9	30	11.3	11	24	48	11.1
				22.10.98	17:10:43	6[b]	−141.0	−172.2	6.2		6.2	24.6	5	2345	9	9	18	11.2	11	9	30	11.3	11	24	48	11.1
A	−348.0	−192.0	1.0	17.11.98	15:46:32	6[b]	−139.1	−453.8	17.3		17.3	13.0	3	17419	4	26	48	11.2	10	19	42	10.4	9	23	48	11.0
B	348.1	−189.0	1.0	18.11.98	02:27:45	6[a]	782.1	−1162.6	14.9		14.9	23.9	3	8266	3	28	45	11.2	10	12	27	9.3	11	14	33	11.0
C	18.8	189.0	1.0	18.11.98	02:30:20	6[a]	522.8	342.8	11.0		11.0	23.4	3	203	4	26	39	11.2	11	6	12	9.2	8	18	36	11.0
				18.11.98	02:30:23	6[a]	514.6	−350.7	11.0		11.0	23.5	3	203	4	26	39	11.2	11	6	12	9.2	8	18	36	11.0

[a] Data from Shark 6 with pressure and depth-sensing transmitter **a**

[b] Data from Shark 6 with similar sensors on transmitter **b**; note that at similar depths, 17.3 and 14.9 m, *T* (13 °C) of transmitter **b** on sea floor is 10.9 C° lower than *T* (23.9 °C) of Unit **a** because the latter is contained in stomach of Shark 6

companions. The following formula was used to estimate the distance (D) moved between successive positions (Riddle 1982):

$$D = \sqrt{\left((x_2 - x_1)^2 + (y_2 - y_1)^2 (z_2 - z_1)^2\right)} \ . \qquad (1)$$

Travel distance was determined in two dimensions (x, y) for Sharks W1 to W5 with beacons, and in three dimensions (x, y, z) for W6, with the depth recorded by the pressure sensor serving as the third dimension. The distance moved, divided by the elapsed time, yielded a rate of movement for a shark between two successive positions. This was a minimum estimate of speed, assuming the shark traveled along a straight line.

Because positions were not recorded simultaneously for all sharks, the distance between individuals was determined in the following manner. We found the distance to Shark B from an imaginary point interpolated on a straight line extending from the last position of Shark A during each listening period to its first position during the next listening period (Fig. 3). Three positions were needed to calculate a separation distance: (1) the position x_1, y_1 of Shark A at time t_1, (2) position x_1, y_1 of Shark B at t_1, and (3) the next position x_2, y_2 of Shark A at time t_2. An imaginary position x_1', y_1' of Shark A existed at time t_1', when Shark B was at Position x_1, y_1. The following procedure was used to calculate the imaginary point. Firstly, we determined the vectoral components X and Y of an imaginary straight-line movement of Shark A between times t_1 and t_2:

$$X = (X_2 - X_1); \ Y = (Y_2 - Y_1) \ .$$

Secondly, we found angle θ:

$\theta = arctan|Y/X|$.

Thirdly, we obtained the distance, D', traveled by Shark A from time t_1 to t_1' by multiplying the rate of movement of Shark A by interval $t_1' - t_1$. Fourthly, the distances X_2 between x_1 and x_1' and Y_2 between y_1 and y_1' were calculated: $X_2 = (cos\theta) \cdot D', Y_2 = (sin\theta) \cdot D'$. Next, these two distances were added to the original coordinates, x_1 and y_1, of Shark A at time t_1 to obtain the imaginary coordinates, x_1' and y_1', of Shark A at time t_1' when Shark B was at coordinates, x_1, y_1. Finally, the distance between the positions of Shark A at time t_1' and Shark B at t_1 was calculated using the distance formula (Eq. 1).

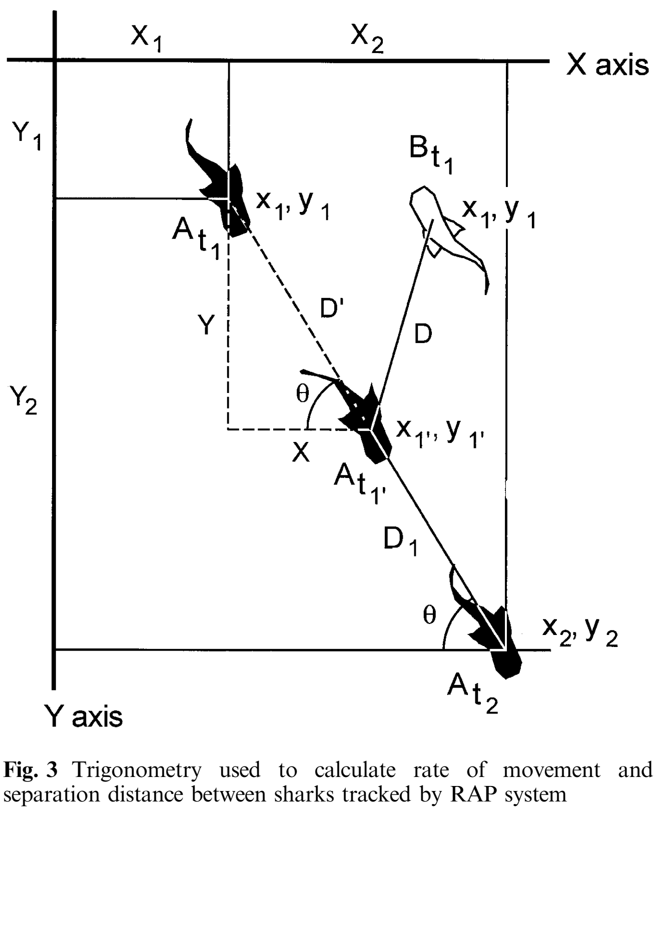


Fig. 3 Trigonometry used to calculate rate of movement and separation distance between sharks tracked by RAP system

An example is presented of the calculation of separation distance between Sharks W1 and W4 (see first RAP record in Table 2). The system obtained five positions of W1 during the 6 s period, starting at 23:27:06 h on 17 October 1997. The fifth position consisted of coordinates, $x = -194.2$, $y = 38.1$. Shark W1 was positioned next 69 s later at 23:28:21 h at coordinates, $x = -221.1$, $y = -16.0$, during the next listening period, after the system had listened for W2, W3, and W4. We then found imaginary coordinates, $x = -214.5$, $y = -2.7$, at 23:28:04 h for W1 on a straight line between its two successive positions. At this time W4 was at its first position, $x = 232.7$, $y = -314.6$, during the former listening period. The interpolated pair of coordinates of W1 and true coordinates of W4 were entered into the distance formula to calculate a separation distance between the two sharks of 545.2 m.

Positional accuracy

The accuracy of a position of an individual, tracked by the RAP system, is related to the ultrasonic transmitter's location relative to the triangular array of sonobuoys. We used a simulation program (Vemco Ltd., PosSim) to identify the degree to which the temporal error in the detection of pulses from the tagged individual reduced the accuracy of position determinations by the RAP system (Fig. 4). We chose a temporal error of ± 0.5 ms for the detection of pulses from the tag. We assigned the same positional coordinates to the sonobuoys that they had on 2 November 1998 when tracking W6 at Año Nuevo Island. The transmitter was given a default depth of 10 m, midway between surface and bottom, as Sonobuoys A and B were over depths of 20 m and Buoy C over a depth of 25 m. We used PosSim to determine the standard deviation (SD) for positions determined at points throughout a 1500×1500 m area surrounding the sonobuoy array. The program determined the times when a pulse emitted from a quadrant (12×12 m) would arrive at the three sonobuoys. The arrival times at each of the buoys were then increased or decreased by a random number ≤ 0.5 ms to simulate the variability in when a signal from a beacon in the center of that quadrant would reach the buoys. The positional error arose from each signal originating from that quadrant following a slightly different path and varying in speed because of temperature stratification in the water column. The distance formula (Eq. 1) was used to determine the distance between each new position based upon modified arrival times and the quadrant's position. A standard deviation SD_d (in m) was calculated from many position calculations for each point in the area around the buoy array.

