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Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the Sea of Cortez, Mexico, and the north Pacific Ocean

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Synopsis

We used satellite-linked radio telemetry to document the geographic and vertical movements and thermal habitats of whale sharks in the Sea of Cortez and as they migrated into the north Pacific Ocean. Of 17 sharks tagged between 1994 and 1996, six dispersed widely in the Sea of Cortez during 12–39 days of tracking. Four others left the Sea of Cortez and ranged extensively in the north Pacific Ocean. Indeed, one whale shark migrated to the western north Pacific Ocean, covering over 13 000 km in 37 months of tracking. The sharks generally occupied areas where sea surface water temperatures were between 28 and 32°C, though several ranged to depths of 240 m or deeper where water temperature reached 10°C or colder. Whale sharks may segregate by size and sex, and their movement patterns appear to be related to oceanographic features, such as sea mounts and boundary currents, where primary productivity may be enhanced. These results have important implications for the global conservation of the world's largest yet least known fish. We think that satellite telemetry is a exceptionally promising tool for learning more about the ecology of whale sharks, especially when combined with conventional methods of telemetry and molecular biology.

Introduction

Past studies

Knowledge of the distribution of the world's largest fish, the whale shark, *Rhincodon typus*, is meager and based largely on anecdotal records of sightings, incidental catches in fishing nets and beach cast animals (see syntheses by Wolfson & di Sciara 1981, Wolfson 1986, 1987, Bishop & Abdul-Ghaffar 1993, Beckley et al. 1997, Colman 1997). The species appears to be globally distributed in tropical oceans between 30°N and 35°S latitudes with occasional records as far north as 41°N and south to 36.5°S (Wolfson 1986). Local apparent abundance may be related to seasonal availability of concentrated prey (Taylor 1996, Clark & Nelson 1997, Colman 1997). Whale sharks are thought to be obligate filter-feeding planktivores that primarily eat small crustaceans, yet a few observations suggest that they may also eat algae and small fish on occasion (e.g. Gudger 1941, Silas[1]). Only recently has it been found that whale sharks are obligate lecithotrophic live-bearers (cf. Baughman 1955, Joung et al. 1996, Chang et al. 1997). Beyond this, virtually nothing is known of their life history, reproduction or population biology.

Whale sharks are known to aggregate seasonally in the Sea of Cortez, Mexico. The best known sites are Bahía San Luis Gonzaga, Bahía de Los Angeles, Bahía de La Paz, El Bajo, and Banco Gordo (Figure 1), though no predictable pattern among years is yet evident (Gudger 1941, Wolfson & di Sciara 1986, Wolfson 1986, 1987). Such aggregations present unusual opportunities to study some aspects of local whale shark biology (cf. Taylor 1989, 1996, Colman 1997) and to

[1] Silas, E.G. 1986. The whale shark (*Rhiniodon typus* Smith) in Indian coastal waters: is the species endangered or vulnerable? Mar. Fish. Infor. Serv. T & E Ser. 66: 1–37.

