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Optimal navigation and behavioural traits in oceanic migrations

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Abstract

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

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

1. Introduction

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

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

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

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

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

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

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

2. Methods

2.1 Model formulation

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

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

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

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

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

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

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

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

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

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

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

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:

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

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.

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

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

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

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

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

2.3 Case studies

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

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

3. Results

3.1 Track generation

3.1.1 Crossing a simple shear flow

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

3.1.2 Migration from Ascension Island to Brazil

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

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).

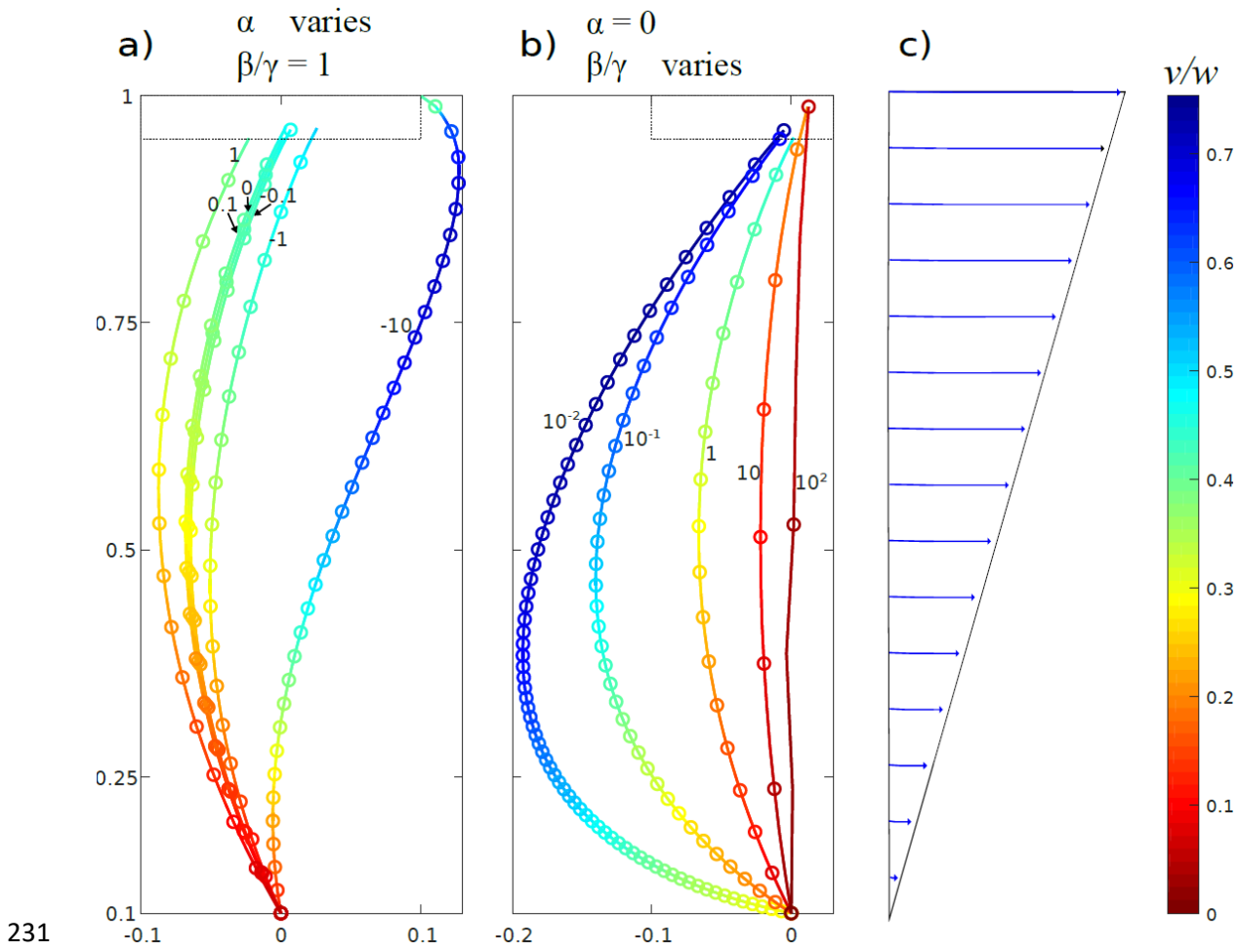


Figure 1 Tracks of migrants crossing a 1 km-long shear flow. The time between two data points is 1 minute, and the colour code shows the ratio between advective and control speed v/w . a) Tracks for different values of α : 1, 0.1, 0, -0.1, 1, 10 (from left to right). b) Tracks for different values of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

