

1 Optimal navigation and behavioural traits in 2 oceanic migrations

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11 Key words: Long-distance migrations, migration routes, behavioural traits, decision making, mechanistic
12 modelling, optimal control

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14 This manuscript is the preprint of the article published in Theoretical Ecology, accessible here:

15 <https://link.springer.com/article/10.1007/s12080-020-00469-4>

16

17 **Abstract**

18 Many organisms perform regular migrations over long distances. These movements are often related to
19 feeding and reproductive periods, and regulated by oceanographic conditions as well as physiological and
20 behavioural traits. Different individual traits and their associated evolutionary constraints will ultimately
21 shape the migratory strategy (and route) of individuals. Optimality theory can provide a framework to
22 assess these inherent trade-offs in individual migrations and identify optimal migration routes in different
23 conditions. Here, we present a model that describes the behavioural trade-off between migration time
24 and energy expenditure and identifies optimal migration routes in realistic ocean conditions. The model
25 explicitly includes a behavioural factor for individual risk management, including risks associated with

26 moving in a stochastic environment. We test this model in three different case studies, one in an idealized
27 theoretical context and two in realistic conditions for sea turtle migrations. We show that behavioural
28 traits can largely influence the optimal routes in long-distance migrations, resulting in major changes in
29 migratory pathways. Further, we assess the ability of the model to infer back behavioural traits given a set
30 of synthetic individual tracks and show relatively good performances. However, further tests are needed
31 to evaluate performances when accurate observations of migrations are used.

32 **1. Introduction**

33 Migrations are common phenomena in terrestrial and aquatic ecosystems typically associated to the most
34 important tasks in the organisms' life history: feeding, survival and reproduction (Dingle 2014). In some
35 groups of birds, marine mammals and fish, these migrations can span thousands of kilometres literally
36 covering the entire planet (Alerstam et al. 2003; Block et al. 2011). Despite the strong selective pressures
37 on migrations, diverse strategies can coexist even within population of the same species including partial
38 migration, different time of departures, distinctive destinations, number of stopovers, moving speed, etc.
39 (Alerstam 2001; Byron and Burke 2014). The existence of these widely variable migration strategies has
40 generated questions regarding the adaptive value of migrations and the relative importance of ecological
41 and evolutionary processes in shaping them (Alerstam et al. 2003; Cardona et al. 2017; Dalleau et al. 2019).

42 The details of migration patterns have been studied for a range of marine species (see e.g. Nichols et al.
43 2000; Bonfil et al. 2005; Aarestrup et al. 2009; Block et al. 2011), and several mechanisms have been
44 suggested for both proximate and ultimate causes driving such processes. Genetic, physiological and
45 behavioural adaptations are considered key attributes for the evolution of migrations (Alerstam et al. 2003;
46 Dingle 2014; Lennox et al. 2016). Generally, migrants undergo these long journeys to find more favourable
47 conditions such as better food, reduced predator pressure, better environmental conditions (Alerstam et
48 al. 2003; Shaffer et al. 2006; Block et al. 2011). The knowledge of migration routes can be innate, learnt
49 through natal homing or taught by other individuals. (Fagan et al. 2013; Mueller et al. 2013; Scott et al.
50 2014). Specific physiological adaptations have been identified in long distance migrants which can expose
51 them to potential vulnerabilities under environmental disturbances including climate change (Feder et al.
52 2010; Lennox et al. 2016). On the other hand, plasticity in behavioural traits can directly affect migration
53 routes adapting them to changing food availability, temperature and ocean currents (Jørgensen et al. 2006;
54 Block et al. 2011; Hays et al. 2014b) .

55 In particular, advection by ocean currents can have a large impact on the realized migration routes
56 (Thomson et al. 1992; Luschi et al. 2003; Metcalfe et al. 2006; Hays et al. 2014a). The impact can be either
57 negative in case of counter-current or lateral drift, or positive when favourable ocean currents allow
58 reaching the destination faster and/or with less energy. While it is well known that migrating birds can
59 adjust their speed in response to local wind conditions (i.e., increasing it in headwinds and reduce it in
60 tailwinds (Bloch and Bruderer 1982)), mechanisms for navigation and active control of speed and heading
61 in marine organisms are less clear (Hays et al. 2003; Åkesson and Hedenström 2007).

62 Optimality methods can be used for the analyses of behavioural strategies and adaptations in the long-
63 distance migrations of several species (Hedenström 2003; Alerstam 2011) but presently few applications
64 can be found for marine organisms (but see Hays et al. 2014a). An optimality approach may assist in
65 providing reference solutions to compare against observed migrations tracks and to infer whether specific
66 individual behaviour is directed towards saving energy, reduce migration time, avoid competition and
67 predators, maximize reproduction, etc. (see e.g. Carmel and Ben-Haim (2005) in the case of foraging
68 theory). In the case of movements in ocean currents the optimality solution to minimize migration time is
69 analogous to solving Zermelo's navigation problem (Zermelo 1931) where a boat crossing a shear flow at
70 constant speed can reduce navigation time by deviating its route from a simple straight line linking initial
71 and final destination points. However, animal migrations are subject to additional physiological and
72 behavioural constraints that could modify the identification of optimal tracks when only a minimization of
73 migration time is considered.

74 In this paper, we present a minimal theoretical mechanistic framework to investigate optimal migratory
75 routes in relation to ocean currents, behavioural and physiological constraints. The model links a
76 description of different behavioural traits to the external factors during migration (e.g. ocean currents and
77 turbulence) and provide the optimal navigational strategy in a stochastic environment. This approach is a
78 generalization of Zermelo's navigation problem where noise as well as animals' behavioural and
79 physiological constraints are specifically included.

80 The model is illustrated for the case of sea turtle migrations in realistic conditions and contrasting ocean
81 regions, where detailed description of migration routes are available in the literature. Hundreds of random
82 tracks are generated in those areas, and the model outputs are compared with available observations.
83 Further, the model is used to infer back the underlying behavioural traits shaping such migration routes,
84 demonstrating skills and limitations of the proposed approach. We suggest that the optimality model

85 presented here could be combined with high-resolution animal tracking technologies to gain insight about
86 the specific behaviour ecology of the migrants.

