Review

Hunting and migratory movements of white sharks in the eastern North Pacific

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Abstract: The aim of these studies was to determine local movements of hunting white sharks (*Carcharodon carcharias*) near a seal rookery and global movements during migration. Seven adults were monitored locally with attached ultrasonic tags that received and telemetered animal position and behavior via an array of three-acoustic-positioning (RAP) buoys moored off Año Nuevo Island, California. Migratory movements of 6 adults departing this island and nearby Southeast Farallon Island were tracked for 2–6 months with attached pop-up satellite archival tags. Sharks began hunting seals at Año Nuevo Island in October, spending 40% of the day patrolling the 1 km^2 receptive field within 400 m of the island at a depth of 30 m or less. For six weeks, they did not stray far or long from the area, were equally active at night as by day, were non-territorial, and fed infrequently. This nearshore phase at both island rookeries ended abruptly in winter as the sharks moved offshore to a region of the subtropical eastern Pacific halfway to Hawaii. An adult male went further, traveling to Hawaii where it remained until migrating back to California, only to repeat the journey the following year. Electronic tagging provides vital information on the hunting and migratory behavior of this apex predator.

key words: white sharks, predation, hunting, migration, tracking

Introduction

Much of our understanding of predator-prey relations in mammals comes from studies of large terrestrial carnivores, dogs and wolves (*Canidae*), hyenas (*Hyaenidae*), cats (*Felidae*) and bears (*Ursidae*) and their large prey, a variety of ruminants (*e.g.*, Mech, 1966; Schaller, 1972; Kruuk, 1972; Packer *et al.*, 1990; Bergerud, 1988; Caro, 1994). In contrast, little is known about the predator-prey relationship of large vertebrates in the marine environment. Predation by killer whales, *Orcinus orca*, sharks, *Carcharhinidae*, and polar bears, *Ursus maritimus*, on a variety of seals and sea lions (Stirling, 1974; Kelly *et al.*, 1987; Riedman, 1990) is significant. Leopard seal, *Hydrurga leptonyx*, predation on Antarctic fur seals, *Arctocephalus gazella*, is documented (Boveng *et al.*, 1998). The hunting strategies of the predator and the impact of predation on the population dynamics, life history, and behavior of the prey, however, is unclear. Apex predators can initiate forces that cascade down to successively lower trophic levels affecting not only the prey but also the base of the food web (Paine, 1980; Strong, 1992; Carpenter and Kitchell, 1993). For example, recent killer whale

predation on sea otters, *Enhydra lutris*, in western Alaska is linked with increases in sea urchin biomass and decreases in kelp density (Estes *et al*., 1998; Hatfield *et al*., 1998). Nevertheless, the top-down cascade is difficult to demonstrate in apex predators in the ocean, in part because these predators are thought to feed infrequently in bouts that are widely separated temporally and spatially.

One of the least well understood large predators in the marine environment is the white shark, *Carcharadon carcharias*, an apex predator that preys on fish as a juvenile and pinnipeds as an adult (Tricas and McCosker, 1984; Klimley, 1985). In the northeastern Pacific Ocean, white sharks have been observed feeding on California sea lions, *Zalophus californianus*, harbor seals, *Phoca vitulina*, Steller sea lions, *Eumetopias jubatus*, and their preferred prey, northern elephant seals, *Mirounga angustirostris* (Ainley *et al*., 1981, 1985; Le Boeuf *et al*., 1982; Klimley *et al*., 1992; Anderson *et al*., 1996).

During the last three decades, it has been well documented that white sharks prey on northern elephant seals at rookeries in central California such as Año Nuevo Island and the Farallones. This has been revealed by observed attacks on seals, fresh white shark inflicted bites on seals, and stomach remains in moribund white sharks. On numerous occasions, white sharks have been observed killing and consuming elephant seals in the nearshore waters adjacent to both islands. The victims have been identified as juveniles of both sexes and adults of both sexes. Elephant seals with massive shark bites have washed up dead on Año Nuevo Island and up to 17 living seals per year have been observed in the fall and winter with fresh shark wounds made by white sharks (Le Boeuf *et al*., 1982; Le Boeuf and Crocker, 1996). The effect of white shark predation on the 54% mortality rate of pups from Año Nuevo Island going to sea for the first time (Le Boeuf *et al*., 1994) is unknown. Elephant seal behavior when approaching or departing Año Nuevo Island is consistent with taking precautions to avoid an encounter with this near-surface predator; on the continental shelf near the island, seals dive to and follow the substrate, swim fast, and minimize time at the surface compared to their behavior beyond the continental shelf (Le Boeuf and Crocker, 1996).

