

Annual re-sightings of photographically identified white sharks (*Carcharodon carcharias*) at an eastern Pacific aggregation site (Guadalupe Island, Mexico)

Michael L. Domeier · Nicole Nasby-Lucas

Received: 20 April 2005 / Accepted: 10 May 2006 / Published online: 19 July 2006
© Springer-Verlag 2006

Abstract A systematic, reliable method for identifying white sharks, *Carcharodon carcharias* Linnaeus, from underwater photographs was developed and applied to examine site fidelity at Guadalupe Island, Mexico (29°N, 118°W). The most reliable features for repeat identification in multiple years were the pigment patterns on the gill flaps, pelvic fins, and caudal fins. Pigment patterns in all three regions were asymmetrical on the right and left sides making it necessary to photograph both sides to catalog each individual. However, once cataloged, an individual could be re-identified using a partial body image. Using this method, 73 individuals were identified between 2001 and 2005. Site fidelity was indicated through repeated annual sightings of individuals with 78% of the identified sharks observed over at least 2 years. Males were found to arrive at Guadalupe Island as early as July and females in September. Peak abundances at the site occurred August–December. The sex ratio was not significantly different from unity in 2002, 2004, and 2005. This monitoring technique has shown Guadalupe Island to be an important white shark aggregation site in the eastern Pacific.

Introduction

The white shark *Carcharodon carcharias* is a large (> 5 m) apex predator that occurs throughout temper-

ate and tropical oceans in relatively low densities. Although occasionally targeted by trophy hunters, white sharks have not been subject to large-scale directed fisheries. Incidental mortalities result from longline and gillnet fisheries and mesh enclosures designed to protect swimmers from sharks (Paterson 1986). There are insufficient data for the analysis of population trends, but white sharks have been recognized as particularly vulnerable to rapid stock declines [IUCN Red List as Vulnerable (Baillie and Groombridge 1996) and 2005 listing in CITES appendix II (CITES, convention of the international trade in endangered species of wild fauna and flora)] due to its low intrinsic rate of population increase (Cailliet et al. 1985; Francis 1996; Pratt 1996; Smith et al. 1998; Compagno 2001) and naturally rare occurrence.

Electronic tagging studies have shown that juvenile white sharks have a strong affinity for coastal regions (Dewar et al. 2004) while adult sharks are capable of long distance seasonal migrations, taking them into the pelagic realm (Boustany et al. 2002; Bonfil et al. 2005). Adult white sharks prey extensively on pinnipeds and other marine mammals and have been shown to aggregate seasonally around pinniped haulout sites (Tricas and McCosker 1984; Ainley et al. 1985; Strong et al. 1992; Klimley et al. 1996). Such aggregations have been identified off the Farallon Islands, California (Klimley et al. 1992; Klimley and Anderson 1996; Pyle et al. 1996a), the southern coast of South Africa (Bass et al. 1975; Cliff et al. 1996; Ferreira and Ferreira 1996) and Spencer Gulf, South Australia (Strong et al. 1992, 1996).

The occurrence of white shark aggregations constitutes a period of local vulnerability when directed or incidental harvest could quickly lead to local, if not

Communicated by J.P. Grassle, New Brunswick

M. L. Domeier (✉) · N. Nasby-Lucas
Pfleger Institute of Environmental Research, Oceanside,
CA 92054, USA
e-mail: domeier@cs.com

regional sharp population decline. These aggregations have the potential to become important population monitoring sites, particularly if individuals can be easily and reliably identified. Previous studies used photographic identification (photo-ID) of individual white sharks to help collect data on spatiotemporal differences in sex ratio (Strong et al. 1996) and residency patterns (Klimley and Anderson 1996), as well as short and long distance movements (Anderson and Goldman 1996; Bonfil 2005). These previous white shark photo-ID studies used identifying characters that included distinguishing nicks on the trailing edge of the dorsal and caudal fins, the presence of pigmented spots on the dorsal fin, scars on the flanks, and estimates of total length. The dorsal fin and upper lobe of the caudal fin (the primary characters used in the above studies) can conveniently be photographed from land or the deck of a vessel, but the fact that not all fins have distinguishing marks and that small marks can quickly be erased by a new, larger mark, creates serious problems for long-term monitoring of individuals.

