

TELEMETRY CASE REPORT

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Implications of tag positioning and performance on the analysis of cetacean movement

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Abstract

Background: Satellite-linked animal-borne tags enable the study of free-ranging marine mammals. These tags can only transmit data while their antenna is above the surface for a sufficient amount of time. Thus, the position of the tag on the animal's body will likely influence the quality and the quantity of location estimates. We explored the effects of tag placement and tag performance on the analysis of cetacean movement, by deploying two identical Argos tags 33 cm apart on the dorsal fin of a male killer whale in Norway in January 2017.

Results: The highest placed (top tag) generated 540 location estimates, while the lowest placed tag (bottom tag) generated 245 locations. In addition, the top tag generated locations of higher quality, with less than 50% of the location estimates in Argos class B (the class with the highest estimated uncertainty), compared to the bottom tag (90% Argos class B locations). The distance between two reconstructed paths ranged from 81 m to 31 km. The path based on the top tag was 1.5 times longer, yielding a higher average speed and more extreme turning angles. The estimated uncertainty around the top track was smaller than that of the bottom track. Switches between searching and travelling behaviour, based on data from the top and the bottom tags, occurred at different positions and times. A significant relationship between core utilization areas and a simulated environmental variable was detectable at a finer spatial scale using data collected by the top tag compared to the bottom tag. A literature search yielded no evidence that tag performance or tag placement is commonly discussed in killer whale telemetry articles.

Conclusions: The differences in quality and quantity of location estimates from our two tags had a substantial effect on derived movement metrics, behavioural inferences and significance of a simulated environmental variable. These differences in tag performance are likely linked to the height difference in tag placement of 33 cm. We suggest that tag positioning on free-ranging marine mammals and tag performance should be considered as a covariate in telemetry studies, especially at a fine scale.

Keywords: Marine mammal, Telemetry, Killer whale, Animal movement, Tag placement, Argos tags, Core areas, Animal behaviour, Tag performance

Background

Movement data are crucial to understanding how animals interact with their environment. The collection of these data may be challenging, particularly in the case of elusive animals that inhabit remote areas or roam over large ranges. Animal-borne instruments (hereafter:

tags) have become widely used in various environments and in animal ecology for a variety of taxa from insects to large megafauna [1, 2]. Technological advances in biotelemetry have led to fundamental discoveries in ecology, providing insight into the horizontal and vertical movements of animals and their physiological state (see [1] for a review). Two main types of tags exist: data loggers that record and store data and need to be recovered, and data transmitters that transmit data to a remote platform [3]. Although different methods exist

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for the transmission of data, most of them do not work underwater, because seawater is opaque to radio waves, and signals cannot pass the water–air barrier. Satellite-based transmission forms a viable option for aquatic animals that often use entire ocean basins [4]. However, this mode of transmission requires tag antenna exposure to air for a sufficient duration in order to communicate with a satellite. Satellite communication serves two purposes in telemetry studies: location estimation and data transfer. In the case of the Argos system, messages used solely for location estimation require a transmission of at least 360 ms, while messages containing data collected by sensors on the tag require a transmission of 920 ms [5]. The quantity and quality of estimated locations depend on the number of received messages, the satellite constellation and the temporal pattern of the messages transmission. Location estimation is therefore directly influenced by the amount of time the antenna is exposed to air [4]. Marine mammals present a significant challenge for satellite telemetry as they spend most of their time underwater and are only briefly at the surface to breath. Satellite-linked tags must be placed strategically on the body of a marine mammal in order to maximize the antenna surface exposure while taking into account the animal's potential discomfort to the tag, its drag and the attachment method. In odontocetes, tags can be mounted onto or below the dorsal fin or on the dorsal ridge [6]. For some species, however, the large size of the dorsal fin allows for substantial inter-individual vertical variation in the placement of the tag. This is the case with killer whales (*Orcinus orca*) and especially males, as the dorsal fin of a male killer whale can grow up to 1.8 m in height [7]. This means that tags may be deployed within a potential vertical range of more than one metre, while at the surface, the upper part of the dorsal fin is exposed to air longer and more frequently than the lower part. Thus, the frequency and duration of tag-satellite communication depend on the vertical placement of the tag on the dorsal fin.

In this study, we explore the differences in data collected by two identical tags that were placed at different vertical positions on the dorsal fin of a male killer whale. We discuss how these differences influence various analytical steps, and we discuss the potential consequences for ecological inferences.

Results

Tag performance and location estimation rate

The tag that was positioned the highest on the dorsal fin (hereafter: top tag, Fig. 1a) was transmitting for 430 h, while the lowest placed tag (hereafter: bottom tag) was

transmitting for a total of 448 h. We restricted these datasets to the 423 h during which both tags were operational simultaneously. During this time, the top tag generated more than twice as many location estimates compared to the bottom tag, respectively, 540 and 245 Argos location estimates. This yields a rate of 1.28 location estimates per hour for the top tag, and a rate of 0.58 location estimates per hour for the bottom tag. The top tag transmitted the percentage dry time on 10 days (out of 19 days), while the bottom tag transmitted the percentage dry time only on 2 days. The reported average percentage dry time per hour by the top tag was higher than that of the bottom tag, 4.8% versus 3.0%, respectively.

The quality of the location estimates, as shown by the distribution of Argos classes, differed between the two tags, with the top tag producing higher-quality location estimates (Fig. 2a). Half of the location estimates from the top tag were assigned to class B, the Argos class associated with the largest measurement error, compared to 90% of the location estimates from the bottom tag. The time intervals between consecutive location estimates were shorter for the top tag (Fig. 2b, median 44.5 and 70.5 min for the top tag and bottom tag, respectively).

Path reconstruction

The total cumulative length of the track based on the top tag (hereafter: top track) was 1.5 times longer than the track based on the bottom tag (hereafter: bottom track), respectively, 1338 km versus 896 km. This yields an average speed for the top track of 3.16 km/h versus 2.12 km/h for the bottom track. The distances between the first and the last locations of both reconstructed paths were similar (Fig. 3a, top track: 127.6 km, bottom track: 138.5 km). Distances between locations of both tracks with the same time stamp, measured as distances between paired hourly locations of the two tracks, ranged from 81 m to 31 km (Fig. 3b) with a median distance of 5 km. The turning angles for the top track were more extreme, with a wider distribution around 0 (Watson's two-sample test, test statistic: 3.4681, p value < 0.001, Fig. 3c). The step lengths (distance per hourly locations) were greater for the top track than those for the bottom track (top: mean = 3.16, sd = 2.35, bottom track: mean = 2.35, sd = 1.77—two-sample Kolmogorov–Smirnov test: $D = 0.26714$, p value = $7.763e-14$, Fig. 3d).

