Effects of satellite-linked telemetry tags on humpback whales in the Gulf of Maine: Photographic assessment of tag sites

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ABSTRACT

Hundreds of large whales have been tracked using consolidated (Type-C) satellite tags, yet there have been few studies on their impacts on whale health. In 2011, we initiated the first study designed to evaluate the effects of these tags on a baleen whale. Between 2011 and 2018, we tagged 79 North Atlantic humpback whales (*Megaptera novaeangliae*) in the Gulf of Maine. We initially deployed commonly-used tags with an articulation between the anchor and transmitter (n = 35, 2011–12), before evidence of breakage prompted the development and use of more robust, integrated tags (n = 45). Tagged individuals were photographed immediately before, during and up to 11 years after tagging. They were re-encountered on an average of 41.3 days (SD = 44.3), yielding 2,971 photographed sightings through 2022. An objective scoring system was developed to characterise tag-site tissue responses based on photographs and to identify risk factors for prolonged healing. The initial tissue response to tagging was minimal, followed by skin loss around the tag, sometimes a degree of subcutaneous swelling, occasional extrusion of blubber, changes in skin colour, local depression formation around the implant site, tag loss and skin healing over the tag site, sometimes with a depression remaining. At last sighting, most non-integrated and integrated tag sites exhibited small, shallow skin depressions (58.8% and 66.7%, respectively). Some exhibited deeper depressions with differing adjacent skin coloration (26.5% and 15.6%, respectively) or barely detectable marks (11.8% and 15.6%, respectively). Mild subcutaneous swellings occasionally persisted at the tag site, but this was uncommon for both tag designs (2.9% and 2.2%, respectively). More severe tissue responses were associated with non-integrated tags and placements lower on the body. This study highlights the importance of using robust tag designs to minimise negative effects from Type-C tags. Furthermore, because tag placement was shown to affect outcome, precision equipment, experienced taggers and vessel operators are critical for optimal deployment.

KEYWORDS: HEALTH; MODELLING; PHYSIOLOGY; SATELLITE TAGGING; TELEMETRY

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INTRODUCTION

Monitoring the location and movements of whales can be vital to research and conservation (Hays *et al*., 2019). One approach for collecting such data is the attachment of instruments that record and transmit information, commonly referred to as 'tags'. In the case of baleen whales, the only tags that are consistently capable of collecting data over a period of weeks to months (rather than hours to days) consolidate their electronics and retention elements in a single unit embedded in the body of the whale. These 'Type-C' tags have been deployed on hundreds of whales, including humpback (*Megaptera novaeangliae*), bowhead (*Balaena mysticetus*), fin (*Balaenoptera physalus*), blue (*Balaenoptera musculus*), North Atlantic, North Pacific and southern right (*Eubalaena glacialis, E. japonica* and *E. australis*), gray (*Eschrichtius robustus*), minke (*Balaenoptera acutorostrata*) and sperm whales (*Physeter macrocephalus*) (e.g., Baumgartner & Mate, 2005; Zerbini *et al*., 2006; Mate *et al*., 2007; Gales *et al*., 2009a; Best *et al*., 2015; Zerbini *et al*., 2015; Sepúlveda *et al*., 2018; Willson *et al*., 2018; Zerbini, 2018). Type-C tags are designed to penetrate and anchor in the connective tissue layer underneath the blubber and/or muscle (Mate *et al*., 1983; Andrews *et al*., 2019), which means the associated wounds have the potential to cause pain and discomfort, while also providing a portal for opportunistic infections. This potential for harm not only raises concerns about animal welfare but can also affect the data collected.

Potential impacts of tagging include adverse effects on whale behaviour, health, reproduction and survival (Weller, 2008). These impacts are difficult to determine, due to a range of factors, such as limited repeat sightings of tagged whales, small sample sizes, lack of data from control (un-tagged) whales within the same study populations, and annual variability in reproductive rate and survival (Robbins *et al*., in prep). There have been few studies on the impacts of tags on cetaceans, and a paucity of information on tissue responses and healing of the tag-placement wound, mostly due to a lack of dedicated effort to conduct follow-up studies (Weller, 2008; ONR, 2009; Andrews *et al*., 2019). Prior attempts were based primarily on opportunistic observations of previously tagged 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 & Mate, 2007) and various other whale species tagged by Mate and colleagues (Mate *et al*., 2007; Gendron *et al*., 2015; Norman *et al*., 2018). Evaluating the potential impacts of a tag on whale health can include systematic assessment of health indicators, such as the animal's behaviour, nutritional status, skin condition, hormonal status and parasitic load, as well as assessment of the localised tissue changes at the tag-attachment site. As future studies using tags are developed to inform research and guide conservation, it is essential that concurrent evaluation of the impacts of these studies on individuals is undertaken. Such work has been recommended by the ethical guidelines for scientists from the Society for Marine Mammalogy (Gales *et al*., 2009b) and is critical for informed decisions that balance individual animal welfare with population conservation (Robbins *et al*., 2013; Willson *et al*., 2018; Andrews *et al*., 2019; Papastavrou & Ryan, 2023).

For some species, standardised photographic methods using hand-held or drone-mounted cameras have been developed for photo-identification of individual animals, assessing nutritional and general health (Pettis *et al*., 2004; Bradford *et al*., 2012; Christiansen *et al*., 2019; Hörbst, 2019), as well as injuries from entanglements (e.g., Robbins & Mattila, 2004; Knowlton *et al*., 2012), ship strikes (Hill *et al*., 2017) and predation (e.g., Naessig & Lanyon, 2004; Mehta *et al*., 2007; Steiger *et al*., 2008). This contrasts with the lack of standardised objective criteria for assessment of wounds associated with satellite tagging. Assessing the impact of a penetrating wound or foreign body in a mammal classically involves use of hands-on physical examinations, imaging of tissues using radiology, ultrasound or infra-red technology, and biopsy for histology and microbiology, ideally at serial intervals (Gulland *et al*., 2018). In living, free-ranging whales, examination to date has been limited to behavioral observations and photographic assessments of tag sites, often at a single time point, with qualitative, opinion-based assessments of wound severity (Norman *et al*., 2018).

In 2011, we initiated the first study designed to evaluate the range of potential effects of Type-C tags on humpback whales, while also improving understanding of their seasonal movements and residency patterns. The project was envisioned and implemented as a collaboration between scientists with extensive experience in large whale biology, behaviour, photo-identification, tagging, health assessments and veterinary medicine. It was undertaken with a goal of transparent communication with other scientists, resource managers and permitting agencies. As part of this overarching project, a scoring system was developed for evaluating tag-site wounds based on photographs (Robbins *et al*., 2013; Andrews *et al*., 2019). This system has already been used to evaluate tag-site wounds on Arabian Sea humpback whales (Minton *et al*., 2022) and southern right whales (Charlton *et al*., 2023). Here, we further refine this method and report on its use to characterise the sequence of tissue responses to tagging over a decade in one well-studied population of North Atlantic humpback whales in the Gulf of Maine (GoM). We provide data on the effects of both a widely used tag that exhibited a high incidence of breakage and improved, robust tags that performed as designed.

MATERIALS & METHODS

Gulf of Maine humpback whales

This study focused on humpback whales in the GoM, which arrive on their feeding grounds as early as mid-March and persist in the region through December (Clapham *et al*., 1993; Robbins, 2007). Individual humpback whales were identified in the field based on their natural markings (Katona & Whitehead, 1981). Many animals in this population have extensive sighting and demographic data accumulated over decades. Individuals were selected for tagging by a population expert (JR) based on life history and demographic traits documented in a four-decade GoM humpback whale catalogue curated by the Centre for Coastal Studies (CCS, Provincetown, MA). Individuals with the following characteristics were prioritised for inclusion in the study: (1) regular annual return to the primary study area, Stellwagen Bank in the southwestern GoM; (2) frequent within-season re-sighting rates; (3) known sex and age class, as well as detailed calving history (in the case of females); and (4) apparent good skin health and nutritional status at time of tagging, with no recent history of poor health. Candidates were also selected to achieve a balanced sample of males and females. The sex of individuals was known from prior genetic analysis of a biopsy sample (Palsbøll *et al*., 1992; Bérubé & Palsbøll, 1996a; 1996b) and typically further supported by prior documentation of the genital slit (Glockner, 1983) and/or calving history in the case of females. Finally, the project focused on adults without a dependent calf in the tagging year to maximise sample sizes and minimise survival effects given that juveniles and lactating females were known to have lower annual probabilities of survival (Robbins, 2007). Age class was assigned based on the number of elapsed years since the first sighting, which was based on the year of birth (exact age) or a subsequent sighting after independence (minimum age). Individuals were considered to be juveniles if younger than the earliest known age at parturition in this population (five years; Clapham, 1992).

Satellite tag deployments

Between 2011 and 2018, 79 humpback whales were tagged under permits issued by the U.S. National Marine Fisheries Service under the U.S. Endangered Species Act and the Marine Mammal Protection Act. This research was also reviewed for ethical considerations and to conform to the U.S. Animal Welfare Act by the Internal Animal Care and Use Committee at NOAA's Marine Mammal Laboratory (Seattle, WA).

All tags were designed to penetrate skin and blubber and anchor in or below the fascia between the blubber and muscle, with tags of varying tag lengths (between 28–30cm). Five different designs were used, starting with a tag described by Gales *et al*. (2009a). Each subsequent tag version reflected one or more modification(s) to improve the design based on information provided by this study, as described in detail by Zerbini *et al*. (in prep). The tags deployed in 2011 and 2012 were designed with an articulating anchor that was intended, in part, to reduce injury due to shearing between the blubber and muscle layers (Moore *et al*., 2013; Moore & Zerbini, 2017). However, the present study revealed that structural interfaces in the anchoring system, or between the anchor and the electronics package, could not withstand the forces on deployment and/or as experienced while deployed in the whale. This resulted in tag breakage on or after deployment. The tag design was subsequently changed to increase its robustness by developing fully integrated tag designs in 2013, 2015 and 2018 (Zerbini *et al.*, in prep.). We therefore differentiate between 'non-integrated' tags and the improved 'integrated' tag designs that had no flexible tag parts and more robust interfaces.

Regardless of design, all external tag components were built from surgical-quality stainless steel. Each tag was sterilised with ethylene oxide gas and stored in a sealed autoclave pouch until the time of deployment.

Tag deployments were performed from the bow of a 12.1m twin-screw motor vessel or from a raised platform on a 10.7m, dual-outboard, rigid-hulled boat. Both vessels were equipped with top-side steering, either in the form of a tower or flying bridge. Approaches were made at distances ranging from 3–10m from the whale by a single, expert vessel operator (DKM). Tags were deployed by experienced personnel (ANZ, AK) from the NOAA Marine Mammal Laboratory. All deployments were performed with a modified version of the Air Rocket Transmitting System (ARTS; Heide-Jørgensen *et al*., 2001), with compressed air pressures ranging from 9–11 bars. The tagger attempted to target a position on the whale that was high on the back, either slightly cranial or just ventral to the dorsal fin (Fig. 1). A tag carrier separated from the tag on impact and was collected from the water after the whale moved out of the area (Gales *et al*., 2009a).

In total, 80 tags were deployed on 79 individuals. One whale was retagged four days after the first deployment because the first tag did not penetrate adequately and was shed immediately after deployment. Whales were photographed prior to, during and after tagging. Focal follows were performed for at least one hour after tagging to assess behavioural responses, injuries and tag placement. Behavioural responses are reported in a companion manuscript. Follow-up observations were then attempted on a weekly or bi-weekly basis through December of the tagging year, and then opportunistically in all subsequent years. Follow-up monitoring was also facilitated by a network of opportunistic observers and commercial whale watching vessels. Images obtained from follow-up were shared with the project team once available. The whale identification, tag number, photographed features, photograph date and time, sighting data, and other information, such as sampling details, were assigned to each image to facilitate image retrieval for analysis. In one case (Tag 1, on day 366), a punch biopsy of skin and superficial blubber close to the tag site was obtained by remote biopsy (Palsbøll *et al*., 1991) and fixed in 10% formalin for histological examination.

