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INDIVIDUAL-BASED METHODS FOR SIMULATION OF MOVEMENT BY WCPO SKIPJACK AND OTHER PELAGIC SPECIES

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Abstract

This information paper outlines the work plan and preliminary results from an Australian Research Council Linkage project that is developing an individual-based model (IBM) of WCPO skipjack. It is anticipated that there will be significant overlap between this project and certain recommendations of the WCPFC-SC.

The SC11 summary report WCPFC12-2015-17 notes that:

"*[regarding] information related to identifying changes in the spatial distribution of skipjack (including range contraction) in response to increase in fishing pressure… SC11 recommends that WCPFC12 take note of the analyses completed to date and that further work on this issue be undertaken, including:*

- *more extensive skipjack tagging activities, including in sub-tropical and temperate regions to provide better information on stock connectivity and movement*"

In addition, as part of the 2015/2016 PTTP work plan, SC11-RP-PTTP-02 recommended that data analyses of movement from tagging data should:

"*provide external validation to [movement] estimates from within MFCL and SEAPODYM.*"

An individual-based approach to modelling tuna behaviours allows many of the assumptions and hypotheses underlying movement in MULITFAN-CL and SEAPODYM to be tested in a simulation framework that is structured on the fundamental unit of ecology: the individual. Here, we detail such an approach using WCPO skipjack as an application. The model extends a newly developed Lagrangian ocean particle-tracking simulator from collaborators in Imperial College London, by incorporating directed movement, non-directional kinesis, and random-walk behaviours. We aim to first replicate the spatial density evolution predicted by SEAPODYM in a single cohort of Pacific skipjack, using identical forcing and habitat fields while developing individual-based equivalents of the advection-diffusion-reaction dynamics used in this model. We will then examine the effect on meso- and large-scale distribution of deviating from SEAPODYM by using alternate behavioural scenarios at the individual level, informing behaviour from ecological theory and analyses of the PTTP database (e.g. SC09-RP-PTTP-03, SC10-RP-PTTP-03/-05) wherever possible. Ultimately, we wish to incorporate behavioural feedback mechanisms through conspecific interaction and simulated FAD deployments to explore possible drivers of range contraction and meso-scale changes to distribution.

Although similar IBMs have been developed for the region in the past (e.g. SCTB16-SKJ-4/-BET-4), this project does not aim to predict population dynamics for stock assessment. By focusing on movement, the anticipated longer-term developments of this model are: simulation of tagging experiments to aid design; examining the effect of changing habitat on mixing rates and migration parameters; and quantifying the sensitivity of assumptions in existing pelagic species stock assessment models as part of management strategy evaluation.

Background

The University of New South Wales and the Secretariat of the Pacific Community are the lead partners in an Australian Research Council Linkage project titled "*Understanding the effect of small-scale ocean process on tuna propulations - a new tool to forecast tuna distributions for use in fisheries management*". The aim of the project is to develop a novel tuna behavioural model, using observationally derived information of skipjack tuna where possible. The model will be integrated into a state-of-the-art biophysical model at resolutions capable of reproducing critical meso-scale processes, providing projections of tuna distributions that will aid in developing sustainable management practices. The approach will focus on two main goals:

- We will use a Lagrangian (individual-based) framework to simulate skipjack tuna distribution, which provides a much more efficient environment for hypothesis testing of behaviour over traditional Eularian

        approaches

- We will examine the sensitivity of distribution in the context of connectivity, range contraction and movement estimates, to changes in the behavioural assumptions of models such as SEAPODYM and MULTIFAN-CL

Recommendations from SC11 regarding tropical tuna behaviour included providing better information on stock connectivity and movement (WCPFC 2015), as well as external validation of the movement estimates from MULTIFAN-CL and SEAPODYM (SPC 2015). The purpose of this information paper is to demonstrate the potential of our modelling tool in this regard, raise the scientific committee's awareness of the project, and solicit input from the community as to potential applications and focal areas for the work in the future.

Work plan

Species distribution is a function of behaviour and reproduction, both of which must be included in a model of population dynamics. However, during the early stages of the project it was agreed that attempting to develop an individual-based population dynamics or ecosystem model was beyond the scope of this relatively short project (two years). Similar stock assessment projects have been undertaken for WCPO skipjack in the past (e.g. Kirby et al. 2003), with few lasting outputs. Focussing only on the movement behaviour of young and adult tuna in the context of the assumptions present in currently used stock assessment models allows us to achieve far more pragmatic outputs. These outputs will be both academic and industry-focussed, feeding into scientific advice for RFMOs wherever possible.

The project will have three stages:
1. Implementation of an individual-based version of SEAPODYM skipjack movement in the WCPO
2. Examine the sensitivity of predicted skipjack tuna distribution to the assumptions behind SEAPODYM, by incorporating alternative behavioural scenarios, spatial resolution and ocean forcing
3. Begin development of a more general tagging simulator to quantify the sensitivity of displacement and mixing rates to these different assumptions

Our individual-based model (IBM) of tuna uses a new Lagrangian particle simulator, PARCELS (in development with colleagues from Imperial College London), extending the simulators functionality by implementing active movement behaviours. PARCELS is written in Python, a high level and extendable language, and implements under-the-hood conversion to C routines that speed up the intensive particle movement kernels significantly. The project will focus on the movement behaviours of young and adult tuna, allowing us to ignore many of the population dynamics components of stock assessment models. During stage one we will replicate the density evolution predicted by SEAPODYM under the same biophysical ocean forcing and behavioural assumptions, which will form a baseline from which the IBM will later deviate.