Here we describe a systematic approach to the identification of individual white sharks using photographs taken underwater at Guadalupe Island, Mexico. In applying this method over a 5-year span, we have addressed the following questions: (1) can characters be found to repeatedly identify individuals over several years? (2) do white sharks at Guadalupe Island exhibit site fidelity? and (3) are there temporal patterns to white shark visitation of Guadalupe Island?

Materials and methods

Guadalupe Island is a sheer volcanic island 407 km south–southwest of San Diego, California, and 260 km offshore of Baja California, Mexico (Fig. 1). The island rises out of deep water (> 3,500 m) and stretches 41 km in a north/south direction and 15 km across at the widest point. Guadalupe Island is both a Mexican nature preserve (dedicated in 1925) and a pinniped sanctuary (1975). The island serves as a haulout and pupping site for the Northern elephant seal *Mirounga angustirostris*, the Guadalupe fur seal *Arctocephalus townsendi*, and the California sea lion *Zalophus californianus*.

Multiple trips to Guadalupe Island were made in January and June through December between 1999 and 2005. Underwater visibility at Guadalupe Island was relatively good allowing for excellent quality underwater images of white sharks (*C. carcharias* Linnaeus). Sharks were attracted to the vessel by chumming fish and blood. Photographic images were obtained from video and still cameras operated by a

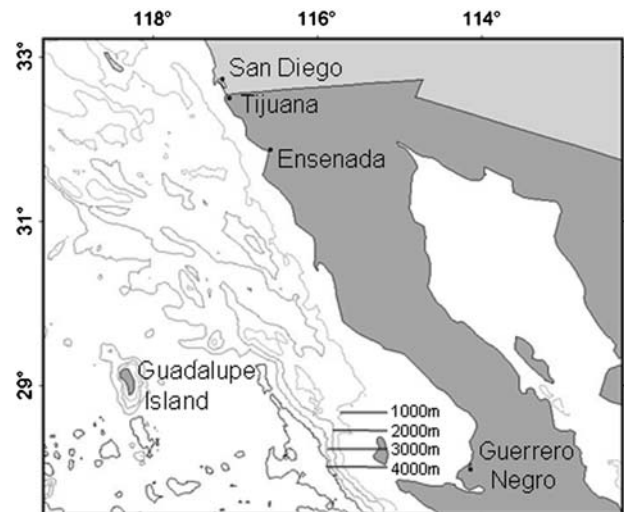


Fig. 1 Guadalupe Island off the coast of Baja with 1,000 m contours

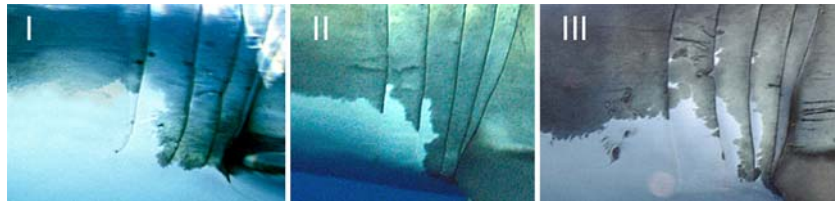
caged diver or through the use of a camera mounted on a hand-held pole. Images were taken by the senior author and divers who volunteered images after visiting the site on commercial cage dive operations that began in 2002. Photographer, date, and location were logged for each photograph.

White sharks exhibit counter-shading, consisting of a dark gray dorsal surface and a white ventral surface; it is the irregular border between the gray and white regions that lends itself to photo-ID of individuals. Three regions of the body proved superior for individual identification, due to consistently high degrees of variability: the gill flaps (extension of the inter-brachial septum), pelvic fin region, and caudal fin region. Multiple pigment pattern types were defined for each of the three body regions to aid in the re-identification process; this allowed the number of possible ID matches to be efficiently narrowed to a few candidate sharks from which the exact unique pigment patterns were then matched to a single shark. Two non-pigment characters were also recorded to aid re-identification: (1) the sex of the fish and (2) permanent trauma-induced markings (i.e., major scars, fin damage, or mutilations).

Gill flap pigment patterns

Three gill flap patterns were defined by the presence of white on individual flaps above the plane of pectoral fin insertion (Fig. 2). Type I (GF I) had white coloration on only the first gill flap, GF II had white on the first and second gill flaps, and GF III had white on the first, second, and third gill flaps. These gill flap types appeared different when a shark was turning, as the amount of overlap between adjacent slits changed, so

Fig. 2 *Carcharodon carcharias*. Examples of gill flap types I–III



the best images were taken when the shark was not turning.

