

Journal of Experimental Marine Biology and Ecology 349 (2007) 52-60

Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

www.elsevier.com/locate/jembe

Why do Argos satellite tags deployed on marine animals stop transmitting?

G.C. Hays a,*, C.J.A. Bradshaw b, M.C. James c, P. Lovell d, D.W. Sims e,f

Institute of Environmental Sustainability, University of Wales Swansea, Singleton Park, Swansea, SA2 8PP, United Kingdom
 School for Environmental Research, Charles Darwin University, Darwin, Northern Territory 0909, Australia
 Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

Received 9 February 2007; received in revised form 22 April 2007; accepted 24 April 2007

Abstract

Identifying the reasons for the loss of signals in satellite tracking studies is important for directing future improvements in transmitter technology and attachment systems, as well as defining the status of the tracked animals (alive or dead) at the end of the tracking period, which is integral to assessing survival rates through established methods. We highlight the importance of transmitted diagnostic data that reveal the status of a tag. We show in marine wildlife satellite tracking that the reasons behind transmitter signal loss can often be identified. Exhaustion of batteries, salt-water switch failure, antenna breakage, animal mortality and premature detachment of tags were all identified as causes of signal loss from transmitters routinely attached to turtles, fish and marine mammals. In principle, battery management systems should allow tracking of individuals for several years, even with existing transmitter technology, although in such long-term deployments in a marine setting, failure of the salt-water switch may persist as the Achilles heel of existing tags.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Argos; Biofouling; Instrumentation; Radio tracking; Seal; Shark; Tagging; Tag failure; Turtle; Whale

1. Introduction

Over the last 20 years, satellite tracking using the Argos system (http://www.clsamerica.com/) has become a standard ecological and conservation tool allowing the movements of many marine and terrestrial species to be documented over a broad range of spatial and temporal scales. The use of the Argos system continues to expand and it seems set to remain a key tool for the animal

tracking community for years to come (see McMahon et al., 2005). While early studies were relatively short-lived (days or weeks) and provided few data (e.g. Hays et al., 1991; Priede, 1984), more recent studies now routinely succeed in tracking individuals for over one year (e.g. Berthold et al., 2004; Bradshaw et al., 2004; Hays et al., 2006; Phillips et al., 2006). There has been a progressive improvement in all the components of the Argos system. Over time there has been an increase in both the number of polar-orbiting satellites that receive signals from tags and the sensitivity of on-board receivers so that more daily locations are calculated for each transmitter.

d Sea Mammal Research Unit, Gatty Marine Laboratory, University of St. Andrews, St Andrews, Fife KY16 8LB, United Kingdom e Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, United Kingdom f School of Biological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, United Kingdom

^{*} Corresponding author. Tel.:+44 1792 295375; fax: +44 1792 295447. E-mail address: g.hays@swan.ac.uk (G.C. Hays).

Simultaneous improvements in transmitter technology have included miniaturization of tags, development of more robust designs and an increase in the number of sensors and quantity of data collected. Consequently, datasets that could once only be collected with data-loggers requiring physical recovery for data download (e.g. dive profiles and temperature-depth profiles) can now be relayed via satellite (e.g. Fedak et al., 2002; Hays et al., 2004; Sims et al., 2003; James et al., 2006). These improvements have led to more refined tracking studies and a large increase in our knowledge of long-distance movements of reptiles (e.g. Luschi et al., 2001, 2003; James et al., 2005b, 2006), fish (e.g. Sims et al., 2005; Weng et al., 2005), birds (e.g. Nel et al., 2001; Phillips et al., 2006) and mammals (e.g. Burns et al., 2004; Bradshaw et al., 2004; Harcourt et al., 2002).

However, a pervasive problem across all tracking studies is the failure of transmitters, often for unknown reasons (e.g. Polovina et al., 2004). Being able to ascribe the cause of signal loss would be useful for several reasons. First, this information could direct improvements to tag design and attachment so that future tags provide data for longer. Second, being able to differentiate between equipment failure versus animal death would be useful in allowing survival estimates to be derived from tracking studies using established procedures (e.g. Kaplan-Meier known-fate models) where the state of the animal at the end of the tracking period is known (Kaplan and Meier, 1958; Pollock et al., 1989; Hays et al., 2003; Bradshaw 2005). Here we consider satellite tracking studies encompassing a variety of taxa and models of transmitter to illustrate the reasons for loss of signals. Importantly, we show in many cases that it is possible to ascribe the reasons for loss of signals by using diagnostic information from tags and interpreting telemetred data and locations of tags prior to signal loss.

