# Navigating the flow: Animal navigation in fluid environments

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**But:** airborne and acquatic organisms must deal with significant and complex flows...







## Talk outline

• A classic navigating problem: homing of green turtles

(Chelonia mydas) to Ascension Island

- Data and modelling
- A multiscale approach: from an IBM to continuous models
- Application to homing.

## **Green Turtle Navigation**

Atlantic adult green turtles return to nest at hatchling sites on Ascension Island:

though far from probable, that the horse may have been born in the Isle of Wight. Even if we grant to animals a sense of the points of the compass, of which there is no evidence, how can we account, for instance, for the turtles which formerly congregated in multitudes, only at one season of the year, on the shores of the Isle of Ascension, finding their way to that speck of land in the midst of the great Atlantic Ocean?

CHARLES DARWIN

Extract from "Perception in the Lower Animals", C. Darwin, Nature 1873.

Classic example of a "homing problem": other well-known examples include homing pigeons, lobsters, salmon, newts...

## **Green Turtle Navigation**

Atlantic adult green turtles return to nest at hatchling sites on Ascension Island:



#### MACROSCOPIC SCALE PROBLEM.

## **Green Turtle Navigation: Theories**

• Geomagnetic information?



Isoclinics and isodynamics in South Atantic (Lohmann 1999).

## **Green Turtle Navigation: Theories**

- Geomagnetic information?
- Chemical cues borne by wind or ocean currents?



## **Green Turtle Navigation: Theories**

- Geomagnetic information?
- Chemical cues borne by wind or ocean currents?
- Orientation with respect to the flow (rheotaxis)?
- Celestial information?
- Sight, sound (when sufficiently close)?
- But: how precise can any of these be?

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#### Controlled behavioural studies:



Experimental apparatus used to monitor orientation responses of hatchling loggerhead turtles to regional magnetic fields. (A) A hatchling loggerhead swimming in a cloth harness. (B) Turtles were tethered to a rotatable tracker arm attached to a digital encoder, which relayed the direction of swimming to a computer in a nearby building. The arena was enclosed by a magnetic coil system capable of replicating magnetic fields found at different locations along the turtles' migratory route. Modified from Lohmann and Lohmann [23].

#### Testing impact of geomagnetic field information on hatchling turtle navigation (Lohmann 2008)

Controlled behavioural studies:



Circular statistics analysis: can be used to generate turning distributions to assess strength of navigating information...

Of course, one should be careful about reading too much information into how such studies translate to "real-life"

#### "Tag, release" experiments:



1950s: Helium balloons attached to nesting turtles.

1990s: Advent of GPS tracking

"Tag, release" experiments:



Individual-level data: generates mean speeds, turning rates, angles...

"Tag, release" experiments:



Block et al (2005), Nature. Electronic tagging of 800 tuna.

For commercially-important species, can even generate population level distributions. Not feasible for turtles....

Ocean currents: publicly available data available from:

- 1. Direct measurements (e.g. buoys, floats, ships, satellite,...)
- 2. Validated ocean circulation models...



#### **Global Ocean Currents Database**

The objective of the Global Ocean Currents Database (GOCD) project is to integrate ocean currents observations from a variety of instruments containing different resolutions and methods, as well as spatial and temporal variability, into a common database.

#### Please cite the use of the GOCD as follows:

Dr. Charles Sun and US DOC; NOAA; NESDIS; National Oceanographic Data Center (2015). NODC Standard Online Product: Global Ocean Currents Database (GOCD) (NCEI Accession 0093183). NOAA National Centers for Environmental Information. Dataset. [access\_date]

Access Ocean Currents Data	
Specify Spatial Range: Help North: 90 West: -180 Global East: 180 South: -90	Warning: Loading approximately 15,000 data positions may take up to 15 seconds. To select an area hold the "shift" key and drag to select an area. Additional Help

Ocean currents: publicly available data available from:

- 1. Direct measurements (e.g. buoys, floats, ships, satellite,...)
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Oceanic flow and surface temperature data (ECCO2, NASA)

## Modelling: fully continuous

Both currents and populations modelled as continuous variables. Typically take the form of diffusion-advection-reaction systems



Ledohey et al (2008). SEAPODYM. Dynamic modelling of tuna population distributions.