Methods

To replicate SEAPODYM, we initially simulate a single cohort of skipjack tuna through time, starting at four months of age. Fishing mortality is removed, with natural mortality acting on the number of fish contained within each 'super-individual', each of which represents a school of tuna. Identical physical forcing and adult tuna habitat fields are used to drive individual movement, derived from the ocean-biogeochemical NEMO-PISCES model at one-degree spatial and one-month temporal resolution (Senina et al. 2008, Senina et al. SC12). Tuna individuals are initially distributed using the spatial density predicted by SEAPODYM for the cohort at four months old, before the simulation then runs forwards, moving individuals using Lagrangian equivalents of the SEAPODYM advection-diffusion-reaction equations. SEAPODYM skipjack density and particle 'super-individual' density is compared each month through time. Two contrasting runs are proposed:

one during the period 2003–2007, where no strong Pacific climate events occurred, and one simulation during 1998–2002, over which a strong El Niño and moderate La Niña occurred.

SEAPODYM advection-diffusion-reaction

SEAPODYM is based on a Eulerian advection-diffusion-reaction approach to modelling the distribution of tuna. Movement of adult tuna in SEAPODYM is represented by advection and diffusion terms of partial differential equations that describe density of fish. Density at age is advected by ocean currents, and through an active taxis that follows the gradient of habitat towards local and more favourable areas. Density is also diffused with a diffusion rate that depends on the quality of that habitat, such that diffusion is enhanced (suppressed) in regions of poor (good) habitat. Recruitment and mortality are governed by the reaction component in this equation. In this project, we focus on the change in density of one cohort of skipjack tuna and assume only natural mortality. The change in density N of a cohort at age a over time is therefor described in a Eulerian framework by:

$$\frac{\partial N_a}{\partial} = -\boldsymbol{\nabla} \cdot (\boldsymbol{U}_a N_a + \boldsymbol{V}_a N_a) + \cdot (K_a \ N_a) - M_a N_a \tag{1}$$

Here, $\boldsymbol{U}_a$ *is* a vector of zonal, *u,* and meridional, *v,* ocean current velocities averaged over the accessible layers (depends on the accessibility as a function of oxygen and temperature, the latter of which varies with age) of the water column.

V_a is a vector of directed velocity (taxis) proportional to the gradient of a spatially and temporally varying quality of habitat index.

K is a spatially and temporally varying diffusivity dependent on the same quality of habit index.

Both K and $\boldsymbol{V}$ depend on a spatially and temporally varying adult tuna habitat. This habitat field is represented in SEAPODYM as a spatial index of forage species biomass accessible by tuna of age a, H_a, estimated from a mid-trophic micronekton sub-model (Lehodey et al. 2010) that depends on forage availability, ocean temperature and dissolved oxygen computed at monthly time-steps. In the case of a single cohort simulation, here we denote this two-dimensional age-dependent adult habitat index as simply H.

Diffusion

In SEAPODYM, maximum diffusivity is scaled non-linearly by the tuna habitat quality, causing biomass to diffuse at its maximum rate σD_m where habitat quality is minimal. Diffusivity is minimal where the habitat quality is maximal, although it remains greater than zero in this maximal case so that a small level of diffusion always occurs. Diffusion is defined as:

$$K_a = \sigma D_m \ (1 - cH^P) \tag{2}$$

where p, c and σ are strictly positive constants.

Senina et al. 2008 suggest that maximal diffusivity is given by

$$D_m \ = \frac{V_m^2 \ t}{4} \tag{3}$$

Where V_{max} is the age dependent maximum velocity of tuna, and t is the model time-step.

Age-dependent maximum velocity of a tuna, $V_{max,}$ is defined as

$$V_m \ = V_m L^b \tag{4}$$

where V_m is the maximum sustainable swimming speed in body lengths per second, L is the mean fork-length at-age in meters per body length, as predicted by the von Bertalanffy growth curve used in MULTIFAN-CL (Rice et al. 2014), and b is a constant slope parameter.

Directed taxis

The advection vector of directed velocity from equation 1, V_a, in x and y are given by the product of maximum swimming speed and the change in H.

$$V_a = V_m \quad H \tag{5}$$

Mortality

Natural mortality, *M*, is both age in months, *a*, and habitat dependent.

$$M_N = M_P \quad e^{(-\beta \ )} + M_S \quad a^{\alpha}$$

$$M_a = M_N \quad (1 - \theta)^{(1 - \frac{H}{2})} \tag{6}$$

Where M_{Pred} is the maximal predation mortality constant, M_{Sen} is the maximal senescence mortality constant, and α and β are slope parameters. A food requirement index affecting mortality is represented by ·.

Individual-based approach

In an individual-based, or Lagrangian, framework, we consider not the density of tuna within a particular area, but rather the movement of a large number of individual particles that represent schools of tuna. These 'super-individuals' occupy continuous positions in space.

The *xy* position of an individual particle *p*, at time *t* + 1, is moved in an equivalent fashion to that simulated by SEAPODYM by the following pair of equations:

$$x_p(t + 1) = x_p(t) + U(x_p, y_p, t) + V_x(x_p, y_p, t) + D_x(x_p, y_p, t) \tag{7}$$

$$y_p(t + 1) = y_p(t) + V(x_p, y_p, t) + V_y(x_p, y_p, t) + D_y(x_p, y_p, t)$$

where *U*, *V* and *D* are the x and y displacements caused by the identical SEAPODYM ocean current forcing, directed taxis, and diffusion terms, respectively. Equation 7 is integrated using a fourth order Runge-Kutta Scheme. Forcing fields are spatially interpolated to the position of particle *p* using linear two-dimensional interpolation.

