Satellite tag effectiveness and impacts on large whales: preliminary results of a case study with Gulf of Maine humpback whales

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ABSTRACT

Satellite telemetry has greatly improved understanding of large whale ecology and conservation. However, long-term attachments are typically invasive and systematic studies of their impacts have been limited. Additionally, satellite tag duration has been highly variable and shorter than battery capacity. The exact causes of tag failure are poorly understood, and could include transmitter or attachment failure, post-impact damage, or removal/rejection. A follow-up study was initiated in the Gulf of Maine to assess tag performance and health impacts in humpback whales (*Megaptera novaeangliae*). Implantable satellite tags were deployed on 35 well-studied individuals with strong prior residency characteristics and known demographic traits. Standard techniques were used to deploy satellite tags equipped with articulated (2011, n=19) or rigid (2012, n=16) anchoring systems. Tagged whales were then regularly re-encountered to assess the state of the tag, wounds at the tag site and the overall condition of the whale. Tagged individuals were re-sighted an average of 10 days (min=1, max=26) within the first tagging season, with those observations spanning 1-136d (average=44d). Twenty-one (60.0%) were documented within a week prior to transmission failure and 15 of these were seen within one day. Ten were also observed within a week after the tag failed. Initial behavioural responses to tagging varied in nature and duration, but no disturbance was noted when tagged whales were re-encountered on subsequent days. Tag site reactions were assessed from photographs and ranged from focal lesions to broad swellings. Broad swellings persisted over extended periods (at least 391 days in one case) and appeared to be related to tag breakage and/or body location. They were more prevalent when the tag was deployed on the lower flank (86.7%, n=13) versus the upper flank/dorsal fin (15.7%, n=3). All of the whales tagged in 2011 were re-sighted in 2012 and their post-deployment coverage now spans more than 600 days in some cases. Females tagged in 2011 returned with a calf as frequently as females that were observed but not tagged. Tag transmissions averaged 26.2 days (d) with a range of 0-97d. Fully implanted tags transmitted for significantly longer than partially implanted ones. Repeated re-sightings of tagged whales after deployment revealed two design flaws that could explain the relatively short and variable tag transmission durations. Articulated anchors failed at the articulation point resulting in premature detachment of the transmitter and part of the anchor being left in the body of the whale in at least five cases. Another weakness was found at the interface between the anchoring system and the electronics resulting in bending and/or breakage of the tag in at least five cases. Because this latter interface is similar to those used in various tagging projects over the past 10 years it is possible that this type of failure occurs regularly but has not been documented. This is the first systematic study of short- and medium-term responses to tagging, and results will be further evaluated as the project continues. Tag modifications arising from this study have already resulted in increased tag duration and are also expected to reduce impacts on individuals. Study of long-term effects will be facilitated by a well-established longitudinal research program. These results highlight the value of follow-up studies to evaluate and improve satellite tagging technology.

KEYWORDS: SATELLITE TAGGING; HUMPBACK WHALE

INTRODUCTION

The use of satellite transmitters to track the movements of large whales (species of the cetacean sub-order Mysticeti and sperm whales, *Physeter macrocephalus*) has greatly improved our understanding of their distribution, seasonal movements and migration, behavior, and the physical characteristics of their habitats (e.g. Mate et al. 1997, 1999, 2000, 2007; Mate and Urbán-Ramirez 2003; Heide-Jørgensen et al. 2003, 2006; Zerbini et al. 2006, 2011; Bailey et al. 2008; Gales et al. 2009, 2010), particularly when these animals move to remote sites (Mate et al. 1997; Zerbini et al. 2006, 2011; Gales et al. 2009, 2010). In some cases, satellite telemetry has revealed the existence of entirely unknown habitats used by whales (Mate et al. 1997; Garrigue et al. 2010). In addition, this technique has yielded important information for determining stock structure and for improving the conservation and management of several species (Baumgartner & Mate 2005; Heide-Jørgensen et al. 2006; Wade et al. 2006; Gales et al. 2009; Zerbini et al. 2011).

