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Evidence of shark predation and scavenging on fishes equipped with pop-up satellite archival tags

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Over the past few years, pop-up satellite archival tags (PSATs) have been used to investigate the behavior, movements, thermal biology, and postrelease mortality of a wide range of large, highly migratory species including bluefin tuna (Block et al., 2001), swordfish (Sedberry and Loefer, 2001), blue marlin (Graves et al., 2002), striped marlin (Domeier and Dewar, 2003), and white sharks (Boustany et al., 2002). PSAT tag technology has improved rapidly, and current tag models are capable of collecting, processing, and storing large amounts of information on light level, temperature, and pressure (depth) for a predetermined length of time before the release of these tags from animals. After release, the tags float to the surface, and transmit the stored data to passing satellites of the Argos system.

A problem noted by several authors using early PSAT models was the occasional occurrence of tags that did not transmit data. Clearly, a tag attached to a moribund fish that would sink to a depth exceeding the pressure limit of the tag casing would be destroyed. To prevent the loss of tags due to mortality events, tag manufacturers and researchers

have developed mechanisms that release tags from dead or dying fish before the structural integrity of the tag is compromised at depth. These mechanisms include both mechanical devices that sever the monofilament tether that attaches the tag to the fish upon reaching a given depth and internal software subroutines that activate the normal electronic release mechanism if the tag either reaches a certain depth or maintains a constant depth for a predetermined length of time.

Despite the addition of these release mechanisms to PSATs, some tags still fail to transmit data. Such failure could result from any of the following events or conditions: mechanical failure of a critical tag component; destruction by fishing crews unaware of or not participating in the present research; excessive epifaunal growth that makes the tag negatively buoyant or prevents the tag from floating with the antenna in a vertical position; or fouling of the tag on the fish, fishing gear, or flotsam. Another cause of failure is that the tags could be lost as a result of ingestion. For example, a free-swimming white marlin (*Tetrapturus albidus*) was observed mouthing and

almost swallowing a free-floating PSAT off the Dominican Republic in May 2002 (Graves, personal observ.). Alternately, the tag could be ingested incidentally with part of the tagged fish, as described by Jolley and Irby (1979) who reported that an acoustic tag on a sailfish (*Istiophorus platypterus*) was eaten along with the fish by an undetermined species of shark. In this note, we present data from PSATs deployed on two white marlin in the western North Atlantic Ocean and on an opah (*Lampris guttatus*) in the central Pacific; the data from these tags indicate that the tags were consumed by sharks.

Materials and methods

White marlin 1 (WM1)

At approximately 10:00 am local time on 1 September 2002, a white marlin was observed on pelagic longline gear set during the night near the southeastern edge of Georges Bank. The fish, which had been caught on a slightly offset, straight-shank J-style hook (size 9/0), was manually guided with the leader alongside the vessel. A PTT-100 HR model PSAT (Microwave Telemetry, Inc., Columbia, MD) was attached to the dorsal musculature approximately 5 cm below the base of the dorsal fin with a large nylon anchor according to the procedure and tether design described in Kerstetter et al. (2003). The tag was activated shortly after the white marlin was first identified, although approximately one hour is required following activation for this tag model to begin collecting data. The tag was programmed to record point measurements of temperature, light, and pressure (depth) in four-minute time intervals and to detach from the animal after 10 days. After release from the fish, the positively buoyant tag was expected to float to the surface and transmit stored and real-time data. For both white marlin

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Table 1

Comparison of depths and temperatures recorded by three pop-up satellite archival tags (PSATs) before and after the tags were ingested by an organism.

Animal	Before ingestion					After ingestion				
	Depth range (m)	Depth mean (SD)	Temp. range (°C)	Temp mean (SD)	<i>n</i>	Depth range (m)	Depth mean (SD)	Temp range (°C)	Temp mean (SD)	<i>n</i>
WM1	145.2	145.2 (±0.00)	11.6–11	11.7 (±0.07)	179	0–564.9	130.0 (±237.50)	12.1–26.5	24.1 (±0.84)	2755
WM2	0–26.9	5.9 (±4.44)	19.8–27.8	24.7 (±0.91)	207	0–699.3	131.0 (±162.61)	18.9–29.5	27.3 (±1.20)	1683
Opah	32–456	221.81 (±92.20)	8–25.6	16.68 (±4.21)	360	0–524	170.56 (±133.83)	26.2–30.6	28.64 (±0.67)	168

tags, minimum straight-line distances were calculated between the point of release and the first clearly transmitted location of the tag following its release (pop-off) (Argos location codes 0–3).