The estimated standard errors in longitude and latitude associated with the two modelled tracks were smaller for the track based on the top tag compared the bottom one (Wilcoxon rank-sum test latitude: $W = 42,763$, p value < $2.2e-16$, longitude: $W = 50,280$, p value < $2.2e-16$, Additional file 1: Fig. S1).

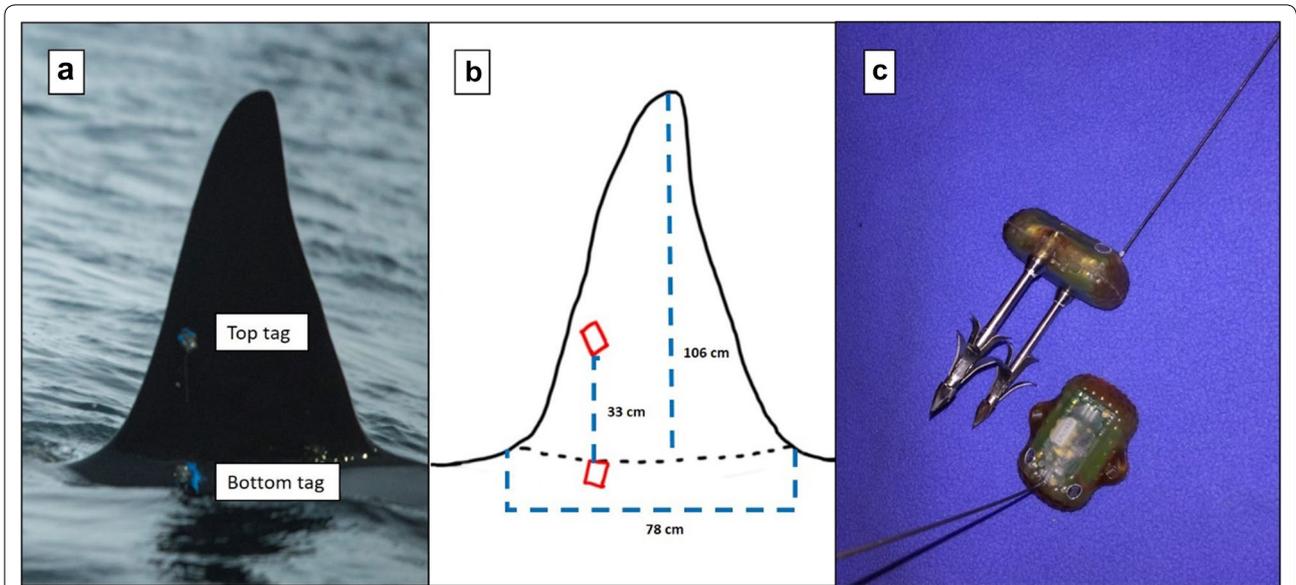


Fig. 1 **a** Photograph of the two tags on the male killer whale instrumented on 9–10 January 2018 in Northern Norway. **b** Schematic of the dorsal fin of the instrumented animal. The estimated measurements of the dorsal fin and the distance between the tags are based on the known dimensions of the tags. **c** Photograph of the type of tags used in this study

