

# Tracking marine mammals in 3D using electronic tag data

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## Abstract

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1. Information about at depth behaviour of marine mammals is fundamental yet very hard to obtain from direct visual observation. Animal borne multi-sensor electronic tags provide a unique window of observation into such behaviours.
2. Electronic tag sensors allow the estimation of the animal's 3-dimensional (3D) orientation, depth, and speed. Using tag flow noise level to provide an estimate of animal speed we extend existing approaches of 3D track reconstruction by allowing the direction of movement to differ from that of the animal's longitudinal axis.
3. Data are processed by a hierarchical Bayesian model that allows processing of multi-source data, accounting for measurement errors, and testing hypotheses about animal movement by comparing models.
4. We illustrate the approach by reconstructing the 3D track of a 52-minute deep dive of a Blainville's beaked whale *Mesoplodon densirostris* adult male fit with a digital tag (DTAG) in the Bahamas. At depth, the whale alternated regular movements at large speed ( $> 1.5$  m/s) and more complex movements at lower speed ( $< 1.5$  m/s) with differences between movement and longitudinal axis directions of up to  $28^\circ$ . The reconstructed 3D track agrees closely with independent acoustic-based localizations.

32 5. The approach is potentially applicable to study the underwater be-  
33 haviour (e.g. response to anthropogenic disturbances) of a wide variety  
34 of species of marine mammals fitted with triaxial magnetometer and  
35 accelerometer tags.

36 *Keywords:* dead reckoning, animal movement modelling, electronic tag,  
37 hierarchical Bayesian modelling, track reconstruction, triaxial  
38 magnetometer and accelerometer, flow noise

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## 39 1. Introduction

40 The use of animal borne autonomous recording tags to collect information  
41 for inferences on movement, ecology, physiology and behaviour is becoming  
42 widespread, providing an unprecedented window into these biological pro-  
43 cesses and leading to otherwise unattainable discoveries, especially at sea  
44 where animal behaviour is hard to observe directly (Ropert-Coudert & Wil-  
45 son, 2005; Bograd *et al.*, 2010).

46 Initially used simply to identify animals, over time tags became equipped  
47 with thermometers and barometers, followed by accelerometers, magnetome-  
48 ters, gyroscopes, microphones, hydrophones, GPSs, and even video (e.g.  
49 Johnson *et al.*, 2009; Burgess, 2009; Marshall *et al.*, 2007; Rutz & Tros-  
50 cianko, 2013). Some tags provide direct information on location while others  
51 do not. For those that do, say via GPS or radio tracking, a common approach  
52 has been to use state space models or hidden Markov models to reconstruct  
53 two dimensional tracks (e.g. Jonsen *et al.*, 2012; Beyer *et al.*, 2013; Langrock  
54 *et al.*, 2014). However, most marine mammals spend a large proportion of  
55 their time at depth, hence accounting for the depth component might be  
56 fundamental, depending on each study's objectives (e.g. Tracey *et al.*, 2014).

57 Published tracks in 3 dimensions (3D) are based on some form of dead  
58 reckoning (Wilson *et al.*, 2007): each position is predicted by updating the  
59 previous time step position considering an estimate of the animal's current  
60 direction and speed. One option is to infer animal 3D speed from 3D orien-  
61 tation (computed from accelerometer and magnetometer data) and vertical  
62 speed (from depthmeter data). However, this is sensitive to error in depth  
63 measurements, notably when animal movement is close to horizontal. This  
64 has led to estimating speed from other sources than depthmeters, namely  
65 tag flow noise (e.g. Simon *et al.*, 2009; Ware *et al.*, 2011). All such methods

66 have required the assumption that the direction of animal movement coin-  
67 cides with the direction of its longitudinal (rostr-caudal for a whale) axis,  
68 i.e. the animal moves towards where it is pointing. If this does not hold, bias  
69 can be expected, and the resulting track will be unreliable (Johnson *et al.*,  
70 2009). Further, errors accumulate over time, a phenomena referred to as drift  
71 (Wilson *et al.*, 2007). Additional drifting due to external factors can occur  
72 (e.g. Shiomi *et al.*, 2008). Therefore, while tags are very useful to establish  
73 relative positions of animals, inferring absolute position is questionable with  
74 existing procedures: the term *pseudo-track* is used to reinforce the notion  
75 that absolute position is unknown (Hazen *et al.*, 2009). Also for this reason,  
76 dead-reckoning tracks are often “anchored” to known positions (e.g. Zimmer  
77 *et al.*, 2005; Hazen *et al.*, 2009; Friedlaender *et al.*, 2009). These are some-  
78 times referred to as *geo-referenced* tracks, to convey the notion of absolute  
79 position on the earth sphere. However, measurement error in positions is typi-  
80 cally ignored, and the way the pseudo-track is combined with these is not  
81 explicitly described (e.g. Davis *et al.*, 2001; Mitani *et al.*, 2003; Tyson *et al.*,  
82 2012). Nonetheless, implementation details can have considerable impact on  
83 the estimated track, as well as (if estimated) on its precision.

84 We consider DTAGs (Johnson & Tyack, 2003) as an example. DTAGs  
85 include triaxial accelerometer and magnetometer sensors, a pressure sensor  
86 (sampling rate up to 50 Hz), and two hydrophones (up to 192 kHz) (Johnson  
87 & Tyack, 2003). Other tags (e.g. “OpenTag”, Loggerhead Instruments, Sara-  
88 sota, FL, USA) include triaxial magnetometers and accelerometers. Around  
89 20 marine mammal species (> 1000 deployments) including whales, dolphins  
90 and pinnipeds have been fitted with DTAGs (Mark Johnson, pers. comm.).  
91 Such tags have become widespread in marine mammal studies, allowing in-  
92 ferences about at depth behaviour and ecophysiology (e.g. Watwood *et al.*,  
93 2006; Shaffer *et al.*, 2013). DTAGs were originally developed to infer be-  
94 haviour and relative movement rather than absolute location, having been  
95 used extensively for this purpose – e.g., recent work on feeding behaviour  
96 in baleen whales (e.g. Simon *et al.*, 2012; Ware *et al.*, 2014, and references  
97 therein). However, DTAG data have been used to reconstruct 3D dives of  
98 animals (e.g. Davis *et al.*, 2001; Mitani *et al.*, 2003; Johnson & Tyack, 2003;  
99 Madsen *et al.*, 2005). Bespoke software is now available to process tag data  
100 into tracks (the R packages `animalTrack`, Farrell & Fuiman (2014), and  
101 `TrackReconstruction`, Battaile (2014), and to depict 3D tracks `Trackplot`,  
102 Ware *et al.* (2006)). An estimated position without an associated measure of  
103 uncertainty can be misleading, providing overconfidence in the reported esti-

104 mate. Nonetheless existing software does not provide uncertainty on position  
105 estimates, so these are never reported.

106 Extending dead reckoning and georeferencing methods described earlier,  
107 we develop a new way to use magnetometer and accelerometer tag data to  
108 reconstruct 3D tracks and estimate associated uncertainty. We explicitly (1)  
109 incorporate measurement error, both from the tag and from estimated posi-  
110 tions, in the input data and propagate this error through to the estimated  
111 track; (2) include information about animal speed both from change in depth  
112 given orientation and from tag flow noise; and (3) utilize the additional in-  
113 formation from both sources of speed information to relax the assumption  
114 that the animal moves in the direction it is pointed. Our model is superfi-  
115 cially similar to well-known 2D random walk models by, e.g., Jonsen *et al.*  
116 (2005), Morales *et al.* (2004) and McClintock *et al.* (2012) in that, like them,  
117 we model animal speed (i.e. step length) and movement direction in dis-  
118 crete time and continuous space, and use Bayesian methods to link models  
119 to data. However, assumptions about animal movement differ. Random walk  
120 models make distributional assumptions about step length and direction (or  
121 turning angle), hence resulting track estimates are a combination of the as-  
122 summed movement model and the input data (filtered through the observation  
123 process); by contrast we do not make such assumptions, hence our estimated  
124 tracks are a function of the data and observation process alone. In this sense,  
125 our approach is more “data focused”, but is also more reliant on having high  
126 frequency, high quality data to produce a realistic track. We return to these  
127 issues in the Discussion.

128 We illustrate our method by reconstructing a 52-minute dive of a tagged  
129 Blainville’s beaked whale *Mesoplodon densirostris* (Laplanche *et al.*, 2015),  
130 for which independent underwater localizations are available. These are not  
131 used in model fitting; instead we use them to evaluate the accuracy of the  
132 estimated track derived from tag data alone. Finally, we discuss the capabil-  
133 ities of the approach and possible improvements.

## 134 2. Materials and methods

### 135 2.1. Tag measurements and coordinate systems

136 We consider three coordinate systems (or frames) to accurately describe  
137 animal movement and tag data: (1) the Earth frame, a cartographic pro-  
138 jected coordinate system ( $x$ -axis south-north, positive north;  $y$ -axis east-  
139 west, positive west;  $z$ -axis bottom-up, positive up; origin is some arbitrary

140 location at the sea surface), (2) the animal frame ( $x$ -axis, longitudinal axis,  
141 positive forward;  $y$ -axis, right-left axis, positive left;  $z$ -axis, dorso-ventral  
142 axis, positive up; origin is the geometric center of the animal), and (3) the  
143 tag frame ( $x$ -,  $y$ -,  $z$ -axes are internally defined; origin is the center of the tag)  
144 – this latter frame is required because the tag is not always placed with the  
145 same orientation on the animal.

146 An animal’s 3D track is the time-series of its 3D location; more specifically  
147 the 3D Cartesian coordinates of the origin of the animal frame in the Earth  
148 frame, denoted  $\mathbf{x}(t) = (x(t), y(t), z(t))$  at time  $t$ . Animal 3D speed is the  
149 time derivative of  $\mathbf{x}(t)$ ; the speed of translation of the animal frame in the  
150 Earth frame, denoted  $\mathbf{v}(t) = (v_x(t), v_y(t), v_z(t))$ . The orientation of a 3D  
151 object in space is unambiguously described in terms of heading  $h$  (rotation  
152 to the  $z$ -axis,  $h \in (-180^\circ, 180^\circ]$ ), pitch  $p$  ( $y$ -axis,  $p \in (-90^\circ, 90^\circ]$ ), and roll  
153  $r$  ( $x$ -axis,  $r \in (-180^\circ, 180^\circ]$ ) with respect to some frame of reference. The  
154 animal’s 3D orientation at time  $t$  is represented by its heading  $h(t)$  (positive  
155 Eastwards), pitch  $p(t)$  (positive upwards) and roll  $r(t)$  (positive rightwards),  
156 with respect to the Earth frame.

157 Tag data are not directly available in the Earth frame. Accelerometer  
158 and magnetometer measure the Earth’s gravitationnal and magnetic fields  
159 in the tag frame. The conversion of Earth’s gravitationnal and magnetic fields  
160 between animal and Earth frames is achieved *via* rotation matrices described  
161 in the next section. The conversion of raw accelerometer and magnetometer  
162 data in the tag frame into the animal frame is achieved in a similar way.  
163 Description of the latter process, together with the processing of acoustic  
164 data into flow noise level, is deferred to Section 2.5.

## 165 2.2. The statistical model

166 We describe the full statistical model here. Approximations used in prac-  
167 tice for computational efficiency are described in Section 2.3.

168 The objective is to use available tag data (Earth’s gravitationnal and  
169 magnetic fields in the animal frame, depth, flow noise level), and independent  
170 positional data, if available, to infer unknown, latent variables characterizing  
171 animal movement ( $\mathbf{x}(t)$ ,  $\mathbf{v}(t)$ ,  $h(t)$ ,  $p(t)$ , and  $r(t)$ ). Our implementation  
172 utilizes a hierarchical Bayesian model (HBM). The overall model structure  
173 is illustrated in Figure 1, relating latent and measured variables as detailed  
174 below. For clarity the model is presented in four sections: (1) estimation  
175 of animal orientation from accelerometer, magnetometer and depth-meter  
176 measurements; (2) estimation of speed from flow noise measurement and

177 direction of movement from a combination of speed, orientation and change in  
 178 depth; (3) track estimation, and (4) incorporation of independent positional  
 179 information.