At the time of tagging, the longline hook used to capture the fish was not visible in the mouth of the white marlin. The leader was therefore cut as close as possible to the fish before the fish was released, following the standard operating procedure for the domestic pelagic longline fleet. The fish was maintained alongside the vessel for less than three minutes for the application of the PSAT and a conventional streamer tag. Although the white marlin was initially active at the side of the vessel, some light bleeding from the gills was noted. After release, the fish swam away slowly under its own power.

White marlin 2 (WM2)

At 9:05 am on 2 August 2003, a white marlin was observed on pelagic longline gear with the same configuration in the same approximate area of Georges Bank as WM1. The fish was caught by a circle hook (size 16/0) in the right corner of the mouth, and although the stomach was everted, the fish appeared to be in excellent physical condition. A PTT-100 HR tag had been activated at 6:30 am that morning, and was therefore collecting data at the time of tagging. After the fish was brought to the side of the vessel, both the PSAT and a conventional streamer tag were attached to this fish in less than three minutes by using the same protocol as that described for WM1, and the fish swam strongly away from the vessel after release without any evident bleeding.

Opah

At 5:52 pm local time on 21 November 2002, a female opah was observed on pelagic longline gear set during the day east of the Island of Hawaii. The fish was brought to the side of the fishing vessel and a Wildlife Computers (Redmond, WA) PAT2 model tag was attached through

the dorsal musculature with a Wildlife Computers titanium anchor. The tag was programmed to record the temperature and depth occupied by the fish in binned histograms, and the minimum and maximum temperatures and depths for 12-hour time periods. However, these 12-hour bins encompassed both day and night periods. The tag was programmed to be released six months after deployment. In the event of a premature release, the tag was programmed to begin transmitting stored data if it remained at the surface for longer than three days. The opah was lively and quickly dived after it was released.