Understanding the predator-prey relationship between white sharks and elephant seals requires extensive knowledge of the life cycles of both species. Although the habits of elephant seals on land and at sea are better known than those of other pinnipeds and many terrestrial mammals (Le Boeuf and Laws, 1994), white shark life history and natural history remains poorly known. Developments in bio-logging science during the last two decades offered the opportunity to close this gap and add significantly to knowledge of the life history and foraging strategies of white sharks, and in so doing, elucidate the predator-prey relationship with elephant seals.

My aim is to summarize two projects on white sharks conducted in central California during the last six years with which I've been associated. Both approaches used bio-loggers. The objectives were to determine: (1) the local movements of white sharks hunting near a seal rookery and (2) the global or migratory movements during the year when away from the rookeries. Additional details of the local movements study can be found in Klimley *et al*. (1998, 2001a, b); details of the global movements study can be found in Boustany *et al*. (2002). The latter study on migratory behavior is continuing and involves the collaboration of several of us from three institutions tagging white sharks at both Año Nuevo Island and Southeast Farallon Island: Barbara Block and Andre Boustany from Stanford University, Peter Pyle and Scot Anderson from Point Reyes Bird Observatory, and Scott Davis and me

from the University of California at Santa Cruz.

Materials and methods

The methods of tagging were an outgrowth of long-term studies at the Farallon Islands near San Francisco Bay that began during the early 1980's, in which it was observed that white sharks return regularly to the rookery at predictable times of year and could be anticipated, located, and tagged (*e.g*., Ainley *et al*., 1981, 1985; Klimley, 1987; several chapters in Klimley and Ainley, 1996).

Two methods of tagging white sharks with bio-logging devices were employed. Habitat and opportunity, which differed at the two island sites, Southeast Farallon Island and Año Nuevo Island, determined which method was used.

The method used at the Southeast Farallon Island exploited the panoramic view of nearshore waters from Lighthouse Hill (elevation, 102 m). From this high post, observers scanned the surrounding waters during daylight hours for evidence of a shark attack or kill, made all the more obvious by the numerous gulls on this island that flocked to the site competing for remains. When a shark kill or attack was sighted, a boat was launched and two researchers motored to the site, gaffed the moribund prey and secured it alongside the boat. As the shark returned to feed on the carcass, it was tagged in the dorsum behind the dorsal fin using a 4 m long pole on the end of which was the instrument attached to a barb by a short cable.

This method was not useful at Año Nuevo Island because its low elevation (6 m) provided limited perspective. Instead, researchers motored up the coast to the outer waters off the island in a 16–25 ft boat. The engine was turned off and a decoy, a plywood cut-out in the shape of a female elephant seal, was set adrift on the surface 10–20 m from the boat (Fig. 1). When a shark rose to the surface to investigate the decoy, it was reeled in slowly until it and the following shark were near the boat. A dead seal wrapped in a burlap sack was stirred in the water over the side to get the shark's attention. When the shark was in range at or near the surface, the barbed tag was plunged into its dorsum using a long pole as described above.

Hunting behavior of white sharks at Año Nuevo Island

The aim of this study was to elucidate the hunting and feeding pattern of white sharks in the waters near Año Nuevo Island, a seal rookery approximately 100 km south of San Francisco, California. We did this by tagging individual sharks with ultrasonic transmitters, continuously tracking them while they were hunting seals near the island, and acquiring a near-continuous record of their behavior with a radio acoustic positioning (RAP) system (VEMCO Ltd., Canada).

