Behavioural responses of southern right whales to satellite tag deployment, with a comparison to biopsy sampling

Emma L. Carroll[1], **Kate R. Sprogis**[2,3], **Robert Harcourt**[3], **Virginia Andrews-Goff**[4], **Tim Button**[5], **Simon Childerhouse**[6], **Ros Cole**[7], **Rochelle Constantine**[1,8], **Kimberly T. Goetz**[9,10], **David Lierich**[11], **David Lundquist**[7], **Mike Ogle**[7], **Holly Raudino**[12], **Esther Stuck**[1], **Glen Sutton**[11], **Kelly Waples**[12], **Alexandre N. Zerbini**[9,13,14] and **Leena Riekkola**[1]

Contact email: e.carroll@auckland.ac.nz

ABSTRACT

Satellite tagging provides vital information about the ecology of whales, not currently obtainable in any other way, but it can elicit short- and long-term impacts on individuals. This study investigates short-term behavioural responses of New Zealand and Australian southern right whales to the deployment of consolidated 'Type C' tags using a standardised behavioural response scale. Whale pre-approach behaviour, tag placement and deployment distance significantly influenced response intensity. Responses were generally weak, and similar to those elicited by biopsy-only sampling, which is also influenced by pre-approach behaviour. Overall, it seems likely that whales' response intensity is primarily influenced by the close boat approach.

KEYWORDS: TELEMETRY; SATELLITE TAGGING; MONITORING; BIOPSY SAMPLING; SOUTHERN RIGHT WHALE

INTRODUCTION

Understanding how cetaceans use their vast ocean habitat is challenging but important given increasing human pressures on the marine environment. Key technologies for understanding habitat use and foraging patterns include dietary markers, such as stable isotope and fatty acid markers (e.g., Derville *et al*., 2023; Groß *et al*., 2024), and satellite (e.g., Cubaynes *et al*., 2019) and telemetry technologies (e.g., Hindell *et al*., 2020). Telemetry

[1] School of Biological Sciences, University of Auckland – Waipapa Taumata Rau, Auckland, Aotearoa New Zealand
[2] The UWA Oceans Institute and School of Biological Sciences, The University of Western Australia, Great Southern Marine Research Facility, Albany, WA, Australia
[3] School of Natural Sciences, Macquarie University, NSW, Australia
[4] Australian Marine Mammal Centre, Australian Antarctic Division, Kingston, Tasmania, Australia
[5] Department of Biodiversity, Conservation and Attractions, Albany District, Albany, Western Australia
[6] Blue Planet Marine, Nelson, Aotearoa New Zealand
[7] New Zealand Department of Conservation – Te Papa Atawhai, Wellington, Aotearoa New Zealand
[8] Institute of Marine Sciences, University of Auckland – Waipapa Taumata Rau, Auckland, Aotearoa New Zealand
[9] Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, Seattle, WA, USA
[10] National Institute of Water & Atmospheric Research, Wellington, New Zealand
[11] Department of Biodiversity, Conservation and Attractions, Blackwood District, Western Australia
[12] Marine Science Program, Department of Biodiversity, Conservation and Attractions, Perth, WA, Australia
[13] Cooperative Institute for Climate, Ecosystem and Ocean Studies, University of Washington & Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA, Seattle, USA
[14] Marine Ecology and Telemetry Research & Cascadia Research Collective, Seabeck, USA

instruments or 'tags' are an increasingly important and commonly used tool, as they can collect and record information on location, dive profile, water temperature and other data over varying periods of time (e.g., Roquet *et al*., 2013; Izadi *et al*., 2018; Harcourt *et al*., 2019; Riekkola *et al*., 2019; Hindell *et al*., 2020). In the case of baleen whales, the only long-term tags that are able to collect such data over a period of weeks to months are the consolidated ('Type C') tags, which have electronics and retention elements in a single unit, and which are embedded in the body of the whale (Andrews *et al*., 2019).

The ethical use of such tags, as with any research tool, requires an understanding of the impact of tagging on individuals and populations, and how this compares to the benefit of information gained for improved management and conservation outcomes (McMahon *et al*., 2012; Andrews *et al*., 2019; Gulland *et al*., 2024). Impact can occur during the close boat approach needed for deployment, the deployment itself, the time period during which the tag is attached to the animal, as well as during the detachment and post-detachment phases (Andrews *et al*., 2019). Previous research has suggested that the close boat approach and deployment of satellite tags can elicit a short-term (0.5–3 min; see Noren & Mocklin, 2012) behavioural response in cetaceans, comparable with that of biopsy sampling, and that the behavioural response can be influenced by various physical and biological factors (Noren & Mocklin, 2012; Reisinger *et al*., 2014; Williamson *et al*., 2016). There has been no evidence of long-term behavioural responses to either tagging or biopsying in the few studies that have examined these questions (Tezanos-Pinto & Baker, 2011; Reisinger *et al*., 2014).

This study investigates the short-term behavioural responses to satellite tag deployment, typically with simultaneous biopsy sampling, on southern right whales (SRWs; *Eubalaena australis*) in Aotearoa New Zealand (hereafter New Zealand) and Australia. Tagging with consolidated tags was conducted on SRW wintering grounds at Maungahuka Auckland Islands, New Zealand (hereafter Auckland Islands) and in Western Australia. The aims of these satellite tagging projects include: (1) understanding SRW migratory movements (including interactions with human threats (e.g., shipping; Zhang *et al*., 2024); (2) identifying foraging grounds and behaviours; and (3) understanding potential overlap between distinct SRW populations on shared foraging grounds (Sprogis *et al*., 2023a; 2024). This work is part of a broader International Whaling Commission – Southern Ocean Research Partnership (IWC – SORP) project on understanding the relationship between foraging ecology, health and population recovery in SRWs. The short-term behavioural response of SRWs to satellite tag deployment is assessed in relation to factors, such as the close proximity required to deploy a tag (~1–5 m) and the behaviour of the whales prior to the close approach. The behavioural response to tagging is then compared with responses to biopsy sampling, which does not require such a close boat approach (~5–15 m), using a published dataset from the New Zealand population (Carroll *et al*., 2022; Riekkola *et al*., 2025).

MATERIALS & METHODS

Fieldwork

Data were collected in the New Zealand subantarctic Auckland Islands (Fig. 1) during the austral winter in August 2020, June/July 2021 and July 2022. New Zealand fieldwork was conducted under New Zealand Department of Conservation Permit 84845-MAR and Marine Reserve Act Permit 87513-MAR, which included consultation with the local Indigenous community (iwi Māori), and following University of Auckland Animal Ethics approved protocol 002072 to E. Carroll. Research efforts in the Auckland Islands were concentrated in Port Ross (Fig. 1), a sheltered and shallow harbour where southern right whales calve and socialise (Carroll *et al*., 2022). Whales were approached using small (≤ 5.5 m), rigid-hulled inflatable boats (RHIBs) each with a single ≤ 30hp four-stroke or two-stroke engine.

Data were collected at three locations in Western Australia: (1) Geographe Bay, Busselton, (2) Flinders Bay, Augusta, and (3) Cheyne Beach (Fig. 1) in September 2022 and August 2023. Fieldwork was conducted under appropriate licenses and approvals obtained under relevant state legislation, and in accordance with a Macquarie University animal ethics approved protocol (2022/006-4) to R. Harcourt. Data collection was conducted using Department of Biodiversity, Conservation and Attractions vessels, either a 6.1 m RHIB with two 90hp four-stroke engines, or a 6.52 m RHIB with two 115hp four-stroke engines.