Photograph review

Photographs were used to assess the appearance of the tag wound as well as potentially relevant tag characteristics, such as placement, penetration depth and retention. These assessments were based on the best available images of each individual per day, hereafter referred to as a 'sighting event'.

Wound characteristics

Photographs were reviewed by one veterinarian (FMDG). Only photographs of adequate quality (based on focus, resolution, glare and angle) were used to evaluate tag sites. The location on the body, angle and penetration depth were also determined. In each photograph, a series of features were evaluated (skin loss, subcutaneous swelling, exudate, blubber extrusion, depression, colour change and cyamid presence) and numerical scores were assigned to each feature based on its appearance as listed in Table 1, with higher scores indicative of more marked changes as illustrated in Figures 2 and 3.

Features of tag sites in different photographs taken on a single day could vary in appearance due to differences in whale-body flexion, lighting, presence of water droplets or photographic angle. If a feature could not be consistently evaluated in a photograph on repeat evaluations, it was not given a numerical score but coded as a 'no score' instead. A multiplier was used to weight total scores on a specific day depending on whether the lesion appeared to be resolving (multiplier score 0.5, thus the total score was halved) or deteriorating (multiplier score 2, thus total score doubled) compared with photographs from immediately preceding re-sight dates. This subjective value adjustment was useful for highlighting periods of wound change and facilitated the second review of the scores. All photographs taken from 2011-18 were reviewed a second time as a batch in 2019. Special care was taken to thoroughly re-evaluate photographs taken during periods of lesion progression or resolution.

Tag and deployment characteristics

Transmission duration was measured as the period between tag deployment and the last transmission received from the tagged whale while tag duration was the maximum number of days of confirmed tag presence. However, a tag part could still be present after transmission ended if breakage occurred. Tag presence was therefore scored as positive when any tag part was visible in any given observation or at any later time. We also assessed the circumferential and cranio-caudal placement on the body. Circumferentially, the tag was categorised as either in the dorsal fin itself, in the upper (dorsal) flank or in the lower (ventral) flank based on its location relative to a crease that was sometimes visible along the flank and/or an inflection point on the slope of the flank as viewed from behind. The slope was typically flat or slightly concave in the upper area ventral to the dorsal fin and became convex on the lower flank. Cranio-caudal positioning was characterised as cranial (cranial of the dorsal fin and the dorsal hump), central (ventral to the dorsal fin and hump), or caudal (caudal to the dorsal fin). Finally, a photogrammetric method was used to estimate the depth that each tag penetrated at the time of deployment. This estimate was based on the length of tag visible outside the skin, the angle of the tag relative to the plane of the body and the known dimensions of the tag, as described in detail in the Supplementary Material S1.

Statistical analyses

Cumulative Link Mixed Models (CLMM) were used to evaluate which variables were predictive of each of the six tag-injury scores (swelling, depression, skin loss, blubber extrusion, cyamids). Binomial generalised linear mixed models (GLMM) were used for the same purpose for binomial injury scores (colour change). Independent variables considered for this model included sex, timing of the sighting event (elapsed days since tagging), tag deployment characteristics (design, circumferential position, craniocaudal position; Fig. S1) and tag presence upon re-sighting. The squared value of the timing of the sighting event was also included in the initial model to account for potential quadratic relationships. The identity of each whale was included in all models as a random effect. The backward elimination procedure informed by the Akaike Information Criterion (AIC) was used for model selection. Significance level was 0.05 for all tests.

Statistical analyses were conducted using *R* 4.3.1 (R Core Team, 2012) with the packages *cowplot* 1.1.1 (Wilke, 2020), *effects* 4.2-2 (Fox *et al*., 2022), *ggplot2* 3.4.3 (Wickham, 2016), *lme4* 1.1-34 (Bates *et al*., 2015), *MASS* 7.3-60 (Ripley *et al*., 2022), *ordinal* 2022.11-16 (Christensen, 2022) and *plyr* 1.8.8 (Wickham, 2022). Mann-Whitney and Kruskal-Wallis tests were respectively used to compare maximum number of elapsed days at re-sighting, number of sightings and tag attachment duration between tag designs and tag models. Local regression (locally estimated scatterplot smoothing (LOESS)) was used to summarise the chronological post-deployment progression of tag-injury feature scores.

RESULTS

Of the 79 tagged whales, 72 were considered suitable for inclusion in the statistical analysis of tag-site effects. Seven whales were excluded from statistical analysis because they had the following atypical characteristics: (a) three whales were tagged on the dorsal fin; (b) one whale had a caudal tag deployment; (c) one whale had a tag that did not penetrate; (d) one whale was never re-sighted after the day of tag deployment; (e) one whale was re-sighted only twice after tag deployment. The other whales were photographed on a cumulative total of 2,971 sighting events, with an average of 41.3 ± 44.3 sighting events per whale (range = 3-218 events). Sighting events spanned an average of 1156.1 ± 986.4 days (range = 1-4,110 days). Tables 1 and S1 provide an overview of tag-site assessment sample sizes for key whale features, tag design and deployment characteristics. Excluding the dorsal fin deployments, mean depth of penetration was estimated at 238.4 ± 40.8 mm (range = 133–294mm) and 195.0 ± 57.4 mm (range = 42–280mm) for non-integrated and integrated tag designs, respectively.

Risk factors for tissue site reactions

Statistical analysis

Location and threshold coefficients of the most supported CLLM/GLMM models used to assess severity of the six tag injury categories are summarised in Table 2 and illustrated in Figures 4-9. Model results suggest that the use of integrated tag designs significantly reduces the probability of observing more severe subcutaneous swelling, skin loss and changes in coloration (Table 2; Figs. 4A, 6A and 8A). Tag design did not influence the severity of depression, blubber extrusion and presence of cyamids (Table 2). Figure 10 illustrates differences in the predicted score of each tag type across the six tag injury categories over two periods for comparison: the first three years after deployment and the whole study period. Predicted scores show that the deployment of integrated tags is less impactful than tags with interfaces or articulations that could lead to breakages.

The severity of all tag injuries was influenced by the time since tagging. Most of the six injury categories were more pronounced at or near the time of tagging, but significantly reduced over time (Table 2; Figs. 4B, 5A, 6B, 7A, 8B, 9A). The presence of a significant quadratic term (time since tagging squared) in the models for all tag injury categories suggests that improvements in the severity scores happen in a non-linear fashion as illustrated in Figure 10.

Tag deployment location was an important predictor for swelling, but not for any other injury category. Model results suggest that tags deployed lower on the body (more ventral position) are likely to result in higher swelling scores (Table 2; Figs. 4D and 4E). The presence of the tag or a tag part (in the case of non-integrated tag designs) was positively correlated (more severe scores) with swelling and skin loss. It was negatively correlated (less severe scores) with depressions, skin loss and cyamids (Table 2; Figs. 4F, 5E, 6D, 8E and 9B).

Some variables included in the CLMM/GLMM models were not significant (e.g., sex and tag penetration depth, Table 2; Figs. 4C, 5B and 5C, 6C, 7B, 8C and 8D), but were retained during model selection for some tag injury scores. This suggests that the models with those variables represent a better fit of the data than those without them and are therefore more appropriate for making predictions of severity scores for the relevant injury categories.

Descriptive assessment of tag-site tissue responses

Tag-site responses followed a common pattern: the initial tissue response to tagging was minimal, then progressively there was skin loss around the tag, sometimes a degree of subcutaneous swelling, occasional extrusion of blubber (including adipose tissue and collagen fibres), skin pallor, local depression formation, tag loss and skin healing over the tag loss site, but with a depression sometimes remaining (see Fig. 10 for a typical sequence of changes). Although included as a feature in the tag-site assessment scoring, exudate was rarely observed, suggesting photographs are an unreliable method to detect exudation if present, probably due to constant washing of the tag site by sea water. For this reason, exudate detection was considered opportunistic and excluded from statistical models. Cyamid infestation within 30cm of the tag site was scored, but was rarely severe (when observed, typically 1–5 individual cyamids). The relative frequency of each type of tag site response observed is summarised in Table 1.

Non-integrated tags

Thirty-five non-integrated tags were deployed on 35 whales in 2011 and 2012. Tissue responses to these tags were influenced by breakage of the tag at the anchor articulation or at the interface between the anchor and transmitter. Tissue reactions were initially minimal, but following transmitter loss, lesions typical of foreign body reactions slowly developed. In 11 cases, tag breakage was visually confirmed and typically (n = 8) involved the retention of either a fragment or the whole anchor after transmissions stopped (Figs. 11 and 12). Confirmed observations of post-transmission part-retention were made up to 846 days (mean = 167.7, SD = 275.9) post tagging. Two of the eight cases were deployments in the dorsal fin and a third was the only caudally-placed tag. The 24 whales without observed tag fragments had tissue reactions similar to these eight whales and the sequence of tissue responses suggested tag breakage also occurred in these whales.

The progression of tissue-change scores following tag insertion is illustrated in Figure 10. Tag insertion was associated with minimal observable immediate skin reaction and no obvious blood loss, with skin margins in contact with the tag at the insertion site. In four whales, there was slight enlargement of the area of penetration in the skin around the tag after 1–4 weeks, resulting in a skin defect up to two times larger than the diameter of the tag that lasted several months. In most cases, however, there was minimal expansion of the skin margin around the inserted tag, with skin edges abutting the tag shaft, suggesting minimal movement of the tag section perforating the skin. In three animals, at about one year (and in one animal, Tag 10, at three years), the skin defect around the tag enlarged to about three times the tag diameter, but the skin had healed at last observation.

Circumferential swelling of the skin around the tag occurred in eight tagged whales within days of insertion. These swellings developed rapidly over 1–3 days, were a uniform shape, colour and size in five animals, irregular shape in three, and persisted for a month to seven years. When tag remnants were visually confirmed, the size of swellings appeared to remain relatively constant over the years, until the remnants were no longer detected. However, the body condition of the whales influenced the appearance of swellings. The lesions were more marked in the first half of the feeding season (through July) compared to later. Presumably, the increased blubber thickness around the tag site masked the appearance of swellings.

In 11 cases, attached segments of blubber (white/pale yellow glistening fatty material) were observed protruding from the tag-wound site as the tag transmitter was shed. Tissue other than blubber, such as muscle or connective tissue, was never observed extruding from the tag site. Protruding blubber was initially white and gradually became grey-yellow, especially at the distal end of the tissue, suggesting gradual necrosis of the fragment due to blood loss and possible secondary microbial or algal colonisation. Once these pieces of blubber were separated from the body, second intention healing of the tag site followed. The skin surface was depressed at the healed tag site, and this was often surrounded by variably shaped patches of paler skin. The depression at the tag site was sometimes so deep that it was not possible to determine if there was umbilicalisation or ulceration of the skin within the depressed area. These depressions may suggest necrosis and possible cavitation of the underlying soft tissues. Cyamids were occasionally present within and around the margins of these depressions. Over a period of months, the depressions became less marked, and were imperceptible by 2022 (see Table S2).

In one-third of the 35 whales, small, raised and smooth cutaneous protuberances (bosselations) or blebs overlaid with skin were observed within the depressed area at the tag site one to three years after tagging. In some cases, the nodular proliferations resolved over months to years. In other whales, these protuberances persisted and were observed 10 years after tag application. In one tagged whale for which frequent sequential photographs of tag-fragment rejection were available (Tag 05), the fragments did not extrude from the skin growths, but adjacent to it (Fig. 12). In a whale that was tagged on the dorsal ridge cranial to the dorsal fin (Tag 17), the tag appeared to have been extruded from the contralateral side to the insertion and a nodule was observed at the exit site.

The first whale tagged in 2011 exhibited a strong, extended behavioural reaction to tagging, and although the tag had fully penetrated, the transmitter was shed by the following day. The reason for this outcome is not known, but it could have been due to tag breakage, adverse psychogenic response, pre-existing health concern or some other process. No tag parts were ever observed in photographs, but the whale's nutritional condition declined over two months post tagging, and a persistent, regional (score 2) subcutaneous swelling developed surrounding the tag-wound site. An exudate was observed once, 366 days post tagging. Histology of a biopsy sample collected near the tag site revealed nonspecific changes of mild dermal fibrosis, perivascular edema and minimal neutrophilic dermatitis. Special stains (periodic acid-Schiff and Gomori's methylene silver) did not detect any fungi. The last photographic assessment of this whale was 391 days post tagging, when the body condition had improved from earlier that summer, the skin over the tag site was pale and swelling could not be assessed from the angle and quality of the photograph, and the whale has not been seen since then. The regional subcutaneous swelling, coupled with purulent exudate and mild dermatitis, suggests that secondary microbial infection of the tag site could have occurred.