Advection by ocean currents

The physical advection components *U* and *V* are calculated simply using velocity fields at the position *(xp, yp)* of a particle over the time-step

$$U = u \quad t \tag{8}$$

$$V = v \quad t$$

Diffusive random-walk behaviours

In an individual-based framework, Eulerian diffusion can be approximated by a pure random walk for individual particles when diffusivity, *K*, is spatially uniform. However, this approach causes spurious accumulation of particles in areas of low diffusivity in a non-uniform diffusivity field (Spagnol et al. 2002). To correct for this, the pure random walk must include an additional deterministic balancing term that moves particles away from these low diffusion areas (Visser 1997).

The movement of particles caused by diffusion in x and y is given by (from Ross & Sharples 2004):

$$D_x = \xi_1 \sqrt[2]{2K\,t/r} + \frac{\partial}{\partial}\,t$$

$$D_y = \xi_2 \sqrt[2]{2K\,t/r} + \frac{\partial}{\partial}\,t$$

(9)

Where ξ_1 and ξ_2 are random numbers drawn from a uniform distribution with zero mean and variance r (e.g. $r = 1/3$ when ξ is drawn from a uniform distribution, $\xi \in [-1,1]$). K remains the spatially varying diffusivity defined in equation 2, at the current position of the particle. An additional deterministic advection $\nabla K \Delta t$ is added to this random walk to counter the accumulation of particles in regions of low K.

Directed taxis

The individual-based equivalent of directed taxis is identical that in SEAPODYM, namely:

$$V_x = V_m \quad H_x$$

$$V_y = V_m \quad H_y$$

(10)

Preliminary Results

A preliminary IBM version of SEAPODYM movement is now complete; although at present there remain some significant differences in the density evolution compared to SEAPODYM that are in the process of being resolved. We have initially focussed on two periods: evaluating the IBM using SEAPODYM velocity and habitat fields for the period 2003–2006 (with no strong El Niño/La Niña effects), and 1997–2001 (strong El Niño and La Niña). Particle positions were integrated forward in time under the influence of ocean advection, taxis and modulated diffusion as described above.

Figure 1 shows the simulated tracks from three schools of adult skipjack, each initialised at the same position and point in time, but exhibiting different combinations of these advection and diffusion behaviours. In this example we can see that the addition of behaviour (via directed movement and modulated diffusion) directs the school towards a region of better habitat.
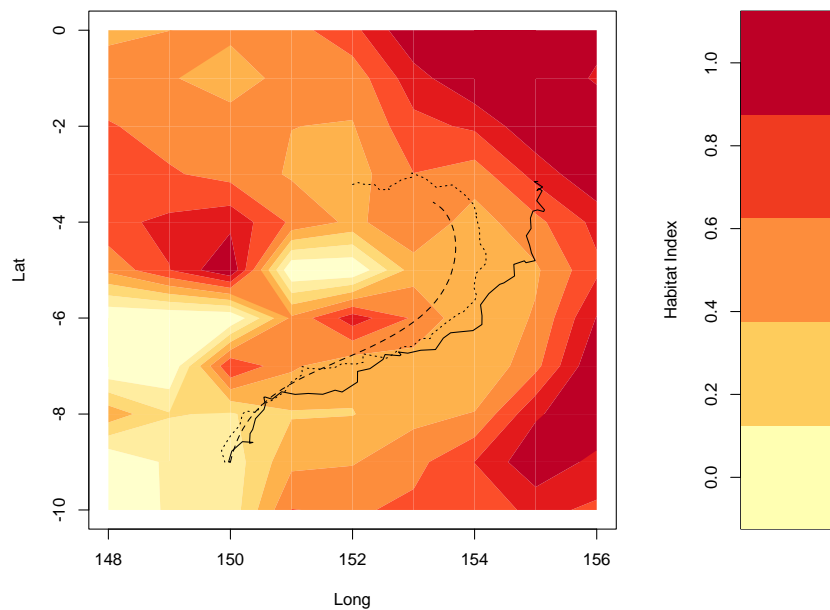
Figure 1. Movement tracks from three tuna schools initialised at the same point and simulated for three months with differing behaviours: school pathway subject to only to ocean current advection (dashed line); advection plus modulated diffusion (dotted line); combined advection, diffusion and directed movement following gradients of favourable habitat. Relative tuna habitat index is contoured underneath.

Particle pathways from an expanded simulation of 500 schools, all initialised at four months of age with positions dictated by SEAPODYM predicted density distribution for the same cohort, show directed movements towards areas of favourable habitat for the 2003 run (figure 2). Appropriate boundary conditions are not yet implemented in our IBM, and so accumulation near coastal zones where habitat quality is high does not always occur correctly at present.

Changes through time in density of tuna in the equatorial region between 5°S and 5°N can be seen through comparative longitude-time plots (figures 3). During the more neutral conditions of the 2003–2006 simulation tuna density quickly becomes concentrated at the start of the simulation, with general movement east and some seasonal variation. Both SEAPODYM and our IBM simulations show high tuna densities remaining in the western Pacific within the Pacific Warm Pool (the edge of which is denoted by the 28°C isotherm). In contrast, the 1997 simulation, during a which a strong El Niño occurred, demonstrated more diffuse concentrations and movements that track the movement of the 28°C isotherm very closely, particularly from 1998 when a moderate El Niña state began. This is consistent with observations of tuna catch variations in response to ENSO (Lehodey et al. 1997).