+'s: Numerically efficient, (somewhat) analytically tractable, directly generate population level detail.

-'s: Hard to parameterise/validate against individual-level data

# Modelling: IBM-continuous hybrid

Individuals immersed as (typically point) Lagrangian particles into a continuous flow. Individual movement could be:

- 1. Simple drifting (e.g. eggs, larvae,...)
- 2. Active swimming and navigating (fish, turtles...)



Blanke et al (2012): European eel larvae dispersal modelled as drifters

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Willis (2011): Salmon in Severn estuary

Putman (2010): Turtle hatchling navigation

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Widely adopted in both academic (animal orientation) and commercial sectors (fish stock forecasting).

+'s: Easy to parameterise against individual-level data; can tailor to incorporate specific individual movement rules; can obtain data at the level of both individuals and populations.

-'s: Computationally intensive (at the population level) and analytically intractable. Difficult to obtain non-parameter specific predictions.



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## **Multiscale approach**



+'s: Formulated, parametrised and validated against individual level data

+'s: A continuous-level model formulated at an individual movement scale

+'s: Analytically & numerically efficient for population-level /macroscopic understanding

It's not all rosy! There are caveats: simplifying approaches must be made and hence its validity will depend on the problem.....

## Multiscale approach: hybrid IBM



Passive velocity field u(x,t)

# Multiscale approach: hybrid IBM

Individuals immersed as point-wise particles into an external flow. Particles do not interact and have negligible impact on the flow. Individual movement from "passive" (external flow) and "active" (swimming /flying) motion:

Key defining parameters/functions:

 $\lambda$  = mean run time;

*s* = mean speed;

q = probability distribution for new velocity.

 $\lambda, s$  v(x,t)

Velocity-jump model

Can be biased to incorporate navigating information

## Multiscale approach: hybrid IBM

Individuals immersed as point-wise particles into an external flow. Particles do not interact and have negligible impact on the flow. Individual movement from "passive" (external flow) and "active" (swimming /flying) motion:

Let  $x_i(t)$ ,  $v_i(t)$  be the position and velocity of an individual *i* at time *t*.

Let u(t, x) be the external flow at time t, position x.

Then for a sufficiently short time step,  $\Delta t$ ,

 $\boldsymbol{x}_{i}(t + \Delta t) = \boldsymbol{x}_{i}(t) + \Delta t(\boldsymbol{v}_{i}(t) + \boldsymbol{u}(t, \boldsymbol{x}_{i}(t)))$ 

 $\boldsymbol{v}_i(t+\Delta t) = \begin{cases} q\big(\boldsymbol{v}|t+\Delta t, \boldsymbol{x}_i(t+\Delta t)\big) & prob.\,\lambda\Delta t\\ \boldsymbol{v}_i(t) & otherwise \end{cases}$ 

Rewrite\* the IBM as a mesoscopic-level continuous transport model:

$$p_t(t, \mathbf{x}, \mathbf{v}) + \overbrace{\nabla \cdot \mathbf{v} p(t, \mathbf{x}, \mathbf{v})}_{\text{active movement}} + \overbrace{\nabla \cdot \mathbf{u} p(t, \mathbf{x}, \mathbf{v})}_{\text{turning}} = \underbrace{\lambda(m(t, \mathbf{x})q(\mathbf{v} \mid t, \mathbf{x}) - p(t, \mathbf{x}, \mathbf{v}))}_{\lambda(m(t, \mathbf{x})q(\mathbf{v} \mid t, \mathbf{x}) - p(t, \mathbf{x}, \mathbf{v}))}$$

p(t, x, v) = particle density with time t, position x and velocity v m(t, x) = macroscopic (or observable) density

$$m(t, \mathbf{x}) = \int_{V} p(t, \mathbf{x}, \mathbf{v}) d\mathbf{v}$$

\* Note: strictly speaking, this is valid only if interactions are "negligible"