Almost all large whale satellite tags are invasive to some extent, with most involving penetration through the skin, blubber, fascia and likely muscle. In recent years, two main broadly defined tag types have been used in large whale satellite tagging studies. The tag design Type 1 (ONR 2009) consists of penetrating tags with both anchoring systems and instrument packages fully or partially implanted in the body of the whale (Fig. 1). These are typically

220-300mm in length and up to 24mm in diameter. Tags are remotely deployed and designed to anchor beneath the fascia/muscle interface for attachment durations of several months to more than a year.

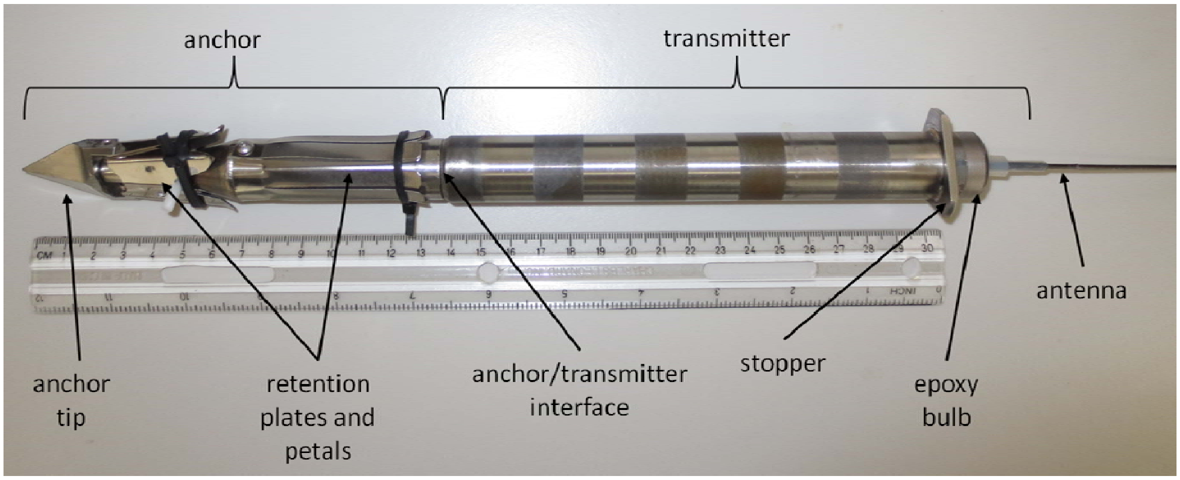


Fig. 1 - Example of an implantable satellite tag currently in use in various large cetacean studies (e.g. Gales et al., 2009) showing various parts referred to in the text. The anchor and transmitter correspond to the anterior and posterior ends of the tag and are connected to each other at the anchor/transmitter interface. The retention plates and petals are shown in the pre-deployment position. Equally spaced etchings along body of the tag are used to assess the rate at it is rejected with photo-identification data.

Despite the clear benefits of satellite tagging for better understanding the ecology and for improving conservation of large whales, there are still a number of concerns with regard to the possible adverse effects resulting from the use of invasive penetrating tags (Weller 2008, Moore et al. 2013). These effects may be short or long term, acute or chronic, and may occur at individual or population levels (Weller 2008). There have been only a few attempts to assess the effects of tagging and to observe wound healing in large whales, mostly because dedicated effort aimed at conducting follow-up studies has been limited (Weller 2008; ONR 2009; Baker et al. 2012). These attempts were based primarily on tagging conducted with fin and humpback whales in Alaska (Watkins et al. 1981; Mizroch et al. 2011), North Atlantic right whales (Kraus et al. 2000), southern right whales (Best and Mate 2007) and in some observations of various whale populations tagged by Bruce Mate and colleagues (Mate et al. 2007). To date, these studies have been opportunistic; for the most part they have been based on relatively small sample sizes and involved tag designs that have been now replaced by improved technology.

Other poorly known subjects in large whale tagging studies include an understanding of the factors that drive tag rejection and wound healing. In most cases, satellite tags stop transmitting before their battery life ends, suggesting that they fail due to damage during deployment, complete removal or damage by the whales (e.g. by rubbing on another whale or the ocean's bottom), migration below the skin surface, or rapid rejection through the expected physiological response to a foreign-body. Reasons for shorter than expected (or designed) tag durations are poorly understood and the tag rejection and healing processes remain to be described in detail.

