Quantifying Rates of Mixing in Tagged, WCPO Skipjack Tuna

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Executive Summary

In the Western and Central Pacific Ocean (WCPO), programmes of large-scale tagging experiments have been carried out on skipjack, yellowfin and bigeye tuna, to aid estimation of movement and mortality parameters through the stock assessment model MULTIFAN-CL. The integration of tagging data in this context includes critical assumptions about the period of time it takes for tagged fish to mix with the equivalent, untagged population in an assessment region. In previous stock assessments, this mixing period has been fixed for all tag release groups, regardless of any perceived difference across regions or time-periods. Sensitivity analyses have shown that the current assessment model for WCPO skipjack tuna is highly sensitive to the selection of a pre-defined mixing period, which has been assumed to be either one or two quarters. However, previous attempts to quantify the degree to which complete mixing of the tagged and untagged populations takes place have generally concluded that the process is likely to be highly variable in space and time.

Here, we apply two existing models of the spatial and fishery dynamics of Pacific skipjack tuna, SEAPODYM and Ikamoana, to examine potential variation in mixing for 20 years of tag releases from the Pacific Tuna Tagging Programme (PTTP) and Japanese Tagging Programme (JPTP). SEAPODYM is a full, Eulerian population dynamics model for tuna-like species, with parameters estimated using Pacific-wide environmental, fisheries, catch and tagging data. Ikamoana provides a Lagrangian, individual-based analogue to the movement and mortality components of SEAPODYM, allowing the tracing of individual fish or school trajectories, and the recording of their mortality over time. Using the most recent SEAPODYM parameterisation for Pacific skipjack tuna as an operating model, we simulate the movement and mortality of tagged skipjack in Ikamoana, alongside the corresponding untagged population, to quantify their degree of mixing under assumed mixing periods of zero to three quarters. We simulated tag release events corresponding to historical events from the PTTP and JPTP and calculated the distribution of overall recapture probability for groups of releases, after allowing dispersion during different assumed mixing periods, as a measure of mixing with the untagged population. Using a non-parametric statistic of dissimilarity to compare these distributions, we provided a quantitative and objective measure of mixing for use in selecting an appropriate mixing period in stock assessments of this species.

Our results show that mixing does indeed vary greatly between release groups. In general, mixing was faster in smaller and more oceanic assessment regions, and poorer in regions where fishing effort was spatially heterogenous and focused in the same area as tag release events. Using different values of the dissimilarity statistic as a minimum level of appropriate mixing, we demonstrate how mixing periods can be assigned at release group level using this approach. This includes some groups having a mixing period of zero quarters which, while impossible in reality, is due to the temporal evolution of their experienced fishing pressure quickly matching that of the untagged population so that effectively, they mix in a much shorter period of time than one quarter.

We discuss these results in the context of improving the choice of mixing period in stock assessments of WCPO skipjack tuna, the design of future tagging experiments, and the appropriate use of tagging data to maximise its ability to inform population level parameters in assessment models.

We invite WCPFC-SC18 to:

- Note the use of tag mixing estimates developed here in the 2022 skipjack tuna assessment
- Adopt the use of the method for selection of mixing periods within assessment model grids
- Support the development of the individual-based model Ikamoana, for hypothesis testing and analysis of tuna data in the WCPO
- Note the utility of the approach for informing future tagging cruises and assessment model spatial structures

Introduction

Capture-mark-recapture (CMR) 'tagging' data are a commonly used tool in fisheries science and management to monitor a subset of the population in order to inform or estimate population parameters (Pine et al. 2003). In the Western and Central Pacific Ocean (WCPO), programmes of large-scale tagging experiments have been carried out on skipjack, yellowfin and bigeye tuna since 1979, and have been directly incorporated into the estimation of such parameters for more than 20 years, through the stock assessment model MULTIFAN-CL (Hampton & Fournier 2001).

The integration of tagging data in this context includes several assumptions, of which two are: (1) the age classes of the tagged subset are representative of the same age classes within the underlying population in a region; and (2) after some period of time the tagged fish have mixed with the untagged population, to a degree that they are both subject to the same processes and probability of capture by the fishing operations in the region (Pine et al., 2003). The former assumption is met by modelling a subset of the population corresponding only to the length frequency of true tag releases, and the latter through including an implicit 'mixing period' during which any recaptured and reported tags are removed from integration into the likelihood calculation. As the possibility of a tagged fish being recaptured commences immediately after tagging, the time-period required to meet this mixing assumption will directly affect the number of tags that can be included into an assessment. Rapid mixing of the tagged with the untagged population implies a greater number of tag returns available for integration in the estimation of population characteristics. The erroneous inclusion of tag recaptures occurring prior to mixing may, however, lead to a significant bias in mortality and movement parameter estimations.

In the case of WCPO skipjack tuna, attempts to quantify the degree to which complete mixing of the tagged and untagged populations takes place have generally concluded that the process is likely to be highly variable in space and time (Kolody & Hoyle, 2015; Sippel et al., 2014). The discrete, 8-region spatial structure used in the assessment consists of areas varying considerably in size, heterogeneity of both environment and fishing effort, and spatial spread of the tagging experiments that have been undertaken within them. Such factors are likely to influence the time over which tagged fish mix with untagged conspecifics. Furthermore, sensitivity analyses have shown that the current assessment model for this stock is highly sensitive to changes in the pre-defined mixing period (Vincent et al. 2019), which are presently assumed to be either three or six months (one or two quarters, the time-step of the assessment model). In previous assessments, the chosen mixing period has been fixed for all tag release groups under a particular MULTIFAN-CL model configuration, regardless of any perceived difference across regions or time-periods.

While sub-regional heterogeneity is not explicitly modelled within MULTIFAN-CL, other, finer-resolution modelling frameworks designed for tuna do provide the means to inform parameters at the coarser regional scale. One such model currently used for scientific advice in the WCPO is the Spatial Ecosystem and Population Dynamics Model, namely its main module for modelling the dynamics of Migratory Age-Structured Stocks (SEAPODYM-MASS, Lehodey et al. 2008, Senina et al. 2020, 2022), which predicts the biomass of modelled species through two-dimensional space, time, and age. It uses classical advection-diffusion-reaction equations in a Eulerian framework to incorporate observed environmental, fisheries catch, effort, size and tagging data for the estimation of the parameters describing passive and active movement, reproduction and both fishing and natural mortality. The model is capable of providing stock assessments of WCPO tuna species, and has previously been used to inform movement parameters at the MULTIFAN-CL regional scale (Castillo

Jordan et al. 2021, Senina et al., 2017). Another modelling tool is the Individual-based Kinesis, Advection and Movement of Ocean ANimAls model (Ikamoana, Scutt Phillips et al. 2018), which uses Lagrangian formulations of the classical Advection-Diffusion-Reaction equations to provide a movement simulator capable of tracing the continuous path of individual animals or schools of fish under a particular behavioural parameterisation. It is suited to examining properties of the population which may be variable at the ecological unit of the individual, such as fishing mortality, reproduction, or environmentally-driven biology and epigenetics.