For macroscopic problems, scaling (see Hillen/P. 2014) used to generate a macroscopic model. Using *moment closure*\*,

$$m(t, \mathbf{x})_t + \nabla \cdot \left( (\mathbf{a}(t, \mathbf{x}) + \mathbf{u}(t, \mathbf{x}))m(t, \mathbf{x}) \right) = \nabla \nabla \left( \mathbb{D}(t, \mathbf{x})m(t, \mathbf{x}) \right)$$
(3)

- 1 Active advection due to swimming/flying
- 2 Passive advection due to flow
- 3 Anisotropic diffusion (uncertainty in active navigation)

\*original methods developed in a physical context and are based on notions of mass, momentum, energy etc. Do these a transfer to biology context? Requires some moment closure condition: here we use a fast flux approximation which states that at the space/time scales of observation, individuals almost instantaneously respond to their environment.

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$$\mathbf{a}(t, \mathbf{x}) = \int_{V} \mathbf{v}q(\mathbf{v} \mid t, \mathbf{x}) d\mathbf{v},$$

i.e. active advection is the expectation of the turning distribution!

$$\mathbb{D}(t,\mathbf{x}) = \frac{1}{\lambda} \int_{V} (\mathbf{v} - \mathbf{a}(t,\mathbf{x})) (\mathbf{v} - \mathbf{a}(t,\mathbf{x}))^{T} q(\mathbf{v} \mid t,\mathbf{x}) d\mathbf{v},$$

i.e. anisotropic diffusion is proportional to the covariance matrix of the turning distribution!

IBM to describe movement in a (continuously) flowing field tu

Inputs: Key parameters/terms are mean speed, turning rate and turning distribution

Reformulate as "mesoscopic" level transport model

Exactly the same inputs as the IBM

Scale to obtain macroscopic/ population-level model Macroscopic terms/parameters depend on statistical properties of the IBM inputs

**Simplification**: assume individuals move with the same mean speed, *s*. Therefore, at each turn, only a new active direction (or heading) is chosen and we specify a suitable directional distribution,  $\tilde{q}$ , over all possible directions.

$$\begin{split} \mathbf{a}(t,\mathbf{x}) &= \int_{V} \mathbf{v}q(\mathbf{v} \mid t,\mathbf{x})d\mathbf{v} \,, \\ &= s \int_{\mathbb{S}^{n-1}} \mathbf{n}\tilde{q}(\mathbf{n} \mid t,\mathbf{x})d\mathbf{n} \,; \\ \mathbb{D}(t,\mathbf{x}) &= \frac{1}{\lambda} \int_{V} (\mathbf{v} - \mathbf{a}(t,\mathbf{x}))(\mathbf{v} - \mathbf{a}(t,\mathbf{x}))^{T}q(\mathbf{v} \mid t,\mathbf{x})d\mathbf{v} \,, \\ &= \frac{1}{\lambda} \int_{\mathbb{S}^{n-1}} (s\mathbf{n} - \mathbf{a}(t,\mathbf{x}))(s\mathbf{n} - \mathbf{a}(t,\mathbf{x}))^{T}\tilde{q}(\mathbf{n} \mid t,\mathbf{x})d\mathbf{n} \,. \end{split}$$

- "Drifters": organisms that simply drift with the external flow,
   e.g. eggs, larvae and small organisms.
- Hence, no active speed (s = 0) and we obtain:  $m(t, \mathbf{x})_t + \nabla \cdot \mathbf{u}(t, \mathbf{x})m(t, \mathbf{x}) = 0$
- As to be expected, a classic drift-equation....