Here, we report on preliminary results from an on-going study to assess the performance and potential health impacts of Type 1 satellite tags in humpback whales (*Megaptera novaeangliae*). Our main goal is to conduct a detailed and systematic follow-up study to better understand short- and medium-term physical and physiological effects of Type 1 tags and to investigate tag rejection, tag failure and loss.

MATERIAL AND METHODS

Study population

Satellite tags were deployed off Cape Cod, Massachusetts (USA) in a population of North Atlantic humpback whales that feeds in the Gulf of Maine. This population was selected because it has been well-studied and has a long residency period in areas with intensive observer effort. Whales arrive from their breeding ground as early as mid-March and persist in the region through December. This period is referred to as the feeding season. Stellwagen Bank, off the coast of Massachusetts, is a well-studied aggregation site, and photo-identification studies there confirm high rates of individual annual return, within-season occurrence and occupancy (Clapham et al. 1993). Directed population research programs have been in place since the 1970s and photo-identification data are also collected on a near-daily basis from commercial whale watching platforms. Catalogued whales are readily recognized in the field and individuals can be selected for tagging based on preferred characteristics.

Tagging

Type 1 tags are divided into two main components: the electronics package or transmitter and the anchoring system or anchor, which correspond to, respectively, the posterior and anterior ends of the tag (Fig. 1). The transmitter used in this study was the location-only Wildlife Computers SPOT5 custom-designed in a 160mm long x 22mm diameter stainless steel cylinder tube. The anchoring system used in this study was the one originally described by Gales et al. (2009). An important feature of this anchor was the presence of a single articulation point designed to allow the tag to compensate for movement between the muscle and the blubber layers and, as a consequence, to minimize potential tissue trauma resulting from shearing forces. In this configuration, the front 80mm of the anchor disarticulates from the back section of the tag post-deployment; a flexible 5mm multi-braided stainless steel wire maintains a coupling between the two parts. The satellite tag is designed to penetrate beneath the skin and hypodermis and anchor the tag within the variable muscle and connective tissue matrix (the fascia) that underlies the blubber. Maximum depth of penetration is 270mm. Retention of the tag is maintained through two actively sprung plates, and a circle of passively deployed 'petals'. All external components of the tag are built from stainless steel and the tag is surgically sterilized prior to deployment.

Tag deployment was conducted during the peak of the feeding season, from July 10-23, 2011 and from July 11-31, 2012. Tagging was conducted from the bow-sprit of a 12.1m twin-screw Jarvis Newman or from a raised platform on a 10.4m rigid-hulled Safeboat inflatable with a flying bridge. Approaches were made at distances ranging from 3 to 10m from the whales. Tags were deployed with a custom-modified pneumatic line thrower (Heide-Jørgensen et al. 2001, Gales et al. 2009) set to a pressure ranging from 8 to 10 bar. A projectile carrier was attached to the rear of the tag by retention teeth. The rapid deceleration of the tag and carrier as they strike the whale leads to the withdrawal of the retention teeth that hold the tag to the projectile carrier and their subsequent disengagement (Gales et al. 2009).

It has been suggested that optimal tag placement on humpback whales is close to the whale's midline, near or just ahead of the anterior insertion of the dorsal fin (e.g. Mate et al., 2007; Gales et al., 2009). While this region of the body corresponded to the main target area for tag placement in this study, deployments in other areas around the dorsal surface of the animals (e.g. below or slightly behind the dorsal hump) occurred. These 'sub-optimal' deployments provided an opportunity to compare tag duration and to assess whether the physical/physiological effects of tag deployment in other parts of the body resulted in tissue reaction that was different from those seen at optimal tag placement areas.

Focal animal selection

Humpback whales were individually identified in the field and selected for tagging based on specific life history and demographic traits. They were prioritized for tagging if they had high prior rates of annual return to the study site, high within-season re-sighting rates, and known demographic traits such as sex, age class and calving history (in the case of females). Tagging was limited to adults and excluded individuals with visual evidence or recent history of impaired health. Other individuals were photo-identified in the area during tagging so that their subsequent behavior and vital rates could serve as a point of comparison to tagged whales.