The theoretical accuracy of positions of tagged sharks when within the sonobuoy array was high. SD_d was < 2 m within a heart-shaped area containing the triangular buoy. The SD_d of positions was < 5 m in front of the island, whose coast lay along a line extending from the coordinates $x = 500$, $y = -600$ to coordinates $x = -300$, $y = -800$ m. A narrow band existed along the coast of the island, with a SD_d of < 10 m. Positions were less accurate (from < 10 to < 20 m) within small triangular areas behind each of the buoys. Either no solution or two solutions existed to the hyperbolic equations at the borders of these areas. These areas of poor accuracy extended outward from the sides of the triangular array. We chose to use the solution to the equation yielding the position closest to the prior position. The chance of that solution being true was considered higher because the shark had to swim a shorter distance between the two consecutive positions.

We estimated the variability with which the RAP system positioned a transmitter moored at a single point within the array. A beacon was attached to a buoy floating 2 m above the bottom. The RAP array located that beacon at the following coordinates, $x = 140.6$ m, $y = -100.5$ m. The mean separation recorded between successive beacon positions over a 2.5 h period was 3.0 m ($SD_d = 1.7$ m, $N = 119$). This SD was similar to the < 2 m SD_d

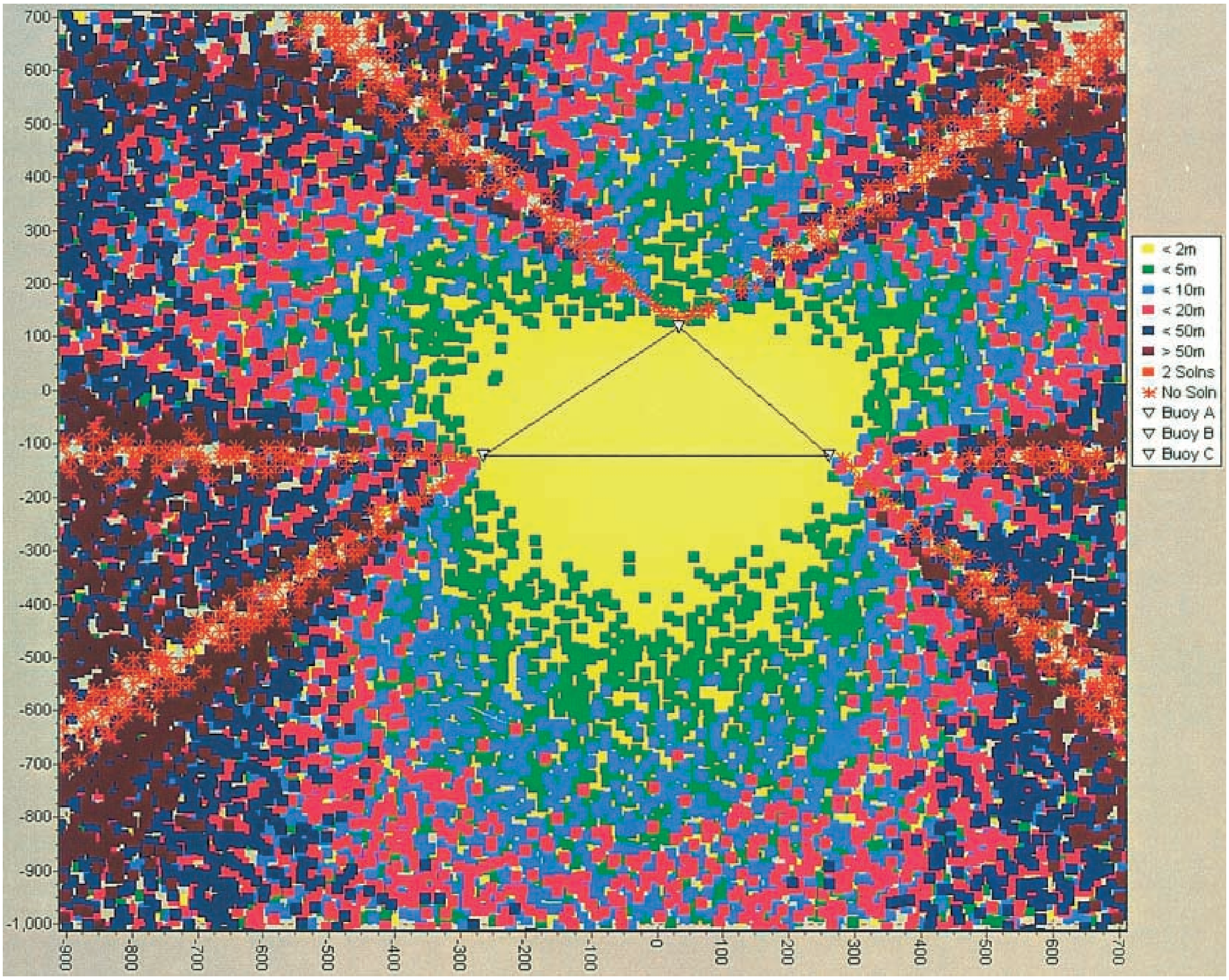


Fig. 4 Simulation plot of the accuracy of positions determined within the detection range of the RAP system with a sonobuoy receiver timing error of ± 0.5 ms and a transmitter depth of 10 m. The buoy separations existed at 15:46:32 hrs on 17 November 1998 (see positions for A–C at bottom, left of Table 2)

found using the PosSim program. The mean rate of movement for this "stationary" beacon was only 0.021 m s^{-1} (SD = 0.113 m s^{-1}, $N = 119$). Both measures varied little over time, except for a peak at 14:30 hrs (Fig. 5). The RAP system thus recorded little motion for a beacon kept relatively stationary on its mooring.

The system's software calculated a SD_{cc} (cc = clock cycles) for those positions recorded for each shark during each listening period based on when the pulses from the shark's transmitter arrived at the three buoys A–C. The times were expressed as intervals by subtracting time taken for the pulse to arrive at the buoy nearest to the transmitter from the times taken to arrive at the two more distant buoys. The interval (I)

$$\bar{I}^A = \frac{\sum I_i^A}{n}$$

$$\bar{I}^B = \frac{\sum I_i^B}{n}$$

$$\bar{I}^C = \frac{\sum I_i^C}{n} \quad (2)$$

for the nearest buoy was set to zero. The average interval was calculated for each buoy from each set of pulses.

The error was then determined for each pulse detected by the three buoys:

$$I_i^{error} = \left(\bar{I}^A - I_i^A\right)^2 + \left(\bar{I}^B - I_i^B\right)^2 + \left(\bar{I}^C - I_i^C\right)^2 \ . \quad (3a)$$

An average error was then computed where $i = 1 - n$, where n = number of pulses in a set of pulses:

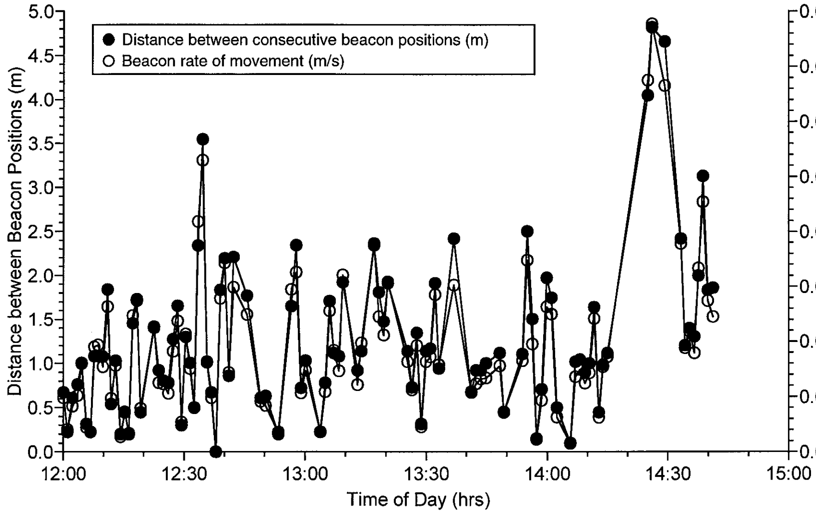
$$\bar{I}^{error} = \frac{\sum I_i^{error}}{n} \quad (3b)$$