Here, we apply both the SEAPODYM and Ikamoana simulation tools to examine potential variation in mixing for 20 years of WCPO skipjack tuna tag releases from the Pacific Tuna Tagging Programme (PTTP) and Japanese Tagging Programm (JPTP). Using the most recent SEAPODYM parameterisation for Pacific skipjack tuna as an operating model, we simulate the movement and mortality of young and adult skipjack in Ikamoana to compare how cumulative fishing pressure experienced by individuals released at tagging sites differs to that of untagged individuals in the region of release, under assumed mixing periods of zero to nine months. The distributions of capture probabilities for these tagged and untagged groups are compared using simple, non-parameteric measures of dissimilarity, providing a consistent framework select mixing period scenarios per release group. Our results are discussed in the context of apparent patterns of mixing rate, incorporation into MULTIFAN-CL assessments, and the future design of capture-mark-recapture experiments for WCPO tropical tuna species.

Methods

Movement and Mortality Model

To simulate the environmentally driven movement and sub-region scale exposure to fishing pressure of WCPO skipjack tuna, the movement parameters, environmental fields, natural and fishing mortality parameters from the most recent SEAPODYM reference model were used (Senina et al. 2020). SEAPODYM has been used to provide scientific advice in the WCPO for over a decade (Senina et al. 2021, 2018, 2016, Lehodey et al. 2012). It uses physical ocean variables provided by the Mercator-Ocean global eddy-permitting NEMO ocean model, the primary production provided by CLS, where it is derived from remote sensing Chl-a data, and the WOA climatology for dissolved oxygen concentration. The physical variables are the ocean hindcast simulated in the ORCA025 configuration under the atmospheric ERA-INTERIM forcing. SEAPODYM assimilates Pacific-wide fisheries, catch and tagging data to estimate the adult movement and mortality parameters used in this study.

Age-dependent, feeding habitat fields were thus generated at ¼° scale with a monthly timestep, which also corresponded to the age-class for all age-dependent movement and mortality processes. This feeding habitat is a function of age-dependent temperature, dissolved oxygen, and micronekton preference parameters. The movement model includes non-directional random movement of biomass away from areas of low-quality feeding habitat, as well as a directed, taxis movement that climbs gradients towards more favourable habitat areas. The mortality model consists of habitat- and age-dependent natural mortality, as well as fishing mortality by fleets operating in the Pacific during the period 1998-2020, aggregated to 15 fisheries. The fishing mortality parameters, comprised of age-dependent selectivity and fishery-dependent catchability terms, were estimated using catch and effort data, available   at between 1° and 5° spatial resolution across fisheries. An overview of the SEAPODYM framework, including the low- and mid-trophic level model and the model for population dynamics with age structure is given in Lehodey et al. (2008) and a full description of the SEAPODYM-MASS model, its numerical solver, configurations and parameter estimation methods are provided in

Senina et al. (2022), with the most recent reference MLE solution for Pacific skipjack used here described in Senina et al. (2020).

Individual-based Simulation Model

The ocean currents and feeding habitat fields described above were used to simulate the movement of fish in the context of different tagging events, within a series of Ikamoana simulations. Ikamoana is an individual-based model, simulating the continuous movement of individual particles representing fish or schools of fish through the ocean (Scutt Phillips et al. 2018). It uses Lagrangian formulations of the advection-diffusion equations that describe movement of fish in SEAPODYM, but where the Eulerian model SEAPODYM describes the density evolution of many individuals in space and time, Ikamoana provides the pathways through space of a discrete number of individuals over time. The position, internal state, and history of these particles are recorded along this pathway, with the approach well suited to examine questions related to connectivity, stochasticity, and how the environment is experienced through time at the level of the individual.

In this application, Ikamoana was used to simulate the age-dependent movement and mortality experienced by different cohorts of skipjack tuna, using SEAPODYM fields and movement/mortality models. The Lagrangian movement model is described in Scutt Phillips et al. (2018), and mortality model in Scutt Phillips et al. (2020). The latter can be summarised as a Lagrangian consideration of the instantaneous mortality model estimated by SEAPODYM, described in Senina et al. (2020). In summary, we consider the effect of these instantaneous mortality rates not as a deterministic reduction of the number of fish within a cell, but rather as a probabilistic function of dying for an individual. Therefore, we consider the total reduction in biomass at each cell over a time step Δt as emerging from the cumulative probability of fish dying or being caught with probability $P(nat)_t$ or $P(catch)_t$, respectively, conditioned on the observed spatial and temporal distribution of fishing effort and/or catch by fishery. When an instantaneous mortality value $Z_{j,t}$ in region j at time t causes a proportion of fish present in a cell to be depleted through the combined effects of fishing and natural mortality, $F_{j,t}$ and $M_{j,l}$ respectively, for simplicity we assume that within that cell the probability that an individual fish is caught is uniform across all the individuals present in the cell.

The probability of an individual dying during time-step t, $P(mor)_t$, is therefore simply a Lagrangian reinterpretation of the Baranov death equation (Baranov, 1918).

$$P(mor)_t = \left(1 - e^{-(Z_{j,t})\Delta t}\right) \qquad (1)$$

Here, instantaneous mortality affects, not the number of individuals N, but the probability of a single individual surviving the time-step. It is important to note that individual particles are never removed from the simulation, but rather that the probability of the individual dying at each time-step t is recorded along each unique pathway of all particles.