2. Material and methods

We made use of several previous studies during which we satellite-tracked marine animals for extended periods: leatherback turtles (*Dermochelys coriacea*), olive ridley turtles (*Lepidochelys olivacea*) and basking sharks (*Cetorhinus maximus*).

2.1. Leatherback turtles

We attached Satellite-Relayed Data Loggers (SRDLs, manufactured by the Sea Mammal Research Unit, University of St. Andrews, United Kingdom, www.smru. st-and.ac.uk) to 10 leatherback turtles that had completed nesting on the Caribbean on the island of Grenada in 2002

and 2003. Location of SRDLs was determined using the Argos system. The SRDLs relayed detailed dive profiles (Hays et al., 2006) and water temperature (McMahon et al., 2005), as well as diagnostic information regarding the status of various components of the tag. For our purposes here, the SRDLs relayed four important types of information.

(1) The status of the salt-water switch that was designed to synchronise transmissions to times when the tag was at the surface (because radio signals do not penetrate well through seawater). The salt-water switch consisted of two stainless steel contacts on the dorsal surface of the tag. Two values describing the status of the salt-water switch were relayed: the driest and wettest condition measured in the preceding three hours. These conditions were measured by recording the resistivity between the two salt-water contacts; immersion in saltwater reduced the resistivity. Resistivity was allocated arbitrary units so that with a new tag the "wet state" was defined by values around 20 and the dry start by values around 150-200, with a value of 50 being used to indicate the change in state from wet to dry and to initiate transmissions when animals surfaced. (2) Information was relayed on how many times the salt-water switch had failed. Failure was defined as the salt-water contacts not becoming dry (i.e. not reaching a value of 50) during the preceding 24 h. For example, failure of the salt-water switch can occur when fouling organisms (e.g. algae, barnacles) grow on the transmitter, so that water fails to drain quickly from the unit when the animal surfaces. (3) The number of transmissions that had been made by the unit. The single D-cell battery in each SRDL allowed a nominal 80,000 transmissions ($\pm 10\%$). Therefore, if the relayed number of transmissions reached 72,000 (i.e., 90% of 80,000), we assumed the batteries were exhausted. Tags were programmed not to exceed a certain maximum number of transmissions each 24-h period to ensure that the batteries lasted a predetermined minimum duration. For tags deployed in 2002, the daily limit on transmissions ensured the batteries should last at least one year, while for the 2003 deployments the daily transmission limit was designed to ensure at least two years of battery life. However, if animals surfaced infrequently, the daily maximum number of transmissions might not be achieved and hence, the battery life might extend beyond the minimum prescribed duration. (4) SRDLs relayed checksums within each uplink (a known sequence of bits within the transmission) so that a distinction could be made between complete transmissions where all checksums were received and incomplete (corrupted) transmissions where not all checksums were received.

These diagnostic datasets (transmission number, saltwater switch dry and wet state, number of salt-water switch failures, checksums) accounted for only 5% of the data relayed via the tags because we were interested in recovering as much dive and temperature data as possible.

2.2. Olive ridley turtles

We also attached SRDLs to four olive ridley turtles in northern Australia and tracked their postnesting movements (McMahon et al., 2007). As with the leatherback turtles study described above, SRDLs relayed a range of diagnostic data about the status of the tags.

2.3. Basking sharks

Pop-up Archival Transmitting (PAT) tags (length: 175 mm; mass in air, 76 g) were attached to 23 basking sharks (Cetorhinus maximus) off south-west England and north-west Scotland during summer in 2001, 2002 and 2004 during surface feeding on zooplankton (Sims et al., 2003, 2006). These tags combine a data-logger that records pressure (swimming depth), water temperature and light level with an Argos-certified transmitter with 0.5 W power output (Wildlife Computers, Redmond, WA, USA). PAT tags archive depth, temperature and light-level data while attached to the host animal. At a user-specified date and time, the tag actively corrodes a metal-alloy pin to which the tether is attached, thus releasing it from the shark. The PAT tag then floats to the surface and transmits summarised information collected over set intervals via the Argos system and provides the position of the tag at the time of surfacing. The summary data transmitted comprises time-at-depth and time-at-temperature histograms, temperature-at-depth profiles, and profiles giving the maximal change in light intensity recorded over specified time periods (dusk, dawn). Battery voltage is also archived and transmitted in status messages.