The standard deviation was the square root of the average error:

$$I^{SD} = \sqrt{\bar{I}^{error}} \ . \quad (3c)$$

We eliminated spurious positions of white sharks by discarding those sets of positions exceeding a threshold SD_{cc}. Shark W6, which was tagged at 09:01 hrs on 22 October 1998, fed later that day at 10:48 hrs on whale meat containing a second temperature- and depth-sensing transmitter (Table 1). This white shark now had two tags within its stomach. We instructed the RAP system to alternately record positions for the two tags, listening to one transmitter for 10 s, the other for the same period, and so forth. This resulted in two tracks for the same shark. We show the two tracks of W6 during a 4 min 29 s period from 17:07:02 to 17:11:31 hrs later on that day (Fig. 6). The standard deviation in clock cycles was varied in Playbacks A to F, decreasing from a maximum SD_{cc} of 1 000 000 to a minimum of 2500.

Fig. 5 Distances between consecutive positions and rates of movement of a "stationary" transmitter suspended 2 m above the bottom inside the triangular sonobuoy array and tracked over a 2 h period on 5 August 1998



The two tracks for the same shark became more similar as the standard deviation was reduced during playback and outlying positions eliminated. Let us compare the tracks of Transmitters (T) 1 and 2 on W6. The positions of T2 were distributed along a straight line leading toward Año Nuevo Island when the track was played back with a SD_{cc} of 1 000 000 (Fig 6a). Shark W6 with T2 swam 270 m in 237 s, resulting in a speed of 1.2 m s^{-1}. This was similar to the rates of movement of white sharks estimated from the distance moved between successive 15 min boat positions (mean = 0.9 m s^{-1}, $N = 145$: Strong et al. 1992; median = 0.80 m s^{-1}, $N = 47$: Klimley unpublished data). It is likely that the shark swam at this time continuously toward the island. Most of the positions of T1 are along the same straight path, except for seven aberrant positions, which were distant from the others. These outlying points were judged erroneous because the shark could not swim fast enough to travel between the widely separated points during the short periods occurring between the consecutive position-determinations. For example, a distance of 361 m separated the outlying position near the bottom of the monitoring area ($x = -142.8$ m, $y = -135.9$ m) recorded at 17:10:03 h and the next position on the straight-line track toward the island ($x = 27.7$ m, $y = -454.3$ m) acquired at 17:10:07 h (Fig. 4c). The shark would have had to swim at an unlikely rate of 90 m s^{-1} to cover the distance between the two points over the given time. This outlier, with a SD_{cc} of 7894.9, was present on the track when the record was played back with a threshold SD_{cc} of 10 000, but not when the playback threshold was set at 7750 clock cycles (see Fig. 6c, d).

The discrepancy between the SD_{cc} of positions recorded for the two transmitters may be due to their different orientation in the stomach of the shark. The piezoelectric transducer on a unit, attached to the stomach wall and hanging downward with its long axis perpendicular to the surface, would propagate its strongest signal outward directly toward the three sonobuoys. However, the same device, resting on the bottom of the shark's stomach parallel to its long axis, would propagate the strongest signal upward and downward toward the sea surface and bottom, respectively. This signal would reflect off these surfaces, depending upon the shark's distance from a sonobuoy. The signal would then reach the nearer sonobuoys directly and farther ones indirectly, producing an aberrant position differing from the shark's true position. The resulting track would be composed mostly of positions along the shark's actual swimming path, yet interspersed with infrequent aberrant positions separated in one direction from the true track of the shark.

By decreasing the SD_{cc}, we arrived at an ideal threshold value (2800 clock cycles), which removed most positions that were judged aberrant but left the majority of positions recorded during the track. The consequence of excluding positions from a track in this manner is that 4 to 5 other good positions recorded during that 12 s listening period would be discarded with that single bad position. We thus played back all tracks of the tagged sharks twice, once with a maximum SD_{cc} of 1 000 000 to view all possible positions of the shark, and again with a SD_{cc} of 2800 to provide a conservative track of the shark. In the end, the unintended ingestion of two tags by W6 provided insight into how to maximize the accuracy of the positions determined by the RAP system.

Rates of movement from records without points removed due to high variability are only relative indices of swimming speed. These measurements, collected during fall 1997 of the study, could not be analyzed with the same rigor as those during fall 1998, when we saved sets of positions only if their cumulative standard deviation was less than the threshold. During the first year of the study, we only used positions based upon the system detecting a signal with the transmitter's frequency and a pulse intervals of 1500 ± 10 ms. This action eliminated many false positions arising from the receivers in the sonobuoys mistaking a high amplitude pulse of noise for the signal of the transmitter. These positions were often so widely separated that it was unlikely that the sharks could swim between the two points in the short time interval separating them. We also eliminated from the records of the sharks those rates of movement >30 m s^{-1}, the highest swimming speed recorded for a fish (Beamish 1978). The majority of these false positions were eliminated during the second year of the study by operating the radio-acoustic positioning system with a SD_{cc} of <2800. The track was also reduced to only those positions recorded separated by a 1 min interval. This resulted in longer distances between position determinations, and reduced the confounding effect of small buoy-movements. We further eliminated rates calculated using positions separated by intervals >1 min, when the shark was less likely to swim directly between the two consecutive points. However, even these more accurate swimming rates are at best indices of activity, as the track vector was the result of both the shark's movement and that of the sonobuoys. We intend to record swimming speed directly with a paddle-wheel sensor on the shark in future, and recommend others to do the same.

The RAP system stored all positions as x, y coordinates in a Cartesian coordinate system with its origin in the center of the triangular buoy array. The x-axis bisects the AC and BC sides of the triangular array; the y-axis bisects the AB side and is perpendicular to the x-axis. Ideally, the tracks of the sharks are viewed on the universal coordinate system, with positions recorded in latitude and longitude. In order to translate x, y positions into global positions, the latitude and longitude of the of the array's origin must first be found from known geographical coordinates for Sonobuoys A–C. The x, y coordinates of each position can then be converted to geographical coordinates