- "Random movers": organisms move actively but (at the observed level) in an essentially random manner.
- Choose uniform probability distributions: defining (2D) polar angle α or (3D) azimuth/polar angles (α,β), set:

(2D)  $\tilde{q}_c(\alpha) = 1/2\pi$ ; (3D)  $\tilde{q}_s(\alpha, \beta) = 1/4\pi$ .

• Substitution and integrating gives:

$$\mathbf{a}(t, \mathbf{x}) = \mathbf{0}$$
, and  $\mathbb{D}(t, \mathbf{x}) = \frac{s^2}{n\lambda} \mathbb{I}_n$ 

• Hence, a drift/isotropic diffusion equation:

$$m(t, \mathbf{x})_t + \nabla \cdot \mathbf{u}(t, \mathbf{x})m(\mathbf{x}, t) = d\nabla^2 m(t, \mathbf{x}) \quad d = s^2/(n\lambda)$$

0

- "Navigators": organisms that actively move in response to environmental navigating cues.
- Example data: hatchling turtle data sets...



- "Navigators": organisms that actively move in response to environmental navigating cues.
- Example data: hatchling turtle data sets...
- "Standard choice" (for 2D) is the von Mises distribution: a circular analogue of the normal distribution:

$$\tilde{q}(\alpha \mid k, A) = \frac{1}{2\pi I_0(k)} e^{k \cos(\alpha - A)}$$

- k is a concentration parameter measuring the navigational strength, while A defines the desired directional choice.
- $I_j(k)$  denotes the modified Bessel function of order *j*.

 "Navigators": organisms that actively move in response to environmental navigating cues

$$\tilde{q}(\alpha \mid k, A) = \frac{1}{2\pi I_0(k)} e^{k \cos(\alpha - A)}$$



Analysis of turtle magnetic orientation datasets: k values 0.5 - 2

- "Navigators": organisms that actively move in response to environmental navigating cues.
- "Fun" integral calculations....

$$\begin{aligned} \mathbf{a}(t, \mathbf{x}) &= s \int_{\mathbb{S}^{n-1}} \mathbf{n} \tilde{q}(\mathbf{n} \mid t, \mathbf{x}) d\mathbf{n} \\ \mathbb{D}(t, \mathbf{x}) &= \frac{1}{\lambda} \int_{\mathbb{S}^{n-1}} (s\mathbf{n} - \mathbf{a}(t, \mathbf{x})) (s\mathbf{n} - \mathbf{a}(t, \mathbf{x}))^T \tilde{q}(\mathbf{n} \mid t, \mathbf{x}) d\mathbf{n} \end{aligned}$$

- "Navigators": organisms that actively move in response to environmental navigating cues.
- "Fun" integral calculations....

$$\begin{aligned} \mathbf{a}(k,A) &= s \frac{I_1(k)}{I_0(k)} (\cos A, \sin A) \,, \\ \mathbb{D}(k,A) &= \frac{s^2}{2\lambda} \left( 1 - \frac{I_2(k)}{I_0(k)} \right) \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \\ &+ \frac{s^2}{\lambda} \left( \frac{I_2(k)}{I_0(k)} - \frac{I_1(k)^2}{I_0(k)^2} \right) \begin{pmatrix} \cos^2 A & \cos A \sin A \\ \cos A \sin A & \sin^2 A \end{pmatrix} \end{aligned}$$

- Advection in direction of dominant angle (obviously).
- Diffusion is anisotropic, depending on A.

• "Navigators": organisms that actively move in response to environmental navigating cues.



- "Navigators": organisms that actively move in response to environmental navigating cues.
- Substitute into macroscopic model and solve...