Follow-up monitoring

We documented the immediate behavioral response of each tagged individual and conducted a one-hour minimum focal follow to evaluate tag positioning, injuries and extended behavioral responses. Behavior was documented with high definition video and behavioral sequencing. We then attempted to regularly re-encounter tagged individuals in order to evaluate the condition of the tag, the state of the wound and the apparent health of the individual. Tagged whales were located by satellite tag fixes while the transmitters were functioning. Otherwise, follow-up monitoring was attempted by targeting areas used previously by the whale or large aggregations more generally. We also actively requested opportunistic documentation from naturalists working aboard commercial whale watching vessels. Re-located individuals were approached for photo-identification and documentation of the tag site. Lateral suites of high resolution images and high-definition video were also taken for visual assessment purposes. When reported, follow-up monitoring observations are expressed in terms of days since tag deployment, where deployment was Day 0.

Analysis

The condition of the tag was visually assessed from follow-up documentation. For the purpose of the analysis presented in this paper, each tag was rated as having been fully implanted (<10% of the tag body exposed) or partially implanted (>10% exposed) 60 minutes after deployment. Visual assessment of the depth of tag penetration was facilitated by equally-spaced transverse grooves etched into the external surface of the transmitter housing (Fig. 1). Additionally the location of the tag was categorized as lower flank, upper flank (just below the dorsal fin), or on the dorsal fin. Upper and lower flanks were differentiated based on a crease that is commonly observed between the relatively flat body surface in the vicinity of the dorsal fin versus the more convex surface below.

Wounds associated with the tag were also visually assessed from photographs. In this paper, wound analysis focused on the frequency and onset timing raised tissue (swelling) and tissue subsidence (divots) at the tag site. We differentiated between local swellings (those limited to tissue adjacent to the tag site) and broad swellings that involved larger areas.

Quantitative comparisons of tag duration were made across tag penetration categories using a t-test for equal variances while equality of variances were tested using an F-test. Other categorical comparisons were evaluated for significance using a G-test.

RESULTS

A total of 35 satellite tags deployed in 2011 (n=19) and 2012 (n=16). During the first season after deployment, tagged whales were re-encountered on an average of 10 days (min=1, max=26), spanning an average of 44 days from deployment (min=1, max=136). Twenty-one whales (60.0%) were documented within a week prior to transmission failure and 15 of these were seen within one day. Ten were also observed within a week after the tag failed. All of the whales tagged in 2011 were re-sighted in a subsequent year, and the span of their coverage currently ranges from 291 to 675 days post-deployment. Half of the whales tagged in 2012 have already been re-sighted in the early 2013 feeding season. Weekly re-encounter histories of individual whales after tagging are presented as Fig. 2, and preliminary assessments of tag performance and impacts to individuals are described below.