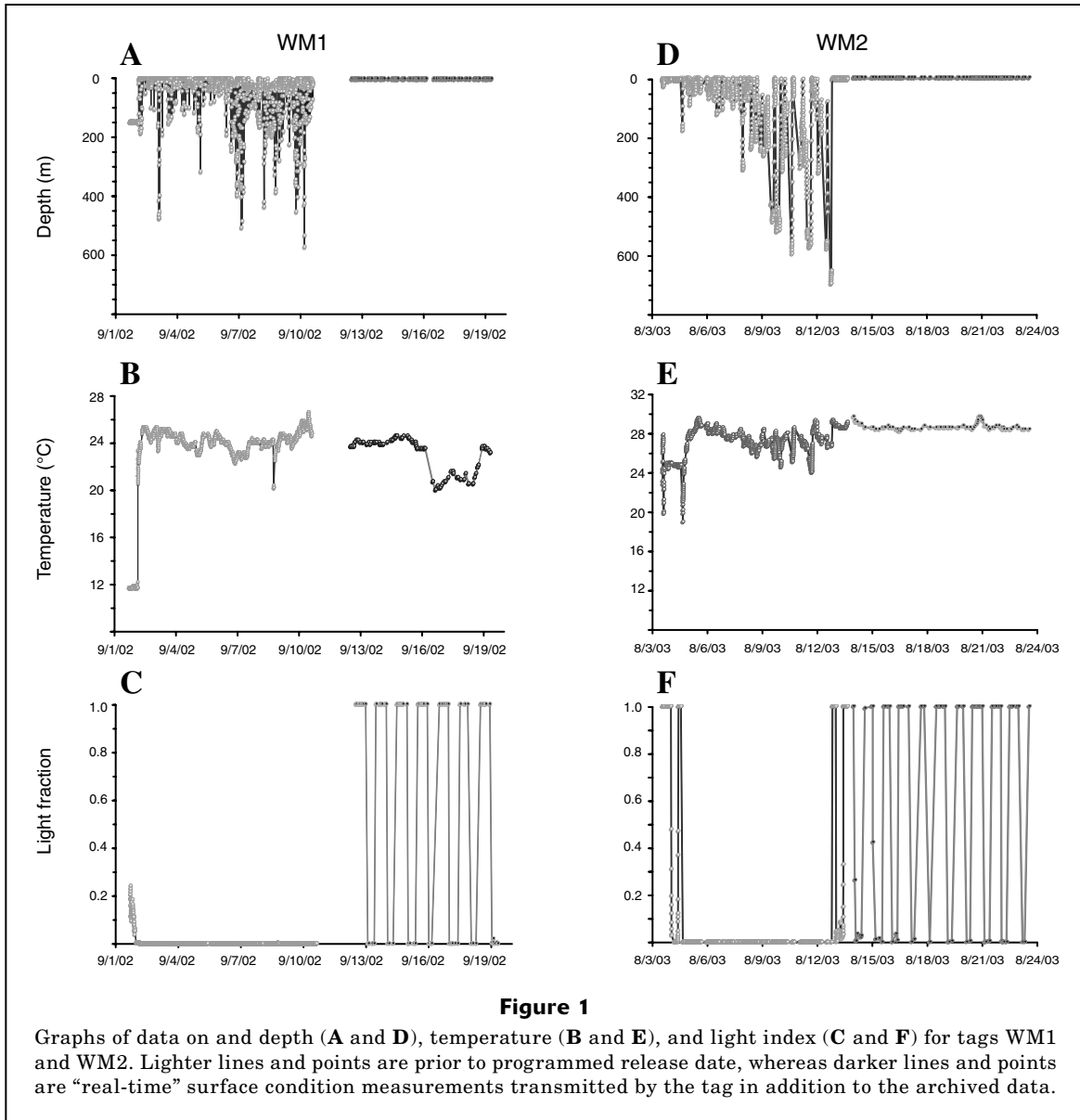
Results

WM1

Release of the PSAT was expected to occur on 10 September 2002 and the tag was expected to begin transmitting data on that date, but the first transmission was not received until almost two days later. At the time of first transmission, the PSAT was 81.3 km (43.9 nmi) west-southwest of the tagging location. A total of 81.5% of the archived light level, temperature, and pressure (depth) data was recovered.

The light level, temperature, and pressure (depth) readings over time are presented in Fig. 1 (A–C) and summarized in Table 1. The first light level measurements indicated that the fish was already in relatively dark waters within one hour following its release. Light levels continued to drop to almost zero during the next ten hours and remained at that level for the next nine days (Fig. 1A). During the next seven-day surface transmission period, the tag recorded real-time day and night differences in light levels, which indicated that the light sensor was functioning properly.

Sea surface temperatures in the area where the gear was set and hauled back, varied from 25.2° to 26.7°C (D. Kerstetter, unpubl. data) and the first temperature



recording by the PSAT (one hour after activation) was 11°C (Fig. 1B). The temperature remained fairly constant at 11°C for a period of approximately ten hours after which there was a rapid rise to 25°C. The temperature of the PSAT remained between 22.5° and 26.5°C for the next nine days (until the programmed release date), with the exception of one brief decrease to 20°C on 8 September. When the tag began transmitting on 12 September, the real-time surface temperature was 23.6°C.

The pressure data (Fig. 1C) indicated that the tag was at a depth of approximately 145 m at one hour following release. The PSAT remained at this depth for a little more than ten hours after which the data suggested that there was a rapid rise to the surface. For the next nine days, the tag reported considerable vertical move-

ment between the surface and depths to 565 m. The tag was at the surface when it began transmitting both archived and real-time data on 12 September.

WM2

The tag reported data as expected on 13 August 2003 and transmitted 57.3% of the archived data. At the time of first transmission, the PSAT was 600.1 km (324.0 nmi) east-southeast of the tagging location. Summary depth and temperature data recorded by the PSAT are included in Table 1.