180 We define  $t_0$  and  $t_{end}$  as the track start and end times,  $t \in [t_0, t_{end}]$ .

181 *2.2.1. Animal 3D orientation*

182 The expected values  $\mathbf{A}^a(t)$  and  $\mathbf{M}^a(t)$  of the 3D Earth gravitational  
 183 and magnetic fields in the animal frame (superscript  $a$ ) at time  $t$  are

$$\begin{aligned} \mathbf{A}^a(t) &= T(t)\mathbf{A}^e \\ \mathbf{M}^a(t) &= T(t)\mathbf{M}^e, \end{aligned} \tag{1}$$

184 where  $T(t)$  is a rotation matrix that switches from the Earth frame to the  
 185 animal frame given by

$$\begin{aligned} T(t) &= \begin{pmatrix} 1 & 0 & 0 \\ 0 & \cos r(t) & \sin r(t) \\ 0 & -\sin r(t) & \cos r(t) \end{pmatrix} \\ &\times \begin{pmatrix} \cos p(t) & 0 & \sin p(t) \\ 0 & 1 & 0 \\ -\sin p(t) & 0 & \cos p(t) \end{pmatrix} \\ &\times \begin{pmatrix} \cos h(t) & \sin h(t) & 0 \\ -\sin h(t) & \cos h(t) & 0 \\ 0 & 0 & 1 \end{pmatrix}, \end{aligned} \tag{2}$$

186 and  $\mathbf{A}^e$  and  $\mathbf{M}^e$  are the values of the 3D Earth gravitational and magnetic  
 187 fields in the Earth frame (superscript  $e$ ) at the tagging location and time.  
 188 Given the relative small scale of most studies, ours included, compared to  
 189 these 3D Earth fields, these can safely be treated as constants. They can  
 190 be either measured or derived from models of the gravitational and Earth  
 191 magnetic fields.

192 Measured (superscript  $obs$ ) values of the Earth gravitational ( $\mathbf{A}^{a,obs}(t)$ )=  
 193 and magnetic fields ( $\mathbf{M}^{a,obs}(t)$ ) in the animal frame at time  $t$  are modelled  
 194 as multivariate Gaussian distributions (MVN)

$$\begin{aligned} \mathbf{A}^{a,obs}(t) &\sim \text{MVN}(\mathbf{A}^a(t), \boldsymbol{\Sigma}_A(t)) \\ \mathbf{M}^{a,obs}(t) &\sim \text{MVN}(\mathbf{M}^a(t), \boldsymbol{\Sigma}_M(t)) \end{aligned} \tag{3}$$

195 where  $\boldsymbol{\Sigma}_A(t)$  and  $\boldsymbol{\Sigma}_M(t)$  are time-dependent covariance matrices (see Ap-  
 196 pendix S1 for details). The observed animal depth is

$$z^{obs}(t) \sim \text{Normal}(z(t), \sigma_z^2), z^{obs}(t) \leq 0, \tag{4}$$

197 where  $z(t)$  is the unobserved true depth of the animal in the Earth frame  
 198 and  $\sigma_z^2$  is the depth-meter measurement error variance.

199 *2.2.2. Animal speed and direction of movement*

200 We explicitly relax what we refer in the following as the *equal pitch as-*  
 201 *sumption*: that the direction of animal movement coincides with the direction  
 202 of its longitudinal axis. Animal speed animal at time  $t$  is

$$\begin{cases} v_x(t) = \cos h'(t) \cos p'(t)v(t) \\ v_y(t) = -\sin h'(t) \cos p'(t)v(t) \\ v_z(t) = \sin p'(t)v(t), \end{cases} \quad (5)$$

203 where  $v(t) = \|\mathbf{v}(t)\|$ ,  $h'(t)$ , and  $p'(t)$  are the Euclidean norm, the heading  
 204 (positive Eastwards), and the pitch (positive upwards) in the Earth frame of  
 205 the speed vector of the animal at time  $t$ . Differences of orientations of the  
 206 longitudinal axis and the speed vector are modeled as differences in respective  
 207 pitch angles

$$p'(t) \sim \text{Normal}(p(t), \sigma_p^2), \quad p'(t) \in (-90, 90], \quad (6)$$

208 where  $\sigma_p^2$  is the variance of the pitch difference  $\Delta p(t) = p(t) - p'(t)$ . We  
 209 refer in the following to this as the *unequal pitch assumption* and to  $\Delta p(t)$  as  
 210 *pitch anomaly*. A positive pitch anomaly occurs when the animal points its  
 211 longitudinal axis higher than expected by its swimming direction, and vice  
 212 versa (Figure 2). Pitch anomaly can be the result of a pitch and/or a heading  
 213 movement in the animal frame depending on the roll. For reasons discussed  
 214 later, we do not consider heading anomaly, hence assuming  $h(t) = h'(t)$ .

215 Animal speed is related to background noise level  $\text{NL}(t)$  at time  $t$  assum-  
 216 ing

$$v(t) \sim \text{Normal}(a_v + b_v \log(\text{NL}(t)), \sigma_v^2), v(t) \geq 0, \quad (7)$$

217 where  $a_v$  and  $b_v$  are regression parameters and  $\sigma_v$  is the residual standard  
 218 error (Appendix S2).

219 *2.2.3. Animal 3D track*

220 Animal Cartesian coordinates at time  $t + \Delta t$  are computed from coordi-  
 221 nates at time  $t$  and speed:

$$\begin{cases} x(t + \Delta t) = x(t) + v_x(t)\Delta t \\ y(t + \Delta t) = y(t) + v_y(t)\Delta t \\ z(t + \Delta t) = z(t) + v_z(t)\Delta t \end{cases} \quad (8)$$

222 *2.2.4. Independent positional information*

223 In our application we only use information about the dive starting po-  
224 sition, assumed to have been observed with known error. We model this  
225 as

$$\begin{cases} x^{obs}(t_0) \sim \text{Normal}(x(t_0), \sigma_x^2(t_0)) \\ y^{obs}(t_0) \sim \text{Normal}(y(t_0), \sigma_y^2(t_0)) \end{cases} \quad (9)$$

226 where  $\sigma_x^2(t_0)$  and  $\sigma_y^2(t_0)$  are known variance terms. If the absolute start  
227 position is unknown, arbitrary values are provided for  $(x^{obs}(t_0), y^{obs}(t_0))$  with  
228 null variances ( $\sigma_x^2(t_0) = \sigma_y^2(t_0) = 0$ ); estimated locations become relative to  
229 this position.

230 Similarly, additional animal positions might be used to improve the track  
231 reconstruction process. When at the surface these could come from visual  
232 observations, animal-borne GPS or satellite receivers. When underwater,  
233 these could come from passive (or active) acoustic localizations.

234 *2.2.5. Priors*

235 Prior distributions are required on all top-level random variables in the  
236 hierarchical model. Observation variance parameters are assumed known,  
237 hence not requiring priors. We also assume the relationship between mea-  
238 sured noise level and speed is known with certainty (see Section 2.3 and  
239 Discussion). These variables are shown as grey boxes in Figure 1. The re-  
240 maining top-level variables are pitch, heading and roll at each time step, for  
241 which uniform distributions are assumed:

$$\begin{cases} p(t) \sim \text{Uniform}(-90, 90) \\ h(t) \sim \text{Uniform}(-180, 180) \\ r(t) \sim \text{Uniform}(-180, 180) \end{cases} \quad (10)$$

242 *2.3. Bayesian computation and approximating model*

243 The model described by equations (1)-(10) is not analytically tractable;  
244 however, samples from the posterior distribution of latent variables can be  
245 simulated via Markov chain Monte Carlo (MCMC). For this, we used Open-  
246 BUGS version 3.2.1, open-source version of WinBUGS (Ntzoufras, 2009).  
247 BUGS code is available as Appendix S3. Tag data preprocessing and output  
248 postprocessing were implemented in R (R Core Team, 2013).

249 Initial runs showed that the full model was highly computer-intensive.  
250 Two procedures were implemented to reduce computing time, both of which  
251 mean we fit an approximation to the full model. Firstly, the model was



252 divided into three stages (and each stage was analyzed in turn): (i) compute  
 253 animal 3D orientation (equations 1 - 4, 10); (ii) calibrate the speed-noise  
 254 relationship (equation 7); (iii) compute animal 3D track (equations 5, 6, 8,  
 255 9). Uncertainty was propagated across stages by modelling stage outputs  
 256 as Gaussians, with mean and variance equal to the corresponding posterior  
 257 values, using this distribution as input to the next stage. However, in moving  
 258 from stage (ii) to (iii) the parameters of the speed-noise model were assumed  
 259 known. Secondly, in computing stages (i) and (iii), the track was divided into  
 260 1-minute pieces. Each piece was run in parallel using a high performance  
 261 computing resource (HPR). Pieces were then joined and uncertainty from  
 262 the end of each piece propagated to the beginning of the next (see Appendix  
 263 S4 for details and discussion for possible impacts).

264 MCMC convergence was assessed by computing the inter-chain variances  
 265 of the simulated latent variable samples across 4 chains. For each chain, once  
 266 convergence was reached, 10,000 samples were simulated; these were thinned  
 267 to 1,000 independent samples per chain, with thinning guided by analyzing  
 268 the autocorrelation function of the posterior samples. Reported point esti-  
 269 mates are posterior means, standard errors are posterior standard deviations  
 270 (reported as mean  $\pm$  standard error), and reported interval estimates are 2.5  
 271 % and 97.5 % posterior marginal quantile estimates.

#### 272 2.4. Alternative models for pitch anomaly

273 The model assumes a fixed pitch anomaly standard deviation  $\sigma_p$  (see  
 274 Discussion for a relaxation of this assumption). To investigate how pitch  
 275 anomaly varied along the track we repeated the above analysis considering  
 276 three different values for  $\sigma_p$ :  $0^\circ$ ,  $5^\circ$  and  $10^\circ$ . These represent three different  
 277 models and we denote them  $\mathcal{M}_0$ ,  $\mathcal{M}_5$  and  $\mathcal{M}_{10}$ , respectively.

278 Models were compared, for each track piece, using the Deviance Infor-  
 279 mation Criterion (DIC Spiegelhalter *et al.*, 2002), a goodness-of-fit index  
 280 penalized for model complexity, similar in spirit to Akaike’s Information Cri-  
 281 terion; smaller values are considered better (see Section 4 for a discussion  
 282 of alternative model selection measures). Following Gelman *et al.* (2003) we  
 283 estimated model complexity as  $p_v = \text{var}\{-2 \log[p(\theta|y)]\}/2$ . The models do  
 284 not share the same complexity:  $\mathcal{M}_0$  is the least complex ( $p'(t)$  is perfectly  
 285 known given  $p(t)$ ), which is less complex than  $\mathcal{M}_5$  ( $p'(t)$  estimated under  
 286 the more relaxed constraint of equation (6) with  $\sigma_p = 5^\circ$ ) which is itself less  
 287 complex than  $\mathcal{M}_{10}$  (even more relaxed constraint with  $\sigma_p = 10^\circ$ ). In the  
 288 Results, we report which model was favoured in each minute of the track.

289 *2.5. Example dataset*

290 For illustration we used a *Mesoplodon densirostris* Blainville’s beaked  
 291 whale adult male tagged on the 5<sup>th</sup> September 2007 (tag on position: 24.3839  
 292 N, 77.5615 W) at AUTECH (Atlantic Undersea Test and Evaluation Center, an  
 293 instrumented US Navy testing range in the Bahamas). AUTECH details and a  
 294 different analysis of this DTAG data can be found in Ward *et al.* (2011). We  
 295 illustrate the methods using the first deep dive, which lasted 51’20’’ (full tag  
 296 deployment: 16 hours, 5 deep dives). *Mesoplodon densirostris* depth profiles  
 297 have been modelled using behaviour states (Langrock *et al.*, 2013), and deep  
 298 dives can be divided in descent, foraging and ascent phases: here the whale  
 299 fluked up and initiated its dive at arbitrarily fixed  $t_0 = 0$ , ended its descent  
 300 and started active searching for prey at  $t_B = 7’50’’$ , stopped active searching  
 301 for prey and initiated its ascent at  $t_C = 35’30’’$ , and reached the surface at  
 302  $t_{end} = 51’20’’$ .