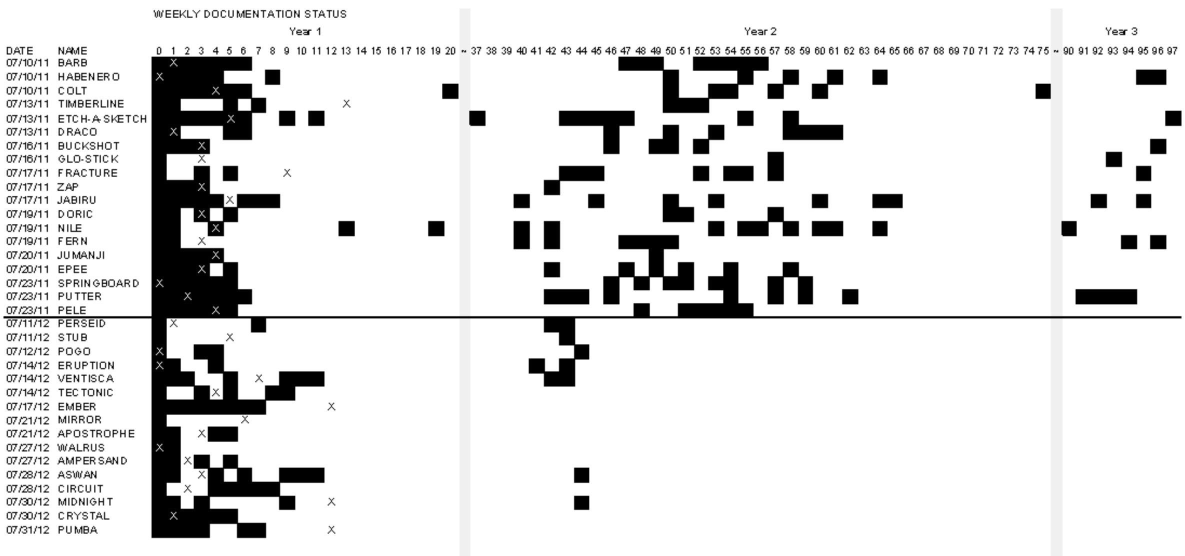


Fig. 2 - Weekly re-sighting histories of individual Gulf of Maine humpback whales after tagging in 2011 or 2012. The first interval (0) is the day of tagging. Black shading indicates that photographic documentation of the tag site was obtained on one or more days in that week. An "X" indicates the week that the tag stopped transmitting. Grey bars are condensed time periods when the whales were largely absent from the region due to seasonal migration.

Tag performance

As shown in Table 1, the average and median tag duration were slightly greater in 2012 than in 2011 for all tags combined, as well for fully or partially penetrated tags. While no statistical difference was observed in tag duration across years in any category, fully implanted tags lasted significantly longer than partially implanted tags in 2011 ($t=2.59$, $df=17$, $p=0.01$) and 2012 ($t=2.28$, $df=14$, $p=0.02$).

When whales were seen within a week after permanent transmission failure (n=10), none still had a transmitter attached. However, there were two tags that stopped transmitting (temporarily or permanently) when the electronics package was confirmed to have been still attached to the animal. The tag on "Nile" yielded only three transmissions in its first 22 days on the whale. Observations were limited to the first two days and indicated no obvious cause of failure. The tag resumed transmissions on Day 23 and the whale was re-encountered with the assistance of telemetry on Day 25, 178-km from the tagging location. Observations at that time confirmed local swelling at the tag site and a coating on the tag and antenna suggested that they had been covered by tissue. Transmissions ceased permanently on Day 28, but the whale was not observed again until Day 91. By that point the transmitter had been shed, but the anchor was still visible (see discussion of breakage, below). The cause of final transmission failure could not be determined.

Table 1 – Summary of tag duration (days) for deployments in the Gulf of Maine humpback whales in 2011 and 2012.

	Mean			Median			Range			n		
	2011	2012	All	2011	2012	All	2011	2012	All	2011	2012	All
All tags	24	28.9	26.2	17	19.5	18	0-97	0-82	0-97	19	16	35
Full	31.9	43.9	36.4	28	43.5	28	13-97	0-82	0-97	13	8	21
Partial	6.8	13.9	10.9	4	12	8.5	0-17	0-34	0-34	6	8	14

The tag on "Ventisca" stopped transmitting for a short period while still fully implanted (Days 3-12). Observations during that period (Days 6 and 8) indicated that the electronics package (but not the antenna) was recessed within the body, likely due to swelling of tissue around the tag. Transmissions resumed on Day 14 and observations on that day confirmed the top of the tag to be exposed. Tag transmissions then resumed as programmed until ending on Day 47. The first subsequent resighting of Ventisca (Day 57) indicated no noticeable outward migration and no visible damage to any tag component. The last sighting of "Ventisca" during the deployment year occurred on Day 79 and by then the transmitter had migrated out only about 3-4 cm. She was re-sighted again on Day 289 without the tag.

Re-sightings of tagged individuals revealed design flaws resulting in breakage or bending of components in at least two locations along the tag body. During the 2011 deployments, at least 5 out of the 19 deployments are thought to have failed because of breakage at the anchor articulation point. In four of these cases, the separated anchor became visible on the whale 3 to 644 days after transmitter failure. Three of these anchors have since been shed (see Fig 3 for an example). Breakage is thought to have occurred within hours to weeks post-deployment, as the tag appeared to perform as expected within the one-hour post-deployment focal follow. Photographic evidence indicates that they failed at the braided cable or at the stop sleeves used to attach the cable to the two anchor sections, possibly due to stress caused by impact forces, by material fatigue, and/or by pulling forces, including shearing. While we do not have direct evidence of the disposition of the anchor in the remaining case, failure is inferred based on the fact that the tag started to migrate outwards immediately after deployment. There may be additional cases of failure that we are not yet able to confirm.