From the depth and temperature data, it appears that the fish survived for approximately 24 hours after release, at which point the light readings dropped to zero (see Fig. 1D) and remained at that level for

the next eight days. The depth record following this change in light level was marked by several discrete diving events, and depths (see Fig. 1F) ranged between the surface and over 699 m. Recorded temperatures for this period varied between 18.9° and 29.5°C, although sea surface temperatures in the area where gear was set and hauled back varied from 20.9° to 26.0°C (Kerstetter, unpubl. data). On 12 August, the light level returned to its maximum value and the tag remained at the surface for approximately one day until its scheduled release date (13 August) when it began transmitting data.

Opah

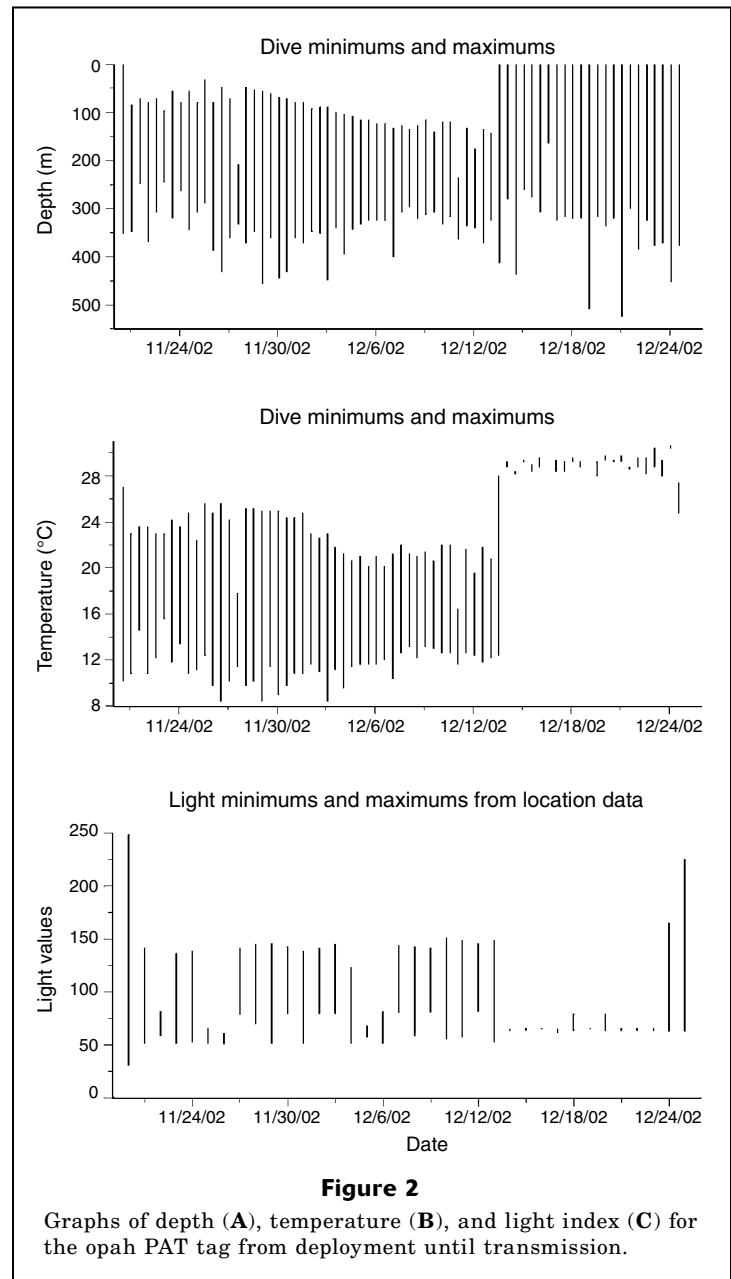
The PAT2 satellite tag was expected to pop-up 6 months after deployment, but the first transmission was received after only 34 days from a location about 330 km (178 nmi) northwest of the deployment site. All the archived binned light level, temperature, and pressure (depth) data from this period were recovered (see Table 1). This tag model collected eight temperature and depth samples during each 12-hour period, resulting in 16 values per day or 528 total values for the deployment period. The two 12-hour blocks were removed from all analyses to more accurately represent the differences in data between specimens: 1) the 12-hour block after tagging in order to allow for the recovery of the animal, and 2) the 12-hour block during which the predation event putatively occurred in order to clarify the potentially distant depth and temperature characteristics of the ingesting animal.