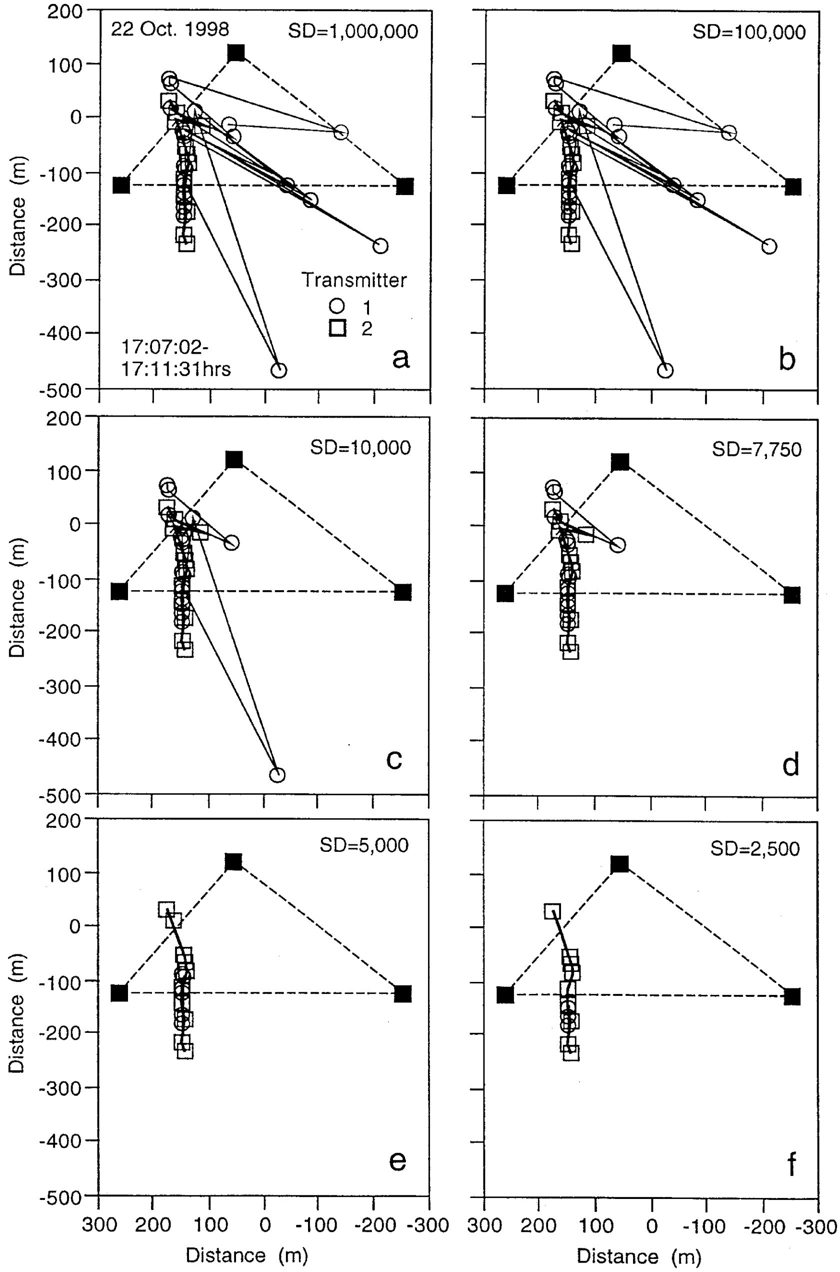


Fig. 6 *Carcharodon carcharias*. Tracks of shark W6 from 17:07:02 to 17:11:31 h on 22 October 1998 showing changes in transmitter positions (○ positions of Transmitter 1; □ positions of Transmitter 2) as standard deviations (SD_{cc}) decreasing from 1 000 000 (*a*) to 2 500 (*f*) clock cycles. Note that with a $SD_{cc} \leq 5\,000$ clock cycles, the paths of both tags coincide and the movement is not erratic but directional. The swimming rate of 1.2 m s^{-1} cycles also resembles that recorded by others for the species

by mathematical rotation using the *x*, *y* and geographical coordinates of the origin of the array and one of the buoys. This permitted us to enter the positions of the sharks into the ArcView GIS environment (ESRI, Inc., Redlands, California), where they can be superimposed on bathymetric records composed of depths referenced to geographic coordinates. This procedure is explained in Table 3.

Results

We present some preliminary results to help evaluate the RAP system. First, we detected multiple animals within the detection areas of the three sonobuoys during daytime versus nighttime. The five sharks, tagged during October 1997, visited the island repeatedly during periods ranging from 11 to 18 d. The sharks stayed near the island during both day and night. They spent an average 39.5% per day within the range of the RAP near the island, a mean percentage of 15 min periods per 24 h that W1 to 5 were detected within the range of the array. We show two records of attendance of W1 to 4 on 20–21 October 1997 (Fig. 7). The above diagram shows when the tagged sharks were within detection range of any one of the three sonobuoys, the most inclusive criterion with the broadest geographic range. The diagram below shows when sharks were within the range of all three sonobuoys. This area consisted of the intersection of all three circular detection ranges of the sonobuoys. Fewer visits, of course, were recorded of the shark within the range of the three sonobuoys than any one of the buoys.

Table 3 Methodology for converting *x*, *y* coordinates into latitude and longitude

1)	Latitude and longitude positions are known for the buoys. These positions are entered into the GIS ArcView field in decimal degrees.
2)	Distances between the buoys can be found using the standard distance formula. (Eq. 1) Degrees of latitude and longitude must be converted to meters in order to have equivalent units. At 37°N latitude, there are 11 0975 meters/°lat., and 89 014 meters/°lon. If buoy separation distances differ greatly from those displayed by VEMCO, buoy positions may need to be adjusted.
3)	In order to rotate the *x–y* data points into a lat./lon. arrangement, the origin of the triangular buoy array must be found in lat./lon. According to VEMCO, the origin in the three buoy system is determined as follows: Buoys A, B and C are arranged in a triangle with the origin half the distance between A and B on the *x*-axis and half the distance between C and D on the *y*-axis. D is not a buoy, but is a point on the line intersecting A and B such that CD forms a right triangle. With this in mind, we proceed to calculate the origin of our lat./lon. buoy positions.
a)	Find the slope of the line connecting buoys A and B: $m_{AB} = (B_{lat} - A_{lat})/(B_{lon} - A_{lon})$ m′, which is the negative reciprocal, will be used in following formulas.
b)	F is the midpoint of AB. The origin of the triangle lies on the line (slope = m′) perpendicular to this midpoint. F is calculated in decimal degrees by finding the average of the positions of A and B: $F_{lat} = (A_{lat} + B_{lat})/2$, $F_{lon} = (A_{lon} + B_{lon})/2$ There is no error due to °lon differences because the average is found in degrees rather than meters.
c)	Distance *CD*, between Buoy C and point D, can be estimated from the VEMCO *x–y* plane in meters.
d)	The latitude and longitude of the origin is found using following formulas: $O_{lat} = \pm \sqrt{[(0.25CD^2)/(1 + 1/m_{AB}'^2)]} + F_{lat}$, $O_{lon} = F_{lon} \pm [(O_{lat} - F_{lat})/m_{AB}']$. Bracketted calculations must be done with measures converted from degrees to meters using the conversions in (Eq. 2). This component is then converted back into degrees and resulted with F_{lat} or F_{lon}.
4)	Once the origin is known in latitude and longitude, a transformation can be done to derive a formula which will convert any *x–y* position into lat./lon.
a)	The transformation is done using the calculated lat./lon. and VEMCO position of the origin ($x = 0$, $y = 0$), as well as the lat./lon. and *x–y* coordinates of a known position (buoy). The *x–y* position of a buoy will vary slightly over a period of study. An average of buoy positions recorded during days of study should be used.
b)	To obtain the coordinates of the buoy in relation to the origin, the lat./lon. positions of the origin and the buoy are subtracted to give a difference in decimal degrees, which is converted to meters.
c)	The following formulas are used to find the buoy's angular relationship to the origin: $B_x = B_{lat}\cos\phi + B_{lon}\sin\phi$, $B_y = -B_{lat}\sin\phi + B_{lon}\cos\phi$ Either equation can be rearranged to solve for sinϕf or cosϕf. The result can be plugged into the additional formula to obtain an equation with a single unknown. Solve for the angle ϕ.
5)	Using the angle ϕ, all x-y points can be transformed into lat./lon. positions using the inverted formulas: $S_{lat} = S_x\cos\phi - S_y\sin\phi$, $S_{lon} = S_x\sin\phi + S_y\cos\phi$ These positions, calculated in meters and converted into degrees, are the position of the shark relative to the origin. The lat./lon. position of the origin must then be added back to S_{lat} and S_{lon} to get the true position of the shark.