87

88

89 2. Methods

90

91 2.1 Model formulation

92 We consider a minimal model for the migration of single individuals that are able to swim and adjust their
93 velocity based on local ocean current conditions. We model the local ocean currents by the sum of a mean
94 velocity component (i.e., $v(x)$) and a white-noise process with diffusion coefficient D . The latter represents
95 small scale fluctuations associated to e.g., mesoscale and/or ocean turbulence processes. We further
96 assume that an organism can control its movement and swim at the control velocity w . Then, the dynamics
97 of the migrant can be described by the following Itô stochastic differential equation (Øksendal 2003):

$$dX_t = (v(X_t) + w(X_t))dt + \sqrt{2D}dB_t \quad (1)$$

98 where X_t is the position of the organism in two dimensions at time t , while B_t is two-dimensional standard
99 Brownian motion. For long-distance regular migrants, evolutionary constraints will benefit behavioural
100 and physiological traits able to minimize the time needed to reach the target while limiting the energy
101 spent on migration. Hence, we can define the total cost of travelling to the target:

$$C = \frac{\gamma}{2} \int_0^T |w(X(t))|^2 dt + \beta T, \quad (2)$$

102 where T is the total duration of the migration event and β and γ are the parameters defining the trade-off
103 between time and energy, respectively. This cost explicitly describes the trade-off between time taken to
104 reach the target and the energy expenditure required to swim at the control velocity w . We assume that
105 the energy expenditure related to swimming scales with the square of the control speed which seems to
106 be consistent with experimental data from turtles (Prange 1976). Other metabolic expenses (e.g., basal
107 metabolism) are assumed to be a linear function of time. We do not consider energy acquisition during
108 the migration (or only implicitly and at a constant rate). Within this framework, when the flow is absent,

109 the optimal control is trivially a straight line from the starting point to the target, but when the flow field
 110 is present the optimal control can lead to a variety of trajectories (Bryson and Ho 1975; Comincioli 2010;
 111 Hays et al. 2014a). Zermelo’s problem was formulated as a deterministic control, while we consider here
 112 a stochastic component to account for both the variability of the ocean currents (e.g. mesoscale dynamics)
 113 and for the noise arising from imperfect decisions of the migrants.
 114 The cost C in Eq. 2 is random so the navigation strategy should minimize some statistic of the cost. Here,
 115 we introduce a risk-parameter α that accounts for the specific risk-sensitivity of the organism. Indeed,
 116 different individuals could weight differently the risk associated in moving under uncertainty conditions
 117 and a combination of risk-averse or risk-prone strategies could emerge (Wolf et al. 2007). This is similar to
 118 economic theory when agents need to consider the long-term implications of their instant decisions and
 119 could employ strategies to minimize the risks of worst case scenarios (Whittle 1990). To introduce a risk-
 120 sensitivity trait in the model we hypothesize that the organism aims at minimizing (Howard and Matheson
 121 1972):

$$F = \frac{1}{\alpha} \log \langle E[\exp(\alpha C)] \rangle \quad (3)$$

122 This risk-sensitivity term adds an additional parameter changing the weight of the best or worst possible
 123 occurrences. As α tends to zero, we recover the risk-neutral strategy where the expected cost $E[C]$ is
 124 minimized. However, if α is small but finite, a Taylor’s expansion shows that the function F becomes a
 125 linear combination of mean cost and variance, with α weighing the importance of the latter with respect
 126 to the former. In general, $\alpha > 0$ corresponds to a risk-averse strategy, where outcomes with high values of
 127 the cost are penalized heavily so that the optimal strategy focuses on these worst-case scenarios (the goal
 128 is to decrease the variance). Conversely, $\alpha < 0$ corresponds to a risk-seeking attitude where the few best-
 129 case scenarios are rewarded (the variance is valued).

130 Given the three behavioural traits α , β and γ the cost F can be computed at all points of the ocean basin
 131 using Dynamic Programming (Bellman 1954; Øksendal 2003). F is then given as the solution to the
 132 following Hamilton-Jacobi-Bellman equation:

$$v \cdot \nabla F + \left(D\alpha - \frac{1}{2\gamma} \right) |\nabla F|^2 + D\nabla^2 F = -\beta, \quad (4)$$

133 with boundary conditions $F=0$ at the target and reflective (Neumann) boundary conditions elsewhere.

134 This equation can be rewritten using the transformation (Dvijotham and Todorov 2011):

$$F = \frac{1}{\delta} \log(Z), \text{ where } \delta = \alpha - \frac{1}{2D}, \quad (5)$$

135 then leading to the following partial differential equation (PDE):

$$v \cdot \nabla Z + D \nabla^2 Z + \delta \beta Z = 0. \quad (6)$$

136 Once this equation is solved, the optimal control velocity at any point can be found using the gradient of
137 the cost:

$$w = -\frac{1}{\gamma} \nabla F \quad (7)$$

138 The derivation of these equations is justified in more details in supplementary material S1. Eq. 6 is solved
139 using COMSOL (COMSOL Multiphysics ® v. 5.2. www.comsol.com. COMSOL AB, Stockholm, Sweden)
140 coupled to MATLAB 2016b (MATLAB 2016b, The MathWorks Inc., Natick, MA, 2000, United States of
141 America) via Livelink. The code needed to run the model described here is available as supplementary
142 material.

143 2.2 Reconstruction of behavioural parameters

144 The objective of the statistical inference is to estimate the behavioural parameters based on observed
145 tracks of the organisms, i.e. sets of points $\xi = (X_i, t_i)_{i \in [1, N]}$, where X_i is the position of the organism at the time
146 t_i . For a given set of behavioural traits, the following quasi log-likelihood is defined:

$$L(\xi \mid \alpha, \beta, \gamma) = - \sum_{i=1}^{N-1} \| (X_{i+1} - X_i) - (v(X_i) + w(X_i)) \cdot (t_{i+1} - t_i) \|^2 \quad (8)$$

147 This log-likelihood function measures the difference between the measured speed vector and the
148 theoretical speed vector at each point of the track. The log-likelihood is maximized numerically with a
149 Nelder-Mead algorithm (Lagarias et al. 1998), thus identifying behavioural traits that fit the migration
150 event the best.