Instruments used and animals tracked:

Ultrasonic tags were attached to seven white sharks shortly after they arrived in the vicinity of the island and began hunting and before inclement winter weather set in. Tracking of the instrumented sharks was done using an array of three RAP buoys anchored in the high-risk zone of shark attack approximately 400 m from the island (Fig. 2). The buoys were linked by radio to a receiving and processing station on the island. Each buoy consisted of an anchor, chain, and line leading to a surface buoy with hydrophone, frequency-synthesizing receiver, microprocessor microcontroller, two-way radio, and antenna. The land base station contained
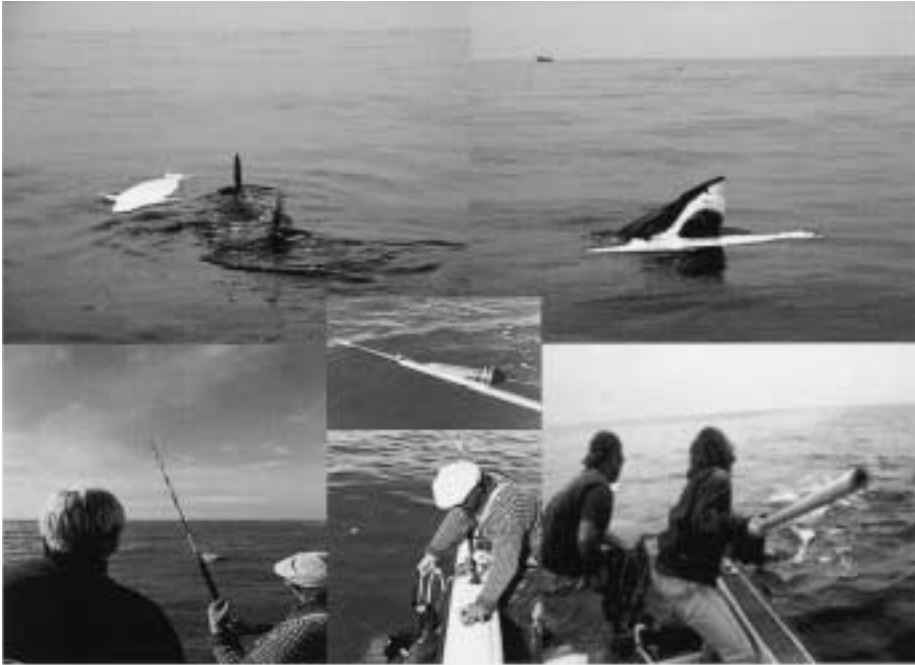
Fig. 1. Photographs illustrating the method of tagging white sharks. Upper left: a white shark approaches the
decoy. Upper right: a large white shark takes the decoy in its mouth, but in this case, did not bite down on
it. Lower left: the decoy is reeled in slowly when a shark approaches it. Lower middle: the water is
chummed with a dead seal to attract the shark close to the boat so that it can be tagged. Middle: a PSAT
tag with barb shown on the end of the tagging pole. Lower right: a white shark is tagged.

a two-way radio, interface with signal timer and decoder, and personal computer. Whenever
the receiver on the buoy detected an acoustic pulse from a beacon or transmitter on a shark,
the two-way radio echoed that pulse in a unique radio frequency. This echo was received by
the two-way radio at the base station, timed by the interface, and used with the times of
unique echoes from the other two buoys to calculate the position of the transmitter and dis-
play its track in real time. An automated scanning circuit in the receiver enabled us to track
multiple sharks in rapid succession, locating the units with the lowest signal frequency first
and tracking it for a preset interval (*e.g*., 5–10 s) before moving to the unit with the next high-
est frequency, and so forth. The receptive field in which the sharks could be tracked was
approximately 1 km^2.

