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An individual-based model of skipjack tuna (*Katsuwonus pelamis*) movement in the tropical Pacific ocean

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ABSTRACT

The distribution of marine species is often modeled using Eulerian approaches, in which changes to population density or abundance are calculated at fixed locations in space. Conversely, Lagrangian, or individual-based, models simulate the movement of individual particles moving in continuous space, with broader-scale patterns such as distribution being an emergent property of many, potentially adaptive, individuals. These models offer advantages in examining dynamics across spatiotemporal scales and making comparisons with observations from individual-scale data.

Here, we introduce and describe such a model, the *Individual-based Kinesis, Advection and Movement of Ocean ANimAls* model (Ikamoana), which we use to replicate the movement processes of an existing Eulerian model for marine predators (the Spatial Ecosystem and Population Dynamics Model, SEAPODYM). Ikamoana simulates the movement of either individual or groups of animals by physical ocean currents, habitat-dependent stochastic movements (kinesis), and taxis movements representing active searching behaviours.

Applying our model to Pacific skipjack tuna (*Katsuwonus pelamis*), we show that it accurately replicates the evolution of density distribution simulated by SEAPODYM with low time-mean error and a spatial correlation of density that exceeds 0.96 at all times. We demonstrate how the Lagrangian approach permits easy tracking of individuals' trajectories for examining connectivity between different regions, and show how the model can provide independent estimates of transfer rates between commonly used assessment regions. In particular, we find that retention rates in most assessment regions are considerably smaller (up to a factor of 2) than those estimated by this population of skipjack's primary assessment model. Moreover, these rates are sensitive to ocean state (e.g. El Nino vs La Nina) and so assuming fixed transfer rates between regions may lead to spurious stock estimates. A novel feature of the Lagrangian approach is that individual schools can be tracked through time, and we demonstrate that movement between two assessment regions at broad temporal scales includes extended transits through other regions at finer-scales.

Finally, we discuss the utility of this modeling framework for the management of marine reserves, designing effective monitoring programmes, and exploring hypotheses regarding the behaviour of hard-to-observe oceanic animals.

1. Introduction

Skipjack tuna (*Katsuwonus pelamis*) is the third most exploited wild fish species in the world (FAO, 2016), with around 70% of the estimated three million tonnes landed globally originating from the Pacific Ocean (IATTC, 2016; Williams and Terawasi, 2016). Current assessments of this species suggest that Pacific stocks are not overfished, but that catches are approaching a fully exploited state (Maunder, 2014; McKechnie et al., 2016a). However, considerable uncertainty exists regarding the spatial parameters of the stock assessment models, such

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as movement rates and recruitment distribution, with models known to be highly sensitive to these parameters (McKechnie et al., 2016a, 2016b).

Gaining a greater understanding of these processes in free-ranging marine predators such as tunas is non-trivial. The behaviour of these animals is a result of many ecological interactions among individuals and their conspecifics (Parrish, 1999), the animals they prey upon (Bertrand et al., 2002; Lander et al., 2011), and abiotic factors associated with their environment (Evans et al., 2013). Technological developments have provided an increased ability to investigate the behaviour of individual marine animals *in-situ*. However, the lack of concurrent information on the local biotic and abiotic environmental conditions means that hypothesis-testing based on data gained from observations such as tagging experiments is difficult (Dagorn et al., 2001; Kirby, 2001). In such situations, the use of simulation models as quantifiable thought-experiments can be a useful tool in exploring hypotheses and bracketing uncertainty (Bélisle, 2005; Di Paolo et al., 2000; Rykiel, 1996).

Current spatial population dynamics models for skipjack and other tunas typically employ state variables of biomass or density, assuming an abstraction at the level of the individual. Most also calculate changes in a population through time in a single fixed location or across fixed points in space (Fournier et al., 1998; Hampton and Fournier, 2001; Lehodey et al., 2008). This approach offers robust parameter optimisation from data, and computational efficiency once these parameters have been estimated. In contrast, Lagrangian framework models examine the evolution of properties following the trajectory of discrete individuals. In an ecological context, these are usually termed individual-based models (IBMs). The IBM approach has a number of benefits over Eulerian and state variable models when simulating the movement and behaviour of animal populations (Grimm and Railsback, 2005); stochasticity in behaviours across individuals can be easily incorporated; simulated individuals can exhibit or adapt their behaviours separately, including in response to other individuals; and the state and position of individuals can be tracked throughout a simulation, making IBMs particularly well-suited to examining connectivity and variability of habitat-use for highly mobile animals. Modelled individuals have trajectories consisting of continuous positions in time and space, and when moved by purely deterministic processes, these trajectories can be simulated backwards in time (Paris et al., 2013). Such individual-scale analysis is not possible using the tracer outputs from Eulerian models. While a number of Eulerian stock assessment and ecosystem models exist for tropical tunas (Hampton and Fournier, 2001; Maury, 2010; Senina et al., 2008), there are few tools to examine movement in the context of tagging, mixing and connectivity.

IBMs simulating the dynamics of oceanic animals have been outlined or developed in a number of studies for both population dynamics (e.g. Brochier et al., 2008; Kirby et al., 2003; Okunishi et al., 2012) or to examine specific questions surrounding movement (e.g. Dagorn et al., 2000; Føre et al., 2009; Huse and Fiksen, 2010). Due to the nature of the pelagic environment, fisheries-independent surveys are usually not feasible, and much of the data obtained on wild animal populations is sampled from observations at the individual level through mark-recapture tagging, biologging, sightings, and catch sampling (Ford et al., 2013; Hare et al., 2015; Leroy et al., 2013a; Scutt Phillips et al., 2017). However, because population dynamics models typically consider large-scale ecological phenomena through mathematical abstractions of these individual-scale processes, informing such models with observations obtained at the individual level remains a challenge (Dagorn et al., 2001; Freon and Misund, 1998; Sippel et al., 2014).

In Eulerian population dynamics models of exploited fish populations, parameters such as catchability, inter-region migration coefficients, and habitat preference aim to encompass the emergent large-scale effect of many small- and individual-scale mechanisms. These assumptions can be tested using IBMs that are informed directly by individual-level observations incorporated into the behaviour of individuals in the model. The emergent properties of the IBM can be examined at a relevant scale for comparison with the population model, identifying if current parameters or model structure are appropriately encompassing dynamics as well as bracketing the uncertainty around such processes.

Here, we introduce an IBM suited to the purpose of testing the assumptions of Eulerian models regarding connectivity and movement dynamics of animal populations: the Individual-based Kinesis, Advection and Movement of Ocean ANimAls model (Ikamoana[1]), parameterised for skipjack tuna in the Pacific Ocean. Simulating a single cohort (fish of a single age class) through time using physical ocean circulation and skipjack tuna habitat fields derived from a tuna-forage sub-model, we replicate the predicted distribution of this cohort from an existing Eulerian numerical ecosystem model parameterised for the same species: the Spatial Ecosystem And POpulation DYnamics Model (SEAPODYM: Lehodey et al., 2008; Senina et al., 2008). We first detail the movement assumptions of SEAPODYM, before describing how they are implemented in a Lagrangian framework within our Ikamoana model. Two simulations using forcing fields from different temporal scenarios are carried out, one during a largely ENSO neutral period (2003–2007), the other during a period of large variations in ENSO phase (1997–2001). We then show how individual trajectories can be used to examine movement and connectivity between stock assessment regions used for fisheries management, and compare these results to connectivity estimates from a second Eulerian model (MULTIFAN-CL: Fournier et al., 1998; Hampton and Fournier, 2001; McKechnie et al., 2016a), used by the Pacific Community for assessing the impact of fishing on the western and central Pacific ocean (WCPO) skipjack tuna stock. Finally, our results and approach are discussed in the context of further informing stock assessment of tropical tuna species, and examining assumptions on movement behaviour in free-roaming oceanic animals.

2. Materials and methods

2.1. Movement model

Here, we briefly describe the movement model of SEAPODYM, alongside the calculation of forcing components and key equations, before detailing the required individual-based reformulation of these terms in Ikamoana.