However, throughout the course of an individual's proper time-at-liberty, τ, this value $P(mor)_t$ is not independent, as death of an individual fish can only occur once. Therefore, the probability of an individual dying after proper time τ, occurring after τ time-steps of t, is conditional on survival until $t = \tau-1$, which is simply the product of all probabilities of the individual having not died during time-steps number $t = 0$ to $t = \tau - 1$.

$$P(surv)_{\tau-1} = \prod_{t=0}^{\tau-1}(1 - P(mor)_t) \qquad (2)$$

Therefore, the probability of an individual's death at time-at-liberty $\tau=t$ is given by

$$P(mor)_\tau = P(surv)_{\tau-1} \cdot P(mor)_t \qquad (3)$$

These probabilities were recorded along the trajectory of all individuals through each Ikamoana simulation, their values changing in response to the individual's position, age, and decreasing chance of survival throughout its time-at-liberty τ.

In the context of fishing pressure estimated by the recapture of tagged fish, the principal process that is informed by the CMR experiments of the PTTP, we wish to compare the probabilities of recapture between fish released at tagging event locations and the corresponding cohort of untagged fish within a region, under differing assumed periods of mixing. This probability of recapture at time-at-liberty t, $P(catch)_t$, is the proportion of total instantaneous mortality Z caused by fishing at time t.

$$P(catch)_t = \frac{F_{j,t}}{Z_{j,t}}P(mor)_t \qquad (4)$$

Substituting (1) into equation (4), it becomes analogous to the Baranov catch equation (Baranov, 1918).

Thus, the overall probability of recapture during an individual's proper time-at-liberty τ is simply the sum of all $P(catch)_t$

$$P(recap)_\tau = \sum_{t=0}^{\tau} P(catch)_t \qquad (5)$$

In the limit, this value of $P(recap)_\tau$ will necessarily asymptote with increasing τ, as additional exposure of an individual to fishing pressure results in decreasing chance of recapture due to preceding mortality. We use the asymptotic value of $P(recap)_\tau$ as the chief metric for comparison between groups in this study, that is the total probability that the individual is captured during its time-at-liberty.

Tagging Events and Data

Skipjack tuna tag release events from the Pacific Tuna Tagging Programme (PTTP) and Japanese Tagging Programme (JPTP) during the period 1998 to 2018, corresponding to available SEAPODYM forcing, were collated for simulations.

For clarity, we here define the vocabulary used to describe different groups of tagging data in this analysis:

1. *True Release Events*
   These refer to historical releases of tags, on a particular day, at a particular location, and with a particular length frequency.
2. *Simulated Release Events*
   These are combined true release events, with location rounded to the nearest 1x1° cell location, length frequencies rounded to the nearest mean length at monthly age class, and dates rounded to the nearest mid-quarter date, as described above.
3. *Release Groups*
   This is the unit at which mixing assumptions are applied in MULTIFAN-CL, and here they

consist of multiple simulated release events that corresponding to all those within a particular assessment region and quarter.

Each true release event consisted of a time rounded to the nearest day, location rounded to the nearest 1° of latitude and longitude, and distribution of fork lengths for all released fish. As both the movement and mortality parameters in SEAPODYM are age-dependent, first the releases of each one-centimeter length bin were assigned to an age class by grouping them to their nearest mean-length at age, as defined in SEAPODYM (Senina et al. 2020), effectively providing release numbers by age class and hence by assumed cohort.

To reduce computational costs of simulations, some filtering and collating of events was undertaken. First, any tagged fish from cohorts with less than 100 releases across the entirety of either the PTTP or JPTP programmes were removed. As each true release event occurred on a separate date, to reduce the combination of cohort/date simulations required, release event dates were also rounded to the mid-point of the nearest quarter. This corresponded to the temporal resolution of the MULTIFAN-CL release groups, at which mixing comparisons were later made (see *Tag Mixing* below). Finally, the resulting quarterly, 1° cell release groupings by cohort were filtered for any cohorts with less than 30 tag releases for the PTTP, and less than 10 releases for the JPTP, per date/location combination.

The final list of release events to simulate represented 87.9% (254,418) of all PTTP, and 20.9% of all JPTP (33,935) skipjack tuna tags. Summaries of these datasets are provided in tables 1 and 2, respectively, and the numbers of simulated release events are shown spatially in figure 1.
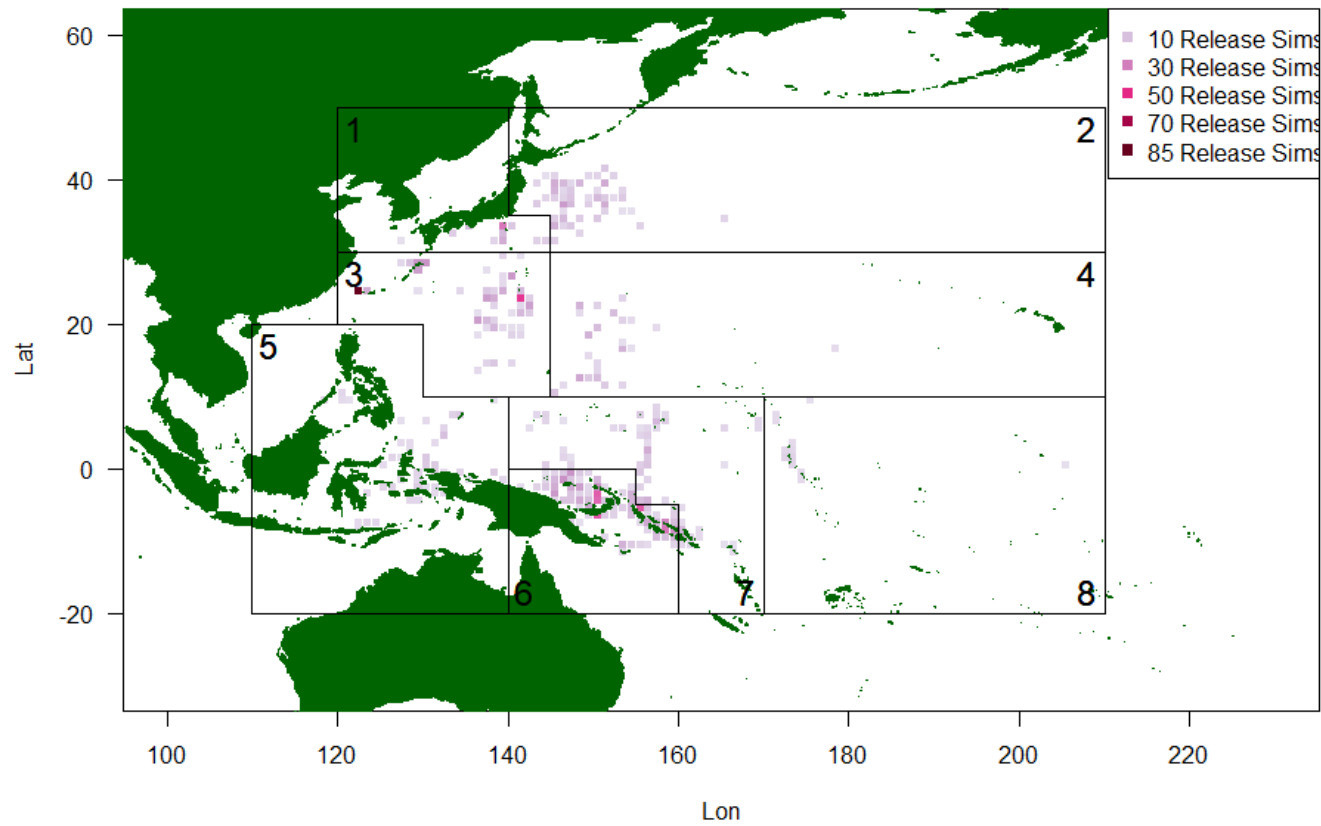
Figure 1. Spatial distribution of all simulated release events in this study, each consisting of a single combination of quarterly date, age class and 1° cell.