151 Note that the two parameters we aim to reconstruct are α and β/γ . This is because varying β and γ
152 together is redundant when $\alpha = 0$ and only the cost ratio β/γ matters. Conveniently, this ratio is also the
153 most interesting value in an ecological context representing the relative allocation between swimming and
154 metabolic expenditures. Similarly, we are interested in identifying the main patterns in risk-averse or risk-
155 seeking behaviour, hence we only focus on the sign of α more than on its absolute value. Indeed the exact
156 value of α is difficult to associate to specific life-history characteristics and can also be expected to rapidly
157 change over time.

158 When α is very small, we recover the cost ratio C from eq. (2) and thus the control w is invariant if we
159 multiply both β and γ by a constant λ :

$$160 \quad w = \frac{-1}{\lambda\gamma} \nabla(\lambda F) = \frac{-1}{\gamma} \nabla F.$$

161 The diffusivity D is given and considered constant throughout the migration event. A value of $D =$
162 $1000\text{m}^2 \cdot \text{s}^{-1}$ is used corresponding to an average horizontal turbulent diffusivity in the oceans (Cole et
163 al. 2015). The effects of different values of the diffusion term have been analysed in more details in the
164 supplementary material. Eq. 8 has been selected after testing different log-likelihood functions including
165 those reconstructing the diffusivity values. We selected the log-likelihood function that reconstructed the
166 behavioural traits in the theoretical case with the smallest error.

167 To test the method, artificial trajectories with random behavioural traits were generated. Then
168 behavioural traits could be inferred using eq. (8) and compared with the initial ones to evaluate the
169 accuracy and precision of the reconstructing method. α could vary between -10 and 1, and β/γ between
170 10^{-2} and 10^2 .

171 To better compare the reconstruction between different scenarios, the cost ratio has been
172 adimensionalised, meaning that it is defined as $\beta/(\gamma|w|^2)$, with $|w|$ the mean control speed during the
173 migration. For each reconstructed parameter X (α or the adimensional cost ratio), we calculate the
174 reconstruction error as $\frac{X_{generated} - X_{reconstructed}}{X_{generated}}$.

175

176 **2.3 Case studies**

177 Three case studies have been investigated ranging from purely theoretical to more realistic scenarios: (1)
178 organisms crossing a shear flow ($\vec{v} = c\vec{e}_x$) from different starting points; (2) migrations of sea turtles from
179 Ascension Island to the Brazilian coast mimicking observations on green turtles (Luschi et al. 1998); (3) sea
180 turtle migrations from Diego Garca in the Indian Ocean to the Somalian coast (a migration route that was
181 also observed for green turtles (Hays et al. 2014b)). The last two study cases used realistic oceanic
182 conditions, with averaged ocean currents corresponding to the relevant migration periods obtained from
183 the Operational Mercator global ocean analysis and forecast system (available at
184 <http://marine.copernicus.eu>) with a frequency of one day and a spatial resolution of 10km. The
185 oceanographic current field considered is the multi-year average (2007-2016) surface currents in the

186 region during the migration windows of the green turtles. To this average current velocity, we added the
187 diffusivity term modelled as in Eq. 1. For the the Atlantic Ocean case, the migration window considered
188 was between April and August (Luschi et al. 1998), and for the study case in the Indian Ocean between
189 October and February (Hays et al. 2014b).

190

191 **3. Results**

192 **3.1 Track generation**

193 3.1.1 Crossing a simple shear flow

194 Different behavioural traits values (α, β, γ) generate substantially different trajectories when crossing a
195 shear flow (Figure 1). Typically, lower values of α yield longer migration routes, as individuals would reduce
196 their instantaneous cost to a minimum and swim actively only when it is necessary to reach the final
197 destination. Risk-averse individuals tend to avoid regions of high currents pointing towards unfavourable
198 directions. There is an inverse proportionality between β and γ hence their ratio regulate the shape of
199 the migration route. A high ratio β/γ means that the optimal strategy is achieved by reducing the
200 migration time more than minimizing energy expenditures. Thus with high β/γ organisms should rely less
201 on the currents, resulting in trajectories that are generally straighter and with a higher control speed,
202 hence shorter navigation time. Varying γ with a fixed β would give the same results as varying β with a
203 fixed γ (Figure 1).

204 3.1.2 Migration from Ascension Island to Brazil

205 Using random values for (α, β, γ) in an Atlantic Ocean setup and starting point on Ascension Island, we
206 obtain tracks converging nicely to the Brazilian coast which is the assumed target destination region. The
207 geographical locations of these tracks vary from northern routes (using the fast equatorial current in the
208 north) to southern migrations with a course correction as approaching the Brazilian region. The simulated
209 tracks resemble those observed in the feeding migration of green turtles although model tracks are
210 generally straighter than the ones recorded. Indeed, some turtles have been observed to arrive at more
211 northern regions than our tracks, making use of the southern edge of the Equatorial current (Luschi et al.
212 1998). The obtained mean control speed in our simulations is in the range 0.74-1.69 km/h (1st and 3rd
213 quartile, median 1.58 km/h) with the fastest migration at 3 km/h on average (supplementary material).

214 Interestingly, these optimal migration speeds are consistent with recorded transit speeds for green turtles
215 from Ascension Island (0.9 and 3.1 km/h from Luschi et al. (1998) and Akesson et al. (2003)).

216

217

218 3.1.3 Migration from Diego García to Somalia

219 The monsoon-driven circulation in the Indian ocean (Schott and McCreary 2001) yields average ocean
220 currents having a more complex spatial structure than those in the Atlantic Ocean case study. As a result,
221 small changes in the behavioural traits can result in large displacement of the optimal migration tracks (Fig.
222 3). Migrations are generally northwards but with different latitudinal gradients, resulting in routes close
223 to a straight line to those displaying several course corrections patterns. The recorded migration patterns
224 of green turtles in the Indian Ocean vary a lot indicating the potential role as milestones of the many small
225 island in the region (Hays et al. 2014b). This factor—together with course correction driven by other
226 environmental cues (e.g., temperature and salinity gradients, geomagnetic field (Akesson et al. 2003;
227 Åkesson and Hedenström 2007))— is not included in the model, but on a qualitative level the simulated
228 tracks are consistent with the observations. Optimal control speeds are somewhat low in this region (1st
229 and 3rd quartiles are 0.62 and 0.92 km/h), which is slower than the total speeds recorded in the area for
230 migrating turtles, between 2 and 2.8 km/h (Hays et al. 2014b).