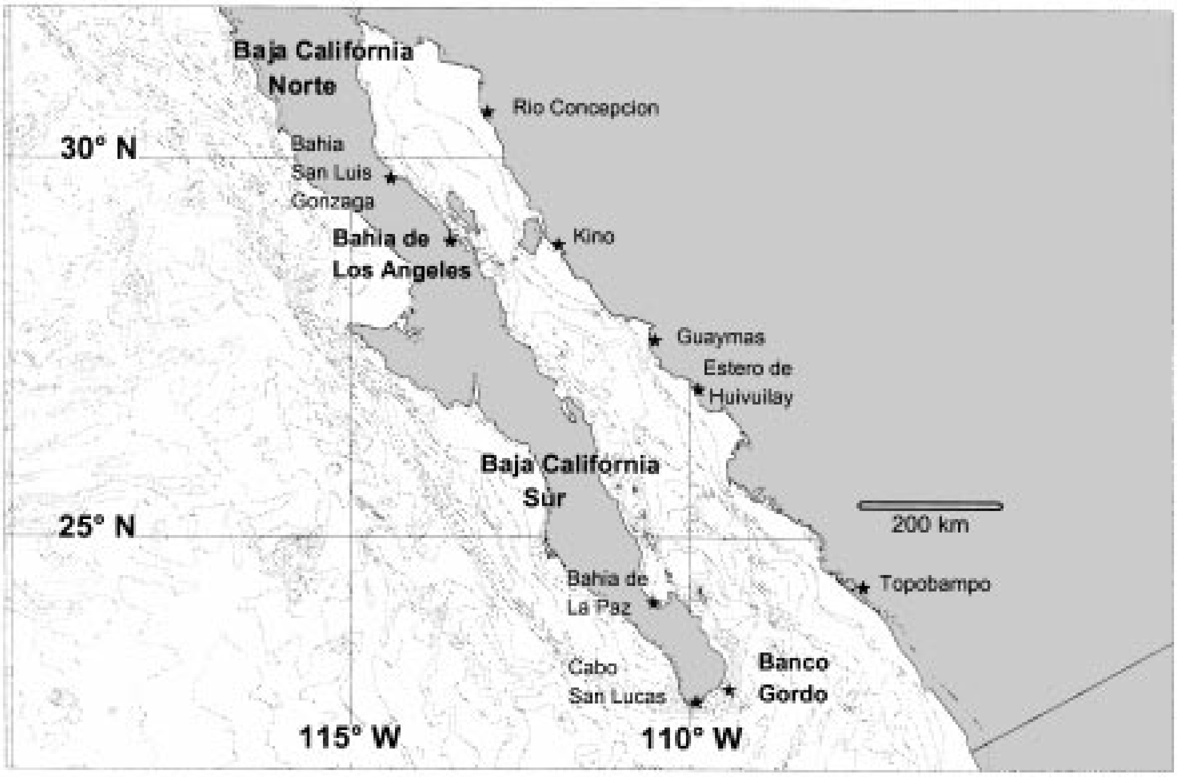

Figure 1. Baja California, the Sea of Cortez, and whale shark tagging sites at Bahía de Los Angeles and Banco Gordo.

allow more detailed study of their ranging behavior using remote sensing techniques. Consequently, to further the long-term interests of Hubbs-Sea World Research Institute in whale shark ecology (e.g., Wolfson & di Sciara 1981, Wolfson 1986, 1987) and owing to our recent applications of satellite-linked radio-telemetry to track the movements and behaviors of a variety of marine vertebrates (e.g., Stewart et al. 1989, 1996, 1998, Heide-Jorgensen et al. 1992, Stewart & DeLong 1995, Eckert & Sarti[2], Stewart 1997), we chose to evaluate the application of radio-telemetry technology to the study of whale sharks in the Sea of Cortez, Baja California, Mexico.

A variety of fishes have been tracked using short-range radio telemetry, though periods of monitoring have generally lasted only a few hours or, occasionally, a few days (e.g., Yuen 1970, Sciarotta & Nelson 1972, Dubsky 1974, Laurs et al. 1977, Nelson et al. 1977, Standora & Nelson 1977, Stasko & Pincock 1977, Carey & Robinson 1981, Carey et al. 1982, Carey & Scharold 1990, Nelson[3], Carey & Clark 1995, Cohen et al. 1999). Satellite-linked tracking and telemetry has become widely used in recent years in studies of terrestrial and marine mammals and various species of birds, but it has only rarely been applied to fishes, and the results have generally been poor (e.g., Priede 1984, Kingman[4], J. Stevens personal communication). One exception is the recent tracking of bluefin tuna, *Thunnus thynnus thynnus*, with timed-release, bouyant transmitters to document gross, short-term movements (Block et al. 1998, Lutcavage et al. 1999).

In the marine environment, satellite telemetry has been most successful in studies of seals and sea lions (pinnipeds), and sea turtles owing to their frequent appearance at the sea surface to breathe which allows

[2] Eckert, S.A. & L.M. Sarti. 1997. Distant fisheries implicated in the loss of the world's largest leatherback nesting population. Marine Turtle Newsletter 78: 2–7.

[3] Nelson, D. R. 1990. Telemetry studies of sharks: a review with applications in resource management. U. S. Nat. Mar. Fish. Serv. Tech. Rept. 90: 245–262.

[4] Kingman, A. 1996. Satellite tracking blue sharks. Shark News 7: 6.

sufficient contact with earth-orbiting satellites for data collection and location determination. Proven techniques for attaching the instruments, by gluing them to the animal's hair or shell or by attaching with a harness, have also been key to reliable short and long term tracking. The infrequent appearance of large fishes at and near the sea-surface means that buoyant satellite transmitters must either be towed behind the animal with a long tether which may allow the transmitter to occasionally break the sea surface often and long enough to make good contact with orbiting satellites (e.g., Priede 1984), or be secured close to the animals body with an in-line corrodible link to allow timed-release of the instrument which can then float to the surface and begin transmitting (e.g., Block et al. 1998, Lutcavage et al. 1999). The former approach may allow the determination of a number of serial locations and thus detailed documentation of migratory routes. The latter, however, may allow only the determination of the location of the animal when the instrument is released relative to where it was attached, but little detail on whereabouts in-between. Moreover, the tracking of the animal is terminated once the transmitter is released. Generally, sufficient opportunities have not been available to test these techniques with large free ranging marine fish to improve the prospects for long-term pelagic tracking, though the miniaturization of transmitter electronics and improved performance of high density batteries are cause for some enthusiasm.

Our goal was to determine whether whale sharks that appear seasonally in some areas of the Sea of Cortez reside there year-round, only appearing near the surface seasonally, or whether they disperse or migrate elsewhere in the Pacific. To accomplish that goal, we tested several methods of configuring and attaching radio transmitters to whale sharks and then document the sharks' geographic and vertical movements remotely using satellite-linked tracking techniques.