2.2. SEAPODYM

SEAPODYM is based on a Eulerian advection-diffusion-reaction approach to modelling the distribution of pelagic fish, as if the density of the fish were a continuous tracer in a two-dimensional (longitude, latitude) field. The reaction component governs the change in abundance of fish through recruitment and mortality at different life stages. However, for comparison with our movement IBM, we focus only on the movement of young and adult tuna in SEAPODYM by following a single, unfished cohort through time with natural mortality set at zero.

Three distinct processes are assumed in order to simulate the movement of young and adult tuna in SEAPODYM. First, physical ocean currents (derived from the Nucleus for European Modelling of the Ocean, NEMO) provide velocity fields for the passive advection of tuna. Second, an active taxis represents directed movements following the gradient of an age-dependent habitat field derived from a tuna forage sub-model (see below), thus driving fish density towards more favourable areas (Grünbaum, 1999). Finally, a non-directional kinesis component accounts for small scale and assumed random movements characteristic of searching behaviour (Okubo and Levin, 2001; Turchin,

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[1] A word existing across several Polynesian languages meaning ‘ocean fish’, from *ika* ‘fish’ + *moana* ‘ocean’.

1997). By diffusing tuna density at a rate that is inversely proportional to the quality of local habitat, diffusion is greater in regions of poor habitat and vice versa. Detailed information on the modelling assumptions and functional forms of movement parameters can be found in Lehodey et al. (2008) and Senina et al. (2008). The SEAPODYM model parameters were fitted using maximum likelihood estimation (MLE) on catch and effort data, size data, and information from tag returns. Model evaluation included examination of spatial residuals and cross-validation using proportions of these data not used in fitting. Full details of these evaluations can be found in Senina et al. (2008, 2016).

The change in density N of a cohort at age a over time, excluding recruitment and mortality, is therefore described in a Eulerian framework by:

$$\frac{\partial N_a}{\partial t} = -\nabla\cdot(U^c N_a + U_a^t N_a) + \nabla\cdot(K_a \nabla N_a) \tag{1}$$

Here, $\boldsymbol{U^c}$ *is* a vector of zonal and meridional ocean current velocities averaged over upper ocean model layers accessible to tuna (which is an age dependant function of oxygen and temperature). $\boldsymbol{U_a^t}$ is a vector of directed zonal and meridional velocity (taxis). K_a is a spatially and temporally varying diffusion coefficient (Eq. (3)). Eq. (1) is approximated in SEAPODYM as a discrete-continuous system on a regular grid of cells at a given spatial resolution, and a discretised time step of Δt (see Lehodey et al., 2008).

Both K_a and $\boldsymbol{U_a^t}$ depend on spatially and temporally varying age-dependent habitat. This habitat field is related to the biomass of forage species derived from a mid-trophic micronekton sub-model (Lehodey et al., 2010). The habitat index is a function of the forage biomass accessible to tuna of age a, and is represented as an index, H_a, which varies between zero and one. Accessibility to forage depends on ocean temperature and dissolved oxygen. All parameters of the habitat index are estimated in MLE approach (Senina et al., 2016, 2008).

The vector of directed taxis from Eq. (1), $\boldsymbol{U_a^t}$, represents the directed movement of tuna towards more favourable habitat. It is proportional to age, maximum sustainable swimming speed, V_{max}, and the change in H_a in the zonal (x) or meridional (y) direction and is calculated using central differencing with forward or backward differencing at the boundaries such that,

$$U_a^t = \frac{V_{max}(L_a)^b \nabla H_a}{\max(\|\nabla H_a\|)} \tag{2}$$

where V_{max} is the maximum swimming speed in body lengths per second, L_a is the mean fork-length-at-age in meters per body length, as predicted by a von Bertalanffy growth curve for Pacific skipjack tuna (Rice et al., 2014), and b is a constant slope parameter. Taxis velocity therefore tends towards the maximal sustainable speed of a fish at a given length where the habitat gradient also tends towards its maximum value.

The final term in Eq. (1) ($\nabla\cdot(K_a \nabla N_a)$) represents the stochastic movement of tuna sampling their environment, with searching distance becoming larger as the habitat becomes less favourable. The diffusion coefficient, K_a of tuna is spatially varying and is non-linearly related to the age-dependant tuna habitat quality index. This causes tuna to diffuse at their maximum rate, σD_{max_a}, where habitat quality is minimal ($H_a = 0$), and at their minimum rate, $(1-c)\sigma D_{max_a}$ where the habitat quality is maximal ($H_a = 1$). The diffusion is given by:

$$K_a = \sigma D_{max_a}(1-cH_a^p) \tag{3}$$

where p, c and σ are positive constants estimated using a MLE approach based on observed catch and mark-recapture tagging data (Senina et al., 2016).

Maximal diffusivity is given by

$$D_{max_a} = \frac{V_{L_a}^2 \Delta t}{4} \tag{4}$$

where V_{La} is an age-dependent velocity fixed at one body length-at-age per second, and Δt is the time step of the discretised model.

For conditions that result in a combined velocity from advection and taxis exceeding two degrees per two days, velocity is set at two degrees per two-days. No corresponding limit is set on large movements resulting from diffusion.

2.3. Ikamoana

In an individual-based, or Lagrangian, framework, we do not consider the density of tuna within a particular area, but rather the movement of 'particles' representing individual or cohesive groups of animals occupying continuous positions in space. For our application to skipjack tuna these individual particles represent small, discrete schools of animals (see *Model Implementation* below), which are referred to using the term 'school'.

The x, y position of an individual particle representing a school of skipjack tuna p, over the discretised time step dt, is given by:

$$\begin{aligned}\frac{dx}{dt} &= D_x^c(x_p, y_p, t) + D_x^t(x_p, y_p, t) + D_x^d(x_p, y_p, t)\\ \frac{dy}{dt} &= D_y^c(x_p, y_p, t) + D_y^t(x_p, y_p, t) + D_y^d(x_p, y_p, t)\end{aligned} \tag{5}$$

where D^c, D^t and D^d are the x and y displacements related to the ocean currents, active taxis, and diffusion terms, respectively. To the extent that it is possible, these terms are the Lagrangian reformulation of the SEAPODYM advection, taxis and diffusion terms. In a Lagrangian framework, the interpretation of these terms must be reconsidered. At the temporal scale of our model, the effect of physical ocean currents can be assumed to act on a cohesive school of fish homogenously. Similarly, the phenomena of diffusion is known to emerge from the random movements of many individual agents (see below). The taxis behaviour of SEAPODYM implies knowledge of the underlying habitat gradient. Schooling is known to provide more effective environmental sampling and information transfer for fishes (Pitcher and Parrish, 1993). Our Ikamoana implementation for skipjack tuna is structured at the ecological scale of the school, and so we may assume that some environmental sampling and information exchange between individuals occurs that is not explicitly simulated as part of the SEAPODYM movement model replicated here.

The physical ocean advection components (D_c) are calculated using velocity fields at the position (x_p, y_p) of a school over the time step. Similarly, the distance moved via taxis is the product of the velocity field given by $\boldsymbol{U_a^t}$ (Eq. (2) over the time step. A fourth order Runge-Kutta scheme is used to integrate both of these deterministic advection terms through time (Butcher, 2016; van Sebille et al., 2017).

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

The movement of schools associated with a non-uniform diffusivity is given by (from Ross and Sharples, 2004):

$$\begin{aligned}D_x^d &= \xi_1 \sqrt[2]{2K\Delta t/r} + \frac{\partial K_a}{\partial x}\Delta t\\ D_y^d &= \xi_2 \sqrt[2]{2K\Delta t/r} + \frac{\partial K_a}{\partial y}\Delta t\end{aligned} \tag{6}$$

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, $\xi \in [-1, 1]$). The first term on the right-hand side represents an unbiased random walk, while the second term is the additional deterministic advection correction that counters the accumulation of schools in regions of low K_a. This stochastic diffusion component of equation (5) is numerically integrated using a simple Euler-forward scheme. The values of all constant parameters are given in

Table 1
List of parameters and values estimated from catch, effort and tagging data (Senina et al., 2016).