 $m(t, \mathbf{x})_t + \nabla \cdot \left( (\mathbf{a}(t, \mathbf{x}) + \mathbf{u}(t, \mathbf{x})) m(t, \mathbf{x}) \right) = \nabla \nabla \left( \mathbb{D}(t, \mathbf{x}) m(t, \mathbf{x}) \right)$ 



- "Navigators": organisms that actively move in response to environmental navigating cues.
- Can also be done for 3D data sets. Uses the spherical von-Mises/Fisher distribution:

 $\tilde{q}(\alpha,\beta \mid k,A,B) = \frac{k}{4\pi\sinh k} e^{k(\cos\beta\cos B + \sin\beta\sin B\cos(A - \alpha))}$ 

• Even more fun calculations give...

 $\mathbf{a}(k, A, B) = s \left( \coth k - \frac{1}{k} \right) \mathbf{w} , \\ \mathbb{D}(k, A, B) = \frac{s^2}{\lambda} \left( \left( \frac{\coth k}{k} - \frac{1}{k^2} \right) \mathbb{I}_3 + \left( 1 - \frac{\coth k}{k} + \frac{2}{k^2} - \coth^2 k \right) \mathbf{w} \mathbf{w}^T \right)$ 

Important for problems with both vertical and lateral movement....

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## **Goal Navigation**

- **Problem**: navigation to a specific goal under external flows.
  - Marine turtle navigation to island beaches...
  - Moths flying to a pheromone source...
  - Salmon returning from oceans to freshwater rivers...
- Flows can easily exceed an individual's swimming/flying speed.
- Individuals must correct or compensate for the flow in order to home.
  - Correction requires periodic reassessment of active heading, but not actual detection of the flow.
  - Compensation requires actual detection of the external flow.
- Here we assume correction only (believed to be the case for turtles).
- How strong does the orienteering capacity need to be?

- Constant and uniform flow  $\mathbf{u} = (u_x, 0)$  from west to east.
- Assume circular goal of radius r centred on the origin.
- I.C.s: releases NE/SW from the goal or uniformly distributed.



- Navigating: use VM dist. with dominant direction pointing to the origin and constant navigating strength k.
- Non-dimensional form: set  $s = \lambda = 1$ , r = 5, R = 100.
- Key parameters: flow u\_x and navigating strength k.
- Success Measure: % that reaches target by t = T (=1000).

Flows: Weak (25% of s); Moderate (50%); Powerful (75%).

**Navigation**: Average (k = 1), Strong (k = 1.5).



Does the macroscopic model provide an acceptable representation of IBM population level statistics?



Does the macroscopic model provide an acceptable representation of IBM population level statistics?



Hence, can exploit the superior analytical efficiency of the macroscopic model.

Parameter sweep through navigational strength/flow speed space to assess population homing success:



Seemingly sharp threshold between k and u\_x: quantifiable?

Use method of characteristics: gives a continuous dynamical system for the path,  $\mathbf{x}(t) = (\mathbf{x}(t), \mathbf{y}(t))$ , of an "average" individual. For the macroscopic model we have:

$$\frac{d\mathbf{x}}{dt} = \mathbf{u}(t, \mathbf{x}) + \mathbf{a}(t, \mathbf{x}) - \nabla \cdot \mathbb{D}(t, \mathbf{x})$$

Flow is constant,  $\mathbf{u} = (u_x, 0)$ , and navigation is determined from the VM distributional choice. Gives...

$$\begin{aligned} \dot{x} &= u_x - c_1 \frac{x}{\sqrt{x^2 + y^2}} - c_3 \frac{x}{x^2 + y^2}; \\ \dot{y} &= -c_1 \frac{y}{\sqrt{x^2 + y^2}} - c_3 \frac{y}{x^2 + y^2}. \end{aligned}$$
$$c_1(k) &:= s \frac{I_1(k)}{I_0(k)}, \qquad c_2(k) := \frac{s^2}{2\lambda} \left( 1 - \frac{I_2(k)}{I_0(k)} \right), \qquad c_3(k) := \frac{s^2}{\lambda} \left( \frac{I_2(k)}{I_0(k)} - \frac{I_1(k)^2}{I_0(k)^2} \right). \end{aligned}$$

Compare MC trajectories with earlier IBM simulations:



Phase plane analysis reveals 2 or 3 steady states:

- **1** The target (i.e. the centre of the goal) unstable node;
- **2** Upstream saddle;
- Ownstream stable node when it exists.