PAT tags are not designed to transmit to satellites during the period of attachment prior to specified release times, so the failure of tags to transmit via Argos is only usually apparent when the pop-up time is exceeded. Because transmission of data including status messages only occurs when a pop-up is successful, if a tag does not uplink with the Argos system, no information can be obtained directly from it to shed light on why a failure has occurred. In the course of our study some PAT tags were physically recovered after having been washed up on beaches or found floating at sea. In these situations it was possible to investigate possible causes of failure by the assessment of various parameters in data still archived in (but never recovered via Argos) the recovered tags. The pressure (depth) record indicated whether the tag released

prematurely, the intactness of the corrodible pin showed whether the tag popped-up but did not transmit, while archived battery voltage readings indicated available power for making Argos uplinks. Visual inspection of the integrity of the tag's antenna and outer casing also provided diagnostic clues as to possible failure.

3. Results

In several cases we were able to make an informed assessment of the reasons underlying loss of signals from satellite transmitters.

3.1. Salt-water switch failure

A case example for leatherback turtle 15119 illustrates salt-water switch failure (Fig. 1). This turtle was tracked during 2002 and 2003, leaving the Caribbean before spending the next year in the equatorial Atlantic. The dry state of the salt-water switch progressively declined, from an initial value of around 170, down to around 50 after 20 days. On day 64, diagnostic data revealed that the salt-water switch had failed for the first time and the failure was accompanied by a reduction in the uplinks received. The switch continued to work intermittently until day 209 when it resumed normal functioning, before working intermittently again from day 314 onwards. Immediately prior to the final uplinks being received on day 374, diagnostic data revealed the salt-water switch was not working. The total number of transmissions made by the unit was 63,168 or 79% of the nominal battery life. We conclude that the cessation of uplinks

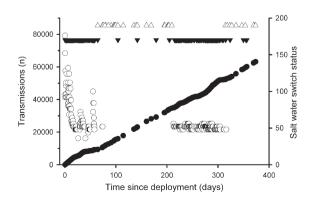


Fig. 1. An example of the diagnostic data received from tag 15119 attached to a leatherback turtle. Solid black circles show cumulative transmission number. Open circles show dry state of the salt-water switch. Filled triangles show diagnostic data indicating the salt-water switch was performing as designed. Open triangles show diagnostic data revealing the salt-water switch had failed.

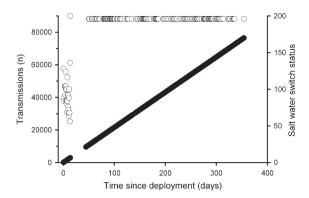


Fig. 2. Diagnostic data from leatherback turtle 15120. On day 14 after tag attachment on the island of Grenada in the Caribbean, this tag came ashore on the neighbouring island of St Vincent and moved inland where it remained for many months. Battery exhaustion was inferred as the reason for final loss of signals. Open circles indicated dry condition of the salt-water switch. Filled black symbols (which appear as a solid black line due to the data volume) show the number of battery transmissions. After 354 days, no more signals were received from the tag, probably due to battery failure. After the tag came ashore, the "dry state" of the salt-water switch was maintained consistently until the tag failed.

from this tag was caused by the failure of the salt-water switch while there was still some battery life remaining.

In some cases the salt-water switch failed a relatively short period prior to the cessation of signals. For example, leatherback turtle 29358 was tracked for 358 days. On day 337, diagnostic data revealed that the salt-water switch had failed for the first time.

3.2. Removal of tag/animal mortality

In some cases the end of tracking may be caused by capture of the study animal, although the tag may continue to function subsequently after it has been removed and/or the study animal killed. This scenario occurred with one of our tracked leatherback turtles (15120). The turtle was tracked moving northwards from Grenada to the neighbouring island of St Vincent where dive data indicated it came out of the water and tracking data indicated the tag travelled inland where it remained for many months (see battery exhaustion section below). A visit to St Vincent confirmed that the turtle had been killed for local consumption and the tag was kept in an unidentified house. We were unable to recover the tag even though we knew its location.

3.3. Battery exhaustion

In some cases diagnostic data revealed that the cessation of signals was caused by exhaustion of the

battery. For example, for leatherback tag 15120 (see Section 3.2 above), we continued to receive transmissions from the tag after it had travelled ashore, before the tag finally stopped transmitting after 354 days. The number of transmissions made by the unit was 76,547, within 10% of the nominal battery life of 80,000 transmissions (Fig. 2). We conclude that eventual cessation of signals was caused by battery exhaustion. For one other tag attached to a leatherback turtle that was tracked moving around the equatorial Atlantic (tag id 15121), battery exhaustion was also implicated as the reason behind the cessation of signals.

3.4. Aerial breakage

Damage to the aerial will degrade the intensity of transmissions and consequently more incomplete messages would be expected. For example, evidence for aerial failure was seen in one of the tags attached to an olive ridley. For olive ridley tag 21914 there was a marked increase in the proportion of incomplete uplinks received towards the end of the tracking period (Fig. 3).