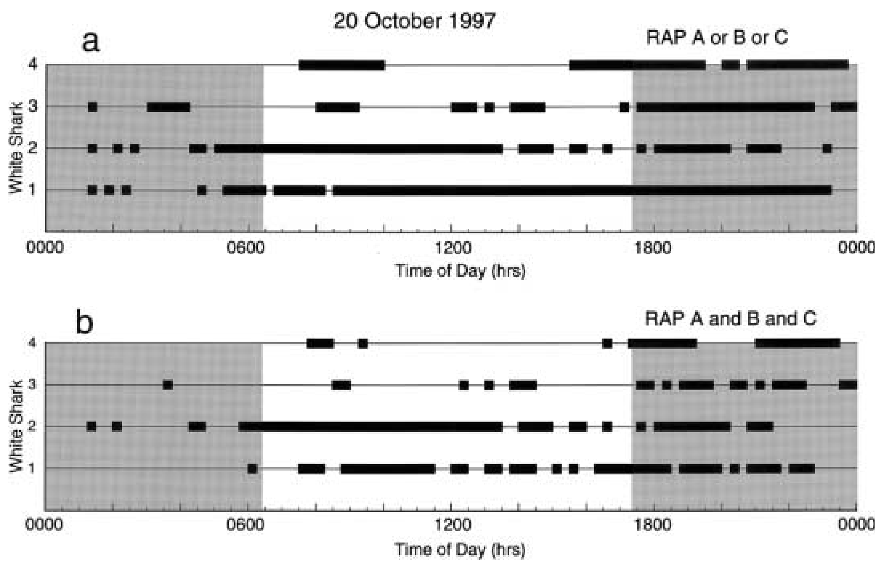


Fig. 7 *Carcharodon carcharias*. The occurrence of four white sharks (W1–4) within the detection range of the sonobuoys on 20 October 1997. Individuals are identified by the symbol ■ if they were detected within 15 min period during 24 hour cycle [*white area* daytime; *stippled area* nighttime; *A or B or C* sharks detected by any one of 3 sonobuoys **(a)**; *A and B and C* sharks detected by all 3 sonobuoys **(b)**]

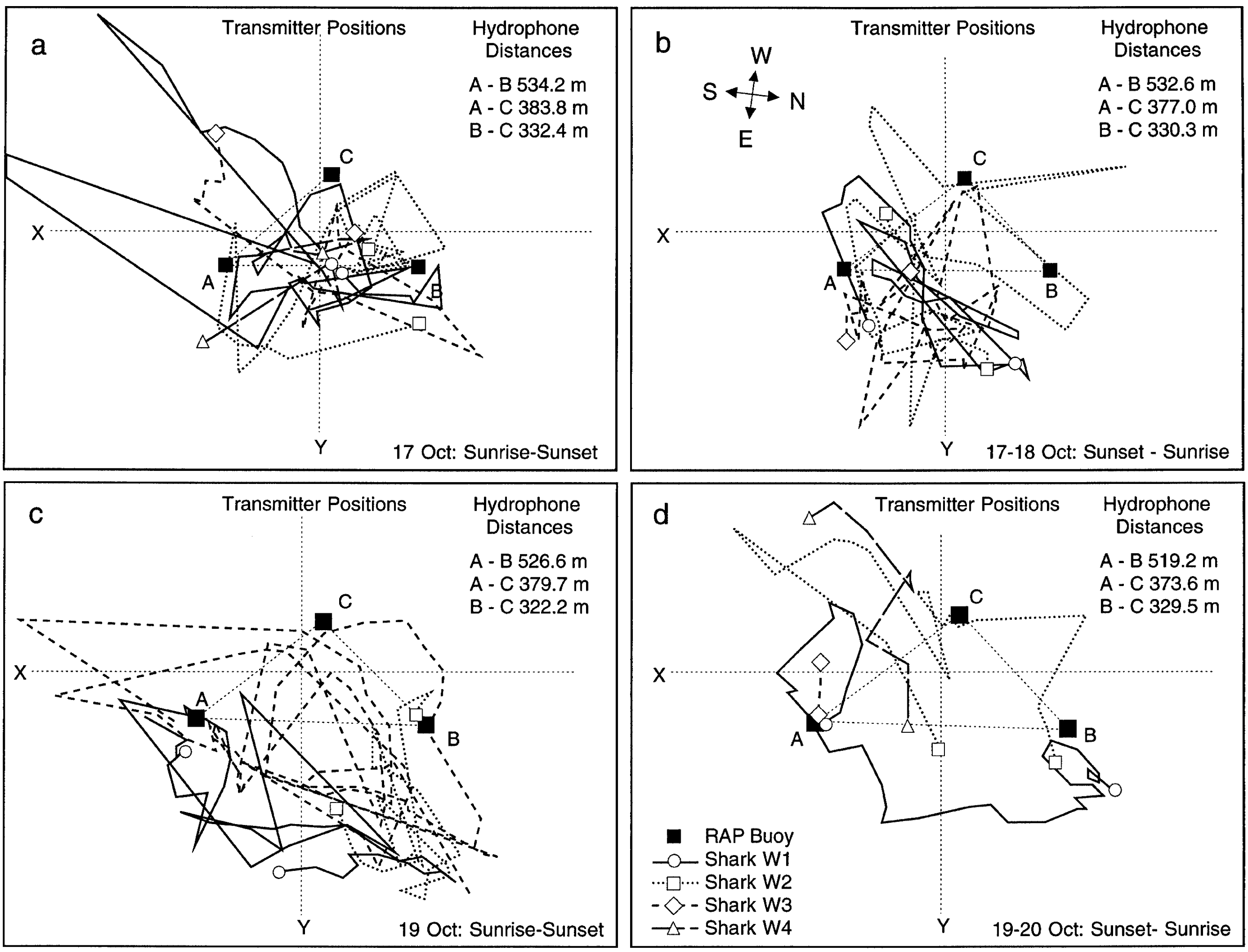
Yet this exclusive area, where sharks were simply detected (see coarse stippling, Fig. 1), was larger than the area where *x*, *y* positions of sharks were recorded by the RAP system. The boundary of this area (see fine stippling), formed by connecting the outermost positions to make the maximum convex polygon (for definition, see

Hooge and Eichenlaub 1997), did not extend to the edge of the exclusive receiving range farthest from the island. This was consistent with the sharks patrolling close to the island where their chance of intercepting a seal swimming to and from the island was highest. Few positions were recorded in the shadow zones outside the triangular array and behind the buoys, where no solutions existed to the hyperbolic equations yielding tag positions (see red asterisks, Fig. 4).

The paths of the tagged sharks can be plotted when the signal from the beacon is detected by the three sonobuoys. We show the day and night tracks of W1–4 during two 24 h periods (Fig. 8). Each shark is assigned a unique style of line that shows its path with unique symbols at the start and end points. The sharks were tracked near Año Nuevo Island both during day and night. For example, W1–3 were present at Año Nuevo Island both during daytime and nighttime on 17/18 October (Fig. 8a,b). The same three sharks were present during daytime two days later (Fig. 8c) with W4 visiting the island only briefly during nighttime (Fig. 8d). Note that the vectors comprising the tracks were often aligned along a southwesterly-northeasterly axis. A channel of deeper water exists along this axis, through which seals and sea lions may move to and from the island.

The spatial distribution of the positions of the different sharks to each other also can be compared while the sharks are within the range of the RAP array. This type of analysis gives an idea of whether a particular shark has a preferential location and whether this differs from that of another shark. Fig. 9 presents a 3-D view of the percentages of positions of W1 and W2 recorded within 100 m^2 cells in a 1100 × 1000 m area close to the coast of Año Nuevo island. The locations of the buoys provide a spatial reference (white circles in Fig. 9); Año Nuevo Island is to the right outside the plotted area. Shark W1 had two favored areas of peak activity off the center of the island, one closer to shore than the other (Fig. 9a). Shark W2 frequented the area close to the island, but rarely was recorded offshore of the center

Fig. 8 *Carcharodon 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 included for all positions in **a**, but only for initial and final positions in **b–d**. (■ RAP sonobuoys; ○ positions of Shark W1; □ positions of W2; ◇ positions of W3; △ positions of W4)



of the island (Fig. 9b). Shark W1 visited the northern end of the island more often than W2. One cannot determine from a frequency distribution alone, without reference to time, whether a particular individual (W1) interacts with another (W2), despite overlapping areas of peak activity.