Parameter	Value	Description
V_{max}	2.226	Maximum sustainable swimming speed (body lengths/second)
b	0.834	Slope parameter for maximum sustainable swimming speed to fish length relationship
σ	0.176	Scaling parameter for maximum diffusivity, D_{max}
c	0.662	Diffusivity function habitat coefficient
p	3	Exponent parameter for diffusivity function
r	1/3	Variance of random uniform probability distribution

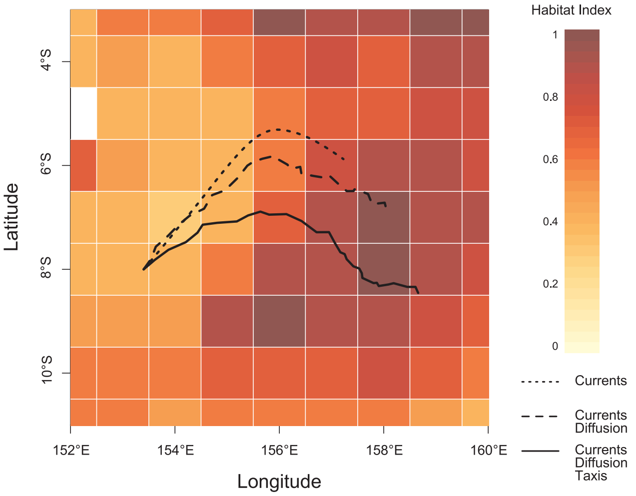


Fig. 1. Movement trajectories from three individual schools initialised at the same point and simulated for three months: one representing a school solely under the influence of physical ocean currents, one moved by both currents and diffusive behaviours, and one combining advection, diffusion, and an active taxis that follows the gradients of favourable habitat. Skipjack tuna habitat index is plotted by cell underneath.

table 1.

An example of the effect of ocean advection, active taxis and biased random walk on the trajectory of a single school is shown in Fig. 1. After the addition of taxis behaviour the school quickly moves to the centre patch of consistently high habitat.

2.4. Model implementation

Ikamoana is built upon the recently developed open-source Lagrangian particle simulation framework *Parcels* (Lange and van Sebille, 2017). In this study, we used physical ocean current and habitat forcing fields identical to those driving recent SEAPODYM solutions for skipjack tuna (detailed below). To replicate the same methodology as SEAPODYM, we used nearest-neighbour interpolation when sampling advection and habitat fields at school locations, and no temporal interpolation between time steps was undertaken. The habitat field was bounded by missing values at the edge of the model domain, pathways to the Indian Ocean through the Timor and Andaman Seas and the Southern Ocean, and large landmasses. In the Lagrangian formulation, if the random, ‘diffusive’ movements resulted in individuals moving outside of these boundaries, the probability distribution of potential displacements was randomly searched by recursively re-drawing the stochastic component of equation (6) until a valid move kept the individual inside the domain.

Like many pelagic fishes, skipjack tuna are known to school, and so it is not necessary to simulate each individual fish. For our study, we assume that the simulated cohort can be packaged into ‘super-individuals’, representing the minimum number of fish that naturally form a school. This is appropriate when these super-individuals share homogenous properties (Hellweger et al., 2016), which in this case is school behaviour and position in space. Although multiple schools may move to the same location in the model to simulate the formation of temporary large schools, which persist for as long as conditions drive these schools to the same location before reforming, it is important that the total population is not packaged into super-individual schools of sizes that would overestimate density projections due to an erroneous school-size assumption. We therefore required an estimate of the approximate minimum number of fish that might form a school of age five-month skipjack tuna.

A representative number of fish within a school can be estimated from observer sampling of catch in the WCPO purse seine fishery. Estimated total tonnage by species and length-frequency sampling are available for each purse seine set made during the period 2004–2016. However, skipjack tuna of five-months age are ‘pre-recruits’ and only incidentally caught by purse seine gears. In order to provide an indicative estimate of a minimum number of fish of this age that could form a cohesive school, we examined mono-specific sets containing only adult skipjack tuna of narrow length distribution (± 2 cm fork length). We used the observer-estimated weight and length of fish in each of these sets to calculate the approximate age and number of fish that would have been present in the school at time of capture, using established length-at-age and weight-at-length relationships (Rice et al., 2014), respectively. The number of fish from a school that had contained this many fish at time of capture was reduced using an inverse natural mortality function (McKechnie et al., 2016a) to estimate the number of fish present when aged five months. This approach makes a somewhat simplistic assumption that natural mortality was the only mechanism responsible for changing school size prior to entry into the purse seine fishery. The smallest 5th percentile in this distribution of projected school-sizes was around 1000 fish, which we assumed to be an appropriate estimate for a minimum super-individual size within our simulation.

We replicated the simulated skipjack tuna distribution from a recent SEAPODYM solution estimated using fisheries and mark-recapture tagging data (Senina et al., 2016). Physical and biogeochemical forcing fields were used, taken from the NEMO-PISCES ocean model (Aumont et al., 2015), with at-age skipjack tuna habitat fields calculated from a tuna-forage sub-model (Lehodey et al., 2010). Forcing fields were at a $1^{\circ} \times 1^{\circ}$ resolution and updated at monthly intervals assumed to be 30 days, beginning in February and running for five years. The movement behaviours of a single cohort of SEAPODYM-defined young to adult skipjack tuna were simulated through time from five months of age, with no natural or fishing mortality included as we wished to examine only the “pristine” distribution of this cohort as an emergent property of our movement model.

The total number of individuals in the cohort was packaged into a smaller number of ‘super-individuals’, which we define here as individual schools. Movements of these schools were calculated at two-day time steps, resulting in 15 positions each monthly period. The ages of skipjack tuna schools were incremented at the end of each month, when school density by grid cell was also calculated.

2.5. Simulation experiments

The distribution of simulated skipjack tuna cohorts was examined across two five-year periods with contrasting environmental conditions: the period 2003–2007, representing a relatively neutral period with respect the El Niño Southern Oscillation (ENSO, the largest driver of inter-annual ocean changes in the tropical Pacific region), and 1997–2001, which includes both a strong El Niño (1997/98) event and La Niña (1998/99) event. The initial distribution of five-month old skipjack tuna was obtained by Monte Carlo sampling the spatial distribution of SEAPODYM projected density for tuna at the same age.

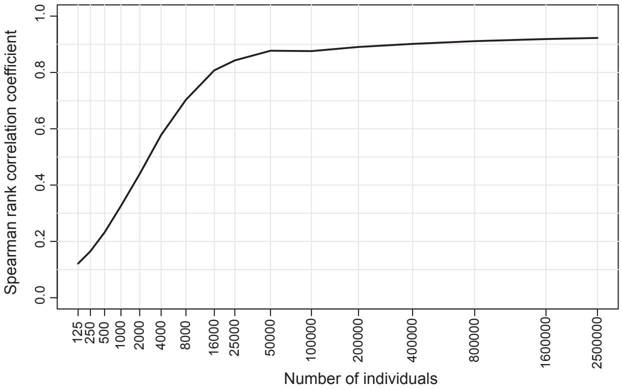


Fig. 2. Spearman's rank correlation coefficient between SEAPODYM and Ikamoana 1° × 1° cell relative density at time 0.

Each school was placed at a random location within a cell, which was selected with probability equal to the relative proportion of the cohort population present in that cell as simulated by SEAPODYM. Comparing density values of a Eulerian field with an approximation of the same solution using a finite number of individual schools in a Lagrangian model necessarily results in some discrepancies. Even at the time of initialisation there were small differences in the distribution of densities for the two models, when by definition the distribution of individual schools in Ikamoana is a direct function of the distribution of density in SEAPODYM. The Spearman rank correlation coefficient between the density distribution of this initial time step between SEAPODYM and Ikamoana was calculated for increasing numbers of schools (Fig. 2). Correlation between the two models increased sharply until 10,000 schools, and began to asymptote after 1 million.