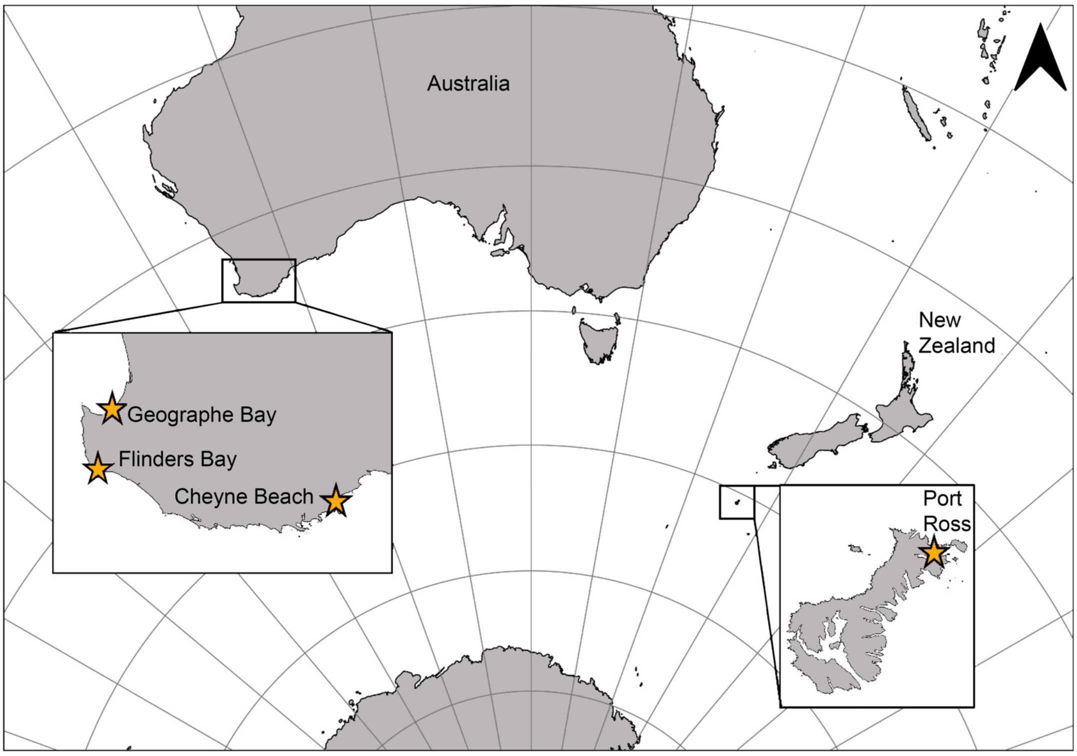

Figure 1. Map of tag deployment locations in Western Australia (Geographe Bay, Busselton; Flinders Bay, Augusta, Cheyne Beach) and in Auckland Islands, New Zealand (Port Ross).

Initial assessment of pre-approach behaviour was done by consensus among all observers onboard the vessel from a distance of approximately 300 m, with continued monitoring of the whale and its behaviour during the slow, steady approach. Pre-approach behaviours were the same as reported in Carroll *et al*. (2022):

(1) Logging: whale is resting at the surface, only moving slightly to breathe.

(2) Travelling: directional forward movement that resulted in change of location.

(3) Socialising: two or more adults interacting at the surface (physical interaction).

(4) Milling: movement that is not directional in nature.

If the whale being approached exhibited clear avoidance behaviour to the approaching vessel (e.g., repeated diving and surfacing away from the vessel, high-speed swimming away from the vessel), the encounter was terminated either by stopping the boat and allowing the whale to move away or by slowly manoeuvring the boat away from the whale. Such encounters and responses were not recorded in this study.

If the whale did not exhibit avoidance behaviour, a close vessel approach (< 25 m) and tagging encounter were considered initiated, and data were collected following previously described methodology (Carroll *et al*., 2022). At all sites, close vessel approaches to whales were conducted at no-wake speeds (< 5 knots), with a consistent course and speed and very few or no gear changes. Data collected included the date, time, location (GPS position), demographic class (unaccompanied adult, or cow with a calf) and pre-approach behaviour of the whale. Cows were defined as individuals in close proximity to a calf, which was less than half the length of the accompanying adult (Van Waerebeek *et al*., 1998; Carroll *et al*., 2011a). All other animals were considered unaccompanied adults, as classifying juveniles or sub-adults can be difficult due to the fact that right whales can reach 75% of their adult length in the first year of life (Fortune *et al*., 2012).

Fully integrated, consolidated (Type C, Andrews *et al*., 2019) Wildlife Computers' (Redmond, Washington, USA) SPOT-372 and SPLASH10-373 Argos satellite tags (n = 40, Fig. 2, Annex 1, Zerbini *et al*., 2025) were deployed on mature animals (identified based on the relative size of head vs. body, and length relative to the vessel on

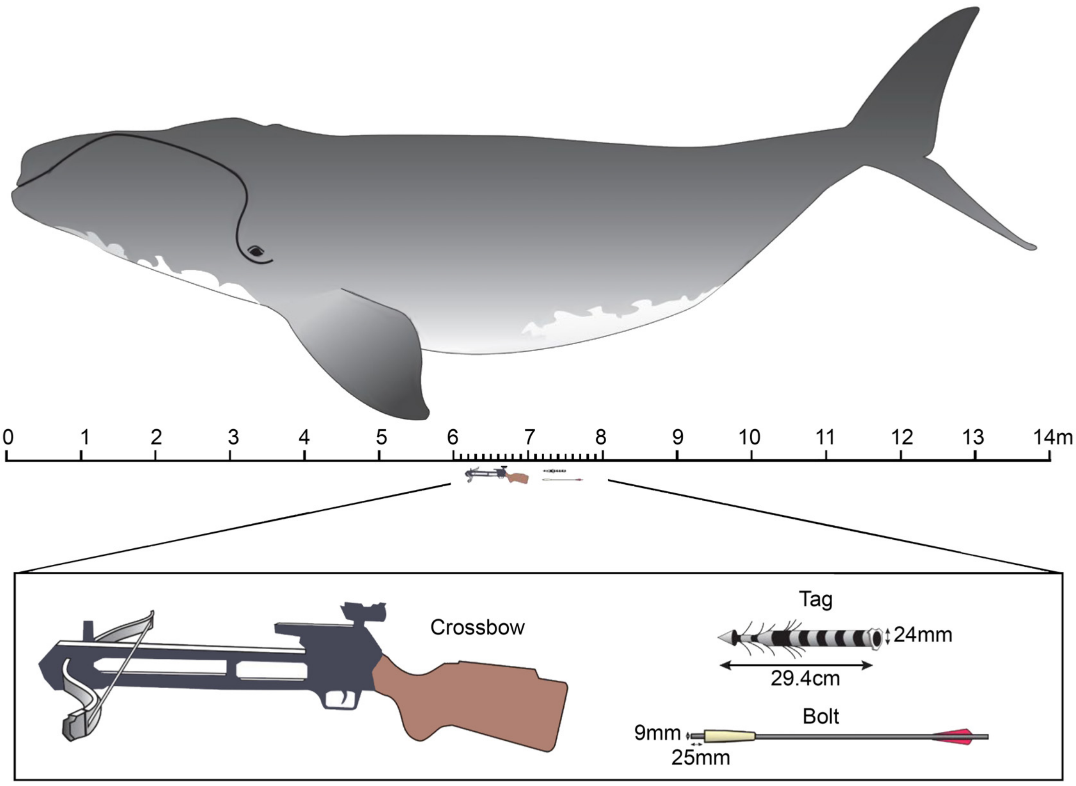

Figure 2. Relative length of the biopsy equipment (crossbow and bolt) and a satellite tag (29.4 cm, and 390 grams), to each other and to an adult southern right whale (Christiansen *et al*., 2023). Dimensions of the satellite tag and the biopsy tip are shown. Note: this figure is of a ~12 m long adult whale (length measured from the tip of the head to fluke notch).

close approach) that were in excellent body condition (i.e., with well developed 'fat rolls'; Pettis *et al*., 2004). In New Zealand, tag deployment was conducted from the bow of a RHIB, typically at distances ranging from 1–5 m, using a custom-modified pneumatic line thrower (ARTS system: Heide-Jørgensen *et al*., 2001) set at a pressure of 12–14 bar. In Australia, tagging was conducted from the bow/front deck of the vessel in 2022, and from a specially designed tagging bowsprit in 2023 (~1 m raised above water level).