Table 1. Summary of Pacific Tuna Tagging Programme yearly releases simulated in this study, grouped by assumed monthly age class.

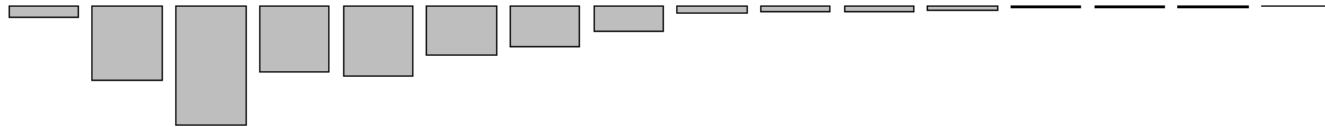| Monthly Age	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Release Event Simulations	Annual Tag Releases	
Mean Length	26.43	30.72	34.73	38.49	41.99	45.27	48.33	51.19	53.86	56.36	58.7	60.88	62.92	64.83	66.61	68.27	69.83			
Year																				
2006	0	343	1889	2358	2254	1956	1355	1307	400	155	124	85	50	36	34	0	0	100	**12346**	
2007	0	649	4216	8814	3212	6816	4358	2696	1008	150	124	39	0	0	0	0	0	139	**32082**	
2008	169	1695	9523	18856	6636	2226	1486	2535	2688	725	622	723	439	121	119	175	89	264	**48827**	
2009	0	572	9417	14768	11303	11483	5508	4775	2336	417	240	150	128	38	0	0	0	271	**61135**	
2011	0	896	2570	3754	3270	4689	3888	3615	2779	570	156	131	130	87	0	0	0	152	**26535**	
2012	0	187	4708	5877	5222	4972	3358	1665	692	209	101	73	0	0	0	0	0	114	**27064**	
2013	0	1441	5713	6970	2196	1708	1052	894	1074	531	243	148	33	34	0	0	0	90	**22037**	
2017	0	120	1848	2497	1269	3298	4857	3815	1972	747	813	1327	1169	471	143	46	0	115	**24392**	
Totals	169	5903	39884	63894	35362	37148	25862	21302	12949	3504	2423	2676	1949	787	296	221	89	1245	254418	

Table 2. Summary of Japanese Tagging Programme yearly releases simulated in this study, grouped assumed monthly age class.

