Animal Biotelemetry

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Evaluating outcomes of long-term satellite tag attachment on leatherback sea turtles

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Abstract

Attachment methods for satellite tags deployed on marine animals must optimize data collection and minimize potential adverse effects on the study subjects. The smooth, oily carapace of the leatherback turtle contrasts with the keratinized scutes of other sea turtles and has required the development of novel approaches to tag attachment. Early leatherback satellite tracking work focused on non-invasive methods, namely the use of custom-fitted harnesses, which have now largely been replaced by the direct attachment of tags to the carapace. The present study represents the first long-term assessment of satellite tag retention, recovery, and attachment site condition for leatherback sea turtles. We compare outcomes for female, male, and sub-adult turtles tagged using both harness ($n = 43$) and direct attachment methods ($n = 43$) in a foraging area off Nova Scotia, Canada. We demonstrate that the typical operational lifespan of harness-attached tags (median 227 days) was similar to that of directly-attached tags (median 235 days). However, harness tags may be more likely to be lost at high latitudes than directly-attached tags. Mating interactions may be a primary source of tag loss for female leatherbacks because, irrespective of tag attachment method, tracking data suggest that females are more likely to lose their tags at low latitudes than either males or sub-adult turtles. High re-encounter rates (~ 50%) on nesting beaches after tagging in Canadian waters indicate that both female turtles with harness tags and directly-attached tags continue to nest successfully, many in the first nesting season following tagging. Differences in tag attachment methodologies did not appear to affect turtle survival or nesting success; however, follow-up examinations suggested divergence in the scale of impact to contact tissue. Direct attachment was characterized as a benign tagging method, as associated impacts were typically superficial, limited to the footprint of the tag itself, and nearly imperceptible following tag loss. This stands in contrast to harness tags, which have been characterized by impact to multiple body parts in contact with harness materials and potential long-term or permanent disfigurement and/or scarring of the body. Moving forward, we encourage all wildlife telemetry practitioners to continue to optimize tag characteristics and attachment methods to improve animal welfare.

Keywords: Leatherback sea turtle, *Dermochelys coriacea*, Satellite tag, PTT, Telemetry, Direct attachment, Harness, Canada, Atlantic Ocean

Background

Challenges associated with the study of marine megafauna often arise from characteristics of their life histories, which span large spatio-temporal scales in a dynamic seascape [1]. Research on the distribution, behaviour, and eco-physiology of such species at times and in locations that are inaccessible for direct observation has been facilitated, in part, through the development of a broad suite of archival and satellite-linked data loggers [2]. Insights from biotelemetry have been particularly important for the conservation of marine organisms with protected status, such as sea turtles, as the collection of empirical ecological data is essential for successful management and recovery planning [3, 4].

While satellite telemetry has contributed much towards our understanding of the movements and ecology of marine animals like sea turtles, there are still limits on the quantity and quality of data collected and/or relayed, and the lifespan of the associated instruments. Many

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of these limitations relate to the challenges of deploying electronic equipment in the marine environment; the mass, shape, memory, battery capacity, and sensor resolution of available tags; and the relatively narrow bandwidth through which data must be transmitted via satellite [5]. Furthermore, tags only collect and transmit data for a finite period, during which time they may be dislodged. For tags that are retained until battery power is depleted, release typically occurs through tag and/or tag attachment materials fatiguing or failing (e.g., via UV exposure or corrosion), growth of the study subject, or other factors [5].

In addition to the technical capacity of the available instruments, researchers are ethically bound to consider animal welfare implications associated with using telemetry instrumentation [2, 6]. There may be potential for injury, physical suffering, increased risk of predation, or fitness costs associated with capture, tag attachment, and tag retention; these have been assessed in many taxa (e.g., [7–10]). For this reason, preference should be given to tags that minimize detrimental impact on study subjects by optimizing the mass, shape, attachment location, and retention time of the instrument [2, 6].

Leatherback sea turtles (*Dermochelys coriacea*) have been the subject of numerous satellite-tagging studies spanning more than 20 years. In the Northwest Atlantic, this giant (up to 700 kg) marine reptile undertakes long migrations between subtropical and tropical nesting beaches and high-latitude foraging grounds, where it feeds on gelatinous zooplankton prey [11, 12]. The species is listed as endangered across much of its range (e.g., Species at Risk Act, Canada; Endangered Species Act, USA). Leatherbacks differ morphologically and physiologically from other sea turtles, most notably in the structure of their carapace, which is covered by smooth, oily skin [13–17]. As a result, satellite tags cannot be attached to leatherbacks using the fibreglass or epoxy resins that work well on the hard, keratinous scutes of cheloniid sea turtles [1, 13–17]; therefore, alternative methods have been pursued.

Traditionally, there was a focus on using non-invasive, indirect tag attachment methods for tracking leatherback turtles via satellite. Initial work used a custom-fitted harness system, structured like a backpack, to hold a satellite tag in place above the carapace [13, 18]. The first documented use of this approach (circa 1987) on a leatherback departing a nesting beach in French Guiana [19] was criticized, as the transmitter design was bulky and clearly lacked hydrodynamic efficiency [1]. Another nesting leatherback, this time in St. Croix, USVI, was equipped with a harness and transmitter circa 1993 [20]. The turtle was re-encountered nesting 18 days later. Chafing from the harness was observed on the animal, prompting researchers to remove the harness and transmitter [20]. Other early attempts at satellite tracking of leatherback turtles (circa 1996) used large, buoyant tags that were towed on a tether anchored through the caudal tip of the carapace [21]. Modern adaptations of this equipment using alternative tag types continue to be employed to this day [22].

Further refinements to the harness design and miniaturization of satellite tags, including platform terminal transmitters (PTTs) specifically, fuelled a suite of leatherback movement research projects using harness-attached tags (e.g., Fig. 1a), beginning around the year 2000 (e.g., [23–29]). These studies yielded substantial insights into leatherback movements and behaviour. However, in 2006 and 2008, detailed reports on the condition of two turtles observed nesting with harnesses attached for 635 days and 665 days generated concern about the potential for the harnesses to cause the animals discomfort and injury—including shoulder calluses, scarring, and deformation of the carapace [15, 16]. Fortunately, subsequent encounters with both turtles revealed healing of their injuries once the harnesses were removed [15, 16].

While these cases demonstrated rapid recovery from impacts of harness materials in contact with body parts, concerns about the possibility of physical injury and/or potential fitness costs related to harness hydrodynamic drag remained. This prompted increased interest in exploring the potential of directly attaching satellite tags to the carapace, an approach that had been then used in only a handful of short-term leatherback biotelemetry studies between 1999 and 2007 with limited success [14, 30, 31]. However, the direct attachment method, even at its most refined, is invasive, requiring drilling of the turtle's highly-vascularized cartilaginous carapace. Channels are drilled through the longitudinal carapacial ridges (e.g., Fig. 1b). Wire, ties, or other foreign materials are then laced through the drill channels to secure the instruments. This effectively precludes complete healing for as long as these materials are in place.