3.5. Premature release/stranding

We deployed 23 PAT tags on basking sharks making foraging movements over the western European continental shelf and received data via Argos from a total of only 10 tags (43.5%). Successful transmissions, where pop-up location was also determined from Argos, were even lower (35% of total tags deployed). Six of the 23 tags deployed were physically recovered on land; three had successfully transmitted data whereas no uplinks were received for the remaining three tags. As shown by the depth records, two of these failed tags released

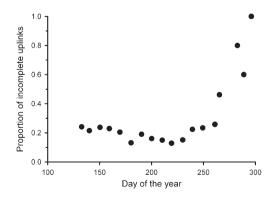


Fig. 3. An example of diagnostic data suggesting the aerial had broken. For olive ridley tag 21914, for each 10 day period during tracking, the proportion of incomplete uplinks is plotted (as measured using checksums relayed within each uplink).

prematurely due to failure of the attachment tether. These tags were programmed to start transmitting a certain time after deployment. They washed ashore prior to this time and hence communication with the Argos satellites may have been impeded by the tags lying horizontally, which is suboptimal for transmitting signals into space. The case of the third failed tag that was physically recovered is described below.

3.6. Unknown reasons for failure

For several of the tags attached to olive ridley turtles we could not definitively establish the reasons underlying tag failure, although we could reasonably exclude battery exhaustion and failure of the salt-water switch. To illustrate, consider the diagnostic data received from tag 21923 attached to an olive ridley turtle (Fig. 4). The last uplink was received from this tag 136 days after deployment. At this time 35,636 transmissions had been made corresponding to 45% of the nominal battery life. Throughout the period of data acquisition diagnostic data revealed that the salt-water switch was working and there was no progressive decline in the dry state of the salt-water switch that preceded switch failure in the leatherback turtle deployments. For most of the PAT tags that failed (11 of 13; see above) there was no clear reason for the underlying causes. One of the failed tags that was retrieved had released at the correct time from its shark, as was evident from the archival depth record and the absence of a corrodible pin. However, no uplinks were received from this tag, the reasons for which remain unknown.

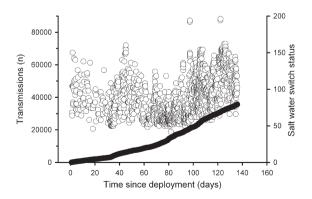


Fig. 4. Diagnostic data relayed from tag 21923 attached to an olive ridley turtle. Filled black symbols (which appear as a solid line due to the data volume) show the number of cumulative battery transmissions. Open circles show dry state of the salt-water switch. Throughout the period when data were received, the salt-water switch continued to function well. However, signals ceased to be received well before the battery had expired.

Table 1 A summary of the satellite tracking results with two species of sea turtle

Species	Tag ID (days)	First SW switch failure	Final battery level (%)	Length of time signals received (days)	Inferred reason for final failure
Leatherback	15119	64	21	374	SW switch
Leatherback	15120	Never	0	354	Battery
Leatherback	15121	105	0	330	Battery
Leatherback	21914	289	19	563	SW switch
Leatherback	21915	148	24	455	SW switch
Leatherback	21920	237	29	320	SW switch
Leatherback	21923	88	19	486	SW switch
Leatherback	29358	337	45	358	SW switch
Leatherback	4394	113	52	184	SW switch
Leatherback	4395	250	43	423	SW switch
Olive ridley	21914	Never	80	162	Antenna
					damage
Olive ridley	21923	Never	55	136	unknown
Olive ridley	21915	Never	85	83	unknown
Olive ridley	21920	Never	56	167	unknown

For each tag, the time of the first failure of the salt-water (SW) switch is shown along with the final battery level relayed prior to the cessation of signals.

3.7. Summary of reasons for tag failure

Using the criteria outlined above, we examined the reasons for the cessation of signals for 14 satellite tags attached to leatherback turtles (n=10) and olive ridley turtles (n=4) (Table 1). For leatherback turtles the most common reason for cessation of signals was failure of the salt-water switch. For olive ridley turtles we received signals for less time and the reasons for premature tag failure could often not be established.

In basking sharks, from the original 23 tags deployed, three of the six tags that were recovered had failed (or would have failed) to make transmissions for reasons not related to early recovery, low battery power, tag damage or biofouling. This level of failure rate among recovered PAT tags was similar to that found in our deployments as a whole (43.5%; see above) and

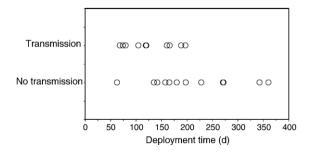


Fig. 5. Relationship between transmission success of PAT tags attached to basking sharks and the programmed deployment time.

suggests our small sample size reflects broader trends in tag failure rate. Overall, successful transmissions were obtained for tags that had programmed deployment times between 68 and 197 days (mean=128; median=120; n=10), whereas failures occurred between 63 and 360 days (mean=206; median=180.5; n=13) (Fig. 5). No successful transmissions from tags were obtained>197 days deployment time, even though 26% of tags were programmed with times exceeding this (Fig. 5). In our study, it appears that PAT tags with shorter deployment times were less likely to fail.