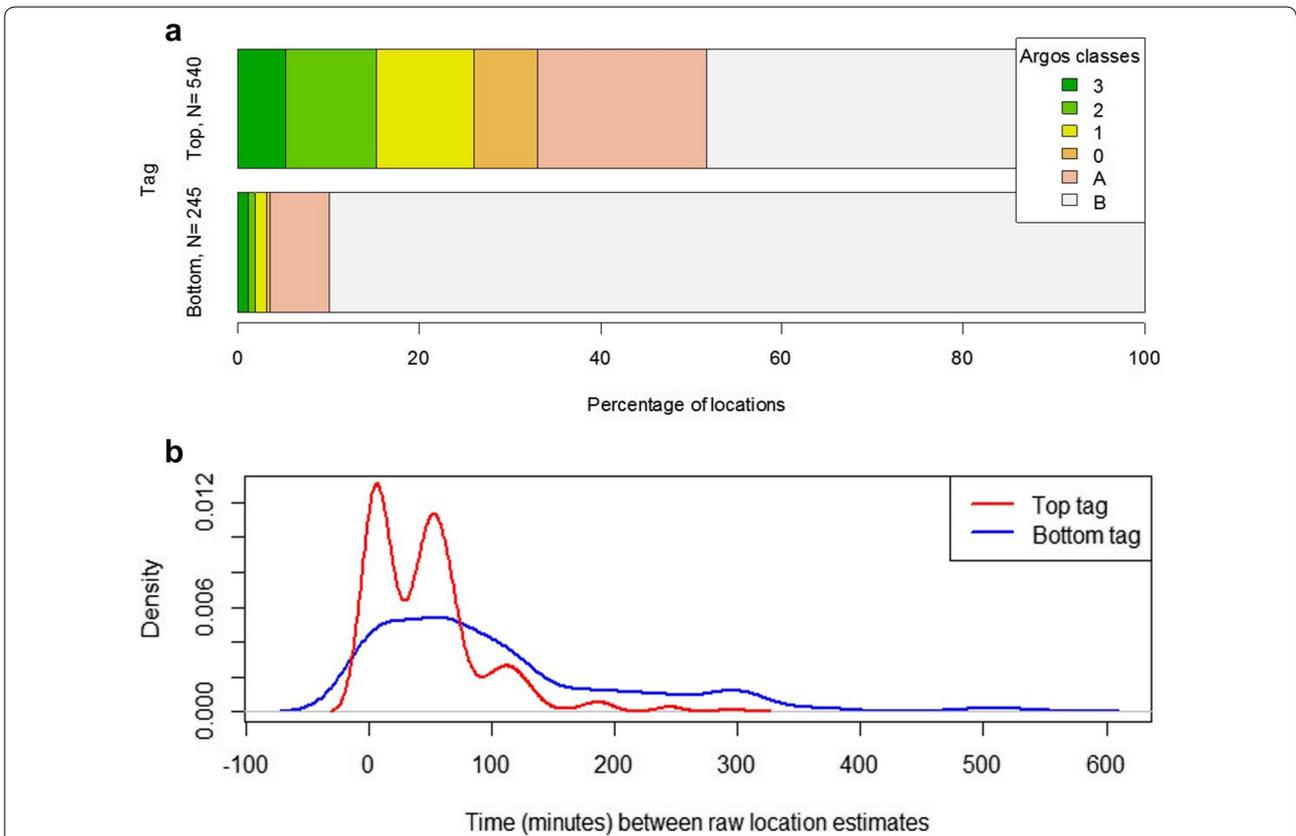
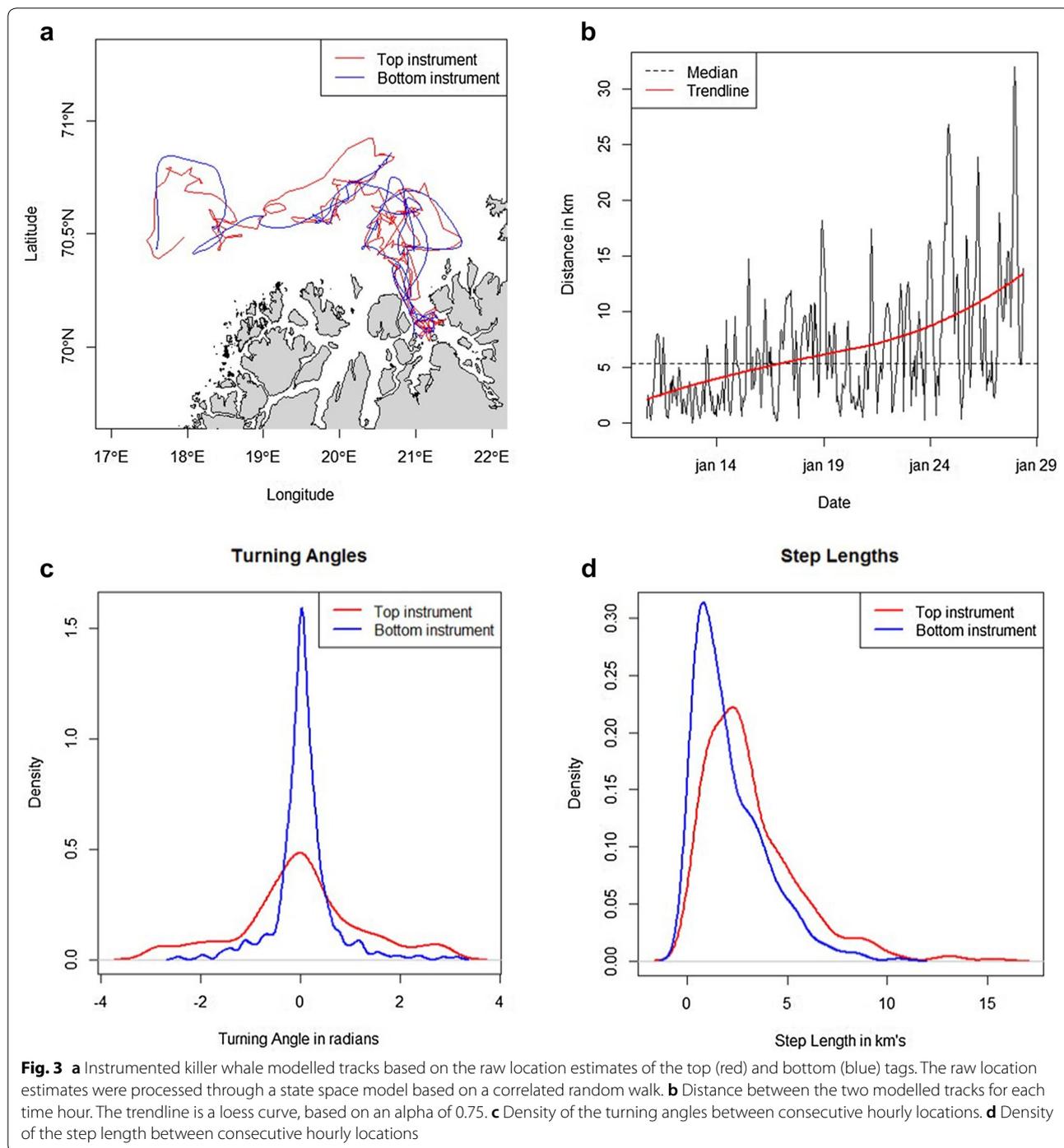


Fig. 2 **a** Proportion of Argos classes associated with the raw location estimates from the two tags. Location classes are colour-coded based on the estimates associated with the smallest positional error (class 3) to the largest (class B). **b** Density plot of the time intervals between two consecutive raw location estimates acquired by the top (red) and bottom (blue) tags



Core area of high utilization

We define the area of high utilization (hereafter: the top or bottom core area, respectively) as the 95% contour of the utilization distribution (UD, hereafter top or bottom UD, respectively). The top core area was approximately 17% smaller than the bottom core area (5399 km² vs. 6293

km², Fig. 4a, b). Eighty per cent of the top core area was included in the bottom core area.

Behavioural analysis

First passage time (FPT)

The variance of log(FPT) based on the top track showed a distinct maximum at 12 km, indicating that the animal was concentrating its search effort within a 12 km radius

(Additional file 2: Fig. S2A). The maximum of the bottom track falls within the error range of estimated error around each location. This means that it cannot be properly interpreted. Any other peak in the graph may be caused by the artificial tortuosity around the track, as a result of the estimated error (Additional file 2: Fig. S2B).

Hidden Markov model (HMM)

We distinguished two behavioural states, “searching” and “transit” along each of the modelled tracks, using a hidden Markov model (Fig. 4a, b). The total number of the

424 locations assigned to either behavioural states was similar for the modelled tracks resulting from both tags (top tag: 234 searching and 190 transit, bottom tag 232 searching and 192 transit). However, these behavioural states did not occur at the same locations nor at the same time. Thirty per cent of the paired locations were not assigned to the same behavioural state (Fig. 4c).

Relationship to environmental variables

We studied whether an environmental variable that is associated with the top track would also be associated