Materials and methods

Study area

Whale sharks have been periodically reported in two main areas in the Sea of Cortez, Bahía de Los Angeles in Baja California Norte (BCN) and Banco Gordo in Baja California Sur (BCS) (Figure 1). We observed and tagged sharks in the former location in autumn of 1993, 1994, and 1995 and in the latter area in early spring of 1996. We also made several aerial surveys, using a Cessna 182, along the eastern coast of Baja California to document whale shark abundance there. Moreover, local residents and fishermen, biologists, and tourists alerted us to the appearance of whale sharks in various areas.

Telemetry

We used satellite-linked radio transmitters (platform transmitter terminals, or PTTs) to monitor the vertical and geographic movements of whale sharks and to collect data on the amount of time that sharks spent at various depths and water temperatures. Transmissions from these PTTs were detected and processed by the Argos Data Collection and Location System (Argos DCLS) and then reported to us monthly in digital format.

Briefly, the Argos DCLS consists of two operational satellites that orbit the earth, in near-polar paths, every 101 minutes and which may detect signals from earth-bound transmitters between 6 and 28 times each day depending on the latitude where the PTT is located. If two or more signals are received by a satellite during a single orbit, then a location may be calculated from Doppler shift of successive transmissions. The accuracies of locations vary with several factors but they are often between a few hundred meters to tens of kilometers. The Argos DCLS codes accuracies of locations as either LC1, LC2, or LC3. The predicted accuracies of those locations are all within several kilometers of true. Other locations, primarily determined for tracking of wildlife, are coded as LC0, LCA, and LCB. The accuracies of those locations are not predicted by the Argos DCLS, though previous studies have found that they may often be within several kilometers of true locations (e.g., Argos 1996, Stewart & DeLong 1995, Stewart 1997). Full details of the Argos DCLS may be found elsewhere (Fancy et al.[5], Harris et al.[6], Stewart et al. 1989, Heide-Jorgensen et al. 1992). The key element for our purposes is that a PTT must break the sea surface and transmit while a satellite is overhead for either data to be collected or for a location determined.

We mainly used LC1, LC2, or LC3 locations to describe shark movements, though we also accepted

[5] Fancy, S.G., L.F. Pank, D.C. Douglas, C.H. Curby, G.W. Garner, S.C. Amstrup & W.L. Regelin. 1988. Satellite telemetry: a new tool for wildlife research and management. U.S. Dept. Int., Fish Wildl. Serv. Res. Publ. 172: 1–54.

[6] Harris, R.B., S.G. Fancy, D.C. Douglas, G.W. Garner, S.C. Amstrup, T.R. McCabe & L.F. Pank. 1990. Tracking wildlife by satellite: current systems and performance. U.S. Dept. Int., Fish Wildl. Serv., Fish Wildl. Tech. Rep. 30: 1–52.

LC0 locations if their position relative to the former locations was reasonable relative to prior locations and travel speed. We calculated summary statistics on distance covered and time elapsed between sequential locations to estimate rates of movement.

PTT design and attachment

We used three PTT designs during the study. One was based on an ST-10 transmitter (1/4 watt power output ; Telonics, Inc., Mesa Arizona), powered by a 3 volt lithium battery supply (two 2/3A size), encased in electrical potting resin, and then mounted in a float of syntactic foam with a hydrodynamic shape (Type I PTT, Figure 2a). The transmitters were programmed to transmit for 8 h each day. A conductivity circuit prevented transmission when the instrument was submerged. These tactics were used to conserve battery power, extend transmitter life, and ensure spontaneous transmission during brief surface periods if the instrument was submerged for more than 40 s.

A second instrument (Type II PTT, 1/2 W output, Wildlife Computers, Redmond, Washington; Figure 2b) included a microprocessor controller that stored time profiles of depth and water temperature. That instrument and its power supply (four C-cells with a 50 000 transmission capacity) were encased in a buoyant, cylindrical float of syntactic foam (5 cm diameter and 42 cm long). We programmed the microprocessor to measure and store depth and temperature data in a series of intervals which would later yield several frequency histograms for each six-hour time period of each day.

The third instrument was a hybrid of the other two, with a simple ST-10 transmitter that was encased in a Type II float. It was powered by 4 C-cell lithium batteries. Each transmitter float was attached to a 3.0–12.1 m length of either monofilament line (114 kg-test) or braided stainless steel cable (57 kg-test). A swivel was placed in line to prevent kinking. The line was then tethered to a shark using one of several barbed points which was inserted several cm subdermally just behind the first dorsal fin. Three subdermal dart styles were used to attach the tethered buoy. One was a modification of a Floy FII-69 stainless steel dart tag, with the identification streamer replaced by a monofilament tether. Another dart style was a Bandito #108/87 dual wing spear point and the third was a Bandito #21 slip-tip spear point, both commonly used in sport spearfishing.