Pelvic fin pigment patterns

Three pigment patterns were described for the pelvic fin region (Fig. 3). Pelvic fin type I (PF I) was defined as gray pigment continuously extending from the body onto the pelvic fin; in PF II the pigment between the body and pelvic fin was discontinuous but the gray on the fin extended dorsally above the plane of fin insertion; in PF III the gray pigment was discontinuous between the body and the pelvic fin and the gray on the fin itself did not extend above the plane of fin insertion.

Caudal fin pigment patterns

For all sharks examined, the upper lobe of the caudal fin was entirely gray above the dorsal edge of the caudal peduncle. The variable pigmentation on the lower lobe of the caudal fin was classified into four distinct patterns (Fig. 4). In Type I (CF I) the lower lobe of the fin was completely gray; in CF II the lower lobe was almost entirely gray except for a small islet of white; in CF III the only white was along the leading edge of the lower lobe and the remainder was gray; in CF IV there was white along the leading edge of the lower lobe and extending toward the center of the lower lobe, either as a small islet (as in CF II), or as a larger patch extending toward the posterior edge of the caudal keel.

Initial identification and cataloging of each white shark required good reference images on both sides of the entire shark because pigment patterns are asymmetrical. Video footage was invaluable in identifying both sides of individual sharks but reference images

required good 35-mm or digital full-body images as well as close-ups of the gill flaps, pelvic, and caudal fins. The close-ups were often obtained by enlarging the sections of high-resolution full-body images. Individual catalog entries were augmented by images of disfigurements or other unique markings when applicable. Sharks were assigned numbers in the order they were identified and the years and months the individuals were sighted at the island were logged. Images of only one side of a shark that could not be matched up to the opposing side were termed orphans, until the record was completed by subsequent sightings. When possible, estimates of lengths were made from the deck of the vessel using known dimensions of the vessel as a guide.

Results

Over 9,000 photographs and 24 h of video of *C. carcharias* were taken at Guadalupe Island during the peak months of August through December (2001–2005). The number of photographs collected increased over the study period, with approximately 100 photographs in 2001, 90 in 2002, 1,640 in 2003, 4,130 in 2004, and 3,290 in 2005. Comparing photographs of known individuals from 2001 through 2005 demonstrated stability of pigment patterns in all the three of the body regions. Any one of the three body regions allowed individual sharks to be easily re-identified over several years. There were a few instances of subtle pigment changes around the gill flaps, but these did not affect the ability to re-identify the sharks. For example, lacerations to the gill region exposed more white pigment below the gills flaps but in most cases the pigment pattern