One can look for the non-random associations between tagged individuals by comparing real separation distances to randomized separation distances. We calculated the former between W1 and 5 over an 18 d period during 1997 and compared them to "randomized" separations. Randomization consisted of supplanting the coordinates of each neighboring shark with coordinates recorded for the same shark at another time. The order of these positions was altered using values taken from a table of random numbers. This positional exchange resulted in a distance between a shark at its present position and the next shark in the listening cycle at a place occupied at another time. For example, the median true-separation distance between W1 and W3 (median = 205 m, $N = 185$) was less than the median random separation distance (median = 299 m) indicating that these sharks may have associated with each other. Indeed, they once swam within potential visual contact, since their 6 m minimum separation distance was less than the occasional

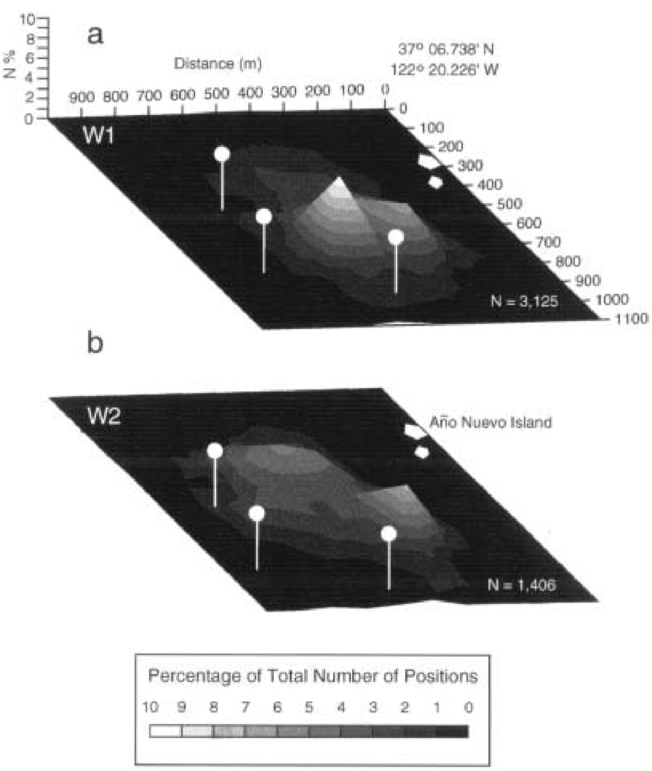


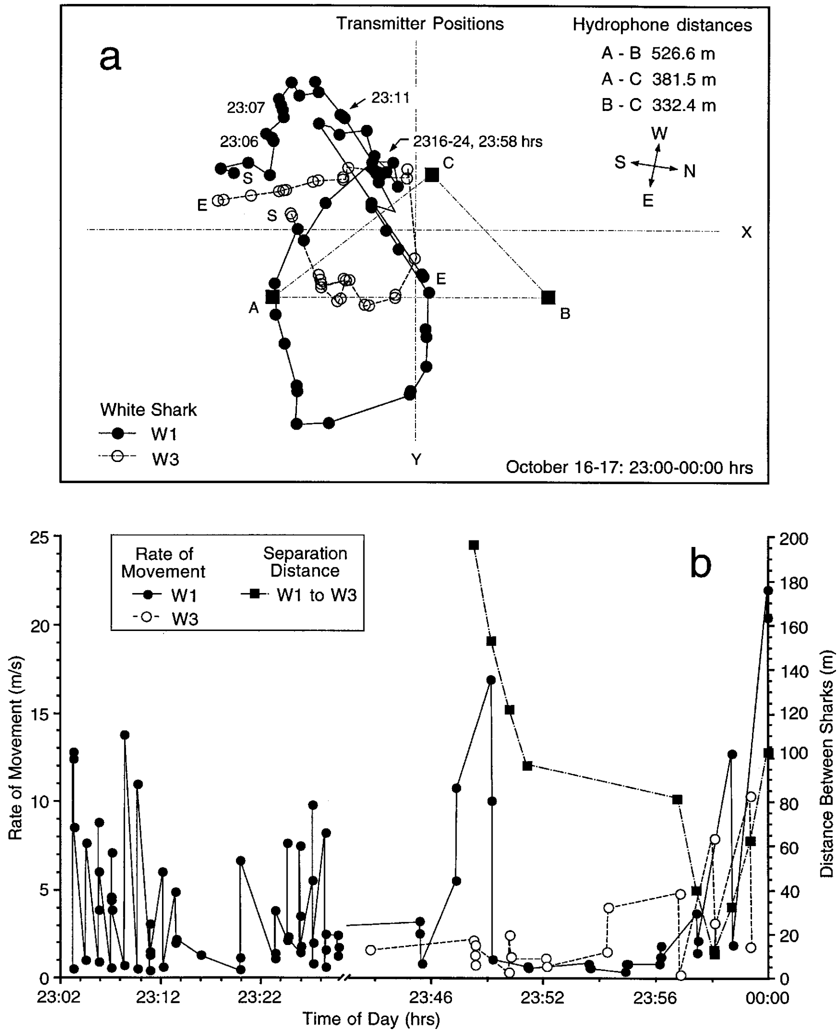
Fig. 9 *Carcharodon carcharias*. 3-D Contour maps formed from grid of 100 × 100 m cells, with the percentages of positions of Sharks W1 (**a**) and W2 (**b**) within 1000 × 1100 m area west of Año Nuevo Island (*white circles* sonobuoys A–C; *each contour* = 1% of total number of position determinations recorded for that shark during study)

water visibility at Año Nuevo Island. We will show next that W3 approached to within 6 m of W1 when the latter exhibited behavior consistent with feeding on a pinniped. For another pair of sharks, W1 and W2, there was little difference between the true- and random-separation distances (medians: 301 vs 307 m, $N = 427$), implying neither association nor avoidance of other sharks.

Finally, the RAP system can eventually be used to identify and describe specific behavioral activities of sharks such as feeding. We present the following record solely to demonstrate the potential of this system. One first must search the long-term computerized records for evidence of a particular behavior based on prior knowledge of that pattern. For example, a shark's rate of movement would increase if it were chasing prey, and its speed would decrease if it were to circle and feed on the prey in one place. Furthermore, the separation distance between individuals would decrease if competing sharks were attracted. We searched low temporal resolution (24 h) plots of rates of movement and separation distances for W1 to W5 for rapid bursts of speed associated with small separation distances. Fig. 10 shows a brief record from 23:06 to 23:58 h on 16 October 1997 consistent with W1 capturing and feeding on a pinniped. This shark accelerated twice at 23:06 and 23:07 hrs, as though chasing prey (Fig. 10). These bursts of speed are apparent as two peaks in the rate of movement (Fig. 10b), and clusters of 3 and 4 positions on the track (Fig. 10a). The shark then swam slowly in a straight line at 23:11 hrs consistent with carrying a massive seal or sea lion in the mouth. The positions on the track were tightly clustered from 23:16 to 23:24 hrs near Sonobuoy C, as though W1 were staying at the prey. Shark W1 then swam away from this site along a clockwise circular path to a distance of 500 m, and returned to the same site at 23:58 hrs. The shark paused here, as is evident by the clustered positions in Fig. 10a. Shark W1 may have returned to feed upon the carcass of the prey. Shark W3 then appeared at 12:49 h at a distance of 200 m from W1 (Fig. 10a), came within 10 m from W1 at 23:58 h, and left in a westerly direction (Fig. 10b). This interpretation of the record is consistent with surface-based observations of predatory attacks on seals and competition among sharks for the prey (for description see: Klimley 1994; Klimley et al. 1996).