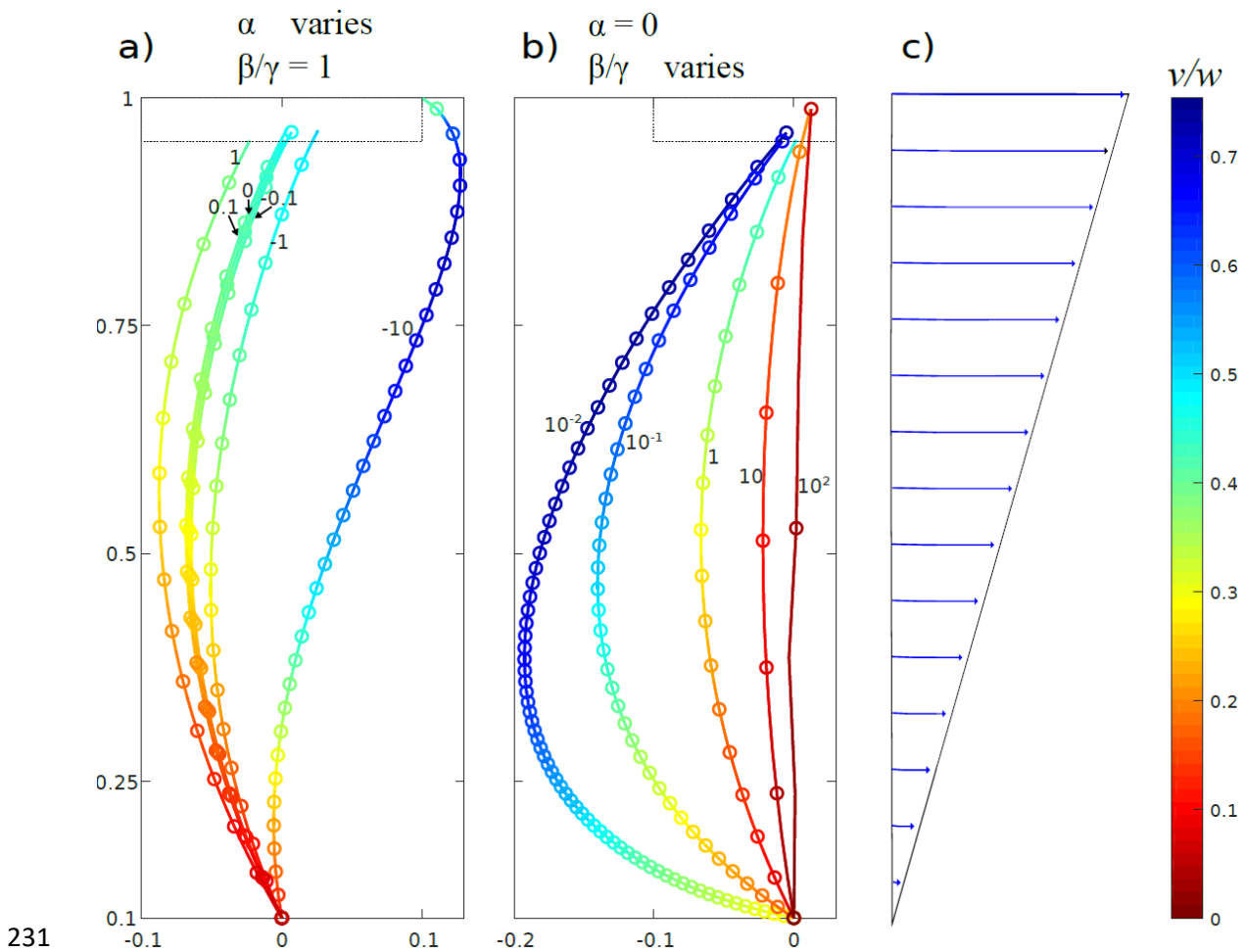


Figure 1 Tracks of migrants crossing a 1 km-long shear flow. The time between two data points is 1 minute, and the colour code shows the ratio between advective and control speed v/w . a) Tracks for different values of α : 1, 0.1, 0, -0.1, 1, 10 (from left to right). b) Tracks for different values of β/γ : 10^{-2} , 10^{-1} , 1, 10, 100 (from left to right). c) Representation of the shear flow used.