In the current SEAPODYM solution for skipjack tuna, there are no density-dependent mechanisms for young and adult life-stages. The estimate of the total abundance of the five-month-age cohort obtained as a result of MLE procedure is around 2.5 billion individual fish. Using both an assumed minimum school size of 1000 fish aged five months, and accurate representation of fish density at 1° grid cells after 1 million schools, we therefore ran full simulations consisting of 2.5 million individual schools, using school density evolution through time to compare to SEAPODYM.

Ikamoana monthly cohort density was compared to those simulated by SEAPODYM without natural or fishing mortality for the same period at 1° × 1° resolution. For comparisons we used root mean square error and correlation metrics between the relative density of skipjack tuna simulated by each approach, through time. The individual-based framework then allowed us to examine connectivity between commonly used assessment regions for skipjack tuna by analysing the simulated trajectories of individual schools. Connectivity was quantified through regional transition matrices, which are comparable to estimated regional 'block transfer' rates used in the existing stock assessment model for skipjack tuna in the WCPO: MULTIFAN-CL (Hampton and Fournier, 2001; McKechnie et al., 2016a). Changes to these movement connectivity measures were also examined across varying ENSO conditions. Finally, trajectories were examined individually to demonstrate how broad movements may involve significant movement through other regions for a quantifiable proportion of the population.

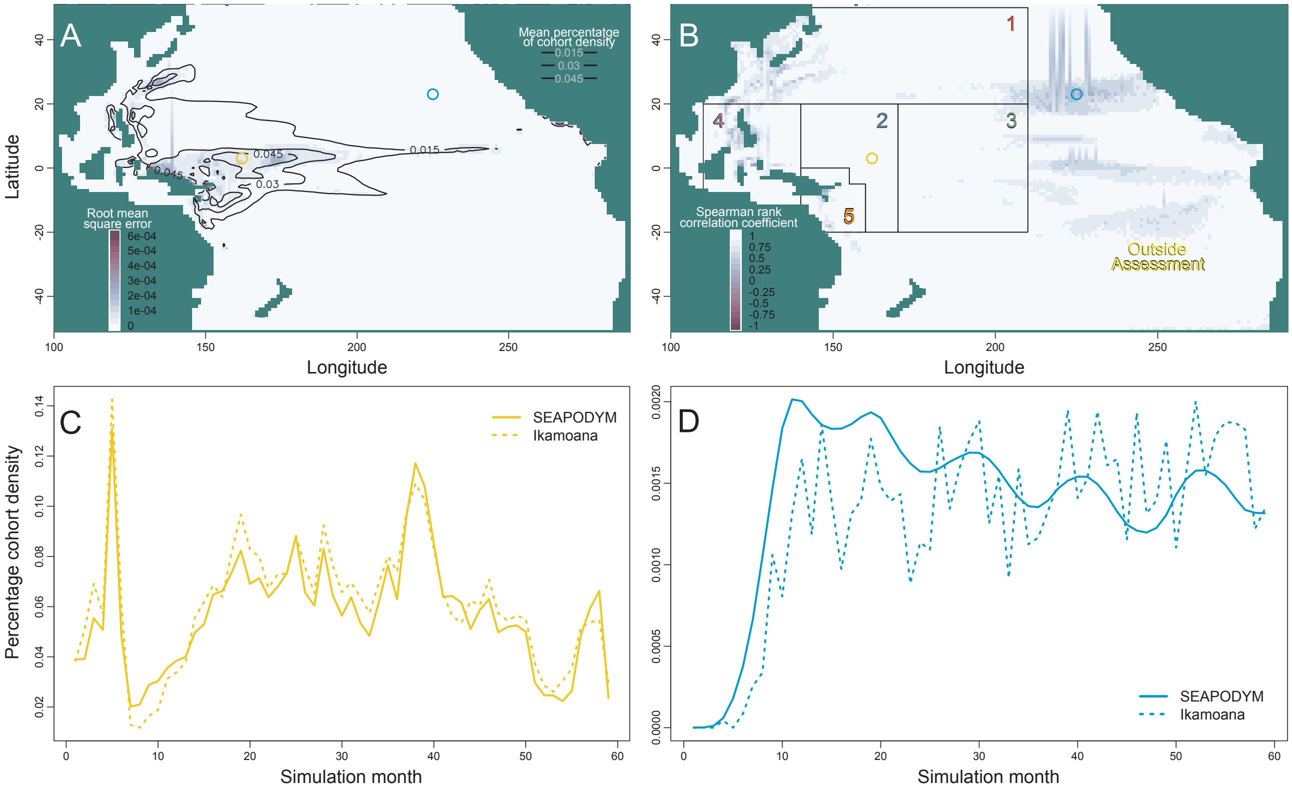
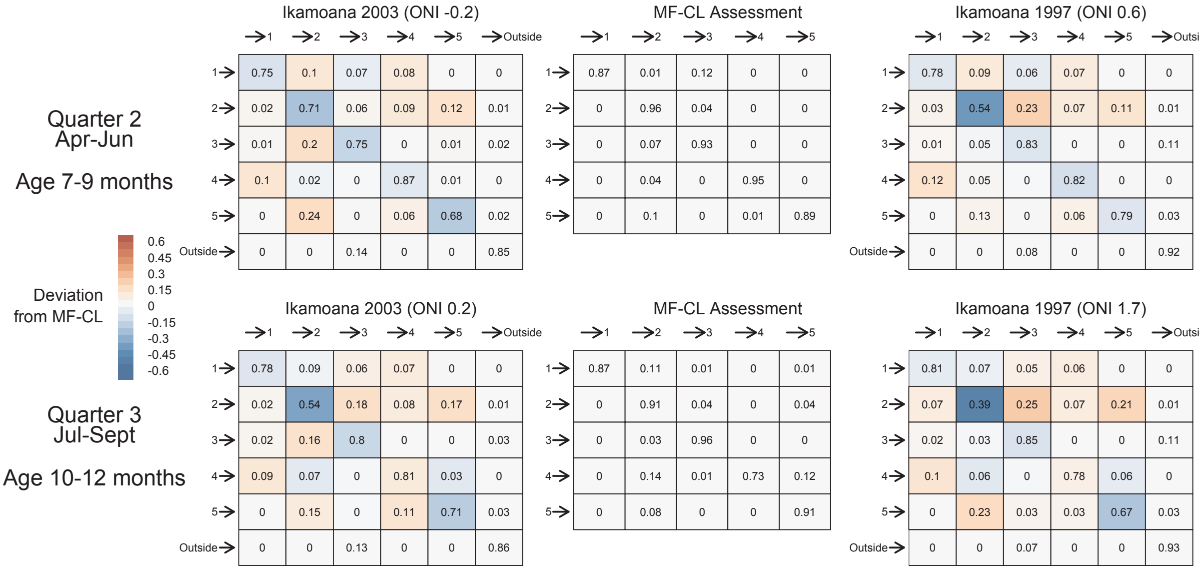


Fig. 3. Plots comparing the relative density evolution of skipjack tuna simulated by SEAPODYM and Ikamoana. (A) Root mean square error through time for each cell, with mean relative density from SEAPODYM contoured. (B) Spearman rank correlation through time for each cell, with recent skipjack tuna assessment regions overlaid. (C) Simulated relative density through time for an example cell in the western warm pool (gold circle in panels A & B). (D) Simulated relative density from a cell in North East Pacific (blue circle in panels A & B). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Quarter 2, Apr-Jun, Age 7-9 months

Ikamoana 2003 (ONI -0.2)

	→1	→2	→3	→4	→5	→Outside
1→	0.75	0.1	0.07	0.08	0	0
2→	0.02	0.71	0.06	0.09	0.12	0.01
3→	0.01	0.2	0.75	0	0.01	0.02
4→	0.1	0.02	0	0.87	0.01	0
5→	0	0.24	0	0.06	0.68	0.02
Outside→	0	0	0.14	0	0	0.85