One can introduce a transmitter with a temperature-sensing thermistor into the stomach of a shark to obtain a more direct indicator of feeding. This should be indicated by an elevation of gastric temperature when the shark consumes the warm-bodied prey. Shark W6 was tagged with a temperature- and depth-sensing-transmitter on 22 October 1999 and tracked over a 28 d period (Table 1). We never recorded a sustained elevation of gastric temperature during the 12 d when W6 was within the range of the array, during a mean 21.6% of each day (max. = 55.2%; min. = 6.3%). The shark usually swam back and forth 200 to 300 m from the shore of Año Nuevo Island, where it was ideally posi-

Fig. 10 *Carcharodon carcharias*. Paths of two sharks (*W1* and *W3*) during putative predatory attack on pinniped (**a**), and plots of sharks' rates of movement and distances between sharks from 23:02 to 00:00 hrs on 16/17 October 1997 (**b**). Spurious positions could not be eliminated because threshold SD was unknown for records during Year 1, resulting in exaggerated rates of movement (● positions of Shark W1; ○ positions of W3 in **a**; ● rates of movement of W1; ○ rates of movement of W3 in **b**; ■ separation distances between W1 and W3)



tioned to intercept seals and seal lions departing and returning to the pinniped rookeries (Fig. 11). The shark did slowly move away from the island at 12:49 h on 2 November 1998 in a southwesterly direction, consistent with stalking a seal or sea lion moving along the canyon leading offshore from the island. Shark W6 also displayed two bursts of speed on the same day, consistent with actively chasing prey at 21:02 and 21:43 hrs (Fig. 12b). The shark first swam rapidly toward the surface, as though attempting to ambush prey (Fig. 12a). During this upward movement, from a depth of 18 to 6 m (Fig. 12c), the stomach temperature of the shark rose from 18.0 °C to a value close to the mean stomach temperature for that day (mean = 26.3 °C, $N = 947$; Fig. 12d). The lower temperature may have resulted from cool ambient water contacting the temperature sensor as the shark swallowed water when moving downward during a previous dive. Shark W6 also accelerated with a speed of 7 m s^{-1} downward at 21:43 hrs, consistent with searching for prey near the bottom. The shark expelled one of its two transmitters from its stomach on 17 November 1998, and the unit

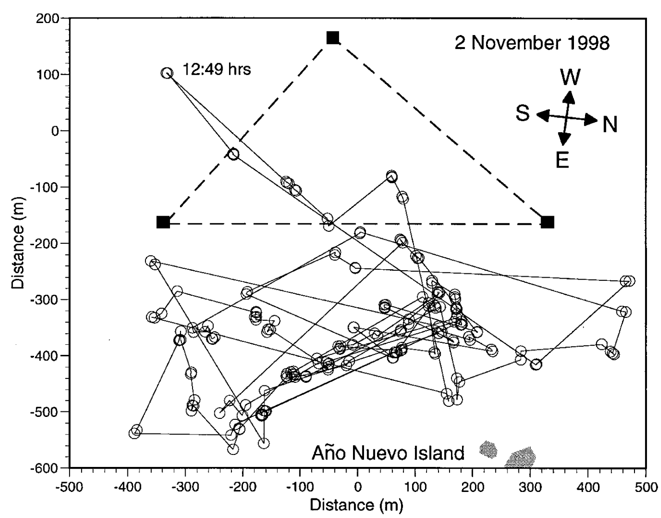


Fig. 11 *Carcharodon carcharias*. Path of Shark W6 on 2 November 1998. Note swimming movements back and forth in front of island, with single excursion away from island possibly to stalk a pinniped (■ RAP sonobuoys; ○ positions of W6)

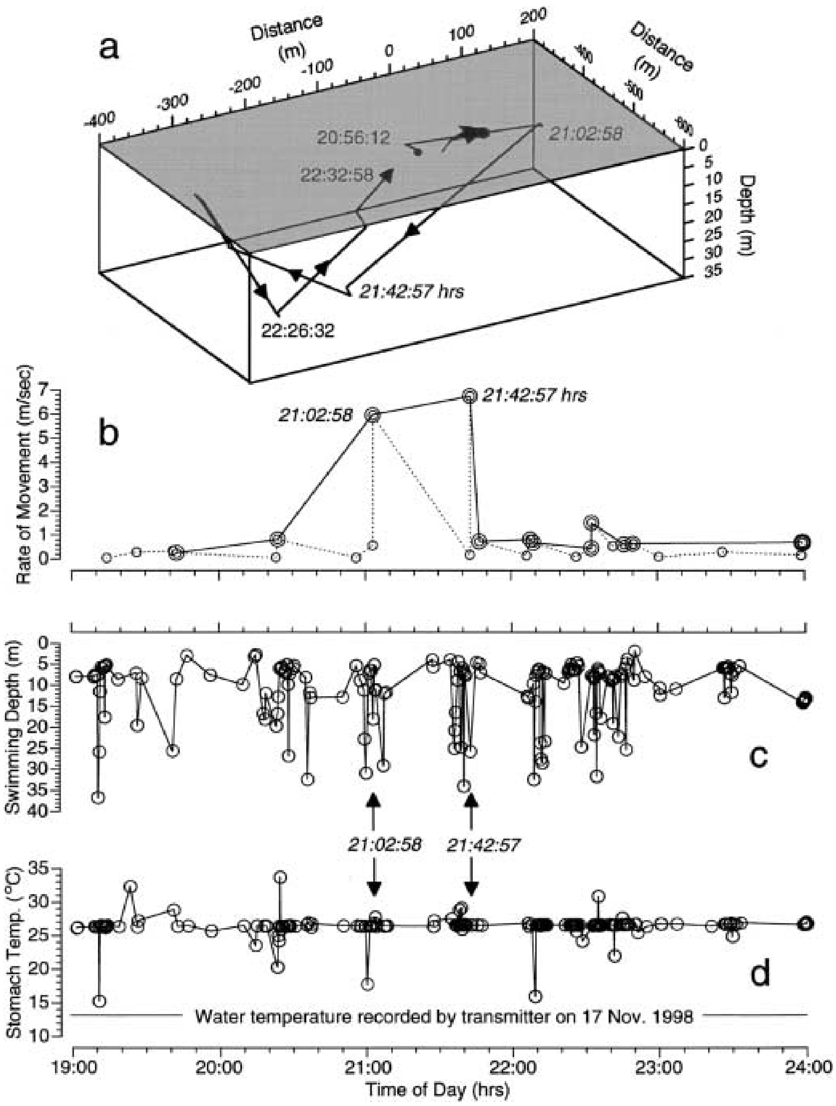


Fig. 12 *Carcharodon carcharias*. 3-D track of Shark W6 on 2 November 1998, showing rise to the surface at 21:02:58 hrs and dive to bottom at 21:42:57 hrs (**a**), and rates of movement (**b**), swimming depths (**c**), and stomach temperatures (**d**) from 19:00 to 00:00 hrs (*dotted line* in **b** rates of movement with intervals between positions separated by one min; *continuous line* in **b** rates with intervals ≥1 min)

recorded a water temperature at the bottom of 13.0 °C (see bottom data set in Table 2).

Discussion

System performance

The radio-acoustic positioning system was capable of accurately tracking sharks (*Carcharodon carcharis*) within an area of 1 km^2. The system localized a stationary beacon in the center of the sonobuoy array with an error (±2 m) identical to that predicted by software simulation (Fig. 4) using a timing error of 0.5 ms. Such high accuracy is consistent with the detection of small upward and downward movements of a diver holding a beacon in a 1 to 2 m swell by a similar RAP deployed off South Africa (O'Dor et al. 1998). However, the positional error was greater when tracking a moving white shark carrying a transmitter. We reduced this error by using only sets of positions with minimal separation between successive points. Use of a threshold standard deviation (SD) of 2800 clock cycles resulted in a linear alignment to the positions of two transmitters implanted within the stomach of the same shark. The resulting tracks were along the same path with the shark moving in a straight-line course toward Año Nuevo Island with a plausible speed of 1.2 m s^{-1}. The shark's swimming speed was slightly slower than the 1.32 m s^{-1} ($N = 268$) recorded from an adult using a paddle–wheel sensor (Klimley unpublished data). The shark's speed also resembled rates of movement estimated by tracking white sharks from a boat and calculating speed from the distance between successive 15 min boat positions; i.e. adult: mean = 0.90 m s^{-1}, $N = 145$, Strong et al. 1992; juvenile: 0.80 m s^{-1}, $N = 43$, Klimley unpublished data.