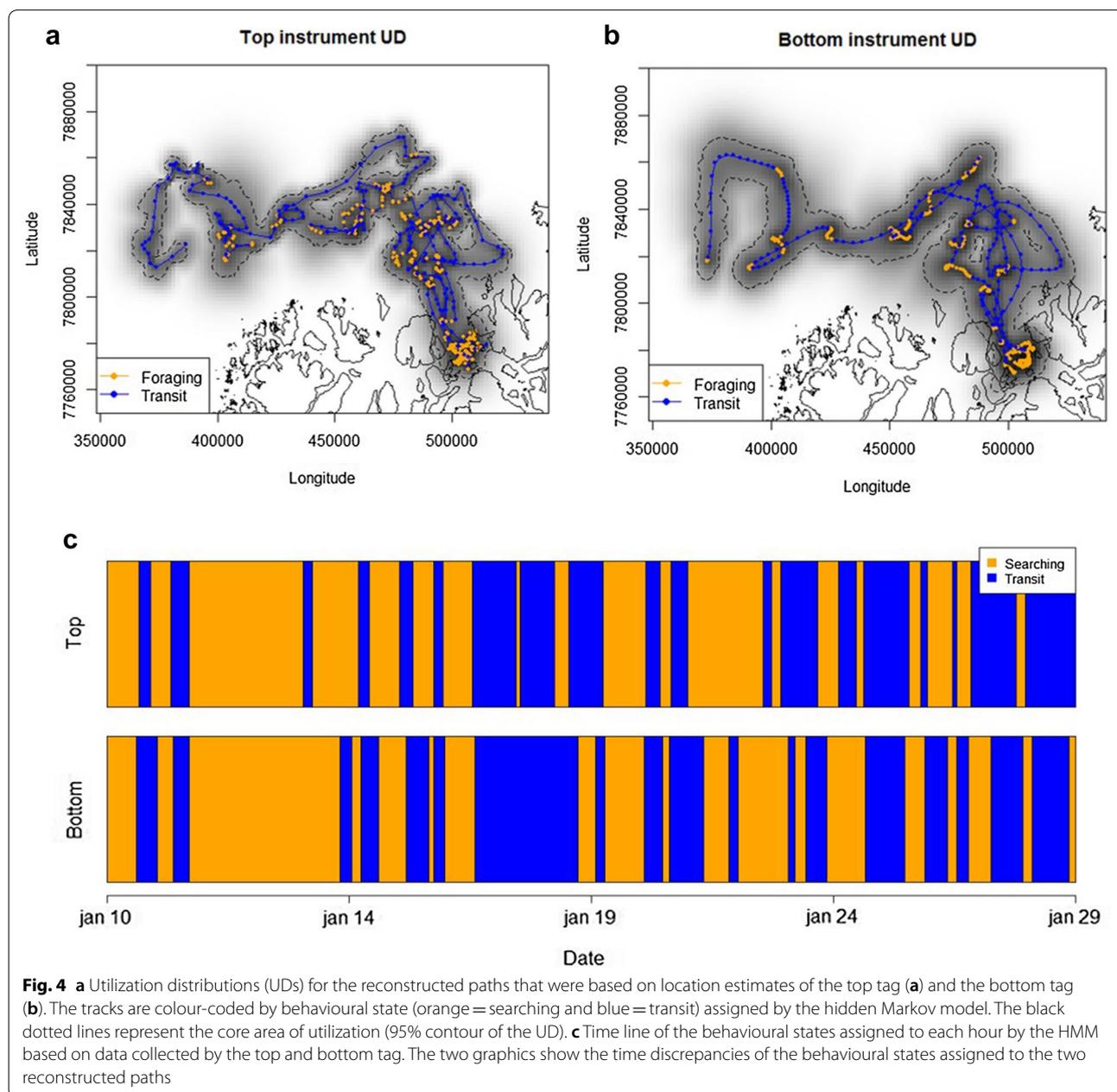


Fig. 4 a Utilization distributions (UDs) for the reconstructed paths that were based on location estimates of the top tag (a) and the bottom tag (b). The tracks are colour-coded by behavioural state (orange = searching and blue = transit) assigned by the hidden Markov model. The black dotted lines represent the core area of utilization (95% contour of the UD). c Time line of the behavioural states assigned to each hour by the HMM based on data collected by the top and bottom tag. The two graphics show the time discrepancies of the behavioural states assigned to the two reconstructed paths

with the bottom track, and the influence of the size of environmental structures on these relationships. To incorporate the uncertainty around each track, we used the UD's rather than the tracks themselves. The bottom track was only significantly related in one scenario: the scenario without any level of randomness, and with an environmental structure radius of 4 km (Fig. 5). In contrast, the top track was significantly related to environmental variables with environmental structure radii of 2 km or more and with up to 50% randomness added to the environmental variable.

Literature review

The tag model that was used in our study has been deployed on 307 animals and 18 species, including killer

whales, between 2006 and 2015 [6]. We focused on (male) killer whales because they represent an extreme example of potential variety in tag placement, due to the size of their dorsal fin. We found no evidence that the influence of tag performance or tag placement on the quality of data output is commonly discussed as an influential factor on the analysis of killer whale data.

Three studies used 12, 19 and 37 instrumented killer whales, respectively, but did not specify the tag positions on the animals [8–10]. Two other studies using two and five killer whales reported tag positions either on the dorsal fin [11], at the base of the dorsal fin or near the saddle patch [12]. Three studies used both females and males [8, 9, 11], while in [12] the animals were identified as either adult females or sub-adult males. One study did