Another design limitation was found during the 2012 season, after the articulated anchors were replaced by rigid ones. In current Type I tags, the transmitter attaches to the anchor via a 10-18mm long and 6mm diameter threaded pin. This pin is welded to the base of the transmitter housing and screws into the anchor until both tag parts are flush against each other. Thread lock glue and/or epoxy are used to secure the anchor/transmitter interface and to prevent the transmitter from unscrewing from the anchor. Breakage and or bending of this interface was documented for 5 out of 16 deployments. One broken tag was confirmed to have been shed in its entirety, but at least four anchors were visually confirmed to be present after the electronics had been shed. Two anchors have subsequently been shed. The reason for tag breakage is still unknown but potentially caused by impact force on the tag upon deployment, or forces on the tag after deployment. However, when whales in this study were re-sighted after tag failure, none exhibited new injuries or abrasions in the vicinity of the tag site that suggested physical contact (i.e., with other whales or the environment) significant enough to have broken the tag.

Effects on individuals

The immediate behavioral response to tagging typically included rapid submergence and acceleration, in most cases preceded by a tail flick. The duration of the subsequent response was highly variable, with some whales returning to normal behavior within a few minutes and others exhibiting evidence of disturbance for an hour or more (at least 4.5 hours in the most extreme case). No behavioral disturbance was evident when tagged whales were re-encountered on subsequent days.

In the 34 cases for which it could be assessed, at least 47.1% (n=16) of tagged whales developed localized or regional swelling at the tag site. Swelling occurred as quickly as the day of deployment (n=1), but was otherwise detected at some point within the first month after tagging. Significant swellings persisted in a relatively stable form over extended periods (at least 391 days in one case). They were significantly more prevalent ($G=17.86$, $df=1$, $p<0.001$) when the tag was deployed on the lower flank (86.7%, n=13) than the upper flank/dorsal fin (15.7%, n=3). They were slightly more common in 2011 (52.6%, n=10) than in 2012 (40%, n=6) although the differences between years were not significant. For individuals seen in the year after deployment, 38.5% (n=5) of swellings had resolved. The cause of swelling could not be determined from photographs, but likely involved local inflammation and soft tissue injury that did not compromise the animal's ability to locomote, forage or reproduce.

Divots were observed in at least 35.3% (n=12) of cases. Tissue subsidence began no earlier than the third week after deployment and typically began to form around the tag before the transmitter was shed. One example of tissue responses to a tag over time that ultimately resulted in a divot are shown in Fig. 3. In four cases from 2011, a discrete bulge of tissue was also observed to develop at the tag site after the transmitter had been shed. In one case, the anchor has been observed emerging from within this bulge on Day 675. The outcome in other cases and the prevalence of this in 2012 cases is still pending.

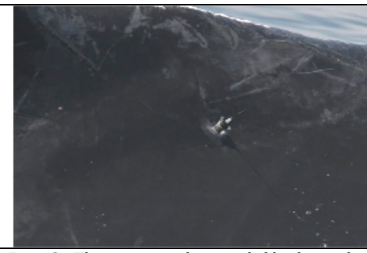
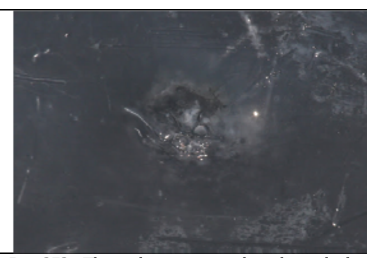
		
Day 0 (deployment). The top of the tag is flush against the body of the whale. This tag was fully implanted.	Day 9: View of the tag from behind, showing the extent of migration (nearly exposing the second set of rings).	Day 12: A plug of tissue has been expelled around the base of the tag.
		
Day 14: The tissue plug has migrated out and is beginning to separate from the tag.	Day 15: The tissue plug has been shed. Note the extent of tag migration since Day 9. More than two sets of rings are now exposed.	Day 23: The transmitter has receded back into the body (only one set of rings is now exposed). This likely occurred because the transmitter was no longer connected to the anchor and so could be pushed back toward it in the wound.
		