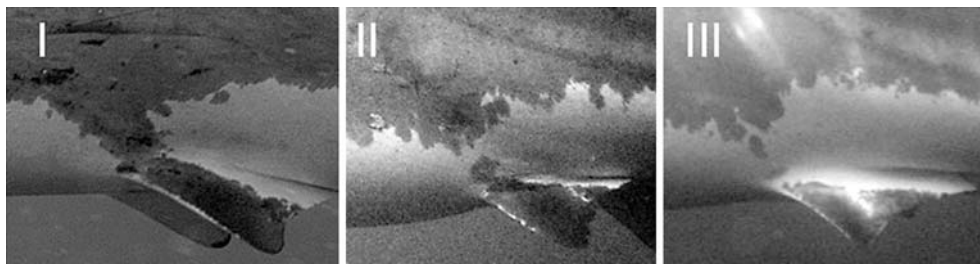


Fig. 3 *Carcharodon carcharias*. Examples of pelvic fin types I–III

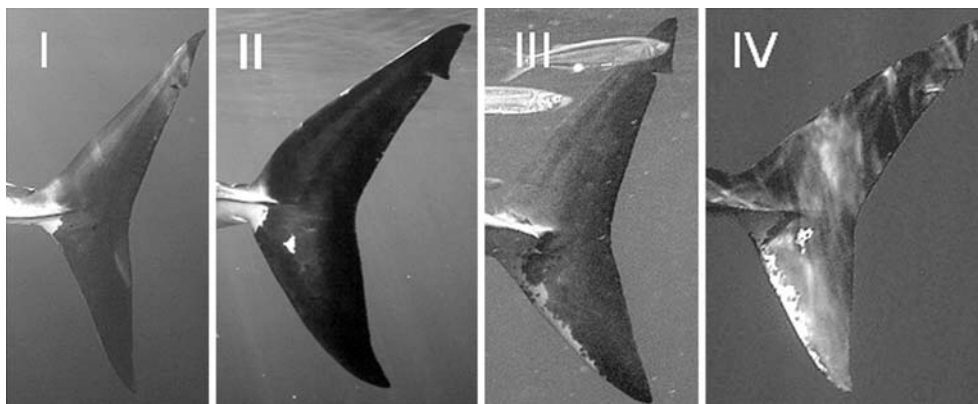


Fig. 4 *Carcharodon carcharias*. Examples of caudal fin types I–IV

returned to its original state as the gill flaps healed. Several sharks also had unusually dark pigment spots, especially near the gill flaps which changed in size and/or shape from year to year (Fig. 5), although the margin between gray and white did not change.

With some exceptions, individual sharks were symmetrical with respect to defined pigment patterns at a given body region, but at a finer scale markings were found to be asymmetrical, making it necessary to fully photograph both sides of each shark before an ID number could be assigned. Of the sharks that were found to be asymmetrical with respect to general pigment pattern type, 11 individuals had asymmetrical GF types, 15 had asymmetrical PF types and 6 had asymmetrical CF types. No shark had asymmetrical defined pigment patterns in all the three body regions.

Unique trauma-induced marks were also used as identifying characters when present. Bite marks from conspecifics were common on both sexes, particularly around the gill region. These bite marks varied from minor lacerations to potentially life-threatening wounds; in one case the gill flaps were torn off leaving gill arches exposed. Minor lacerations and abrasions aided in identification for several months but were not useful from year to year, while large wounds led to permanent marks (i.e., fin damage, deep scarring) that were used for identification between years. Because even large wounds can heal and become indistinguishable (Fig. 6), the pigment patterns were the most useful for identification.

The photographic and video records collected between 2001–2005 led to the complete photographic identification of 73 individual white sharks from Guadalupe Island consisting of 40 males and 33 females. An additional 23 orphans from the left side and 17 orphans from the right side have not yet been matched. These orphans represent 23 additional sharks yet to be added to the catalog, implying that at least 96 individual sharks have been photographed at Guadalupe

Island. Of the 73 individuals with complete records, 13 were photographed in 2001, 25 in 2002, 39 in 2003, 53 in 2004, and 52 in 2005. Fifty-seven sharks have been sighted in multiple years. Of the 57 sharks identified in multiple years, 5 were identified in all 5 years (all male), 5 in 4 of the 5 years (4 males, 1 female), 27 in 3 of the 5 years (18 males, 9 females), and 20 in 2 of the 5 years (7 males, 13 females) (Fig. 7).

White sharks were present at Guadalupe Island minimally between the months of July and January with August through December being the peak months. The maximum number of individual sharks observed during the peak months was 15 in August (2004), 34 in September (2005), 32 in October (2004), 26 in November (2003), and 16 in December (2004). White sharks have not been observed at Guadalupe Island during the months of May (1 trip) or June (3 trips), while only 1 shark has been spotted in July (3 trips) and only 2 sharks were seen in January (3 trips). No sampling occurred from February through April.

The sex ratio for all white sharks identified at Guadalupe Island was not significantly different from 1:1 [sex ratio 1.21 (male:female); Chi Square $P = 0.41$]. When sex ratio was examined by year, all years were biased toward males but only 2003 differed significantly from unity (ratios of 1.5, 2.0, 1.3, and 1.7 in 2002–2005, respectively; chi-square $P = 0.32, 0.04, 0.34, \text{ and } 0.05$ in 2002–2005, respectively).

The timing of shark visitation to the island differed between males and females. Males were sighted between July and January (photographed between August and December) while females were sighted and photographed from September through December. From 2001–2005, 18 females were identified in at least two consecutive years (55%), 5 were identified only during odd or even numbered years (15%), and 10 were sighted only once (30%). Thirty-two males were identified in at least two consecutive years

Fig. 5 *Carcharodon carcharias*. Photographs in consecutive years showing changes in darker pigmentation spots (shown inside *squares*) not used in identification of individuals **a** shark #11, **b** shark #5