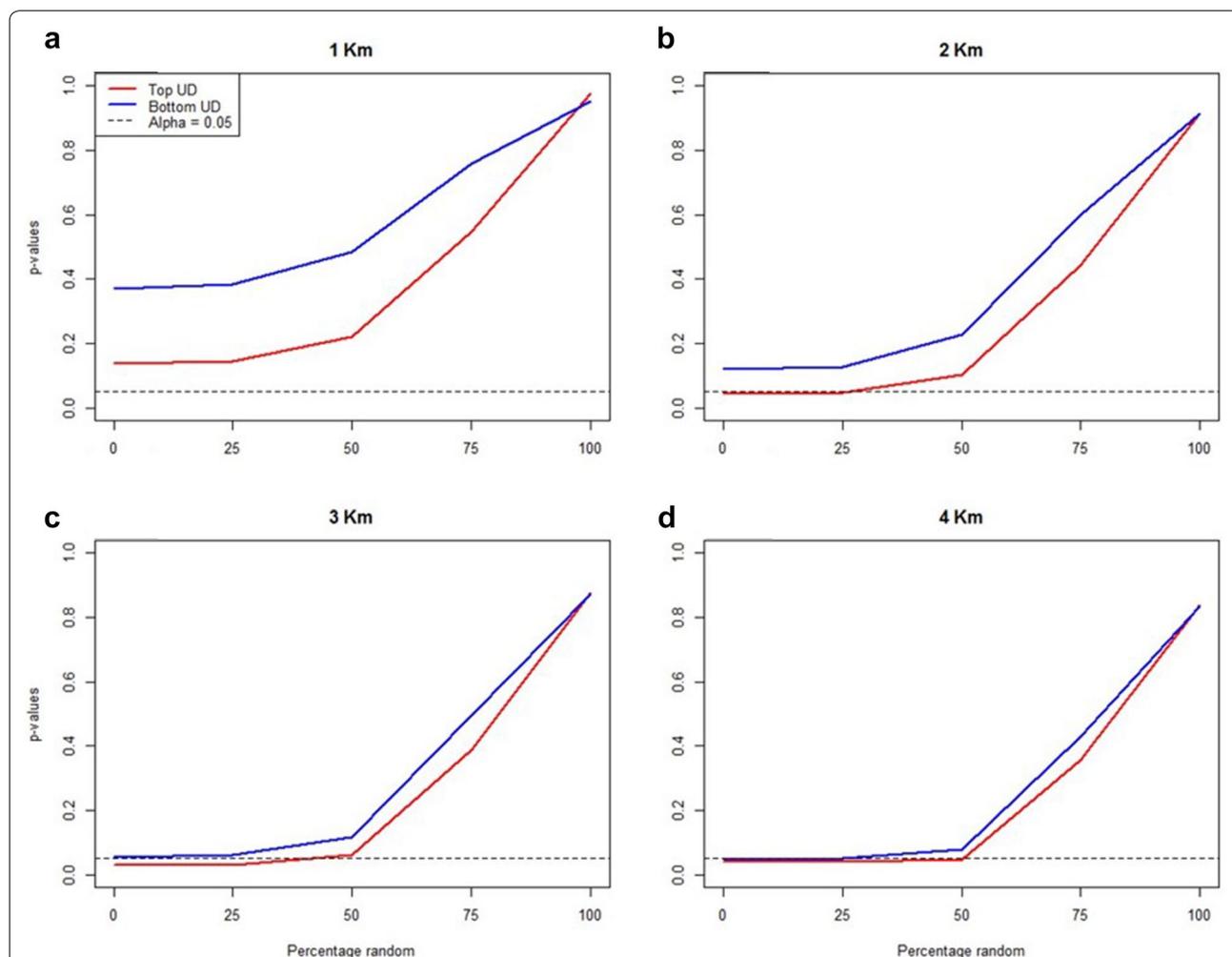


Fig. 5 Relationships between the top (red line) and bottom utilization distributions (blue line) and a range of hypothetical environmental variables. The four plots represent four different scales, expressed as radii of environmental structures. The y-axes show the *p* values from generalized linear models, while the x-axes represent a range of environmental variables, ranging from highly associated to the top track (0% random) to a completely random scenario (100%). The black dotted line represents a threshold value of 0.05

not specify sex [10]. While tag performance was mentioned in three studies (as location estimates per day, in some cases only an average was given for all animals), it was not discussed or taken into account in the analyses [8–10]. One study reported an average of four location estimates of Argos class 1 or better throughout the study [9], while [8, 10] reported averages of between 10 and 20 locations per day, or approximately 0.4 and 0.8 locations per hour.

Discussion

This double-tagging experiment on a male killer whale has allowed us to explore how tag performance influences movement metrics associated with a free-ranging animal's path and the behavioural and ecological inferences. In the present study, these differences are most likely caused by a small vertical difference of 33 cm in tag placement. Aquatic animals that spend long periods submerged are problematic for satellite-linked techniques due to the instrument's reliance on signal transmission through air and real-time communication with satellites [13]. In addition, the location estimates provided by the satellite are prone to measurement error giving an approximation of an animal's real locations. More locations of higher quality should increase the accuracy (how close is the estimated location to the real location) and precision (how large is the uncertainty around an estimated location) of the reconstructed path and associated metrics [14]. To obtain more and better location estimates, the air exposure time of the tag antenna must be maximized. A tag that is exposed to air longer and more often than another tag, is likely to generate more and higher-quality location estimates. This is because it is more likely to send a message while satellites are passing. In addition, it is less likely that messages are interrupted by water splashing on the conductivity sensor. Indeed, we have shown that the placement of an Argos-linked tag on a male killer whale affects the quality and the quantity of collected data with the less exposed bottom tag providing less and lower-quality location estimates compared to the top tag. These differences were significant even though the vertical distance between both tags was just 33 cm. The performance of the bottom tag, expressed in location estimations per hour, is comparable to tag performance described in the literature, while the top tag generated more location estimates per hour. However, since tag performance is most commonly described only briefly and as an average of multiple tags, the range that we found is only a crude approximation of the actual range of location estimates per unit of time. Percentage dry time was only transmitted during some days, and more often by the top tag, presumably because the top tag was exposed to air for longer stretches of time. The transmission of

data messages takes at least 920 ms, during which the antenna must be dry. Therefore, the length of time a tag is exposed to air, and not affected by waves is even more important for data messages which require longer transmission time. Tag performance may also have been influenced by the repetition rate with which the tags transmit. After each transmission, the tag would wait 45 s before re-transmission, which means that it is unlikely that a single surfacing event from the killer whale would have allowed for multiple transmissions from either tag. Both tags were restricted to sending 15 messages per hour, which could cause one or both of the tags to transmit all 15 messages within the first part of each hour. However, we found no indications that the location estimates were clustered to the beginning of each hour.

Based on the differences in raw data, tag placement appears to affect both the accuracy and the precision of the reconstructed paths and identification of behaviour. The two reconstructed paths were noticeably different. The distance between the two tracks, ranging from 81 m to 31 km, indicates a clear difference in accuracy. We assume the top track to be more accurate, as it is based on location estimates of better quality and quantity, compared to the bottom track. The top track was also more precise, with smaller error estimates around the locations compared to the bottom track. The distance between the two tracks appears to increase over time (Fig. 3b). This is most likely caused by the animal's behaviour. Based on the HMM output, the animal is transiting more towards the end of both reconstructed paths, thus spending less time at the surface. This means that consecutive locations of the reconstructed paths are further apart. Slight discrepancies between the two reconstructed paths may thus be amplified, resulting in an increase in distance between the reconstructed path towards the end of both recordings.

Movement metrics, calculated from reconstructed paths, such as travel distances and average velocity, are approximations of 'true' metrics. The length of a reconstructed path can be longer than the real path the animal has taken. The error around location estimates can artificially inflate the track length. However, if path reconstruction is based on relatively few raw location estimates per hour, the model is likely to underestimate the track length, as there is not enough information to accurately reconstruct the meandering movement of the animal. We argue that this is the case for our reconstructed paths, which are based on either 0.58 or 1.28 raw Argos location estimates per hour (bottom or top track, respectively). Since the bottom track is based on fewer raw Argos locations, it is likely missing more of the animals' fine-scale movement. This explains why the bottom reconstructed path is 1.5 shorter than the top reconstructed path.

Metrics that are calculated from track length, such as average speed, are therefore also likely to be underestimated if the rate of location estimation is low. Given the rate of location estimations reported in the literature, we argue that track length and associated metrics are often underestimated.

These metrics are commonly reported metrics in killer whale studies [8, 11, 12]. However, the effect of tag placement or tag performance on these metrics is not commonly taken into account.