Reports of the first long-term deployments of PTT satellite tags directly attached to leatherbacks (2005–2009) included analyses of movements and dive behaviour [17, 25, 32]. They suggested that leatherbacks equipped with directly-attached tags had improved hydrodynamic performance and reduced energetic costs versus those with harness-attached tags. However, these preliminary studies comparing the effectiveness of harnesses versus direct attachment techniques and investigating potential tagging effects were limited to relatively short-term behavioural analyses with relatively small sample sizes (Fossette et al. [17], $n=2$ directly attached, $n=3$ harnessed; Byrne et al. [32], $n=2$ directly attached, $n=6$ harnessed; Sherrill-Mix and James [16], $n=0$ directly attached, $n=42$

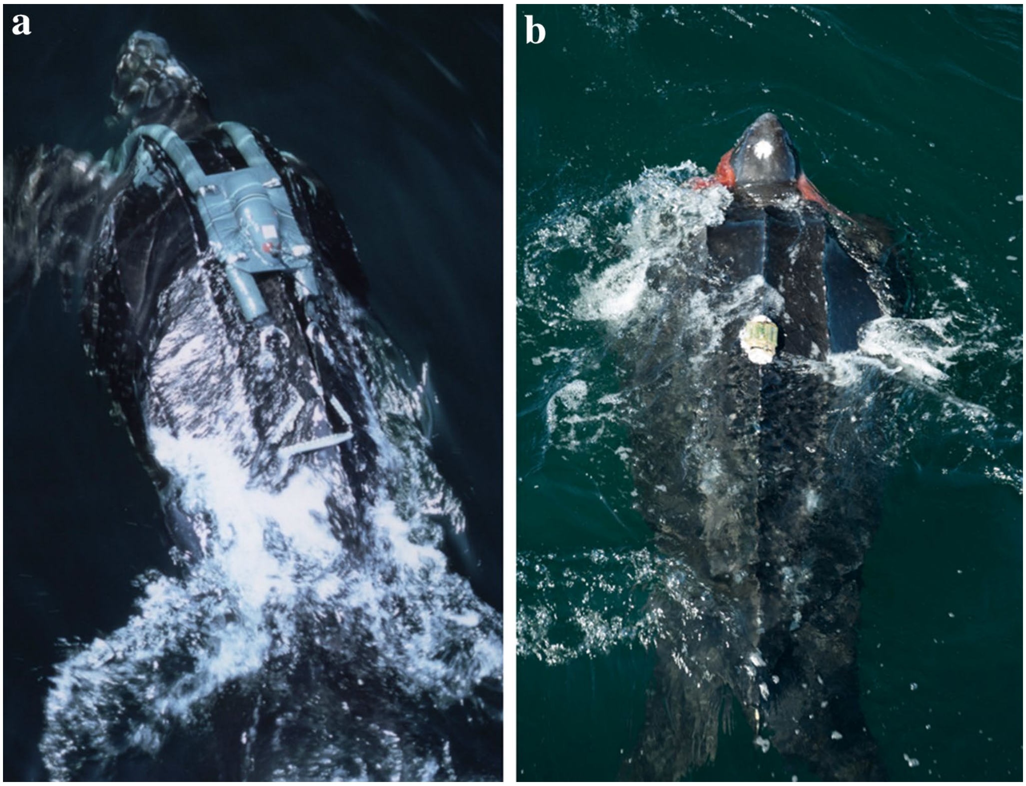

Fig. 1 Satellite tags attached to leatherback sea turtles using **a** harness attachment and **b** direct attachment to the carapace. *Photo credits*: Canadian Sea Turtle Network

harnessed), and did not provide insight into long-term outcomes for tagged turtles.

Direct attachment of satellite tags to leatherbacks is now a mainstream tagging technique. However, to date, there have been no long-term studies of leatherbacks equipped with satellite tags via direct attachment which assess individual survival, nesting success, tag retention, or the condition of the tag attachment site through time. Biologists implementing tagging studies, and particularly those focused on protected species, have a responsibility to ensure not only that such research contributes to the sound management of the species in question, but also that animal welfare concerns are clearly identified and effectively addressed. Thus, an evaluation of both the efficacy of direct carapacial attachment of satellite tags to leatherback turtles and its suitability from an animal welfare perspective is long overdue.

Here we reference the largest dataset of satellite-tagged leatherbacks in the Atlantic. We build upon evidence collected by Sherill-Mix and James [16] to assess and compare potential impacts to, and fates of, turtles subjected to harness or direct attachment tagging methods. All turtles were tagged during directed fieldwork in eastern Canada, a region that hosts one of the largest seasonal foraging populations of leatherbacks in the world [12, 25, 33], comprising turtles from nesting populations throughout South and Central America, southern USA, and the Caribbean [34]. In the present study, we evaluate satellite tag attachment methods, operational lifespan, and retention. We also describe subsequent observations of turtles equipped with satellite tags, including condition of the carapace at the attachment site following long-term tag retention and healing of impacted areas following release or removal of directly-attached tags.

Methods

Tag deployment methods and tag retention

Platform terminal transmitter (PTT) satellite tags were deployed on leatherback turtles from 1999 to 2016 off Nova Scotia, Canada. Each satellite tag was attached using either a harness method (years 1999–2004; modified from Eckert and Eckert [13]; see James et al. [25, 35]; Fig. 1a) or direct carapace attachment (years 2008–2016; see [32]; Fig. 1b). During direct carapace attachment, satellite tags were anchored to the medial ridge of the carapace via plastic zip-ties or nylon-coated wire ties passed through two small (~4 mm diameter) drill channels in the medial ridge. The ties are designed to become brittle and break following prolonged UV exposure (zip ties) or corrode (wire ties), releasing the tag from the turtle. Approximately 250 g of Equine Putty is moulded to the medial ridge at the attachment site to support the base of the tag before it is tightened in place.

The satellite tags deployed ($n=86$) included models from various manufacturers: Wildlife Computers SDR-SSC3 ($n=14$), SDRT-16 ($n=2$), MK10-AF ($n=15$), MK10A ($n=21$), SPLASH10 ($n=1$), SPOT3 ($n=7$), SPOT4 ($n=1$), SPOT5 ($n=6$), Sirtrack KiwiSat101 ($n=18$), and Telonics ST-10 ($n=1$). Geolocation data were obtained from CLS Service Argos (Argos, www.argos-system.org).

We obtained a suite of data for each satellite-tagged turtle, including the original capture condition (i.e., live-captured or entangled in fishing gear), sex, location and date of tag deployment, tag attachment method, make and model of tag, date of receipt of final transmission (end of operational lifespan, irrespective of cause, defined by the last date successful Argos-derived location estimates were received from the tag), and duration of active tracking.

