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A review of shark satellite tagging studies

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ABSTRACT

Recent advances in satellite tagging technologies have provided scientists growing opportunities to resolve previously unknown spatial ecology of marine predators, including sharks. Such an understanding is particularly important at this time given recent declines in shark populations worldwide. Here we reviewed 48 studies published in the primary literature between 1984 and 2010, addressing the most basic questions regarding the use of satellite tagging for studying shark behavior and ecology. For each study, the following aspects were analyzed: tagging location; species tagged; study focus; technology employed; sample size; tag attachment and deployment technique; duration of tracking; tag failure rate; and study limitation. The potential impacts of tagging on shark behavior and physiology are considered. Finally, we discuss how satellite tagging has furthered our current knowledge of shark behavior and consider the possibility of new tag developments that can improve our ability to resolve the mechanisms underlying shark habitat use.

Contents

1. Introduction

Apex predators can impact community structure and function through top-down density- and risk-driven effects on the distribution and abundance of their prey (Creel and Christianson, 2008; Heithaus et al., 2008). Thus, understanding the habitat use and foraging ecology of these animals is important for predicting how they, and their communities, are likely to respond to anthropogenic impacts (Morris, 2003; Frid et al., 2008; Hammerschlag et al., 2010). In the past, documenting the movements and behaviors of large marine predators has been challenging, due largely in part to their high vagility and the visually concealing nature of the marine environment (Myrberg, 1987; Klimley et al., 1992; Bres, 1993; Martin et al., 2009). However, recent advances in satellite tagging and tracking technologies have provided scientists the opportunity to improve measurements of home range, movements and habitat use of marine predators including tunas (Wilson et al., 2005), billfishes (Prince and Goodyear, 2006), sharks (Weng et al., 2008), whales (Bailey et al., 2010) and albatrosses (Tuck et al., 1999).

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Besides providing estimates of position, some satellite tags can also measure water depth, temperature, and other environmental factors (Teo et al., 2009). This provides valuable insights into the movements of marine animals and the physical oceanographic properties encountered during their movements (Biuw et al., 2007). Subsequently, these new technologies are transforming the science underlying fisheries management (discussed in Greene et al., 2009).

The purpose of this study was to review the primary literature to address the most basic questions pertaining to the use of satellite tagging for studying shark behavior. Questions addressed in this study included: why, where and how have shark satellite tagging studies been performed? What types of satellite tags have been used and what types of data have they provided? What are the negative impacts of tagging on shark behavior and physiology and how can they be minimized? How can tag technology be improved to further advance our understanding of shark habitat use patterns? The results provided by this study will offer guidance and useful information for those conducting satellite tracking studies of apex predatory fishes, particularly sharks.

2. Methods

The present paper only focuses on satellite tagging studies already published in the primary literature as of July 2010 (Table 1). Publications included in this study were selected based on library and electronic database searches using key word and title searchers for the words 'satellite(s),' 'shark(s),' 'elasmobranch' and/or 'Argos.' In addition, works cited based on papers identified through our electronic database searches were also incorporated.

For each study, the following information was recorded: (1) study location; (2) species tagged; (3) study purpose; (4) satellite tag type; (5) sample size; (6) tag attachment and deployment technique; (7) the minimum and maximum transmission days for each study; (8) shark behavior; and (9) study limitations, if any. Study locations were grouped according to oceanic basin where sharks were originally tagged. Study purpose included: identifying spatial or temporal patterns in habitat use, examining post-release mortality, evaluating if shark movements were correlated with prey availability, etc. Tag attachments and deployment techniques were grouped based on how sharks were captured, tagged and thereafter released. Tag configuration, type of gear used to affix the tag to the shark and use of anti-fouling paint was also noted. The minimum and maximum transmission days reported over the course of each study were determined. Comparisons between the average minimum and maximum number of days an individual was tracked using different tag types were statistically analyzed using t-tests. All analyses were performed using SAS (1990) software and significance was declared at $p<0.05$.

3. Results and discussion

A total of 48 studies were examined between 1984 and 2010 (Table 1).

3.1. Purpose of studies

The majority of shark satellite tracking studies reviewed focused on determining the movement patterns and/or evaluating the depth and temperature preferences of sharks in certain regions. Three of the reviewed studies examined if shark habitat use was linked with prey availability (e.g. Shepard et al., 2006; Sims et al., 2006; Weng et al., 2008). Two studies tracked sharks to evaluate precision and/or accuracy of satellite tags (Teo et al., 2004; Wilson et al., 2007) and another two studies employed satellite tagging to evaluate post-release fishing mortality on sharks (Moyes et al., 2006; Campana et al., 2009). Another study used satellite telemetry to empirically test a long-held belief that basking sharks hibernate during the winter (Sims et al., 2003). Although the technology allows the ability for researchers to deploy tags and "see what the sharks do" or "where they go," we encourage new studies to continue embarking on hypothesis-driven questions.