We located sharks directly from our survey vessel or with the guidance of spotter plane. We then approached the sharks, by swimming or in a skiff, to within several meters and embedded the subdermal darts 2–4 cm off the dorsal midline near the first dorsal fin using either a 3 m fiberglass spear pole or a Mares Cyrano 850 pneumatic spear gun. The penetration of the darts was limited to a maximum depth of 8 cm by a stop on the spear shaft, as skin thickness is 10–15 cm in the targeted area near the first dorsal fin.

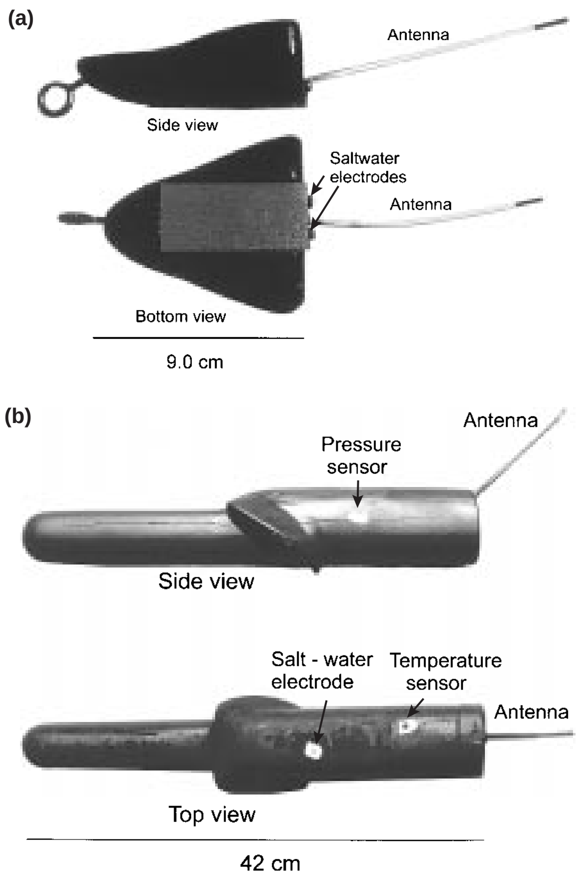

Figure 2. Towed satellite-linked radio transmitter designs used in whale shark tracking: a - type I instrument as viewed from the side (upper) and bottom (lower). b - type II instrument as viewed from the side (upper) and top (lower).

Results

We tagged seven whale sharks (Type I PTT) in Bahía de Los Angeles in September and October 1994 (Table 1). We tagged five more sharks there in early September 1995 (two with Type I PTTs, 3 with Type II PTTs) and then another five further south, at Banco Gordo, in June 1996 (one hybrid Type I PTT, four Type II PTTs).

Geographic movements

No records were obtained for two of the 17 whale sharks tagged. Four of the others were tracked for fewer than 7 days (Table 1). One (#7) of those remained in Bahía de Los Angeles (BLA) for the one day it was tracked, while another (#9) remained there for 3 days until contact was lost. Shark #1 left BLA immediately after it was tagged and moved about 58 km east until contact was lost the following day. Shark #6 remained in BLA for at least 5–7 days until the tag evidently detached and floated ashore where we recovered it 5 days later. Shark #4 remained in BLA for 17 days before contact was lost.

The other ten sharks either moved out of BLA (Figure 3) or out of the Sea of Cortez (Figure 4) and were tracked for 17–1144 days. Four of those sharks (#2, #3, #8, #12) moved into the northern Sea of Cortez until contact was lost, whereastwo (#5, #11) traveled south soon after being tagged (Figure 3). At least four sharks (#10, #13, #14, #15) eventually migrated away from the Sea of Cortez and two of them (#10, #15) traveled substantial distances westward. Indeed, shark #13 covered more than 12 000 km over 37 months (Table 1). Overall, sharks traveled between 23.3 and 12 620 km during 1.1–1144 days of tracking, averaging 4–29 km day^{-1} (Table 1, Figure 5). The weighted mean distance traveled per day was 23.8 ± 0.1 S.E. km (range = 0.1–95.6 km day^{-1}, $n = 14$). They covered more geographic distance when near the surface (23.9 km day^{-1}), when contact was more frequent, than they did at other times when locations occurred less often (17.5 km day^{-1}; Mann-Whitney 'U' test, $p = 0.02$). Average daily distances traveled appeared to correlate with shark size, though the sample is too small for statistical comparison (Figure 6).

Vertical movements

Data on vertical movements and time spent at various depths and in water of various temperatures were obtained from four whale sharks. During the 24 h prior to contacts with orbiting satellites those sharks spent most ($\geq$80%) of their time at depths less than 10 m (Figure 7a). However, the records also indicate that they also spent time in relatively deep water (Figure 7b).

Table 1. Whale sharks tracked with satellite-linked radio transmitters between 1994 and 1998 in the Sea of Cortez, Mexico, and the North Pacific Ocean (BLA = Bahía de Los Angeles, BG = Banco Gordo)[a].