231

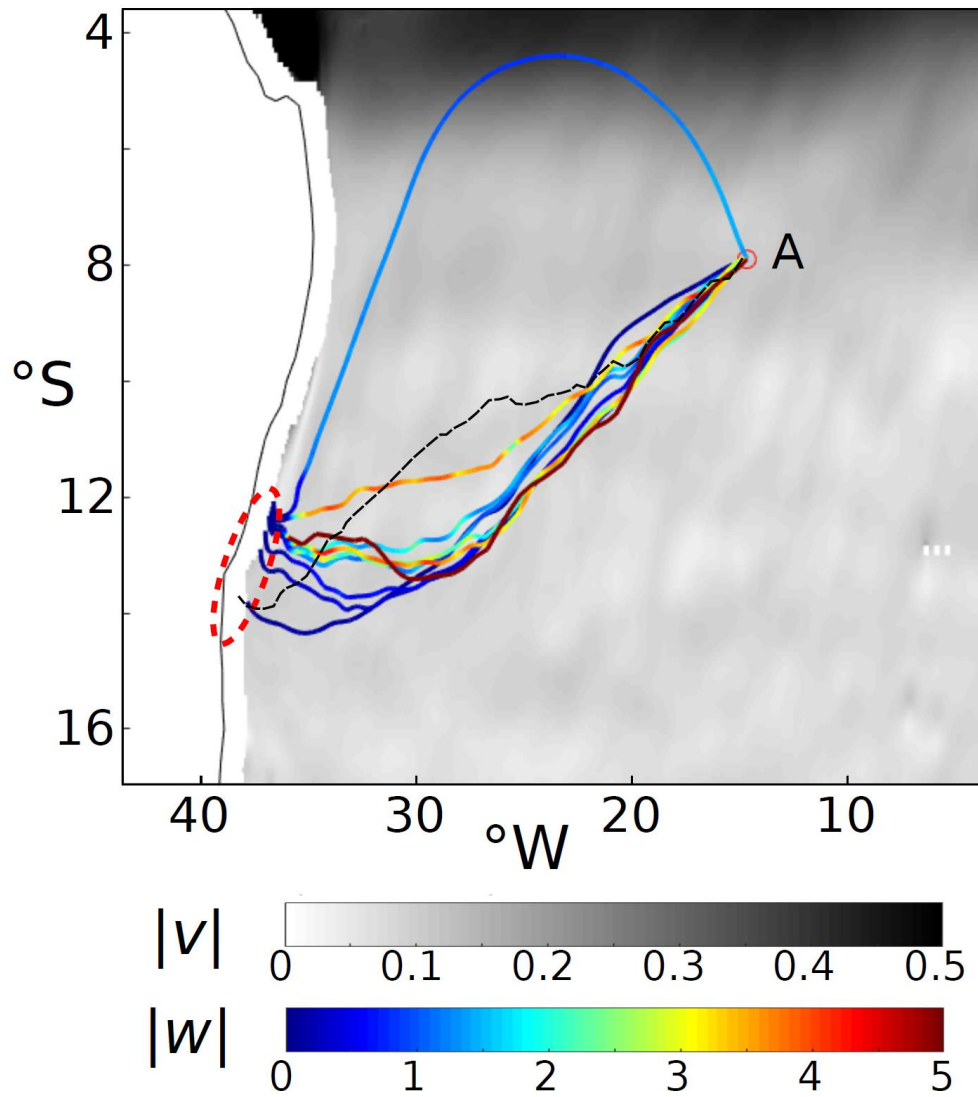
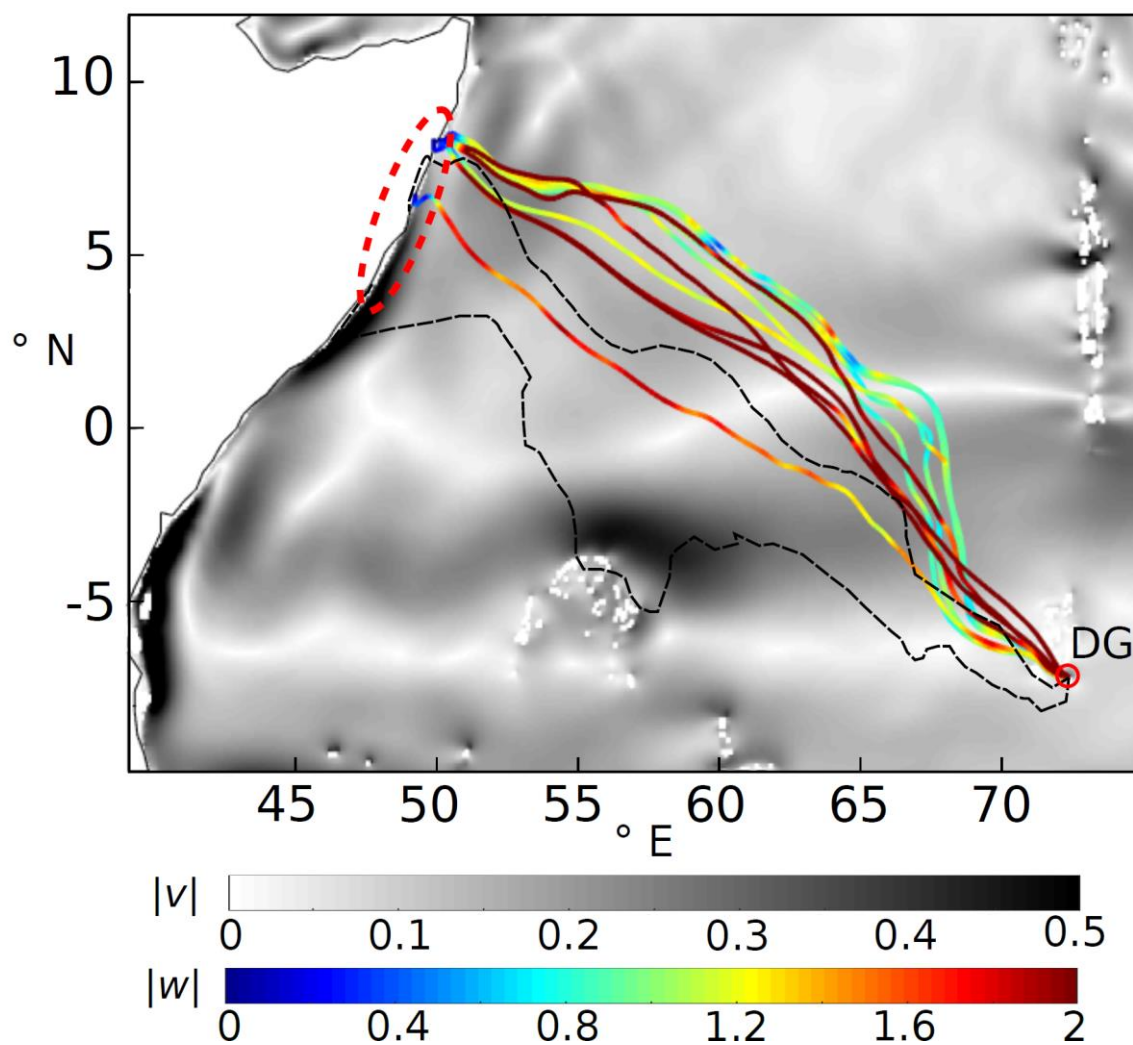


Figure 2 Tracks generated by the model in the Atlantic with random behavioural parameters. The arrival area is the red ellipse, and the departure points is the red circle (A, Ascension Island). Background is the current speed (in m/s), and the track colours represent the control velocity (in m/s). Dashed black line is an original migration track of green turtle, reproduced from Cerritelli et al. (2019).



232

Figure 3 Tracks generated by the model for organisms migrating between Diego García (DG, red circle C) and the Somalian coast (red dashed ellipse) with random behavioural parameters. Background is the current speed (in m/s), and the track colours represent the control velocity (in m/s). Dashed black lines are original migration tracks of green turtles, reproduced from Hays et al. (2014b).