303 The magnetic field was computed by using the IGRF11 (11<sup>th</sup> Genera-  
 304 tion International Geomagnetic Reference Field) Earth’s main magnetic field  
 305 model (International Association of Geomagnetism and Aeronomy, Work-  
 306 ing Group V-MOD, 2010). The magnetic field at the tagging location and  
 307 time was  $\mathbf{M}^e = (25736, 3205, -35522)$  nT (declination: 7.15° W; inclination:  
 308 54.08° down). The gravitational field was  $\mathbf{A}^e = (0, 0, -9.79)$  m/s<sup>2</sup>. Arbitrary  
 309 null values were provided for the location of the whale at the beginning of  
 310 the dive ( $x^{obs}(t_0) = y^{obs}(t_0) = 0$  m with  $\sigma_x^2(t_0) = \sigma_y^2(t_0) = 0$  m).

311 Raw tag-frame accelerometer and magnetometer data were converted into  
 312 animal-frame accelerometer and magnetometer data as described by Johnson  
 313 & Tyack (2003). Accelerometer, magnetometer, and depth-meter data were  
 314 lowpass filtered by using a 1-second, squared-window rolling mean before  
 315 being downsampled at 1 Hz ( $\Delta t = 1$  s). Background noise level was evaluated  
 316 as the median of the absolute value of the acoustic samples over a 1-second  
 317 window before being downsampled at 1 Hz. This simple procedure is robust  
 318 to the presence of transient signals, in our case echolocation signals emitted  
 319 by the tagged animal.

320 Eight independent acoustic localizations with low measurement error were  
 321 available (at 7’40, 10’40, 10’44, 29’21, 29’22, 29’23, 29’24, and 29’33), ob-  
 322 tained by cross referencing data from AUTECH range hydrophones with the  
 323 known times of emission of clicks from the tag (see Ward *et al.* (2011) for  
 324 details). These were ignored in the modelling, providing instead an inde-  
 325 pendent comparison to our location results. For comparison, a conventional  
 326 dead reckoning track was obtained based on a state space model formulation

327 with 4 states ( $x$ ,  $y$ ,  $z$ , speed) and 1 observation (depth). Heading and pitch  
328 were treated as known covariates, fitted via a Kalman filter, implemented in  
329 R.

### 330 3. Results

331 The dive track reconstruction (for all 3 models) on a single MCMC  
332 chain would have required 65 h of computation time on a single core of a  
333 Intel® Xeon E5-2680v2 2.8Ghz 10-core processor. This was reduced to 75  
334 minutes using HPR (Appendix S4).

335 Estimates of whale heading, pitch, and roll for the complete dive are  
336 provided as Appendix S5. The standard deviations of the whale head-  
337 ing, pitch, and roll estimates were  $0.78^\circ$  (average for the whole dive, 95 %  
338 in  $(0.35^\circ, 1.31^\circ)$ ),  $0.35^\circ$  ( $0.18^\circ, 0.54^\circ$ ), and  $0.47^\circ$  ( $0.14^\circ, 1.01^\circ$ ), respectively.  
339 These quantify observation measurement error in heading, pitch, and roll.  
340 Animal speed is linearly predicted from log-transformed flow noise level  
341 ( $R^2 = 0.77$ , Appendix S2).

342 DIC values are shown in Figure 3. Model  $\mathcal{M}_0$  was favoured from 1' to 5'.  
343 Model  $\mathcal{M}_5$  performed better for the rest of the dive except for 4 dive portions  
344 (at 12', 18', 25', 45') where  $\mathcal{M}_{10}$  was favoured.  $\mathcal{M}_0$  better performance at the  
345 beginning of the dive (similar fit with lower complexity) can be explained by  
346 the whale's negligible pitch anomaly at this stage leading to the equal pitch  
347 assumption. The improvement provided by  $\mathcal{M}_5$  and  $\mathcal{M}_{10}$  for the rest of the  
348 dive (better fit despite higher complexity) suggests a non negligible pitch  
349 anomaly and consequent need for equation (6). Model  $\mathcal{M}_5$  performed better  
350 than  $\mathcal{M}_{10}$  for most of the dive (similar goodness-of-fit with lower complex-  
351 ity) indicating that the flexibility introduced by setting  $\sigma_p = 5^\circ$  should be  
352 preferred to  $\sigma_p = 10^\circ$ . Nonetheless,  $\mathcal{M}_{10}$  outperformed  $\mathcal{M}_5$  for some dive  
353 portions (better fit despite higher complexity) with higher amplitude pitch  
354 anomaly. Overall, results strongly favor the unequal pitch assumption and  
355  $\sigma_p = 5^\circ$ . The following results are exclusively based on model  $\mathcal{M}_5$ , but this  
356 choice is not critical, as localization results are similar by using  $\sigma_p = 10^\circ$   
357 (distance between tracks:  $17.4 \pm 14.5$  m). The whale's estimated 3D track  
358 is illustrated in Figure 4 (interval estimates are provided as Appendix S5).  
359 The absolute distance between the results from the independent acoustic  
360 survey localizations and the estimated track from  $\mathcal{M}_5$  is  $38.3 \pm 18.7$  m. For  
361 comparison a standard dead-reckoning track fitted using a Kalman Filter is  
362 also shown (distance between tracks:  $151.6 \pm 88.9$  m). Estimated speed and

363 pitch anomaly is illustrated in Figure 5. The whale initiated its dive with a  
364 strongly negative pitch anomaly ( $-20^\circ$ ), pitch anomaly rapidly reached zero  
365 ( $t \in [0'00, 0'40]$ ) and stabilized (peak-to-peak lesser than  $4^\circ$ ,  $t \in [2'00, 6'00]$ )  
366 and up to  $15^\circ$  for  $t \in [6'00, 7'50]$ ). At depth ( $t \in [7'50, 35'30]$ ), the whale alter-  
367 nated sections with either moderate pitch anomaly variations (peak-to-peak  
368 lesser than  $10^\circ$ ) or strong variations (peak-to-peak up to  $40^\circ$ ). During the  
369 ascent ( $t \in [35'30, 51'20]$ ), the whale had a positive pitch anomaly (between  
370  $5^\circ$  and up to  $28^\circ$ ). At depth, sections of large speed were associated with  
371 moderate pitch anomaly variations and sections of low speed were associated  
372 with strong pitch anomaly variations, suggesting that the whale alternated  
373 complex rotational movements at low speed and more regular movements  
374 at higher speed. During the ascent, the whale always kept a positive pitch  
375 while the vertical speed could be negative (as low as  $-0.40$  m/s) as illustrated  
376 in Figure S2-2 (Appendix S2). The whale alternated active fluking (strong  
377 variations in speed) and passive gliding (no variation) with a strong positive  
378 pitch anomaly for the whole ascent.

#### 379 4. Discussion

380 We used a relatively simple “data driven” model, where expected ori-  
381 entation is a function of accelerometer and magnetometer measurements,  
382 expected speed is a function of measured noise and pitch anomaly is a func-  
383 tion of speed and measured changed in depth. Measurement error on the  
384 observed quantities was assumed Gaussian, with known variance (except for  
385 variance in the speed vs. flow noise relationship, which was estimated). This  
386 approach can be expected to produce a realistic track where high quality  
387 (i.e., low error), high frequency data are available that relate closely to ani-  
388 mal orientation and speed. DTAGs generate exactly such data. By contrast,  
389 where the data give less accurate information about animal movement or po-  
390 sition, and/or are collected much less frequently, then it becomes necessary  
391 to include assumptions about the underlying movement behaviour of the ani-  
392 mal in the model – for example using a biased correlated random walk, with  
393 model parameters representing centres of attraction or repulsion and corre-  
394 lation between time steps (e.g. McClintock *et al.*, 2012). A good example of  
395 such data is Argos satellite tags (see, e.g. McClintock *et al.*, 2015). One ad-  
396 vantage of our approach is that the track is not constrained by assumptions  
397 about movement behaviour. Disadvantages include it: (1) requires high qual-  
398 ity data; (2) does not incorporate biological knowledge of animal movement

399 behaviour (except in the specification of different error variances in differ-  
400 ent diving phases); (3) does not directly allow biological inferences about  
401 movement (in contrast with, e.g., the multi-state models of McClintock *et al.*  
402 (2012) – although such inferences could be made in a second analysis stage;  
403 (4) cannot be used for simulating tracks, since it relies on input data at each  
404 time step. Therefore, the most appropriate approach depends on the data  
405 available and the goals of the analysis.

406 Reconstructing 3D tracks from accelerometer, magnetometer, and depth-  
407 meter data alone, by implicitly assuming that the animal is moving in the  
408 direction of its longitudinal axis, might lead to biased inferences (see Figure  
409 4). As illustrated in Figure S2-2 (Appendix S2), the whale’s movement direc-  
410 tion does not necessarily coincide with its longitudinal axis during the ascent.  
411 Therefore the animal is capable of having a movement direction different to  
412 its own axis, issuing a serious warning against the equal pitch assumption.  
413 The inability to estimate speed when the animal is approximately horizontal  
414 (Appendix S2) represents an additional argument against reconstructing 3D  
415 tracks from accelerometer, magnetometer, and depthmeter data alone.

416 Following previous work (e.g. Simon *et al.*, 2009; Ware *et al.*, 2011) we  
417 estimated speed from an independent source, modeling the speed/noise re-  
418 lationship using the animal’s steep descent phase, formalized via a loglinear  
419 relationship. The estimated track consistency with independent acoustic  
420 locations suggests that this procedure is sensible, at least for the first 30  
421 minutes of the dive when acoustic data were available. However, using flow  
422 noise as a proxy for animal speed has its own limitations. It can be sensitive  
423 to changes in background noise during the dive (e.g. presence of sonar, boat  
424 motor, animal sounds). Difficulties are expected if the goal is to reconstruct  
425 tracks at the surface, when other sources might contribute significantly to  
426 acoustic noise (e.g. wave lapping) – a solution for this is discussed later.  
427 Further, animal speed estimates from flow noise assume that the speed-flow  
428 noise relationship is independent of the animal orientation (discussed in more  
429 detail later).

430 The key advantage of including an independent estimate of speed was  
431 the ability to relax the equal pitch assumption, clearly supported by the  
432 data (Figure S2-2) and by our localization results. For example, the whale  
433 was able to be oriented upwards while moving downwards (e.g. during the  
434 ascent), with differences up to  $28^\circ$  between 3D orientation of its longitudinal  
435 axis and its speed vector. Consequently, accounting for complex animal  
436 movements by dissociating animal translation and rotation movements seems

437 necessary to produce reliable 3D tracks. We have considered a fixed, known  
438 variance for pitch anomaly and concluded that a  $5^\circ$  was a sensible choice for  
439 our example. Another approach might be to consider an unknown variance  
440 for pitch anomaly. Hence, provided a reasonable vague prior, variance would  
441 be estimated while reconstructing the track, and (at least in theory) a time-  
442 dependent variance might be considered.

443 We considered DIC as a model selection metric because it was readily  
444 implemented in OpenBUGS. We acknowledge DIC's use is controversial, and  
445 that other approaches have been suggested (see, e.g., discussion papers fol-  
446 lowing Spiegelhalter *et al.* (2002, 2014)). It may, for example, be possible  
447 to implement a Gibbs Variable Selection or related approach (see O'Hara &  
448 Sillanpää (2009) for review) to estimate the posterior model probability for a  
449 model with 0 variance in pitch anomaly vs a model with a non-zero variance  
450 prior.