| Monthly Age	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Release Event Simulations	Annual Tag Releases
Mean Length	26.43	30.72	34.73	38.49	41.99	45.27	48.33	51.19	53.86	56.36	58.7	60.88	62.92	64.83	66.61	68.27	69.83		
Year																			
1998	0	0	52	10	25	46	0	396	287	37	0	0	0	0	0	0	0	41	853
1999	0	0	101	169	81	128	58	294	74	0	0	0	0	0	0	0	0	49	905
2000	0	0	263	47	11	130	0	0	0	26	82	97	68	0	0	0	0	40	724
2001	0	45	0	145	0	72	89	478	270	188	31	84	10	0	0	0	0	73	1412
2002	0	0	227	363	86	1113	341	192	0	0	0	91	91	65	37	48	0	96	2654
2003	82	0	0	0	65	681	272	379	23	10	0	0	20	48	0	22	49	50	1651
2004	0	41	0	99	0	205	141	128	0	0	0	56	0	0	0	0	0	49	670
2005	0	0	10	87	112	282	36	168	49	0	0	0	0	11	0	0	0	44	755
2006	0	0	46	39	0	64	11	76	56	0	10	61	10	0	29	0	0	29	402
2007	0	0	0	45	86	169	0	43	0	0	0	0	0	0	0	0	0	23	343
2008	0	0	0	0	11	137	0	127	101	0	0	0	0	0	0	0	0	19	376
2009	0	0	0	532	465	461	0	0	0	0	0	0	0	0	0	0	0	62	1458
2010	0	0	0	1871	1168	386	0	36	0	0	0	0	0	0	0	0	0	75	3461
2011	10	0	0	50	0	34	0	55	0	0	0	0	0	0	0	0	0	12	149
2012	0	0	925	3395	504	402	23	0	0	0	0	54	31	21	101	0	0	88	5456
2013	0	210	1212	1569	479	533	0	0	40	0	0	0	0	0	0	0	0	77	4043
2014	0	0	105	321	188	243	0	0	0	0	0	0	0	0	0	0	0	35	857
2015	0	0	34	605	672	470	92	233	0	0	0	0	0	0	0	0	0	56	2106
2016	0	100	497	1330	1116	1128	0	44	0	0	0	0	0	0	0	0	0	114	4215
2017	0	0	192	297	245	334	24	160	0	11	11	0	0	0	0	0	0	72	1445
Totals	92	396	3664	10974	5314	7018	1087	2809	900	272	134	178	97	91	150	0	0	1104	33935
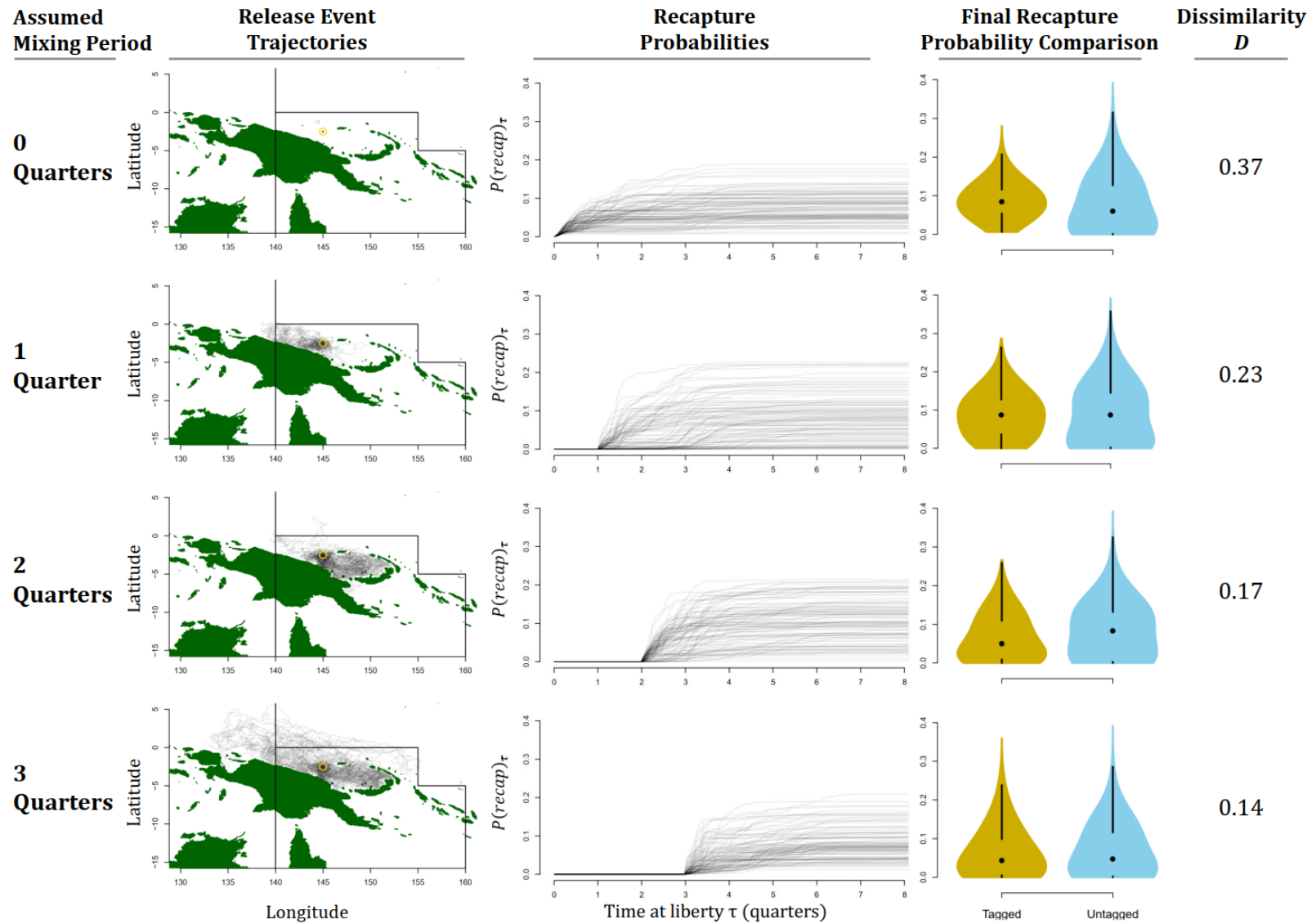
Figure 2. Example of a single, simulated release event in skipjack assessment region six. A sample of 100 trajectories is shown (left) during the four assumed mixing periods (rows), followed by their increase in recapture probability through time (center). Finally, the distribution of $P(recap)_\tau$ in the limit is shown next to that of the untagged population in the region, alongside the calculated dissimilarity D between the two.

Simulation Experiments

A suite of simulation experiments were undertaken using Ikamoana, consisting of paired groups of 'release events' simulations representing cohorts of tagged fish, and 'untagged group' simulations representing the corresponding cohorts of untagged fish. Each individual simulation consisted of individuals of a single cohort of skipjack tuna of a particular start age and date, corresponding to the historical releases summarized above, which were forced forwards through time under SEAPODYM movement and mortality models, ageing and recording their probability of recapture during a proper time τ, $P(recap)_\tau$ along their trajectory. For any particular age and start date combination of simulations, all environmentally-driven movement and fishing mortality fields were identical. Paired groups of simulations differed only in their initial spatial conditions.

Each tagged fish 'simulated release event' was seeded with 100,000 particles representing fish of the appropriate SEAPODYM age class, distributed randomly within a 1° by 1° grid cell given by the rounded release location of historical releases in tables 1 and 2. Where land mask cells lay within this cell, close to the coast for example, particles were redistributed in adjacent cells. Each individual therefore began at time-at-liberty $\tau = 0$ somewhere within this release event cell. The value of 100,000 particles was chosen, not to match the numbers of true tag releases corresponding to historical events in this cell, but rather to accurately sample the evolution through time of potential tagged school trajectories within the simulation, which contains stochastic processes that equate to numerical diffusion (Scutt Phillips et al. 2018). For a given age and start date combination, the number of individual release event simulations ranged from 1 to 85.

In parallel, for each age and start date combination, the Pacific-wide, untagged fish simulation was also run. These simulations were identical to their release event counterparts, save their spatial starting conditions and number of particles. The starting distribution of particles was taken from the mean density of tuna for the appropriate age class and start date, as provided by SEAPODYM, by Monte Carlo sampling of the relative, spatial density to seed particles positions. Three million particles were used in each Pacific-wide simulation.

Each simulation was run in parallel, so can therefore be considered as grouping into one or more tagged 'release event' simulations, each consisting of a release of a single age class with a constrained spatial start position, and a corresponding untagged cohort of the same age class, representing the 'true' distribution of untagged individuals throughout the Pacific.

For all simulations, the spatial extent of the domain was Pacific-wide, running from 45°S to 55°N and 110°E to 70°W. All simulations ran for 735 days following the starting release date, with advection kernels run over a one-day time-step and Runge-Kutta fourth order temporal integration scheme (Lange & van Sebille 2019). Particle trajectory data were output at three-month intervals, to minimise file size. Simulations were run in parallel using resources from Australia's National Computing Infrastructure GADI cluster.