Both models captured the broad patterns of tuna density distribution predicted by SEAPODYM, particularly for areas of highest density. However, it is clear that SEAPODYM is far more diffusive than our IBM at this stage, with our simulation model indicating overly strong accumulation of particles in certain regions. In particular during the 2003 simulation, strong concentrations of tuna develop by the end of the first year in the eastern Pacific region that are not predicted by SEAPODYM.

A comparison of the relative density distribution of individuals through time compared to that projected by SEAPODYM is shown in figures 4 and 5. IBM particle distribution broadly corresponds to the distribution predicted by SEAPODYM, particularly in the first year. After 18 months some clear discrepancies become apparent. In particular, overly strong concentrations of tuna in the eastern and central Pacific, as well as near Japan and Indonesia, persist throughout our current simulations. This issue may be caused by the stochastic

random walk behaviours approximating diffusion, which essentially drive the sampling of the habitat field by individuals. The nature of this sampling drives the ability of active taxis behaviours to effectively find gradients of favourable habitat to climb. If this behaviour is not equivalent to the Eulerian mechanisms in SEAPODYM, then particles may become trapped in local maxima. Some preliminary experiments with temporal interpolation of the SEAPODYM forcing fields, allowing gradients to gradually change through time in place of sudden step changes at a monthly resolution, appear to reduce this spurious concentration of particles.
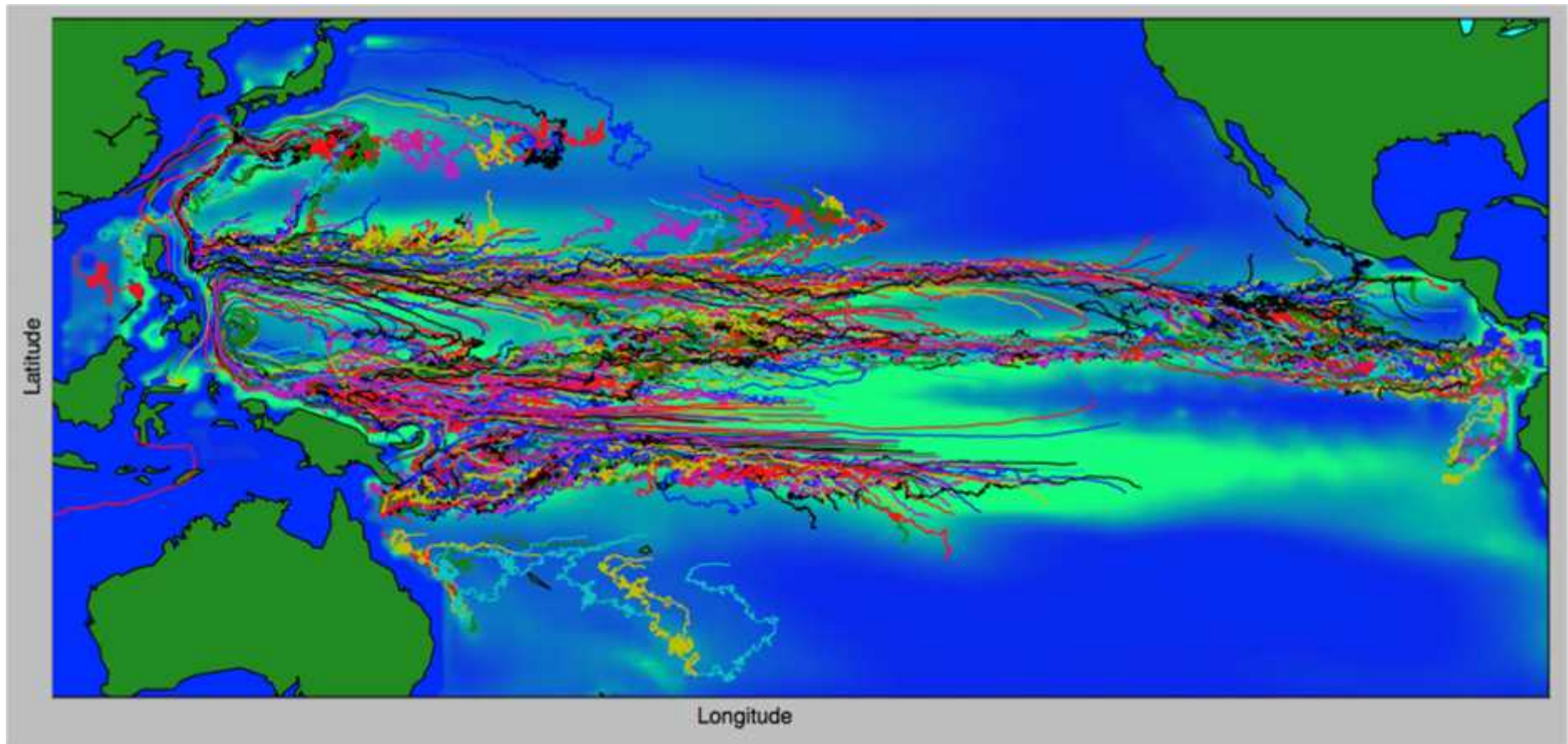
Figure 2. Movement tracks from 500 tuna school individuals simulated over three years with SEAPODYM forcing fields. Relative tuna habitat at the mid-point of the simulation is contoured underneath (green is higher quality, blue lower).
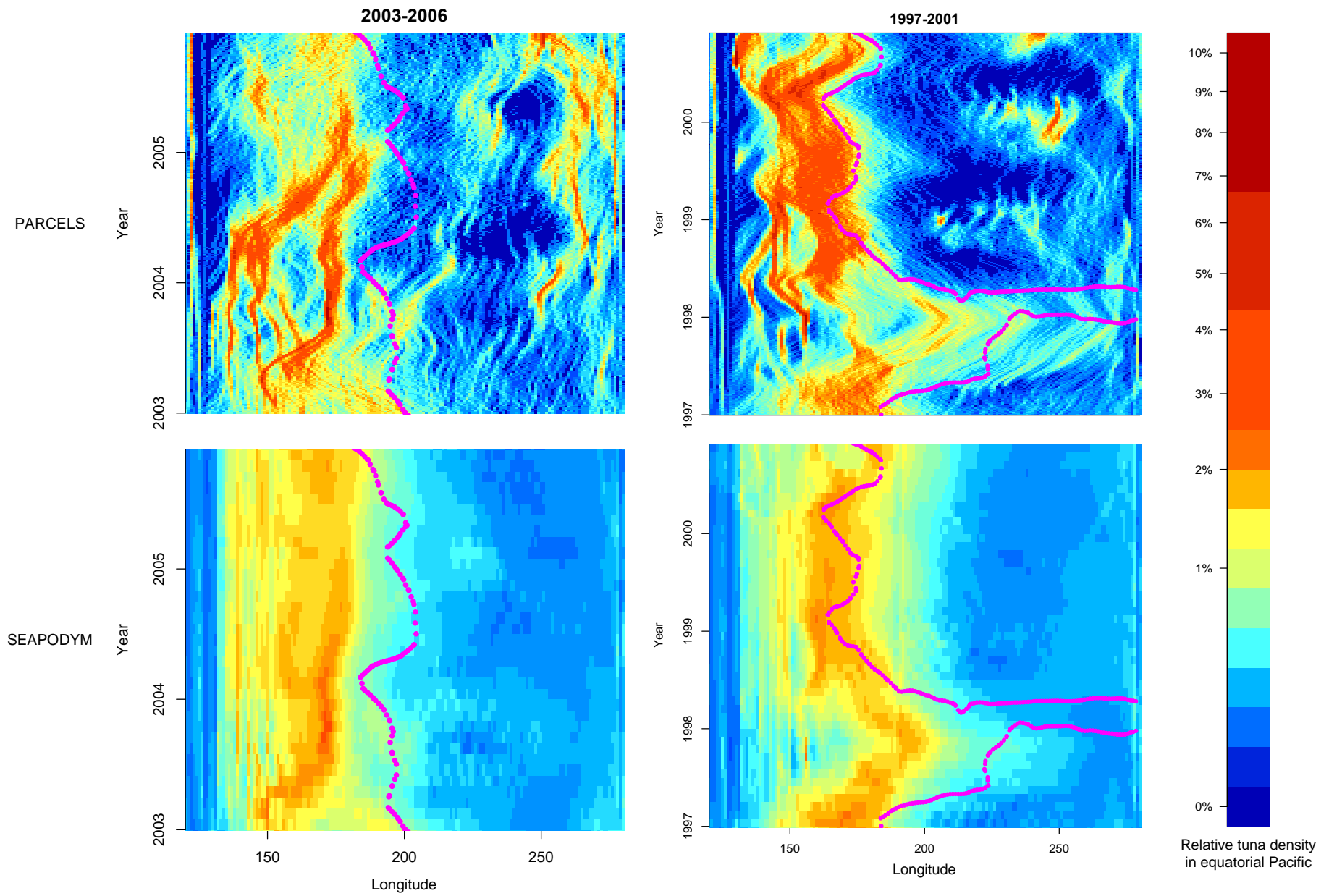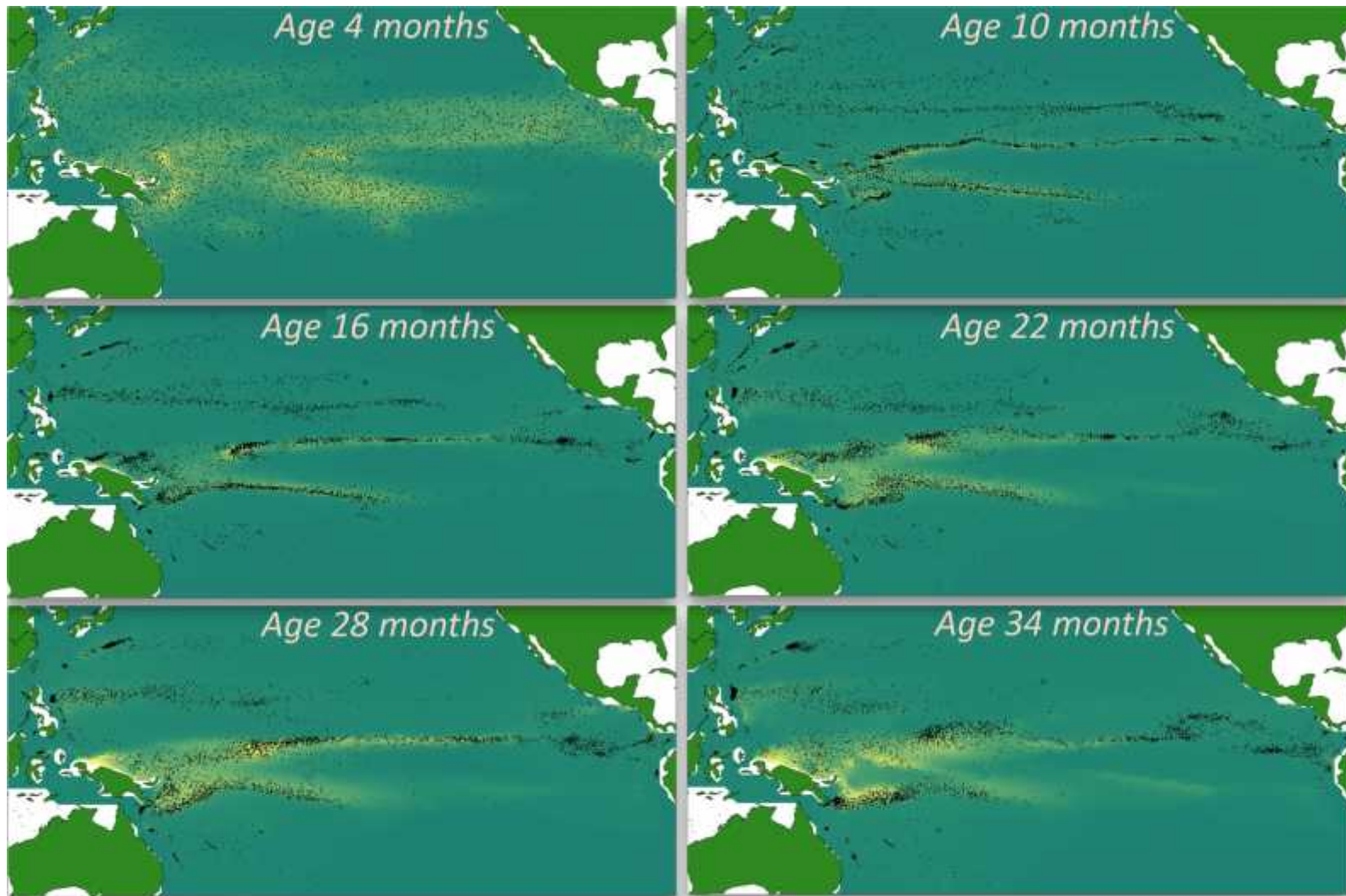
Figure 3. Hovmöller plots of relative tuna density distribution in the equatorial region between 5° N and 5° S for two separate periods in time, as simulated by the IBM (top) and SEAPODYM (bottom). Points in pink represent the longitudinal position of the 28° C isotherm.