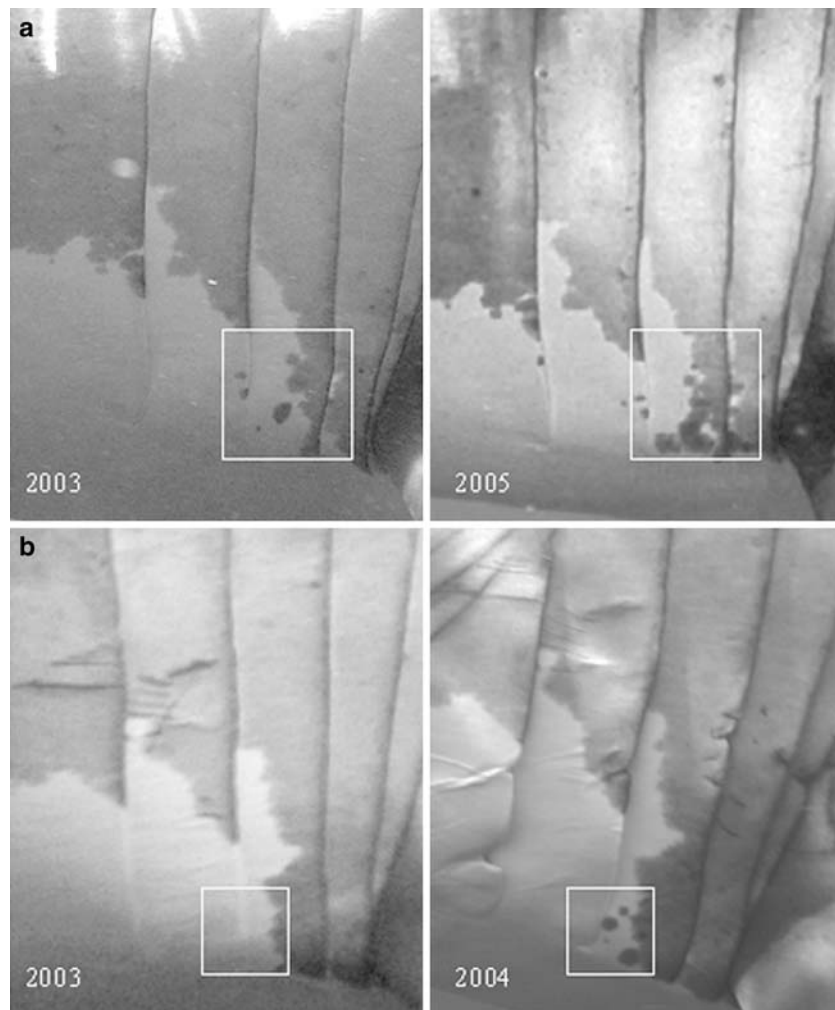
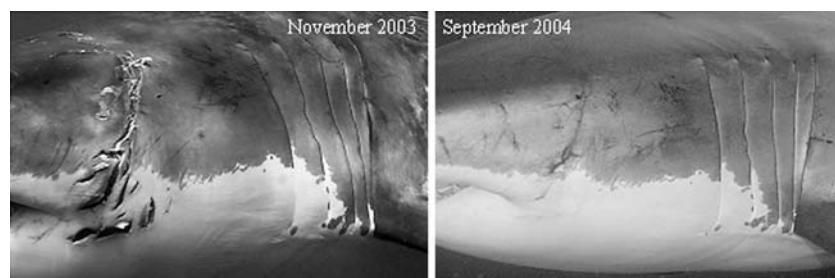


Fig. 6 *Carcharodon carcharias*. Photographs of a bite wound from November 2003 (shark #19) that had healed by September 2004



(80%), 2 every other year (5%), and 6 were identified only once (15%).

Rough length estimates were made 50 times to provide preliminary information on the size structure of this population. Sharks varied in total length from 2.5 to 5.5 m, and most were > 3.5 m long [16 sharks estimated < 3.5 m (32%), 22 between 3.5 and 4.5 (44%), and 12 sharks > 4.5 m (24%)]. For those sharks where sex was verified, 2 females and 10 males were estimated between 2.5 and 3.5 m, 4 females and 13 males were estimated between 3.5 and 4.5 m, and 6 females and 5 males were estimated between 4.5 and 5.5 m (Fig. 8).