4. Discussion

It is clear that interruption or cessation of satellite tag transmissions in marine environments may be attributed to several factors. For example, the batteries of the tag may expire, the transmitter may become physically damaged (e.g. the aerial broken), the transmitter may detach from the host animal and sink, the tracked animal may die or the salt-water switch may fail. Often diagnostic information relayed from satellite tags can be used to identify the reasons for the cessation of uplinks being received. Hence, such data can be a useful inclusion in the data-stream from tags. The SRDL units we have described here with regard to attachments to turtles are also widely deployed on marine mammals (both seals and whales) (e.g. Bradshaw et al., 2004). Hence the arguments we have presented for inferring the reasons behind the cessation of signals should apply widely across different marine taxa. With limited bandwidth available in the Argos system (256 bits per message, with the interval between messages usually >45 s) there is clearly a need for some selection in the type of information one wishes to be relayed. Often the central reason for attaching tags to animals is to reveal their movements and receive information about their behaviour (e.g. diving behaviour and swim speed for marine vertebrates, altitude for flying birds) and environment (e.g. water temperature and salinity for marine vertebrates) (Berthold et al., 2004; Burns et al., 2004; Hays et al., 2006). Such data streams will inevitably take precedence. However, reserving some of the available bandwidth for relaying diagnostic information about the state of the tag itself is particularly desirable when the fate of tags (and inference regarding the fate of their bearers) is also of interest (e.g. Hays et al., 2003).

We have identified several reasons for loss of tracking data and identifying the particular reasons for each failed tag can help direct improvements in tag design, attachment procedure and choice of study animal. Clearly there is little that can be done, in terms of designing future studies, when the animal itself is captured and killed by human or other predators (e.g. Eckert, 2006), although tracking data can still provide useful information about mortality hotspots and help direct conservation efforts (Hays et al., 2003; Bradshaw 2005; James et al., 2005b). The inferences we have made about the mortality rates of marine vertebrates echo those made in studies of terrestrial vertebrates and birds. For example, Combreau et al. (2001) used the loss of altitude and cessation of movement when tracking birds to infer mortality during migration. Similarly, cessation of movement and a change in tag temperature have been used to identify mortality in radio tracking studies of lions (e.g. Woodroffe and Frank, 2005) and mortality sensors (e.g. motion cessation detectors) are a common feature in both terrestrial and aquatic tag deployments to detect mortality events (Stuart-Smith et al., 1997; Millán et al., 2002; Sammons et al., 2003; Clarke and Eastridge, 2006). In some cases in marine studies, mortality of animals may occur in the open ocean with, for example, animals then sinking or being brought onto a ship (e.g. if captured in fishing gear). It is possible that such events can still be inferred from relayed data. For example, some satellite tags are designed to detach if a threshold depth is reached (e.g. a dead animal sinking in the open ocean) and then pop up to the surface and relay data (Graves et al., 2002). For animals brought onto ships from fishing activities (e.g. Chaloupka et al., 2004; Polovina et al., 2004), there may be unusual subsequent movements and, in addition, diagnostic data may reveal the tag is out of the water (Bradshaw, 2005).

Exhaustion of the tag batteries implies that with modified battery management schedules, it will be possible to track those animals for longer. There is now flexible programming available for satellite tags whereby the maximum number of daily transmission is strictly controlled by onboard software. The result is that minimum battery life can be predetermined regardless of the behaviour of the animal. Where batteries have become exhausted, it is therefore a simple matter to modify the software so that battery life is extended in subsequent studies.