   Five adult white sharks, 4.5–5.2 m long, were simultaneously tracked in the fall of 1997.
The beacons on the sharks provided location in the receptive field, from which we calculated
rate of movement and separation distance between neighboring sharks. These sharks were
tracked nearly continuously for 15 days during the period, 13 to 30 October 1997. During
1998, we tracked a single adult female white shark for 12 days (22 October to 13 November)
with a temperature and depth transmitter (TD transmitter) lodged in her stomach as a result
of swallowing a bolus of marine mammal meat with the TD transmitter embedded in it. The
aim was to track movements, identify bouts of feeding, indicated by a rise in stomach tem-
perature, and the pattern of swimming associated with prey capture. We tracked another adult
shark during the fall of 1999, recording measurements of location, swimming speed and
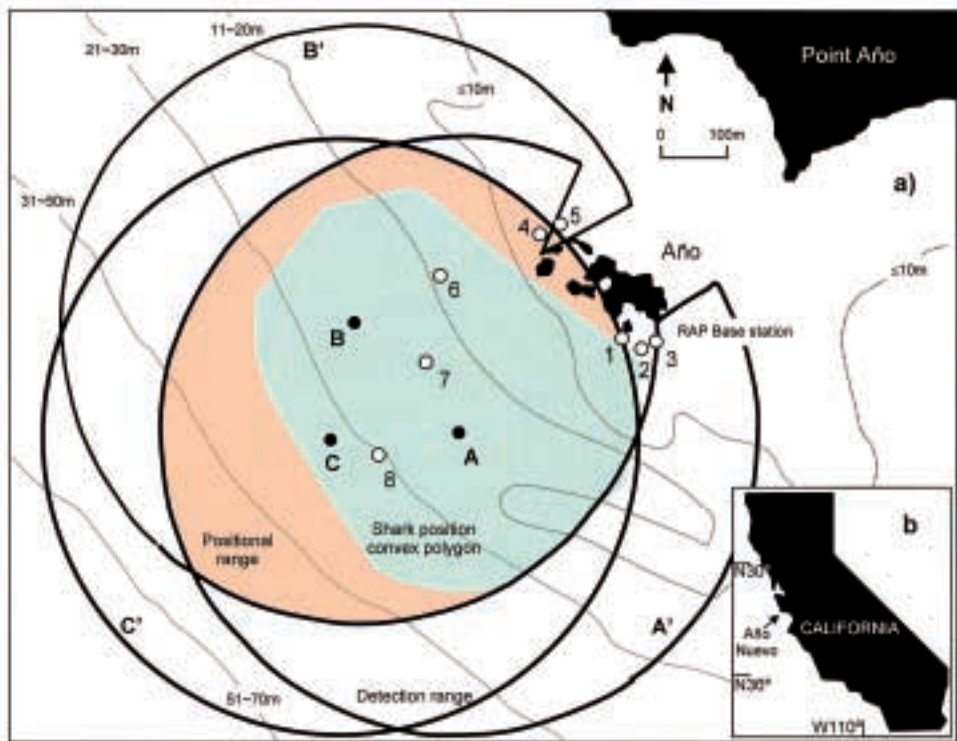
Fig. 2. A schematic map showing the location of the radio-acoustic positioning system (RAP) in relation to Año Nuevo Island and the mainland. A beacon on tagged white shark emits an ultrasonic pulse that is detected by hydrophones on the three-sonobuoy array; this information is sent by radio receiver to a receiving station on the island, where the shark's position is displayed on a computer monitor and stored on disk. Open circles indicate the location where the seven white sharks were tagged. Closed circles indicate the positions of sonobuoys A, B, and C. The large circles, A', B' and C', indicate the receiving range of each sonobuoy. The orange area indicates the area in which positions could be determined. The green area is a concave polygon indicating the home range of the sharks tracked in October and November of 1997–1999. Adapted from Klimley *et al*. (2001a).

swimming depth for three nights during the period, 30 October to 2 November.
Results and conclusions:
Data obtained from these instrument deployments, together with repeated observation of naturally marked sharks, and observation of fresh shark bites on seals on the island, led to the following general conclusions.

1) Time of observation. Adult white sharks of both sexes are observed regularly in the waters near Año Nuevo in the fall with the first observations being in mid-October. Individuals identified by natural markings or streamer tags have been observed here at this time of year for up to six consecutive years.

2) Duration of observation. From observation of tagged and naturally marked individuals, white sharks remained in the vicinity of the island for at least six weeks before inclement weather made it no longer feasible to track them with the RAP system. Studies of global movements (see below) indicate that departure from central California seal rookeries occurs between mid-November and mid-January.

3) Number of sharks. It is estimated that fewer than 10 sharks were in the waters in and around the receptive field near Año Nuevo Island at any one time during the course of this study.

4) Time in the receptive field near the island. Sharks tracked by the RAP system spent a substantial amount of time in the receptive field close to the island. On average, 40% of each day was spent within tracking range of the array. The individual range varied from 29 to 52%. Moreover, the percentage of time per day spent in the receptive field varied from day to day. For example, one male spent 73% of one day in the receptive field followed by only 23% the next day. On average, time in the receptive field lasted 45 min.

5) Excursions away from the rookery. When tracked individuals left the receptive field they did not travel far and returned quickly. Median time away from the receptive field was 60 min. Given a cruising speed of 1.34 m/s, it is estimated that the maximum distance moved from the rookery was 2.4 km.

6) Time of day patrolling the receptive field. The tracked individuals visited the receptive field at all times of the day and were equally active by day, by night and at twilight.