Shark #	Length (m)	Sex	PTT type[b]	Date tagged	Tagging site	Days tracked[c]	Distance traveled (km)	Mean travel rate (km day^{-1})
1	3.7	F	I	6.10.1994	BLA	1	57.7	—
2	4.6	?	I	22.9.1994	BLA	22	—	—
3	3.0	F	I	19.9.1994	BLA	17	320.3	21.7
4	4.6	?	I	20.9.1994	BLA	17	31.7	3.2
5	4.3	?	I	20.9.1994	BLA	39	818.3	23.5
6	4.0	?	I	23.9.1994	BLA	5–7	23.3	8.4
7	4.0	?	I	7.10.1994	BLA	1	11.2	—
8	6.1	F	I	10.9.1995	BLA	12	404.6	23.6
9	3.7	?	I	10.9.1995	BLA	3	8.5	11.1
10	7.1	?	II	12.9.1995	BLA	1144	12620	17.1
11	3.7	F	II	10.9.1995	BLA	18	46.3	2.0
12	?	?	II	9.9.1995	BLA	28	199.6	—
13	15.0	F	hybrid	20.6.1996	BG	111	2863.6	28.8
14	18.0	F	II	19.6.1996	BG	30	206.8	18.2
15	?	F	II	19.6.1996	BG	665	7762	23.3

[a] Instruments on sharks #1 and #2 transmitted continuously. Those on sharks #3, #4, #5, #6, #7, #8, #9, and #13 operated on a cycle of 8 h on and 16 h off while those on sharks #10, #11, #12, #14, and #15 transmitted on a cycle of 24 h on and 36 h off.

[b] Tether materials were as follows: sharks 1, 2, 6, 7 = 13 m long monofilament tether with a Floy stainless steel dart; sharks 3, 4, 5 = 4 m long monofilament tether with Floy stainless steel dart tip; sharks 8, 11, 12 = 13 m monofilament tether with Bandito 108/87 dart tip; sharks 13, 14, 15 = 15.4 m long stainless steel tether with Bandito 21 dart tip.

[c] The transmitters on sharks 2, 3, 6, 8, 11, 12 are known to have become detached when the anchors pulled out and the transmitters were either recovered or determined to be washed ashore by the telemetry locations and data. The fates of the other transmitters are not known.

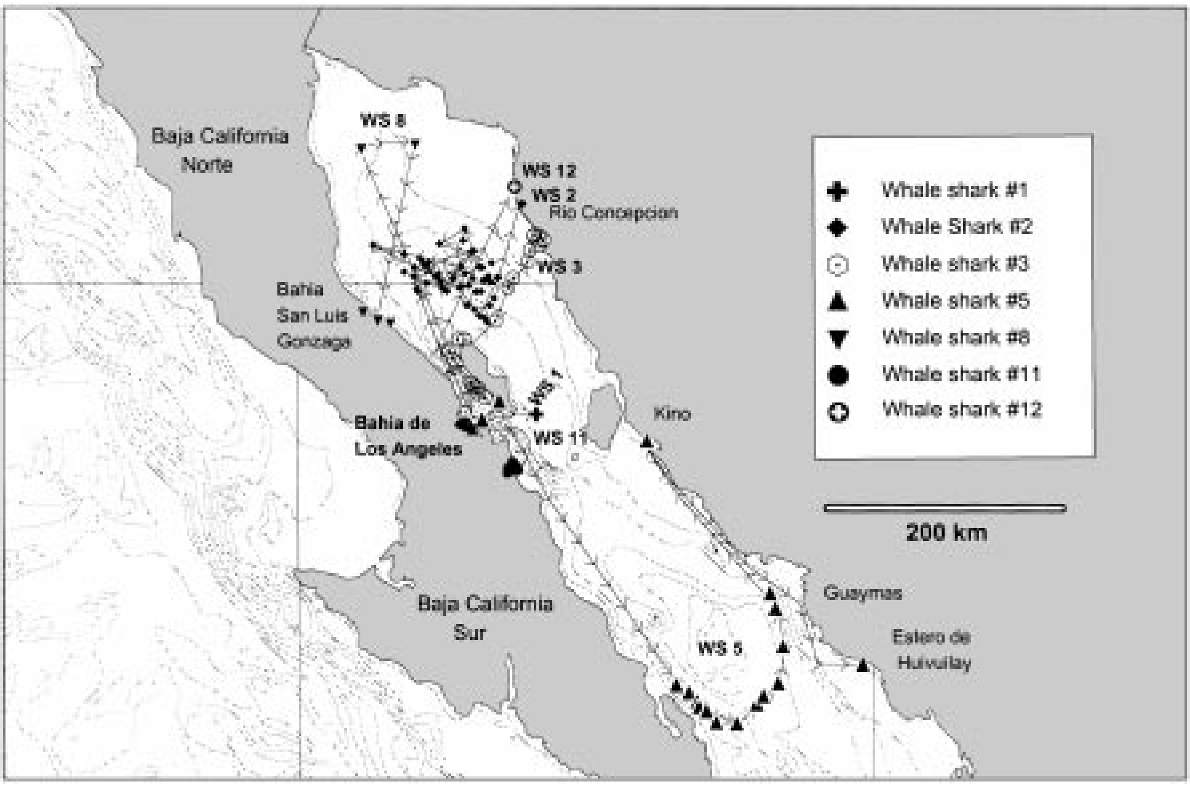

Figure 3. Movements of seven satellite-tagged whale sharks in the Sea of Cortez.