The measured sea surface temperature during the tagging of the opah was 25.9°C. The ranges of dive depths, temperature, and light based on minimum and maximum values over the 12-hour day and night periods showed two distinct patterns (Fig. 2). During the first period (23 days), the dive depths ranged from about 32 to 456 m (Fig. 2A). Water temperatures encountered by the tag during this period ranged from 8.0° to 25.6°C (Fig. 2B) and the light index values ranged from about 50 to 150 (Fig. 2C). During the second period (11 days), the dive depths ranged from 0 to 524 m, temperature ranged from 26.2° to 30.6°C (higher than the 24.2–24.8°C SST recorded by the tag after it was released from the fish), and the light index recorded persistently low values.

Discussion

WM1

Our interpretation of these data is that the PSAT on WM1 was ingested by an animal scavenging the marlin carcass. The first PSAT readings for WM1,



recorded about one hour after its release, indicated that the marlin was already dead or moribund by that time and was descending to the ocean floor. For the next ten hours, the tag and carcass remained at a constant depth of 145 m (the depth of the nearest sounding at the site of release, according to NOAA depth chart 13003 [1998], was approximately 160 m) and at a temperature of 11°C. The light level steadily decreased at approximately 4:30 pm, corresponding to changes in ambient light from the setting of the sun. At approximately 9:00 pm local time, there was a dramatic change in conditions when temperature rapidly rose to near 26°C and depths began to vary between the surface and 600 m.

We cannot attribute these changes to a resuscitation of the fish for three reasons. 1) The measured light levels indicated that the tag was in complete darkness for a period of ten days, even though it was at the surface during daylight hours. A malfunctioning light sensor cannot explain this observation because the tag recorded day and night differences in light levels at the surface during the seven-day transmission period after it was released from the fish. 2) After a rapid increase, the temperature remained relatively constant, between 23° and 26°C, even when the tag was at depths in excess of 300 m. Although dive behavior may be affected by location-specific conditions, previous PSAT observations of more than 20 other white marlin indicated that temperature ranges of individual dive events rarely exceed 8°C when, it is assumed, animals make foraging dives to depth (Horodysky et al., in press). 3) The PSAT recorded several dives in excess of 400 m, and previous observations of white marlin have revealed no dives in excess of 220 m (Horodysky et al., in press). Finally, the PSAT was scheduled to be released from WM1 after ten days on 10 September. Although archiving of light, temperature, and pressure data ceased on that date, the tag did not begin transmitting until 12 September.

WM2

The shallow dive patterns reported by this fish may indicate that it survived for approximately 24 hours following its release. Between 12:45 and 3:07 pm (local time), the light level fell abruptly from the maximum light level value to zero. At 3:08 pm, the temperature was 19.8°C at 166 m depth; by 4:37 pm, the temperature was above 24°C and remained above this value for the remainder of the deployment period. At 5:58 pm on 12 September, the light levels returned to maximum strength from zero—an indication that the tag had likely been egested. For the 19 hours remaining of the programmed deployment period prior to pop-off, the depth, light, and temperature data all indicated that the tag was floating at the surface.