3.2. Tag types deployed

In terms of types of tags deployed, 63% of reviewed studies used pop-up archival tags (PAT tags). Eighteen percent of studies used satellite-linked transmitters (SAT tags), the majority of which are smart position or temperature transmitting tags (SPOT tags, discussed below). The remaining 18% of studies used both PAT and SAT tags. This section provides details of tag function, performance, location accuracy estimates and deployment techniques.

PAT tags have successfully been used to track the movements of large pelagic fishes, including tunas (e.g. Gunn et al., 2003; Wilson et al., 2005) and billfishes (e.g. Takahashi et al., 2003; Prince and Goodyear, 2006) and sharks (Sims, 2010). In the case of sharks, PAT tags are usually affixed to the animal by way of a tether that anchors in the musculature at the base of the dorsal fin. The tag can be applied easily from a boat using a tagging lance. Once deployed, PAT tags record and store measurements of ambient light levels, depth and temperature at pre-programmed intervals. The tags detach from the fish at a pre-programmed date and float to the surface, where they transmit summaries of their stored data to orbiting Argos satellites; and if recovered, all raw data can be obtained. Depth and temperature data provided by PAT tags are highly accurate (Sims, 2010). However, position data from PAT tags are derived from the light levels recorded by the tag during deployment. Daily estimates of latitude and longitude are calculated using algorithms provided by the tag manufacturers. These calculations may be inaccurate due to sources of error associated with natural variability in ambient light levels such as light attenuation, turbidity, clock error and shark diving behavior (Musyl et al., 2001). As a result, several methods have been developed to improve light-based estimates from PAT tags including: (1) filtering outliers (Schaefer and Fuller, 2002); (2) using smoothing procedures like moving averages (Matsumoto et al., 2005); (3) processing raw estimates of location using state-space movement models such as the Kalman filter (Sibert et al., 2003) or the particle filter (Royer et al., 2005); and (4) matching sea surface temperatures (SST) from tags with remotely sensed SSTs (Delong et al., 1992). To date, two studies have compared position estimates from PAT tags with Argos positions from SAT tags in free-swimming sharks (Teo et al., 2004; Wilson et al., 2008). Both studies concluded that by filtering and incorporating tag-measured SST with processed light level data, position estimates can be significantly improved and made suitable for reconstructing large-scale horizontal shark movements (for details see Teo et al., 2004; Wilson et al., 2008). Despite these advances, the spatial accuracy of PAT tag estimates (~60 to 180 km) is not conducive for evaluating small-scale or high resolution movements typical of many species of sharks (Sims, 2010). Thus, PAT tags may be utilized best for examining depth data or tracking large-scale shark movements.

The advantage of SPOT tags is obtaining near-real time tracks that provide horizontal movements that can be analyzed at a much higher resolution than those from PAT tags. SAT tags determine geographic locations of tagged sharks via Doppler-shift calculations made by the Argos Data Collection and Location Service whenever a passing satellite received two or more signals from a tag. To date, nearly all SAT tag studies on sharks have employed SPOT tags. To deploy the tags, most SPOT tags need to be mounted to the shark's dorsal fin (see Weng et al., 2005). This often requires catching and temporarily removing the shark from the water, while tags are attached using a bolt system (e.g. Bonfil et al., 2005). SPOT tags contain a salt-water switch, which initiates tag transmission when above the water's surface. Location accuracy may vary with geometrical conditions of the satellite passes, the stability of the transmitter oscillator, the number of successive transmission/messages collected by the satellite and their distribution in the pass (www.argos-system.org). Argos

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Table 1
Review of satellite tagging studies published between 1984 and 2010.