Day 33: The transmitter has migrated out again to nearly the same extent as Day 15. This is the last sighting with the transmitter. The tissue around the tag has begun to subside slightly.	Day 34: The transmitter has been shed. The last transmission was two hours earlier. Note the narrow diameter of the exit wound, suggesting that the anchor was not shed.	Day 41: The tag site has developed more of a divot shaped appearance.
		
Day 136: It appears that a lump may be forming within the tag site (the divot at the tag site is no longer concave).	Day 347: The anchor is now visible migrating out of the tag site.	Day 373: The anchor appears to have been shed. The wound was relatively stable through the latest sighting of this individual (522 days after deployment).

Fig. 3 - Selected images of "Colt" as an example of the progression of tag shedding and tag site reactions.

All of the whales tagged in 2011 were re-sighted in a subsequent year, and the span of their coverage currently ranges from 291 to 675 days post-deployment. Half of the whales tagged in 2012 have already been re-sighted in the first two months of the 2013 feeding season, with more expected as the season continues. Females tagged in 2011 (n=9) returned with a calf in 2012 as frequently as 18 other females that were also present during tagging.

DISCUSSION

This intensive follow-up study has provided new insight into the frequency and causes of Type 1 satellite tag failure. Images suggested that the single articulation point of the articulated anchor failed in at least some cases in 2011, resulting in premature detachment of the transmitter and shorter than expected tag durations. Discovery of the faulty articulation prompted us to modify the anchor for subsequent deployments by making it fully rigid. This modification led to an improvement in the duration of tags as shown in Table 2. For example, if one considers fully implanted tags, the improvement in the mean duration from 2011 to 2012, albeit not statistically greater, showed an increase of nearly 40%. The single point articulation in anchoring systems was originally designed to compensate for movement (shearing) at the interface between muscle and blubber (Gales et al. 2009). It has been suspected that shearing may have been one of the causes of premature detachment of rigid satellite tags as movement of muscle and blubber at opposite directions near the subdermal sheath could potentially worsen tissue trauma caused by the penetration of rigid satellite tags and promote a faster tag rejection (Weller 2008; ONR 2009; Moore et al. 2013). Gales et al. (2009) implemented the articulated anchor design used in this study with the goal of minimizing trauma and, as a consequence, improving tag duration. While the implementation of the articulation may have been faulty in this case, the development of articulated tag anchors is still desirable to minimize potential shearing issues and deserves further exploration.

Table 2 – Summary of tag duration (days) for deployments on humpback whales off Brazil and the Antarctic Peninsula a reinforcement sleeve was installed in the anchoring systems of implantable satellite tags.

	Brazil – Oct 2012[1] Zerbini et al. (unpublished data)				Antarctic Peninsula – Feb-Mar. 2013[2] Gales et al. (SC/65a/IA12)			
	Mean	Median	Range	n	Mean	Median	Range	n
All tags	50.7	23	0-222	14	62.6	51	5-118	9
Full	72.2	43.3	6-222	10	-	-	-	-
Partial	7.5	7.2	0-23	4	-	-	-	-

[1]One tag was still transmitting 222 days after deployment.
[2]Three tags were still transmitting 118 days after deployment.

It is not known where exactly the anchor/transmitter interface failed in 2012, but it is clear that this region of the tag needs to be made more robust. A temporary solution was implemented for existing tags by placing a reinforcement sleeve around the interface. This reinforced tag was subsequently used in deployments carried out in the latter part of 2012 on a breeding ground off Brazil (Table 2, Zerbini et al., unpublished data), in early 2013 near the Antarctic Peninsula (Table 2, see also SC/65a/IA12), and on Antarctic blue whales in early 2013 in the western Ross Sea (SC/65a/SH03). Preliminary results for the humpback whales show an improvement of the average and maximum duration of fully implanted tags. For example, the mean duration of fully implanted tags deployed in Brazil is 64% greater than one from the Gulf of Maine in 2012.