Tag Mixing

To quantify the degree to which differing assumed mixing periods influence disparity between fishing pressure experienced by tagged and untagged fish, simulated probabilities of recapture were compared after allowing particles of tagged and untagged cohorts to disperse for different periods of time. In each case, $P(recap)_\tau$ was calculated assuming that no mortality was experienced during the

mixing period. For each examined mixing period, T_{mix}, survival after proper time-at-liberty $\tau = T_{mix}$ (equation 2), was therefor set at 1, and $P(recap)_\tau$, being the cumulative effect of fishing pressure from the point of assumed mixing, examined. Mixing periods of zero, one, two and three quarters were examined, where zero is equivalent to no mixing period. Assumed mixing periods of four or more quarters, for skipjack tuna, essentially remove nearly all effective tag recaptures in practice, and so were not examined here.

Tagging data inform parameters using a regional spatial structure within the assessment model MULTIFAN-CL. Tagged fish releases are therefore grouped by both assessment model region and quarter, being the time-step of the assessment model, into so-called 'release groups'. It is at this group level that we aim to examine variation in mixing. Ikamoana simulation results were therefore also grouped regionally, using the currently adopted eight region model for WCPO skipjack tuna (Vincent et al. 2019, Castillo Jordan et al. 2022). For a given region and quarterly release group, as well as for each mixing period examined, all release event simulations corresponding to that release group were filtered to examine only trajectories present in the region at their proper time-at-liberty $\tau = T_{mix}$. When $T_{mix} = 0$, this necessarily included all trajectories, as simulated release event particles had not yet displaced from their release location. Similarly, trajectories from the Pacific-wide, untagged simulations were also filtered to include only those particles located in the region for which comparisons to tagged fish were being made, at $\tau = T_{mix}$. Thus, for each release group mixing scenario, two groups of trajectories were compared. One corresponding to all the tagged fish present in the release region at their proper time-at-liberty $\tau = T_{mix}$, and one group for the untagged fish in the same region.

As a simple comparison of fishing pressure experienced at the individual trajectory level, we used $P(recap)_\tau$ in the limit, where τ is the maximum time-at-liberty for each individual. This can be considered as the overall probability that a fish was captured between the moment of assumed mixing through to a maximum of two-years at liberty, being the timespan of the simulations. Every individual simulated has a unique probability of recapture, as a function of their environmentally driven movement behaviours, and the spatiotemporally dynamic field of fishing mortality through which they have moved.

Thus, for a particular tag release group, there will be a distribution of these recapture probabilities under each tag mixing scenario. The shape of this distribution is dependent on the spatial spread of tagged individuals throughout the domain during their time-at-liberty, and the range of fishing mortality experienced by the group. Naturally, the form of these distributions may vary greatly, being normally distributed, highly skewed, or even multimodal when tagged fish become separated into groups exposed to highly disparate levels of fishing, particularly when this occurs early during time-at-liberty.

Regardless, when tagged fish are well mixed we would expect that the shape of this distribution is very similar to the equivalent distribution from the untagged population, comprised of fish at liberty throughout the region. To make such a comparison, we chose a non-parametric test of dissimilarity, the two-sample Kolmogorov-Smirnoff test (Kolmogorov 1933, Smirnoff 1939). This test assumes no shape of sample distributions, but calculates a dissimilarity statistic D, which is the distance difference between the empirical distribution functions from the two samples. Thus, the two distributions of

P(recap)$_\tau$ from tagged and untagged groups were used as samples with which to calculate a dissimilarity statistic.

We use this *D* statistic as a summary metric with which to quantify the success of different mixing period assumptions for each release group, where success refers to similar distributions of recapture probability between the tagged and untagged groups for an assumed mixing period. A smaller value of *D* indicates less different recapture probabilities between tagged and untagged fish, and thus greater levels of mixing. Each release group was therefore assigned a value of *D* for each assumed mixing period *T*$_{mix}$ of zero to 3 quarters. An example of how the distribution of *P(recap)*$_\tau$ varies under different mixing assumptions for a single, simulated release event, alongside it's dissimilarity *D* with the untagged population, is shown in figure 2.

Results

A total of 2296 separate release simulations were undertaken, alongside 626 simulations corresponding to Pacific-wide, untagged fish, for a total of 2.1 billion particles forced over two years. Five release simulations of historical location-age class releases were located so close to land masses that appropriate ocean cells within the model could not be found, and so these were excluded from the analysis.

Calculated *D* statistics for all release groups combined are summarised by assumed mixing period in Figure 3. As expected, dissimilarity between tagged and untagged fish recapture probabilities tended to reduce with a longer assumed mixing period. Less than 8% of release groups had a calculated *D* of 0.1 or less when no mixing was assumed, compared to over 46% when fish were allowed to mix for three quarters. However, the general rate of decrease in *D* dissimilarity reduced with increasing mixing period. Median decreases were -0.09, -0.05 and -0.01, for an increase from zero to one, one to two, and two to three quarters, respectively.

Examining dissimilarity by region, some regions demonstrated generally faster mixing compared to others (Figure 4). As expected, release groups in smaller regions such as regions one and three were associated with lower values of *D* for short mixing periods. However, when the spatial extent of fishing effort in a region was highly concentrated around the area of tagging, as is the case in regions six and, to some extent, eight, mixing rates appeared slower. This result is attributed to the increased dissimilarity between tagged and untagged cohorts when tagging events have occurred in the areas of high fishing effort. In this case, the simulation of untagged cohort under the SEAPODYM movement model predicts significant biomass away from the areas of concentrated effort. The contrasting scenario can be seen for the large, northern Pacific region two, for which dissimilarity *D* decreases considerably over the first quarter. In this case, despite the large region area and concentrated fishing effort near Japan, little untagged biomass is predicted away from the fishing ground. This means that tagged fish mix throughout the area where fishing occurs at similar rates to those simulated in much smaller regions.