In five cases, the tag was deployed on the dorsal fin (Tags 02, 23, 30 and 32) or dorsal ridge (Tag 17, also discussed above). In two of these cases (Tags 02 and 17), discoloured skin with focal depressions was observed on the contralateral side after tag loss. These changes in skin colour and depression of the tag site could result from changes in blood supply to the area, localised necrosis and cavitation of the fin stroma, secondary microbial involvement with associated inflammation, migration and exit of a tag fragment to the contralateral side, or contraction of scar tissue on the tagged side retracting the tissue internally from the contralateral side. Ten years after tag loss, there were no detectable lesions in the skin at the tag site or the contralateral sides compared with surrounding tissue in these five whales.

At last observation, 11.8% (n = 4) whales tagged with non-integrated tags had re-epithelialisation of the tag sites and barely detectable marks on the skin; 58.8% (n = 20) had small shallow depressions in the skin (1–3 times the diameter of the transmitter shaft); 26.5% (n = 9) had deeper depressions with areas of grayish paler skin than the adjacent area; and 2.9% (n = 1) had a mild subcutaneous swelling around the tag site (Table S2).

The remaining whale was observed only once, on the day after tagging, when there was a mild swelling at the tag-insertion site.

Integrated tags

Forty-five integrated tags were deployed on 44 whales in 2013, 2015 and 2018. The chronology of changes evaluated in each photograph is shown in Figure 10 and a typical sequence of events illustrated in Figure 13. Immediately after tag deployment, minimal tissue responses were observed. Rarely, drops of blood were observed in photographs taken within an hour of tagging, but most often, no discharge was observed, and the skin margins appeared tight against the transmitter body. Within days of tagging, the skin margins typically appeared expanded away from the tag with a skin defect of up to twice the diameter of the transmitter body, with no discharge or tissue extrusion observed. Over the following weeks, variably sized cutaneous swellings were observed around the margins of 25 tag deployment sites, while no swellings were observed at 20 tag-attachment sites. In nine whales, swellings were Score 1, 15 whales had transient swellings assigned as Score 2, and one whale had a Score 3 swelling. In six whales (Tags 46, 51, 54, 57, 61 and 64), small pieces of blubber were observed around the tag that gradually became discoloured and were extruded 2–4 weeks post tagging. Once the tag was ultimately shed, the tissue deficit healed and a depression in the skin surface was apparent at the tag site. Occasionally, the skin around the healed tag site was paler than adjacent skin. The size of depression and area of coloration change corresponded to the size of swellings and areas of skin lost during tag retention. A raised subcutaneous nodule within the depression was observed in one whale.

One year after tag loss, skin depressions at the tag sites were visible in high-quality photographs, but some defects could be missed in photographs taken at greater distances, or those of poor quality. In one whale where the tag was applied just right of the dorsal midline (Tag 79), there were marked bilaterally symmetric depressions of the dorsal ridge, with the depression in the contralateral side larger than the tag-insertion site.

One whale (Tag 48) tagged very close to the midline cranial to the dorsal fin had minimal initial tissue reaction to the tag. At day 56 post insertion, the tag was no longer visible and an irregular erosion, approximately 50cm in diameter, with multifocal ulceration, surrounded the tag site. This lesion healed over days 57–90, and at day 346, the defect had resolved, leaving an irregular shaped area of roughened skin. It is likely that this tag was caught and detached (avulsed) by a foreign object or rubbed out of the animal, abrading a large portion of adjoining epidermis, resulting in this irregular shaped lesion. No evidence of purulent discharge or foreign body in the wound was detected.

An unusual egress event occurred in the case of one integrated tag (Tag 69). This individual was entangled in a boat anchor line 10 days after tagging in 2018. The tag was detached by the entangling rope. The tag site was well-documented minutes prior to the event as well as shortly after the tag was removed. Images show rope emanating from the mouth and trailing aft along the body, sometimes in contact with the tag site. It is our assumption that the entangling gear dislodged the tag. There is no evidence that the tag was a direct or indirect cause of the entanglement. Although there was initial bleeding at the tag site following detachment, no unusual tissue damage was evident at the skin surface. A disentanglement team responded the same day and removed a large portion but not all of the life-threatening gear. While this individual was not re-sighted, it was retrospectively matched by CCS to a whale that was found dead from unknown causes in 2019. No necropsy was conducted in that case.

At last assessment of the 45 whales tagged with integrated tags, all attachment sites were re-epithelialised: 15.6% (n = 7) had no obvious mark at the implant sites; 66.7% (n = 30) had small, shallow depressions (score 1); 15.6% (n = 7) had deeper depressions (score 2); and 2.2% (n = 1) had mild subcutaneous swelling at the tag site (Table S3).

DISCUSSION

The series of photographs in this study provide the most comprehensive description of tissue changes associated with satellite tag deployment in baleen whales to date. Photographic assessments are limited, without additional histological insights or ultrasound examination of tissues, which means any attempt to interpret the significance of features such as swelling is also limited to the sequence of apparent changes over time, unless informed by other data, such as whale behaviour, reproduction, body condition, survival and opportunistic necropsy findings from stranded animals. The availability of many tag-site photographs in individually identified whales over years enabled the development of an objective scoring system to characterise temporal and spatial changes at tag sites. This scoring facilitated comparison of tissue responses amongst whales and tag types, so that factors minimising tissue responses could be identified. Although the addition of a multiplier based on the scorer's decision as to whether the lesion was improving or worsening was subjective, it was useful in focusing attention of the reviewer on periods of change when reviewing hundreds of photographs spanning multiple years. In humans, an objective scoring system for evaluating surgical wound healing using only appearance has been useful for evaluating surgical success and identifying risk factors for prolonged wound repair (Bailey *et al*., 1992; Gorad *et al*., 2021). In wildlife, such a numerical system has only rarely been used, yet has been proposed as a tool for cross-ocean comparison of wounds in whale sharks (Womersley *et al*., 2021) and could also be used for evaluating the impacts of different tag types in cetaceans.

The series of observations in the first years of this study enabled improvements in the tag design to prevent tag breakage, prolonged retention of tag fragments, minimised foreign-body tissue reactions and delayed wound healing. Modifications of the tag design through the study resulted in improved skin healing and minimal residual tissue changes in whales associated with the integrated tag design. The effort undertaken to repeatedly re-sight tagged whales was invaluable to improving tag designs and understanding the causes of prolonged tag-site healing. We have yet to fully quantify the forces on tags during deployment and within the body. Consequently, we recommend that tag design and manufacturing techniques avoid the use of elements that might break, as well as those that could result in tissue shearing.

The tissue responses observed in whales tagged with integrated tags suggest there was moderate local reaction to the insertion of an indwelling integrated tag placed dorsally and in proximity to the dorsal fin of a humpback whale, with post-detachment wound healing by second intention. Typical wound healing by second intention (filling a tissue deficit) involves epithelialisation, angiogenesis, collagen formation, remodeling and finally contraction, in contrast to primary intention healing which occurs when skin margins at a wound site are closely aligned by suturing. The discoloration of the whale skin around the tag site weeks after tagging is likely a consequence of new skin cell production and migration (re-epithelialisation) and blood vessel formation (angiogenesis), while the depressions observed months to years after tag loss likely result from contraction of the wound site following blubber and possible underlying muscle loss and tissue healing. The duration of each phase of wound healing observed after tag loss in this study fit within the expected durations of phases of wound healing observed in large cetaceans injured by other traumatic events (Bruce-Allen & Geraci, 1985; Zasloff, 2011). Exceptions were the skin protuberances observed in association with broken tag fragments that may be fibro-epithelial masses similar to keloids observed in people with delayed skin healing (Murray *et al*., 1981).

Potential causes of the swelling around the tag site include bleeding with haematoma formation; tissue edema; inflammation in response to trauma or saltwater intrusion; or a mixture of these processes. Bleeding or purulent discharge were rarely observed at the tag-implant sites, making hematomas or abscesses unlikely causes of swelling. Although pus was not observed, bacterial infection around embedded tag parts has been detected by histology of tissue from beluga whales (*Delphinapterus leucas*) tagged with 'spider' tags (Burek-Huntington *et al*., 2023). Thus, the lack of purulent discharge in the photographs does not conclude lack of infection, although it is unlikely in these humpback whale cases given the progression of lesion development. More likely causes of swelling are edema, hemorrhage, necrosis and inflammation due to mechanical trauma to tissue, as any disruption of the keratinocyte layer at the skin surface will initiate an inflammatory reaction (Nickoloff & Naidu, 1994). Surgical-grade sterilisation (versus disinfection) of the tags prior to use was likely important in minimising infection post insertion. This practice should be continued despite the additional logistical challenges involved.

The tags used in this study were longer than the minimum distance across the blubber from outer epidermis to underlying muscle, as adult humpback blubber thicknesses at tag-deployment sites reportedly vary between 10–18cm seasonally (Slijper, 1962; Lockyer, 1981; Gabriele *et al*., 2021). There are no recent published data on blubber thickness of adult humpback whales in the GoM, but insights can be drawn from two stranding events involving catalogued adults in recent years. One adult male had a 7cm blubber layer at the mid-lateral thoracic region in the month of January (AMCS013Mn2013, AMSEAS, unpublished data). An adult female had blubber thicknesses along the dorsum cranial to the dorsal fin ranging from 6–7cm in May (IFAW19-287Mn, IFAW/CCS, unpublished data). This information, combined with our photogrammetric tag-penetration estimates, suggest that most tags in this study likely extended below the blubber into the hypodermis and sometimes the muscle. The post-mortem examination of a North Atlantic right whale that had been darted with a syringe and needle to administer antibiotics about a week prior to death revealed the potential for a rigid object traversing the blubber-muscle interface to cause tissue shear and cavitation (Moore *et al*., 2013). Further studies on dolphin carcasses indicated insertion of a rigid needle across the blubber-muscle interface can cause cavitation in the muscle due to shearing action, with the effect more marked further from the dorsal midline (Moore & Zerbini, 2017). Thus, it is possible that the tags were causing necrosis and cavitation with associated hemorrhage and hematoma formation. The subcutaneous more acute swellings may reflect haematomas in the fascial layer or possibly subjacent musculature. However, the speed of swelling development and the lack of change in size over time makes this less likely than tissue edema following trauma. A 16-year time series of photographs of a female blue whale tagged with an old model Type-C tag had a persistent skin lump associated with a retained tag fragment for a decade, yet later shed the tag and the lump resolved (Gendron *et al*., 2015). This persistent lump was associated with a retained tag fragment embedded in the whale for nearly 10 years. Similar swellings have been observed in North Atlantic right whales and gray whales tagged with older versions of Type-C tags (Weller, 2008; Norman *et al*., 2018). These observations reinforce the need to avoid potential tag breakage through improved design and material composition.

The lack of significant cyamid infestation of these tag sites, compared with infestation of wounds associated with some entanglement injuries (Rolland *et al*., 2016), suggest there may be minimal and localised necrosis of epithelium at these tag sites, as cyamids feed on shed epithelial cells (Schell *et al*., 2000). A southern right whale seen with a broken tag 11 years after deployment had no significant tissue response around the tag which was observed at the base of a shallow depression in the skin (Best *et al*., 2015). Fragments of a consolidated tag in the blubber of a gray whale were surrounded by epithelial cells with no external observable swelling (Goley *et al*., 2023). Harpoon heads have been observed in the blubber of bowhead whales with minimal tissue response years or decades after embedment, indicating that foreign bodies can embed in epidermal tissues of baleen whales without obvious health impacts (George *et al*., 1999).