The type of the anchor/transmitter interface used in the Gulf of Maine in 2011 and 2012 is nearly identical across many tag manufactures, and has been employed in many telemetry studies for large whales worldwide (e.g. Heide-Jørgensen et al. 2006, 2012; Wade et al. 2006; Zerbini et al. 2006, 2011; Dalla-Rosa et al. 2008; Gales et al. 2009, 2010; Hauser et al. 2010; Quackenbush et al. 2010; Prieto et al. 2012; Guzman et al. 2012). It is likely that breakage/bending of this nature have been a regular event but not documented because follow-up information was limited and with insufficient temporal resolution to observe tag damage. In addition, this type of problem may explain, at least partially, some of the short tag durations as well as the relatively wide variability in tag longevity reported in prior studies. One of several other theorized explanations for shorter retention times is the behavior of the animals and specifically the potential for contact between them and/or objects in their environment. We have found little evidence to date that external forces were responsible for tag failure, but encourage similar studies on breeding grounds where body contact may be more prevalent.

It is not clear why transmissions ceased before the tag deployed on “Ventisca” was shed. A possible hypothesis is that the epoxy bulb at the back end of the transmitter was cracked upon or after deployment, which slowly allowed for intrusion of salt water into the electronic package and ultimately causing it to fail. Whatever the cause, results from this study indicate that failure of the tag while it is still on the whale appear to be a relatively infrequent event.

The results presented here do highlight the importance of full implantation of satellite tags to maximize tag duration (see also Mate et al., 2010 for similar findings). In both 2011 and 2012, durations of tags that were fully implanted were significantly higher than partially implanted ones.

Follow-up monitoring of tagged whales in the Gulf of Maine is still underway, but already increasing understanding of behavioral responses, wound healing and health impacts in the short and medium term. Previous work on these topics was largely opportunistic, based on relatively small sample sizes and often based on tag designs that have been now replaced by improved technology. In one case, the follow-up period (up to 17 days after tagging) was likely too short to assess physical and physiological effects (Watkins et al. 1981). The tags used with humpback and fin whales in Alaska (Watkins et al. 1981) and with North Atlantic right whales (Mate et al. 1997, Kraus et al. 2000) had different designs and much shorter durations than those currently used with large whales. Observations on the physical effects of tagging based on outdated technology may not be applicable to current satellite tags. For example, the open wound left by penetrating tags serves as a pathway for saltwater and skin cells (and their associated fauna) to be carried into the wound and potentially reach the blood stream or muscle (Weller 2008). Tags with longer duration could potentially result in more persistent physical and physiological responses and possibly greater negative effects for the tagged animal.

Previous reports of immediate behavioral responses to tag deployment have included pronounced reactions (e.g. evasive swimming, underwater exhalations, fin/tail slaps, group disaffiliation), but for the most part they were unnoticeable or mild and transient (Watkins 1981, Alves et al. 2005, Mate et al. 2007). Immediate behavioral responses to tagging in this study were similar to those described previously. However, the extended duration of disturbed behavior in a few cases has not previously been described. It is conceivable that these responses were related to the breakage of the tag (if some damage occurred on impact), but this requires further evaluation as the study continues.

The types of tissue reactions that we observed at the tag site (divots and swellings) have previously been reported for large whales tagged with Type 1 tags (Kraus et al. 2000, Mate et al. 2007). However, regular follow-up monitoring in this study has generated greater resolution on the time frame of these responses, especially in relation to tag shedding (e.g., Fig. 3). One result to date is that visible physiological responses appear to be influenced by the location of the tag, with greater effects observed when tags were placed lower on the body. Tags deployed on the upper flank will likely have a more positive outcome for the whale, in addition to the potential benefits to tag performance.

Prior studies have failed to detect significant changes in survival or reproductive rates of tagged whales relative to untagged animals (Kraus et al. 2000, Best & Mate 2008, Mizroch et al. 2011). A longer suite of observations will be required to fully understand the potential impacts of the tags used here, but results to date do not suggest acute effects on survival or reproduction. All of the whales tagged in 2011 survived to the next year and many have already been re-sighted in Year 3. This is the first study to report on reproductive rates of satellite tagged humpback whales and no significant effect has been detected to date. Use of a control group is useful in studies of this type, in light of the significant annual variation in reproductive rates in this population (Robbins 2007).

Finally, this project is still underway; tagging and follow-up monitoring will continue through the 2014 feeding season. We are providing this preliminary information now to contribute to an open dialogue about Type 1 satellite tag performance and impacts. The current results are already contributing to further development efforts to improve the tag housing as a whole. However, we expect continuing data collection and analysis to further add further to our understanding of these issues.

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