Understanding which environmental features are important for an individual or a species and which behaviours are realized in a certain area can help decision-making processes, for example, in the development of marine protected areas. However, we have shown that the precision and accuracy of a modelled track and associated areas of high utilization affect inferences about how a free-ranging animal interacts with its environment. First, the placement of the tags led to different conclusions from behavioural analyses. We found a spatial scale on which the animal concentrated its search effort, based on locations generated by the top tag. The detection of such a spatial scale can, for example, be used to mitigate human activities in a certain place or during a particular period. We could not reach the same conclusion based on locations generated by the bottom tag. This might be caused by the reduced level of detail in the bottom track, which is a direct result of the relatively low quality and quantity of the locations generated by the bottom tag. While we did detect a similar amount of switches between search-related behaviour and travel-related behaviour along both tracks, these switches occurred at different times along both tracks. This could easily lead to misinterpretation of an animal behaviour at a certain time and place. Second, we have shown that tag placement affects the scale on which animal behaviour can be related to environmental conditions. The top track was significantly related to environmental variables with radii of 2 km or more, while the bottom track was only significantly related when the radius of environmental structures was 4 km. Since both tracks represent the same animal path, this difference is an indication that tag performance influences the spatial scale at which relationships with environmental variables may be detected. This can be explained by the uncertainty around the reconstructed path, which is translated into the size, shape and concentration of the UD. A track with a high level of certainty results in a highly concentrated and relatively narrow UD, while a large uncertainty around the track leads to a larger UD where the values are spread out. This level of uncertainty is the reason why the top track was not significantly related to a very fine scale (environmental structure radius 1 km) environmental

variable, even though one scenario of the environmental variable was directly based on the top track. Since the uncertainty around the reconstructed bottom track is larger than around the top track (e.g. the bottom core area is 17% larger), the values of the UD are also more spread out, which makes it less likely small-scale environmental variable are significantly related. There is a bias in the detectability of the relationships, as one scenario of the environmental variable is directly based on the top track. Our two UD's provide two slightly different representations of the animal's true distribution. Neither of these can be completely accurate, but in this analysis we treat one of them (the top UD) as a more accurate representation. This is because the top UD is based on more and higher-quality raw Argos locations. While it is unlikely that the "true" distribution of the killer whale is identical to the top UD, it is likely more closely associated with the top UD than with the bottom UD.

Tag placement and tag performance are most important for fine-scale movement analysis. Studies of large-scale migrations over long periods might be less dependent on high-quality data. The authors of [8] studied killer whale migration on such a large scale that it is unlikely that tag performance affected the conclusions. [10–12] focused on smaller scales, where tag performance may potentially have affected the results.

We focused on killer whales, as the size of their dorsal fins allows for potential variation in tag placement, which may influence tag performance. We showed the effects of a vertical difference in tag position of 33 cm. Similar vertical differences in tag placement may also occur in female killer whales, or in other cetacean species. For example, pilot whales and false killer whales also have relatively large dorsal fins, although not as extreme as male killer whales. Humpback whales and other large whales are typically tagged under their dorsal fin. Due to their large size, substantial height variation in tag placement may occur in the tagging of these species as well.

Conclusions

We have shown that tag performance can be influenced dramatically by the vertical placement of a tag. A tag placed relatively high on the dorsal fin yields location estimates of higher quality and quantity, since the frequency and duration of the tag's surface are higher compared to a tag placed at the base of the dorsal fin. Tag positioning can be controlled to some extent during deployment, in contrast to other factors that may influence tag performance, such as technical malfunction, individual variation between tags and satellite availability. Furthermore, movement metrics, calculated from reconstructed paths, such as travel distances and average velocity, may be underestimations, specifically when location estimation

rate is relatively low. Tag performance and tag placement can also lead to misinterpretation of behaviour, or misidentification of the occurrence of particular behaviour in space or time. The effect of tag performance and tag placement on inferences about behaviour or the environmental relationships is scale dependent. Conclusions in small spatial scale studies are more likely to be affected by tag performance, especially with regard to fine-scale environmental variation, for example, in coastal waters. We found that the effect of tag placement on the quality or quantity of data and the potential influence of tag performance are not commonly taken into account. It is likely that variation in vertical tag placement, or variation in tag performance, may also occur in other cetacean species. Our study focuses on killer whales as an extreme example of potential variability in tag placement; however, general tag performance regardless of the reason should be discussed in telemetry studies of any species. We advocate that tag placement on a free-ranging animal should be carefully considered prior to tagging and that relative tag performance should be considered as a covariate in telemetry studies, especially at a fine scale.

Methods

Tag and instrumentation procedure

We deployed two identical Argos tags (Limpet spot 6/240) [15] on a male killer whale in Kvænangen fjord, Northern Norway (Fig. 6), in January 2018. The tags measured 54 × 46 × 20 mm (Fig. 1a) and were surface-mounted with two sub-dermal 68-mm titanium anchors [6]. A 15-cm-long antenna of flexible material is mounted on the top of the tag (Fig. 1c). When the tag is placed on the dorsal fin of a killer whale, the antenna is positioned horizontally. Due to the flexibility of the antenna material, the antenna might point downwards (Fig. 1a). Both tags were programmed to transmit up to 15 messages per hour. The standard repetition rate or minimum time between transmissions for this type of tag is 45 s. The SPOT 6 tags operate via an internal clock, rather than a 24-h timer that starts at zero once activated. Argos tags instantly transmit 3-bit messages for location estimation when the dry-wet sensor detects that the tag is dry. The dry-wet sensor is sampled every 0.25 s. Therefore, there is a potential delay of up to 0.25 s when the animal surfaces before the message is sent. Since the transmission