The tags are designed to penetrate beneath the skin and hypodermis (up to a maximum of 290 mm) and anchor at or below the blubber-muscle interface (Tormosov *et al*., 1998; Moore *et al*., 2001; Miller *et al*., 2011) to facilitate long-term (> 3 month) durations. Tags were deployed on the whale's dorsum, to the left or right and just behind the post blow-hole fat roll. The target location for tag placement near the dorsal midline of the body, rather than the flank, minimises tissue responses from a body-penetrating device and allows for better transmissions due to the whales' tendency to float low on the water (Moore & Zerbini, 2017; Gulland *et al*., 2024).

At the time of deployment, the tagger visually estimated the distance (typically ~3 m) between themself and the whale, as well as the percentage of tag implantation based on the length of the tag visible outside the skin (e.g., 100% tag implantation indicates that the tag is fully inserted into the whale up to the stopper; see Annex 2). Tagger identity varied across the field seasons (total of three taggers across New Zealand and Australia), which may have introduced some variability in the parameters estimated at the time of tagging. Two independent and experienced researchers evaluated tag placement post-hoc using photos and videos of the tag deployments. The vertical (dorsal/upper flank or lateral/lower flank) and horizontal (anterior, central or posterior) position of the tag in the body of the whale was categorised following Zerbini *et al*. (2023). There were a small number of discrepancies (n = 4 out of 40 tag placements) in the tag placement assignment that occurred when placement was ambiguous between categories that were then arbitrated by a third experienced SRW researcher (see Annex 1).

During each satellite tagging encounter, attempts were made to simultaneously collect skin biopsy samples to genetically determine the sex and uniquely identify the tagged individuals. Biopsy sampling was conducted concurrently with tagging when possible to minimise boat approaches and reduce disturbance. The biopsy sampler targeted a region caudal to the tag target site to avoid interfering with the tag deployment. Small (20–25 mm length, 9 mm diameter), stainless steel biopsy darts were used, deployed from a crossbow or a modified veterinary capture device (PAXARM; Lambertsen, 1987; Krützen *et al*., 2002), following previously published methodologies (Patenaude *et al*., 1998; Riekkola *et al*., 2025). Skin samples were stored in 95% ethanol and/or frozen in the field and transported to the University of Auckland for analysis. DNA was extracted using either the DNeasy kit (Qiagen) or standard proteinase K digestion and phenol/chloroform methods (Sambrook *et al*., 1989). The sex of each sampled whale was identified by amplification of the male-specific SRY gene, multiplexed with an amplification of the ZFY/ZRX region as a positive control (Aasen & Medrano, 1990; Gilson *et al*., 1998).

Analysis of behavioural response to satellite tagging

Whales' behavioural responses were recorded immediately after a satellite tag deployment as a number ranging from 1–4 (Table 1; Weinrich *et al*., 1992; Noren & Mocklin, 2012). All statistical analyses were conducted in *R* version 4.2.1 (R Core Team, 2022) using *R* packages (denoted in italics below). First, the mode and range of behavioural responses to tagging were summarised for New Zealand and Australian whales separately. Subsequently, the response distributions were tested for significant differences between the two regions using a chi-square test for ordinal data (*coin*; Hothorn *et al*., 2006) to determine whether the data could be analysed in combination.

The response to tagging was then tested for association with the following explanatory variables: field site (New Zealand or Australia), vessel type, tagger identity, whale demographic class and sex, behaviour of whale prior to boat approach (pre-approach behaviour), distance from whale to tagger at tag deployment (deployment distance), tag implantation percentage at deployment (implantation %) and location of tag placement.

In analyses, the variable 'field site' likely encompassed various field conditions, such as the different vessels used, environmental conditions and timing in the migration (e.g., beginning to end of the breeding season). As the 'field site' variable is likely correlated with vessel type and tagger identity, these three variables were fitted individually in separate models to ensure model parameters were as independent as practical. The impact of different explanatory variables on model fit was evaluated using the Akaike Information Criterion (AIC), whereby the candidate model with the lowest AIC score was retained. Similarly, sex and demographic class are linked (e.g., cows are assumed female) and were fitted in separate models and compared. The analyses were conducted using ordinal logistic regressions using *MASS* (Venables & Ripley, 2002) and goodness of fit was assessed using Pearson's chi-squared test in *gofcat* (Ugba, 2022) given the relatively small sample size.

Table 1

Definitions of cetacean short-term behavioural response categories to satellite tag deployment and biopsy-only sampling, derived from Noren & Mocklin (2012).

Behavioural response category	Description
1 – No response	Animal continues pre-biopsy behaviour with no detectable change.
2 – Low/weak response	Brief and mild change in behaviour (e.g., startle, dive, acceleration, small tail flick).
3 – Moderate response	More forceful, but not prolonged response (e.g., moderate swimming, single tail flick or slap, breaching, trumpet blow).
4 – Strong response	Succession of forceful activities (e.g., breaches, multiple tail flicks or slashes, numerous trumpet blows, fast swimming).

Comparison of behavioural response to satellite tagging and biopsy-only sampling

During all field seasons, biopsy samples and associated data were collected for population monitoring purposes (e.g., for assessing population abundance, genetic diversity, animal culture or foraging ecology; Carroll *et al*., 2011b; 2013; 2015; 2022; Derville *et al*., 2023), and the whales' responses to biopsy-only sampling were recorded using the response categories reported in Table 1. Biopsy-only response data from 748 biopsy sampling events (excluding biopsies of the tagged whales) conducted in Port Ross (Auckland Islands) have been presented in Riekkola *et al*. (2025). This analysis showed that behavioural response to biopsy sampling was significantly impacted by pre-approach behaviour and a combined demographic class/sex variable (i.e., calf, cow, adult-female, adult-male).

Simultaneous data collection provided the opportunity to test the hypothesis that the short-term behavioural response to satellite tagging (with the simultaneous biopsy sampling, hereafter 'tagged') was significantly different to that of biopsy-only sampling, while accounting for pre-approach behaviour, whale demographic class/sex, as well as the different sample sizes of the two approaches (for New Zealand data only). Specifically, the responses of adult males were examined, which was the demographic class with the largest sample size of all tagged whales (n = 12). Due to the difference in sample sizes between tagged and biopsy-only individuals, the biopsy-only dataset was subsampled. To account for the significant effect of pre-approach behaviour, 100 biopsy encounters of adult males were randomly selected (with replacement) while maintaining the same proportion of pre-approach behaviours as for the adult male whales that had been satellite tagged. The mode and range were calculated for each dataset, and then the tagging and biopsy-only datasets were tested for statistically significant difference in response intensity using a chi-square test for ordinal data.

RESULTS

Satellite tagging data summary

A total of 25 tag deployments from New Zealand and 15 from Australia had complete field data and were included in the analysis. Behavioural response (both mode and range of the response category) to tagging varied between the field sites: mode = 3 (range = 1–3) for New Zealand and mode = 2 (range = 1–4) for Australia (Fig. 3). The distribution of the behavioural response data was not significantly different between the two field sites (ordinal chi-square = –0.23, p = 0.86) and so the datasets were combined for further analyses.

Figure 4 shows the distribution of the characteristics of tagged whales and potential explanatory variables used in the ordinal logistic regression analyses. The most common demographic class was 'unaccompanied adult' (85%). Genetic sex identification was possible for 28 of 40 whales (70%), with 14 females (including four cows and 10 unaccompanied adults) and 14 males (all unaccompanied adults) tagged. The most common pre-approach behaviour was logging (55%), followed by socialising (30%). The estimated distance of deployment ranged from 1 to 7 m, with a mean of 3.3 m (SD = 1.8 m). Implantation percentage was recorded to be 100% in 27 (68%) of the 40 deployments, with a minimum value of 50% and a mean of 94% implantation (SD: 12%, median: 100%; Annex 2).

There was a non-significant negative relationship between deployment distance and the percent tag implantation into the whale (Pearson correlation coefficients R = –0.21, p = 0.19; Fig. 5A). There was no significant difference in deployment distance based on pre-approach behaviour (Kruskal-Wallis test chi-squared = 1.66, df = 3, p-value = 0.65; Fig. 5B). Pairwise comparisons using Dunn's test indicated that deployment distance was significantly closer for deployments with a response category 3 compared to response category 1 (p = 0.01). No other differences between deployment distance and response intensity were statistically significant (Fig. 5C).