In addition to tag type and design, another important predictor of tissue responses to tags was the site of placement on the body. Dorsal insertion, anterior to the dorsal fin, was associated with the least swelling. More deeply implanted tags, reflecting a shallower angle of insertion, were associated with less skin loss. Lower photographic scores following tagging were associated with less detectable marks on the skin years after tagging. Based on these results, every effort should be made to target the dorsum in the vicinity of the dorsal fin, both to optimise the research and for the tagged individual's welfare. Experienced taggers and vessel operators are therefore critical for optimal deployments, as are equipment that increase deployment precision, such as tagging platforms and properly-calibrated rifle aims.

Despite the variation in intensity and duration of tissue responses after tagging, most whales had minimal long-lasting changes in the skin surface years after tagging. At the end of this study, there were some cases where the skin depression was not detectable, some cases where the depression was detectable to an experienced observer with knowledge of the earlier tag site, but not to an uninformed observer, and some cases where the detectable depressions were slightly larger than 2–4 times the tag diameter. In one whale (Tag 79) with two depressions either side of the dorsal fin, the position of the two depressions, and the larger size of one depression contralateral to the tag insertion site, suggest the tag might have migrated through the whale to exit on the opposite side from tag entry, although no such migration was observed. This is possible but unlikely as the tag is fitted with a stopper preventing inward migration. In gunshot animals, bullet exit holes are larger than entry holes, with everted skin margins (Moore *et al*., 2013; Harnish *et al*., 2019). Alternatively, the contralateral lesion could have resulted from fluid discharge tracking along the fascia, exiting the body contralaterally.

The impacts of pain on animal welfare are not possible to assess from these photographic data and remain subjective. Future research on tag effects could focus on methods to evaluate the potential for pain assessment, such as changes in behaviour and stress hormone levels in blow, blubber, baleen or faeces (Hunt *et al*., 2014a; Hunt *et al*., 2014b; Hunt *et al*., 2017; Hunt *et al*., 2019). In addition, continued collaboration amongst the whale research and health-monitoring community is vital to ensure all known tagged whales are examined if a carcass should be found, even if years after tagging. Some tissues hold years of whale history and could shed light on stress hormones, reproduction and even feeding ecology changes in tagged whales (Gabriele *et al*., 2021). Concurrently, efforts should continue to improve tag designs to prevent tag breakage, petal detachment and fragment retention and decrease the length and/or diameter of the attachment components to minimise tissue reaction without reducing duration/efficacy. Advanced tag features, such as antimicrobial coatings, may potentially enhance biocompatibility and thereby increase retention while minimising adverse impacts to the host (Smies *et al*., 2022). The ongoing efforts of regional stranding networks are also critical to understanding tagging impacts, which further depends on good communication between these networks and both tagging programmes and population studies. Although one tagged whale in this study was found dead following a life-threatening entanglement, no necropsy was possible, the tag wound was not observed, and the individual was also not successfully linked to its life-history records until three years later. As a result, there are no relevant observations or samples to further clarify the impacts of the tag. Furthermore, it is important to note that the tag site of an individual could not necessarily be assessed in all sightings, including, in some cases, its most recent sighting year. Therefore, tag site re-sight data do not represent whale survival, which is presented separately in Robbins *et al*. (in prep).

In conclusion, tag deployments on 79 whales, with up to a decade of post-tagging observations, revealed that, despite a range of local tissue responses, mostly influenced by tag design leading to breakage, and position of insertion, the long-term effects detectable at the tag site were minimal, with skin healing and scar contraction. This study led to improved tag designs with robust components, reducing local trauma to tissue resulting from retained tag fragments (Zerbini *et al*., in prep.). It also enabled recognition of the sites on the body least prone to tissue reactions to tag insertion. This decade of observations highlights the value of long-term studies on individually identifiable whales not only to improve understanding of whale ecology but also to evaluate research methods and their impacts on individual animals. The photographic evaluation scores have contributed to international guidelines for best practices in cetacean tagging (Andrews *et al*., 2019). These results inform researchers as they work to meet ethical and animal welfare standards for research on individual animals while providing valuable information to inform population level conservation.

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FIGURES & TABLES

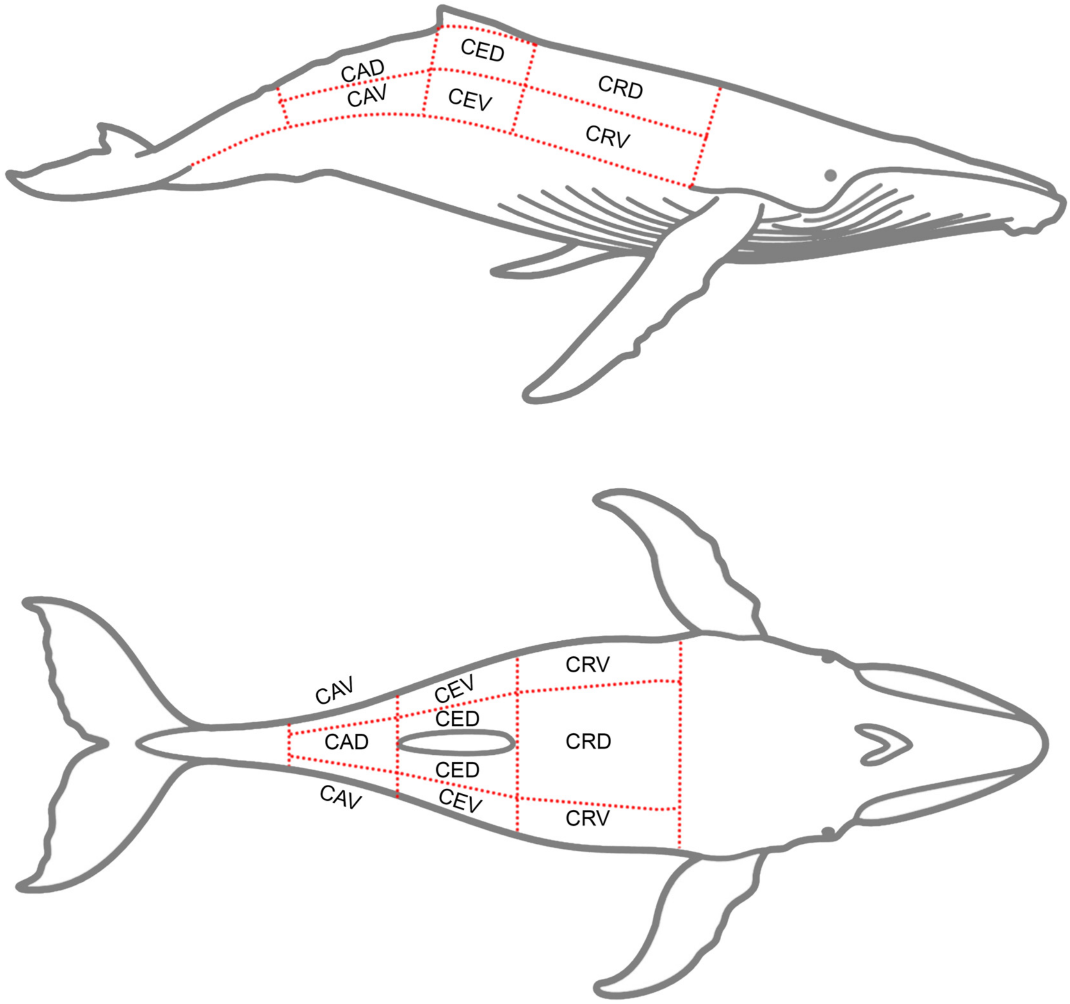


Fig. 1: Tag placement by craniocaudal position (CR = cranial, CE = central, CA = caudal) and circumferential position (D = dorsal, V = ventral).

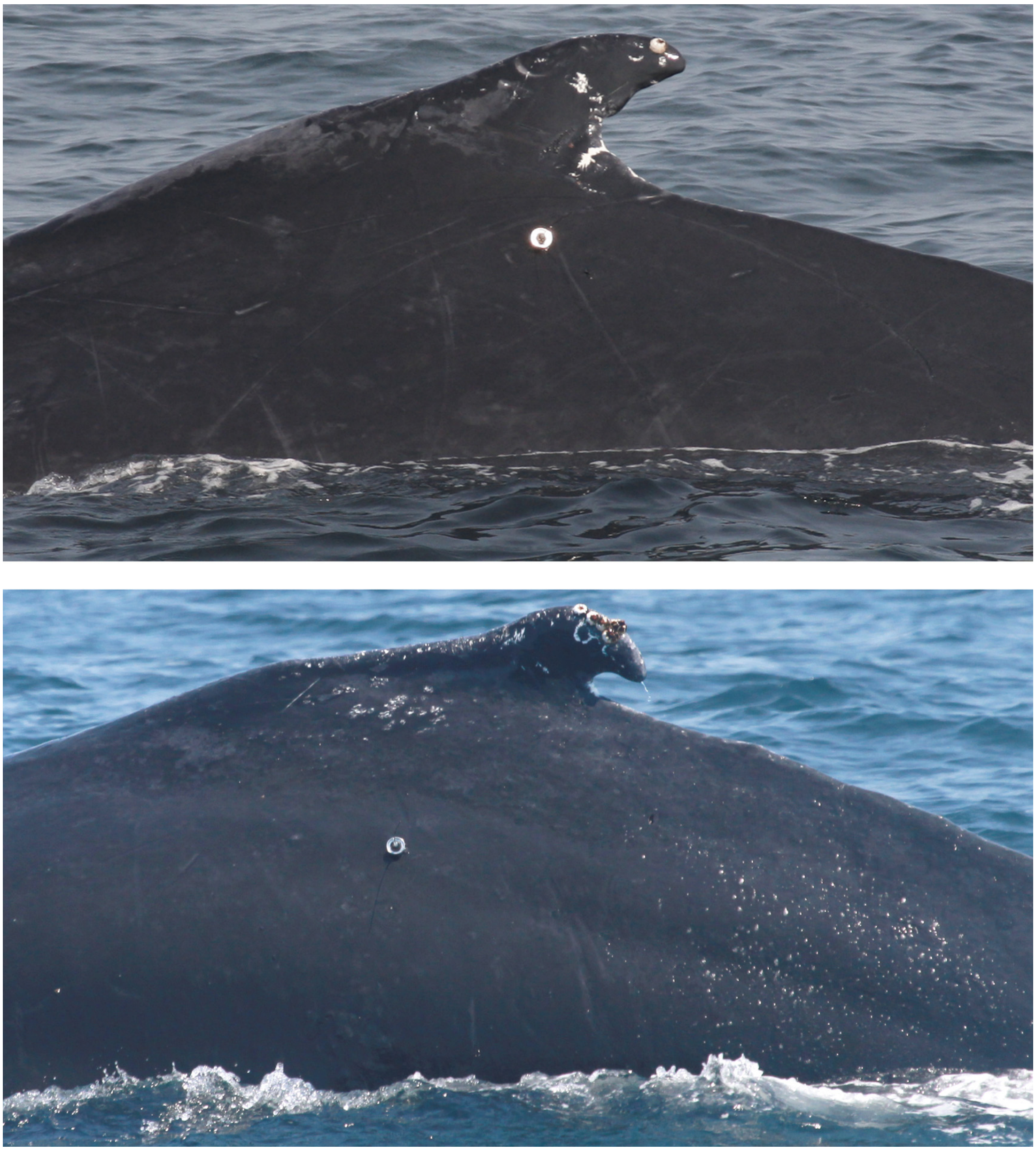


Fig. 2: Two GoM humpback whales before any site effects were detected (i.e., Score 0). The cranio-caudal positioning of both was central (under the dorsal fin), but the top image shows an upper flank deployment while the other tag was on the lower flank. Image credits: CCS.