We used rate of movement as an index of relative activity of the sharks while within the range of the RAP array. The rates determined by the system are often overestimates of the shark's true swimming speed.

Aberrant high rates resulted when widely separated positions were not eliminated because they exceeded a known threshold positional standard deviation. Such exaggerated rates were present in the record of the putative predation by Shark W1 on 16/17 October 1997 (Fig. 10). We removed much of this variability from the records of W6 during the following year by eliminating sets of positions with a SD exceeding 2800 (2 Nov. 1998; Fig. 12). However, we also calculated rates only from points separated by 1 min to further reduce the RAP system's tendency to overestimate the tagged individual's swimming speed. These steps reduced the mean swimming speed of W6 on 2 November from 1.90 to 0.68 m s^{-1}, the latter being more comparable to the above-mentioned measurements of swimming speed in the field. We recommend that investigators, who are interested in describing the swimming capabilities of the species, measure swimming speed directly, using a paddle-wheel sensor.

Remote sensing of movements and behavior

Tag-detecting sonobuoys can provide diverse information about the movements and behaviors of a species. Firstly, they indicate when animals are present at a specific locality. It was evident from the plots of the presence and absence, that white sharks visited Año Nuevo Island during both daytime and nighttime in October 1997. Sonobuoys placed at a seamount in the Gulf of California showed that 18 tagged individuals were present only during daytime (Klimley et al. 1988). However, sharks emigrated as a group during daytime when the seamount was covered by a cold water mass, and returned when it was immersed in warm water (Klimley and Butler 1988). Tunas repeatedly visited fish aggregating devices (FADs) over a 9 mo period off Hawaii (Klimley and Holloway 1999) and a seamount in the Gulf of California (Klimley personal communication) over a year-long period at specific times during both daytime and nighttime with high temporal precision. Both hammerheads and tunas moved in and out of the range of the sonobuoy simultaneously consistent with a schooling habit, and returned to the site of tagging in preference to adjacent sites with sonobuoys (Klimley et al. 1988; Klimley and Holloway 1999). On the other hand, white sharks tracked during this study did not spend more time within the range of any particular sonobuoy. It would be difficult to obtain such long-term and continuous records of the occurrence of animals at these sites by tracking individuals with a boat. Yet manual tracking provided for hammerheads and tunas a description of their nightly excursions away from the sites outside the beacon-detection ranges of the sonobuoys (Klimley and Nelson 1984; Holland et al. 1990 a, b; Klimley 1993).

We have shown tracks of the sharks during daytime and nighttime for 17/18 and 19/20 October 1997, when the sharks swam within the range of three sonobuoys, an area of ca. 1 km^2. The sharks actively patrolled near the pinniped rookeries during the night as well as day. We have presented indirect evidence that the sharks fed once during night. We would have greater confidence in this interpretation if we had a better indicator of feeding. One potential indicator of feeding would be to place on a shark a "crittercam", a small camcorder in a waterproof housing equipped with an electronic time-release, acoustic, and radio beacon to permit localization and retrieval once the unit is shed from the shark and floats to the sea surface. These cameras, along with timed depth recorders, have been placed on a diversity of marine vertebrates including the white shark (Marshall 1998). We placed two crittercams on sharks during 1998, but were unable to recover them. A limitation of this technology is presently the brevity of the continuous sampling period (≥6 h) and the resulting low probability of recording infrequent behavioral events such as feeding or mating.

Another more direct method of detecting feeding would be to record continuous measurements of an individual's stomach temperature. Toward this end, we implanted a transmitter with a temperature sensor in W6 during fall 1998 to identify feeding by an increase or decrease in the shark's gastric temperature associated with feeding upon warm- or cold-bodied prey. The stomach temperature of white sharks varies from 23.4 to 27.8 °C (McCosker 1987; Goldman et al. 1996; Goldman 1997; present study), which is substantially higher than the ambient water temperatures 11 to 15 °C and lower than the 37.5 °C $\pm$ 1.0 °C body temperature of elephant seals (McGinnis and Southworth 1971). We anticipated that body temperature would increase substantially after feeding, with the duration of the temperature elevation increasing with the size of the meal. For example, bluefin tuna, *Thunnus thynnus*, showed elevations in stomach temperatures after ingestion of food 10 to 15 °C above ambient water temperature over a 12 to 20 h period (Carey et al. 1984). If a shark were to swallow a large part of an elephant seal, the latter's body temperature would be expected to raise the shark's stomach temperature by ≥10 °C. However, we observed no sustained elevation or depression of the stomach temperature of W6 during the 13 d period it spent near Año Nuevo Island.

Shark W6 moved back and forth parallel to the coastline, within 400 to 600 m of the shore, over a 2 wk period, consistent with waiting to intercept a seal or sea lion moving to and from the island. The spatial scale of this shark's movements was on the same scale at which feeding and reproduction occurs in many other large marine animals. For example, leopard seals feed upon Adelie penguins close to beaches in the Antarctic (Penney and Lowry 1967). Furthermore, nurse sharks court and copulate within a restricted area in the shallow waters off the Dry Tortugas (Klimley 1980), and squids perform a nuptial dance on a similar spatial scale in pelagic waters off South Africa (O'Dor et al. 1989; Sauer et al. 1997).

We believe that the RAP system has potential for monitoring the movements and behavior of large marine animals. The RAP system is most useful for tracking species that remain within a relatively small zone to feed or reproduce where buoys can be moored, the weather is reasonably good, and a homebase is near at hand for reception of the radio signal transmitted by the buoys. The system avoids two shortcomings of acoustic tracking. First, the RAP system remotely triangulates the position of the animal, whereas the course of a ship only roughly approximates the path of the subject and may frighten the individual, altering its natural movement and behavior. Second, the system operates autonomously, and is thus capable of recording the positions of animals and acquiring behavioral information over a longer time scale than the labor-intensive manual tracking aboard ship. The two systems can be used in a complementary fashion, with shipboard tracking of individuals once they move outside the restricted range of the RAP system.

A RAP system has certain advantages over data-storage or "archival" tags. The former operates in real time, immediately storing data on disk. Archival tags store their data in their electronic memory. The data from low-cost tags are retrieved when the tagged animal is recaptured. The rate of recapture of predatory fishes is usually low, ranging from 0.55% in the blue marlin to 9.4% in the shortfin mako shark (Klimley et al. 1994). More advanced archival tags will soon transmit their stored information to shore–based retrieval stations via satellite. However, these tags will do this only after release from the subject and floating to the surface, from where they will communicate by radio signal with a satellite each time it passes over. Future "smart" listening stations could also retrieve the contents of these tags, transmitted to the stations via an acoustic signal while the subject remains within range (Klimley et al. 1998). Once the listening station acquires the contents of the tag, the unit can clear its memory and begin again to collect and store information while the subject is away from the station. Although the range is limited, a RAP system can position an animal with an acoustic tag with high accuracy, at best with an error of only ± 2 m. Data-storage tags can collect information over a much greater geographical range, but must estimate their position from light measurements. "Geoposition" estimates by these tags are thought to be at best $\pm 1°$ ($+111$ km) for an actively swimming individual moving up and down in the water column under constantly changing light conditions (Hill 1994; Klimley et al. 1994). This promising technology will be most effective in tracking the long-distance movements of highly migratory species only when the method of position determination is improved. The RAP system, however, provides real-time monitoring of the movements and behavior of species with higher spatial accuracy but on a smaller geographic scale.

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