7) Patrolling. The sharks exhibited back and forth patrolling movements along the shore, a pattern consistent with being in position to intercept seals or sea lions departing and returning to the rookery. Some of these movements were roughly perpendicular to the shore, perhaps indicative of stalking or chasing. Most of the shark movements were within 700 m offshore of the island, with some sharks approaching to within 2 m of the shore. The mean daily swimming depth of the shark monitored in 1998 was 12.2 m (range = 7.8–15.3 m). This shark spent most of its time patrolling 200–300 m from shore. Most of the time the shark cruised at 1.34 m/s but rare bursts of 6–7 m/s were observed. The mean stomach temperature while patrolling was 26.9°C.

8) Site specificity. Although some sharks showed a preference for certain areas, such as close to one buoy or another, there was no evidence of territorial defense. All of the sharks moved over the same areas at one time or another.

9) Solitary strategy. Hunting was solitary. Tracked sharks did not swim in close proximity to each other while patrolling near the island. The median distance separating the five sharks tracked simultaneously in 1997 was 80 to 420 m. Three sharks tagged on the same day near a sea lion kill did not associate with each other more frequently than with other sharks tagged on a subsequent occasion. That is, the three sharks seen together at initial tagging did not hunt together as a social group. The simultaneously tracked sharks showed no evidence of attraction or avoidance of each other. Most likely, each individual searched for prey alone but "eavesdropped" on others to be ready to come to the site to compete for a share of a kill made by any one of them.

10) Feeding pattern. Feeding was evidently infrequent since we observed no kills or attacks on prey and there were only two potential predatory attacks discernible in the tracking records of the five sharks studied in 1997. These two episodes consisted of bursts of rapid swimming, abrupt change in direction and distance of swimming in or away from the receptive field, and the proximal concomitance of two sharks in the same area, all of which suggest chasing and possible killing of prey. The conclusion also follows from the lack of clear evidence that the shark with a stomach probe in her stomach fed during intermittent monitoring totaling 12 days over a 28-day period.

Migratory behavior and global movements

Previous tracking studies of white sharks were limited to seasonal investigations near coastal seal rookeries (*e.g*., Campagno, 1984; Klimley, 1985; Goldman *et al*., 1996). From these local tracking studies and scattered observations as sea, white sharks along the west coast of North Amercia are thought to be restricted to shallow coastal waters over the continental shelf. Based on 109 records, Klimley (1985) proposed that females give birth in late summer and early fall south of Point Conception in southern California and that later in the fall adult sharks move northward to feed on pinnipeds.

The objective of this study was to determine large scale movements of white sharks during the year. We were interested in questions such as: Where do the sharks go when they leave off hunting near the central California seal rookeries? What is the annual pattern of global movements? What depth of water do they prefer? What is the range of water temperatures to which they are exposed? Are they restricted to shallow waters over the continental shelf? Did they move up and down along the coast between breeding and feeding?

Instruments and animals tracked:

We attached pop-up satellite tags (PSATs) to six adult sharks of both sexes (four males and two females), 3.7–5.0 m long, hunting at Año Nuevo Island or Southeast Farallon Island in the fall of 1999 and 2000. The barbed tags were placed in the dorsal musculature using one of the two methods described above. The tags (see Block *et al*., 1998, 2001) recorded pressure (swimming depth), water temperature, and light level data every two minutes, and stored the information onboard. Location was estimated from the light level data (Hill, 1994; Welch and Eveson, 1999). The tags were programmed to detach from the fish after 4–6 months, float on the water surface, and transmit a summary of the stored data via the Argos satellite system.

Results and conclusions:

After tagging, all sharks exhibited the near-shore behavior characteristic of hunting seals described above in the RAP study (Klimley *et al*., 2001a, b). Most of their time was spent between the surface and 30 m and they were exposed to water temperatures ranging from 10 to 14°C. Two tags popped to the surface prematurely after only 15 and 27 days, while the sharks were still hunting in the near-shore phase.

After approximately two weeks of hunting near the seal rookery, the other four sharks, two males and two females, moved offshore headed due west across the continental shelf into deep waters of the Pacific (Fig. 3). They remained in this exclusively pelagic phase for 4–6 months until the tags popped up and stopped recording. One individual (shark 5, a male) traveled 3800 km to the waters off the west coast of the Hawaiian Island of Kahoolawe, near Maui. The other three sharks moved to a region of the subtropical eastern Pacific about half way between Hawaii and the west coast of the North American continent. Shark 5 reached Hawaii in 40 days, traveling at a minimum velocity of 71 km/day. He remained there for almost four months before the tag stopped recording.