Count	Reference	Ocean	Shark species	Sample size	Tag type	Attachment type	Min tacking days	Max tracking days	Prop. tag failure	Prop. pre-mature pop-offs
1	Priede (1984)	Atlantic	*Cetorhinus maximus* (basking)	1	SAT	Dart	17	17	0	NA
2	Eckert and Stewart (2001)	Pacific	*Rhincodon typus* (whale)	17	SAT	Dart	0	1144	12	NA
3	Boustany et al. (2002)	Pacific	*Carcharodon carcharias* (white)	6	PAT	NR	15	180	0	NR
4	Sims et al. (2003)	Atlantic	*Cetorhinus maximus* (basking)	5	PAT	Dorsal dart anchor	52	198	0	NR
5	Dewar et al. (2004)	Pacific	*Carcharodon carcharias* (white)	1	PAT	Dart	28	28	0	NR
6	Skomal et al. (2004)	Atlantic	*Cetorhinus maximus* (basking)	1	PAT	Dart	71	71	0	100
7	Teo et al. (2004)	Pacific	*Lamna ditropis* (salmon)	2	SAT and PAT	Fin mount and Dart	123	123	0	0
8	Teo et al. (2004)	Pacific	*Prionace glauca* (blue)	4	SAT and PAT	Fin mount and Dart	28	104	0	25
9	Weng and Block (2004)	Atlantic and Pacific	*Alopias superciliosus* (bigeye thresher)	2	PAT	Dart	27	60	0	NR
10	Bonfil et al. (2005)	Indian	*Carcharodon carcharias* (white)	17	PAT	Dart	9	39	0	59
11	Bonfil et al. (2005)	Indian	*Carcharodon carcharias* (white)	7	SAT	Fin mount	30	363	0	NA
12	Loefer et al. (2005)	Atlantic	*Isurus oxyrinchus* (mako)	1	PAT	NR	60	60	0	0
14	Stokesbury et al. (2005)	Pacific	*Somniosus microcephalus* (Greenland)	2	PAT	Dart	66	66	0	0
15	Weng et al. (2005)	Pacific	*Lamna ditropis* (salmon)	48	SAT and PAT	Fin mount	0	1162	31	NR
16	Bruce et al., 2006	Pacific	*Carcharodon carcharias* (white)	6	SAT and PAT	Fin mount and Dart	0	221	17	NR
17	Brunnschweiler and Van Buskirk (2006)	Atlantic	*Carcharhinus leucas* (bull)	6	PAT	Dart	4	24	0	100
18	Graham et al. (2006)	Atlantic	*Rhincodon typus* (whale)	11	PAT	NR	0	206	55	NR
19	Hulbert et al. (2006)	Pacific	*Somniosus pacificus* (Pacific sleeper)	36	SAT and PAT	Dart	0	336	67	6
20	Moyes et al. (2006)	Pacific	*Prionace glauca* (blue)	23	PAT	Fin loop	0	NR	52	64
21	Shepard et al. (2006)	Atlantic	*Cetorhinus maximus* (basking)	6	PAT	Dorsal dart anchor	7	229	0	NR
22	Sims et al. (2006)	Atlantic	*Cetorhinus maximus* (basking)	20	PAT	Dart	0	213	65	NR
23	Wilson et al. (2006)	Indian	*Rhincodon typus* (whale)	19	PAT	Dart	0	216	37	NR
24	Chapman et al. (2007)	Atlantic	*Carcharhinus perezi* (Caribbean reef)	6	PAT	Fin loop	7	20	0	100
25	Gifford et al. (2007)	Atlantic	*Rhincodon typus* (whale)	5	SAT	Dart	2	132	0	NA
26	Heithaus et al. (2007)	Indian	*Galeocerdo cuvier* (tiger)	5	SAT	Fin mount	0	67	0	0
27	Rowat et al. (2007)	Indian	*Rhincodon typus* (whale)	1	SAT	Dart	9	9	0	NA
28	Weng et al. (2007a)	Pacific	*Carcharodon carcharias* (white)	29	PAT	Dart	0	367	31	NR
29	Weng et al. (2007b)	Pacific	*Carcharodon carcharias* (white)	6	PAT	Dart	24	182	0	NR
30	Wilson et al. (2007)	Indian	*Rhincodon typus* (whale)	1	SAT and PAT	Fin mount and Dart	147 (SAT)/ 50 (PAT)	147 (SAT)/50 (PAT)	0	100 (PAT)
31	Domeier and Nasby-Lucas (2008)	Pacific	*Carcharodon carcharias* (white)	75	PAT	Dart	0	386	21	NR
32	Gore et al. (2008)	Atlantic	*Cetorhinus maximus* (basking)	2	PAT	Dart	41	82	0	100
33	Weng et al. (2008)	Pacific	*Lamna ditropis* (salmon)	68	SAT	Fin mount	6	1335	0	NA
34	Brunnschweiler et al. (2009)	Indian	*Rhincodon typus* (whale)	2	PAT	Dart	7	87	0	100
35	Campana et al. (2009)	Atlantic	*Prionace glauca* (blue)	40	PAT	Dart	0	210	8	33
36	Jorgensen et al. (2009)	Pacific	*Sphyrna lewini* (scalloped hammerhead)	1	PSAT	Dart	74	74	0	100
37	Pade et al. (2009)	Atlantic	*Lamna nasus* (porbeagle)	4	PAT	Dart	22	90	0	25
38	Priede and Miller (2009)	Atlantic	*Cetorhinus maximus* (basking)	1	SAT	Dart	1	1	0	NA
39	Skomal et al. (2009)	Atlantic	*Cetorhinus maximus* (basking)	25	PAT	Dart	0	423	28	4
40	Bonfil et al. (2010)	Pacific	*Carcharodon carcharias* (white)	4	PAT	Dart	0	181	25	75
41	Jorgensen et al. (2010)	Pacific	*Carcharodon carcharias* (white)	97	PAT	Dart	0	362	30	NR
42	Papastamatiou et al. (2010)	Pacific	*Carcharhinus melanopterus* (blacktip)	4	SAT	Fin mount	30	45	0	NA
43	Stevens et al. (2010)	Pacific	*Prionace glauca* (blue)	9	SAT and PAT	Fin mount and Dart	0	159	22	100