Figure 4. Simulated movement of tuna individuals (black points) at six monthly intervals during the period 2003–2006. Individuals begin at age four months. SEAPODYM predicted relative density for the same period is plotted underneath (yellow is higher density).
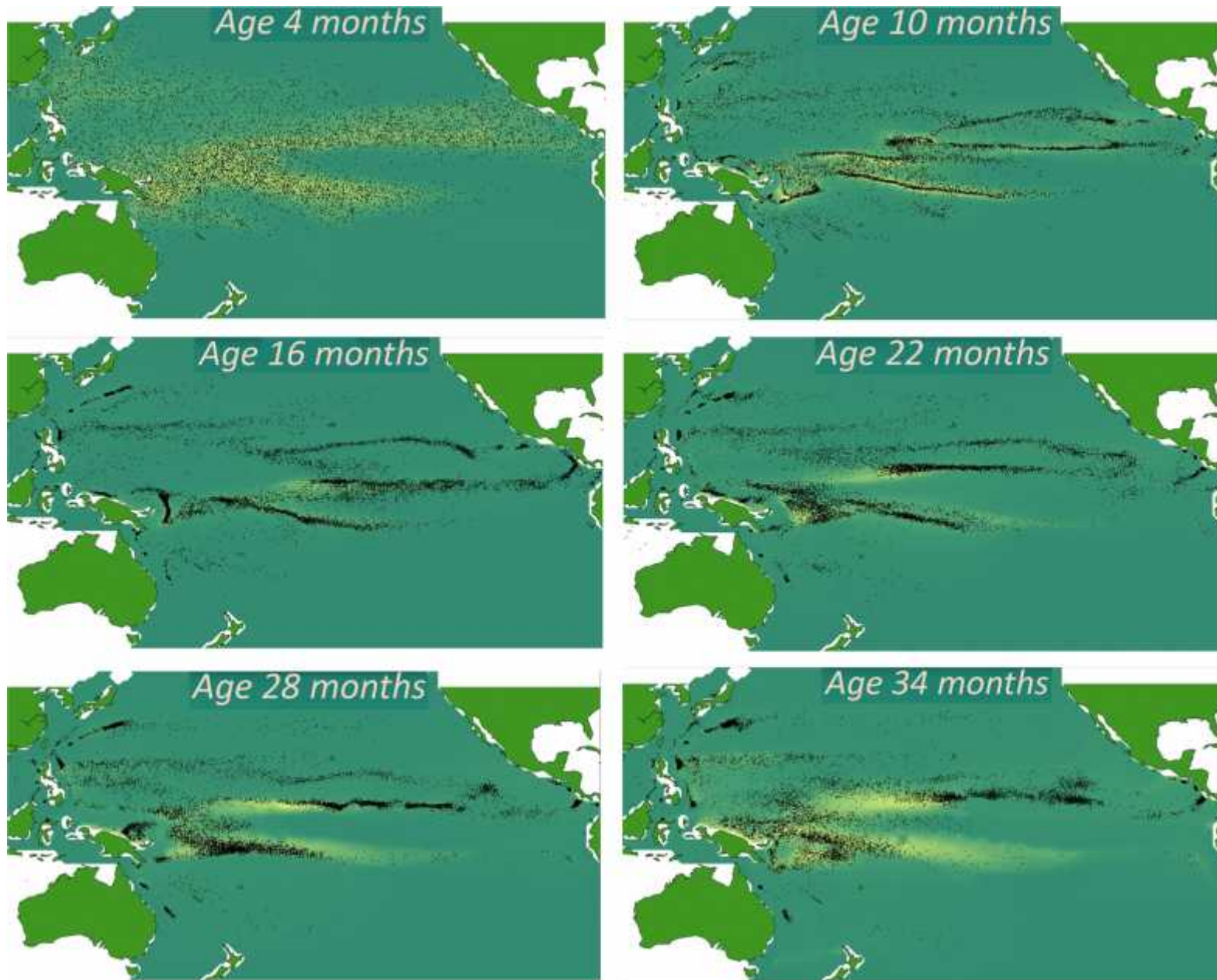
Figure 5. Simulated movement of tuna individuals (black points) at six monthly intervals during the period 1997–2000. Individuals begin at age four months. SEAPODYM predicted relative density for the same period is plotted underneath (yellow is higher density).