451 Pitch anomaly does not necessarily describe a pitch movement of the  
452 animal in its own frame; instead it is the difference between the animal's  
453 longitudinal axis pitch and the pitch of its speed vector (both on the Earth  
454 frame). Depending on the animal's roll, pitch anomaly can be the result of  
455 a pitch movement (in the animal frame) if roll is null or equal to  $\pm 180^\circ$ , of a  
456 heading movement (in the animal frame) if roll is equal to  $\pm 90^\circ$ , or a com-  
457 bination of both. Average roll was  $4.9^\circ$  (95 % in  $(-39.6^\circ, 20.5^\circ)$ ) during the  
458 descent,  $-5.0^\circ$  ( $-53.7^\circ, 35.2^\circ$ ) at depth, and  $1.0^\circ$  ( $-15.8^\circ, 23.0^\circ$ ) during the  
459 ascent. Consequently, variations in pitch anomaly here mainly depict pitch  
460 movements (in the animal frame) slightly combined with heading movements.  
461 We have not included heading anomaly in the model. Similarly as for pitch,  
462 heading anomaly could be defined as the difference between the heading  
463 of the longitudinal axis of the animal and the heading of its speed vector.  
464 A positive heading anomaly would represent movements when the animal  
465 points its longitudinal axis more on the starboard side than expected by its  
466 swimming direction, and vice versa. The reason for not including heading  
467 anomaly in the model is that it is not possible, given the available data, to  
468 compute both pitch and heading anomalies. Considering only pitch anomaly  
469 is a parsimonious choice: the most likely explanation for the discrepancy be-  
470 tween measured depth and the depth predicted by the 3D orientation of the  
471 animal and its speed norm is through a vertical shift of the speed vector, i.e.  
472 pitch anomaly.

473 The model handles four sources of errors: observation measurement errors  
474 on accelerometer/magnetometer data ( $\Sigma_A$  and  $\Sigma_M$ ), on depth data ( $\sigma_z^2$ ), and

475 internal errors due to differences between 3D orientations of the animal body  
476 and speed ( $\sigma_p^2$ ), and on the prediction of speed from flow noise ( $\sigma_v^2$ ). The  
477 model propagates measurement and process errors into parameter estimate  
478 errors. However, it still apparently underestimates the location estimates  
479 precision, as indicated by the independent acoustic localizations (Figure 4  
480 and Appendix S5). Variances of parameter estimates are conditional on the  
481 model being true. This is strictly unrealistic, as the model still represents  
482 an oversimplification of the mechanism underlying animal 3D displacement  
483 and flow noise. Therefore, while ignoring them should be avoided, confidence  
484 intervals associated with locations should be handled with caution.

485 There are (at least) 4 additional sources of errors ignored by the model:  
486 (1) Strictly, the speed considered is the speed of the animal with respect  
487 to the water mass. We consequently reconstructed the track in the water  
488 mass frame, not in the Earth frame. If water speed (in the Earth frame)  
489 is not negligible with respect to animal speed (in the water mass frame),  
490 track reconstruction might be biased. Were current speeds available one  
491 could incorporate them by adding a correction term in equation (8); (2) the  
492 calibration of the orientation of the tag to the whale frame was assumed  
493 to be an error free process, and potential tag shift over time ignored. An  
494 option would be to estimate calibration angles while reconstructing the track  
495 to propagate calibration errors to uncertainties on animal 3D orientation.  
496 Further research on the impacts of this calibration procedure on DTAG based  
497 by-products is welcome; (3) while errors on the prediction of the speed from  
498 the noise level are considered (equation (7)), errors on the parameters of the  
499 relationship ( $a_v$ ,  $b_v$ ,  $\sigma_v$ ) or on the relationship itself are ignored – the use  
500 of a more advanced relationship, calibrated while reconstructing the track is  
501 an interesting perspective; (4) a known error-free variance  $\sigma_p^2$  was used. As  
502 mentioned earlier, an option would be to estimate  $\sigma_p^2$ . The consequences of  
503 assuming a known calibrated speed-noise relationship and a known variance  
504  $\sigma_p^2$  on the track reconstruction process are explored in Appendix S6.

505 No explicit track smoothing was implemented. The reconstructed track  
506 regularity (Figure 4) is the consequence of the estimated speed regular-  
507 ity (Figure 5), itself the consequence of flow noise regularity, caused by  
508 smooth animal movement. Another option to smooth the track would be  
509 to consider explicitly autocorrelation in animal 3D orientation and speed.  
510 This might help when speed could not be inferred from flow noise (e.g.  
511 tags without acoustic sensors). One possible implementation is to add two  
512 sets of latent variables, angular speeds ( $v_h(t)$ ,  $v_p(t)$ ,  $v_r(t)$ , e.g.  $v_h(t) =$

513  $(h(t + \Delta t) - h(t))/\Delta t$  and accelerations  $(a_x(t), a_y(t), a_z(t)$ , e.g.  $a_x(t) =$   
514  $(v_x(t + \Delta t) - v_x(t))/\Delta t$ ), assumed unbiased with known behavioral state de-  
515 pendent variances, . As an illustration, the angular speed statistics (mean  
516  $\pm$  standard deviation) of our whale differ across behavioral states: descent  
517 (pitch:  $-1.0 \pm 3.7^\circ/\text{s}$ ; heading:  $0.0 \pm 2.0^\circ/\text{s}$ ; roll:  $0.5 \pm 3.0^\circ/\text{s}$ ), at depth  
518 ( $-0.8 \pm 5.5^\circ/\text{s}$ ;  $-0.1 \pm 5.0^\circ/\text{s}$ ;  $0.0 \pm 5.0^\circ/\text{s}$ ), and ascent ( $-0.2 \pm 3.0^\circ/\text{s}$ ;  
519  $0.0 \pm 2.5^\circ/\text{s}$ ;  $0.0 \pm 2.2^\circ/\text{s}$ ). Acceleration (3 coordinates altogether) also differ  
520 across states: descent ( $0.000 \pm 0.091 \text{ m/s}^2$ ), at depth ( $0.001 \pm 0.200 \text{ m/s}^2$ ), and  
521 ascent ( $0.000 \pm 0.081 \text{ m/s}^2$ ). The latter values could also be used to smooth  
522 animal tracks computed from acoustic surveys, as described by Laplanche  
523 (2012).

524 One of the advantages of implementing the model in a Bayesian frame-  
525 work is that incorporation of additional data sources and propagating corre-  
526 sponding observation errors is conceptually straightforward. Acoustic based  
527 localization could be used as direct observations or provide time of arrival  
528 differences (TDOA) data instead of computed localization, by combining our  
529 model with that of Laplanche (2012), which would deal with propagating  
530 TDOA errors to localization estimates.

531 We made some approximations to speed up model fitting computations:  
532 (1) we broke the full model into three parts (3D orientation, speed-flow noise  
533 and track reconstruction) and (2) analyzed some parts in one minute chunks,  
534 using Gaussian distributions to cascade uncertainty between chunks (see Sec-  
535 tion 2.3 and Appendix S4). These approximations are expected to have a  
536 negligible influence on the estimated track since they concern only the vari-  
537 ance of orientation and position. Nevertheless, we see four main drawbacks  
538 in our implementation: (1) it is not compatible with additional independent  
539 positional information (GPS or acoustic based), except for at the first time  
540 point; (2) it removes the possibility to correct for animal acceleration while  
541 computing animal orientation from accelerometer data. Although animal  
542 acceleration is negligible for large species, like the beaked whale considered  
543 here, it would be questionable for smaller, rapid species like dolphins or pin-  
544 nipeds; (3) it prevents calibrating tag orientation while reconstructing the  
545 track, and (4) it removes the possibility to account for animal orientation  
546 and speed to predict flow noise and compare to data for the whole dive.

547 Clearly HPR are a valuable tool, giving the potential to speed up exten-  
548 sive computations. Whether this potential is realized is case specific: in our  
549 case, because of the independence of some latent variables over time, parts  
550 of the computation could be carried out in parallel with almost no loss in



551 inference accuracy. This might no longer be the case if the model were ex-  
552 tended. Another option to reduce computation time might be implementing  
553 the model in a likelihood based approach, e.g. via an extended Kalman-filter,  
554 another research avenue we are pursuing.

555 Reconstructing tracks from accelerometer, magnetometer and depthmeter  
556 tag data happens routinely regardless of potential hidden dangers in doing so.  
557 The need for methods incorporating observation error and providing preci-  
558 sion measures on estimated tracks is clear. We have shown that the approach  
559 described here, allowing (1) the estimation of speed from flow noise and con-  
560 sequently (2) the dissociation of the 3D orientation of the animal longitudinal  
561 axis and the 3D orientation of its speed vector, is an important step towards  
562 such goal. We suggest that practitioners should evaluate the validity of the  
563 equal pitch assumption on their species before reconstructing 3D tracks. Our  
564 methods – considering equal/unequal pitch assumption, comparing outputs  
565 and fits, and using independent localization – are an option. It allowed us  
566 to design a new descriptor on marine mammal movement: pitch anomaly.  
567 We believe that making assumptions explicit via a mathematical model is  
568 a relevant approach in gathering current knowledge about animal behavior,  
569 identifying gaps, and allowing new insights.

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585 **Data Accessibility**

586 The DTAG data used to illustrate the methods is available from the Dryad  
587 Digital Repository: <http://dx.doi.org/10.5061/dryad.138cg>

588 **Supporting information**

- 589 • **Appendix S1.** Statistical model for accelerometer and magnetometer  
590 measurement errors.
- 591 • **Appendix S2.** Statistical model for speed from background noise  
592 level.
- 593 • **Appendix S3.** BUGS code.
- 594 • **Appendix S4.** Procedure to distribute track computations on a High  
595 Performance Resource (HPR).
- 596 • **Appendix S5.** Point and interval estimates of the heading, pitch, roll,  
597 and coordinates of the whale for the complete dive.
- 598 • **Appendix S6.** Investigating sensitivity to variance in pitch anomaly  
599 and flow noise relationship.

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745 hypothesis. *The Journal of the Acoustical Society of America*, **117**, 1473–  
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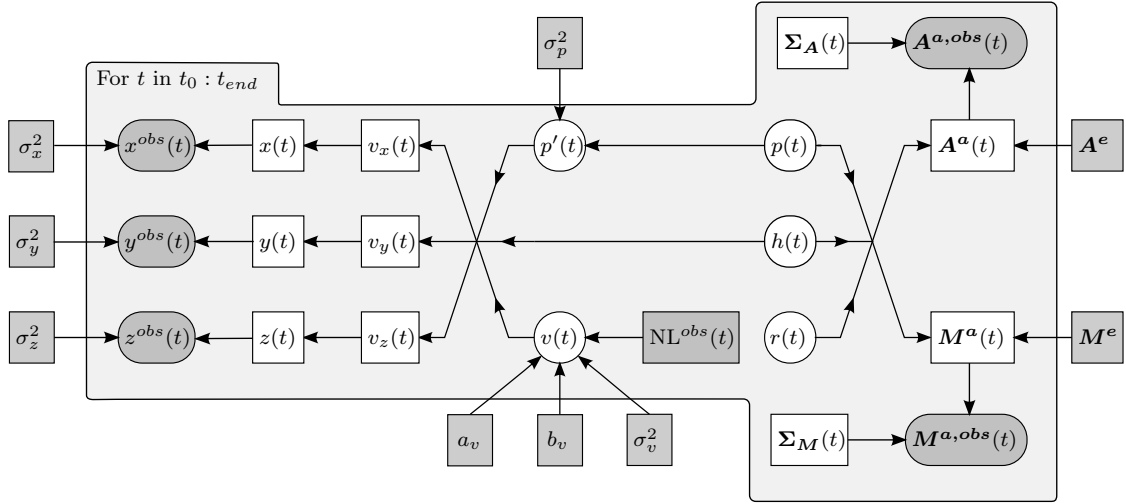


Figure 1: Directed acyclic graph (DAG) illustrating the relationship between model parameters and measured variables. Measured variables (in dark grey) are either modeled as random variables (circles and rounded rectangles) or are considered as known (rectangles). Parameters (in white) are either defined by a stochastic formula (circles and rounded rectangles) or are deterministic resultants of upstream nodes (rectangles). Variables indexed with  $t$  are time-dependent (grey polygon). The 3D orientation of the animal ( $h(t)$ ,  $p(t)$ ,  $r(t)$ ) is estimated from the accelerometer and magnetometer ( $\mathbf{A}^{a,obs}(t)$ ,  $\mathbf{M}^{a,obs}(t)$ ) data. The 3D orientation and norm ( $h(t)$ ,  $p'(t)$ ,  $v(t)$ ) of the animal speed vector is used to compute the 3D speed vector ( $v_x(t)$ ,  $v_y(t)$ ,  $v_z(t)$ ) and resulting track ( $x(t)$ ,  $y(t)$ ,  $z(t)$ ). The model allows for the possibility that the animal has a swimming direction ( $p'(t)$ ) that is distinct from, yet statistically related to, the 3D orientation of its body ( $p(t)$ ).