For our longest successful deployments, several lasting over one year, we were able to infer that it was rarely battery exhaustion that caused the cessation of signals but rather failure of the salt-water switch that is used to synchronise transmissions with surfacing. The most parsimonious explanation is that with time biofouling organisms accumulate around the salt-water switch so that eventually when the tag comes to the surface, water remains between the salt-water contacts so that the tag fails to register a "dry" state. In some cases, direct evidence of epibiont biofouling of tags has been seen (Troëng et al., 2006). For example, Fig. 6A

shows a dorsal view of a SRDL that was attached to an internesting turtle in the Caribbean. After 12 days, the tag was removed when the turtle returned to nest, at which time a ~ 1 cm-long goose barnacle was attached to the tag close to the salt-water switch. Fig. 6B shows a frontal view of an extremely biofouled SRDL that had been attached to a loggerhead turtle (Caretta caretta) in the Mediterranean for 6 months. Applying antifouling paint to the tag might potentially reduce salt-water switch failure by inhibiting or delaying epibiont colonisation, although the salt-water contacts themselves will need to remain unpainted to function. Moreover, most antifouling paints are ablative and must be reapplied regularly, so their long-term efficacy is therefore limited. In addition, it may be possible to change the material type used for the salt-water switches





Fig. 6. (A) Dorsal view of an SRDL that had been attached to a leatherback turtle for only 12 days during the internesting interval in the Caribbean. During this time a goose barnacle had settled near one of the salt-water contacts. (B) Frontal view of a SRDL that had been attached to a loggerhead turtle in the Mediterranean for 6 months (photograph courtesy of Sandra Hochscheid).

so that fouling is less of a problem. For example, copper contacts, rather than stainless steel, are currently being trialled for some satellite tags. Clearly the salt-water switch of satellite tags is a problematic issue for longterm marine studies and warrants further consideration by manufacturers. Intermittent failure of the salt-water switch is presumably caused by the level of biofouling changing over time. For example, we have found that satellite tags deployed on some leatherback turtles in temperate waters will function well until the animals spend extended periods in tropical waters during the winter months. At this point, transmissions may cease altogether, then resume as turtles return to temperate waters the following year (James et al., 2005a). We attribute such intermittent tag performance to fouling of the salt-water switch by tropical epibionts, which die and slough off the tag as the turtle moves into much cooler, northern waters.

In contrast to our studies with leatherback turtles, for tags attached to olive ridley turtles we often did not receive diagnostic data to indicate the cause of tag failure. Certainly the habit of hard-shelled sea turtles to wedge themselves between rocks and corals can threaten the integrity of the most robust of aerials. In cases of unexplained failure, we can surmise that there might have been very sudden catastrophic physical damage to the tag (e.g. most likely to the aerial) or that the tag was no longer attached to the turtle. If damage to the aerial occurs slowly it may be revealed in diagnostic data (e.g. Fig. 3), but if the aerial suddenly breaks off there might be instantaneous signal loss. Unequivocally identifying detachment of the tag is difficult without re-sighting the tagged animal. One solution is to attach two satellite tags to each individual and then monitor if both tags fail simultaneously. However, this approach may only be useful for large, well-funded studies because the trade-off between tag cost and sample size usually limits the number of deployments possible.

In the case of PAT tags attached to basking sharks it was evident that deployments over about 6 months were never successful, suggesting that further developments of this technology are needed. Increased mortality of basking sharks over time is unlikely to have contributed to the high proportion of failures observed because basking sharks are long-lived species with low natural mortality, although capture by fisheries (Southall et al., 2006) may have contributed to some tag failures. However, the high proportion of failures in relation to apparent catch rates of basking sharks, which seem relatively low (58 sharks per 1000 trawls; Francis and Duffy, 2002), suggests factors such as internal malfunction or premature release to be the most likely sources of tag failure. PAT tags have a

premature release feature whereby a tag will release and begin transmitting if initiated by the recorded depth remaining unchanged for a user-specified period of time (a measurement analogous to classic mortality motion cessation sensors). With this feature enabled, PAT tags assume an animal to be dead or the tag detached if depth remains the same for the specified time. However, this feature was turned off for deployments on basking sharks because they sometimes spend long periods at a single depth during the course of normal behaviour (Sims et al., 2005). However, all tags deployed on sharks were attached in the same way and would float even if they detached prematurely with the attachment tether and corrodible pin intact. Premature release probably did not preclude successful transmissions if the tag was working. However if a tag washed up on land before the programmed release time fewer uplinks would be expected. Clearly improving the detection of detached tags through on-board analysis of depth data might improve data recovery.

In summary, by identifying the reason for satellite tag failure, efforts to extend the tracking period in future studies can be targeted. SRDLs provide unparalleled diagnostic data and we have tried to indicate the utility of these data. Argos satellite tags are made by a number of manufacturers, but the diagnostic data relayed are generally much less than by SRDLs. Hence we would encourage other manufacturers to incorporate more diagnostic data into the data streams relayed via Argos so that the causes of cessation of signals from their units can be established more objectively. While it might not always be possible to identify the reasons for tag failure, for example, where tags have become detached and the animal is not seen subsequently, diagnostic data from the tag can still be used to exclude other possibilities (e.g. battery or salt-water switch failure). Furthermore, increasing the diagnostic data relayed via tags will provide more information to ascertain and quantify the reasons underlying signal loss to be objectively assessed. Where diagnostic data are not relayed, then often the only way to determine the reason for signal loss will be to re-sight the study animals or recover the tag — both of which may be unlikely events for animals moving large distances. With ongoing improvements to battery management, attachment techniques and salt-water switch design, we can look forward to tracks of several years being routinely available.