We assigned sex to leatherbacks with curved carapace length (CCL) > 145 cm based on tail length dimorphism [36, 37]. Sex assignments were also possible for a small number of turtles with CCL < 145 cm when the phallus was everted during handling [37] or the animal was recorded on a nesting beach. All other turtles for which a reliable sex could not be determined were classified as sub-adults (i.e., CCL < 145 cm, with neither nesting history nor phallus display [36]).

Re-observation of satellite-tagged turtles

In addition to collecting data on tag attachment method and operational lifespan, details of nesting observations of turtles equipped with satellite tags in Canada were compiled to identify the locations and dates of nesting following tag deployment. These reports were provided by partnering nesting beach monitoring organizations that reported rear flipper tags from the Canadian tag series (ID code beginning with "CAN") found during tagging patrols. For these satellite-tagged turtles, the number of days between tagging and first reported observation on the nesting beach was calculated. From these reports, we were able to elucidate the state of the tag upon re-observation (i.e., tag still attached vs. partially attached vs. missing; tag still functioning vs. no longer functioning).

Tag recovery and examination of tag attachment site

In several cases, satellite tags directly attached to the carapace in Canada were recovered from nesting turtles, facilitating assessment of the tag attachment site. For a subset of these turtles, we were able to obtain documentation of healing of the drill channels following tag removal. In a few rare cases, recorded observations were supported by photographs documenting the physical impact of the tag on the carapace.

Carapacial healing was documented for one additional leatherback (Turtle Y), live-captured while foraging in Canada and later equipped with a satellite tag while nesting in Trinidad (see Results: "Recovery of satellite tags and condition of the attachment site"). This turtle was excluded from some analyses, since she was not tagged in Canada. However, a description of her case was included here, as she exhibited an outcome of direct tag attachment not documented in other turtles in our sample.

Data analysis

All analyses were conducted using R Statistical Computing Software [38]. Results are reported as mean ± standard deviation, unless otherwise indicated. The *maptools* [39], *rgdal* [40], and *GISTools* [41] packages were used to map the spatial distribution of satellite tag signal loss based on the final Argos position for each tag with location class A, 0, 1, 2, or 3 (as per Vincent et al. [42]).

Results

Tag deployment and retention

There were 86 satellite tags deployed on leatherback turtles off Nova Scotia, Canada, between June and September 1999–2016. Of these tags, 90.7% ($n=78$) were deployed on free-swimming turtles; 8.1% ($n=7$) on turtles found entangled in fishing gear; and one on a free-swimming turtle captured while trailing gear (lobster pot, gear subsequently removed).

Of the 86 tags, 50% ($n=43$) were deployed using harnesses (years 1999–2004) and 50% ($n=43$) were directly attached to the carapace (years 2008–2016). Leatherback research in Nova Scotia has used the direct attachment tagging method exclusively since 2008. There were 50 tags (58.1%) deployed on female turtles (21 harnesses, 29 direct attachments), 21 (24.4%) on male turtles (10 harnesses, 11 direct attachments), and 15 (17.4%) on presumed sub-adults for which sex could not be reliably determined (12 harnesses, 3 direct attachments). Mean curved carapace length (CCL) for all tagged turtles was 151.1 ± 8.5 cm (range 125.5–174.5 cm), with no significant difference between the CCL of harnessed (148.8 ± 8.95 cm) verses direct-attachment animals (153.3 ± 8.9 cm).

Operational lifespan (to final transmission) of tags attached via harnesses (270.4 ± 208.3 days; median 227 days; range 53–838 days) was not significantly different ($p=0.3$, Mann–Whitney *U* test) from that of those attached directly to the carapace

(257.1 ± 132.1 days; median 235; range 56–682 days). There was also no statistically significant relationship between CCL and tag tracking duration ($R^2 = 0.03$, $p = 0.12$). However, tracking durations were significantly different based on sex ($p = 0.03$, Kruskall–Wallis test). Using multiple comparison tests [43], neither male/female nor male/sub-adult tracking durations were significantly different, but female/sub-adult tracking durations were significantly different ($\alpha = 0.05$). Tags attached to sub-adult turtles appeared to transmit longer than those attached to males (harness attachment) or females (both methods), with females having the shortest tracking durations (Fig. 2).

Locations of final tag transmission were widely distributed, particularly in oceanic regions, but also in the vicinity of nesting beaches at low latitudes (Fig. 3). This is in contrast to where these animals spent most of their time during the active tracking period, which tended to be at high latitudes (Additional file 1: Fig. S1). When evaluating cessation of receipt of tag transmissions as a function of latitude, there appeared to be a bimodal distribution, with one primary mode at ~ 10–15°N and a secondary mode at ~ 35–40°N (Fig. 4). Tags on harnessed turtles appeared to be more likely to cease

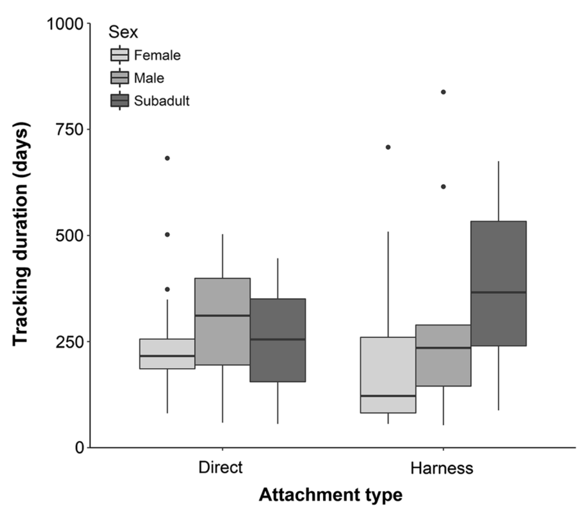

Fig. 2 Tracking duration boxplots for satellite tags deployed on female, male, and sub-adult leatherback sea turtles off Nova Scotia, Canada, using both harness and direct-attachment methods

transmission at higher latitudes relative to turtles with directly attached tags (Fig. 4a). Transmissions from tags attached to males and, in particular, sub-adults appeared to be more frequently lost at higher latitudes than was the case for females (Fig. 4b). Transmissions from tags attached to females were more likely to cease at low latitudes.

A message indicating the battery voltage of the tag at final transmission was available for 50% ($n = 43$; all Wildlife Computers models) of the tagged turtles (Additional file 2: Fig. S2). Of these tags, the vast majority ($n = 40$) had battery voltage at last transmission < 4.0 V. More specifically, 30.2% ($n = 13$) had voltage of 3.0 V or less, and 2 of these had voltage < 2.7 V. Voltage decline to ~ 3.0 V suggests imminent loss of battery function and a threshold of ~ 2.7 V indicates battery death (A. Rupley, Wildlife Computers, pers. comm., 17 November 2016); thus, loss of battery function was relevant to some instances of satellite tag transmission loss, but was likely not a factor in most (~70%) cases.