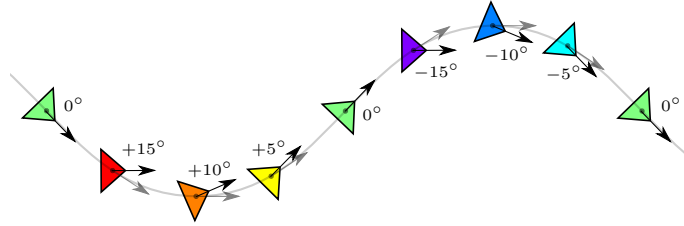


Figure 2: Pitch anomaly  $\Delta p(t) = p(t) - p'(t)$  is the difference between the pitch ( $p(t)$ ) of the orientation of the animal's longitudinal axis (black arrows) and the pitch ( $p'(t)$ ) of the animal's speed vector (grey arrows). A positive pitch anomaly highlights movements when the animal points its longitudinal axis higher than expected by its swimming direction, and vice versa. The 3D whale track (grey line) and vectors are projected on a vertical plane. The color legend for pitch anomaly is the same as what is used in Figure 4 (green: no anomaly; from yellow to red: increasing positive anomaly; from cyan to violet: decreasing negative anomaly), angles between pairs of arrows have been inflated in the current plot for the ease of representation.

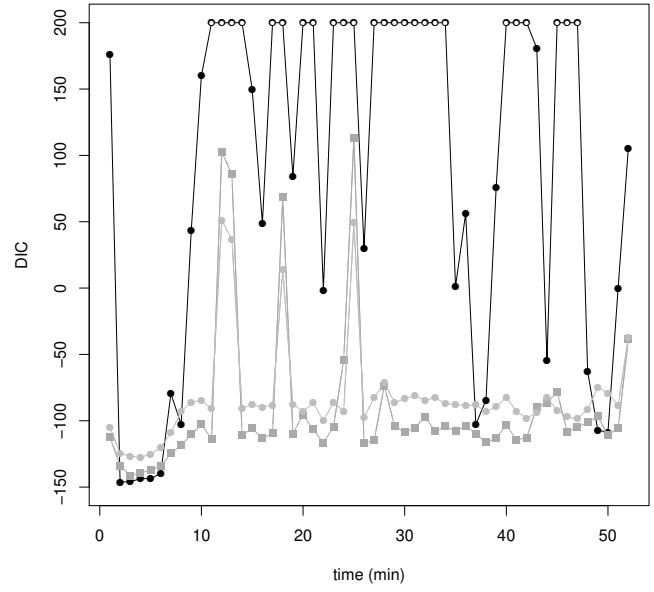


Figure 3: DIC values computed separately for each minute of the dive for models  $\mathcal{M}_0$  (black dots, values greater than 200 are represented as empty dots),  $\mathcal{M}_5$  (dark grey squares), and  $\mathcal{M}_{10}$  (light grey circles).

748

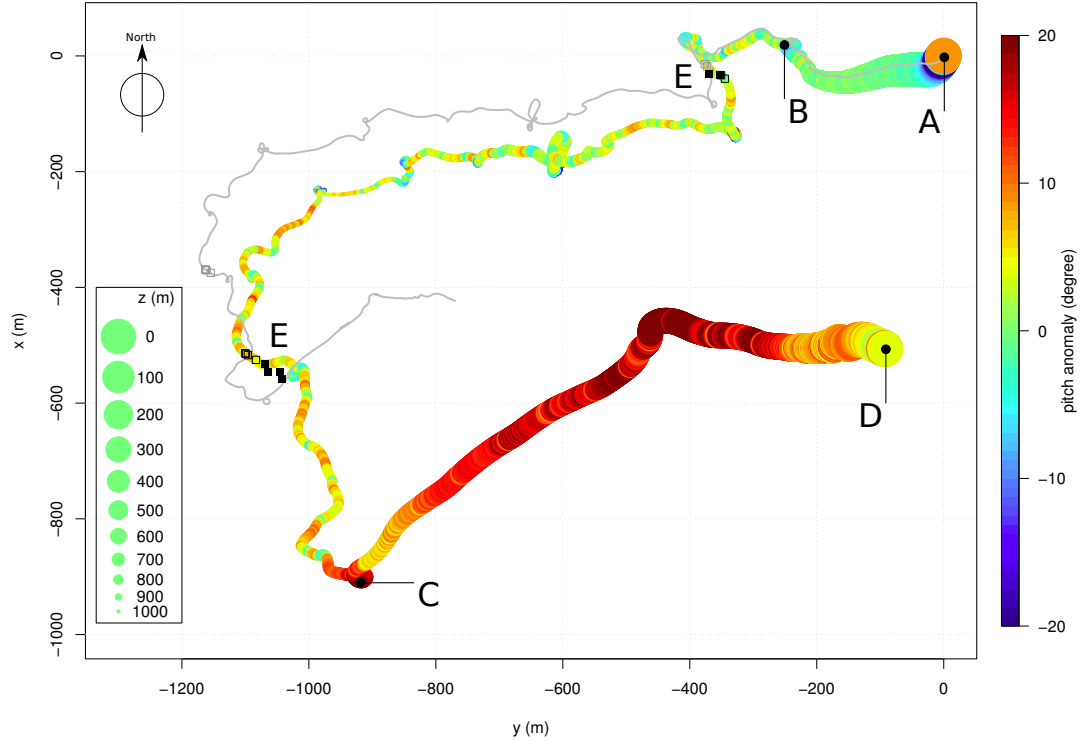


Figure 4: Estimated 3D whale track (x-axis, y-axis, dot size) and pitch anomaly (color). The whale dives at  $t_0 = 0$  (A), ends its descent and starts to actively search for prey at depth at  $t_B = 7'50$  (B), starts to res ascend at  $t_C = 35'30$  (C), and resurfaces at  $t_{end} = 51'20$  (D). Independent acoustic localization from surrounding AUTECH hydrophones are represented (full black squares, E) together with points on the estimated track at the same timing (empty black squares). The whale covers a total curvilinear distance of 5170 m (descent (AB): 895 m; at depth (BC): 2845 m; ascent (CD): 1430 m). Estimated whale track by processing accelerometer, magnetometer, and depthmeter data with a Kalman filter is represented (grey line) together with location at acoustic localization timing (grey squares).

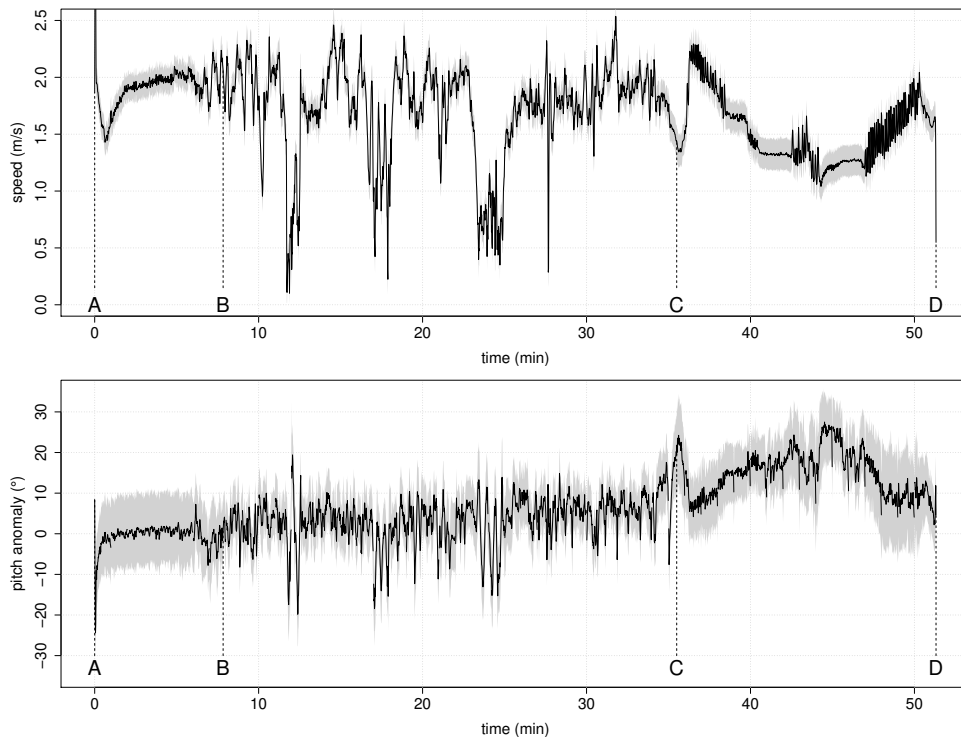


Figure 5: Point estimate of whale speed (top, in black) and pitch anomaly (bottom, in black). Descent (AB), at depth (BC), and ascent (CD) phases are defined in Figure 4. Mean speed during the descent is  $1.91 \pm 0.17$  m/s,  $1.72 \pm 0.42$  m/s at depth, and  $1.51 \pm 0.28$  m/s during the ascent. Mean pitch anomaly is  $-0.5 \pm 2.9^\circ$  during the descent,  $3.5 \pm 5.6^\circ$  at depth, and  $14.8 \pm 5.5^\circ$  during the ascent. Interval estimates are also represented on the plots (in grey). At depth, sections of large speed are associated with small pitch anomaly variations, and vice versa.

## Appendix S1 – Statistical model for accelerometer and magnetometer measurement errors

Accelerometer and magnetometer measurements normalized with respect to the norms of the earth gravitational and magnetic fields,  $\mathbf{A}^{a,obs}(t)/\|\mathbf{A}^e\|$  and  $\mathbf{M}^{a,obs}(t)/\|\mathbf{M}^e\|$ , would have a constant unit norm if earth gravitational and magnetic fields were the only components in accelerometer and magnetometer measurements. In practice, both norms are time-dependent, as a result of other sources of acceleration, plus noise. By modelling errors on each of the 3 accelerometer coordinates as independent and normally distributed (discussed below) with variances  $\sigma_A^2(t)$ , the variance of the squared norm  $\|\|\mathbf{A}^{a,obs}(t)\|/\|\mathbf{A}^e\|\|^2$  is  $6\sigma_A^4(t) + 4\sigma_A^2(t) \simeq 4\sigma_A^2(t)$  (by neglecting the fourth-order term, since  $\sigma_A \ll 1$ ; see values below for  $\sigma_A(t)$ ). One can find a similar formula for the variance of the squared norm  $\|\|\mathbf{M}^{a,obs}(t)\|/\|\mathbf{M}^e\|\|^2$ . Consequently, the time-dependent covariance matrices in equation (3) are here diagonals,  $\Sigma_{\mathbf{A}}(t) = \sigma_A^2(t)I$  and  $\Sigma_{\mathbf{M}}(t) = \sigma_M^2(t)I$ , with variances  $\sigma_A^2(t)$  and  $\sigma_M^2(t)$  equal to a quarter of the variances of the norms  $\|\mathbf{A}^{a,obs}(t)\|/\|\mathbf{A}^e\|$  and  $\|\mathbf{M}^{a,obs}(t)\|/\|\mathbf{M}^e\|$  which are directly measurable. Plots of  $\|\mathbf{A}^{a,obs}(t)\|$  and  $\|\mathbf{M}^{a,obs}(t)\|$  (not shown) strongly suggest consideration of distinct but constant variances for the animal descent, active searching for prey, and ascent (sequences AB, BC, and CD illustrated in Figure 4). Computed values are respectively for these three stages 1.12, 1.90, and 1.12 % for  $\sigma_A(t)$  and 0.61, 0.97, and 0.33 % for  $\sigma_M(t)$ .