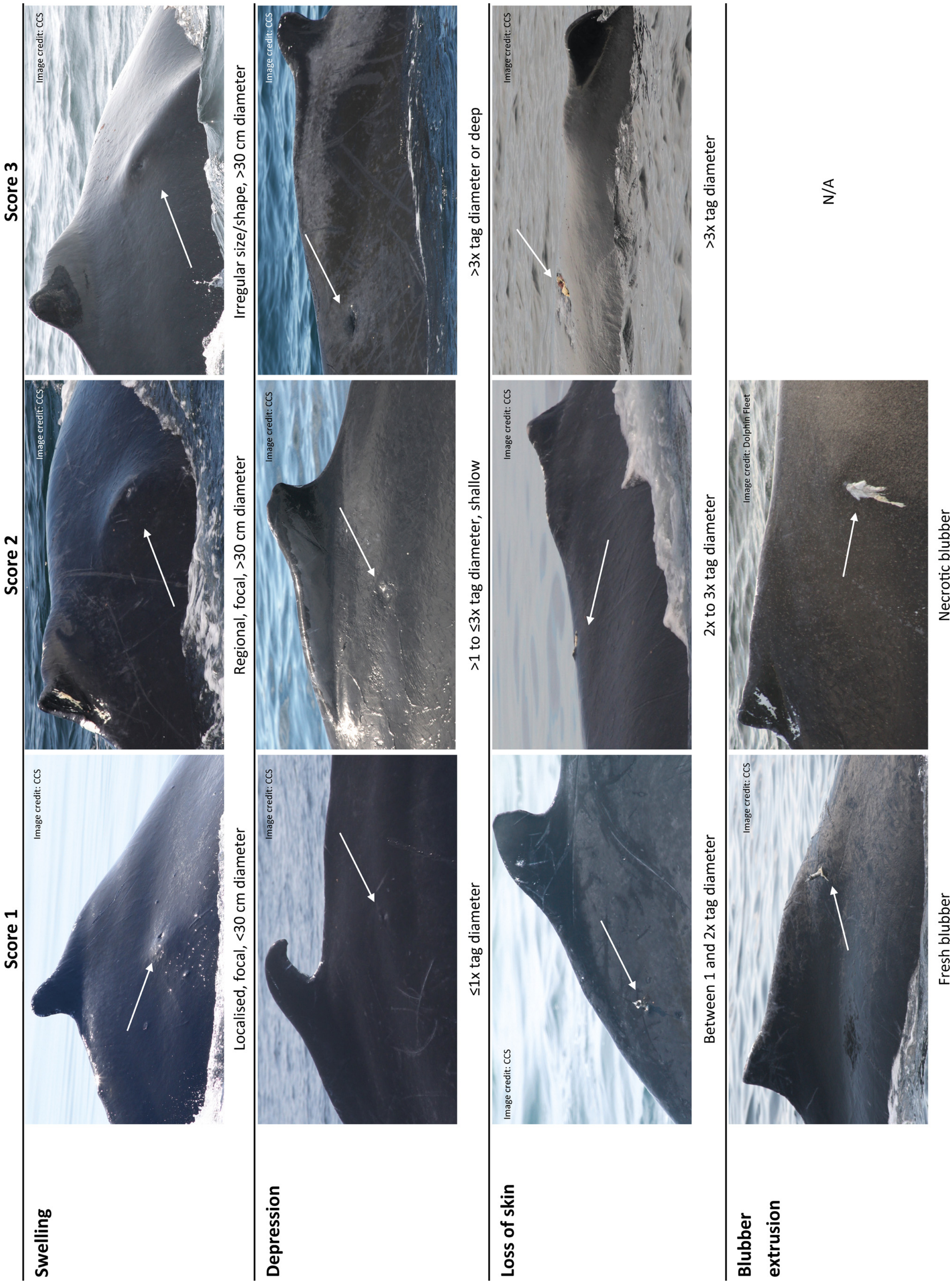


Fig. 3a: Examples of tag site scoring for all injury features associated with deployment of consolidated satellite transmitters in GoM humpback whales.

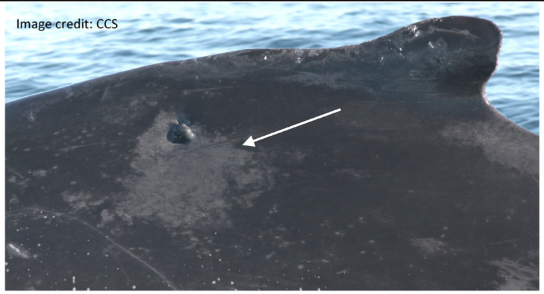
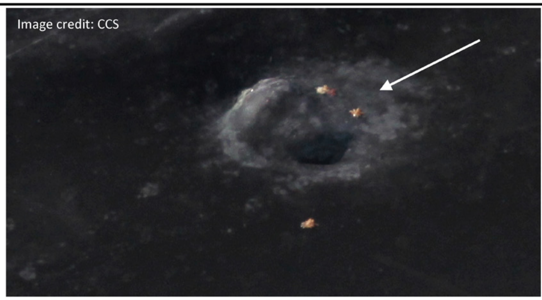
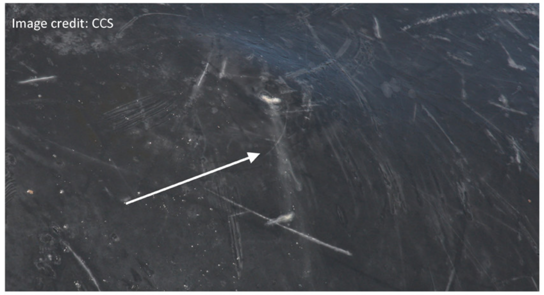
	Score 1	**Score 2**	**Score 3**
Colour change	 Colour change around the tag site	N/A	N/A
Cyamids	 Sparse (≤10 cyamids) within 30 cm of the tag	 Abundant (>10 cyamids) within 30 cm of the tag	N/A
Exudate	 Exudate visible	N/A	N/A

Fig. 3b: Examples of tag site scoring for all injury features associated with deployment of consolidated satellite transmitters in GoM humpback whales.

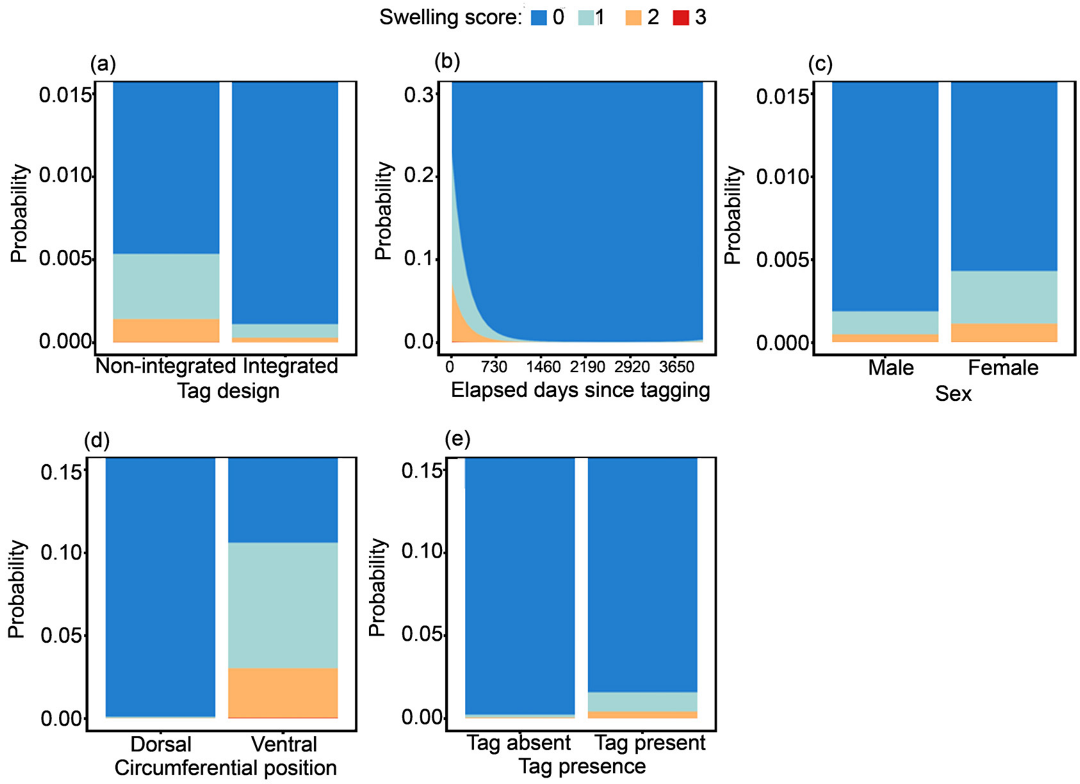


Fig. 4: CLMM effects plots for the 'swelling' tag injury score: (a) tag design; (b) elapsed days since tagging; (c) sex (not statistically significant, see Table 2); (d) tag circumferential position; and (e) tag presence.

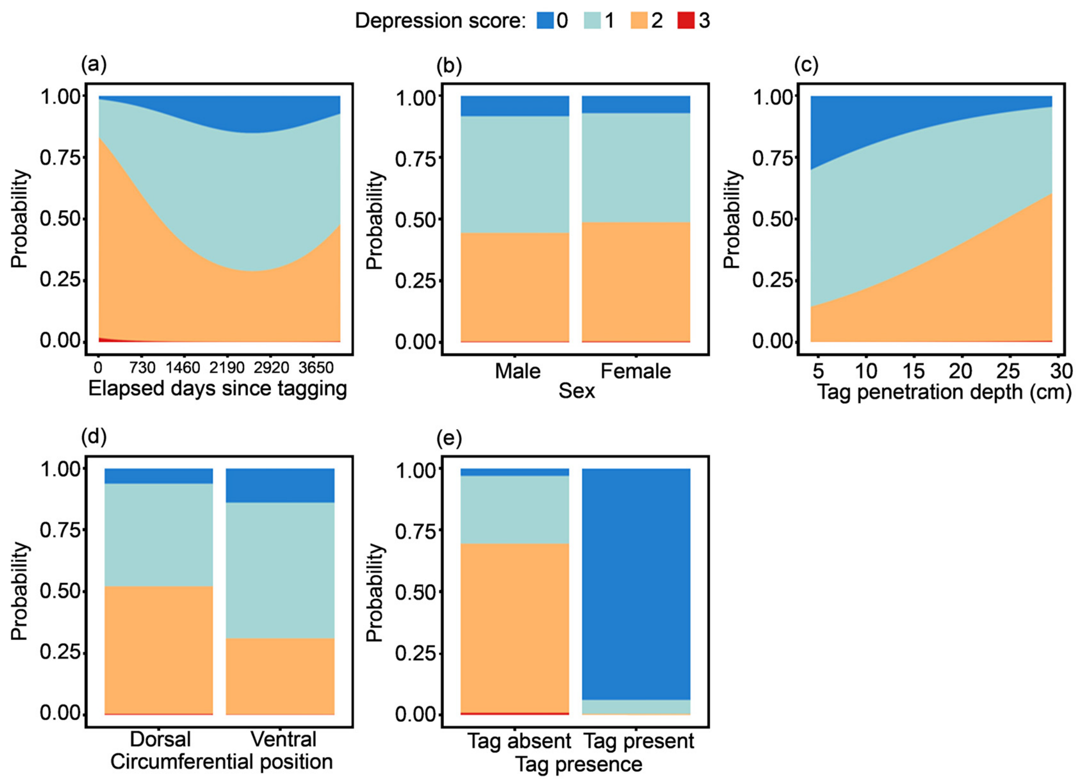


Fig. 5: CLMM effects plots for the 'depression' tag injury score: (a) elapsed days since tagging; (b) sex; (c) tag penetration depth; (d) tag circumferential position; and (e) tag presence. Only 'elapsed days since tagging' and 'tag presence' were statistically significant (see Table 2).