Interestingly, the number of tag release simulations, that is, combinations of release locations and age classes, that constituted a particular release group, did not appear to consistently improve values of dissimilarity *D* across regions and mixing period assumptions. When combining all regions, there was

an apparently negative relationship between the number of simulated release events and D (i.e. a positive relationship with mixing) when zero or one quarter mixing periods were assumed, which reversed for two and three quarter mixing periods (Figure 5). Dissimilarity D was clearly highly variable across release groups, but may show evidence of a non-linear relationship with the spread of release locations and age classes, particularly when increasing from low numbers.
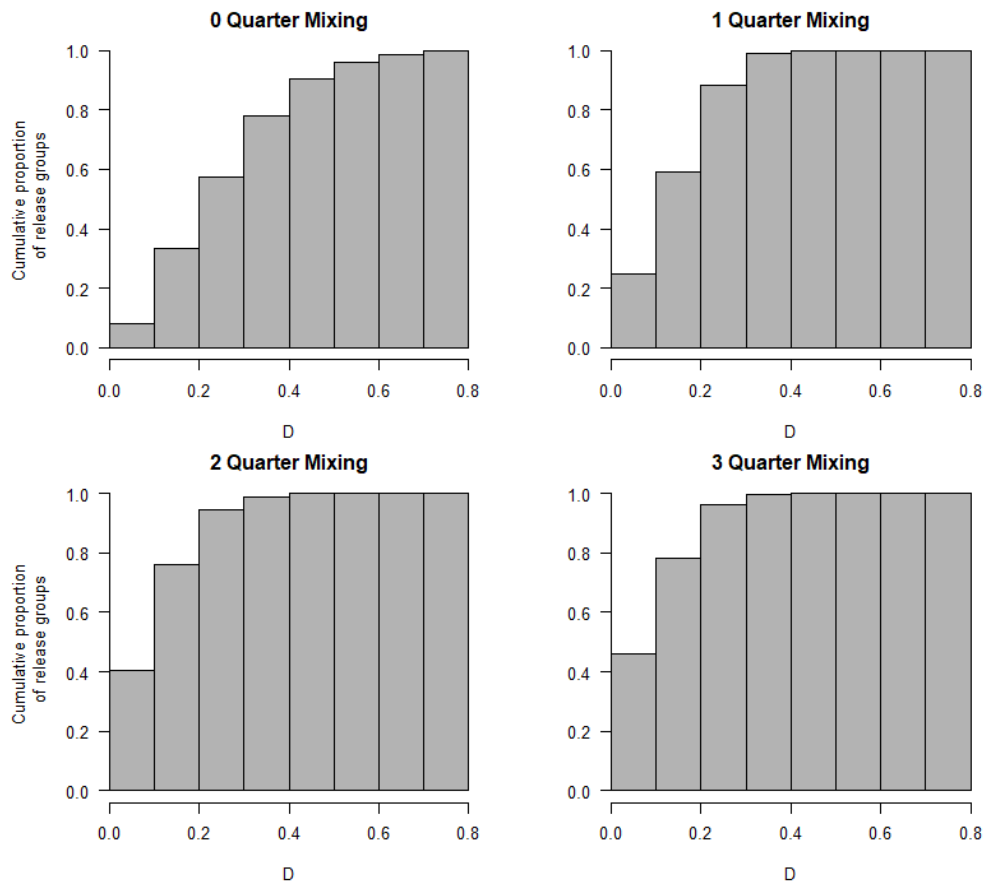
Figure 3. Histograms showing proportion of all release group dissimilarity *D* statistics, under all four mixing period scenarios examined here.
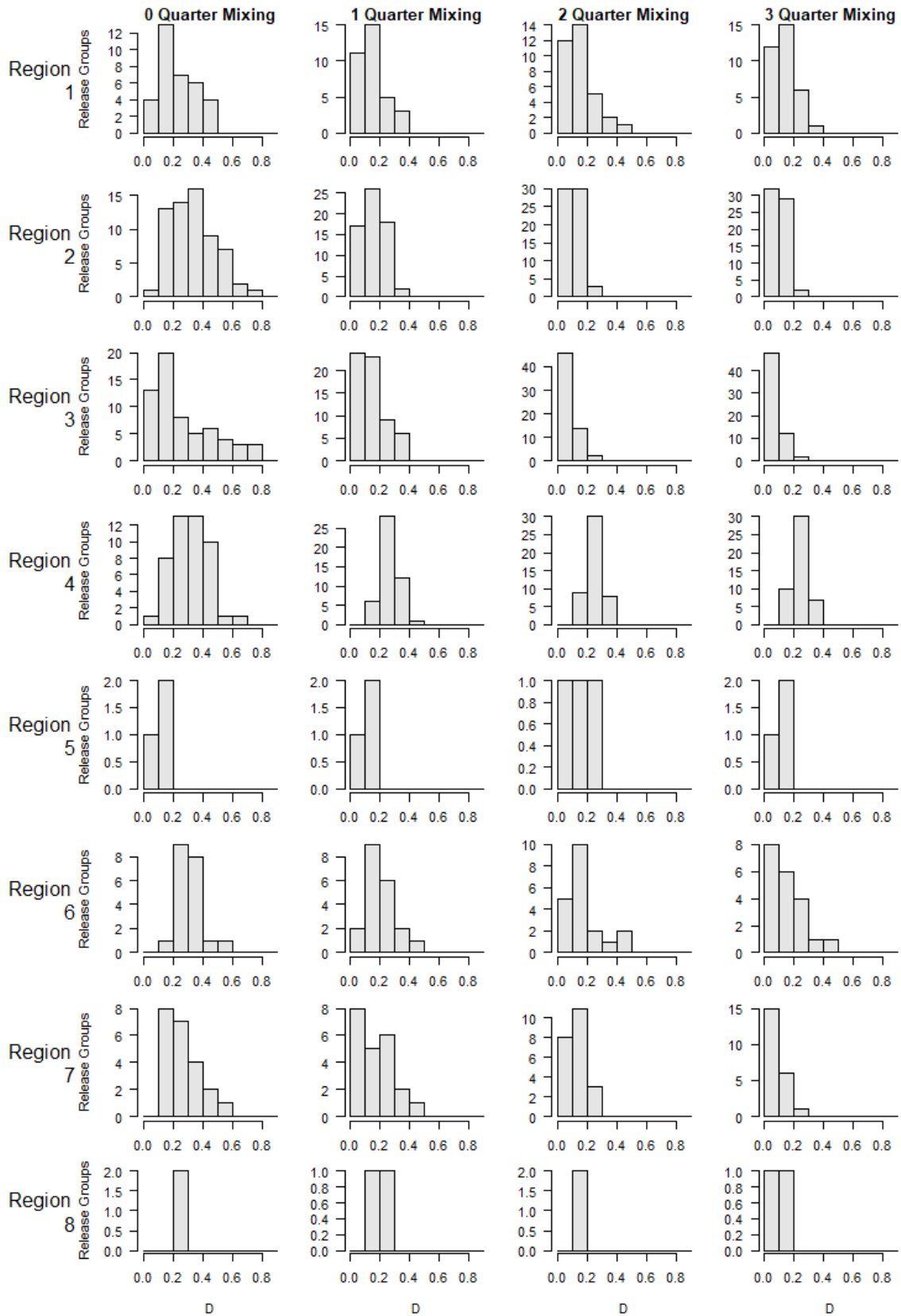
Figure 4. Distribution of calculated dissimilarity *D* statistics in numbers of release groups, separated by region (rows) and assumed mixing period in quarters (columns).
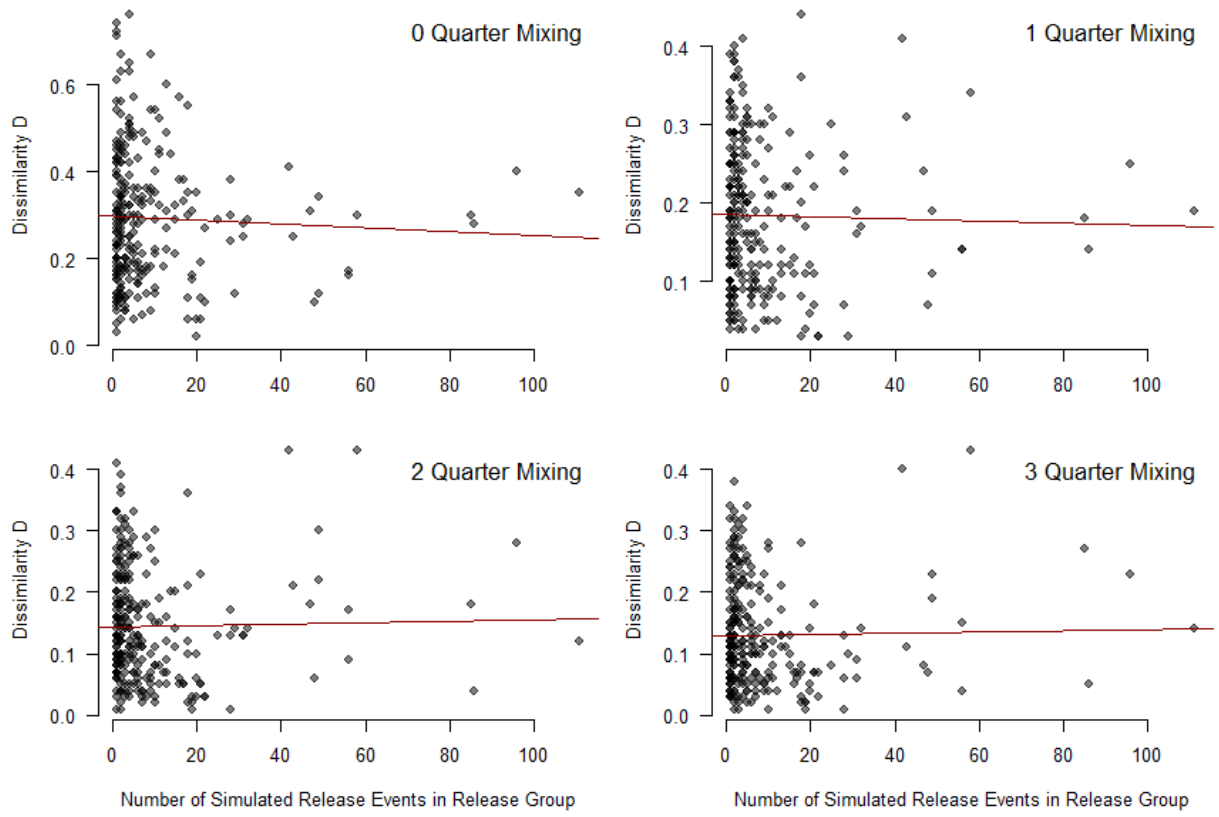
Figure 5. Estimation of dissimilarity *D* between tagged release groups and the untagged population under each mixing period assumption, by number of simulated release events included in the group. A linear regression is shown in red.