Low resulting errors on orientation estimates (standard deviations on orientation angles are  $0.78^\circ$  on average, cf. main document’s results section) and location estimates could be potentially biased, as discussed in the main document. Errors in orientation and location estimates are computed assuming the model is true. Possible improvements to the error structure might include (i) considering correlated errors across the three magnetometer and accelerometer axes, leading to non diagonal covariance matrices  $\Sigma_{\mathbf{A}}(t)$  and  $\Sigma_{\mathbf{M}}(t)$ , (ii) considering auto-correlated errors, and (iii) using non-Gaussian distributions, particularly distributions defined on the circle.

## Appendix S2 – Statistical model for speed from background noise level

Animal speed can theoretically be estimated ( $v^{est}(t)$ ) from accelerometer, magnetometer, and depthmeter data alone

$$v^{est}(t) = |v_z(t)|\sqrt{1 + 1/\tan p(t)} \quad (\text{S2-1})$$

where  $v_z(t) = (z(t + \Delta t) - z(t))/\Delta t$  is the vertical speed computed from depth meter data and  $p(t)$  is the pitch of the animal computed from the accelerometer and magnetometer. The use of equation (S2-1) is problematic for two main reasons. The first is that accelerometer, magnetometer, and depthmeter data provide no information on animal speed when the animal is horizontal (equation (S2-1) does not apply if  $p(t) = 0$ ). As a corollary, the computation of animal speed from accelerometer, magnetometer, and depthmeter data with low pitch values is unreliable and highly sensitive to measurement error. The second reason is that, as considered in the present paper, animal orientation is not necessarily the orientation of its speed vector  $\mathbf{v}(t)$ , and consequently speed computed from accelerometer, magnetometer, and depthmeter data could be misleading. One could, however, use Equation (S2-1) to compute a reliable estimate of the speed norm from accelerometer, magnetometer, and depthmeter for periods of high pitch when the equal pitch assumption is likely to hold. As Simon et al. (2009), we consider the section of the dive when the animal is fluking and steeply descends from the sea surface to reach the foraging depth, and hence when the equal pitch assumption is most likely to hold. We apply equation (S2-1) to all samples ( $n = 384$ ) during the animal descent for which the pitch is greater than  $60^\circ$  (an arbitrary threshold).

Background acoustic noise level is expected to increase with animal speed as a consequence of water flow on the sensor. Figure S2.1 shows the observed relationship between estimated speed for the above data versus measured noise level on the tag (on a logarithmic scale). An ordinary linear regression yielded the relationship, for data from descent with pitch  $> 60^\circ$  of  $E\{v(t)\} = 4.53 + 1.16 \log_{10}(\text{NL}(t))$ , with a residual standard error  $\sigma_v = 0.08$  m/s ( $R^2 = 0.77$ ). The fit is shown in Figure S2.1.

Also shown in Figure S2.1 are the samples ( $n = 330$ ) during the animal ascent for which the pitch is greater than  $60^\circ$ . A similar regression on these data yielded somewhat different regression parameters ( $E\{v(t)\} = 4.73 + 1.37 \log_{10}(\text{NL}(t))$ , with a residual standard error  $\sigma_v = 0.12$  m/s,  $R^2 = 0.84$ ). We postulate that ascent should not be considered to calibrate the speed-noise relationship, as during this stage the direction of the movement differs

from the animal's axis (Figure S2.2: on two occasions a positive pitch, i.e. head oriented upwards, is observed concurrently with a negative vertical speed, i.e. animal moving downwards). We hypothesize that the discrepancy between the descent and ascent calibration results (Figure S2-1) is that for the latter movement direction can differ from the animal's longitudinal axis. We therefore calibrated the speed-noise relationship with descent data, when the animal is actively navigating downwards, to predict animal speed from the noise level for the rest of the dive.

Currently this model does not consider differences of flow noise due to animal orientation and does not propagate errors on estimates  $a_v$ ,  $b_v$ , and  $\sigma_v$  to location uncertainties. This is discussed in the main document.

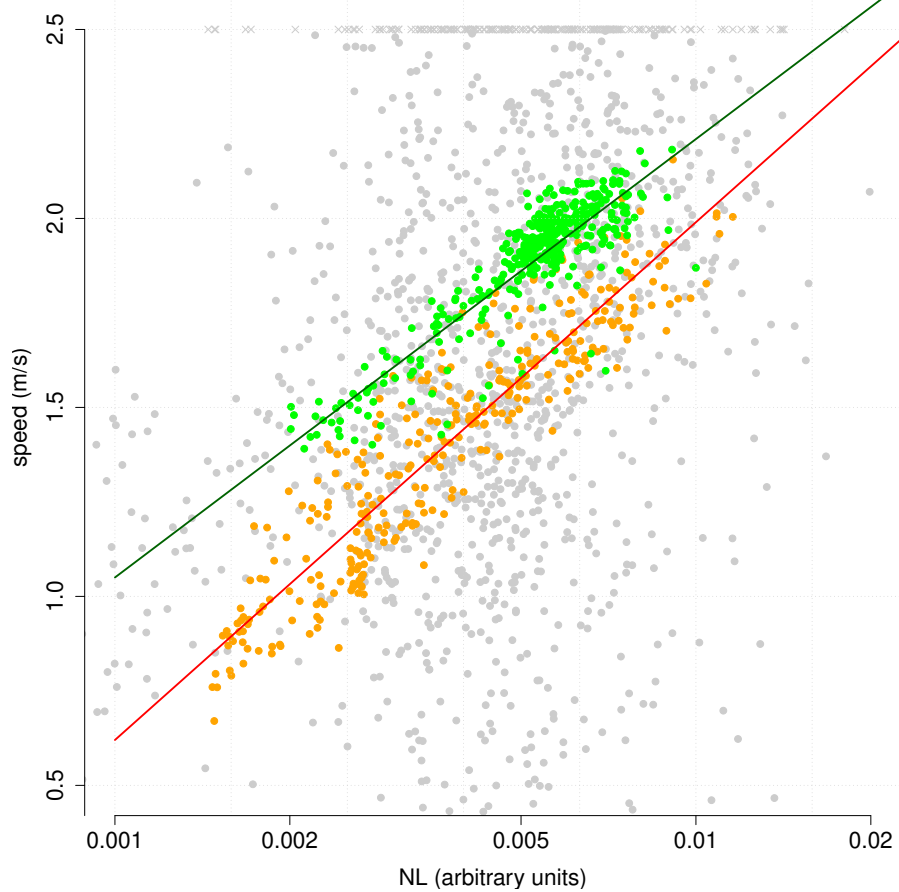


Figure S2.1: Measured noise level (NL) and speed norm ( $v$ ) computed by dead reckoning from accelerometer, magnetometer, and depthmeter data. Samples with pitch angle  $p(t) \geq 60^\circ$  during the whale descent ( $t \in [0, 470]$  s; 384 samples; in green), during the ascent ( $t \in [2130, 3080]$  s; 330 samples; in orange), and remaining points (in grey; for a better presentation of points during the descent and the ascent, speed values greater than 2.5 m/s are censored and are represented as crosses). Speed is linearly related to the logarithm of the noise level by using data from the descent ( $R^2 = 0.77$ ; green line) or the ascent ( $R^2 = 0.84$ ; red line). Data from the descent are used to calibrate the relationship connecting  $v$  to NL. Predicted speed norm is  $E(v) = a_v + b_v \log_{10}(\text{NL})$  ( $a_v = 4.53$ ,  $b_v = 1.16$ ), standard error is  $\sigma_v = 0.08$  m/s.



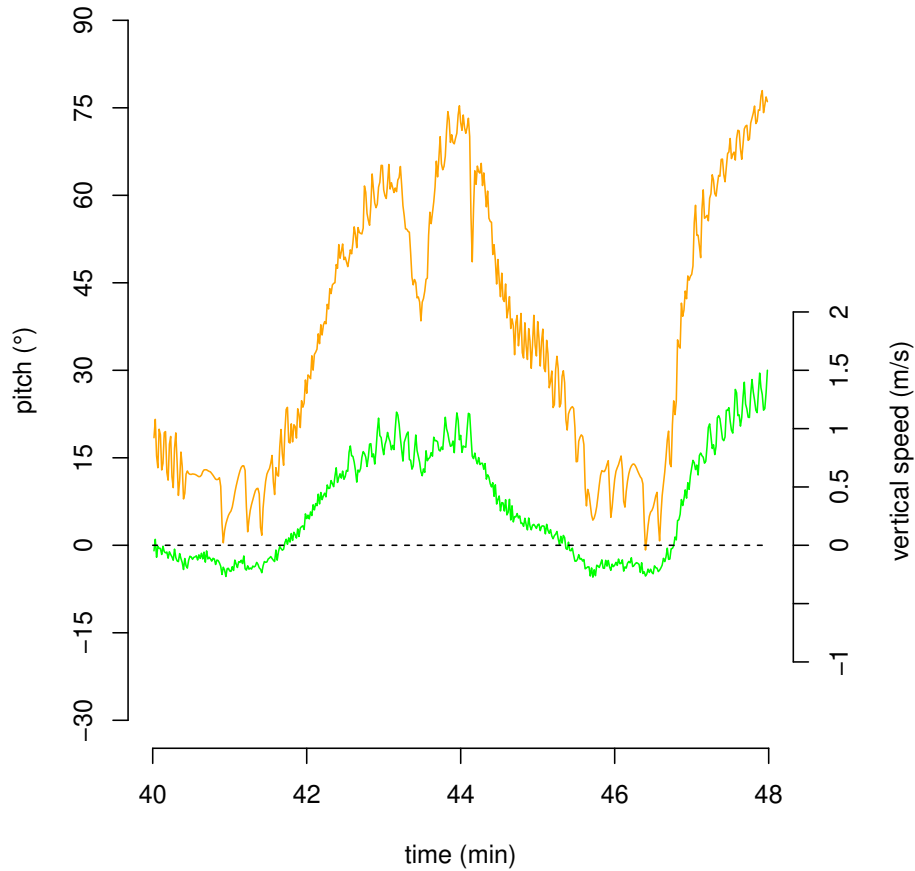


Figure S2.2: Pitch and vertical speed during the whale ascent. Pitch is computed from the accelerometer and accelerometer data (orange) and vertical speed is computed from the depth sensor data (green). On two occasions (around  $t = 41$  and  $t = 46$  minutes), the animal is oriented upwards (pitch is positive) while moving downwards (vertical speed is negative), showing that the direction of the animal movement is different from its longitudinal axis. Therefore, the equal pitch assumption does not hold during the ascent, and the calibration of the relationship from the noise level during this stage is ill-advised.

## Appendix S3 – BUGS code

As detailed in Appendix S4, computations are completed in three steps (CS 1, CS 2, CS 3). First, animal 3D orientation is computed from accelerometer and magnetometer data by simulating BUGS model `orientation` (code below). Second, parameters of the relationship connecting speed to noise level are found by regression (Appendix S2). Third, animal 3D track is computed from the animal orientation found in CS 1, regression parameters found in CS 2, and depth and noise level data, by simulating BUGS model `track` (code below). Propagation of errors from measurements to 3D track is described in Appendix S4.

Index  $i \in \{1, \dots, I\}$  is an index over time stamps,  $I$  is the number of time stamps, and time for index  $i$  is denoted  $\mathbf{t\_i}[i]$ . Although the track considered in this study was processed at a constant, 1-second time step, the BUGS code has been written to deal with any time step (smaller, larger, or adaptive). Time stamps are provided as data to the BUGS models.