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Table 1 *(continued)*

Count	Reference	Ocean	Shark species	Sample size	Tag type	Attachment type	Min tacking days	Max tracking days	Prop. tag failure	Prop. pre-mature pop-offs
44	Stevens et al. (2010)	Pacific	*Isurus oxyrinchus* (mako)	1	PAT	Dart	88	88	0	100
45	Stevens et al. (2010)	Pacific	*Alopias vulpinus* (common theresher)	1	PAT	Dart	177	177	0	100
46	Stevens et al. (2010)	Pacific	*Alopias superciliosus* (bigeye thresher)	1	PAT	Dart	14	14	0	100
47	Carlson et al. (2010)	Atlantic	*Carcharhinus leucas* (bull)	18	PAT	Dart	0	85	13	100
48	Brunnschweiler et al. (2010)	Atlantic and Pacific	*Carcharhinus leucas* (bull)	20	PAT	Dart	0	53	40	100

Attachment type refers to whether tag that was affixed via dart tag into dorsal musculature (Dart), mounting to the dorsal fin (Fin mount), anchor through the dorsal (Dorsal dart anchor) or fin tether looped through the dorsal (Fin loop); Prop. = proportion; Min = minimum; Max = maximum.

provides SAT/SPOT tag derived positions on a decreasing location class (LC) scale: 3, 2, 1, 0, A, B, and Z. Argos provides the following accuracy estimates for the following location classes: LC 3, >250 m; LC 2, >500 m and LC 1, >1500 m (www.argos-system.org). These accuracy errors are assumed to be isotropic and characterized by a radius of error, one standard deviation (sigma) of the estimated location error. Argos does not provide estimates for LC 0, A, B, and Z; but it has been reported in the literature that LC A was accurate to >1 km radius and LC B was accurate to >5 km radius (Tougaard et al., 2008). Class Z indicates that the location process failed and estimates of position are highly inaccurate. Successive transmissions received by the satellite in short time intervals improve the accuracy of each position. To obtain a LC of 3 to 0, an orbiting satellite needs to receive 4 successive transmissions from the tag. For a LC of A and B, 3 and 2 successive transmissions, respectively, need to be received by the satellite. Accordingly, the major disadvantage of using SPOT tags on sharks is the need for the tags to surface for prolonged periods to allow for successive transmissions for obtaining accurate position data. The latter makes shark species which rarely surface less suitable candidates for SPOT tag deployment. However, when deploying SPOT tags on sharks that do frequently surface, locations can be improved by programming tags with short repetition rates (<30 s). This alteration increases the likelihood of a tag sending multiple transmissions to an orbiting satellite.

There is a new Argos-linked satellite tracking technology, called “fast-GPS” tags. These tags provide the ability to achieve accurate GPS locations, while only requiring the tag antenna to be above the surface for less than one second (www.wildlifecomputers.com). No studies to date have been published using this tag type for sharks, but use of this “fast-GPS” technology may improve the ability for researchers to obtain useful data for sharks that surface briefly.