Acknowledgements

We thank all the people who helped with field deployments of satellite tags. Funding was provided by

the Natural Environment Research Council (NERC). DWS was supported by a NERC-funded MBA Research Fellowship. Discussions between GCH and DWS were facilitated through the European Tracking of Predators in the Atlantic (EUTOPIA) programme in the European Census of Marine Life. This work was conducted as part of a Ray Lankaster Investigatorship awarded to GCH from the Marine Biological Association of the United Kingdom. [SES]

References

- Berthold, P., Kaatz, M., Querner, U., 2004. Long-term satellite tracking of white stork (*Ciconia ciconia*) migration: constancy versus variability. Journal of Ornithology 145, 356–359.
- Bradshaw, C.J.A., 2005. Survival of the fittest technology problems estimating marine turtle mortality. Marine Ecology. Progress Series 287, 261–262.
- Bradshaw, C.J.A., Hindell, M.A., Sumner, M.D., Michael, K.J., 2004. Loyalty pays: life-history consequences of fidelity to marine foraging regions by elephant seals. Animal Behaviour 68, 1349–1360.
- Burns, J.M., Costa, D.P., Fedak, M.A., Hindell, M.A., Bradshaw, C.J.A., Gales, N.J., Mcdonald, B., Trumble, S.J., Crocker, D.E., 2004. Winter habitat use and foraging behavior of crabeater seals along the Western Antarctic Peninsula. Deep-Sea Research II 51, 2279–2303.
- Chaloupka, M., Parker, D., Balazs, G., 2004. Modelling post-release mortality of loggerhead sea turtles exposed to the Hawaii-based pelagic longline fishery. Marine Ecology. Progress Series 280, 285–293.
- Clarke, J.D., Eastridge, R., 2006. Growth and sustainability of black bears at White River National Wildlife Refuge, Arkansas. Journal of Wildlife Management 70, 1094–1101.
- Combreau, O., Launay, F., Lawrence, M., 2001. An assessment of annual mortality rates in adult-sized migrant houbaru bustards (*Chlamydotis [undulata] macqueenii*). Animal Conservation 4, 133–141.
- Eckert, S.A., 2006. High-use oceanic areas for Atlantic leatherback sea turtles (*Dermochelys coriacea*) as identified using satellite telemetered location and dive information. Marine Biology 5, 1257–1267.
- Fedak, M.A., Lovell, P., McConnell, B.J., Hunter, C., 2002. Overcoming the constraints of long-range radio telemetry from animals: getting more useful data from smaller packages. Integrative and Comparative Biology 42, 3–10.
- Francis, M.P., Duffy, C., 2002. Distribution, seasonal abundance and bycatch of basking sharks (*Cetorhinus maximus*) in New Zealand, with observations on their winter habitat. Marine Biology 140, 831–842.
- Graves, J.E., Luckhurst, B.E., Prince, E.D., 2002. An evaluation of pop-up satellite tags for estimating post release survival of blue marlin (*Makaira nigricans*) from a recreational fishery. Fishery Bulletin 100, 134–142.
- Harcourt, R.G., Bradshaw, C.J.A., Dickson, K., Davis, L.S., 2002. Foraging ecology of a generalist predator, the female New Zealand fur seal. Marine Ecology. Progress Series 227, 11–24.
- Hays, G.C., Webb, P.I., Hayes, J.P., Priede, I.G., French, J., 1991.
 Satellite tracking of a loggerhead turtle (*Caretta caretta*) in the Mediterranean. Journal of the Marine Biological Association of the UK 71, 743–746.