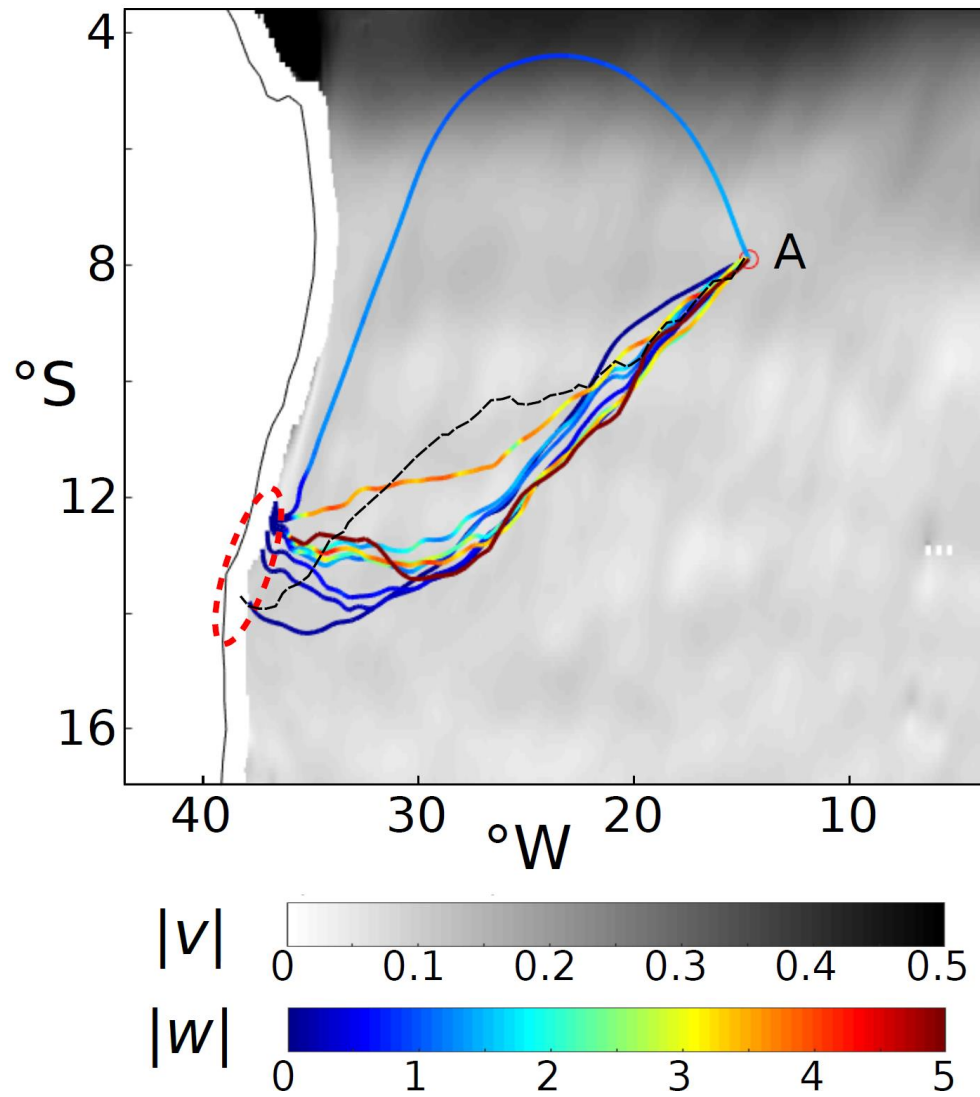


Figure 2 Tracks generated by the model in the Atlantic with random behavioural parameters. The arrival area is the red ellipse, and the departure points is the red circle (A, Ascension Island). Background is the current speed (in m/s), and the track colours represent the control velocity (in m/s). Dashed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