Opah

Based on recovered data, our conjecture is that the tag was attached to the live opah for the first 23 days. Then, sometime during the 12-hour period from 2:00 pm 13 December to 2:00 am 14 December the tag was ingested. From our data, we cannot discern whether 1) the tag was detached prematurely from the opah and was floating on the surface when it was ingested, 2) an animal

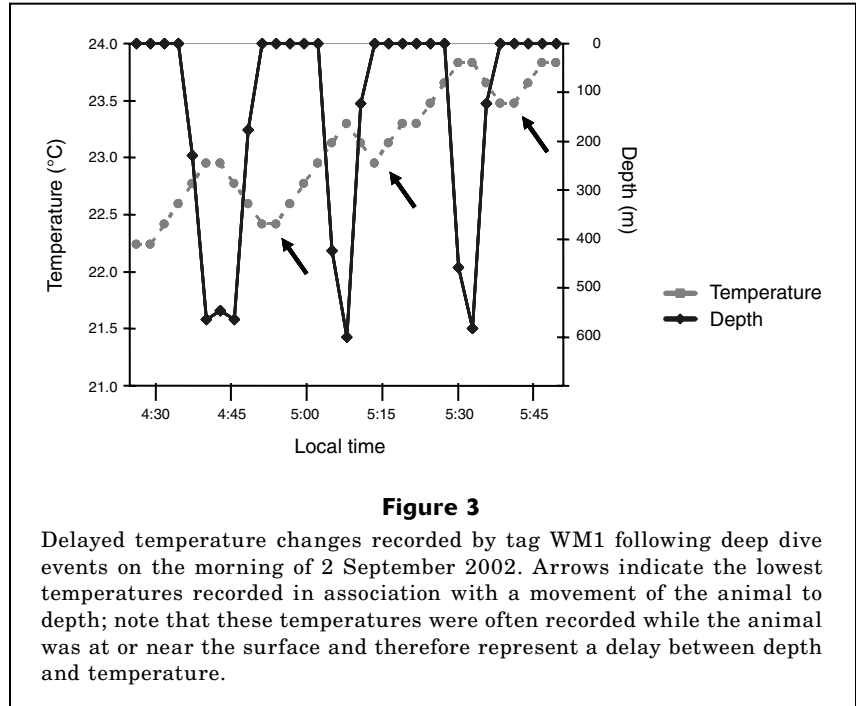


Figure 3

Delayed temperature changes recorded by tag WM1 following deep dive events on the morning of 2 September 2002. Arrows indicate the lowest temperatures recorded in association with a movement of the animal to depth; note that these temperatures were often recorded while the animal was at or near the surface and therefore represent a delay between depth and temperature.

attacked the opah and ingested the tag incidentally, or 3) an animal ingested the tag alone. However, it is unlikely that the opah died, sank to the ocean floor, and was scavenged because the ocean floor in the area where the opah was tagged is below 2000 m. We have observed from other tags on opahs what we believe are mortalities; these occur shortly after tagging and show that the tag reaches depths in excess of 1000 m before detaching when the emergency pressure release in the tag is triggered. We did not observe depths below 600 m at any time during this record, and therefore the pressure-induced detachment mechanism on the tag was not triggered.

The ingestion hypothesis for the failure of these three tags to transmit data is supported by several lines of evidence. First, the light level readings were consistent with a tag residing in the complete darkness of an alimentary canal. Second, although temperature variations occurred during the deployment period, the delay in temperature changes during dives to depths indicates that the tags were not directly exposed to ambient water (see Fig. 3 for an example from WM1, as well as the comparisons in Table 1) and further may indicate that the scavenger was either endothermic or of large enough size to mitigate heat loss at depth.

There are several organisms that could have eaten these PSATs, whether by scavenging a carcass or attacking a moving fish. Clearly, each of these organisms was sufficiently large to ingest the tag without seriously damaging it. It is unlikely that a cetacean was responsible for any of these events because internal temperatures for odontocete whales (including killer whales, *Orcinus orca*) range between approximately 36° and 38°C (Whittow et al., 1974)—well above the range of temperatures recorded by the PSATs.