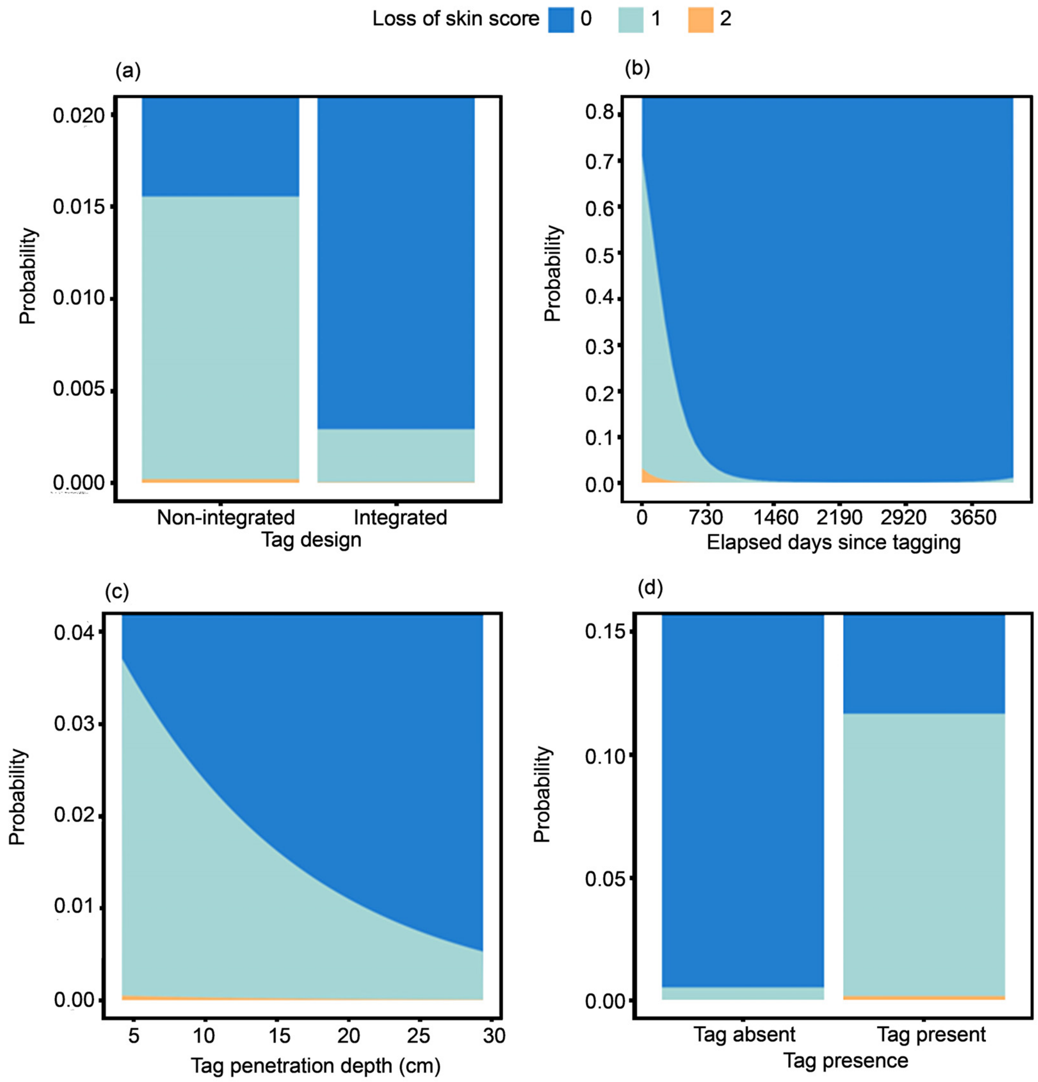


Fig. 6: CLMM effects plots for the 'loss of skin' tag injury score: (a) tag design; (b) elapsed days since tagging; (c) tag penetration depth (not statistically significant, see Table 2); and (d) tag presence.

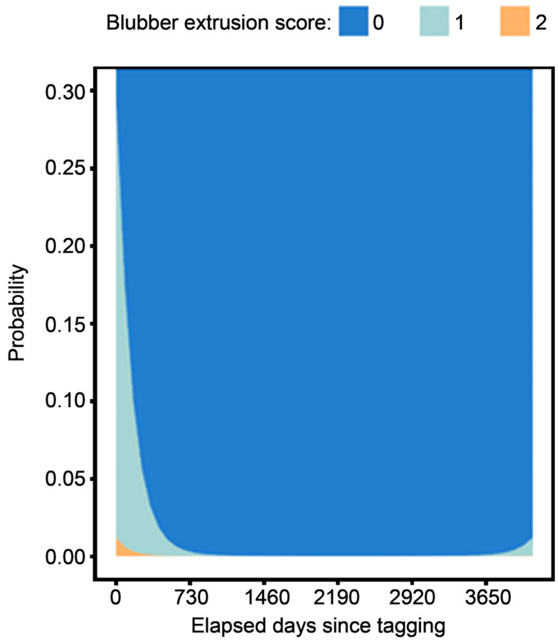


Fig. 7: CLMM effect plot of elapsed days since tagging for the 'blubber extrusion' tag injury score.

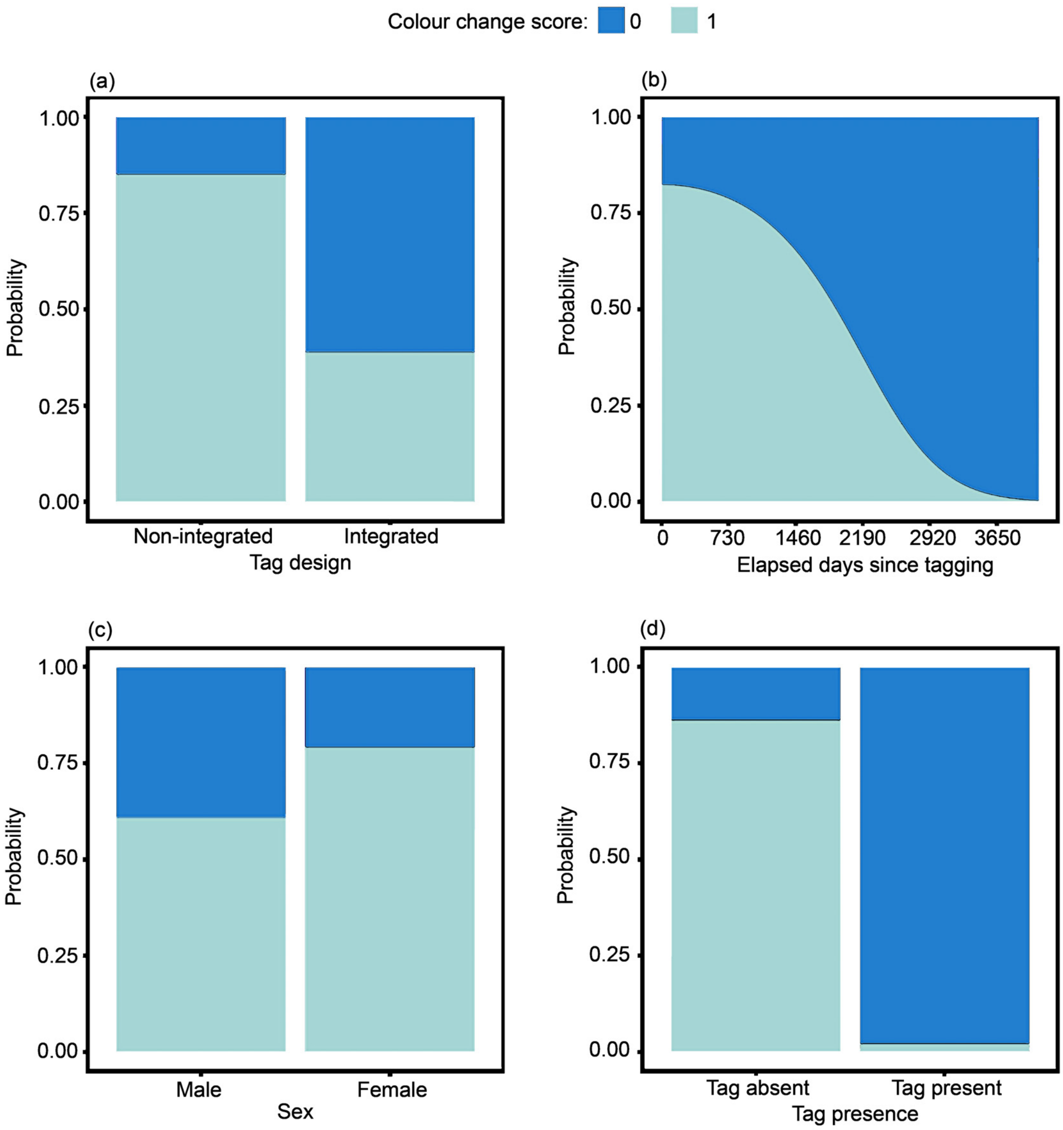


Fig. 8: GLMM effects plots for the 'colour change' tag injury score: (a) tag design; (b) elapsed days since tagging; (c) sex (not statistically significant, see Table 2); (d) tag penetration depth; and (e) tag presence.

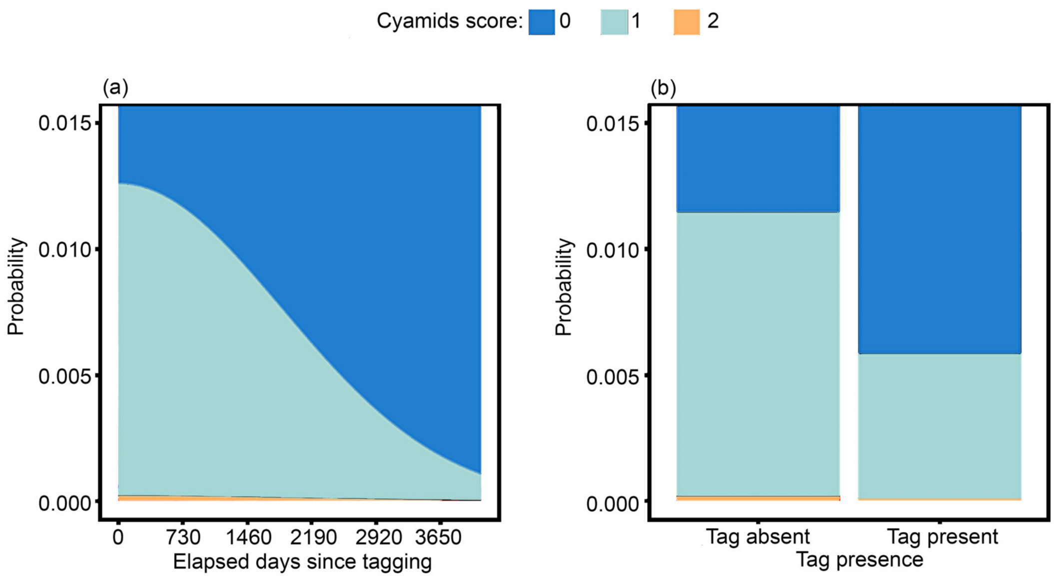


Fig. 9: CLMM effects plots for the 'cyamids' tag injury score: (a) elapsed days since tagging; and (b) tag presence (not statistically significant, see Table 2).