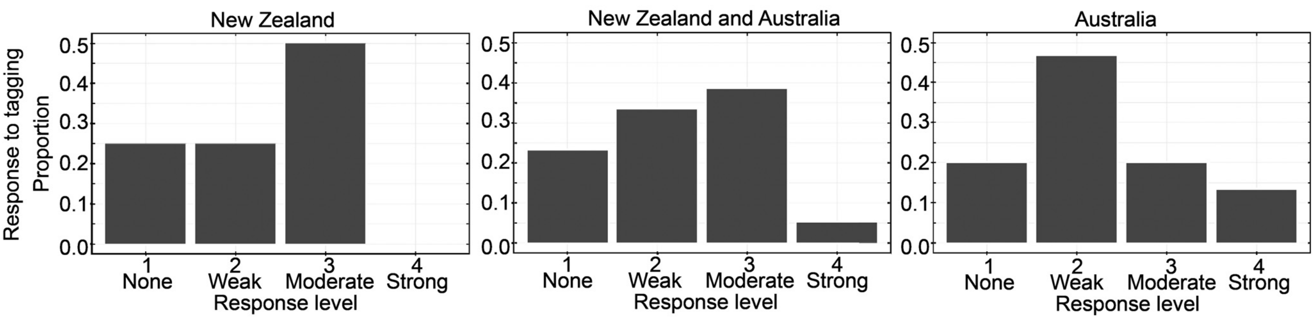

Figure 3. Proportion of responses to tagging (and simultaneous biopsy sampling) for New Zealand (n = 25), Australian (n = 15), and pooled New Zealand and Australian (n = 40) southern right whales.

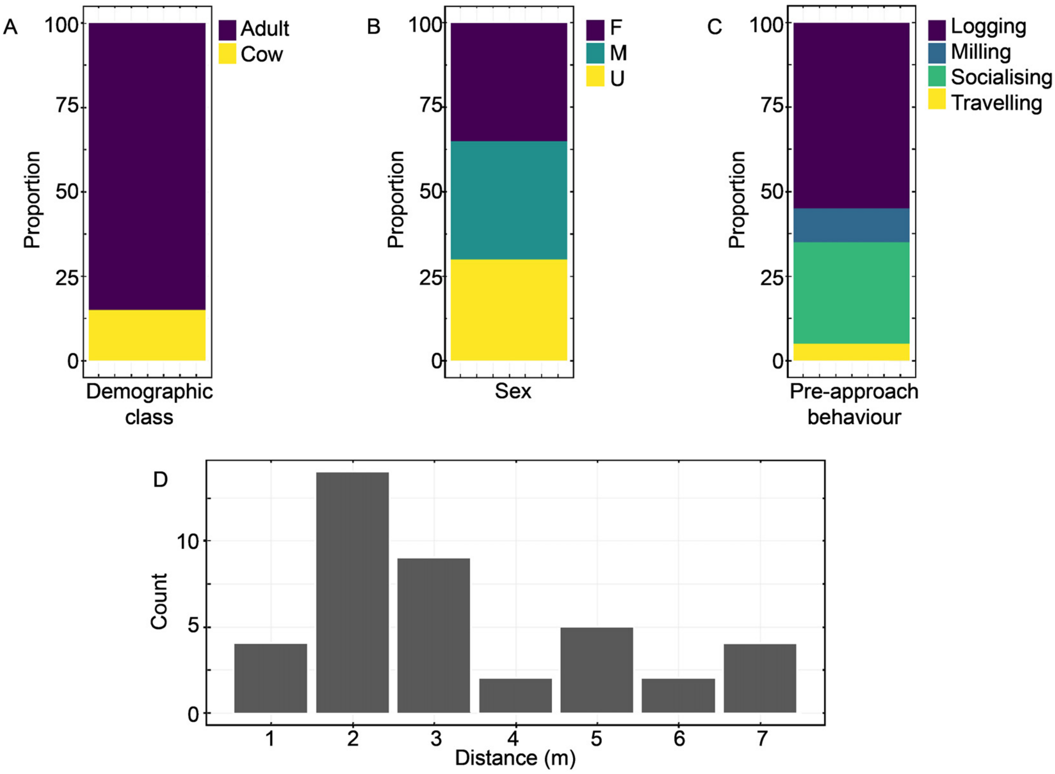

Figure 4. Summary of encounter and deployment characteristics of the 40 tag deployments made on New Zealand and Australian southern right whales. A–C shows proportion of deployments by demographic class (A), genetically identified whale sex (B, F: female; M: male; U: unknown), and pre-approach behaviour (C). Panel D shows the distribution of estimated distances between the whale and the tagger at time of tag deployment.

Ordinal logistic regression analyses

Video and/or photographic footage to assess tag placement post-hoc was not available for n = 5 cases (Annex 1). Given the already small sample size, the first modelling steps were conducted without the tag placement variable to avoid additional loss of data points. Based on AIC scores, the candidate model with the 'tagger identity' covariate fit the data better than candidate models with 'field site' or 'vessel type'. In addition, candidate models with 'demographic class' fit the data better than those with 'sex'. Demographic class and the percentage of tag implantation did not have statistically significant impacts on the behavioural response elicited by tagging and were therefore excluded from further analyses. Tagger identity showed a marginal significance ($p = 0.07$) and was retained. The final model was fitted both with and without the tag placement variable to assess its impact. Regardless of its inclusion, tagger identity did not have a statistically significant impact on the behavioural response (Table 2).

The final ordinal logistic regression model indicated that pre-approach behaviour, tag placement and distance of deployment had a significant effect on the intensity of tag response (Table 2). Compared with logging animals, whales that were milling, socialising or travelling were 52–100% less likely to show a stronger response to a tagging event, however the only statistically significant difference was between logging and travelling animals. Out of the 35 cases where tag placement could be assessed, it was categorised to be on the anterior dorsal ('AD') section of the whale in 27 (77%) cases, followed by central dorsal ('CD', n = 6, 17%), and anterior lateral ('AL', n = 2, 6%), with no instances of central lateral placement. Only the difference between AD and CD placements was significant ($p = 0.05$), whereby tags in the central dorsal placement elicited a significantly elevated behavioural response compared with tags deployed on the anterior dorsal side. In addition, for every 1 m increase in distance at deployment, there was a 78% decrease in response to tagging.

The effect of tagger identity was not statistically significant, however the large estimated-effect-size reflected a combination of small sample size and differing variability in responses between taggers. Specifically, tagger A