The only other natural predators of large pelagic fishes are various species of sharks. Several species of lamnid sharks maintain elevated body temperatures, including the shortfin mako (*Isurus oxyrinchus*) and the white shark (*Carcharodon carcharias*), both of which are found in the area of Georges Bank (Cramer, 2000) and the Central Pacific (Compagno, 1984). Several shortfin makos were caught by the same longline vessel during the week following each white marlin PSAT deployment (WM1: $n=4$, 95–189 cm FL; WM2: $n=3$, 94–199 cm FL) (Kerstetter, unpubl. data). The opah tag record closely resembles the relatively constant temperature noted for lamnid sharks, despite the independence of stomach temperature with ambient water for these endothermic sharks as reported by Carey et al. (1981). It is also interesting to note that although precipitous temperature fluctuations were generally absent, a rapid drop in temperature from 24° to 20°C was observed with tag WM1 on 8 September at 32.3 m depth—a fluctuation that could have resulted from another feeding event that brought cool food matter into the stomach. Similar reductions in stomach temperatures due to feeding have been noted for white sharks (McCosker, 1987). The range of temperatures recorded by each of the two white marlin tags appears rather broad for an endothermic shark, however, and although the temperature at depth was not measured, the delay in stomach temperature closely resembles the pattern of blue shark internal temperatures (*Prionace glauca*) measured in the Mid-Atlantic (Carey and Scharold, 1990).

The diving behavior recorded by the three tags also corroborates ingestion of the tags by sharks. Carey et al. (1982) reported that a tagged white shark off Long Island, New York, made frequent dives to the bottom during a 3.5-day acoustic tracking period. White sharks are known to dive to depth while scavenging whale carcasses (Dudley et al., 2000; Carey et al., 1982). A juvenile white shark also tracked by Klimley et al. (2002) spent far more extended times at depth than either white marlin tag. Although the programming of the tag on the opah precludes such fine-scale analyses of diving behavior, the available data are not inconsistent with the mako tracks in the study of Klimley et al. (2002). However, the short duration dives with frequent returns to the surface seen with the two white marlin tags most closely resemble those of blue sharks (Carey and Scharold, 1990) and were notably missing from the tracks of three shortfin makos observed by Klimley et al. (2002).

If sharks were indeed the scavenging animals, it is likely that the tags were regurgitated, rather than egested through the alimentary canal, whereupon the PSAT floated to the surface and was able to transmit the archived data. The narrow diameter of the spiral valve in the elasmobranch gastrointestinal tract would likely be too narrow to allow the undamaged passage of an object the size of a PSAT, even for a large shark. Although the available literature describing regurgitation abilities of pelagic sharks is rather limited, Hazin et al. (1994) reported that 35% of blue sharks brought aboard for scientific study had everted and protruding

stomachs. Economakis and Lobel (1998) also stated their belief that regurgitation of ingested ultrasonic tags was the primary cause of lost tracks for grey reef sharks (*Carcharhinus amblyrhynchos*) on Johnston Atoll in the central Pacific Ocean.

Conclusions

The temperatures and dive depths recorded by the opah tag and both white marlin tags after apparent ingestion share similarities, yet also contain sufficient information to indicate the different identities of the ingesting organisms. The dive depths in all cases ranged from the surface to over 500 m, whereas the temperatures remained relatively constant at several degrees above the background SST, even during deep dive events. Temperature ranges alone strongly indicate sharks rather than odontocete whales were the ingesting organisms. However, limited literature on the internal stomach temperatures of the various pelagic sharks forces us to rely on telemetered diving behavior data for further species identification, which we used in the present study to suggest that blue sharks ingested the two white marlin tags (on account of the broad range of recorded temperatures) and that an endothermic shark ingested the opah tag.

It is not possible to account for all of the factors that may result in the failure of satellite tags to transmit data, but the results from these three PSATs indicated that biological activities such as predation and scavenging may play an important role. We believe that the most consistent explanation for the data transmitted by these three tags is that they were ingested by large sharks. One cannot calculate the probability that a tag could be engulfed whole without physical damage to the tag, survive for several days in the caustic environment of a digestive system, and be regurgitated with sufficient battery power to transmit data to the Argos satellites, but we suspect that the probability is not very great. We expect that a far greater number of tags may have had similar fates, that is to say, they were damaged by predation or scavenging and digestion processes or were regurgitated later in the transmission cycle, when the PSAT batteries had insufficient remaining power for successful data transmission. The failure of satellite tag to transmit data is frequently considered to be the result of internal tag malfunction or user error. However, these three data sets clearly indicate that the failure of PSATs to function may also be due to predation or scavenging events.

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