Re-observation of tagged turtles

Of the 50 turtles in our sample classified as mature females, nearly half (n= 24; 48%) were reported on nesting beaches at least once after being tagged (Table 1). These included 10 turtles originally equipped with harnesses and 14 turtles that had satellite tags applied via direct attachment (Table 1). The first reported re-observations of turtles on nesting beaches occurred from 209 to 1332 days following satellite tag attachment, with harnessed turtles recorded an average of 562.2 ± 399.4 days (median 311.5 days) after tagging, and turtles with directly-attached satellite tags recorded an average of 450.9 ± 290.6 days (median 291.5 days) after tagging (Table 1). There was no significant difference in time to first nesting observation between harnessed and direct-attachment turtles ($p = 0.17$, Mann–Whitney U test). Of the 24 re-observed turtles, 15 (62.5%) were found nesting the season immediately following satellite tagging in Canadian waters (< 365 days post-tagging; Table 1). There was no significant difference between the number of turtles found nesting in the season immediately after tagging based on their tag attachment type ($n = 6$ harness; $n = 9$ direct attachment; $p = 0.27$, two-proportion z-test).

For 70.8% ($n = 17$) of the turtles re-observed after tagging (harness: $n = 7$; direct attachment: $n = 10$), all reported re-observations occurred in the same nesting season. In the other 7 cases (29.2%; harness: $n = 3$, direct attachment: $n = 4$), the turtles were re-observed across multiple subsequent nesting seasons. On average, 3.0 ± 2.6 nesting beach encounters were reported for those turtles that were re-observed post-tagging, with many turtles ($n = 9$) re-observed one time only. The longest reported nesting history post-satellite tagging was for a turtle observed during 11 post-tagging nesting events spanning two nesting seasons over a three-year period (Turtle L in French Guiana; Table 1).

Documentation from nesting beach patrols suggested that all previously tagged turtles were observed performing normal nesting behaviours. These nesting events

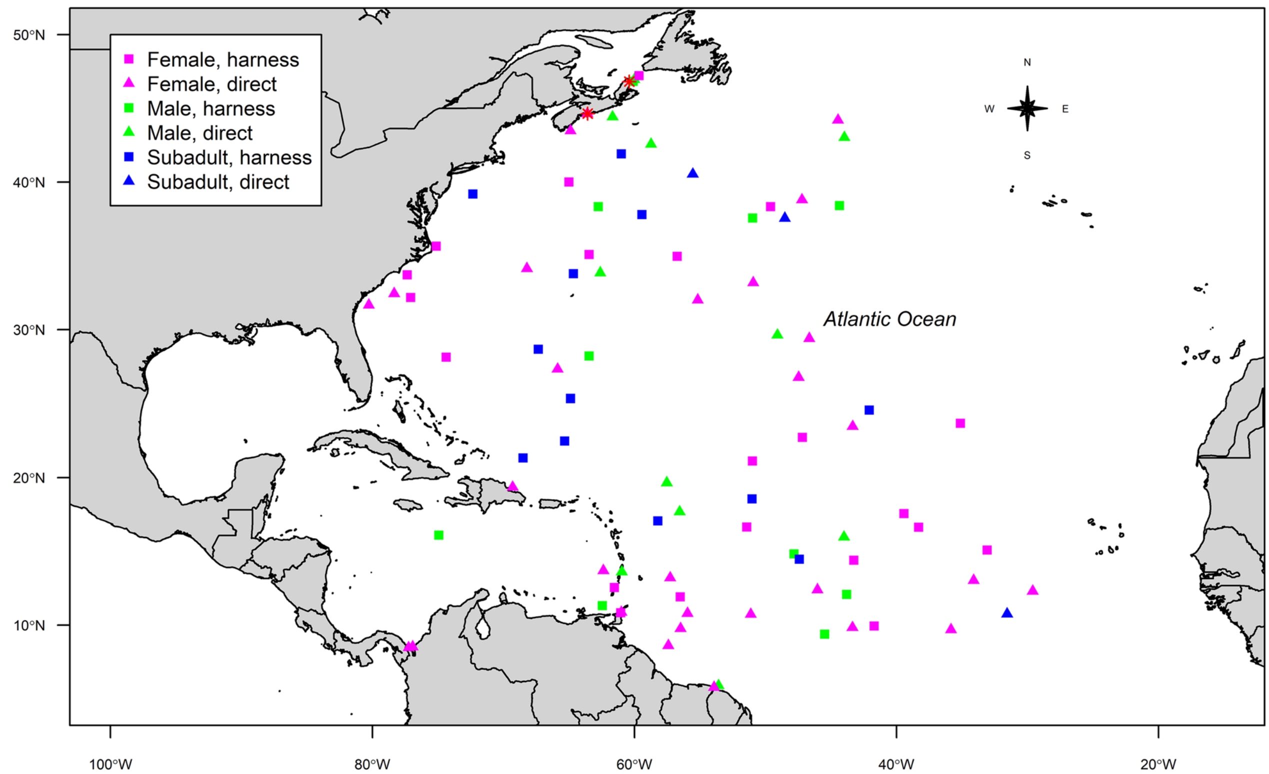

Fig. 3 Geographic distribution of signal loss for satellite tags deployed on leatherback sea turtles off Nova Scotia, Canada. Red stars indicate field research sites from which tags were deployed. Colours (green, magenta, blue) denote the sex of the turtle, while symbols denote whether the satellite tag was attached via harness (square) or directly attached to the carapace (triangle)

($n=72$ total) occurred in Colombia ($n=11$), Costa Rica ($n=2$), French Guiana ($n=24$), Panama ($n=14$), Suriname ($n=2$), and Trinidad and Tobago ($n=19$). Multiple re-observations of the same turtles were normally reported from the same country, but Turtles E and F had nesting events split between beaches in Panama and Costa Rica, and Turtle J had nesting events split between French Guiana and Suriname (Table 1).

One additional female turtle (Turtle Z; tagged in Nova Scotia on 21 July 2003) was excluded from the above analyses, as she was never reported nesting by beach patrol teams. However, in this one case, satellite tag data were available during the pre-nesting period such that presumed nesting could be inferred on 21 April 2005 (see "Turtle A" in Bond and James 2017 [44]). This conclusion was based on the large number of high-quality satellite-derived locations indicating that the turtle-borne transmitter was dry for an extended period of time on Shell Beach, Guyana, a known nesting area for this species.