In the orientation BUGS model, `sigma_A` and `sigma_M` refer to the standard deviations of the norms of  $\|\mathbf{A}^{a,obs}(t)\|/\|\mathbf{A}^e\|$  and  $\|\mathbf{M}^{a,obs}(t)\|/\|\mathbf{M}^e\|$  (see Appendix S1). Such values are behavioral state-dependent and are therefore indexed by `I_state` (descent: 1, searching for prey: 2, ascent: 3). Variables `sigma_A_i[i]` and `sigma_M_i[i]` refer to  $\sigma_A(t)$  and  $\sigma_M(t)$ , which are equal to half `sigma_A` and `sigma_M` (Appendix S1). Since `sigma_A_i[i]` and `sigma_M_i[i]` represent the standard deviation of the average accelerometer and magnetometer error over a time step of duration  $\mathbf{t\_i}[i+1]-\mathbf{t\_i}[i]$  – while `sigma_A` and `sigma_M` are values for a 1-second time step – values `sigma_A_i[i]` and `sigma_M_i[i]` need to be adjusted in case of time steps smaller or larger than 1 second, which is achieved, by still assuming independent accelerometer and magnetometer errors, by dividing by `sqrt(t_i[i+1]-t_i[i])`.

```
model orientation {
  # heading, pitch, roll of the whale
  # earth frame
  for(i in 1:I){
    # heading
    h_i[i] ~ dunif(-180,180)
    h_cos_i[i] <- cos(h_i[i]/180*pi)
    h_sin_i[i] <- sin(h_i[i]/180*pi)
    # pitch
    p_i[i] ~ dunif(-90,90) # used by the acc/mag data model
    p_cos_i[i] <- cos(p_i[i]/180*pi)
```

```

p_sin_i[i] <- sin(p_i[i]/180*pi)
# roll
r_i[i] ~ dunif(-180,180)
r_cos_i[i] <- cos(r_i[i]/180*pi)
r_sin_i[i] <- sin(r_i[i]/180*pi)
}
# acceleration and magnetic field
# earth frame
for(i in 1:I){
  Ax_earth_i[i] <- 0#ax_i[i]
  Ay_earth_i[i] <- 0#ay_i[i]
  Az_earth_i[i] <- -g#az_i[i]
  Mx_earth_i[i] <- bx
  My_earth_i[i] <- by
  Mz_earth_i[i] <- bz
}
# acceleration and magnetic field
# whale frame
for(i in 1:I){
  Ax_whale_i[i] <- p_cos_i[i]*h_cos_i[i]*Ax_earth_i[i]+p_cos_i[i]
    *h_sin_i[i]*Ay_earth_i[i]+p_sin_i[i]*Az_earth_i[i]
  Ay_whale_i[i] <- (-r_cos_i[i]*h_sin_i[i]-r_sin_i[i]*p_sin_i[i]
    *h_cos_i[i])*Ax_earth_i[i]+(r_cos_i[i]*h_cos_i[i]-r_sin_i[i]
    *p_sin_i[i]*h_sin_i[i])*Ay_earth_i[i]+p_cos_i[i]*r_sin_i[i]
    *Az_earth_i[i]
  Az_whale_i[i] <- (r_sin_i[i]*h_sin_i[i]-r_cos_i[i]*p_sin_i[i]*
    h_cos_i[i])*Ax_earth_i[i]+(-r_sin_i[i]*h_cos_i[i]-r_cos_i[i]
    *p_sin_i[i]*h_sin_i[i])*Ay_earth_i[i]+r_cos_i[i]*p_cos_i[i]
    *Az_earth_i[i]
  Ax_whale_mes_i[i] ~ dnorm(Ax_whale_i[i],pi_A_i[i])
  Ay_whale_mes_i[i] ~ dnorm(Ay_whale_i[i],pi_A_i[i])
  Az_whale_mes_i[i] ~ dnorm(Az_whale_i[i],pi_A_i[i])
  Mx_whale_i[i] <- p_cos_i[i]*h_cos_i[i]*Mx_earth_i[i]+p_cos_i[i]
    *h_sin_i[i]*My_earth_i[i]+p_sin_i[i]*Mz_earth_i[i]
  My_whale_i[i] <- (-r_cos_i[i]*h_sin_i[i]-r_sin_i[i]*p_sin_i[i]
    *h_cos_i[i])*Mx_earth_i[i]+(r_cos_i[i]*h_cos_i[i]-r_sin_i[i]
    *p_sin_i[i]*h_sin_i[i])*My_earth_i[i]+(p_cos_i[i]*r_sin_i
    [i])*Mz_earth_i[i]
  Mz_whale_i[i] <- (r_sin_i[i]*h_sin_i[i]-r_cos_i[i]*p_sin_i[i]*
    h_cos_i[i])*Mx_earth_i[i]+(-r_sin_i[i]*h_cos_i[i]-r_cos_i[i]
    *p_sin_i[i]*h_sin_i[i])*My_earth_i[i]+(r_cos_i[i]*p_cos_i[i]
    *Mz_earth_i[i]
  Mx_whale_mes_i[i] ~ dnorm(Mx_whale_i[i],pi_M_i[i])
  My_whale_mes_i[i] ~ dnorm(My_whale_i[i],pi_M_i[i])
  Mz_whale_mes_i[i] ~ dnorm(Mz_whale_i[i],pi_M_i[i])
}

```

```

}
# standard deviations and precisions
# accelerometer and magnetometer data
for(i in 1:I){
  # the sd of one 3d coordinate component is half the sd of the
  norm
  # A and M are averages over t_i[i+1]-t_i[i] samples
  sigma_A_i[i] <- sigma_A[I_state[i]]/sqrt(t_i[i+1]-t_i[i])/2
  sigma_M_i[i] <- sigma_M[I_state[i]]/sqrt(t_i[i+1]-t_i[i])/2
  pi_A_i[i] <- 1/(sigma_A_i[i]*sigma_A_i[i])
  pi_M_i[i] <- 1/(sigma_M_i[i]*sigma_M_i[i])
}
}

```

```

model track {
# heading , pitch , roll of the whale
# EARTH frame
for(i in 1:I){
  # heading
  h_i[i] ~ dnorm(h_mes_i[i],pi_h_i[i])I(-180,180) # from the acc
  /mag data model
  # pitch
  p_i[i] ~ dnorm(p_mes_i[i],pi_p_i[i])I(-90,90) # from the acc/
  mag data model
  pprime_i[i] ~ dnorm(p_i[i],pi_p)I(-90,90)
  dp_i[i] <- p_i[i]-pprime_i[i]
}
# speed (m/s)
# EARTH frame
for(i in 1:I){
  v_pred_i[i] <- a_v+b_v*log(noiselevel[i])/log(10)
  v_i[i] ~ dnorm(v_pred_i[i],pi_v)I(0,)
}
for(i in 1:I){
  vx_i[i] <- cos(h_i[i]/180*pi)*cos(pprime_i[i]/180*pi)*v_i[i]
  vy_i[i] <- -sin(h_i[i]/180*pi)*cos(pprime_i[i]/180*pi)*v_i[i]
  vz_i[i] <- sin(pprime_i[i]/180*pi)*v_i[i]
}
# location (m)
# EARTH frame
x_i[1] <- 0
y_i[1] <- 0
z_i[1] ~ dnorm(0,1.0E-8)I(,0)
for(i in 1:I){
  x_i[i+1] <- x_i[i]+vx_i[i]*(t_i[i+1]-t_i[i])
}

```

```

    y_i[i+1] <- y_i[i]+vy_i[i]*(t_i[i+1]-t_i[i])
    z_i[i+1] <- z_i[i]+vz_i[i]*(t_i[i+1]-t_i[i])
  }
  # whale known location
  for(i_mes_xy in 1:I_mes_xy){
    x_mes_i[i_mes_xy] ~ dnorm(x_i[i_mes_xy_i[i_mes_xy]],pi_x_i[
      i_mes_xy])
    y_mes_i[i_mes_xy] ~ dnorm(y_i[i_mes_xy_i[i_mes_xy]],pi_y_i[
      i_mes_xy])
  }
  # whale depth (from depth-meter)
  for(i in 1:(I+1)){
    z_mes_i[i] ~ dnorm(z_i[i],pi_z_i[i])I(,0)
  }
  # standard deviations and precisions
  # known location
  for(i_mes_xy in 1:I_mes_xy){
    pi_x_i[i_mes_xy_i[i_mes_xy]] <- 1/(sigma_x_i[i_mes_xy_i[
      i_mes_xy]]*sigma_x_i[i_mes_xy_i[i_mes_xy]])
    pi_y_i[i_mes_xy_i[i_mes_xy]] <- 1/(sigma_y_i[i_mes_xy_i[
      i_mes_xy]]*sigma_y_i[i_mes_xy_i[i_mes_xy]])
  }
  # depth
  for(i in 1:(I+1)){
    sigma_z_i[i] <- sigma_z
    pi_z_i[i] <- 1/(sigma_z_i[i]*sigma_z_i[i])
  }
  # speed
  pi_v <- 1/(sigma_v*sigma_v)
  # angles
  pi_p <- 1/(sigma_p*sigma_p)
  for(i in 1:I){
    pi_p_i[i] <- 1/(sigma_p_i[i]*sigma_p_i[i])
    pi_h_i[i] <- 1/(sigma_h_i[i]*sigma_h_i[i])
  }
}

```

## Appendix S4 – Procedure to distribute track computations on a High Performance Resource (HPR)

The HBM presented in the main document could theoretically be used to process tag data and compute animal 3D orientation and location for the complete track. Computation time for this is, however, prohibitive given the large number of parameters (3D orientation, speed and location at each time step) to be simulated by the MCMC sampler. In order to speed up computations, the parameter estimation procedure is completed in three consecutive steps. First (later referred to as Computation Step 1, CS 1), point estimates of the heading, pitch, and roll (denoted  $h^{est}(t)$ ,  $p^{est}(t)$ , and  $r^{est}(t)$ ) and respective variances ( $\sigma_h^2(t)$ ,  $\sigma_p^2(t)$ , and  $\sigma_r^2(t)$ ) are computed from the accelerometer and magnetometer data by simulating the HBM defined by equations (1) to (4). The BUGS code for this reduced model is provided in Appendix S3. Second (CS 2), parameters of the relationship connecting speed to noise level are found by using noise level data, depth data, and point estimates of the animal pitch found in CS 1 (details are provided in Appendix S2). Third (CS 3), animal 3D track is computed from the orientation found in CS 1, regression parameters found in CS 2, depth data, and noise level data. In CS 3, the animal location and orientation are simulated by using the priors

$$\begin{cases} h(t) \sim \text{Normal}(h^{est}(t), \sigma_h^2(t)) \\ p(t) \sim \text{Normal}(p^{est}(t), \sigma_p^2(t)) \end{cases} \quad (\text{S2-2})$$

together with the HBM defined by equations (5) to (10). The BUGS code for this reduced model is also provided in Appendix S3. Initializations for CS1 were computed by adding noise to accelerometer and magnetometer data (using noise model described in Appendix S1) before calculating heading, pitch, and roll as suggested by Johnson & Tyack (2003). Initializations for CS3 were computed by adding noise to heading and pitch output from CS1 (using equation S2-2) as well as to depth measured values and by reconstructing tracks by dead-reckoning.