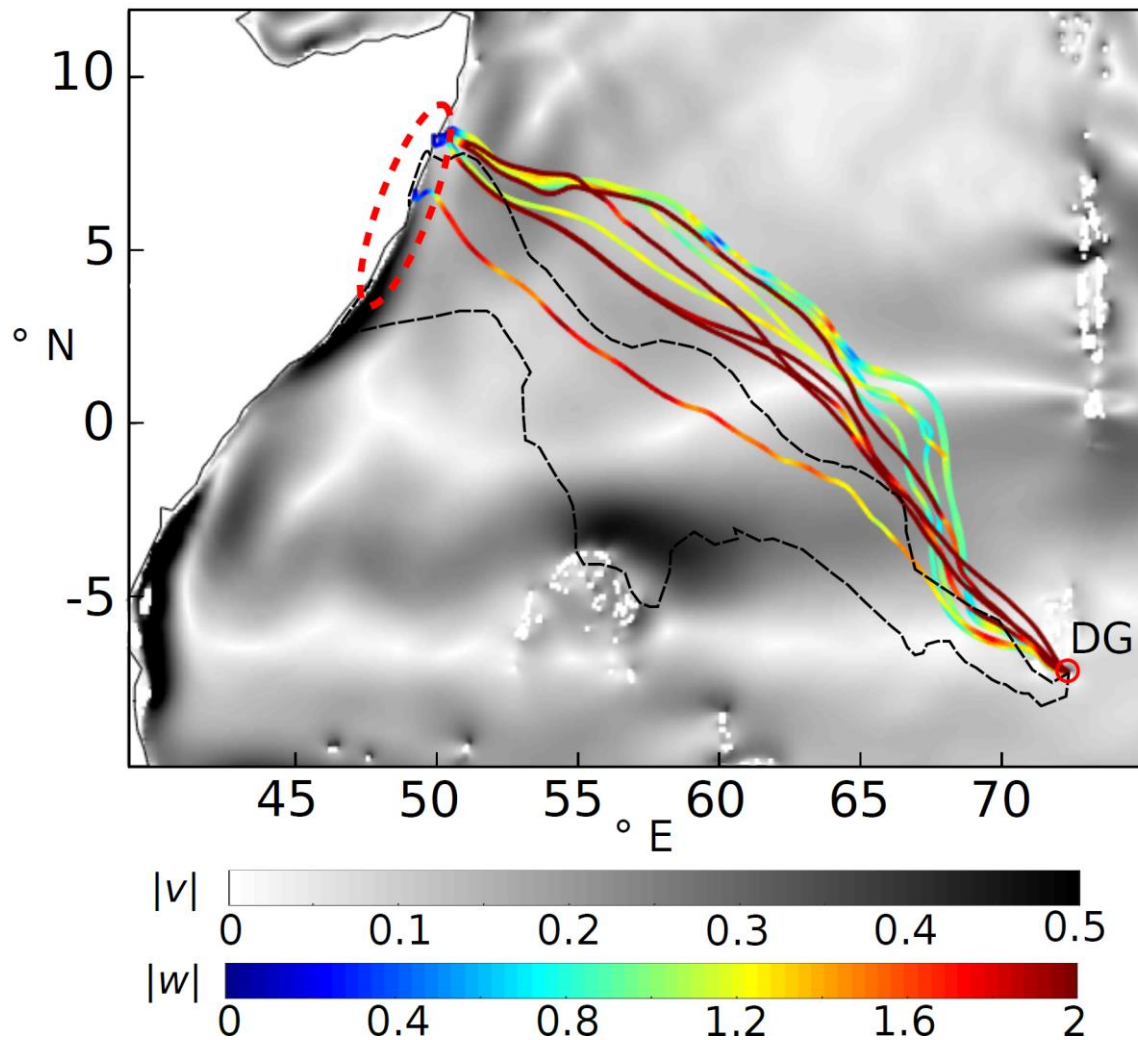


Figure 3 Tracks generated by the model for organisms migrating between Diego García (DG, red circle C) and the Somalian coast (red dashed ellipse) with random behavioural parameters. Background is the current speed (in m/s), and the track colours represent the control velocity (in m/s). Dashed black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