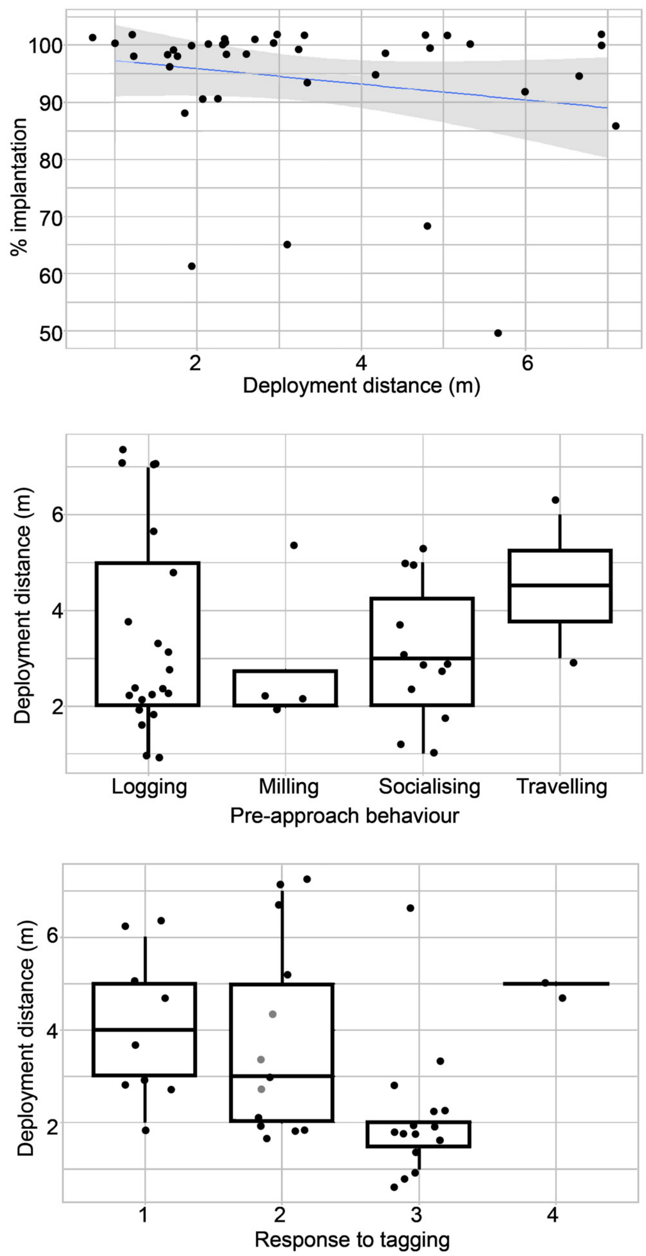

Figure 5. Relationship between satellite tag deployment distance and (A) percent tag implantation, (B) pre-approach behaviour and (C) response to tagging. The data are plotted with 'jitter,' i.e., by adding a small amount of variation to the position of each point along both axes to reduce overplotting.

deployed only three tags, all of which elicited a response of category 3, whereas tagger B's deployments were associated with greater variability in recorded responses (range: 2–4, SE = 2.34). As the model estimates the odds of a response being at or above each reaction level relative to the reference group, in this case tagger A, the higher number of stronger responses (scores of 3 and 4) associated with tagger B resulted in elevated odds of higher reactions.

Comparison of tag and biopsy responses

The behavioural response of adult male SRWs in New Zealand to tagging was compared with biopsy-only response data previously reported by Riekkola *et al*. (2025). Prior to the tag deployment approach, 58% of the tagged adult males were logging, 8% were milling and 33% were socialising (New Zealand data only, n = 12). To control for the effect of pre-approach behaviour in our comparison, which significantly influenced behavioural response

Table 2

Factors influencing the behavioural response to tagging in southern right whales in New Zealand and Australia as identified by ordinal logistic regression modelling. Sample size (N), log odds ratios (LogOR), effect sizes (back-transformed through the exponential function) and significance (p-value – bold when significant) are reported. For categorical variables, one level of the variable was used as the basis ('–' in the table) to which all other levels (in italics) were compared. Deployment distance was modelled as a continuous variable.

Explanatory variable	Level	N	Log(OR)	Effect size	p-value
Tagger identity	Tagger A	3	–	–	–
	Tagger B	8	2.90	+1710%	0.22
	Tagger C	29	–1.71	–82%	0.29
Pre-approach behaviour	Logging	22	–	–	–
	Milling	4	–1.38	–75%	0.29
	Socialising	12	–0.73	–52%	0.41
	Travelling	2	–16.89	–100%	**0.00**
Deployment distance (m)		40	–1.50	–78%	**0.00**
Tag placement	Anterior dorsal	27	–	–	–
	Anterior lateral	2	0.00	0%	1.00
	Central dorsal	6	3.17	+2280%	**0.05**

intensity to both tagging (Table 2) and biopsying (Riekkola *et al*., 2025), 100 biopsy encounters were randomly selected to match these proportions of pre-approach behaviours.

The biopsy and tagging datasets for adult male SRWs (New Zealand data only) showed some differences in the distribution of responses. Biopsy sampling had a peak (mode) in responses in category 2 (mean = 2.5) and several category 4 responses, the latter of which were not present in the tagging group (Fig. 6). In comparison, the tagging group showed a right skewed distribution with a peak (mode) in response category 3 (mean = 2.33; Fig. 6). Ordinal chi-square test showed there was a statistically significant difference between the response distributions of tagged vs. biopsied whales (p-value = 0.03), likely reflecting the difference in modes. The influence of distance of deployment on behavioural response was not able to be accounted for, as these data were not available for the biopsy-only response data.

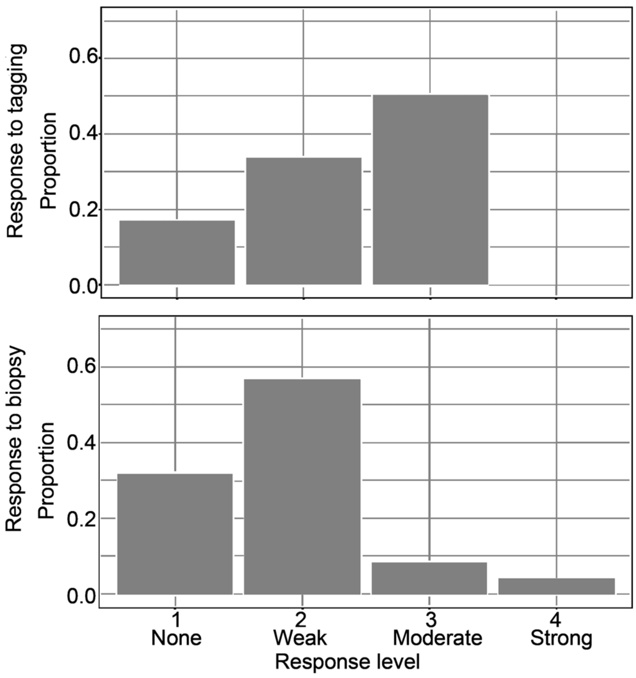

Figure 6. Comparison of responses to tagging (n = 12) and biopsy for adult male southern right whales (New Zealand only). For biopsy response, 100 biopsy encounters with adult males were randomly selected that had the same proportion of pre-approach behaviours as for the adult male whales that were satellite tagged (biopsy response data from Riekkola *et al*., 2025).

Table 3

Summary of genetically identified whales that were biopsy sampled one or more times at separate encounters to tagging.

Individual	Sex	Demographic class	Pre-approach behaviour	Tag/biopsy-only	Response	Date dd/mm/yy
A	M	Adult	Social	Biopsy	1	02/08/20
			Milling	Tag	1	17/08/20
B	M	Adult	Logging	Biopsy	2	15/07/21
			Social	Tag	2	16/07/21
C	M	Calf	Milling	Biopsy	3	17/08/20
		Adult	Logging	Tag	3	21/07/21
D	F	Adult	Social	Biopsy	2	08/07/22
			Milling	Tag	2	11/07/22
			Milling	Biopsy	1	12/07/22
E	M	Adult	Logging	Biopsy	1	14/07/21
			Social	Biopsy	2	17/07/21
			Logging	Tag	3	18/07/21

Anecdotally, genetic identification further revealed that, out of all the tagged whales, five individuals were biopsy sampled at separate encounters to tagging (Table 3). The time difference between tagging and biopsy-only events ranged from one to 338 days. Three male whales had the same response at both tagging and biopsy-only encounters, one female had a category 2 response to tagging and categories 1 and 2 to biopsy, while another male whale had a milder reaction (category 1 and 2) when biopsied compared to tagging (category 3; Table 3).

DISCUSSION

Satellite tagging is an essential research tool that provides important information on migratory movements and foraging behaviour of cetaceans with insights for conservation and management (e.g., Reisinger *et al*., 2022). Here information is provided on the short-term behavioural responses of SRWs to satellite tagging with simultaneous biopsy sampling off New Zealand and Australian wintering grounds, showing that most short-term behavioural responses to tagging were weak to moderate. For the New Zealand wintering ground, results show that the behavioural responses to tagging and biopsy-only sampling were not substantially different when controlling for demographic class and pre-approach behaviour, and in some cases for the individual whale.