Future work

The immediate future of the project will see continued improvement to the individual-based representation of SEAPODYM advection-diffusion dynamics. We will also begin stages two and three, which we briefly outline here.

Stage 2. Alternative scenarios

The purpose of stage two is to expand the capabilities of the IBM to include alternative environmental and behavioural scenarios, with the aim of examining the sensitivity of the baseline SEAPODYM density distribution to alternative assumptions. These scenarios will be informed from ecological theory and real data wherever possible.

While the individual-based version of SEAPODYM described in above is Lagrangian, it still relies heavily on Eulerian assumptions. Diffusive and directed movement of particles are functions of the habitat index gradient, and as such assume that individual schools of tuna have complete information about their local environment. Even the algorithms that approximate Eulerian diffusion are not true random walks, and can cause individuals to move faster than their maximum theoretical speed. In the real world, animals are bound by their physiological and perceptual limits, and gain knowledge about their environment through spatial sampling, sensory triggers and biotic or abiotic environmental clues.

This stage will see us begin to move away from the behavioural assumptions of this Eulerian approach by simulating alternative behavioural scenarios at the individual school level. This will form the framework for a new stand-alone tool that can be used to simulate different advection (physical ocean movements), kinesis (non-directional behaviours) and active movements of pelagic animals. In the case of skipjack, alternative random walk and other movement behaviours will be explored, which will include tuna schools independently sampling their local habitat to build up gradient information. This school-level knowledge will then influence future movement and therefore future sampling.

Furthermore, eddy-resolving ocean forcing resolutions or models will also be explored if possible. SEAPODYM habitat fields are integrated over the water column through accessibility functions that represent the vertical habitat-use and physiological limits of tuna. In an individual-based model context, fairly moderate developments can lead to a third dimension of particle movement. These behaviours can be parameterised from electronic tagging analyses to directly simulate the interaction between tuna and depth-dependent prey fields (e.g. Leroy et al. 2014, Scutt Phillips et al. 2015).

Finally, mechanisms for interaction and feedbacks will be implemented. We anticipate focussing on two key areas: interactions between conspecifics, and interactions with fish aggregating devices. Interaction between individuals can be directly simulated in IBMs, without relying on abstract density dependence terms, although this can become computationally expensive. Incorporating these feedback mechanisms will allow us to examine potential range contraction due to competition for habitat under simple ideal free distribution assumptions, as well as the effect on mesoscale distribution that aggregation at FADs causes.

Simulation models can be considered as tools for constructing opaque thought experiments that can be effectively used in the assessment of underlying assumptions (Rykiel 1996, Di Paolo 2000). The simulation model we will develop is anticipated to provide such a tool, acting as an "assumption analyser" rather than a predictive model, and feed wherever possible into management strategy evaluation (MSE).

Stage 3. Tagging simulation

The third stage of the project is the development of a simple but generic tagging simulator for pelagic species, using the separate models built earlier in stages one and two. Quantifying the distribution of hypothetical displacement and mixing rates with regional populations from simulated tagging events are valuable applications of an IBM. For example, release events can be simulated at the same point at two different periods. Given the changes to underlying ocean and habitat forcing, alongside the behavioural assumptions of SEAPODYM, we will show how predicted displacement and mixing may differ between these two periods. These hypotheses will be compared to the results of empirical analyses of tagging data (e.g. Kolody & Hoyle 2015). Alternative behaviours,

such as attraction to FADs or density-feedbacks, could also be included. Such simulation experiments can feed into tagging program design, as well as the evaluation of currently assumed mixing and stock transfer rates in MULTIFAN-CL. It must be noted that a simple harvest/fisher model will need to be developed to accurately simulate effort and recapture rates.