Recovery of satellite tags and condition of the attachment site

Satellite tags were removed from 6 turtles (turtles A, K, L, N, Q, and U) when they were encountered by nesting beach patrols (Table 1). Three of these tags (on turtles K, L, and U) were still actively transmitting at the time they were removed; regular Argos positions from these tags in the days prior to recovery helped facilitate organization of dedicated search effort. Turtles A, N, and Q had satellite tags that ceased transmitting prior to nesting; therefore, these tags were recovered incidentally. Turtles H, O, and X shed their tags prior to re-observation on the beach; however, written observations or photographs helped clarify the condition of the tag attachment site on the carapace.

While 11 turtles originally equipped with harnesses were later documented nesting, only one turtle was encountered with the harness still attached (Turtle A, Table 1). This turtle presented with calluses around the shoulders, abrasion on the carapacial ridges, and mild deformation of the carapace corresponding to placement of a fitting strap under the plastron, as previously documented by Sherill-Mix and James [16]. Turtle H

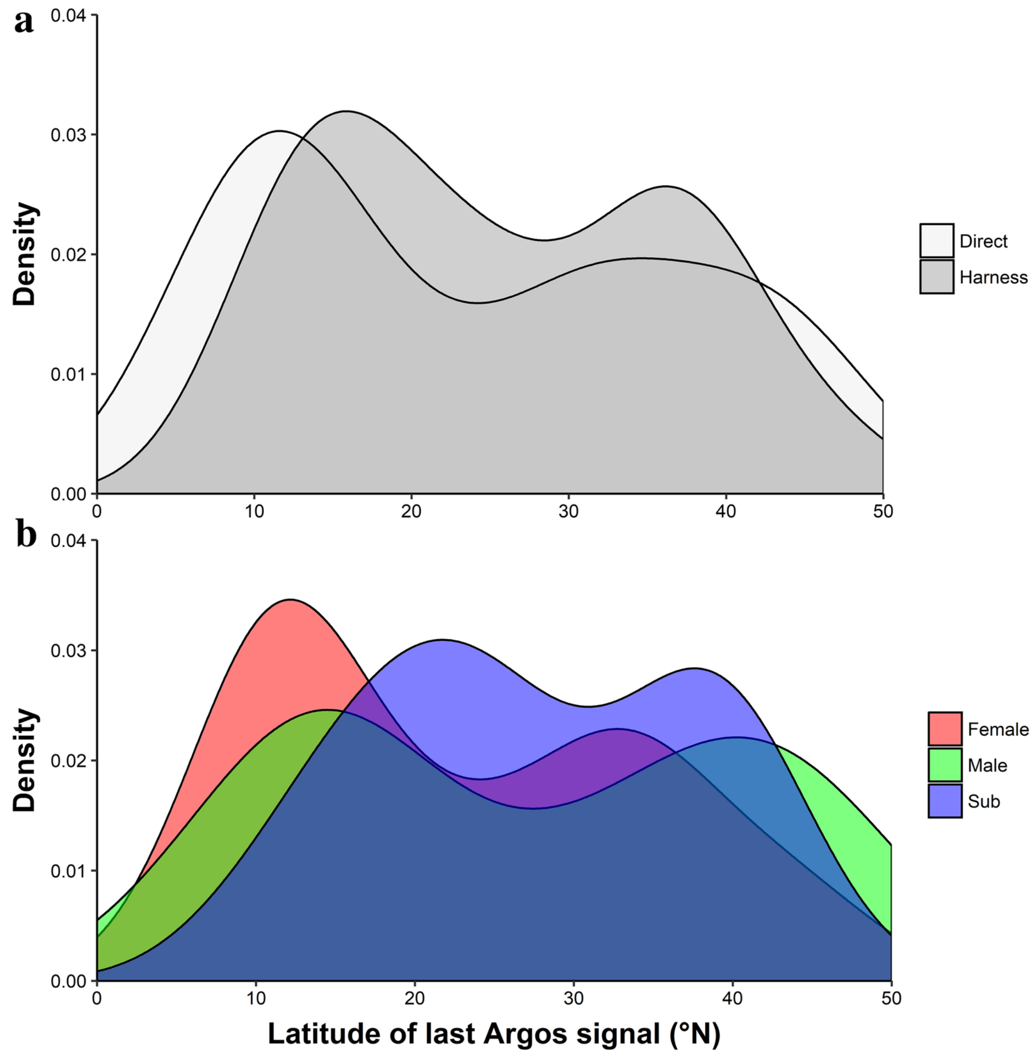

Fig. 4 Probability density of tag signal loss as a function of latitude for satellite tags deployed on leatherback sea turtles off Nova Scotia, Canada, based on **a** harness versus direct attachment methods and **b** sex (female, male, or sub-adult)

also presented with scarring and notches on her carapace attributed to harness materials.

Turtles re-observed with directly-attached tags did not typically display visible injuries or scarring, apart from the development of very small, round scars (~ 6 mm diameter) corresponding to the two drill channels in the medial ridge (Fig. 5; Additional file 3: Fig. S3). The other notable visible condition associated with long-term direct attachment turtles was minor temporary discolouration (lightening) of the dark epidermis corresponding to the original footprint of the cold-curing silicone hoof putty (Equinox, Smooth-On, PA, USA) contoured to the ridge to support the overlying satellite tag (e.g., Turtle U; Additional file 3: Fig. S3). In one case (Turtle Y; Additional file 4: Fig. S4), a pair of healed notches in the medial ridge observed nearly two years following tag attachment (15 May 2017), suggested the tag anchor loops had eroded through the drill channels on the medial ridge, releasing the tag. This was a unique case and could potentially reflect the fact that Turtle Y was the only animal in the present sample that was equipped with a satellite tag on the nesting beach (Trinidad: 30 June 2015) versus in Canadian waters. It was established as a northern foraging animal from an earlier live capture (Nova Scotia: 6 September 2003).

Longer-term assessment of medial-ridge satellite tag attachment site condition was possible for Turtles L and Q, both of which were re-observed multiple times in the nesting season immediately following tag deployment.