The short-term behavioural response of New Zealand and Australian SRWs to tag deployment was typically a weak to moderate response, based on the standardised response scale of Noren & Mocklin (2012). While this methodology is best-practice for evaluating short-term behavioural responses in cetaceans, ongoing technological and methodological developments should be monitored to enable more detailed measurement of the behavioural and physical impact of tagging. For example, monitoring physiological responses through external tags, drones or developments to the tags themselves may be possible in future to more accurately measure impact (e.g., Gulland *et al*., 2024; Kennedy *et al*., 2024; Yaney *et al*., 2025, McKnight *et al*., 2025, Zerbini *et al*., 2025). The majority of tags were deployed on the anterior dorsal section of the whale, which elicited the weakest short-term behavioural response. Anterior dorsal tag placement might also be recommended, as it is likely to improve transmissions (by allowing the tag to remain above water when the whale is lying low), and minimise tissue responses to a body-penetrating device, as suggested in previous studies (Moore & Zerbini, 2017; Gulland *et al*., 2024). However, it is not yet clear how these factors contribute to the quality of data collected, which is essential for making informed conservation decisions. Furthermore, due to the small and uneven sample sizes in this study, further investigation is required to confirm the effect of tag placement on short-term behavioural response (e.g., the stronger response to central dorsal placement).

Closer boat approaches (as characterised by distance at tag deployment) elicited significantly stronger behavioural responses. Whales whose pre-approach behaviour was logging (resting) exhibited stronger responses than whales who displayed other behaviours. Logging whales (55% of tagged individuals) and small social groups were preferentially approached due to an expectation that these behaviours could increase the chance of reaching the optimal deployment distance compared with other behaviours. However, no pre-approach behaviour (e.g., logging) was shown to enable a closer tag deployment distance.

It has been suggested that the increased response intensity due to pre-approach behaviours characterised as resting (e.g., logging) and tagging distance are related to the close boat approach, at least partly due to the associated underwater boat noise. For example, SRW cow-calf pairs are recorded to react to boat approaches from more than 1 km away (Barrett, 2000; Sprogis *et al*., 2023b), and louder vessel noise has been found to elicit significant behavioural changes (e.g., decrease in resting, and increase in swim speed) in humpback whales (*Megaptera novaeangliae*; e.g., Sprogis *et al*., 2020). The boat approaches for tagging SRWs were typically conducted at slow and consistent speeds with a constant heading to avoid gear changes or other acoustic disturbances that might elicit a behavioural response from the whale. However, noise levels would still have increased as the boat moved closer to the whale. Furthermore, in the field, it was noted that whales often began reacting shortly before the tag deployment or biopsy attempt. It is therefore likely that the whales were responding to the proximity and noise of the approaching boat rather than the tagging and/or biopsy. For example, Williamson *et al*. (2016) showed that close boat approaches may cause small, temporary behavioural changes in humpback whales, with changes being greater and longer lasting in cow-calf groups, while other studies have found that humpback whale cows showed a stronger reaction to boat approaches compared to actual biopsy sampling (Clapham & Mattila, 1993; Garrigue & Derville, 2022). It may also be that, in logging whales, a behavioural response to disturbance is obvious, i.e., the whale begins swimming in response to the close boat approach rather than continuing to log on the surface (Sprogis *et al*., 2020).

Previous studies have reported similar findings to these, with resting humpback whales (Cantor *et al*., 2010) and northern bottlenose whales (*Hyperoodon ampullatus*; Hooker *et al*., 2001) exhibiting the greatest response to biopsy sampling. It is likely that logging individuals were sleeping or otherwise relaxed and were woken up or startled by the sudden disruption of the close boat approach or by the physical contact arising from tagging (or biopsy sampling), thus eliciting a strong startle response or a more obvious shift in behavioural state (e.g., from logging to travelling). As tags were deployed with a consistent 14 bar of pressure regardless of tagging distance, an additional factor might be that the closer the tagger was to a whale, the more forcefully the tag struck the whale. The same would apply to a simultaneous biopsy dart shot from a crossbow, whereas the pressure can be easily adjusted to account for different distances when using other biopsy systems, such as the PAXARMS system.

Although the negative relationships between percentage tag implantation and deployment distance, and between reaction intensity and deployment distance, were statistically non-significant, researchers must weigh the trade-offs associated with varying deployment distances. While deploying tags from a greater distance may reduce the immediate behavioural response of the whale, it raises the risk of a missed shot or a partially implanted tag with a shorter deployment duration (as the body expels the foreign-body; e.g., Mate *et al*., 2007). Given that satellite tagging inherently disturbs the whale and involves penetrating the skin and blubber, it is essential to ensure that the data obtained justify such impacts. A partially implanted tag could cause a similar short-term behavioural disturbance and potential for pathogen entry as a fully implanted one, without the benefit of long-term data collection.

SRW behavioural responses to tagging were compared with biopsy-only sampling in the New Zealand population while controlling for variables found to affect response intensity: pre-approach behaviour, and demographic class/sex (in the case of biopsy response; Riekkola *et al*., 2025). The mode for tag response was slightly higher in adult males (three, compared with two for biopsy, albeit with similar means) and the distribution of behavioural responses were statistically different, consistent with a closer approach and likely more forceful impact of the tagging method. While the strongest reactions in the New Zealand dataset occurred with biopsy-only sampling, this could be due to the greater sample size for biopsies, and the low overall incidence of strong reactions. The results of comparing tagging and biopsy-only responses were similar if there was no control for sex and demographic class, and, instead, the responses of all adult whales (i.e., males and females, but excluding 'cows'; Annex 3) were examined. Unfortunately, it was not possible to compare satellite tagging and biopsy-only sampling while accounting for distance at deployment – a significant determinant of behavioural response to tagging – as these data were not recorded for biopsy-only sampling. However, given the average distance for tagging was 3.3 m (2 m being the most common deployment distance), while biopsy-only sampling typically occurs at 5–15 m, (Riekkola *et al*., 2025), the closer distance between boat and the whale likely explains the slightly stronger response to tagging compared with biopsy.

While response to tagging and biopsying are not analogous due to the difference in required approach distance and methodological approach, it is interesting to note that four whales that were biopsy sampled at separate encounters to tagging showed the same response at each encounter. Our results therefore suggest that, while satellite tagging is undeniably more invasive, it does not necessarily elicit a stronger short-term behavioural response than biopsy-only sampling, and that some individuals may be more sensitive and reactive than others. This is similar to the findings of Reisinger *et al*. (2014) in a study on killer whales (*Orcinus orca*), which found that, while there were slightly stronger reactions to tagging than biopsy-only sampling, the type of sampling (tagging vs. biopsying) was not a significant determinant in whether a whale responded or not.

This study only assessed short-term behavioural responses to tagging, in comparison with biopsy sampling. Wound healing or longer-term impacts directly of either biopsy or tagging were not able to be investigated, and despite recommendations (Andrews *et al*., 2019), little information is available from tag development on their likely physical impacts (although see Mate *et al*., 2007; 2017; Gulland *et al.*, 2024; Zerbini *et al*., 2025). Previous research suggests that biopsy sampling wounds heal over within 24 hours for cetaceans (Funasaka *et al.*, 2024) and are completely healed within a few weeks to months (Weller *et al*., 1997; Jefferson & Hung, 2008). Evaluation of drone-based photogrammetry photos of SRWs from the Auckland Islands did not show any evidence of skin lesions, wounds or other anomalous skin presentations that could be linked to biopsy or tagging (Carroll *et al*., 2022). Furthermore, there is no evidence of long-term impact of tagging on SRW survival or reproductive output in South Africa (Best & Mate, 2007; Mate *et al*., 2011; Best *et al*., 2015) or SRW body condition and reproduction in Australia (Charlton *et al*., 2023).