MF-CL Assessment

	→1	→2	→3	→4	→5
1→	0.87	0.01	0.12	0	0
2→	0	0.96	0.04	0	0
3→	0	0.07	0.93	0	0
4→	0	0.04	0	0.95	0
5→	0	0.1	0	0.01	0.89

Ikamoana 1997 (ONI 0.6)

	→1	→2	→3	→4	→5	→Outside
1→	0.78	0.09	0.06	0.07	0	0
2→	0.03	0.54	0.23	0.07	0.11	0.01
3→	0.01	0.05	0.83	0	0	0.11
4→	0.12	0.05	0	0.82	0	0
5→	0	0.13	0	0.06	0.79	0.03
Outside→	0	0	0.08	0	0	0.92

Quarter 3, Jul-Sept, Age 10-12 months

Ikamoana 2003 (ONI 0.2)

	→1	→2	→3	→4	→5	→Outside
1→	0.78	0.09	0.06	0.07	0	0
2→	0.02	0.54	0.18	0.08	0.17	0.01
3→	0.02	0.16	0.8	0	0	0.03
4→	0.09	0.07	0	0.81	0.03	0
5→	0	0.15	0	0.11	0.71	0.03
Outside→	0	0	0.13	0	0	0.86

MF-CL Assessment

	→1	→2	→3	→4	→5
1→	0.87	0.11	0.01	0	0.01
2→	0	0.91	0.04	0	0.04
3→	0	0.03	0.96	0	0
4→	0	0.14	0.01	0.73	0.12
5→	0	0.08	0	0	0.91

Ikamoana 1997 (ONI 1.7)

	→1	→2	→3	→4	→5	→Outside
1→	0.81	0.07	0.05	0.06	0	0
2→	0.07	0.39	0.25	0.07	0.21	0.01
3→	0.02	0.03	0.85	0	0	0.11
4→	0.1	0.06	0	0.78	0.06	0
5→	0	0.23	0.03	0.03	0.67	0.03
Outside→	0	0	0.07	0	0	0.93

Fig. 4. Comparison of Ikamoana estimated transition matrices for two different age classes and quarterly periods (left and right columns), with temporally matching movement rates between different skipjack tuna assessment regions estimated using MULTIFAN-CL. Colours represent larger (red) and smaller (blue) transition coefficients than those from MULTIFAN-CL rates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Model validation

To test the accuracy of our model in correctly formulating the movement assumptions of SEAPODYM, the relative density distribution of all schools simulated at each time step in Ikamoana was compared with relative density distribution simulated by SEAPODYM, at a 1° × 1° grid resolution.

Both root mean square error (RMS) and Spearman rank correlation coefficients were calculated for each cell through time (Fig. 3a and b, respectively, shown for 2003 scenario). As expected, RMS was greater where mean cohort density through time was also greater, in particular within the western warm pool region. Conversely, correlation was consistently higher in areas with a high mean cohort density, and 95% of cells had correlation coefficients greater than 0.72. Correlation was poorest in areas where density of skipjack tuna was low, and some land-boundary cells.

Changes in skipjack tuna density, relative to density of the entire cohort, are shown for two contrasting example cells in Fig. 3c and d. Fig. 3c shows a cell of fluctuating but generally high relative skipjack tuna density (mean SEAPODYM cohort density = 0.057%), for which RMS was moderate but correlation was high (Spearman's rank coefficient = 0.92). Predicted density by Ikamoana tracked that of SEAPODYM well, overestimating relative density over the course of the simulation (mean Ikamoana cohort density = 0.061%). Fig. 3d shows a cell of low skipjack tuna density (mean SEAPODYM cohort density = 0.0013%), for which correlation with Ikamoana was poor (Spearman's rank coefficient = 0.33). Due to low density, the relative density simulated by Ikamoana fluctuated as small numbers of individual schools moved in and out of the cell, and the density evolution did not track that of SEAPODYM. However, the time-mean relative density was similar (0.0012%).

Temporally, the Spearman rank spatial correlation coefficient over the whole domain at each timestep remained stable throughout the simulation, with a mean of 0.98, and never fell below 0.96.

3.2. Tracking school trajectories

Using IBMs, it is possible to track the trajectories of individuals throughout the simulation, quantifying the environment experienced and movement across a variety of temporal and spatial scales (Video 1). Connectivity of Pacific skipjack tuna can be examined using our Ikamoana simulation. Here we examine movement between five spatial regions defined in recent stock assessments for WCPO skipjack tuna (McKechnie et al., 2016a), and a sixth region constituting that part of the Pacific Ocean outside WCPO convention area. These regions form the spatial stratification of another Eulerian state variable model, MULTIFAN-CL (Fournier et al., 1998), used for stock assessment of many tuna species in the WCPO. In this model, tuna biomass present in each region is transported to other regions over quarterly time periods using estimated stock transfer movement parameters, which vary each quarter and by age-class, but do not exhibit inter-annual variability.

These stock transfer parameters can be arranged in a transition matrix, representing the proportion of the biomass in each region that moves to each other region over each three-month time step. In an IBM context, transition matrices can be thought of as describing the probability that an individual school present in one region will move to another region over the given period of time. Regional persistence, which is the probability of beginning and ending a period in the same region, is given by the diagonal of this matrix.

In Ikamoana, it is possible to calculate comparable transition matrices by summarising the trajectories of all schools as they move between region boundaries over a three-month period. To appropriately compare to MULTIFAN-CL, the region occupied at the start and end of a quarterly period by each school is used to populate the transition matrix, which is then compared to the MULTIFAN-CL stock transfer movement parameters for the same age-class of skipjack tuna. Here, we compare transition matrices across two quarterly periods from both our temporal scenarios, for fish aged between 7 and 12 months (Fig. 4).

The connectivity between assessment regions, simulated by Ikamoana is greater than that recently estimated in MULTIFAN-CL (MF-CL) for skipjack tuna in most cases. Regional persistence during quarterly periods was lower than in MF-CL across all regions, that is, Ikamoana simulates greater movement of schools away from their starting regions for a given quarterly period. In particular, skipjack tuna in the western warm pool (region 2) showed far less persistence and greater movement into the central tropical Pacific (region 3), and to the east of Papua New Guinea and northern Australia (region 5) than in MF-CL. This movement rate was strongest during quarter three for skipjack

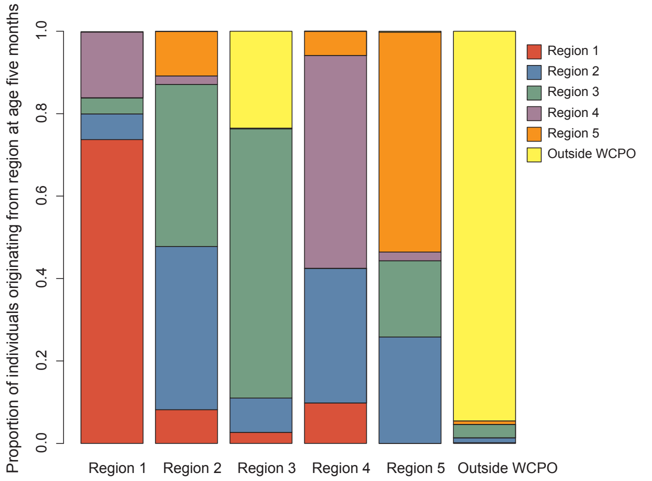


Fig. 5. Proportion of skipjack tuna by region, of age ten-months (i.e. at entry into the purse seine fishery), which originated from each other region at the start of the 2003 simulation scenario, when tuna are age five months.

tuna aged 10–12 months, when the probability of schools beginning and ending the quarter in region 2 was 0.54 and 0.39, compared to 0.91 estimated by the assessment model, for the 2003 and 1997 scenarios, respectively. The quarterly transfer of fish from region 5 to regions 2 and 3 was also greater than that of the MF-CL assessment.