- Hays, G.C., Broderick, A.C., Godley, B.J., Luschi, P., Nichols, W.J., 2003. Satellite telemetry suggests high levels of fishing induced mortality for marine turtles. Marine Ecology. Progress Series 262, 305–308.
- Hays, G.C., Houghton, J.D.R., Isaacs, C., King, R.S., Lloyd, C., Lovell, P., 2004. First records of oceanic dive profiles for leatherback turtles (*Dermochelys coriacea*) indicate behavioural plasticity associated with long distance migration. Animal Behaviour 67, 733–741.
- Hays, G.C., Hobson, V.J., Metcalfe, J.D., Righton, D., Sims, D.W., 2006. Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. Ecology 87, 2647–2656.
- James, M.C., Eckert, S.A., Myers, R.A., 2005a. Migratory and reproductive movements of male leatherback turtles (*Dermochelys coriacea*). Marine Biology 147, 845–853.
- James, M.C., Myers, R.A., Ottensmeyer, C.A., 2005b. Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. Proceedings of the Royal Society of London. B 272, 1547–1555.
- James, M.C., Davenport, J., Hays, G.C., 2006. Expanded thermal niche for a diving vertebrate: a leatherback turtle diving into nearfreezing water. Journal of Experimental Marine Biology and Ecology 335, 221–226.
- Kaplan, E.L., Meier, P., 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53, 457–481.
- Luschi, P., Åkesson, S., Broderick, A.C., Glen, F., Godley, B.J., Papi, F., Hays, G.C., 2001. Testing the navigational abilities of oceanic migrants: displacement experiments on green sea turtles (*Chelonia mydas*). Behavioural Ecology and Sociobiology 50, 528–534.
- Luschi, P., Hays, G.C., Papi, F., 2003. A review of long-distance movements by marine turtles and the possible role of ocean currents. Oikos 103, 293–302.
- McMahon, C.R., Autret, E., Houghton, J.D.R., Lovell, P., Myers, A.E., Hays, G.C., 2005. Animal-borne sensors successfully capture the real-time thermal properties of ocean basins. Limnology and Oceanography: Methods 3, 392–398.
- McMahon, C.R., Bradshaw, C.J.A., Hays, G.C., 2007. Satellite tracking reveals unusual diving characteristics for a marine reptile, the olive ridley turtle (*Lepidochelys olivacea*). Marine Ecology. Progress Series 329, 239–252.
- Millán, J., Gortázar, C., Tizzani, P., Buenestado, F.J., 2002. Do helminths increase the vulnerability of released pheasants to fox predation? Journal of Helminthology 76, 225–229.
- Nel, D.C., Lutjeharms, J.R.E., Pakhomov, E.A., Ansorge, I.J., Ryan, P.G., Klages, N.T.W., 2001. Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. Marine Ecology. Progress Series 217, 15–26.
- Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V., 2006. Year-round distribution of white-chinned petrels from South Georgia:

- relationships with oceanography and fisheries. Biological Conservation 129, 336–347.
- Pollock, K.H., Winterstein, S.R., Bunck, C.M., Curtis, P.D., 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53, 7–15.
- Polovina, J.J., Balazs, G.H., Howell, E.A., Parker, D.M., Seki, M.P., Dutton, P.H., 2004. Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. Fisheries Oceanography 13, 36–51.
- Priede, I.G., 1984. A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote sensing. Fisheries Research 2, 201–216.
- Sammons, S.M., Maceina, M.J., Partridge, D.G., 2003. Changes in behavior, movement, and home ranges of largemouth bass following large-scale *Hydrilla* removal in Lake Seminole, Georgia. Journal of Aquatic Plant Management 41, 31–38.
- Sims, D.W., Southall, E.J., Richardson, A.J., Reid, P.C., Metcalfe, J.D., 2003. Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. Marine Ecology. Progress Series 248, 187–196.
- Sims, D.W., Southall, E.J., Tarling, G.A., Metcalfe, J.D., 2005. Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. Journal of Animal Ecology 74, 755–761.
- Sims, D.W., Witt, M.J., Richardson, A.J., Southall, E.J., Metcalfe, J.D., 2006. Encounter success of free-ranging marine predator movements across a dynamic prey landscape. Proceedings of the Royal Society B 273, 1195–1201.
- Southall, E.J., Sims, D.W., Witt, M.J., Metcalfe, J.D., 2006. Seasonal space-use estimates of basking sharks in relation to protection and political-economic zones in the NE Atlantic. Biological Conservation 132, 33–39.
- Stuart-Smith, A.K., Bradshaw, C.J.A., Boutin, S., Hebert, D.M., Rippin, A.B., 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. Journal of Wildlife Management 61, 622–633.
- Troëng, S., Solano, R., Diaz-Merry, A., Ordoñez, J., Taylor, J., Evans, D.R., Godfrey, D., Bagley, D., Ehrhart, L., Eckert, S., 2006. Report on long-term transmitter harness retention by a leatherback turtle. Marine Turtle Newsletter 111, 6–7.
- Weng, K.C., Castilho, P.C., Morrissette, J.M., Landeira-Fernandez, A.M., Holts, D.B., Schallert, R.J., Goldman, K.J., Block, B.A., 2005. Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. Science 310, 104–106.
- Woodroffe, R., Frank, L.G., 2005. Lethal control of African lions (*Panthera leo*): local and regional impacts. Animal Conservation 8, 91–98.