Long-term follow up studies at our research sites, in particular Auckland Islands, are hindered by their remoteness and resulting logistical difficulty and cost of conducting fieldwork. Research into the impacts of tagging other marine mammal species is more advanced. Recently, Gulland *et al*. (2024) showed that long-term effects at the tag site were minimal in 72 humpback whales resighted, on average, three years after tagging. While there have been concerns that rigid, implanted devices that span the cetacean blubber muscle interface where the muscle moves relative to the blubber could have negative health impacts (Moore *et al*., 2013), the use in this study of a recently developed integrated tag design (Zerbini *et al*., 2025) substantially reduces the chance of negative tag site outcomes compared with non-integrated tags (Gulland *et al*., 2024). Non-integrated tags have been associated with long-term swelling in one tagged Australian SRW (1,446 days post-tagging; Charlton *et al*., 2023), however this whale did not have significantly different body condition metrics than non-tagged whales of the same demographic class and population. Studies using different tag types, such as Reisinger *et al*. (2014) found no evidence of mid (1 month) or long-term (< 24 months) behavioural changes in killer whales due to tagging. While Burek-Huntington *et al*. (2023) reported cases of beluga whales (*Delphinapterus leucas*) with tag wounds whose infection may have been a factor in that whale's death, this could not be conclusively determined. Similarly, one of the Australian SRWs tagged in this study was found dead 12 days after tag deployment. Without a comprehensive necropsy to examine the carcass, the cause of death was deemed inconclusive, but the circumstances of the event were consistent with a ship-strike (see Harcourt *et al*., 2025 for the full report). Another Australian SRW tagged in 2024, though its data are not part of this study, also subsequently died with cause of death inconclusive. However, this 2024 whale had a fractured skull and no major pathology, and vessel strike could not be ruled out in this case either (R. Harcourt, unpublished data). However, as invasive tags will always present at least some level of risk to the tagged animal, rigorous best practice efforts (e.g., Andrews *et al*., 2019; DCCEEW, 2025) should be followed and continuous efforts should be made towards understanding medium and long-term impacts.

CONCLUSION

Satellite tagging allows researchers to gain important information on whales over extended periods of time in vast and remote oceanic regions where direct observations are difficult or not possible. Yet, the ethical use of any tags which require a close boat approach that may disturb the whales, and which may or may not penetrate into a whale's body, necessitates a thorough understanding of the impacts on individuals and populations compared to the benefits gained for improved management and conservation outcomes. This study provides insight into one facet of the impact: short-term behavioural response. Such responses of SRWs to tagging using 'Type C' consolidated tags (Andrews et al., 2019) were mild, and similar to the responses to the less invasive biopsy sampling. Furthermore, deployment distance, or more accurately, the closeness of the boat approach, was an influential factor of short-term responses. This suggests that recommendations to minimise impact to whales should recognise the trade-offs between deployment distance and deployment accuracy and duration. However, these results may not be applicable to all whale populations or species, given that differential responses to biopsy sampling have already been recorded between species, populations and demographic classes (Weinrich et al., 1991; Brown et al., 1994; Gauthier & Sears, 1999; Reisinger et al., 2014; Garrigue & Derville, 2022). Similarly, 'Type C' tags are not suitable for all species, highlighting the importance of conducting case-by-case studies of tag impacts. Given the increasing use of tagging technologies to study marine mammals, monitoring of both short- and long-term responses to tagging should therefore continue, and be conducted on a range of species. Furthermore, the development and use of standard procedures for recording behavioural responses could help facilitate cross-population comparisons.

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Supplementary Material

ANNEX 1

Complete field data records used for analysing short-term behavioural responses of southern right whales to satellite tagging

Relevant metadata:

- Date: formatted as dd/mm/yyyy
- Field site: NZ = New Zealand, Auckland Islands, AU = Western Australia
- Vessel: During the first field season in New Zealand (2020), there was an engine failure with the four-stroke small boat engine, and a back-up two-stroke engine was used. This issue was rectified prior to the next field seasons when only the four-stroke engine was used.
- Sex: F = female, M = male, U = unknown (no biopsy sample, or sex identification was unsuccessful)
- Deployment distance in meters (m)
- % tag implantation: the tag is approximately 29.4 cm long. For reference on the scale, see Figure 2 in the main text. See Annex 2 for example images of different implantation percentages
- Tagger identity: represents three individuals (A, B and C) – real initials not used
- Tag placement: NA = no video/photo material to review; A = anterior; C = central; D = dorsal; L = lateral

Table S1

Date dd/mm/yy	Field site	Vessel	Demographic class	Sex	Pre-approach behaviour	Tag number	Deployment distance	% tag implantation	Tagger identity	Tag placement	Behavioural response category
05/08/20	NZ	Black Betty_25 hp_4stroke	Adult	U	Logging	203575	2	90	C	NA	3
05/08/20	NZ	Black Betty_25 hp_4stroke	Adult	U	Logging	203573	3	100	C	AD*	3
07/08/20	NZ	Black Betty_25 hp_4stroke	Adult	U	Logging	203572	2	100	C	AD	2
07/08/20	NZ	Black Betty_25 hp_4stroke	Adult	U	Milling	205015	2	100	C	AD	2
07/08/20	NZ	Black Betty_25 hp_4stroke	Adult	U	Logging	203571	1	100	C	AD	3
17/08/20	NZ	Black Betty_25 hp_4stroke	Adult	M	Milling	203574	2	95	C	AD	1
16/07/21	NZ	Black Betty_25 hp_4stroke	Adult	M	Socialising	215259	3	100	C	AD	2
17/07/21	NZ	Black Betty_25 hp_4stroke	Adult	M	Socialising	215262	2	100	C	AD	2
17/07/21	NZ	Black Betty_25 hp_4stroke	Adult	M	Socialising	215258	1	100	C	AD	3
18/07/21	NZ	Black Betty_25 hp_4stroke	Adult	M	Socialising	215261	1	100	C	AD	3
18/07/21	NZ	Black Betty_25 hp_4stroke	Adult	M	Socialising	46955	2	100	C	AD	3
21/07/21	NZ	Black Betty_25 hp_4stroke	Adult	M	Logging	215263	2	100	C	AD	3
21/07/21	NZ	Black Betty_25 hp_4stroke	Adult	M	Logging	46950	2	90	C	AD	3
21/07/21	NZ	Black Betty_25 hp_4stroke	Adult	M	Logging	212499	2	100	C	AD	3
21/07/21	NZ	Black Betty_25 hp_4stroke	Adult	U	Logging	46635	2	60	A	AD	3
21/07/21	NZ	Black Betty_25 hp_4stroke	Adult	F	Logging	212500	2	100	A	AL	3
25/07/21	NZ	Black Betty_25 hp_4stroke	Adult	U	Logging	46633	2	90	A	AD	3
07/07/22	NZ	Black Betty_25 hp_4stroke	Adult	M	Logging	235400	3	100	C	NA	1
07/07/22	NZ	Black Betty_25 hp_4stroke	Adult	M	Travelling	235403	3	95	C	AD	1
08/07/22	NZ	Black Betty_25 hp_4stroke	Adult	M	Socialising	235402	3	100	C	AD	1
10/07/22	NZ	Black Betty_25 hp_4stroke	Adult	F	Socialising	235401	4	95	C	AD	1
10/07/22	NZ	Black Betty_25 hp_4stroke	Cow	F	Socialising	235404	5	100	C	AD	1
11/07/22	NZ	Black Betty_25 hp_4stroke	Adult	F	Logging	197853	2	100	C	AD	2
11/07/22	NZ	Black Betty_25 hp_4stroke	Adult	F	Milling	235399	2	100	C	AD	2
12/07/22	NZ	Black Betty_25 hp_4stroke	Cow	F	Logging	208742	6	90	C	CD**	1
08/09/22	AU	Leeuwin_90hp_4stroke	Cow	F	Logging	235621	7	100	B	CD	2
09/09/22	AU	Leeuwin_90hp_4stroke	Adult	F	Logging	235410	7	100	B	CD†	2
09/09/22	AU	Leeuwin_90hp_4stroke	Cow	U	Logging	235411	4	100	B	NA††	2
10/09/22	AU	Leeuwin_90hp_4stroke	Cow	U	Logging	235622	5	100	B	CD	4
11/09/22	AU	Leeuwin_90hp_4stroke	Adult	U	Socialising	235413	5	100	B	CD	4
16/09/22	AU	Eclipse_115hp_4stroke	Cow	F	Logging	235407	7	95	B	CD	3
19/09/22	AU	Eclipse_115hp_4stroke	Adult	U	Logging	235114	7	85	B	AD	2
19/09/22	AU	Eclipse_115hp_4stroke	Adult	U	Logging	235405	3	65	B	AD	2
07/08/23	AU	Leeuwin_90hp_4stroke	Adult	F	Travelling	235411	6	NA	C	AL	1
10/08/23	AU	Leeuwin_90hp_4stroke	Adult	M	Socialising	235408	3	100	C	AD	1
10/08/23	AU	Leeuwin_90hp_4stroke	Adult	M	Logging	235409	1	100	C	AD	3
11/08/23	AU	Leeuwin_90hp_4stroke	Adult	F	Socialising	235412	3	100	C	NA	3
12/08/23	AU	Leeuwin_90hp_4stroke	Adult	F	Socialising	245752	5	70	C	NA	1
13/08/23	AU	Leeuwin_90hp_4stroke	Adult	F	Logging	245751	3	100	C	AD	2
13/08/23	AU	Leeuwin_90hp_4stroke	Adult	F	Milling	245754	5	100	C	AD	2