To take advantage of high performance resources (HPR), animal location and orientation (CS 1 and 3) are computed by splitting the whole track into  $m$  consecutive pieces (time stamps are relabeled  $t_{j,i} = t_0 + \sum_{j'=1}^{j-1} \Delta t_{j'} + i$ ,  $\Delta t_j$  is the duration of piece  $j \in \{1, \dots, m\}$ ,  $i \in \{0, \dots, \Delta t_j\}$ ). Tag data at time  $t \in [t_0, t_{end}]$  provide information on the orientation of the animal only for time  $t$  and information on the location of the animal only for subsequent timing  $[t, t_{end}]$ . Consequently, computation of animal orientation (CS 1) for all pieces can be carried out independently of each other and computation

of animal location (CS 3) can be carried out sequentially. The error on the animal estimated location at the end of some piece  $j \in \{1, \dots, m - 1\}$  is propagated as an error on the 'observed' location at the beginning of piece  $j + 1$ . This could be achieved by updating equation (9) accordingly, the 'observed' coordinates of the animal at time  $t_{j+1,0}$  would be in that case

$$\begin{cases} x(t_{j+1,0}) \sim \text{Normal}(x^{est}(t_{j,\Delta_j}), \sigma_x^2(t_{j,\Delta_j})) \\ y(t_{j+1,0}) \sim \text{Normal}(y^{est}(t_{j,\Delta_j}), \sigma_y^2(t_{j,\Delta_j})) \end{cases} \quad (\text{S2-3})$$

where  $x_j^{est}(t_{j,\Delta_j})$ ,  $y_j^{est}(t_{j,\Delta_j})$  are the point estimated  $x$ - and  $y$ - coordinates of the animal at time  $t_{j,\Delta_j}$  and  $\sigma_x^2(t_{j,\Delta_j})$ ,  $\sigma_y^2(t_{j,\Delta_j})$  their respective variances. Computations for pieces  $j \in \{1, \dots, m\}$  would still need to be carried out one after the other (simulation of piece  $j$  requires the output for piece  $j - 1$ ) and could not be parallelized in order to take benefit from HPR. Another option is to carry out CS 3 for all pieces independently of each other and to propagate localization errors by post-processing. In that case, CS 3 is performed by setting  $x(t_{j,0})$  and  $y(t_{j,0})$  to zero with null variances ( $j \in \{1, \dots, m\}$ ). For  $j = 1$  to  $j = m - 1$ , the point estimate and the variance of the location estimate at time  $t_{j,\Delta_j}$  are added to the point estimates and variances of the location estimate for times  $t_{j+1,0}$  to  $t_{j+1,\Delta_{j+1}}$ . This option, enabling the distribution of track computations on a HPR, has been applied in order to produce the results presented in the main document.

The complete track was split into 51 1-minute consecutive pieces and a remaining 20-second piece ( $m = 52$ ,  $\Delta t_j = 60$  for  $j \in \{1, \dots, 51\}$ ,  $\Delta t_{52} = 20$ ). Computation of the orientation of the animal (CS 1) and of the location of the animal (CS 3) required the simulation of 11,000 and 20,000 samples per chain, respectively (see Section 2.3 for more details). For each 1-minute piece, and for each chain, CS 1 and CS 3 respectively required 20 s and 75 minutes of computation time on a single core of an Intel® Xeon E5-2680v2 2.8Ghz 10-core processor. The computation time for the complete dive is consequently of approximately 65 h, which is reduced to 75 minutes by using HPR on 52 cores. Simulation of 4 chains required 5 hours, which could have been reduced to 75 minutes by using 208 cores.

The HPR used in this study (EOS) is structured into 1224 Intel® Xeon E5-2680v2 2.8GHz 10-core processors which are scheduled and controlled by the SMURL resource manager. Simulations were dispatched to 6 processors (60 cores) by using CHDB software running with Intel® MPI library. CHDB (<http://www.calmip.univ-toulouse.fr/spip/spip.php?article465>) was originally designed for bioinformatics purposes to drive the processing of large number of data files on a cluster by the repeated use of a single program. In our case, we used CHDB to process BUGS batch files – one file

per track piece and initialization – with BUGS software. An example of a batch file (here first initialization of the first track piece) is provided below.

```
modelCheck('model/m6_track.R')
modelData('data/data_m6_tC1.txt')
modelCompile(1)
modelInits('init/init_m6_tC1_chain1.txt',1)
modelUpdate(1000,10)
modelSaveState('log/state_m6_tC1_chain1.txt')
samplesSet('deviance')
samplesSet('h_i')
samplesSet('p_i')
samplesSet('pprime_i')
samplesSet('dp_i')
samplesSet('x_i')
samplesSet('y_i')
samplesSet('z_i')
samplesSet('v_i')
modelUpdate(1000,10)
samplesStats('*')
modelSaveState('log/state_m6_tC1.txt')
#samplesCoda('*','coda/coda_m6_tC1_chain1.txt')
modelQuit()
```

BUGS output files (table containing parameter statistics) were later loaded into R and merged together (post-processing described earlier) by using R code below:

```
TRACK=read.table(paste('track/track_tC1.txt',sep=''),header=TRUE)
for(i_traj_id in 2:52){
  traj_id=paste('C',i_traj_id,sep='')
  TRACK_i=read.table(paste('track/track_t',traj_id,'.txt',sep=''),
    header=TRUE)
  # point and interval estimates for heading (h), pitch (p), roll
  (r), speed norm (v)
  # just copy-paste
  TRACK[c('h','p','p2','r','v','h_val2.5pc','h_val197.5pc','p_val2
    .5pc','p_val197.5pc','r_val2.5pc','r_val197.5pc','p2_val2.5pc
    ','p2_val197.5pc','v_val2.5pc','v_val197.5pc','dp_val2.5pc','
    dp_val197.5pc')][nrow(TRACK),]=TRACK_i[c('h','p','p2','r','v
    ','h_val2.5pc','h_val197.5pc','p_val2.5pc','p_val197.5pc','
    r_val2.5pc','r_val197.5pc','p2_val2.5pc','p2_val197.5pc',
```



```

    v_val2.5pc', 'v_val97.5pc', 'dp_val2.5pc', 'dp_val97.5pc'))][1,]
# point estimates for horizontal location (x and y)
# add
TRACK_i['x']=TRACK_i['x']+TRACK['x'][nrow(TRACK),]
TRACK_i['y']=TRACK_i['y']+TRACK['y'][nrow(TRACK),]
# variances for horizontal location (x and y)
# add
TRACK_i['x_sd']=sqrt(TRACK_i['x_sd']^2+TRACK['x_sd'][nrow(TRACK)
,]^2)
TRACK_i['y_sd']=sqrt(TRACK_i['y_sd']^2+TRACK['y_sd'][nrow(TRACK)
,]^2)
TRACK=rbind(TRACK, TRACK_i[-1,])
}
# interval estimates for horizontal location (x and y)
TRACK$x_val2.5pc=TRACK$x-2*TRACK$x_sd
TRACK$x_val97.5pc=TRACK$x+2*TRACK$x_sd
TRACK$y_val2.5pc=TRACK$y-2*TRACK$y_sd
TRACK$y_val97.5pc=TRACK$y+2*TRACK$y_sd
write.table(TRACK, 'track_full.txt', quote=FALSE)

```

## Appendix S6 – Investigating sensitivity to variance in pitch anomaly and flow noise relationship

Animal track in this study was reconstructed by using the speed-noise relationship calibrated using data from the animal descent ( $a_v = 4.53$ ,  $b_v = 1.16$ ,  $\sigma_v = 0.08$ ) with a moderate pitch anomaly ( $\sigma_p = 5^\circ$ ). One could theoretically calibrate the speed-noise relationship using data from the animal ascent, although this appears strongly ill-advised since during this stage the direction of the movement differs from the animal's axis (Appendix S2). One could also consider a higher pitch anomaly ( $\sigma_p = 10^\circ$ ), although once again this seems ill-advised since model comparison strongly suggested to consider the more moderate value  $\sigma_p = 5^\circ$ . Nevertheless, to explore the sensitivity of the localization process to such choices, we compare the animal track's reconstruction considering the 4 possible combinations of: (1) either the animal descent or ascent to calibrate the speed-noise relationship and (2) either moderate ( $\sigma_p = 5^\circ$ ) or high ( $\sigma_p = 10^\circ$ ) pitch anomaly (Figure S6-1). The distance between the track presented in the main document and (respectively) the track using data from the animal descent and  $\sigma_p = 10^\circ$ , data from the animal ascent and  $\sigma_p = 5^\circ$ , and data from the animal ascent and  $\sigma_p = 10^\circ$  are  $17.4 \pm 14.5$  m,  $124.6 \pm 70.5$  m, and  $173.9 \pm 92.6$  m. As discussed, the model, while considering various sources of errors, assumes that parameters  $a_v$ ,  $b_v$ ,  $\sigma_v$ , and  $\sigma_p$  are perfectly known. We therefore highlight (i) the critical choice for 'known' parameters (in this case  $a_v$ ,  $b_v$ ,  $\sigma_v$ , and  $\sigma_p$ ) in the track reconstruction process and the need, as was done here, to support the choice of their values from data, and (ii) the underestimate of confidence intervals width on estimated locations since variances of parameter estimates are conditional on the model being true, which ignores additional variability not accounted for in the model. In our case, results ignore errors originating from the divergence between the truth and the model for the speed-noise relationship (inaccurate parameter values or relationship) and the pitch anomaly process (inaccurate parameter value or relationship).

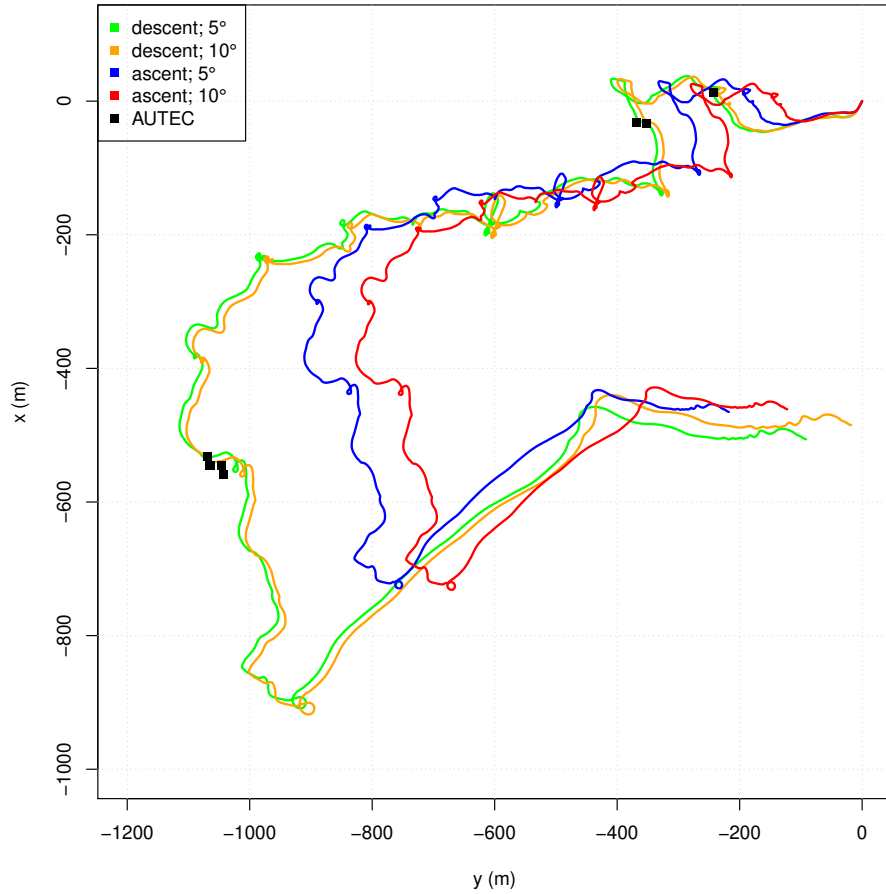


Figure S6.1: Reconstructed track for different options of calibration of the speed-noise relationship and different amplitude of pitch anomaly. The track presented in the main document (green; color line in Figure 4) has been reconstructed by calibrating the speed-noise relationship using data from the animal descent with a moderate pitch anomaly ( $\sigma_p = 5^\circ$ ). Other options are considered (orange: calibration using data from the descent,  $\sigma_p = 10^\circ$ ; blue: ascent,  $\sigma_p = 5^\circ$ ; red: ascent,  $\sigma_p = 10^\circ$ ). Locations found from the independent acoustic survey are also plotted (black dots).