An example proof of concept tagging simulation application is shown in figure 6. A release of 1000 adult skipjack individuals was simulated at the same point and season as a true tagging release event that occurred as part of the PTTP in 2009 near Tarawa, Kiribati. Skipjack individual positions were integrated forward in time as described in this paper, and a subset of their positions was sampled at the same monthly temporal distribution as the returned tags from the true tagging event (i.e. 1% during the first month after release, 30% during the second, 11% during the third etc.). Habitat and ocean forcing fields from 2009 were not available at the present time, and so fields from the same season during 1997 were used. Furthermore, field data at one-degree grid cell resolution do not contain the kinds of meso-scale dynamics that are likely to affect tuna recapture locations at the scale of months and single release events. We present these results here purely as example of how our IBM might be used in tagging simulation. In this case, all individuals initially move east before the movement tracks bifurcate and pass both north and south of the original tagging location. Such behaviour is an example of how interactions with a dynamic habitat can result in recapture close to a tagging location, despite an individual fish potentially mixing with the wider population more extensively than their mark-recapture displacement suggests.

While a fully realised tagging simulator tool is beyond the scope of the current project, it is anticipated that preliminary analyses using the PARCELS extensions developed in stages two and three will provide input into the MSE scheduled for 2017. The project team welcomes any potential collaboration for future development and application to WCPO tuna or other pelagic species (please contact corresponding author).
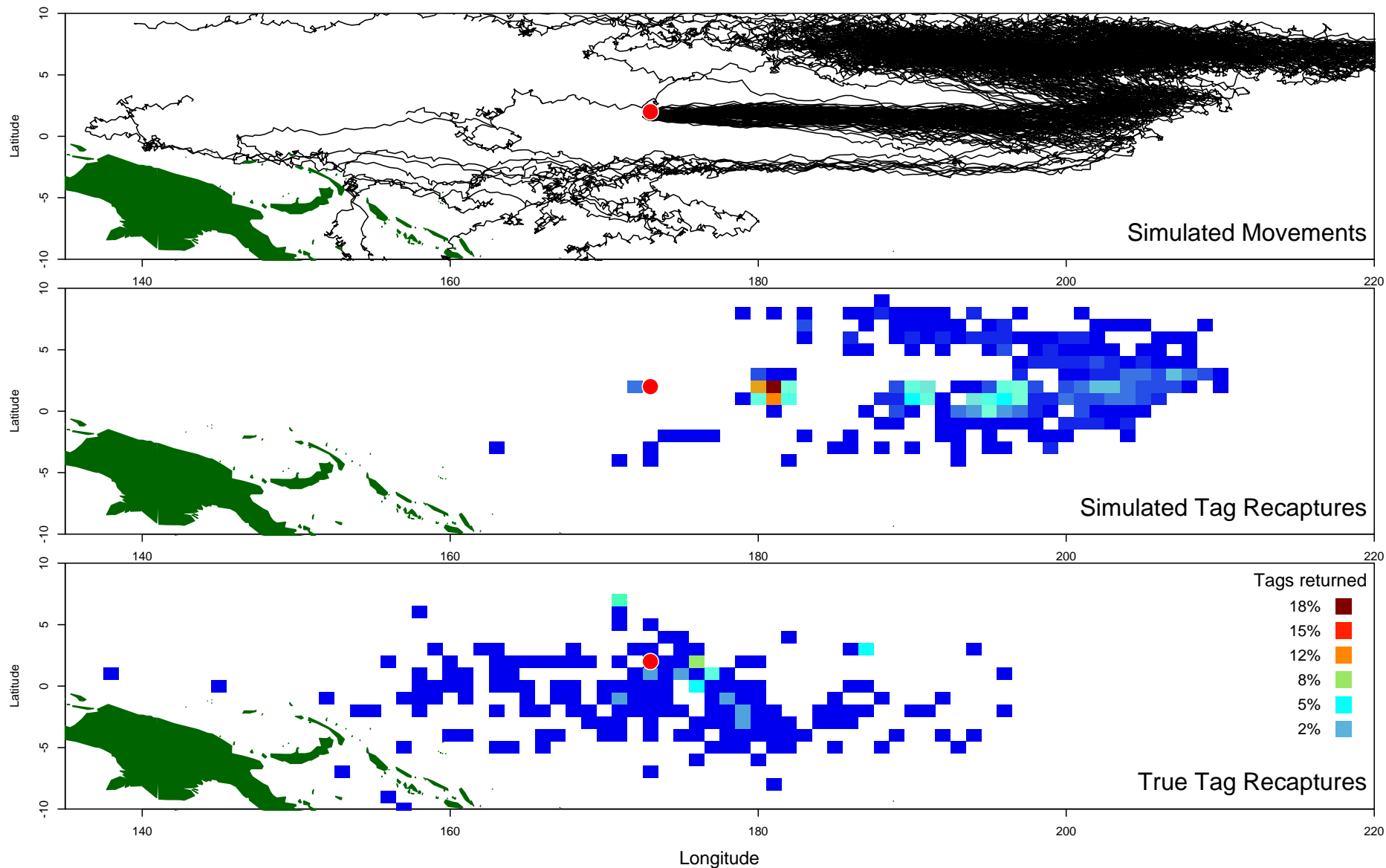
Figure 6. Comparison of a simulated tagging event with a true release of tagged skipjack undertaken in 2009 (location indicated red spot). Top panel: a subset of the complete movement tracks of 100 tuna individuals. Middle panel: positions of individuals sampled through time from the same monthly distribution of returns from the true release event. Bottom panel: positions of recaptures from the true tag release.

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