Discrepancy cases in the tag placement assignment: *first evaluators assigned as AV or CV, third and final assignment as AD; **first evaluators assigned as CD or AD, third and final assignment as CD; †first evaluators assigned as CV or CD, third and final assignment as CD; ††first evaluators assigned as AD or AV, third and final assignment as AV.

ANNEX 2

Examples of different percentage tag implantations

For a scale of the tag relative to the whales and a biopsy dart, see Figure 2 in the main manuscript above.

Figure S1. 50% implantation.

Figure S2. 65% implantation.

Figure S3. 90% implantation.

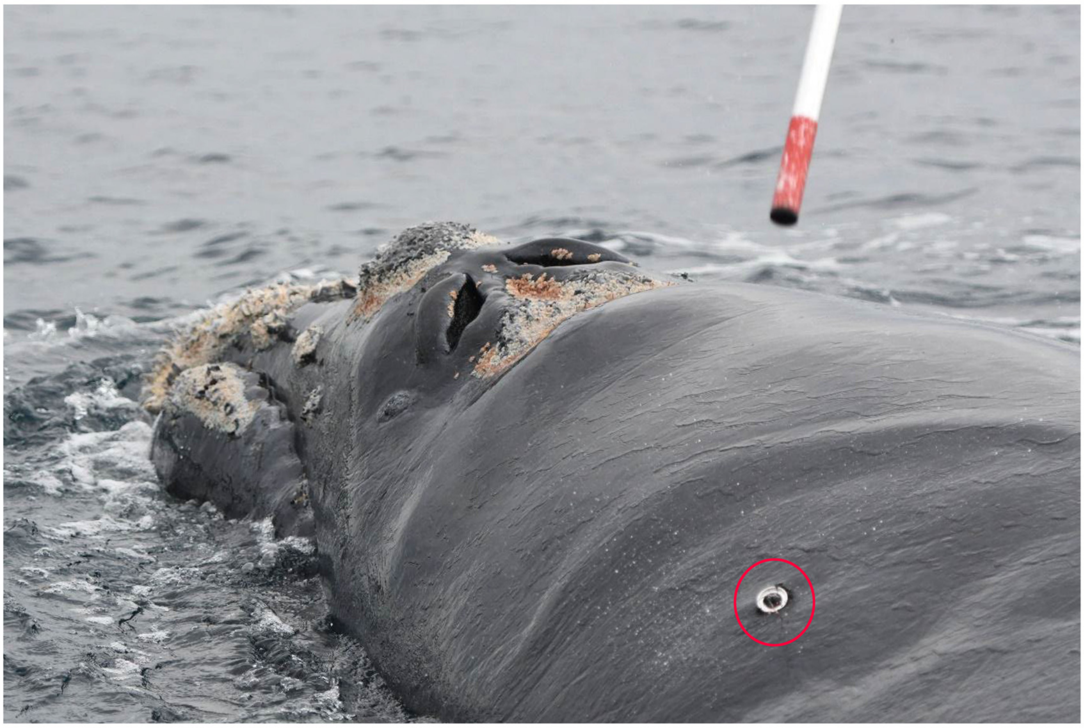

Figure S4. 100% implantation.

ANNEX 3

Comparison of tag and biopsy response of all unaccompanied adult southern right whales

Behavioural responses to tagging and biopsy-only events in New Zealand were initially compared using unaccompanied adult male SRWs, as this was the demographic class with the largest sample size of all tagged whales (n = 12; see main text), and as demographic class was shown by Riekkola *et al*. (2025) to significantly impact the behavioural response to biopsy sampling. In order to maintain as large a sample size as possible, this analysis was also repeated for all unaccompanied adult whales (i.e., males and females, but excluding 'cows', n = 23), while accounting for pre-approach behaviour, which was also shown by Riekkola *et al*. (2025) to significantly impact the behavioural response to biopsy sampling. Due to the difference in sample sizes between tagged vs. biopsy-only individuals, the biopsy-only dataset was subsampled. To account for the significant effect of pre-approach behaviour, 100 biopsy encounters involving unaccompanied adult whales were randomly selected (with replacement) while maintaining the same proportion of pre-approach behaviours as for the unaccompanied adult whales that had been satellite tagged. The mode and range were then compared and tested for statistically significant difference in response intensity between the tagged and biopsy-only groups using a chi-square test for ordinal data.

Prior to the tag deployment approach, 61% of the tagged unaccompanied adult whales were logging, 13% were milling and 26% were socialising (New Zealand data only). The tagging and biopsy-only datasets for all unaccompanied adult whales showed differences in the distribution of responses. Biopsy sampling had a peak (mode) in responses in category 2 and several category 4 responses, the latter of which were not present in the tagging group, while the tagging group showed a right-skewed distribution with a peak (mode) in response category 3. The distributions were compared using an ordinal chi-square test, which showed there was a statistically significant difference between the response distributions of tagged vs. biopsied whales (p-value < 0.001). It was not possible to account for the influence of distance of deployment on behavioural response, as these data are not available for the biopsy-only response data. These results are similar to those observed when only considering unaccompanied adult males that were tagged vs. biopsy sampled, while accounting for pre-approach behaviour (see main text).

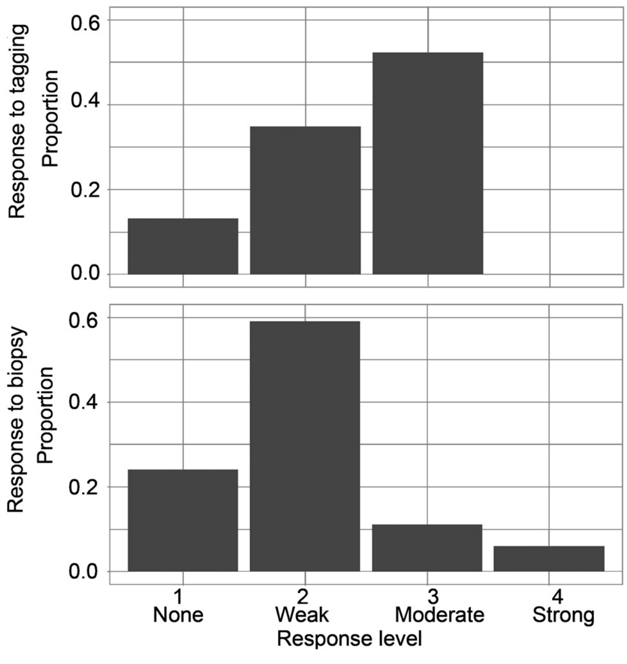

Figure S5. Comparison of responses to tagging (n = 23) and biopsy for adult southern right whales (i.e., excluding cows). For biopsy response, we randomly select 100 biopsy encounters with adult whales that had the same proportion of pre-approach behaviour as for the adult whales that were satellite tagged (biopsy response data from Riekkola *et al*., 2025).