Ikamoana can also be used to determine the locations of schools at previous time steps (Video 1, Fig. 5). For instance, where ten-month skipjack tuna (a typical age at which they recruit into the purse seine fishery) in each region were located five months earlier. Specifically, in the north-western Pacific (region 1), 74% of ten-month old tuna were located within region 1 at age five-months, with 15% coming from region 4, 6% coming from region 2, and 4% from region 3. Region 5 received the largest influx of fish from another region, with 26% of fish at entry into the purse seine fishery coming from region 2 and most of the remainder coming from region 3. Overall, the majority of individual schools began and ended the five-month purse seine recruitment period in the same region (mean 63%, s.d. 19%), although this did not necessarily mean that schools remained in the region during the entirety of this period.

We also examined broad environmental drivers on regional connectivity by constructing movement transition matrices from the movement of schools between the beginning of October and the end of the year, during which a strong El Niño and moderate La Niña event began to build during separate years of our 1997 scenario. We compared the regional transition matrices to the same age fish from the same period in our 2003 scenario, where ENSO phases were more neutral (Fig. 6).

During the El Niño period, skipjack tuna had a much lower probability of remaining in region 2, which lies in the western warm pool area, instead moving east into region 3 and north into region 1, when compared to the ENSO neutral period. Similarly, for tuna that were already present in region 3, there was less movement west into region 2, and greater movement further east into the region outside the assessment area. In contrast, during the La Niña event schools showed far greater persistence in region 2, and skipjack tuna outside the assessment area had a greater probability of moving into the central Pacific region 3. Interestingly, during both the El Niño and La Niña periods, there was greater exchange of fish from the archipelagic region 5 into the more oceanic region 2, when compared to ENSO neutral periods.

As with our comparison of quarterly movement probabilities with MULTIFAN-CL, these transition probabilities do not capture potential short-term movements through other regions, nor multiple exchanges between regions. Using the individual school trajectories output from Ikamoana, we are able to quantify inter-region movements that may be occurring at higher temporal resolutions. An example is given in Fig. 7, which describes the movement of all schools that moved from region 4 to region 2 over the three-monthly period 1st October 1997 to 1st January 1998 (i.e. the period of strong El Niño).

This movement was undertaken by 0.5% of the cohort, and from the transition matrix in Fig. 6, it can be seen that schools moving from region 4 to region 2 accounted for about 7% of all skipjack tuna in that region. However, individual pathways indicate that this set of quarterly movements also included schools which moved into other regions. Three school trajectories are highlighted as examples, each of which undertook contrasting routes during this period. Summarising across all schools that made this movement from region 4 to region 2, we can calculate that during this three-month period, 53% of the time was spent in the original region 4 and 37% in the destination region 2. However, 9% and 1% of time was also spent in regions 5 and 1, respectively.

4. Discussion

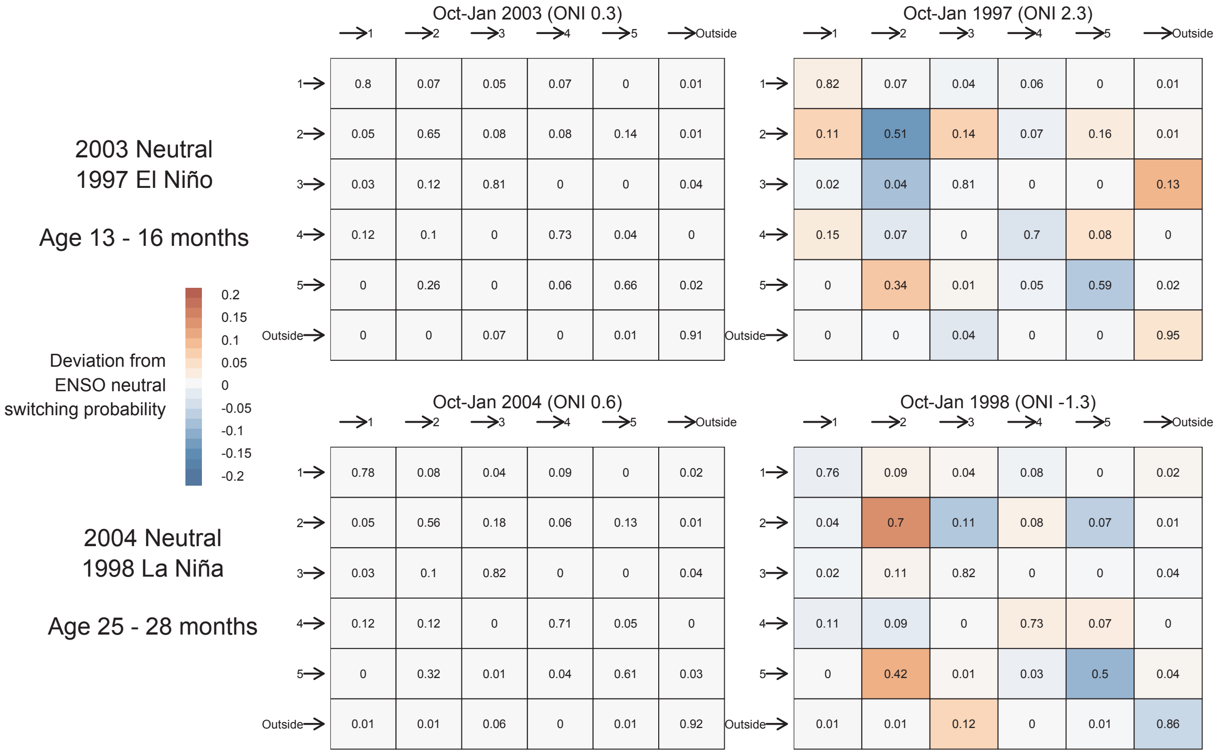
4.1. Replication of SEAPODYM

In this study, we have outlined an approach for an IBM equivalent to the established SEAPODYM Eulerian movement model for skipjack tuna in the Pacific Ocean. Our results show that the Ikamoana IBM can accurately reproduce the evolution of the skipjack tuna density distribution simulated by SEAPODYM. Moreover, the individual-based framework means that it is possible to track individual school trajectories to quantitatively answer questions on movement and connectivity that are difficult to answer using the Eulerian approach. Our simulation of skipjack tuna density exhibits low deviation, both spatially and temporally, with those of SEAPODYM. Unsurprisingly, model differences are highest in areas where skipjack tuna density is low, and at certain land-boundary cells. When density is low, deviations to SEAPODYM are driven chiefly by the stochastic nature of small numbers of individuals moving in and out of areas of consistently low density. This could be improved by increasing the number of individuals in the simulation. The numerical diffusion implicit in the advection-diffusion-reaction solver of SEAPODYM may also account for some discrepancies between our models. This diffusion represents a spurious additional term in the Eulerian model (Sibert et al., 1999). Greater deviations from SEAPODYM in land-boundary cells are likely due to the boundary conditions of our IBM, which randomly searches for legal moves from the probability distribution of habitat-dependant diffusion. This approach differs from the Neumann boundary condition implemented in SEAPODYM. Alternative boundary conditions for Ikamoana, such as reflective edges (e.g. North et al., 2011), are being explored.

4.2. Comparison to skipjack tuna assessment models

It is non-trivial to quantify the connectivity of continuous tracer within a Eulerian model, when the aim is to identify the conditional route of that tracer over multiple time steps. For population dynamics models of exploited marine species, this tracer represents a number of individual mobile animals, which move through a habitat in which they may be exposed to a spatially-varying mortality, either natural or from fishing. Quantifying the trajectories of these movements is important to accurately capture the likely exposure of individuals to these habitat and mortality fields, which are assumed to be homogenous below the spatial stratification of a Eulerian or state variable model.