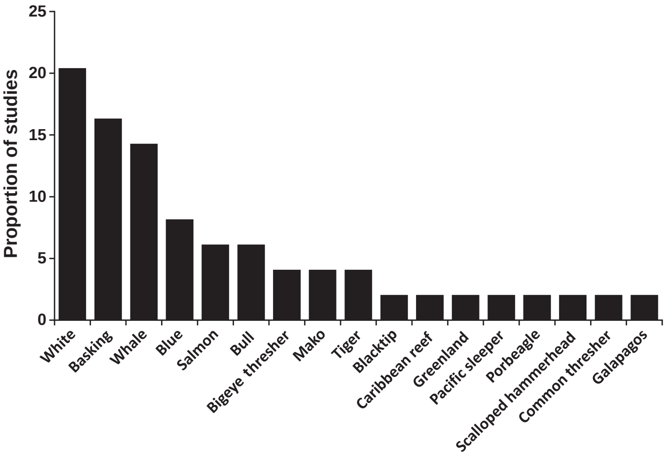

Fig. 1. Proportion of satellite tagging studies by species. To date, 17 shark species, representing 7 families (Alopiida, Carcharhinidae, Cetorhinidae, Rhincodontidae, Dalatiidae, Somniosidae, Sphyrnidae) from 4 orders (Lamniformes, Carcharhiniformes, Orectolobiformes, Squaliformes) have been satellite tagged.

3.3. Species and geographic regions

To date, 17 shark species, representing 7 families from 4 orders have been satellite tagged (Fig. 1). The majority of tagging studies have focused on the white (*Carcharodon carcharias*) (20%), basking (*Cetorhinus maximus*) (16%) and whale shark (*Rhincodon typus*) (14%). Focus on these species is likely due to a couple primary reasons. First, all three species congregate in localized areas around the globe at specific times of year to feed at or near the surface, which is highly conducive to tagging. Secondly, all three species are considered at high risk for global extinction by the IUCN (International Union for Conservation of Nature; www.iucnredlist.org, accessed July 2010), thus generating significant scientific and conservation interest.

The spatial distribution of studies examined covers various areas in the Atlantic, Pacific and Indian Oceans (Fig. 2). We failed to identify any published studies to date from the Arctic and southern (Antarctic) oceans, probably due to the difficulties imposed by traveling to and conducting research in these remote geographic regions. The majority of studies (~50%) have been conducted in the Pacific Ocean. This was mainly due to the efforts of the TOPP Program (Tagging of Pacific Predators), which began in 2000 as a major component of the Census of Marine Life. TOPP has attached satellite tags to more than 2000 animals of 22 different species in the Pacific, including sharks (Boustany et al., 2002; Dewar et al., 2004; Weng and Block, 2004; Weng et al., 2005; 2007a; b; 2008; Jorgensen et al., 2009; http://www.topp.org/topp_census, accessed 18 July 2010).

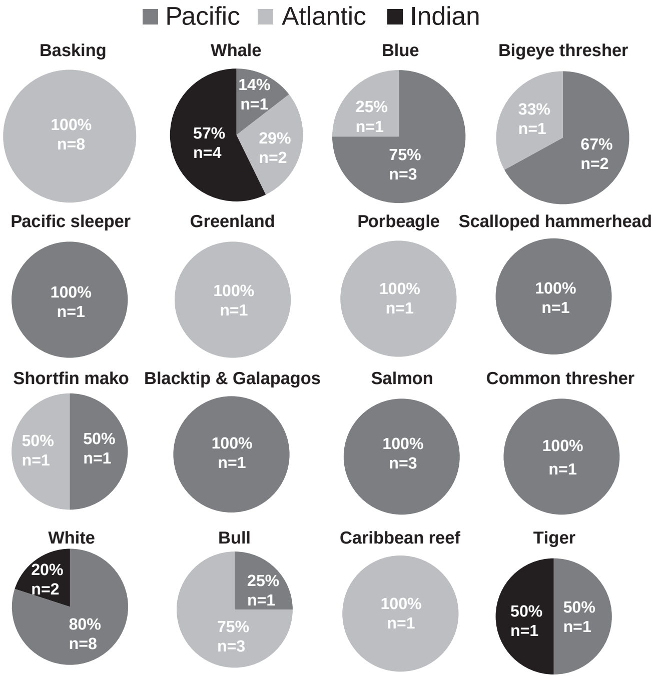

Fig. 2. Proportion of satellite tagging studies by species within each ocean basin.