233

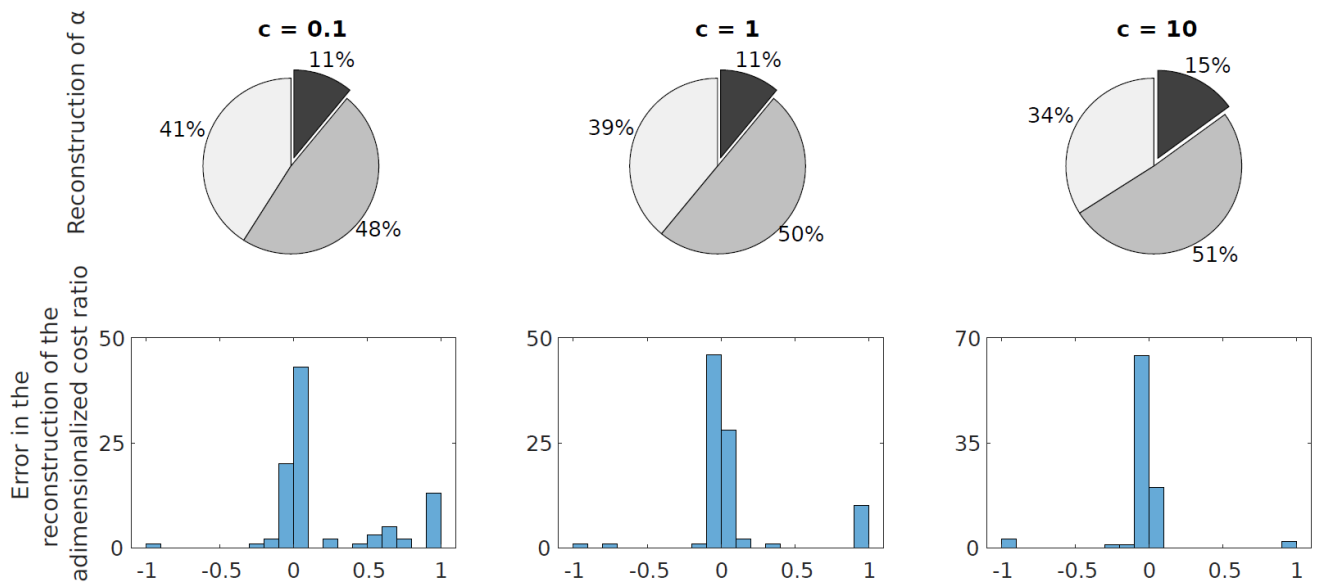
234 3.2 Behavioural parameter inference

235 3.2.1 Reconstruction for the theoretical case

236 Out of the 100 Monte-Carlo simulations of the model with different behavioural traits, some do not lead
 237 to viable trajectories. Moreover, a few iterations of the reconstruction algorithm do not converge. In total,

238 out of 100 simulations, 90 to 93 converge to a proper migration track and lead to a successful
 239 reconstruction.

240 Inference of the sign of the risk-attitude parameter are reasonably accurate (Fig 4). Depending on the
 241 current strength, between 85 and 89% of the risk parameter signs are reconstructed correctly. Inference
 242 of the cost ratio is also relatively accurate: For a small current ($c = 0.1$), 63% of the points are correctly
 243 reconstructed within 10% accuracy. Within the same accuracy envelope, this fraction increases to 74% and
 244 84% when $c=1$ and when $c=10$, respectively.



245 **Figure 4** Top: Reconstruction of the sign of the risk parameter α and of the adimensionalized cost
 ratio in the theoretical cases. For the risk attitude: the dark share of the chart represents the
 misreconstructed signs, the dark grey the correct positive (risk-averse) reconstruction, and the
 light grey the correct negative (risk-seeking) reconstructions. Bottom: For the cost ratio: the
 histograms were constrained between -1 and 1, and all more extreme values were assigned to -1
 (if negative) or 1 (if positive). Each bar represents 10% of error.

246
 247 3.2.2 Reconstruction for oceanic migrations

248 The reconstruction of the risk-attitude is better than in the theoretical case, with between 94 and 98% of
 249 correct reconstructions. The accuracy of the inference of the cost ratio reconstruction is also high: 72% of
 250 the tracks in the Atlantic Ocean (80% in the Atlantic Ocean) lead to reconstructions within 10% accuracy.
 251 However, despite these relatively good performances for such cases, there are a few outliers. For example,
 252 in the Atlantic case, 18% of the reconstructions lead to a cost ratio with an error of more than 200%.

253

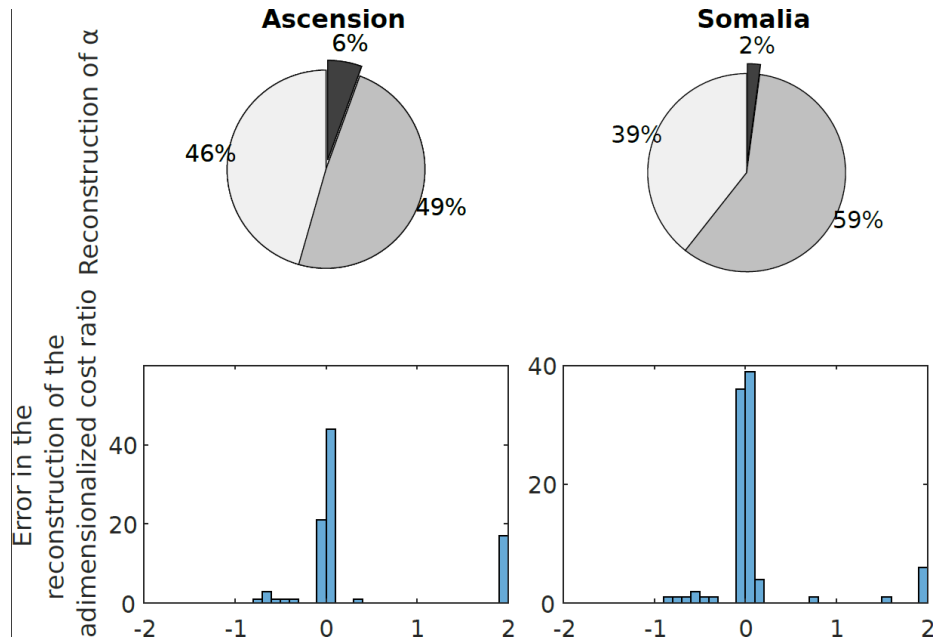


Figure 5 Top: Reconstruction of the sign of the risk parameter α and of the adimensionalized cost ratio in the oceanic cases. For the risk attitude: the dark share of the chart represents the misreconstructed signs, the dark grey the correct positive (risk-averse) reconstruction, and the light grey the correct negative (risk-seeking) reconstructions. Bottom: For the cost ratio: the histograms were constrained between -2 and 2, and all more extreme values were assigned to -2 (if negative) or 2 (if positive). Each bar represents 10% of error.