Our ability to structure a transition matrix from the simulated movements in Ikamoana, with the appropriate spatial and temporal framework from another model (MULTIFAN-CL), demonstrates another useful application of our approach. By tracking school trajectories, we have shown that the simulated connectivity between skipjack tuna assessment regions is far greater with the SEAPODYM estimated movement than that estimated in a recent stock assessment using



Oct-Jan 2003 (ONI 0.3)

	→1	→2	→3	→4	→5	→Outside
1→	0.8	0.07	0.05	0.07	0	0.01
2→	0.05	0.65	0.08	0.08	0.14	0.01
3→	0.03	0.12	0.81	0	0	0.04
4→	0.12	0.1	0	0.73	0.04	0
5→	0	0.26	0	0.06	0.66	0.02
Outside→	0	0	0.07	0	0.01	0.91

Oct-Jan 1997 (ONI 2.3)

	→1	→2	→3	→4	→5	→Outside
1→	0.82	0.07	0.04	0.06	0	0.01
2→	0.11	0.51	0.14	0.07	0.16	0.01
3→	0.02	0.04	0.81	0	0	0.13
4→	0.15	0.07	0	0.7	0.08	0
5→	0	0.34	0.01	0.05	0.59	0.02
Outside→	0	0	0.04	0	0	0.95

Oct-Jan 2004 (ONI 0.6)

	→1	→2	→3	→4	→5	→Outside
1→	0.78	0.08	0.04	0.09	0	0.02
2→	0.05	0.56	0.18	0.06	0.13	0.01
3→	0.03	0.1	0.82	0	0	0.04
4→	0.12	0.12	0	0.71	0.05	0
5→	0	0.32	0.01	0.04	0.61	0.03
Outside→	0.01	0.01	0.06	0	0.01	0.92

Oct-Jan 1998 (ONI -1.3)

	→1	→2	→3	→4	→5	→Outside
1→	0.76	0.09	0.04	0.08	0	0.02
2→	0.04	0.7	0.11	0.08	0.07	0.01
3→	0.02	0.11	0.82	0	0	0.04
4→	0.11	0.09	0	0.73	0.07	0
5→	0	0.42	0.01	0.03	0.5	0.04
Outside→	0.01	0.01	0.12	0	0.01	0.86

Fig. 6. Comparison by monthly age class of estimated transition matrices between assessment regions for periods of contrasting Oceanic Niño Index (ONI). Top row: Neutral (left) and strong el niño (right). Bottom row: Neutral (left) and moderate la niña (right).

MULTIFAN-CL. In particular, Ikamoana simulates more movement between region 5, around the Solomon Sea and Papua New Guinea, and region 2, in the western equatorial Pacific. While around 15–30% of the schools simulated in our experiments moved from the archipelagic waters of region 5 to the more oceanic region 2, regardless of age or simulation period, a counter-movement of only 12–20% occurred from region 2 to region 5. It may be that while the two sub-populations are well mixed, the relatively small region 5 seeds the larger region 2 with juvenile skipjack tuna newly recruited in the population. It is also important to note that regional movement rates in MULTIFAN-CL do not contain inter-annual variation. During the parameter estimation process, contrasting movements such as those associated with El Niño and La Niña conditions, may lead to averaging of contrasting environmentally driven connectivity.

In contrast, schools present in the large domain outside the assessment area showed more consistent residence within this region. For the time during which the cohort aged from five-months to entry into the purse seine fishery, the largest exchange of fish with the non-assessment area was a result of fish leaving region 3 at the start of the simulation until they recruit into the purse seine fishery at ten-months of age ($< 5\%$, Fig. 5.). Immigration into assessment regions from the non-assessment area was minimal for all regions except region 3 ($> 20\%$). Although our IBM is driven by a different movement model to that used for stock assessment of WCPO skipjack tuna, this presents independent justification for the appropriateness of the spatial boundary used in the MULTIFAN-CL assessment model.

However, we have also shown that during the movements between regions at broad time-scales there can exist potentially significant detours through other regions, which may be subject to different fishing mortality and other forcings. Using the IBM approach, we can quantify this for a cohort or population of individuals. Understanding the proportion of a sub-population that is exposed to differing mortality rates during broad scale movements has considerable implications for modelled population dynamics in stock assessment.

It is important to stress that while both SEAPODYM and MULTIFAN-CL use the same catch data (at different spatial aggregations) to estimate their parameters, they have fundamentally different approaches to modelling the spatial distribution of skipjack tuna. Furthermore, we do not include any spatially-varying mortality as a result of fishing, which alters the emergent connectivity of our simulated tuna. As some areas are subject to a greater depletion of fish, the relative transfer of individuals between regions will result in different transition matrices than those we have calculated here. However, in the majority of regions, the fishing mortality for skipjack tuna peaks for fish aged nine to 15 months (McKechnie et al., 2016a), and so the transition matrices for young fish presented here should be approximately comparable to those of MULTIFAN-CL.

4.3. Environmental drivers

Simulated connectivity associated with different ENSO phases on skipjack tuna schools of comparable age was consistent with previous literature and SEAPODYM experiments examining the effect of climate on skipjack tuna (Lehodey et al., 2013, 2008). During El Niño, waters of the warm pool region in the west expand eastward as trade winds reduce and currents from the eastern Pacific weaken or reverse. In the context of tropical tuna ecology, this results in changes in distribution via two processes: changes in cold water boundaries and associated habitat that cause nektonic tunas to generally move eastward to follow productive waters (Lehodey et al., 1997) and changes to spawning habitat and associated larval success which results in generally increased and spatially-differential recruitment of juveniles (Lehodey, 2006; Lehodey et al., 2003). Our application includes only young and adult tuna and so the changes to connectivity we present during the strong 1997/98 El Niño are due solely to the former process of nektonic tunas actively following positive habitat, and showing increased movement eastwards, across region 5, 2 and 3. Residence times decreased across all regions when compared to the ENSO-neutral period, except for the north Pacific region 1 and the area outside the WCPO assessment.