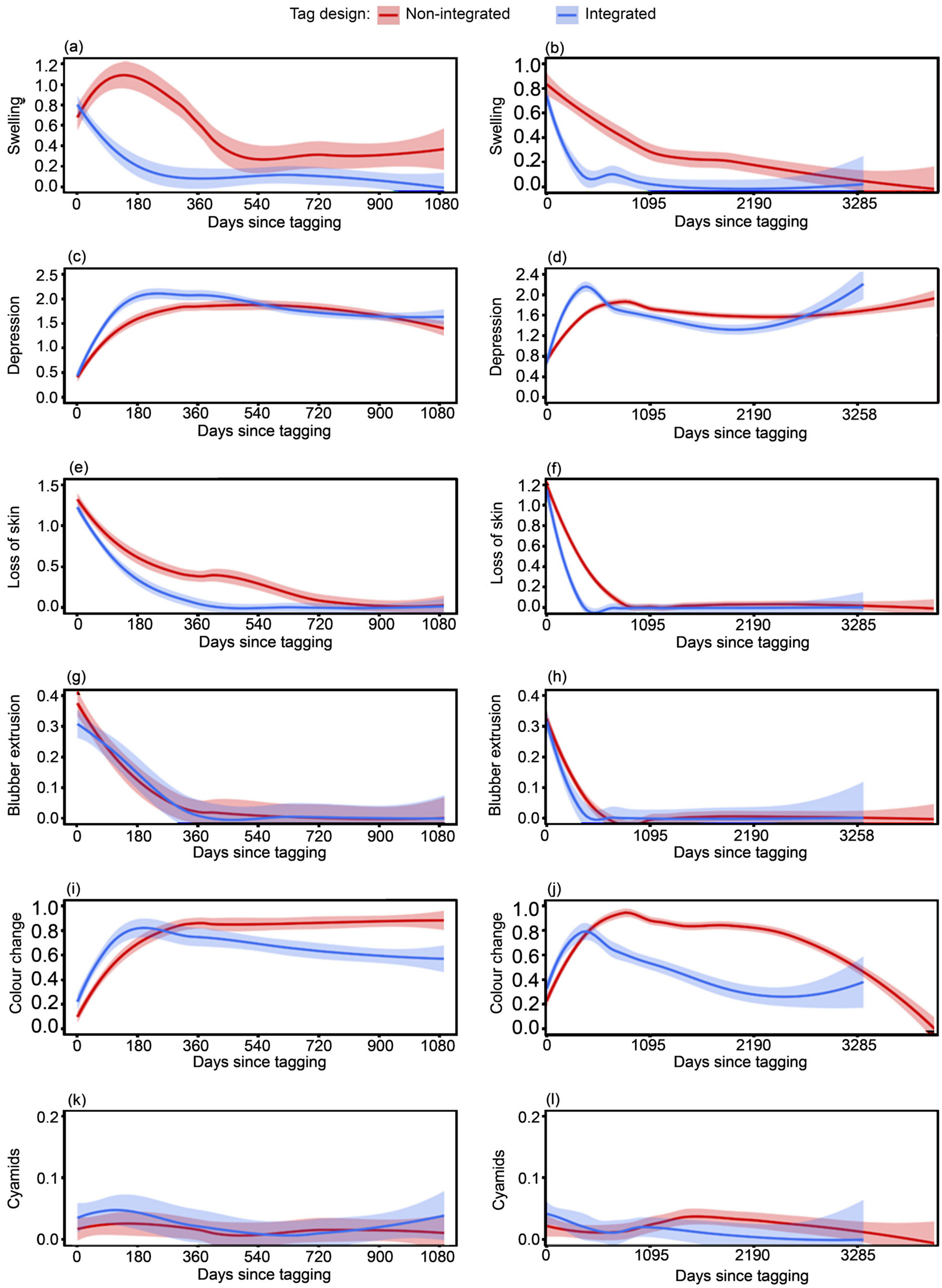
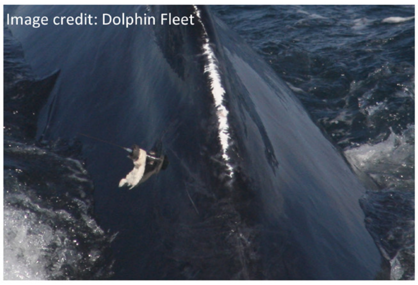


Fig. 10: Comparison of the chronology (local regression curve) of tag injury scores among whales that received tags with integrated and non-integrated designs. Lines represent the local regression using data from sightings during the first three years post-deployment (A, C, E, G, I, and K) or during the entire study period (B, D, F, H, J, and L). Shaded areas represent their corresponding 95% confidence intervals.

Day 0
This tag was fully implanted on deployment

Day 9
View of the tag from behind, showing the extent of egress.

Day 12
A blubber plug is visible around the base of the tag.



Day 14
The blubber plug has migrated out and is beginning to separate from the tag.

Day 15
The blubber plug has been shed and no further tissue discharge was observed.

Day 23
The transmitter has moved inward. The transmitter had likely been moving freely within the wound.

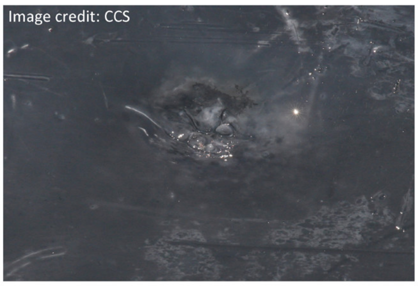
Day 33
The transmitter has migrated out to nearly the same extent as Day 15. This is the last sighting with the transmitter. The skin surface around the tag has begun to subside.

Day 34
The transmitter has been shed. The last transmission was two hours earlier.

Day 41
The tag site has developed more of a sunken appearance (a depression).

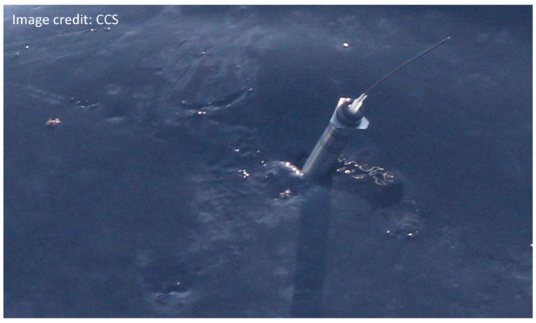
Day 135
A raised area has formed at the tag site.

Day 347
The anchor is now visible migrating out of the tag site.



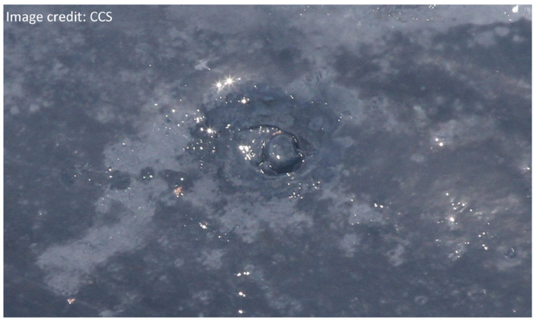
Day 373
The anchor appears to have been shed. This depression was relatively stable through the latest sighting (Day 1592).

Fig. 11: Typical sequence of changes in the tag site during tag rejection and healing in a humpback whale instrumented with a non-integrated satellite transmitter in the GoM (Tag 3).



Day 20
Ten days before transmitter was shed

Day 31
One day after transmission failure.



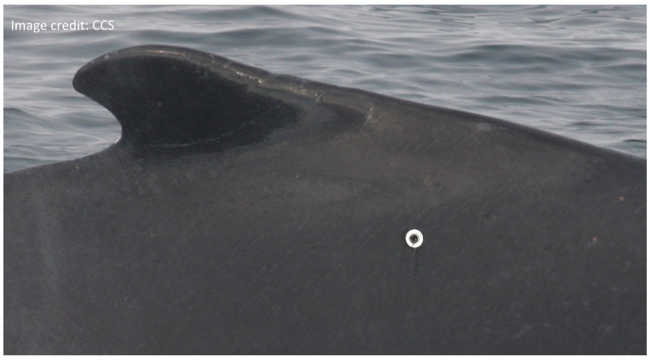
Day 323
"Bleb" of tissue forming at tag site

Day 675
First evidence of the anchor emerging at tag site

Day 846
Another portion of anchor becomes visible

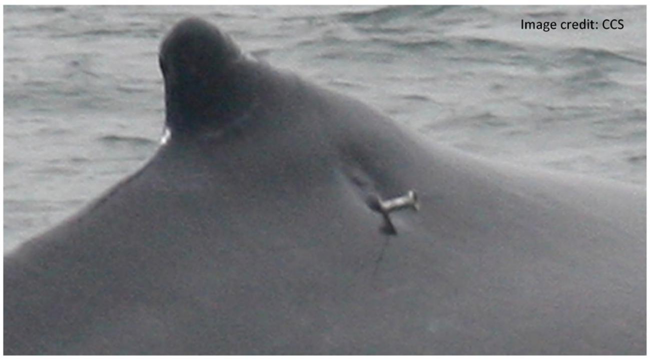
Day 1126
Tag parts were no longer visible as of Day 1028.

Fig. 12: Example of tag site appearance during rejection and healing in the presence of broken tag parts on a humpback whale tagged with a non-integrated satellite transmitter in the GoM (Tag 5).



Day 1
a) Lateral view

b) posterior view



Day 27
a) Lateral view

b) posterior view

Day 47
a) Lateral view two days before transmissions ceased

b) posterior view

Day 56
a) Lateral view seven days after transmissions ceased.

b) posterior view

Fig. 13a: Example of tag rejection and healing on a humpback whale tagged with an integrated satellite transmitter in the GoM (Tag 68).

Day 56

a) Lateral view seven days after transmissions ceased.

b) posterior view

Day 75 Last day seen in deployment year.

Day 768

Day 1123

Day 1522

Fig. 13b: Example of tag rejection and healing on a humpback whale tagged with an integrated satellite transmitter in the GoM (Tag 68).

Table 1

Summary of tag injury definitions and sample sizes for statistical analyses. The latter included scores recorded at the individual level (highest score across all re-sighting events) and for all sighting events. Skin loss scores 2 and 3 were combined in statistical analysis and exudate (presence/absence) was scored but not included in the analysis.

	Non-integrated tags				Integrated tags			
	Individuals		Resightings		Individuals		Resightings	
Tag injury score	N	%	N	%	N	%	N	%
Swelling								
0 – None	8	27.6	1,513	81.2	17	39.5	874	86.6
1 – Localised, focal, under 30 cm diameter	8	27.6	78	4.2	10	23.3	51	5.1
2 – Regional, focal, over 30 cm diameter	6	20.7	211	11.3	15	34.9	82	8.1
3 – Irregular size and shape, over 30 cm diameter	7	24.1	62	3.3	1	2.3	2	0.2
Depression								
0 – Diameter equal to tag diameter or less	0	0	225	12.0	3	7.0	163	16.1
1 – Up to 3× tag diameter, shallow	3	10.3	492	26.3	7	16.3	262	25.9
2 – Up to 3× tag diameter, deep	20	69.0	1,064	56.8	28	65.1	536	53.1
3 – Larger than 3× tag diameter, deep	6	20.7	91	4.9	5	11.6	49	4.9
Loss of skin								
0 – Less than 1× tag diameter	2	6.9	1,519	81.3	7	16.3	772	76.3
1 – Between 1× and 2× tag diameter	12	41.4	233	12.5	19	44.2	181	17.9
2 – Between 2× and 3× tag diameter	15	51.7	116	6.2	16	37.2	55	5.4
3 – Larger than 3× tag diameter	0	0	0	0	1	2.3	4	0.4
Blubber extrusion								
0 – None	6	20.7	1,774	94.9	16	37.2	931	92.0
1 – Fresh tissue	20	69.0	90	4.8	26	60.5	77	7.6
2 – Necrotic tissue	3	10.3	5	0.3	1	2.3	4	0.4
Color change								
0 – No change	1	3.4	539	28.9	8	18.6	495	49.0
1 – Change in skin color around tag site	28	96.6	1,327	71.1	35	81.4	515	51.0
Cyamids								
0 – None	16	55.2	1,809	97.9	31	72.1	985	97.8
1 – Sparse (≤ 10 individuals) within 30 cm of tag	12	41.4	38	2.1	12	27.9	22	2.2
2 – Abundant (> 10 individuals) within 30 cm of tag	1	3.4	1	< 0.1	0	0	0	0
Exudate								
0 – Absent	21	72.4	1,860	99.5	35	81.4	995	98.4
1 – Present, clear	7	24.1	8	< 0.1	8	18.6	16	1.6
2 – Present, blood or pus	1	3.4	1	< 0.1	0	0	0	0

Table 2

Summary of the statistical models to predict tag-injury feature scores recorded upon a resighting event. Location and threshold coefficients are expressed as 'estimate (standard error)'.