For example, shark #10 spent at least 1% of its time deeper than 240 m. No diel patterns were apparent in vertical movements for any of the sharks.

Thermal habitats

Sharks spent much of their time in areas where sea surface temperatures were between 20 to 32°C. Nonetheless, colder water did not appear to constrain their movements as several spent substantial time in subsurface water of 10°C or cooler (Figure 8). There was no apparent relationship between vertical movements and time of day.

Transmitter performance

The proportion of LC1, LC2, and LC3 locations differed substantially among the three types of instrument. The Type II transmitter, with its cylindrical shaped float and greater power output, performed best (Figure 9). We think that its better performance was primarily due to greater effective power of transmissions, particularly since the hybrid tag, which was housed in the same float as the Type II, performed no better than a Type I transmitter.

Performance of attachment and application method

We cannot easily evaluate the relative performance of the tether materials or the subdermal anchors because we did not systematically match them to the instrument types nor do we know how deeply the anchors penetrated or how well they seated. Nonetheless, instruments with the Bandito 21 anchor appeared to remain on longer (mean = 391 days) than the Bandito 108/87 (mean = 19.3 days) and the Floy (15.4 days) anchors. There were no clear differences in performance among the tethers.

Discussion

This is the first long-term tracking of whale sharks and indeed the first to document long-term

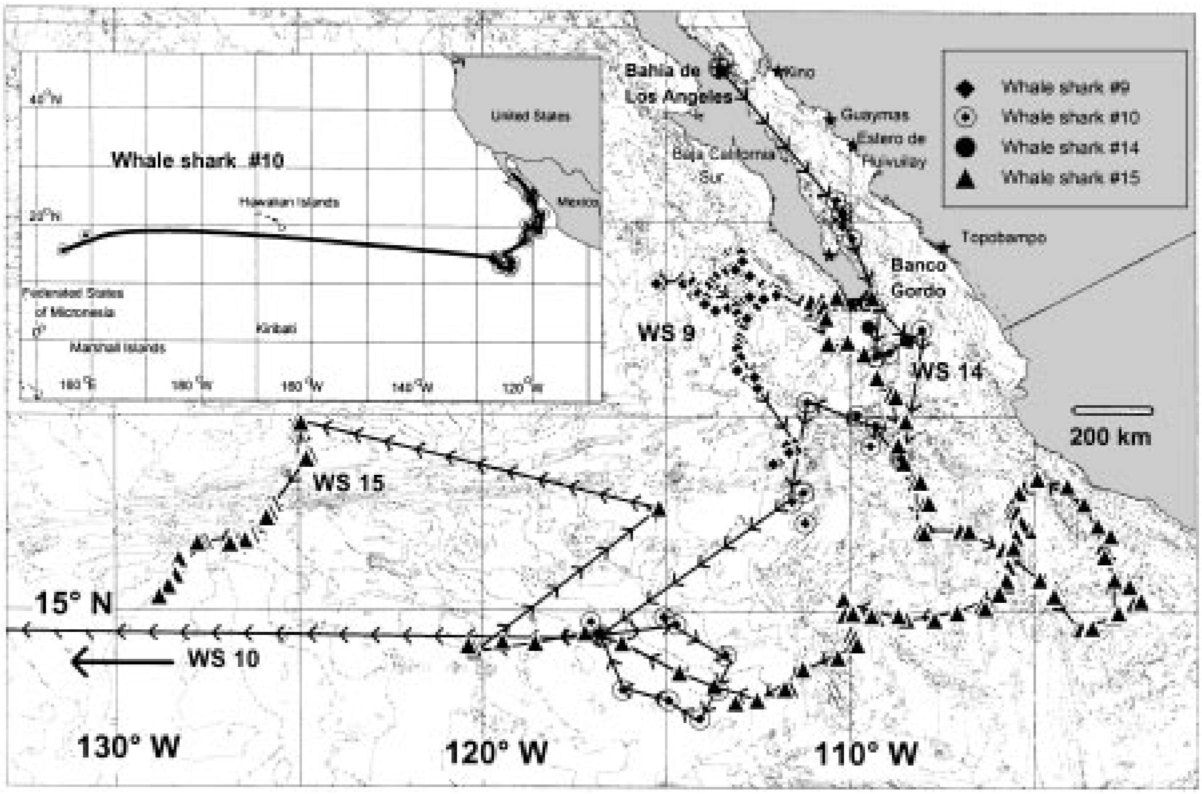

Figure 4. Movements of four satellite-tagged whale sharks that moved out of the Sea of Cortez into the North Pacific Ocean.