254

255 4. Discussion

256 We introduced a simple model to simulate optimal migrations under different behavioural traits and
 257 environmental conditions. The model makes explicit the trade-off between energy saving strategies and
 258 arrival time and includes the effects of navigational errors and ocean mesoscale, all considered important
 259 aspects in animal movements (Luschi et al. 2003; Åkesson and Hedenström 2007; Shamoun-Baranes et al.
 260 2010). Additionally, a risk-averse behavioural trait is introduced to identify strategies minimizing the risk
 261 of incurring in large (i.e., above average) costs during the migrations. A few other works have explored
 262 Zermelo’s problem in relation to migration before (e.g., in turtles (Hays et al. 2014a) or birds (McLaren et
 263 al. 2014)), but they did not consider time and energy constraints together and the different optimal
 264 strategies that may arise due to behavioural discrepancies between individuals. Additionally we note that
 265 we do not impose the swimming speed, but both navigation speed and headings are output of the model.

266 Our model generates optimal migration strategies under different behavioural and oceanographic
267 scenarios. When applied to simulate sea turtle migrations in realistic conditions, the model is able to
268 reproduce some of the patterns observed by GPS-tracking. But not all behavioural strategies can lead to
269 viable migrations, as animals cannot reach the target or the target is reached but outside a suitable time
270 window. When provided with a large set of simulated tracks, the model can also be used to infer back the
271 behavioural traits of the organism. Inference of these behavioural traits is proven to be often accurate but
272 errors in the reconstruction are also reported. The model can provide new insight in the behavioural
273 ecology of long distance migrations when used in combination with accurate high-resolution data on
274 animal tracks.

275

276 *Learning and optimization of migration routes*

277 The way organisms select their migration route varies largely between species making it difficult to identify
278 common mechanisms (Mueller et al. 2013; Dingle 2014). However, in different groups, individual learning,
279 social learning and genetic constraints are all considered important components of successful migrations.
280 For example, humpback calves learn their routes during their first years, while they are migrating with
281 their mothers (Clapham and Mayo 1987). This results in later-stage migrations towards mother-defined
282 feeding grounds (Weinrich 1998). Moreover, since whales migrate in pods (at least the females) they can
283 possibly benefit from the social transmission of knowledge (Weinrich 1998), as it has been also
284 hypothesized for other species such as tuna (De Luca et al. 2014) and birds (Mueller et al. 2013). Opposite
285 to the mechanism of learning via social information transfer, turtle hatchlings are completely independent
286 during their first migration (Carr 1987). Hence most likely they have limited, if any, social information about
287 the migration route to take and the hypothesis is that they might rely on the initial dispersal phase to learn
288 migration pathways between nesting site and feeding areas (Hays et al. 2014b; Scott et al. 2014).

289 Regardless of how marine migrants learn their destination, it seems reasonable to assume that strategies
290 minimizing migration time and energy expenditure are favoured in repeated migration events, as it has
291 been found in birds and ungulates for example (Alerstam and Lindström 1990; Alerstam 2001; Bischof et
292 al. 2012). However, results for adult turtles demonstrate that they are not following routes minimizing
293 migration time alone (Hays et al. 2014a). Still they follow routes that are not far from this optimum and
294 able to bring them to their goal. This could indicate that turtles have evolved a successful migration
295 strategy to cope with the year-to-year variability of the ocean circulation, making it interesting to explore

296 optimal migration strategy against multi-year average ocean conditions. It has been suggested that
297 migrating adult turtles cannot effectively perceive current deflection or that their navigation map is not
298 accurate enough to allow optimum route finding (Hays 2017). Here we suggest that including swimming
299 cost and/or differences in individual behaviour could provide a more general framework to assess
300 optimality conditions in long-distance migrants.

301

302 *Risk-attitudes and ocean currents*

303 Ocean currents are highly variable in space and time hence optimization should work on expected
304 conditions over repeated migrations. In the model presented here, we considered average ocean current
305 conditions in the relevant migration period and include a random term to simulate mesoscale activity or
306 likewise to describe year-to-year variability. This should be conditions relevant for the emergence of
307 optimal migration strategies in an environment with known stochasticity.

308 The relationship between expected value and variability is introduced as an additional parameter in the
309 model (α , Eq. 3). If α is zero the optimal strategies would only consider the average ocean currents, while
310 for non-zero values the variance will matter. If α is positive the goal is to decrease the variance, i.e. to
311 avoid worst-case scenarios in migrations. At first, it seems reasonable to assume that organisms may
312 behave as to minimize the likelihood to encounter these high cost events during migration (showing risk-
313 averse behaviour). However, we cannot exclude that some migrants could optimize for a more general
314 trade-off, where an increased risk of high cost would possibly lead to an increased fitness (early arrival
315 may mean the possibility to claim, for example, the best feeding or nesting grounds). In our simulations,
316 we found that when adopting a risk-seeking attitude, some organisms will complete their migration in a
317 more efficient way than risk-neutral or risk-averse individuals, thus reducing their energy expenditure. In
318 some cases, risk-seeking migrants would of course have a worse outcome than organisms more prone to
319 risk mitigation but this behaviour may still prove advantageous in the long run.

320 In more general settings, behavioural experiments highlighted the potential benefits of a bold (or risk-
321 seeking) behaviour (Sundström et al. 2004; Hulthén et al. 2017): bolder fish tend to be more dominant
322 than others, have a higher ingestion rate but also suffer a higher predation rate than shy individuals.
323 Consequently, what risk attitude parameter may emerge for migration events is then a bit unclear, and
324 would probably vary from population to population, and most likely among individuals too. Moreover, we
325 only consider here the risk-attitude as either being risk-seeking or risk-averse. In reality, the risk-parameter

326 α is a continuous variable, and any level of risk may emerge. The reconstruction of the absolute value of
327 the risk parameter is quite poor in our case (see supplementary material), and refining the reconstruction
328 is needed before any conclusion on the absolute risk value of the organisms can be drawn.