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Trajectories swept out.

Trajectories attracted to 3

Phase plane analysis reveals 2 or 3 steady states:

- **1** The target (i.e. the centre of the goal) unstable node;
- 2 Upstream saddle;
- Oownstream stable node when it exists.



Trajectories swept out.



If (SS3) lies inside goal then we have eventual homing success

Overlay on earlier parameter sweep suggests that this gives a good proxy for population success:



Can also investigate more complicated flows: e.g. adding a "whirlpool" between the individual's starting location and the goal.

$$\dot{x} = \gamma (66 - 0.1x - y) - c_1 \frac{x}{\sqrt{x^2 + y^2}} - c_3 \frac{x}{x^2 + y^2}$$
$$\dot{y} = \gamma (x - 0.1y - 54) - c_1 \frac{y}{\sqrt{x^2 + y^2}} - c_3 \frac{y}{x^2 + y^2}$$



Increasing gamma

- Turtles swim from South America coastal waters to Ascension Island to breed/lay eggs once every few years.
- Breeding season is from late December/January to June/July.



Fig. 2. Temporal distribution of nesting activities of green turtles on Ascension Island during the 1998/1999 season. For each beach, the

• Most females lay multiple clutches of eggs during the season.

- Highly difficult to track full navigation pathway.
- Instead, females at AI are displaced and tracked.



Fig. 2. Satellite tracks of adult female green turtles displaced by ship and released at sea at eight different sites around Ascension Island. (A) Female green turtles classified as searching for Ascension Island, but were not able to locate it, and (B–D) turtles

- Consider the 2D ocean surface centred about Ascension Island (turtles spend the majority of the time at/near the surface).
- Simulate displacement experiments:



- Consider the 2D ocean surface centred about Ascension Island (turtles spend the majority of the time at/near the surface).
- Simulate displacement experiments.
- Parameter set:
  - Active swimming speed s = 0 80 km/day (i.e. ranges from a passive drifter to upper ends of energetically feasible limits)
  - Turning rate 12 per day (roughly, once every couple of hours).
  - Navigational strength k = 0 3 (i.e. ranges from a random mover to a "strong" navigator).
- "Success" measures:
  - P\_100: Population percentage that return within 100 days.
  - $T_{1/2}$ : Time by which half the population has successfully returned.



s = 50 km/day, k = 1, Release date: 01/01/14



s = 50 km/day, k = 1, Release date: 01/01/14



s = 50 km/day, k = 1, Release date: 29/01/14



s = 50 km/day, k = 1, Release date: 01/01/14



s = 30 km/day, k = 1, Release date: 01/01/14



Comparison between IBM and macroscopic model:



Comparison between IBM and macroscopic model:



Simulations: IBM takes order of an hour while the macroscopic model takes order of minutes....

Sweep across mean speed/navigating strength parameter space:

















(b)

(a)

## Summary

- Multiscale framework for movements in flowing environments.
   Beyond navigation, potential applications in:
  - Modelling fish (egg, larval and adult stages) distributions
  - Insect infestations etc.
- Current work: more detailed modelling of different hypotheses for turtle navigation.
- Challenges: efficient and stable solvers for anisotropic diffusion equations (also has important consequences in image processing).
- Challenges: "Mean free passage time what is the expected time for individuals to reach a target?" Solved for isotropic diffusion in the absence of flow, but not for the more complicated model here.

## **References/Thanks**

Thanks to my collaborator: mathematician and jazz pianist:

Thomas Hillen (University of Alberta)



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