Discussion and conclusions

The multiple pigment characters we developed as the basis for cataloging individual white sharks, *C. carcharias*, proved to be stable and reliable over a period of years. Once a shark was logged into the catalog it was possible to re-identify it from partial body images since any one character was often enough to make a positive identification. The application of this method (2001–2005) resulted in the largest white shark photo-ID catalog of its kind, with complete photographic records of 73 white sharks and partial

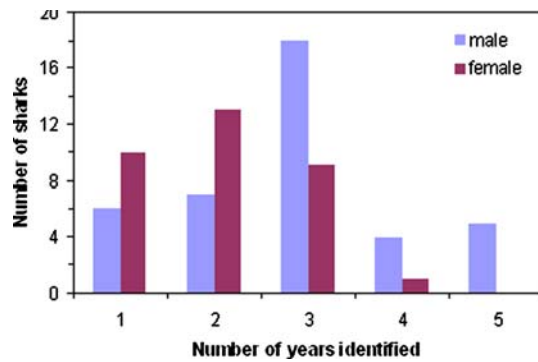


Fig. 7 *Carcharodon carcharias*. Number of years male and female white sharks were re-sighted at Guadalupe Island ($n = 73$)

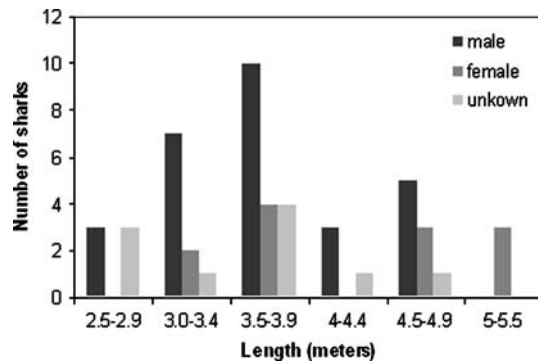


Fig. 8 *Carcharodon carcharias*. Distribution of size structure by sex of white sharks observed at Guadalupe Island ($n = 50$)

photographic records of 23 additional sharks, for a total of 96 individuals.

The photo-identification catalog has allowed us to track the presence of white sharks at Guadalupe Island over time. White sharks were seasonally observed at the island between July and January with peak numbers of individuals sighted between September and November. Identified sharks were routinely observed on more than one occasion, with 78% being sighted in more than 1 of the 5 years of the study. These documented return rates provide clear evidence of seasonal site fidelity of white sharks around Guadalupe Island.

The sex ratio of Guadalupe Island white sharks was essentially 1:1, but the sexes displayed different temporal patterns of island visitation with males appearing at Guadalupe Island about 45 days earlier than females. Spatial and temporal segregation of the sexes has been reported previously in white sharks (Casey and Pratt 1985; Klimley 1985; Bruce 1992; Ferreira and Ferreira 1996; Strong et al. 1996). Some sites have shown heavy sex bias toward females and others toward males. Other aggregation sites have also shown seasonal changes in sex ratio, but when all sites are compared

there is no clear global seasonal pattern to the presence or absence of each sex; in fact, an aggregation at Dangerous Reef, Australia, was once biased toward males but is now biased toward females (Strong et al. 1996).

The timing of seasonal presence and site fidelity observed at Guadalupe Island are similar to those observed at the Farallon Islands (Klimley and Anderson 1996), although return patterns of males and females may differ between these two eastern Pacific aggregation sites. Anderson and Pyle (2003) observed an every-other-year female white shark visitation pattern to the Farallon Islands while many of the Guadalupe Island females (55%) were seen in consecutive years, although some of the largest females were not seen in consecutive years. Anderson and Pyle (2003) suggested that the pattern observed at the Farallon Islands is indicative of a 2-year reproductive cycle for females. It is possible that once females reach sexual maturity their seasonal movement patterns change. Unfortunately we cannot apply accurate length measurements to all our identified sharks, but clearly such in situ length data (e.g., Klimley and Anderson 1996) would provide invaluable data to study sex-specific behavioral patterns. We have made attempts at using a paired laser system to measure the sharks, but more work must be done before these data are reliable.

The majority of the world's known white shark aggregations are centered on dense pinniped populations (usually an island) suggesting that concentrated food supply may be the primary reason these aggregations occur. Although northern elephant seals, Guadalupe fur seals, and California sea lions occur at Guadalupe, we have never witnessed a shark feeding on a pinniped and have learned of very few anecdotal accounts of such predation. This is in stark contrast to a white shark aggregation site off the coast of South Africa, where over 2,000 predatory attacks on pinnipeds have been documented between 1997 and 2003 (Martin et al. 2005). Predation on pinnipeds was also routinely observed at the Farallon Islands (Pyle et al. 1996b). Guadalupe Island white sharks were frequently observed preying on yellowfin tuna (*Thunnus albacares*) that had been hooked on rod-and-reel (we once witnessed 50 25–35 kg yellowfin tuna taken from a single recreational fishing boat over a period of hours). A large white shark was also observed feeding on a free-swimming 2-m blue shark (Harper, personal communication) at Guadalupe Island. Whether free-swimming tuna are regularly preyed on by white sharks at Guadalupe Island is unknown, but the lack of observed attacks on pinnipeds is noteworthy.