3.2 Behavioural parameter inference

3.2.1 Reconstruction for the theoretical case

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

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

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

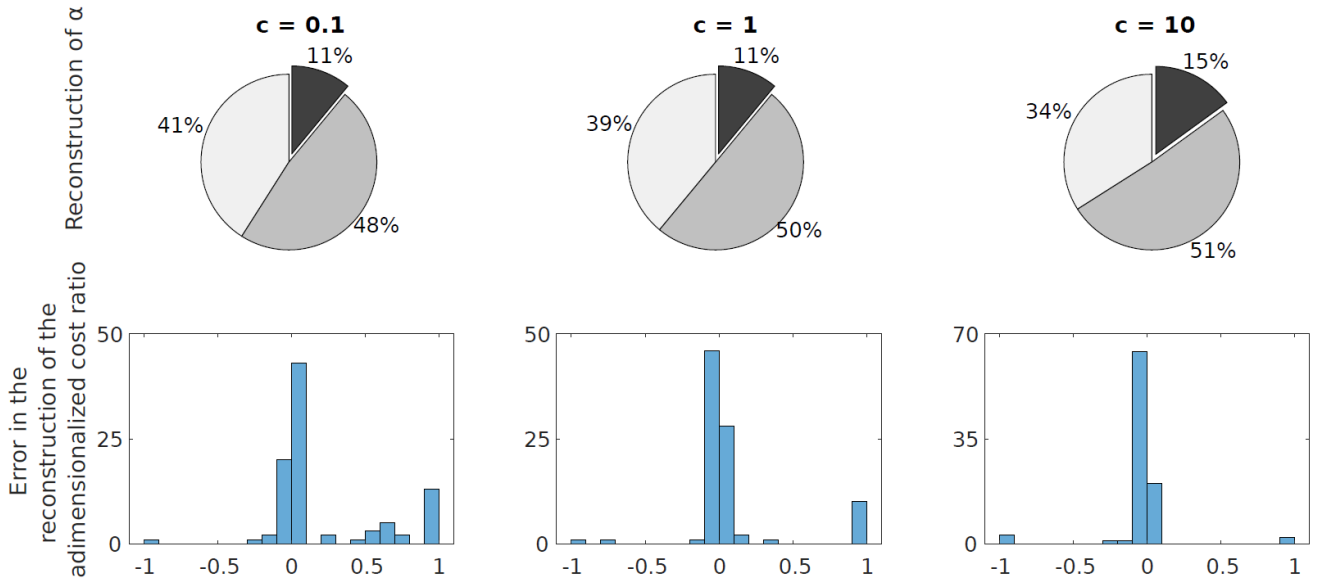


Figure 4 Top: Reconstruction of the sign of the risk parameter α and of the adimensionalized cost ratio in the theoretical cases. For the risk attitude: the dark share of the chart represents the misreconstructed signs, the dark grey the correct positive (risk-averse) reconstruction, and the light grey 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.

3.2.2 Reconstruction for oceanic migrations

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

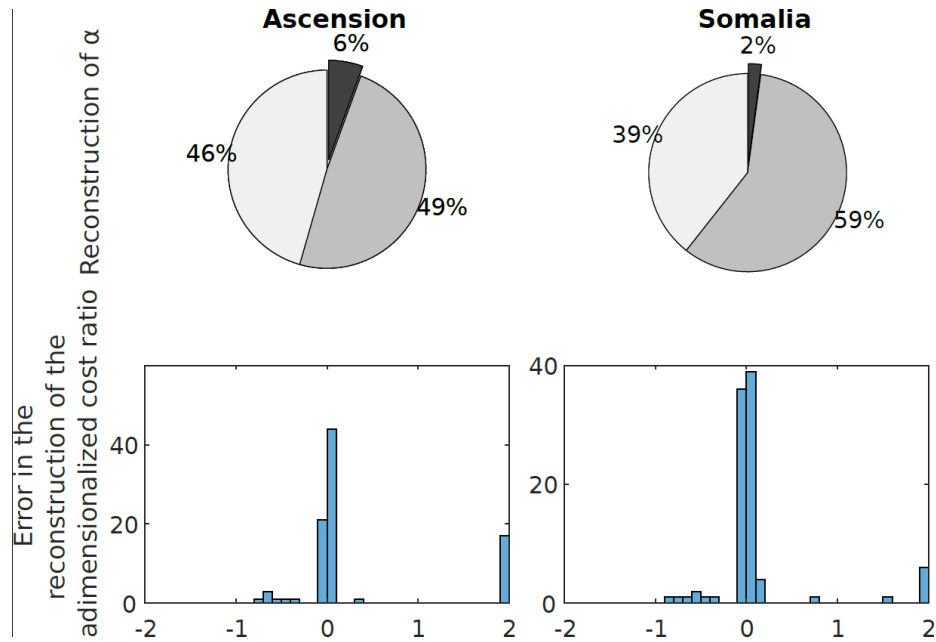


Figure 5 Top: Reconstruction of the sign of the risk parameter α and of the adimensionalized cost ratio in the oceanic cases. For the risk attitude: the dark share of the chart represents the misreconstructed signs, the dark grey the correct positive (risk-averse) reconstruction, and the light grey the 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.

4. Discussion

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

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

Learning and optimization of migration routes

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

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

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

Risk-attitudes and ocean currents

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

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

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

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

Model limitations and ecological implications

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

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

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

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

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

Statistical inference

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

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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.