Table 1 Re-observation of Canadian-tagged leatherback turtles on nesting beaches in South and Central America and the Caribbean

Turtle ID	Date tagged	Attachment type	Max tag date	Nesting date	Δ*t* (days)	Country	Attachment state	Tag recovery
A	2001-07-19	Harness	2002-05-08	2003-04-15	635	TT	Tag attached, not functioning; carapace scarred and disfigured	Yes
				2003-05-14	664	TT		
				2003-06-03	684	TT		
				2003-06-13	694	TT		
				2005-04-09	1360	TT		
				2005-05-11	1392	TT		
B	2001-08-14	Harness	2002-05-22	2004-03-28	957	CL	Details unavailable	No
				2004-04-09	969	CL		
				2004-04-28	988	CL		
C	2001-08-15	Harness	2002-03-29	2005-04-08	1332	PN	Details unavailable	No
				2005-05-11	1365	PN		
D	2002-08-30	Harness	2002-11-22	2003-07-14	318	SR	Details unavailable	No
E	2002-09-09	Harness	2002-12-03	2003-06-13	277	PN	Tag missing; injury details unavailable	No
				2005-03-24	927	PN		
				2007-04-07	1671	PN		
				2007-04-18	1682	PN		
				2007-04-26	1690	PN		
				2007-05-23	1717	PN		
				2007-05-31	1725	CR		
F	2002-09-11	Harness	2002-11-16	2003-04-15	216	PN	Details unavailable	No
				2003-05-05	236	CR		
				2003-05-13	244	PN		
				2003-05-22	253	PN		
G	2003-07-18	Harness	2003-09-18	2004-05-18	305	TT	Details unavailable	No
H	2003-08-27	Harness	2004-03-06	2006-06-03	1011	TT	Tag missing; carapace scarred	No
I	2004-08-26	Harness	2004-10-31	2005-06-23	301	FG	Tag missing; injury details unavailable	No
J	2004-09-06	Harness	2005-02-08	2005-06-03	270	SR	Tag missing; injury details unavailable	No
				2007-06-14	1011	FG		
K	2008-07-17	Direct	2009-05-22	2009-05-21	308	CL	Tag attached, functioning	Yes
L	2008-07-24	Direct	2009-03-22	2009-03-22	241	FG	Tag partially attached, functioning; drill channels healing	Yes
				2009-04-02	252	FG		
				2009-04-24	274	FG		
				2009-05-02	282	FG		
				2009-05-12	292	FG		
				2009-05-23	303	FG		
				2009-05-31	311	FG		
				2009-06-10	321	FG		
				2009-06-21	332	FG		
				2011-04-08	988	FG		
				2011-04-18	998	FG		
M	2008-07-27	Direct	2009-07-11	2010-05-16	658	TT	Details unavailable	No
N	2009-07-15	Direct	2010-01-17	2010-04-10	269	PN	Tag partially attached, not functioning; injury details unavailable	Yes

Table 1 (continued)

Turtle ID	Date tagged	Attachment type	Max tag date	Nesting date	Δ*t* (days)	Country	Attachment state	Tag recovery
				2010-05-02	291	PN		
				2010-05-13	302	PN		
O	2009-08-21	Direct	2009-11-10	2010-04-17	239	FG	Tag missing; faded epidermis under tag, drill channels healing	No
				2010-05-05	257	FG		
P	2009-08-24	Direct	2010-01-03	2010-03-24	212	TT	Details unavailable	No
				2010-04-12	231	TT		
				2010-04-27	246	TT		
Q	2012-06-22	Direct	2013-04-01	2013-04-20	302	CL	Tag attached, not functioning; faded epidermis under tag	Yes
				2013-05-01	313	CL		
				2013-05-11	323	CL		
				2013-05-21	333	CL		
				2013-05-29	341	CL		
				2013-06-11	354	CL		
				2016-03-09	1356	CL		
R	2012-07-04	Direct	2013-02-01	2014-05-10	675	TT	Details unavailable	No
				2017-04-11	1742	TT		
S	2012-07-06	Direct	2013-01-29	2015-05-23	1051	FG	Details unavailable	No
				2015-06-27	1086	FG		
				2015-07-06	1095	FG		
T	2012-07-15	Direct	2013-02-17	2013-04-22	281	FG	Tag missing; details unavailable	No
				2013-06-19	339	FG		
				2015-05-21	1040	FG		
				2015-06-08	1058	FG		
				2015-06-18	1068	FG		
				2015-06-30	1080	FG		
U	2013-08-25	Direct	2014-03-22	2014-03-22	209	TT	Tag attached, functioning; faded epidermis under tag	Yes
				2014-04-25	243	TT		
V	2014-07-25	Direct	2015-12-09	2016-04-09	624	TT	Tag missing; details unavailable	No
W	2014-08-03	Direct	2015-02-11	2017-04-02	973	TT	Tag missing; details unavailable	No
X	2014-08-05	Direct	2015-03-28	2015-05-02	270	TT	Tag missing; faded epidermis under tag, drill channels healing	No

"Max Tag Date" denotes the last time the tag transmitted. "Δ*t*" indicates the difference in days between the deployment of the tag and the observation of the turtle on the beach. Countries: TT = Trinidad and Tobago, CL = Colombia, PN = Panama, SR = Suriname, CR = Costa Rica, FG = French Guiana. "Attachment State" indicates any notes on the state of the tag or attachment point on the carapace upon re-observation of the turtle. "Tag Recovery" indicates whether the tag was recovered by the nesting beach team that intercepted the turtle

Turtle L was tagged in Canadian waters on 24 July 2008 and tracked to a beach in French Guiana, where her tag was recovered on 22 March 2009, her first nest of the season. This turtle was reported re-sighted on the beach more than any other turtle in our sample; she was encountered 9 times in 2009, and twice in 2011, when she returned to nest at the same beach. A series of photographs taken by beach patrols demonstrated rapid healing of the drill channels in the weeks following tag removal and only minor scarring (Fig. 5).

Turtle Q was a unique case because she was originally satellite tagged at sea (Nova Scotia: 22 June 2012); was re-encountered during the nesting season following tagging, at which time her tag was removed (Colombia: 20 April 2013); and then was recaptured at sea 2 years later (Nova Scotia: 26 August 2014) only a few hundred kilometres