During transit to these distal locations, all four sharks exhibited a daily bimodal preference for depths of 0–5 m and 300–500 m. Up to 90% of the day was spent at these depths and little time was spent at intermediate depths. The swimming and diving pattern changed again when the sharks reached their ultimate destination. For example, when shark 5 reached Hawaiian waters, his time was rather equally distributed between the surface and 300 m throughout his stay there. Thus, three swimming/diving patterns were exhibited across the
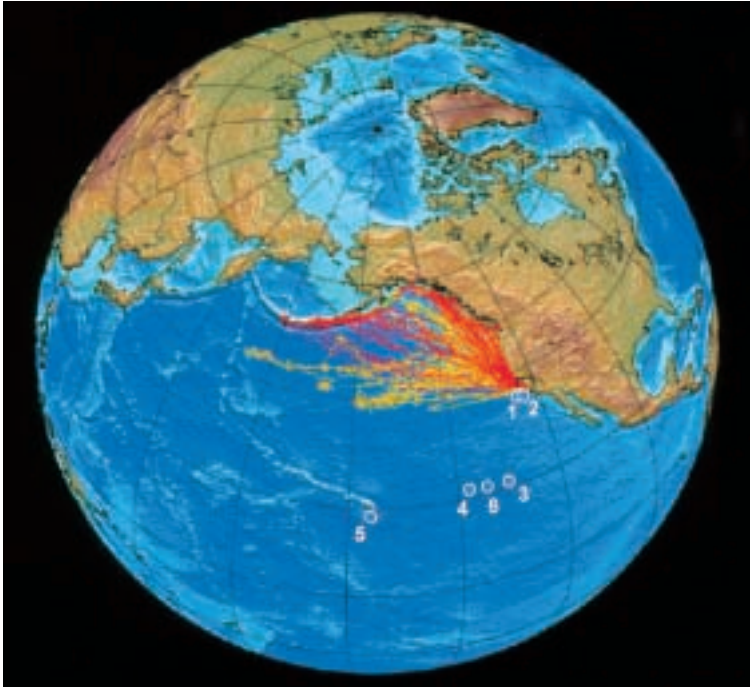
Fig. 3. PSAT pop-up locations of six white sharks (open circles) tagged near Año Nuevo and Southeast Farallon
         Islands in central California seal in 1999–2000 (dark square), in relation to the migratory paths of adult
         male (red) and adult females (yellow) to and from the Año Nuevo seal rookery during the spring and fall
         of 1995–1997. Adapted from Le Boeuf *et al*. (2000) and Boustany *et al*. (2002).

three phases: shallow swimming in the near-shore phase while hunting near seal rookeries in central California, a daily bimodal depth swimming pattern during transit, and a daily swimming/diving pattern evenly distributed by depth at the distal migratory destination.

During the southwest transit the maximum dive depths increased abruptly beyond the continental shelf and the sharks experienced a broader range of temperatures. Sea surface temperatures rose from about 13°C near the coast to about 26°C in Hawaii. Minimum temperatures at the greatest depths (650 to 680 m) dropped to 4.8°C, showing that white sharks can withstand a broad temperature range.

Deployments in 2001 produced similar results; shark 5 returned to the Farallones in the fall and was tagged again, and again returned to Hawaiian waters for the winter months (Pyle *et al*., 2003). Evidently, some individual white sharks are reliable creatures of habit judging by their repeated timely appearance at distal destinations in their migration as well as at seal rookeries in California. At Año Nuevo Island, individuals have been observed annually in the fall for six consecutive years. At the Farallones, a female was observed every other year over a ten-year period (Pyle *et al*., 2003).

These results reveal a different annual cycle than was previously thought. The white shark range contains not only an inshore continental shelf hunting phase but a long pelagic phase involving extensive open ocean travel. The latter phase lasts five or more months and must be an important aspect of the animal's natural history. It is not clear what function this pelagic phase serves. The white sharks are not following their elephant seal prey from the

rookeries as the latter migrate north and northwest (Fig. 3). The pelagic phase suggests breeding insofar as many migrating animals usually move from feeding to breeding and vice versa (*e.g.*, gray whales, Swartz, 1986; elephant seals, Le Boeuf *et al.*, 2000). We know that the white sharks are feeding near central California rookeries during the near-shore coastal phase. But if the shark migration from California is to breed, it is puzzling that the pelagic phase is so long in duration. Moreover, the great depth of swimming and diving, and the range of temperatures to which the sharks are exposed, are greater than expected.