329

330 *Model limitations and ecological implications*

331 The mathematical framework proposed is general enough as it relies on few assumptions on the
332 interactions between turbulent flow and animal behaviour. The model is applied on oceanic migrations of
333 turtles but it could similarly be of use in analysing long-distance migrations of other groups such as birds,
334 whales, fish, etc. A major assumption is on the cost function (quadratic form for energy consumption and
335 linear relation with time) enabling to reduce the mathematical system to a relatively simple linear PDE
336 that is then solved with inputs on behavioural traits, current field and migration goal. A more general
337 formulation of the cost function would consider the drag force on the migrants to be quadratic – as for
338 the general case at high Reynolds number. This would then result in a metabolic cost of swimming which
339 scales as the third power of the velocity, which would then complicate the numerical solution of the model
340 as the linearized version will be no longer valid. However, for the specific case analysed here a quadratic
341 metabolic cost is a good approximation for turtles swimming (Prange 1976).

342 The cost function is also regulated by the details on the physiology of different organisms and by the way
343 organisms perform in a turbulent flow. For example, whales can easily overcome the currents and swim
344 towards their destination (Horton et al. 2011), while fish and turtles have been found to rely more on
345 ocean currents (Luschi et al. 2003; Girard et al. 2006). Consequently, migrations in turtles should give
346 greater importance to energy saving strategies when compared to whales. This is a prediction that could
347 be tested when accurate tagging data become available in the future.

348 The feeding regime of organisms may also influence energy constraints during migrations. Some species
349 can feed and replenish energy reserves while migrating (Åkesson and Hedenström 2007; Stamation et al.
350 2007). Others such as green turtles cannot feed in the open ocean, and therefore need to manage
351 cautiously their energy expenditure (Carr and Goodman 1970). The amount of control velocity an
352 individual need to invest during migrations could be also regulated by the extent of the geographic shift.
353 For example, in migrations towards high latitudes, seasonality is important and therefore a precise timing
354 may be necessary to ensure sufficient time to complete tasks such as reproduction or feeding before it is
355 time to migrate again (Both et al. 2010). When the migration is in more temperate regions, the timing may

356 be less critical, and the constraints on arrival time less important. Thanks to the recent effort in assembling
357 global database on movement patterns (e.g. Sequeira et al. (2018), these hypotheses could now be tested
358 with the model by inferring behavioural traits across different biogeographical regions.

359 Organisms can in reality swim or fly in a three dimensional space and not only in a horizontal plane. In the
360 case of sea turtles, this approximation is valid as they remain the vast majority of the migration close to
361 the surface (Hays et al. 2001), where the vertical structure of horizontal currents does not change much.
362 However, for other species diving deeper or flying, individuals may select the area with winds or currents
363 that minimize migration cost (Gauthreaux 1991), subsequently optimizing their migration route in a 3D
364 space rather than a 2D horizontal plane.

365

366 *Statistical inference*

367 The method used for the statistical inference of the behavioural traits performs reasonably well in case
368 of strong flows, while reconstruction errors increase when conditions in ocean currents are weaker. This
369 is not unexpected as weaker ocean currents yield weaker constraints in the migration model hence lower
370 accuracy of the reconstruction algorithm. Different functions have been tested in our analyses of the
371 river case and the results shown here are for the method that provides the best results. However, aiming
372 at reconstruction of behavioural traits from tracking observations, further analyses are required to
373 systematically assess the performance under more general environmental conditions. The algorithm
374 used here (Nelder-Mead simplex algorithm, (Lagarias et al. 1998)) is robust and relatively time-efficient,
375 but other algorithms may be more efficient in the case of local minima leading to inaccurate behavioural
376 traits reconstructions. Finally, the performance of the log-likelihood, as all parameter estimation
377 methods, depends on the type of observations available. Hence, quality observations with many GPS-
378 data points are more likely to yield reliable estimates (and thus, to provide us with insights on the
379 behavioural ecology of long-distance migrants) than observations with lower resolution.

380 **Acknowledgements**

381 This work was supported by the Centre for Ocean Life, a VKR Centre of excellence funded by the Villum
382 Foundation. We thank Susanne Åkesson and Paolo Luschi for the discussions on turtle migrations that
383 motivated the approach presented in the manuscript.

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529

5. Figure captions

Figure 2 Tracks of migrants crossing a 1 km-long shear flow. The time between two data points is 1 minute, and the colour code shows the ratio between advective and control speed v/w . a) Tracks for different values of α : 1, 0.1, 0, -0.1, 1, 10 (from left to right). b) Tracks for different values of β/γ : 10^{-2} , 10^{-1} , 1, 10, 100 (from left to right). c) Representation of the shear flow used.

Figure 2 Tracks generated by the model in the Atlantic with random behavioural parameters. The arrival area is the red ellipse, and the departure points is the red circle (A, Ascension Island). Background is the current speed (in m/s), and the track colours represent the control velocity (in m/s). Dashed black line is an original migration track of green turtle, reproduced from Cerritelli et al. (2019).

Figure 3 Tracks generated by the model for organisms migrating between Diego García (DG, red circle C) and the Somalian coast (red dashed ellipse) with random behavioural parameters. Background is the current speed (in m/s), and the track colours represent the control velocity (in m/s). Dashed black lines are original migration tracks of green turtles, reproduced from Hays et al. (2014b).

Figure 4 Top: Reconstruction of the sign of the risk parameter α and of the adimensionalized cost ratio in the theoretical cases. For the risk attitude: the dark share of the chart represents the misreconstructed signs, the dark grey the correct positive (risk-averse) reconstruction, and the light grey the correct negative (risk-seeking) reconstructions. Bottom: For the cost ratio: the histograms were constrained between -1 and 1, and all more extreme values were assigned to -1 (if negative) or 1 (if positive). Each bar represents 10% of error.

Figure 5 Top: Reconstruction of the sign of the risk parameter α and of the adimensionalized cost ratio in the oceanic cases. For the risk attitude: the dark share of the chart represents the misreconstructed signs, the dark grey the correct positive (risk-averse) reconstruction, and the light grey the correct negative (risk-seeking) reconstructions. Bottom: For the cost ratio: the histograms were constrained between -2 and 2, and all more extreme values were assigned to -2 (if negative) or 2 (if positive). Each bar represents 10% of error.