Aggression was commonly observed between white sharks at the island and many sharks, both male and

female, carried wounds that were inflicted by conspecifics. It has been suggested that white sharks refrain from escalating aggression to the point where life-threatening wounds are inflicted (Barlow 1996); however, many of the bite marks observed at Guadalupe were on or near the gill flaps. One large female was observed with gill flaps torn off and the gill arches exposed. Attacks on the gill region are evidence of more serious aggression, which could lead to the death of the loser. It has also been suggested that bite marks on the flanks of females are a result of a mating ritual where the male grips the side of the female, often near the gills (Francis 1996). These types of bite marks were observed on both sexes suggesting that although mating rituals may produce such marks on females, the presence of these marks does not necessarily indicate mating. Although bite marks were very prevalent among the sharks at Guadalupe Island they made poor characters for photo-ID because of the ability of this species to regenerate tissue.

This study identified Guadalupe Island, Mexico, as an important white shark site in the eastern Pacific and our systematic approach to identifying individual sharks has provided valuable baseline data. Over time it should be possible to accurately estimate the total Guadalupe Island white shark population using mark and recapture statistics, allowing us to track population trends and new recruitment to the aggregation. A great deal could be learned by applying the photo-ID methods we developed at Guadalupe Island to other known white shark aggregation sites, particularly where cage diving activities already exist. Movement of individuals between aggregation sites could be documented without expensive tagging methods and population trends could be compared between sites. These methods can be cost effective when cage diving operations are included in the sampling plan, although caution and further study are needed to insure cage diving operations do not negatively affect the white sharks, nearby seals, or other components of the local ecosystem.

Acknowledgments We would like to thank Tom Pflieger whose field assistance, interest and funding made this project possible. We would like to acknowledge the help of Jessica Harper whose interest and persistence in tracking photographs of white sharks helped give this project momentum, Patric Douglas and Lawrence Growth for access to their photographs and videos, and Steve Drogin for allowing us to use his shark cage. This project was funded by a grant through the George T. Pflieger Foundation. We would like to acknowledge all photographers whose photographs were used in our database, namely Scott Aalbers, Paul Adie, Tony Baskeyfield, Chris Bouton, Eric Cheng, Phil Colla, Luke Cresswell, Robin Criman, Dean Cross, Jonathan Gershon, Mark Grindley, Dave Haas, Tim Harris, Guy Harvey, Jeff Hoover, Bill James, Chris Limon, Andy Lineseisen, Keith Ludwig, James MacIntosh, Chris Marshall, Jay Marzolf, Antonio

Mondragon, Bonnie Pelnar, Doug Perrine, Daniel Preston, Jeff Prevet, Simon Rogerson, Toshimi Sakurai, Chugey Sepulveda, Phil Streather, Mike Urciuoli, Bery Wells, Rick Westphal, Chris Zacharias, and Phil Zerofski. We thank Dr. Felipe Galván Magaña for Mexican permitting assistance. All research was conducted in accordance with permits through Centro Interdisciplinario de Ciencias Marinas Instituto Politecnico Nacional.