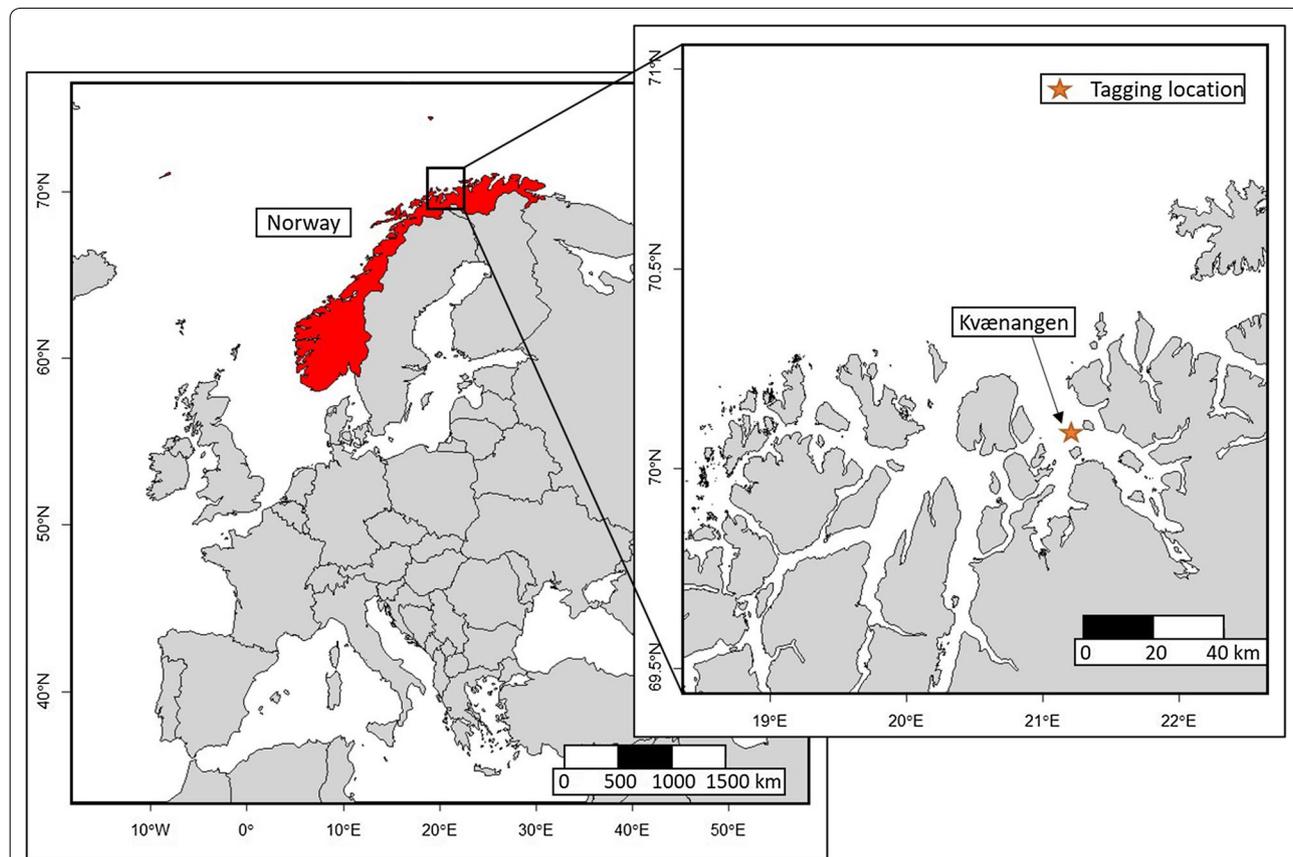


Fig. 6 Map of Europe, with Norway highlighted in red. The inset shows a close-up of the area where the male killer whale was instrumented. The star shows the tagging location

time of a standard location message is 0.36 s, the potential required time for one successful location transmission is 0.51 s. During the transmission, at least 10% of the antenna needs to be above the surface [16, personal communication].

The animals were approached from a 26-ft open RIB boat while they were feeding in groups of 30–150 animals in the vicinity of purse-net herring fishing vessels. The tags were deployed with an ARTS tag applicator (using a pressure of 8 bar at a distance < 10 m), similar to the tag applicator described in [17] and the anchors were cleaned with 70% alcohol prior to the deployment. The bottom tag was deployed at the base of the dorsal fin (Fig. 1a) on 9 January 2018 at 11:55, while the top tag was deployed at approximately 60 cm from the tip of the dorsal fin on 10 January 2018 at 15:51. The vertical distance between the two tags was estimated to be 33 cm. We estimated the dorsal fin to be 106 cm in height, and 78 cm at the base, based on the known dimensions of the tags (Fig. 1b).

The placement of two tags on one individual male was not a planned event and precautions were taken during this study to minimize the risk of tagging the same individual twice: (1) the target animal was always followed prior to the tagging event in order to manoeuvre the boat in a proper position facilitating the tag placement, (2) tagged animals were identified, based on characteristics of the dorsal fin and the saddle patch and photographed, (3) all animals were tagged on the same side of the dorsal fin, and (4) tags were only deployed from a distance of less than 15 m. However, light and weather conditions during the winter in Northern Norway can be challenging. In this particular tagging event, the first tag was placed at the base of the dorsal fin and was poorly visible when the animal was at the surface. Upon the discovery that we double tagged an animal, the Norwegian Food Safety Authority (Mattilsynet) was contacted immediately. This body is the responsible authority for animal research in Norway. After investigation, Mattilsynet decided that all required precautions had been taken and that our methods were in line with our tagging permit. Mattilsynet agreed that although unplanned, this event could benefit marine mammal research by providing insight into the functioning of electronic tags that are placed at different heights on the body of a cetacean. They fully support the present study and granted permission to double tag one animal a posteriori.

No reaction was observed during either tagging occasion, and the animal continued to feed with the other animals from its group, alongside the fishing boats. Tagging procedures were approved by the Norwegian Food Safety Authorities (Mattilsynet), under the permit: FOTS-ID 14135, and evaluated by an accredited veterinarian (Mattilsynet Report nr. 2017/279575).

Raw data and path reconstruction

We restricted the analysis to data recorded between 10 January 2018 17:00 and 28 January 2018 08:00 (423 h), when both tags transmitted simultaneously. The Argos system provides irregular location estimates associated with an error ellipse, depending on the location quality class [18, 19]. Argos location estimates are classified into 6 quality classes: 3, 2, 1, 0, A and B. The classes 3–0 associated with the highest accuracy have an estimated error ranging from < 100 m (class 3) to > 1500 m (class 0). The classes A and B do not have an estimated error, since they are based on less than 4 Argos messages. We compared the number of location estimates, the quality class distributions, the time intervals between locations, the number of location estimates per hour and the transmitted percentage dry time (recorded as average per hour) between the tags. The hourly percentages dry time are transmitted 10 times for each day, to increase the chance the message is recorded by a passing satellite. All data preparation, comparison and analysis were performed in R [20].

In order to obtain an estimate of the most probable path taken by the animal, we fitted a continuous-time correlated random walk (CRW), based on a state space model framework (SSM), on the raw Argos locations [21]. The CRW is an extension of a Random Walk and assumes that the movement rate at a location is correlated with the movement rates at previous locations [22]. Path reconstruction using a CRW does not require the exclusion of any location but takes into account the error associated with each ARGOS location estimate. The model also provides an estimated error around the track [23]. We used the “ssmTMB” package in R [24], and we computed location estimates at 1-h intervals.

We calculated summary metrics of the reconstructed paths based on the data from the two tags [25]. We used total displacement, cumulative track length, average speed, hourly speed step lengths and turning angles. Step length refers to the straight distance between hourly location estimates, while turning angles refer to the changes in direction between two consecutive location estimates. We compared the cumulative distribution functions (CDF) of the step lengths for both modelled tracks with a Kolmogorov–Smirnov test. The distributions of the turning angles were compared using a Watson’s two-sample test of homogeneity. In addition, an unpaired two-sample Wilcoxon test was used to compare the distributions of the standard errors that were estimated by the CRW model for latitude and longitude for the two modelled tracks. Finally, we calculated the distance between the two reconstructed paths at each hourly time step.