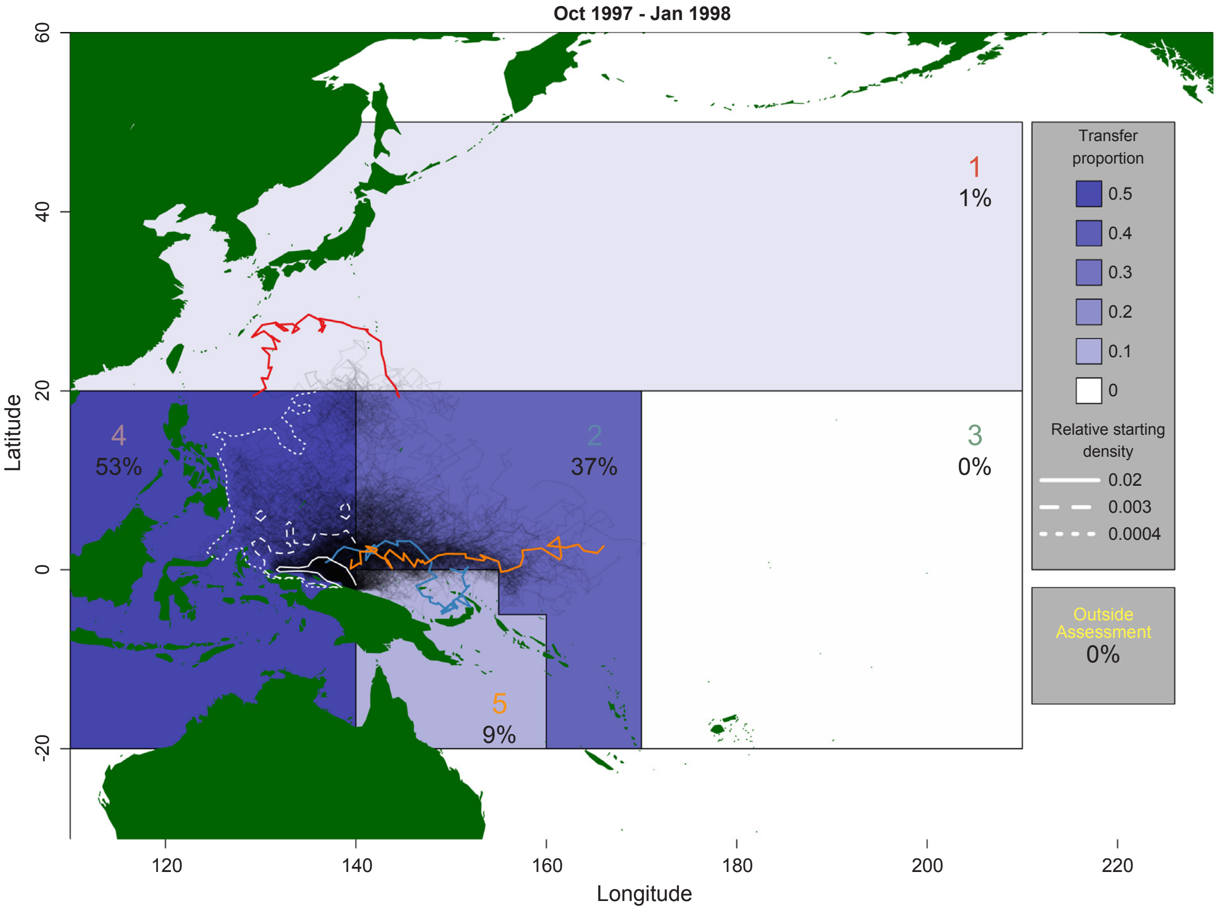


Fig. 7. Example school trajectories from 500 simulated schools that moved from assessment region 4 to region 2 during the period October 1997 to January 1998 (N = 14628). Three individual schools are highlighted, each taking contrasting routes. Assessment regions are coloured by the total proportion of time spent by all individual schools transferring from region 4 to region 2 during the period. The density of region 4 schools prior to moving is contoured in white.

During La Niña, contrasting oceanographic conditions occur, with increased trade wind and intensified westward currents, compressing the warm pool region into a more confined area with a deeper thermocline. Our results during this period show that the principal change is greater westward movement from outside the assessment region, and greater persistence in region 2. These ENSO-driven changes to connectivity are reflected in observed changes to catch distribution data (Lehodey et al., 2003), on which SEAPODYM parameters have been estimated, and here we see this consistently reproduced in the distribution of skipjack tuna simulated by SEAPODYM (Senina et al., 2008) and Ikamoana.

It is interesting to note that during both strong ENSO phases there appeared to be increased movement from the archipelagic waters of region 5 into the oceanic waters of region 2 when compared to more ENSO neutral periods. It appears that, over a quarterly time-scale, skipjack tuna leave the area around Papua New Guinea and the Solomon Sea for oceanic habitats during these El Niño and La Niña events. In the case of the 1997–98 El Niño period, this movement appears to be driven by more heterogeneous habitat quality in region 5 compared to the ENSO neutral period, with high habitat gradients moving individual schools east into region 2 via taxis. For the 1998–99 La Niña, a consistent area of high quality habitat is present during the ENSO-neutral period in the south of region 5 does not develop. As a result, diffusion drives more schools to leave this region into region 2 during the La Niña period.

4.4. Fisheries applications and further development

In this study, we have demonstrated a number of uses of the Ikamoana model, chiefly in the context of connectivity and current stock assessment spatiotemporal stratification. The strength of our approach is in the IBM's ability to examine these dynamics at varying spatial (from regions to individual school positions) and temporal scales (from years to days). In particular, extension of the examples that we have presented would inform stock assessment model parameters and help in quantifying the uncertainty regarding the movement of subpopulations.

As regional transfer rates are estimated parameters in MULTIFAN-CL, the transition matrices describing assessment region connectivity, based on the movement assumptions formulated in SEAPODYM, may be best incorporated as prior values for the estimation of those parameters during optimisation of MULTIFAN-CL. The need for greater understanding of skipjack tuna movements in the WCPO, and potential for new assessment region definitions or protected areas, has been identified as a critical area of improvement for stock assessment in the WCPO (Evans et al., 2015; Kiyofuji and Ochi, 2016; PTTP, 2015), and other regions (Fonteneau, 2015; Kaplan et al., 2014). Given the expense in undertaking tagging studies, and the uncertainty present in the resulting data (Leroy et al., 2013a), use of simulation models to examine differing scenarios would appear to be a useful tool in the optimisation of such tagging experiments. This could take form of providing independent prior values for stock assessment model parameter estimation, or providing movement input to alternative operating models in management strategy evaluations.

Such tuna tagging programmes are designed to obtain information on not only movement, but also mortality and fleet-specific catch rates (Leroy et al., 2013a). Conventional mark-recapture tagging experiments assume that a tagged group of individual fish are representative of the wider population at some spatial scale, after fully mixing with this population after a period of time. As we have shown here, movement and residence may be highly variable within and between broad-scale regions, and reviews of tagging data suggest that such mixing may vary greatly or even never occur in reality (Kolody and Hoyle, 2013; Sippel et al., 2014). Ikamoana provides an intuitive framework to simulate how tagged individuals may distribute in relation to an untagged population over varying temporal and spatial scales. The examples we have given here would necessarily use the movement model of SEAPODYM, but alternative behaviours could be used in an ensemble sensitivity approach.

Such alternative behaviours could be informed from ecological theory, hypotheses, or patterns in real-world data. Information across the individual-, group- and population-level on the behaviour and distribution of oceanic animals such as tuna is increasingly being obtained through electronic tagging studies (Block et al., 2011; Leroy et al., 2010; Schaefer et al., 2009), genomics (Grewe et al., 2015; King et al., 2015; Wu et al., 2014), trophic analysis (Young et al., 2015), microchemistry and isotope studies (Carlisle et al., 2012; Graham et al., 2006), acoustic monitoring (Bertrand, 2003; Lopez et al., 2017) and integrated analysis of fisheries data (Evans et al., 2008). IBMs are particularly well-suited to integration across data sources because they can be examined at variable scales. For example, quantitative models of individual behaviour in both horizontal and vertical dimensions (e.g. Patterson et al., 2009; Scutt Phillips et al., 2015) can be used to drive simulated individuals movement, the emergent distributions of which are then examined in relation to an identified or potential genetic subpopulation (e.g. Dammannagoda et al., 2011). The taxis behaviour of SEAPODYM, here replicated in a Lagrangian framework for skipjack tuna, requires that these animals have a perfect knowledge of habitat distribution in their local area. In a Eulerian approach, assuming that a cell of tracer represents a sufficiently high density of individuals over a large enough area, movement in the direction of the favourable habitat emerges as result of the collective movements of individuals to local cues (Grünbaum, 1999). For our study, we have described how the schooling nature of our simulated skipjack permits similar assumptions of environment sampling and knowledge of the underlying distribution of habitat over our two-day temporal time step. However, in reality no individual or group of animals has perfect knowledge of their environment. Using Ikamoana, habitat gradient fields could be removed and replaced with habitat distribution information gathered at the individual-scale from a random walk behaviour. Similarly, alternative age, spatial and temporal structuring via the implementation of continuous ageing, spatial interpolation schemes, and arbitrary time steps are already complete in Ikamoana, built on the Parcels framework. The effect on the emergent distribution of skipjack tuna from these many differing approaches should be examined.

Such applications will also allow the impacts of alternative assumptions regarding mixing and connectivity on emergent distribution to be realised during the course of a simulation. In studies of exploited marine species, fishing mortality is generally aggregated at fixed spatial scales. However, like animal movement, real fishing operations occur at the scale of individual boats and fleets that also have their own individual behaviours. While spatial and temporal aggregation may be sufficient to capture the experienced mortality in some cases, feedbacks between fishers and fish, such as occur with the use of free-floating fish aggregating devices in tuna fisheries, may cause significant local-scale changes to both fleet and tuna behaviour (Dagorn et al., 2013; Leroy et al., 2013b; Maufroy et al., 2016). More broadly, the incorporation of IBMs alongside Eulerian models as two components of a hybrid-approach that have the flexibility of robust parameter estimation, yet can examine dynamics across varying spatiotemporal scales should be developed for modelling of marine species distribution (Rose et al., 2015; Tyutyunov and Titova, 2017). We suggest that Ikamoana provides an ideal framework for such further work.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.pocean.2018.04.007.

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