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In terms of species by region (Fig. 2), the majority of satellite tagging in the Pacific has been done on white sharks, followed by blue (*Prionace glauca*) and salmon sharks (*Lamna ditropis*). In fact, 80% of white shark studies have been conducted in the eastern Pacific. The remaining studies were conducted in the Indian Ocean; comprising the waters of Australia, New Zealand and South Africa. Thus far, basking sharks have only been satellite tagged in the northwest and northeast Atlantic Ocean. Although whale sharks have been satellite tagged in the Atlantic, Pacific and Indian Ocean, over 60% of published studies have been conducted in the Indian Ocean. The majority of blue, bigeye thresher (*Alopias superciliosus*) and salmon shark studies have also been conducted in the Pacific (Fig. 2). For the remaining species which have been satellite tagged, there have been two or fewer tagging studies occurring in the Pacific, Indian or Atlantic. Subtropical and tropical regions have been relatively underrepresented for satellite tagging studies, especially in the Atlantic Ocean.

3.4. Tracking times

Tracking times ranged from 0 days to 1335 days (Table 1). Across studies, the minimum number of days an individual was tracked averaged 25 days (SE ± 5, N = 48); while the maximum number of days an individual was tracked averaged 201 days, (SE ± 39, N = 48). Across studies, we found no significant difference in the average minimum number of days an individual shark was tracked using PAT versus SAT tags (mean ± SE = 26 ± 6 days, N = 34, versus 24 ± 10 days, N = 17; $p > 0.05$). However, there was a significant difference in the average maximum number of days an individual shark was tracked using PAT versus SAT tags (mean ± SE = 139 ± 19 days, N = 34, versus 325 ± 106 days, N = 17; $P < 0.05$). Several reasons may be responsible for this pattern. PAT tags are usually applied from a boat using a tagging lance, where the tag is imbedded within the shark skin using a dart anchor. This method is highly conducive to tag shedding, which can result in premature tag pop-off. In fact, based on our review, we found that PAT tag premature releases averaged 66% (SE ± 8, N = 27) across all studies reporting this data. For this reason, PAT tags are usually programmed for relatively short deployment periods of 30, 60 or 90 days; rarely being programmed for a period of longer than a year. In contrast, the SAT tag system is less conducive to rapid shedding. These tags are designed to transmit as long as the tag stays attached and battery life permits (generally greater than a year).

3.5. Tag failure

Out of the 48 studies reporting tag failure data, 39 studies contained tags that transmitted less than 30 days; 17 studies had tags that failed to transmit a single position. Further, across all studies reporting data on tag failure, an average 10% of all tags deployed per study failed (N = 48 studies). This being said, there have been constant advances in the field over the past decade and with it an associated lowering in tag failure rates. From 1984 to 2006 (N = 21 studies), tag failure rate averaged 13.5% per study; but, between 2007 and 2010 (N = 30 studies), tag failure rate averaged only 7.2% per study.

Hays et al. (2007) examined various reasons why satellite tags deployed on marine animals may stop transmitting. Over short periods of time, Hays et al. (2007) suggested that tag failure resulted from animal mortality, salt-water switch failure, antenna breakage and premature detachment (Hays et al., 2007). However, they found that over longer deployment periods (i.e. >year), tag failure was likely a result of salt-water switch malfunction. Their data suggested that bio-fouling organisms (e.g. algae and barnacles) that accumulated over the salt-water switch caused tag failure. Hays et al. (2007) proposed that changing the stainless steel salt-water switches, used in all previously published studies to date, to copper may result in lower growth rates of bio-fouling organisms.

The use of anti-fouling agents applied to tags has been proposed to limit growth of bio-fouling organisms. In all the papers reviewed, only one shark study (Gifford et al., 2007) reported use of any anti-fouling agents (although several studies may have used them). We caution the use of boat paints containing heavy metals as anti-fouling agents. In addition to their potential environmental impacts, the metals in the paints can cause irritation or damage to shark tissue, which could result in tag shedding. We have been experimenting with a non-toxic, non-metallic, anti-fouling agent comprised of several different types of silicone resins. This product, Propspeed (www.propspeedusa.com), produces a coating over the tag's surface that inhibits attachment of marine growth. Although our investigation is still in its infancy, we recaptured one of our tiger sharks (*Galeocerdo cuvier*), equipped with a Propspeed-coated SPOT tag, three weeks after initial tag deployment. We found no evidence of bio-fouling on the treated tag, nor any signs of skin irritation around the tag. We caution these preliminary observations, since further testing is required before we can draw any long-term conclusions relating to the effectiveness of Propspeed.

On many occasions, divers have observed PAT-tagged lemon sharks (*Negaprion brevirostris*) swimming upside down, scraping their tags against the seafloor. These sharks were described by divers as appearing to try and rid themselves of their tracking devices (J. Abernethy, pers comm). Such behaviors could cause both tag damage and/or shedding. In Fiji, scientists have also made several observations of PAT tags on bull sharks (*Carcharhinus leucas*) being plucked off and eaten by predatory fishes, resulting in tags failing to transmit (G. Adkinson, pers comm). Similarly, Caribbean reef sharks (*Carcharhinus perezi*) have been observed trying to bite the tags and loggers off conspecifics (A. Maljkovic, pers comm).