Identification of areas of high utilization

To incorporate the error around the reconstructed paths, as estimated by the CRW, we developed a modified version of a utilization distribution (UD). A UD can be described as the distribution of animal locations over a period of time [26]. We selected 20 locations from the standard error ellipse (based on the CRW output) around each location, creating 20 sets of locations for each track. Around each of these sets, we estimated the probability of occurrence across a regularized raster (1069×825 m resolution) using Brownian bridges, following a similar procedure as [21, 27]. The resulting 20 distributions were then combined into one average UD by taking the mean value for each raster cell. This approach generates an average UD for each of the two reconstructed paths (hereafter: top UD and bottom UD) that accounts for the estimated uncertainty around each reconstructed path. In order to compare the two areas of utilization, we used the 95% contours of the top and bottom UDs to create a core area of high utilization. We compared the size of the core areas, and we calculated the percentage overlap.

Identification of behavioural states

We used the first passage time (FPT) method and a hidden Markov model (HMM) in order to partition each track according to two behavioural states [21, 28–32]. The FPTs, the time an animal spends within a circle of a specific radius centred at each hourly location, were calculated along the two modelled tracks. We calculated the variance of the log (FPT) at radii that ranged from 0 to 30 km at 1-km intervals. The radius for which the variance of the log(FPT) is at a maximum provides an estimate of the spatial scale within which the search effort of an animal is concentrated [33]. We used the R package *adehabitatLT* [34].

We used a state space model to infer the behavioural state of the killer whale based on its movements, e.g. [30, 35]. An SSM estimates model parameters to predict different states (e.g. searching and travelling behaviour). These states themselves are unknown, but they are described by a process model, which is fitted to observed data (e.g. movement metrics) [23]. Hidden Markov models (HMMs) are a special case of SSM, which predict discrete, rather than continuous states (see [36] and references therein). In this study, we used an HMM to predict parameter estimates for step lengths and turning angles of two discrete behavioural states “searching” and “transit”, following the approach by [21]. We fitted the two modelled tracks separately in a HMM, using the *momentuHMM* package [37]. We used the Viterbi algorithm to assign behavioural states to predicted locations of the reconstructed paths. A Viterbi algorithm estimates the most likely sequence of states, based on the parameter

estimates from the HMM, where the behavioural state is dependent on the previous state [37].

Relationship with environmental variables

Animal movement and distribution studies often develop models assessing the importance of one or several environmental characteristics, e.g. [38, 39]. However, the statistical significance of the relationship between environmental variable and animal movement depends on their resolution and the accuracy of the estimated tracks. We aimed to test if an environmental variable that was associated with one track would also be associated with the other track. Second, we aimed to study how the relationship between the environmental variable and the animal tracks was affected by changing the radius of environmental structures.

A range of environmental variables was created for this analysis, based on a number of environmental structures. We define the term environmental structure as an area that influences killer whale movement. This may include a school of fish, but it may also represent, for example, an area with a specific surface temperature. Each environmental variable consisted of 30 structures; the number 30 is arbitrary. First, we varied the locations of the environmental structures. Second, we varied the radius of the structures, between 1 and 4 km. For the first step, we created two scenarios with different environmental structure locations. We also created intermediate scenarios by taking the weighted means of these two scenarios (0.25–0.75, 0.5–0.5, 0.75–0.25). The first scenario was created by randomly selecting 30 locations from the same grid that was used to create the UDs. In the second scenario, one of the two reconstructed paths is treated as a more accurate representation of the animals true path. We selected the top track for this role, since it is based on more, and more accurate location estimates than the bottom track. This scenario was created by selecting 30 locations from the highest values of the top UD, which can be interpreted as the top track with the uncertainty around it.

For the second step, we varied the radius of the environmental structures. We used a multivariate distribution to distribute 10,000 points around the locations of the scenarios that we created in the previous step. We then varied the radius of all the structures between 1 and 4 km at 1-km intervals. We then summed the number of points in each grid cell, using the same grid cell that was used to create the UDs. These summed values per grid cell were normalized so that we could compare the values of the different structure radius variants.

The relationship between both tracks and each variation of the environmental variable was tested in a series

of simple GLMs. We used the UD to represent each track and the uncertainty around it in the following model structure: GLM (UDs grid cell values ~ environmental variable). The *p* value of each model was recorded and compared with the *p* values of the other models (Additional file 3: Fig. S3).

Literature review

We conducted a literature search to study whether researchers take tag placement into account in their analysis. We focused on published, peer-reviewed articles using the search engines Google Scholar and Biological Abstracts, using various combinations of the keywords: “killer whale”, “telemetry”, “satellite”, “tag”, “PTT”, “Argos”, “transdermal”. We looked for information on the placement of killer whale tags in these studies and whether tag performance (number of location estimates per unit of time) was evaluated or taken into account during the analysis. We focused on killer whale literature and tag models that were similar to the SPOT 6 tags that we used. The focus on killer whales was directed by the size of their dorsal fin and the potential vertical variation in tag placement.

Additional files

Additional file 1: Fig. S1. Latitude (A) and Longitude (B) of the reconstructed paths.

Additional file 2: Fig. S2. Variance of the log-transformed first passage time.

Additional file 3: Fig. S3. Simulated environmental variables.

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Authors' contributions

EM and AR conducted the fieldwork, and AR deployed the tags. EM, MAB and MB analysed the data. EM, MAB, MB and AR wrote the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

Ethics approval

The placement of two tags on one individual male was not a planned event and precautions were taken during this study to minimize the risk of tagging the same individual twice: (1) the target animal was always followed prior to the tagging event in order to manoeuvre the boat in a proper position facilitating the tag placement, (2) tagged animals were identified, based on characteristics of the dorsal fin and the saddlepatch and photographed, (3) all animals were tagged on the same side of the dorsal fin, (4) tags were only deployed from a distance of less than 15 m. However, light and weather conditions during the winter in Northern Norway can be challenging. In this particular tagging event, the first tag was placed at the base of the dorsal fin and was poorly visible when the animal was at the surface. Upon the discovery that we double tagged an animal, the Norwegian Food Safety Authority (Mattilsynet) was contacted immediately. This body is the responsible authority for animal research in Norway. After investigation, Mattilsynet decided that all required precautions had been taken and that our methods were in line with our tagging permit. Mattilsynet agreed that although unplanned, this event could benefit marine mammal research by providing insight into the functioning of electronic tags that are placed at different heights on the body of a cetacean. They fully support the present study and granted permission to double tag one animal a posteriori. No reaction was observed during either tagging occasion, and the animal continued to feed with the other animals from its group, alongside the fishing boats. Tagging procedures were approved by the Norwegian Food Safety Authorities (Mattilsynet), under the permit: FOTS-ID 14135, and evaluated by an accredited veterinarian (Mattilsynet Report nr. 2017/279575).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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