	Swelling	Depression	Loss of skin	Blubber extrusion	Colour change	Cyamids
Model method	CLMM	CLMM	CLMM	CLMM	GLMM	CLMM
Location coefficients						
Integrated tag (ref: non-integrated)	–1.580 (0.888) *	·	–1.685 (0.572) **	·	–2.191 (0.702) **	·
Time since tagging squared (10^3 days)	0.967 (0.114) ***	0.368 (0.045) ***	1.208 (0.113) ***	1.753 (0.209) ***	–0.426 (0.025) ***	–0.147 (0.064) *
Time since tagging (10^3 days)	–5.060 (0.429) ***	–1.925 (0.174) ***	–6.266 (0.431) ***	–8.060 (0.752) ***	·	·
Female (ref: male)	0.834 (0.864) ^{ns}	0.173 (0.494) ^{ns}	·	·	0.893 (0.689) ^{ns}	·
Tag penetration depth (mm)	·	0.088 (0.471) ^{ns}	–0.078 (0.051) ^{ns}	·	·	·
Ventral position (ref: dorsal)	4.766 (0.958) ***	–0.884 (0.543) ^{ns}	·	·	·	·
Tag present (ref: absent)	1.948 (0.285) ***	–6.181 (0.226) ***	3.205 (0.273) ***	·	–5.633 (0.279) ***	–0.679 (0.404) ^{ns}
Threshold coefficients						
Scores 0|1	2.569 (0.913)	–3.259 (1.085)	–2.817 (1.285)	0.880 (0.178)	–2.640 (0.633)	4.259 (0.328)
Scores 1|2	3.901 (0.921)	–0.639 (1.084)	1.459 (1.285)	4.388 (0.376)	not applicable	8.443 (1.046)
Scores 2|3	8.328 (0.962)	4.925 (1.093)	not applicable	not applicable	not applicable	not applicable
Standard deviation of random effects	3.269	1.992	1.963	0.973	2.741	1.263
Observations	2,870	2,879	2,880	2,881	2,873	2,855

Legend: '·' not included in model, ^{ns} not significant but included in model, * P < 0.05, ** P < 0.01, *** P < 0.001.

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Supplementary Materials

PHOTOGRAMMETRY

A photogrammetric method was used to measure features of interest in follow-up photographs. Initially, a range finder was used in the field to measure the distance from the camera to the whale (e.g., Jaquet, 2006). However, the Jaquet (2006) approach limited measurements to photographs with paired range-finder data and also required that each camera/lens combination be calibrated across the relevant subject distances and focal lengths. This study used images from 21 different camera models, including contributions from opportunistic observers. An alternative measurement method was therefore used that took advantage of the fact that an object of known size (the tag) had been placed on the whale.

Photogrammetric measurements were conducted for all whales with suitable photographic coverage. Known-sized objects were measured using the programme ICY (de Chaumont *et al*., 2012) to establish a scale (mm/pixel) for objects at approximately the same distance in each image. The tag was initially used as the scale, but we also measured persistent natural features on the whale to act as reference marks when the tag was no longer present.

Two reference marks were chosen for each tagged whale. These marks were selected based on their persistence across years, proximity to the tag site and size. The two marks selected were typically substantially different in size and as orthogonal to each other as possible. Measurements were made on the subset of photos that were taken approximately perpendicular to the feature of interest, which was either along the long axis (i.e., anterior/posterior axis) of the whale or directly behind it. The distance from the camera to the whale was typically much greater than the size of the objects being measured and therefore slight deviations from the preferred angle (i.e., within 15°) were expected to produce minimal error. A direct comparison of this approach with the Jaquet (2006) method suggested comparable accuracy, but greater ease of use and wider applicability to the data in this study. The maximum depth of tag penetration was calculated based on a measurement of the minimum length of tag exposed on the day of deployment, the insertion angle and the known length of the tag (Fig. 8). It was calculated as follows:

$$\text{Depth}_{max} = (\text{Length}_{embedded} * \sin \Theta) * \sin \Phi$$

where: $\text{Length}_{embedded} = \text{Length}_{total\ tag} - \text{Length}_{exposed}$, Θ = angle in the dorsal-ventral plane and Φ = angle in the anterior-posterior plane.

Angles were measured using the Angle Helper tool in programme ICY. Photos taken perpendicular to the dorsal-ventral and the anterior-posterior planes were used to calculate the angle incident to each. These were selected such that the view of the surface of the skin surface at the point of tag insertion was approximately normal to the camera lens. An anterior-posterior angle was also estimated assuming that the measured length of the exposed tag was one length of a right-angle triangle and the slope from the base of the tag to the top, as viewed from above the tag, was the opposite length. When possible, this second method was used as a check of anterior-posterior angle calculations.

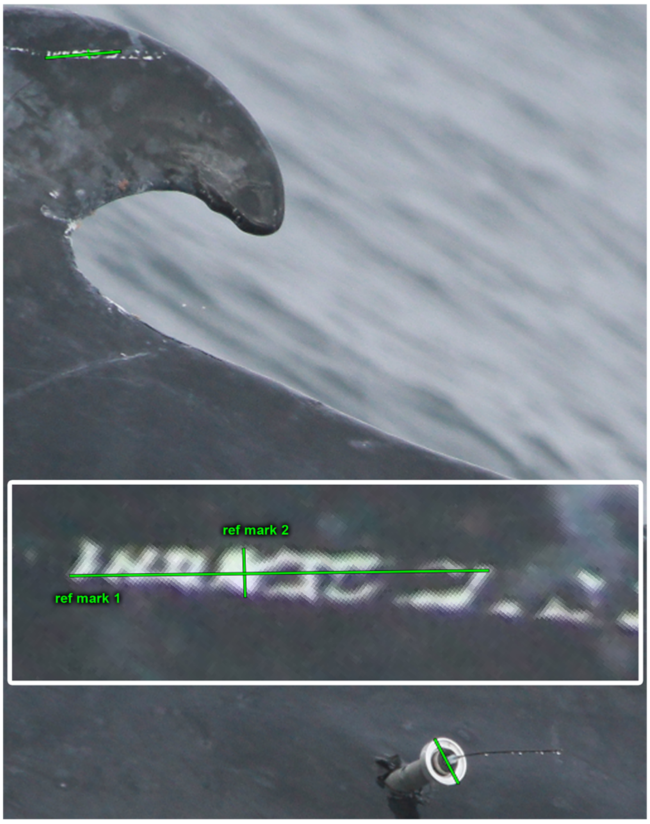
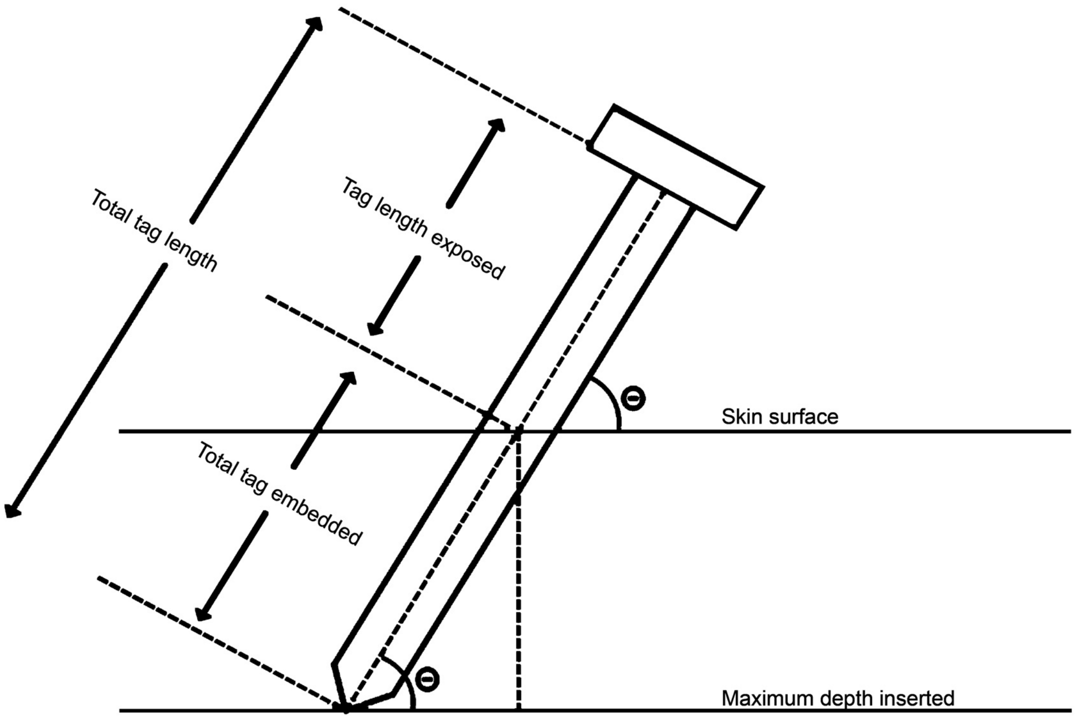


Fig. S1: Example of reference marks established for photogrammetry. Natural marks on the dorsal fin were measured while a tag of known size was present to establish a scale. The inset shows greater detail of the tag and natural markings that were measured. Image credit: CCS.



sin ϴ = maximum depth inserted/tag length embedded

Maximum depth inserted = sin ϴ * tag length embedded

Fig. S2: Schematic of measurements used to estimate maximum penetration depth.

RESULTS

Table S1

Summary of sample sizes used for statistical analyses according to whale sex, year of tag deployment, tag design and tag placement on the body.

Variable	Individuals	Sightings
Sex		
Female	35	1,204
Male	36	1,764
Unknown	1	3
Year of tag deployment		
2011	18	1,534
2012	11	414
2013	7	260
2015	21	540
2018	15	223
Tag design		
Integrated	43	1,023
Non-integrated	29	1,948
Tag position		
Dorsal – Cranial	20	804
Dorsal – Central	30	1,463
Ventral – Cranial	5	127
Ventral – Central	17	577
Total	72	2,971

Table S2

Status of the tag site at last photographed sighting for whales tagged with non-integrated tags (n = 35). Colour codes are as shown below. Note: * = individual last seen in poor health.

Higher scores				**Lower scores**
Moderate swelling (Score 3) or depression (Score 2–3)	Mild swelling (Score 2) or deep depression (Score 3)	Small swelling (Score 1), deep depression (Score 3) or skin colour change (Score 1)	Small depression (Score 1–2)	Depression in skin barely detectable

Deployment no.	Year tagged	Year and status at last assessed sighting					
		2012	2018	2019	2020	2021	2022
1	2011						
2	2011						
3	2011						
4	2011						
5	2011						
6	2011						
7	2011						
8	2011						
9	2011						
10	2011						
11	2011						
12	2011						
13	2011						
14	2011						
15	2011						
16	2011						
17	2011						
18	2011						
19	2011						
20	2012				*		
21	2012						
22	2012						
23	2012						
24	2012						
25	2012						
26	2012						
27	2012						
28	2012						
29	2012						
30	2012						
31	2012						
32	2012						
33	2012						
34	2012						
35	2012						

Table S3

Status of tag site at last photographed sighting for whales tagged with integrated tags. Colour codes are shown below. Notes: * = individual died in 2019 but was involved in a life-threatening entanglement event that dislodged the tag 10 days after tagging. ** = no adequate tag-site image in 2022, so an image from 2023 was analysed.

Higher scores				**Lower scores**
[red]	[yellow]	[light green]	[green]	[dark green]
Moderate swelling (Score 3) or depression (Score 2–3)	Mild swelling (Score 2) or deep depression (Score 3)	Small swelling (Score 1), deep depression (Score 3) or skin colour change (Score 1)	Small depression (Score 1–2)	Depression in skin barely detectable

Deployment #	Year tagged	Year and status at last assessed sighting					
		2017	2018	2019	2020	2021	2022
36	2013						[green]
37	2013						[light green]
38	2013						[green]
39	2013						[green]
40	2013						[dark green]
41	2013						[light green]
42	2013						[light green]
43	2013						[green]
44	2015						[green]
45	2015						[dark green]
46	2015					[green]	
47	2015						[green]
48	2015						[green]
49	2015						[light green]
50	2015						[dark green]
51	2015						[dark green]
52	2015						[green]
53	2015						[dark green]
54	2015						[green]
55	2015						[green]
56	2015						[green]
57	2015						[green]
58	2015						[green]
59	2015						[green]
60	2015	[green]					
61	2015						[green]
62	2015			[green]			
63	2015		[green]				
64	2015		[green]				
65	2015						[dark green]
66	2018					[green]	
67	2018						[green]
68	2018						[green]
69	2018		[yellow] *				
70	2018						[light green]
71	2018						[green]
72	2018						[green]
73	2018						[green]
74	2018						[green]
75	2018						[green]
76	2018				[dark green]		
77	2018						
78	2018		[green]				
79	2018						[light green]
80	2018						[green] **