3.6. Impacts of satellite tagging on physiology and behavior

The process of applying or inserting tags into animals can lead to varying short and long term physiological consequences (Weimerskirch et al., 2002). In sharks, the dorsal musculature is widely accepted as the most suitable region for PAT tag application due to a tough placoid scale epidermis that covers a highly convoluted region of thick muscle fibers, cartilage, and pterygiophores (Campana et al., 2009). Forceful insertion of the tagging unit into the dorsal musculature decreases the probability of premature release or shedding. However, exposed injuries and lesions at the site of insertion can increase an individual's susceptibility to bacterial infection (Mote Summary, 2002–2007). Moreover, the PAT tag dorsal anchor and tether often remain embedded in the musculature of sharks, long after the tag has detached (Fig. 3), providing attachment sites for parasites.

SPOT tags are usually mounted to shark fins using biocompatible materials. The attachment process includes punching or drilling holes

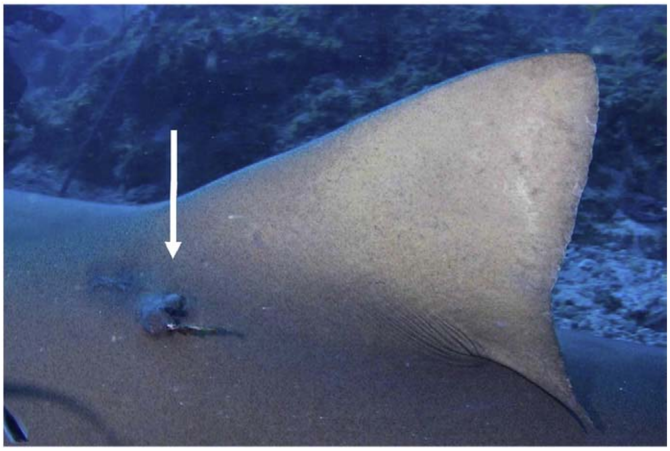

Fig. 3. (A) Remnant of an anchor and tether from a detached PAT tag in the dorsal musculature of a lemon shark *Negaprion brevirostris* showing tissue damage and possible infection (arrow). Image and reports courtesy of J. Abernethy.

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through the dorsal fin tissue, where after the tag is affixed using bolts or pins, and finally secured with nuts made of a corrodible material. This design theoretically allows the tag to shed after battery exhaustion. However, tissue degradation and infection due to a foreign body response may result. To our knowledge, there are no published reports of this condition on the dorsal fins of satellite tagged sharks, however this pattern of fin damage from tagging has been described in other predatory marine animals such as dolphins (Balmer et al., 2010).

Once deployed, the actual satellite tag becomes an extension to the shark's body. The most obvious behavioral consequence of tagging is a change in swimming efficiency due to hydrodynamic drag incurred by the tag. Transmitters have been linked with abnormal swimming behavior and increased energetic demands in dolphins (e.g. Irvine et al., 1982) and marine birds (e.g. Wilson et al., 1986; Wilson and McMahon, 2006). Various studies have examined possible effects of electronic tags or data loggers on the swimming efficiency of sharks, but results have been variable (Holland et al., 1993; Heithaus et al., 2007; Gleiss et al., 2009).

Another factor rarely considered is satellite tag color and how this may impact shark behavior (Wilson and McMahon, 2006). It is well documented that white sharks rely on stealth and ambush to successfully capture and subjugate seal prey (Martin et al., 2005; Hammerschlag et al., 2006). A vigilant seal may be cued into the presence of a white shark prior to an imminent attack by detecting a colored satellite tag, resulting in predator avoidance. We have been able to consistently distinguish colored electronic tags on approaching white sharks below the surface, before visualizing the actual shark (Authors, unpublished data). Brightly colored tags should be avoided due to their potential to alter predator–prey relationships (Hawkins, 2004).