References

- Ainley DG, Henderson RP, Huber HR, Boekel-heide RJ, Allen SG, McElroy TL (1985) Dynamics of white shark/pinniped interactions in the Gulf of the Farallones. *South Calif Adac Sci Mem* 8:109–122
- Anderson SD, Goldman KJ (1996) Photographic evidence of white shark movements in California water. *Calif Fish Game* 82:182–186
- Anderson SD, Pyle P (2003) A temporal, sex-specific occurrence pattern among white sharks (*Carcharodon carcharias*) at the South Farallon Islands, California. *Calif Fish Game* 89:96–101
- Baillie J, Groombridge B, Compilers (eds) (1996) 1996 IUCN red list of threatened animals. IUCN, Gland, Switzerland
- Barlow GW (1996) Behavior of the white shark: an emerging picture. In: Klimley AP, Ainley DG (eds) *Great white sharks: the biology of Carcharodon carcharias*. Academic, San Diego, pp 257–260
- Bass AJ, D'Aubrey JD, Kistnasamy N (1975) Sharks of the east coast of Southern Africa. 4. the families Odontaspidae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. *Invest Rep Oceanogr Res Inst Durban S Afr* 39:1–102
- Bonfil R, Meyer M, Scholl MC, Johnson R, O'Brien S, Oosthuizen H, Swanson S, Kotze D, Paterson M (2005) Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* 310:100–103
- Boustany AM, Davis SF, Pyle P, Anderson SD, Le Boeuf BJ, Block BA (2002) Expanded niche for white sharks. *Nature* 415:35–36
- Bruce BD (1992) Preliminary observations on the biology of the white shark, *Carcharodon carcharias*, in South Australian waters. *Aust J Mar Freshw Res* 43:1–11
- Cailliet GM, Natanson LJ, Weldon BA, Ebert DA (1985) Preliminary studies on the age and growth of the white shark *Carcharodon carcharias*, using vertebral bands. *South Calif Acad Sci Mem* 9:49–60
- Casey JG, Pratt HL (1985) Distribution of the white shark, *Carcharodon carcharias*, in the western North Atlantic. *South Calif Acad Sci Mem* 9:2–14
- Cliff G, Van Der Elst RP, Govender A, Witthuhn TK, Bullen EM (1996) First estimates of mortality and population size of white sharks on the South African coast. In: Klimley AP, Ainley DG (eds) *Great white sharks: the biology of Carcharodon carcharias*. Academic, San Diego, pp 393–400
- Compagno LJV (2001) *Sharks of the world. An annotated and illustrated catalogue of the shark species known to date. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes)*. FAO Species Catalogue for Fisheries Purposes No 1, vol 2. Rome, FAO p 269
- Dewar H, Domeier M, Nasby-Lucas N (2004) Insights into young of the year white shark, *Carcharodon carcharias*, behavior in the Southern California Bight. *Envir Biol Fishes* 70:133–143
- Ferreira CA, Ferreira TP (1996) Population dynamics of white sharks in South Africa. In: Klimley AP, Ainley DG (eds)

- Great white sharks: the biology of *Carcharodon carcharias*. Academic, San Diego, pp 381–391
- Francis MP (1996) Observations on a pregnant white shark with a review of reproductive biology. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic, San Diego, pp 157–172
- Klimley AP (1985) The arial distribution and autoecology of the white shark, *Carcharodon carcharias*, off the West Coast of North America. South Calif Acad Sci Mem 9:15–40
- Klimley AP, Anderson SD (1996) Residency patterns of white sharks at the South Farallon Islands, California. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic, San Diego, pp 365–373
- Klimley AP, Anderson SD, Pyle P, Henderson RP (1992) Spatio-temporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. Copeia 1992:680–690
- Klimley AP, Pyle P, Anderson SD (1996) The behavior of white sharks and their pinniped prey during predatory attacks. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic, San Diego, pp 175–191
- Martin RO, Hammerschlag N, Collier RS, Fallows C (2005) Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. Mar Bio Ass UK 85:1121–1135
- Paterson R (1986) Shark prevention measures working well. Aust Fish March:12–18
- Pratt HL Jr (1996) Reproduction in the male white shark. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic, San Diego, pp 131–138
- Pyle P, Anderson SA, Ainley DG (1996a) Environmental factors affecting the occurrence and behavior of white sharks at the Farallon Islands, California. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic, San Diego, pp 281–291
- Pyle P, Anderson SA, Ainley DG (1996b) Trends in white shark predation at the South Farallon Islands, 1968–1993. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic, San Diego, pp 375–379
- Smith SE, Au DW, Show C (1998) Intrinsic rebound potentials of 26 species of Pacific sharks. Mar Freshw Res 49:663–678
- Strong WR Jr, Murphy RC, Bruce BD, Nelson DR (1992) Movements and associated observations of bait-attracted white sharks, *Carcharodon carcharias*: A preliminary report. Aust J Mar Fresh Res 43:13–20
- Strong WR Jr, Bruce BD, Nelson DR, Murphy RD (1996) Population dynamics of white sharks in Spencer Gulf, South Australia. In: Klimley AP, Ainley DG (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic, San Diego, pp 401–414
- Tricas TC, McCosker JE (1984) Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. Proc Calif Acad Sci 43:221–238