Discussion

The development of bio-logging science has made it possible to obtain fundamental information about the hunting and migratory behavior of white sharks. This new information requires a substantial revision in our understanding of what these animals really do. The preliminary studies reviewed here show that we are just beginning to understand some elementary aspects of the life history and ecology of this apex predator. This is a necessary step in understanding the predator-prey relationship of white sharks and northern elephant seals.

The impact of white shark predation on elephant seals remains an open question but the studies summarized suggest general limits. White sharks are resident near the seal rookeries in central California in fall and early winter; they are in the pelagic phase from mid-winter to late summer. Elephant seals are resident on the central California island rookeries at all times of year but colony composition by sex and age changes. In fall, juveniles of 1–3 years of age are returning from foraging trip at sea, followed by subadult males in late fall. In early winter, these animals return to sea as adult males and pregnant females begin arriving for the breeding season. It is important to note that white sharks are in their pelagic phase when the naïve, fat weaned pups depart the rookery for their first foraging trip. During 1971–1988, the mortality rate of weanlings during the first trip to sea from the Año Nuevo rookery was 54% and ranged from 35 to 61% (Le Boeuf *et al.*, 1996), which accounts for most of the high mortality during the first year of life (mean = 63.2% of pups born). These juveniles are at sea from April through September. Although the location of foraging of these juveniles is unknown, most likely they take a northward path as do older juveniles and adults (Le Boeuf *et al*., 1996). If so, they would be most prone to predation when returning to the rookery. Yet, many things remain unclear. Do most sharks exhibit the migratory pattern observed? Are some sharks hunting near the rookeries in winter, spring and fall? Do the predators prefer adults or juveniles? Are white sharks responsible for the high juvenile mortality rate of elephant seals, and if so, what proportion?

The RAP system is especially useful for revealing high accuracy in real time positioning for marine animals that inhabit a relatively small area (< 1 km^2), such as for feeding or breeding. It is especially useful in showing the movements of one animal in relation to others, *i.e*., addressing coordinated, cooperative or social movements. This is much more evident in graphic presentations with animation than in a two dimensional figure on a journal page.

The RAP system, however, has severe drawbacks for research projects requiring monitoring animals continuously for a month or more in the open ocean. The receiver/buoys must be recharged every eight days which means retrieving and then redeploying them. Solar charging is a partial solution but this is an added expense. The buoys are heavy and danger-

ous to anchor and retrieve especially when the sea state is moderate or worse. Moreover, buoys in the open ocean break loose and must be retrieved. One must monitor the sea state closely and be prepared to remove the buoys before the sea state worsens to prevent them from losing their moorings and being lost. Once the buoys are removed for any reason, it may be days before the weather moderates allowing the buoys to be redeployed. This makes it difficult and dangerous to monitor instrumented animals continuously.

Pop-up satellite tags permit one to learn fundamental aspects of the behavior of large marine animals like sharks and tunas that are extremely difficult to observe and study by other means. Secure attachment of tags is essential. This is relatively simple, inexpensive and effective for the white shark but considerably more expensive for tunas, because larger boats are required (Block *et al.*, 1998, 2001). PSATs are particularly good at revealing large scale movements, water temperature ranges to which the animals are exposed, and the general swimming/depth pattern. The results can provide excellent preliminary data that benefit from follow-up studies using other methods. For example, the Boustany *et al.* (2002) study, that illustrated the distal locations of white shark migration from central California, suggests further study of these locations to address the function of the migration using other methods of study.

The disadvantages of PSATs are that the location positions are general and the diving/swimming data are summarized or binned. This is useful for preliminary studies but more precise locations and more detailed records of diving and swimming behavior, such as one gets from archival tags on some pinnipeds (*e.g.*, elephant seals, Le Boeuf *et al.*, 2000), are desirable and would facilitate understanding their behavior.

We remain far from attaining the goal of demonstrating top-down cascade effects in this apex predator. Bio-logging science, however, is helping us to understand heretofore unknown fundamental aspects of their natural history.

Acknowledgments

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