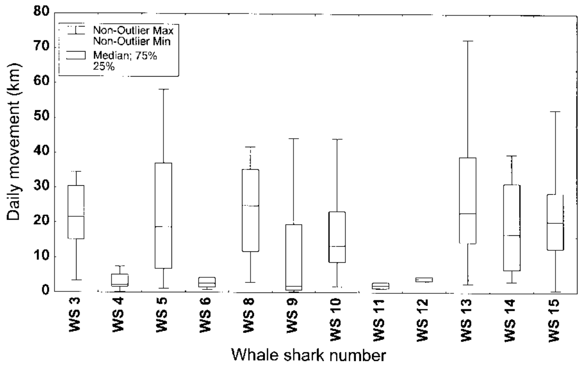

Figure 5. Daily travel distance of 12 whale sharks tagged with satellite-linked radio transmitters in the Sea of Cortez.

movement routes of any fish using satellite telemetry, notwithstanding the recent origin-to-destination tracking of bluefin tuna (Block et al. 1998, Lutcavage et al. 1999). Our results demonstrate the utility of the use of towed satellite-linked radio transmitters to study the ecology of whale sharks and perhaps other large pelagic fishes. Moreover, they indicate rather extensive use of vertical and geographic marine habitats by whale sharks and suggest that whale sharks may range widely, in the North Pacific Ocean at least, and perhaps make migrations that take several years to complete. The tracking of one shark over three years and across the North Pacific Ocean is particularly noteworthy as there has been no prior data to support the hypothesis that whale sharks from local populations (e.g., the eastern and western North Pacific) may mix. Still, there are too few data to determine whether individual whale sharks regularly return to the Sea of Cortez, as they apparently do in waters off western Australia (cf. Taylor 1996). Indeed, our data suggest that they may not, though additional studies are clearly needed to test that hypothesis.

Our data also suggest that whale sharks may segregate by size and sex while in the Sea of Cortez. Virtually all whale sharks that we encountered in the northern Sea of Cortez were less than 4 m long, whereas all of those encountered in the southern reach of the Sea of Cortez were three times that length (Table 1) and all sharks

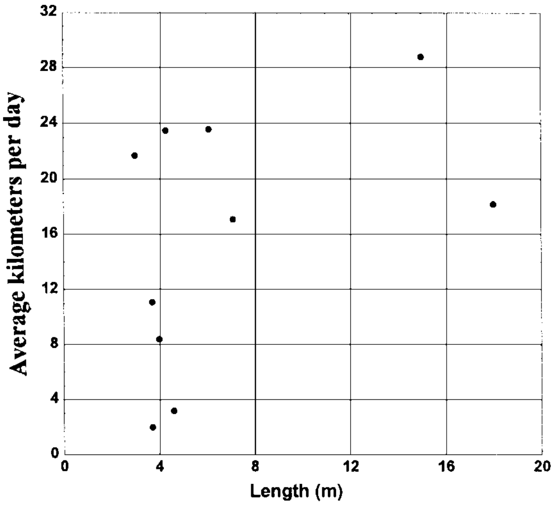

Figure 6. Daily distance traveled versus body length for 12 satellite-tagged whale sharks.

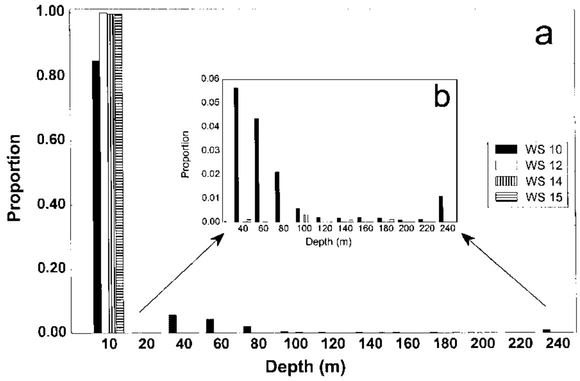

Figure 7. Proportion of time spent at depth for 4 satellite-tagged whale sharks in the Sea of Cortez, Mexico, and the North Pacific Ocean: a – depth profiles show that during the 24 hours preceding radio contact, the majority of time was spend in the upper 10 m of the water column. b – depth profiles show that sharks also spent time in waters substantially deeper than 10 meters and to 240 m and deeper.

that we found in the latter area were females (most of those appeared to be gravid).