3.7. Satellite tagging as a tool for shark conservation

An increasing number of studies worldwide have demonstrated rapid declines of large sharks over the last decades due to over-fishing practices (Baum et al., 2003; Myers and Worm, 2005; Dulvy et al., 2008; Ferretti et al., 2008, 2010). As such, there has been a growing concern globally for shark conservation. However, policy makers and managers have for the most part been unable to put appropriate regulations in place to protect sharks, largely due to a lack of scientific data. Although useful, conventional identification tagging does not provide the appropriate data needed for policy makers, nor can the methodology be improved to help fill this need (Kohler and Turner, 2001). Conventional tagging relies on the ability to recapture previously tagged individuals to make inferences about their whereabouts while at large; and requires a large number of tags to be employed to make these efforts valuable. Satellite technology can provide data on behavioral, spatial and population ecology of fishes which can be used to inform managers (Greene et al., 2009; Sims, 2010). A great example of this successful integration comes from studies of Atlantic bluefin tuna (*Thunnus thynnus*). Through satellite tagging, Block et al. (2005) demonstrated that there are at least two populations of bluefin tuna in the North Atlantic, which share common foraging areas, but utilize distinct breeding areas. The level of mixing estimated from the tracking studies was higher than previously assumed by the International Commission for the Conservation of Atlantic Tunas (ICCAT) stock assessment models, which were used in setting management quotas for the tuna that resulted in overfishing (Block et al., 2005).

3.8. So what have we really found out and where can we go from here?

With the increase of shark satellite tagging over the past decade, scientists have been able to describe previously unknown migration patterns, diving behavior as well as depth and temperature preferences for a variety of species. This technology has revealed some unexpected and impressive insights into shark biology; for example, white shark transoceanic migrations of over 10,000 km (Bonfil et al., 2005), whale shark deep dives exceeding 1 km (Rowat et al., 2007; Brunnschweiler et al., 2009) and hibernation in basking sharks (Skomal et al., 2009). However, most satellite tagging studies have only been able to describe the "what" rather than the "why" aspects of shark behavior and ecology. This is best exemplified in the most highly satellite tracked shark species on the planet: the white shark. For example, recent research has revealed that white sharks migrate from the central Californian coast and neighboring areas to Hawaii and back, spending the majority of the year in the middle of the Pacific Ocean, in a localized area between the two coasts, termed the "Shared Offshore Forage Area or SOFA" (Boustany et al., 2002; Dewar et al., 2004; Domeier and Nasby-Lucas, 2008; Weng et al., 2007a,b; Jorgensen et al., 2009). Despite cumulatively deploying an impressive 216 satellite tags (SPOT and PAT tags) on white sharks in the eastern Pacific region, it still remains unknown *why* exactly the sharks are spending the majority of the year in the SOFA as well as undertaking migrations of over 4000 km to Hawaii. Mating, feeding, and/or parturition have been suggested as possibilities, but empirical evidence is lacking.

In order to get at the important "why" questions, scientists will need to incorporate a variety of tools and develop new satellite tagging technologies. A variety of transmitters and sensors already exist which are useful for measuring subtle changes in shark behavior, such as swimming speed, sound, tail–beat frequency, muscle contraction and acceleration (Sundström and Gruber, 1998; Lowe et al., 1998; Lowe, 2001; Lowe and Goldman, 2001; Meyer et al., 2007; Papastamatiou et al., 2007; Whitney and Crow, 2007). Animal-borne video systems are now available, which can provide continuous video recordings from the shark's view-point (Marshall et al., 2007). In addition to providing location estimates, current satellite tags already have the sensors and capabilities of recording and transmitting measurements of water depth, temperature, and chlorophyll content (Teo et al., 2009). Future work should seek to couple tools, such as accelerometers and video systems, into a single satellite tag. If such a tag were developed, we could use a transmitter to track shark migration, swimming speed and tail beat frequency. If an irregular or abrupt change in swimming speed or tail–beat frequency occurred, a built-in mini camera could record a series of photos and videos. Subsequently these data could be archived and transmitted to orbiting satellites, making them accessible for researchers. With the right tools, time, funding and effort, manufacturers and scientists could work together to develop more advanced tags, affording researchers opportunities to answer some of the critical "why" questions that continue to go unanswered.

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Glossary

Bio-fouling: the unwanted accumulation and subsequent growth of fouling, micro-organisms such as plants, algae and invertebrates onto surfaces of devices or structures.

Density effects: effects of predators on prey through killing and consumption.

Doppler-shift: this is the change in frequency of a sound wave or electromagnetic wave when a transmitter and a receiver are in motion relative to each other.

Drag: the forces that oppose the relative motion of an object through a medium such as air or water.

Physiological stress: the collective bodily response of an organism in relation to a non-favorable, exhaustive or extreme metabolic or respiratory demand (such as exercise, impaired breathing, etc). These physiological consequences can be traced through various animal tissues and metabolites.

Risk effects: when prey alter their behavior in response to predators (i.e., anti-predator behavior).

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