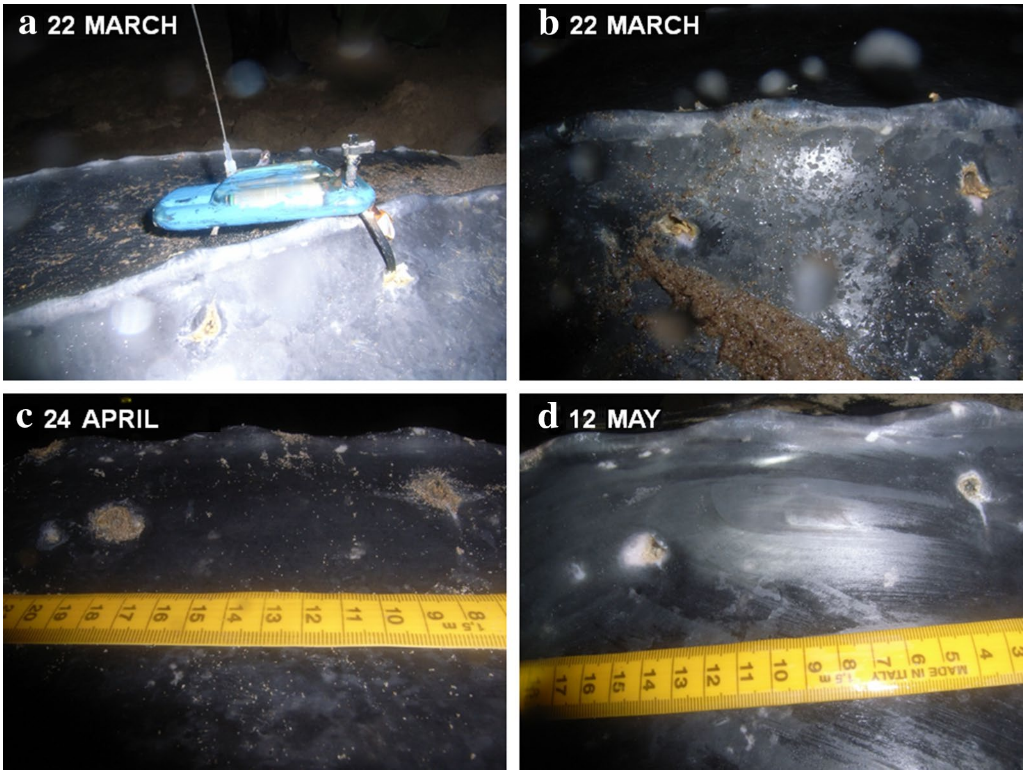

Fig. 5 Condition of the carapace at the attachment site following long-term deployment of directly-attached satellite tag off Nova Scotia, Canada, on 24 July 2008: **a** first re-observation, French Guiana, 22 March 2009; **b** drill channels in the medial ridge immediately following tag removal (22 March 2009); **c** drill channels 33 days after tag removal (24 April 2009); and **d** drill channels (healed) 51 days after tag removal (12 May 2009). *Photo credit*: Centre National de la Recherche Scientifique (French Guiana)

from where she was originally tagged. When she was recaptured in Canadian waters a year after nesting, careful examination of the original satellite tag attachment site on the medial ridge revealed complete healing of the drill channels and a return of dark pigmentation to the epidermis (Additional file 3: Fig. S3). Turtle Q was later observed nesting in Colombia (9 March 2016), and was recorded again in Nova Scotia on 5 August 2018. To our knowledge, this represents the only extant record of a leatherback turtle satellite tagged in a northern foraging area and then re-encountered both at a low-latitude nesting area and back at a high-latitude foraging area.

Discussion

The present study evaluates satellite tag operational lifespan and host turtle survival and nesting success for leatherbacks equipped with tags via harnesses and direct medial ridge attachment as part of a long-term, in-water research project in Atlantic Canadian waters. Associated data from a large sample of satellite-tagged turtles suggests that neither direct attachment nor harness methods are likely to result in long-term fitness or health effects, provided the impermanence of both approaches is guaranteed. However, our review and evaluation of visible injuries after long-term tag retention and the progression of post-attachment healing, coupled with the findings of previous research on tag hydrodynamics and associated energetic costs [45], provide compelling evidence for the preferential use of direct attachment, as it is associated with fewer animal welfare concerns.

Tag deployment and retention

In contrast to nesting beach-based telemetry research on sea turtles, which is limited to sampling of mature females, in-water studies in foraging areas are more representative of the broader population because, as in the present case, they can include sampling of turtles of both sexes and of different life stages (mature and immature). Previous research with harness-tagged leatherbacks in Canadian foraging habitat has revealed potential capture or tagging effects, including accelerated rates of travel and initiation of southward movements, for up to ~ 1 week post-tagging [16]. However, such unusual short-term behaviour is rarely exhibited by leatherbacks following direct attachment of satellite tags to the medial ridge, and turtles tagged this way have been opportunistically observed actively foraging within hours of release (M.C.J.; e.g., Fig. 1b). These observations suggest that capture and handling effects related to live sampling leatherbacks at sea may be minimal and that short-term post-capture effects indicated from earlier telemetry studies using harnesses may largely be a product of the harness itself.

Locations associated with satellite tag signal loss were broadly distributed throughout the North Atlantic Ocean, suggesting that cessation of transmissions was likely related to multiple variables. We did not attempt to elucidate the cause of signal loss for each of the satellite tags in our sample, but possibilities include technical failure, battery depletion, premature tag detachment, tag damage (e.g., via biofouling, attempted predation, mating, debris), or death of the turtle [5]. Evaluation of voltage at last transmission for a portion of the tags enables us to infer that battery depletion was likely a primary factor in signal loss for only ~30% of tags; operational lifespan of ~70% of tags was cut short due to other factors.

Previous research using a limited sample size [17] has suggested that the operational lifespan is reduced for directly-attached tags relative to harness-attached tags. Our results, substantiated by a much larger sample size, demonstrate that the duration of data collection does not differ significantly between deployments of harnessed and directly-attached tags. It should be noted that this finding is confounded by the fact that our directly-attached tags were also newer models than those used in initial trials. However, tags attached by harness also appeared to be more likely to cease transmissions at high latitudes compared to directly-attached tags, perhaps indicating premature detachment of the harness itself ("harness shedding") during migration [16]. Female turtles with either tag type had significantly lower tracking durations than sub-adult turtles (males were not significantly different from either group).

Transmissions ceased for the largest number of tags between 10 and 15°N, a zone that may represent a "hot-spot" for tag loss. Preliminary analysis of leatherback movement data in this latitudinal range identifies this area as a probable location of mating activity [44]. Therefore, it is possible that a large number of tags may be damaged or detach during mating interactions given the contact between the plastron of the male and the carapace of the female during copulation [46]. In particular, the low latitude mode of tag transmission loss (Fig. 4) appears to be driven by female turtles, suggesting that interactions with males off the nesting beach may figure prominently in tag loss there.

Alternatively, tags may cease transmission at low latitudes as a result of increased biofouling in subtropical and tropical waters [5, 47]. This may explain why males (whose tags would be less affected by mating interactions) and sub-adults (turtles presumably not engaged in mating) also exhibited a mode in tag transmission loss at relatively low latitudes (Fig. 4). This phenomenon of tropical biofouling has been implicated in tag signal loss in previous leatherback studies in the Northwest Atlantic, during which tag signals were lost and then regained upon turtles moving to higher latitudes [48]. Continuing to assess and explain the reasons for tag signal loss (e.g., turtle mortality, instrument technical issues, conspecific or predator interactions, biofouling, etc.) is an important future goal for tagging studies, as an accurate interpretation of biotelemetry data can inform the assessment of threat distribution and mortality rates and thus has implications for conservation efforts [5].

Re-observation of tagged turtles

The mature female leatherbacks satellite tagged in Atlantic Canada as part of this work had very high re-encounter rates on nesting beaches (~50%). There were no statistically significant differences in the proportion of turtles re-observed or in the time to first re-observation between turtles with satellite tags attached via harness or via direct attachment. Moreover, over half of re-observed turtles nested in the season immediately following tagging. Together, these results corroborate previous evidence that satellite-tagged leatherbacks successfully complete migrations as well as mating and nesting activities [16]. Thus, early concerns surrounding potential interference of carapace-mounted satellite tags with mating (e.g., [49]) were likely unwarranted.