The whale sharks that we tracked appeared to spend long periods at depth punctuated by briefer bouts of time near the surface, when we were able to locate them. However, we think that the data on their vertical movements may be biased overall towards warmer water temperatures and shallower depths, particularly for those sharks that weretracked for longer periods and consequently located less often. This is because

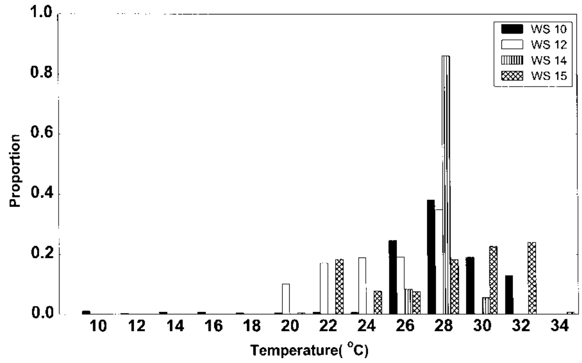

Figure 8. Proportion of time during the 24 hours preceding radio contact that sharks spent in water of various temperature.

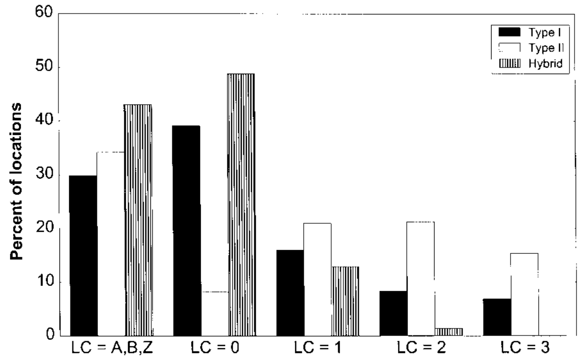

Figure 9. Percentage of locations of various accuracies versus instrument configuration (see Materials and methods for details).

the instruments were programmed to store and transmit data in 24 hour blocks. Consequently, if sharks had spent several days or more in deeper water before occasionally approaching the surface, those data would not have been available in the limited instrument memory to be transmitted. In any event, further work using instruments that archive data for longer periods of time and then transmit some or all of it later when the shark surfaces for extended durations or the tags detach and float at the surface (cf. Block et al. 1998, Lutcavage et al. 1999) could resolve this question. Nonetheless, our data do demonstrate that whale sharks spend time, perhaps substantial amounts, at depths greater than 240 m and in water as cold as 10°C.

Our direct experience while in the water with whale sharks indicates that they are strong, powerful swimmers, for short bursts at least. Similarly, the tracking data indicated occasional travel rates of up to 96 km day^{-1} (3.9 km h^{-1}). Overall, however, the tracking data indicate that they are generally slow swimmers and migrators especially compared with other large pelagic sharks. The overall average travel rates that we documented were around 24 km day^{-1} (1 km h^{-1}). These rates compare with 1.5 km h^{-1} for blue sharks (Carey & Scharold 1990), 3.2 km h^{-1} for white sharks (Carey et al. 1982, Strong et al. 1992), 3.6 km h^{-1} for tiger sharks (Tricas et al. 1981), 2.7–3.4 km h^{-1} for basking sharks (Harden Jones 1973, Priede 1984), and 1.2 km h^{-1} for a megamouth shark (Nelson et al. 1997). When we have observed whale sharks in the Sea of Cortez, they appear to swim continuously, though recirculating in small geographic areas while filter-feeding. They also occasionally remain stationary and vertical in the water column while pumping prey-laden water through their gill slits. Thus the tracking data, as indicators of geographic distance covered per hour or day, may not generally reflect true swim speed.

From the movements of sharks outside of the Sea of Cortez, we think that their distribution may be influenced primarily by oceanographic features which correlate with enhanced upwelling and plankton productivity, like the sea mounts near the Revillagigedo Islands and Clipperton Island and along current boundaries in the central north Pacific Ocean.

Future directions

Though our studies have revealed some data on the vertical and geographic movements of whale sharks in the Sea of Cortez and in the North Pacific Ocean, research is clearly needed to document the behaviors of a larger number of individual whale sharks in these regions and in other oceans. Additional information is needed on the relative and seasonal distributions of adult versus juvenile whale sharks and adult females versus males. Moreover, the genetic relationships of putative whale shark populations is an important issue for the global conservation of this poorly known animal. Tracking the habits of these elusive fish using satellite technology presents the most feasible method of further learning, especially when combined with molecular genetic techniques and conventional radio-telemetry.

Because so little is known about whale sharks, virtually any questions about the species' life history, physiology, foraging ecology, demography, and behavior could be posed as hypotheses. Few of those may be actually testable (i.e., truly falsifiable) though, owing to the sharks' cryptic nature and brief seasonal appearances at a few locations. Nonetheless, in further applications of telemetry (especially satellite-linked) and molecular techniques, we think that the following null hypotheses follow directly from the preliminary and suggestive results that we report here and are the most tractable:

(1) Whale sharks are sedentary local residents year round but occur near the sea surface seasonally and live at depth during the others.
(2) The age and sex structure of local whale sharks is reflective of the population at large and the species does not aggregate by age or sex seasonally or during the species life cycle.
(3) There are no inter-region or inter-ocean genetic differences among populations of whale sharks.

Further studies which address these hypotheses, or are even merely descriptive, should contribute substantially to the knowledge of whale sharks and also effectively structure the approach and direction for additional research.

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