While the post-tagging fates of turtles tagged in this study that have not been subsequently reported on a nesting beach remain unknown, this does not imply that they failed to reproduce or experienced mortality, as most nesting areas for this species in the northwest Atlantic receive only partial or no monitoring coverage. Thus, the repeat observations of our tagged turtles post-tagging must be considered a minimum estimate of true survival and nesting success. Using tracking data to infer nesting events is possible, but high-quality satellite location data confirming nesting behaviour are rare and in this study were only available in one additional case (Turtle Z; [44]). As turtles in different tagging treatment groups (direct or indirect attachment) were all tagged and handled in the same way, and all re-observed turtles—irrespective of tagging treatment—appeared to be in good general health, we do not expect that either method of tag attachment decreased survivorship across the sample.

Recovery of satellite tags and condition of the attachment site

We documented 6 cases in which turtles satellite tagged at high latitudes ($n = 1$ harness and $n = 5$ direct attachment) were observed on nesting beaches with their tags still in place. Such instances are exceedingly rare given the great distances leatherbacks travel, the challenges associated with tag retention, and the variability in nesting beach monitoring effort. High-resolution archival data that is not relayed remotely via the Argos satellite network can only be accessed when tags are physically recovered. Beyond providing valuable access to detailed archival data, we highlight a secondary benefit of satellite tag recovery: the opportunity for researchers to document the condition of the turtle immediately upon tag removal and to monitor changes in the appearance of the attachment site during subsequent nesting events. While the present results suggested that there were no significant differences between performance of harness-attached tags and directly-attached tags in terms of operational lifespan and probability of successful nesting, the nature and extent of injuries sustained by the harnessed turtles documented in previous studies [15, 16] were broader and more disfiguring than the small drill holes associated with direct attachment (which rapidly ossified and healed over) documented here.

Furthermore, the hydrodynamic effects of tags on leatherbacks have been evaluated experimentally using model turtles in a wind tunnel [45, 50]. This work has demonstrated that harness-attached tags have the potential to confer significant, negative hydrodynamic impacts compared to directly-attached tags [45, 50]. Turtles equipped with harnesses in Canadian waters continued to migrate and nest successfully at appropriate intervals and as regularly as turtles with directly attached tags, demonstrating that the negative effects of wearing a harness are sub-lethal; however, it is still recognized that harnesses may impose substantial energetic costs [45, 50]. We assert that the shift from the use of harnesses to direct attachment methods in leatherback biotelemetry research was a positive change for animal welfare.

It is important to note that application of direct attachment tagging methods still confer some level of impact to study subjects, with increased hydrodynamic drag remaining a primary concern. Fortunately, ongoing research and experimentation has helped address this by miniaturizing and streamlining satellite tags. Models of directly-attached tags now available for leatherback tracking studies fit directly over the medial ridge of leatherbacks, negating the use of bulkier platforms previously implemented for attaching the tag to the carapace (see [17]).

Direct attachment methods for leatherback turtle satellite tagging studies in Atlantic Canada have been refined over time. For example, to guard against potential erosion of the drill channels by tag fasteners (as documented on Turtle Y in Additional file 4: Fig. S4), the channels are now lined with narrow tubing. Research conducted in Canada and on nesting beaches has demonstrated that leatherbacks exhibit seasonal plasticity in carapace size and shape in response to changes in nutritional and reproductive status, including distension of the carapace between the lateral ridges associated with deposition of dorsal blubber among turtles foraging off Nova Scotia [51]. Therefore, for Turtle Y, equipped with a satellite tag while nesting, it is possible that localized erosion of the drill channels and subsequent release of the satellite tag resulted from mass gain and the corresponding morphing of the carapace following post-nesting migration to the high-latitude foraging habitat. Additional nesting re-observations of turtles originally satellite tagged on the beach and tracked to high latitude foraging habitat will be required to further clarify this issue. A continued commitment to optimizing tag performance and animal welfare is essential.

Conclusions

Here we have provided the first detailed assessment of the operational lifespan of satellite tags applied to leatherback turtles using two attachment techniques and have compared associated evidence for long-term turtle post-tagging survival, nesting success, and tag attachment site healing. Our results suggest that direct attachment of satellite tags to leatherbacks using methods currently practiced in Atlantic Canada to facilitate long-term tracking are humane and unlikely to have detrimental effects on associated individuals. To continue to improve animal welfare, we encourage wildlife telemetry practitioners to consider the long-term effects of transmitter attachment (e.g., energetic costs) concurrently with acute impacts (e.g., direct injuries to the carapace) when optimizing tag characteristics and attachment methods.

Additional files

Additional file 1: Fig. S1. Probability density of final Argos locations and median daily Argos locations recorded by satellite tags deployed on leatherback sea turtles off Nova Scotia, Canada.

Additional file 2: Fig. S2. Number of satellite tags deployed on leatherback sea turtles off Nova Scotia, Canada, with a given battery voltage at the time of last transmission. The dotted-dashed line indicates the 3.0 V threshold (imminent loss of battery function) and the dashed line represents the 2.7 V threshold (battery death).

Additional file 3: Fig. S3. Long-term healing of drill channels in the carapace of a leatherback sea turtle following direct attachment of a satellite transmitter on 22 June 2012, including **a** state of the carapace immediately after tag removal and recovery (Colombia, 20 April 2013) and **b** state of the carapace 16 months after tag removal (Nova Scotia, Canada, 26 August 2014). Photo credit: **a** Conservacion Ambiente Colombia, **b** Canadian Sea Turtle Network.

Additional file 4: Fig. S4. Healing of drill channels following apparent localized erosion of the medial ridge of the leatherback carapace by satellite tag anchor loops. Turtle first tagged while nesting in Trinidad, 30 June 2015, and re-observed in Trinidad, 15 May 2017. Photo credit: Nature Seekers.

Authors' contributions
KMH lead the analysis and writing of the manuscript. MCJ conceived and secured funding for the study, implemented field research, and contributed to the analysis and writing of the manuscript. Both authors have approved the final manuscript.

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Competing interests
The authors declare that they have no competing interests.

Availability of data and materials
Metadata used and analysed during the current study are available from the corresponding author on reasonable request.

Consent for publication
Consent for publication of photographs by partner organizations was obtained prior to their inclusion in the manuscript.

Ethics approval and consent to participate
Research and associated protocols were reviewed and approved by Dalhousie University Committee on Laboratory Animals or the Fisheries and Oceans Canada Maritimes Animal Care Committee, to meet standards established by the Canadian Council on Animal Care. Research was conducted under scientific license from Fisheries and Oceans Canada and Species At Risk Act (SARA) Section 73 permits.

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