Discussion

This working paper describes an application of the Lagrangian model Ikamoana to quantify levels of WCPO skipjack tag mixing, using an existing behavioural and mortality parameterisation from the ecosystem model SEAPODYM. The aim of this study is to assist the choice of appropriate mixing periods for tag release groups, during the integration of skipjack tagging data into stock assessments, through provision of a quantitative, objective and informed approach to evaluating tag mixing. This contrasts to the current of approach of subjectively applying a single mixing period for all release groups, regardless of region size, fishery dynamics, distribution of true release events, and potential variation in tagged fish movement.

The use of the Kolmogorov-Smirnoff dissimilarity D statistic, calculated from distributions of simulated recapture probabilities that predict the spread of potential movement and fishing pressure experienced for a given tag release group and an equivalent, untagged group, provides such an objective approach. By choosing a particular value of D as a maximum at which a release group can be considered adequately mixed, the shortest mixing period at which such a value is achieved can be assumed for that group. Similarly, sensitivity analyses can be carried out by choosing more or less conservative values at which mixing is considered adequate.

For example, selecting a maximum dissimilarity of 0.1 would lead, for the release groups simulated here, to 8% of groups being included with no assumed mixing period, 17% after one quarter, 15% after two quarters, and 6% after three quarters. The remaining 54% of tags could either be excluded, or included after an even longer mixing period, essentially down-weighting their influence in the assessment model. However, relaxing this maximum dissimilarity value to 0.2 would increase the data used in the assessment by assigning 34%, 25%, 17% and 2% of release groups to zero, one, two and three quarter mixing periods, respectively.

Our analysis also highlights several aspects in the design of both tagging experiments and the interpretation of data within the spatial structure of the current stock assessment model. In particular, the spatial extent of some regions appears to far exceed that of the fishing and tagging effort in that region, causing a lack of mixed, and therefore informative, tagging data. For example, the archipelagic region six is responsible for the vast majority of skipjack tuna tags simulated in this study (more than 170,000). Our results here suggest that, due to a mismatch between estimated skipjack biomass and the concentration of fishing effort in the north of this region, tag releases in the fishing ground are likely to be very poorly mixed even after two quarters (Figure 4). Under the approach we outline here, and using a fairly strict value of dissimilarity D = 0.1 for mixing, no release groups from this region would be included with a mixing period of zero quarters, and only 10% included assuming mixing after one quarter. However, running an alternative mixing scenario in which the extent of region 6 reduced by a southern boundary at 10°S, roughly in line with the southern tip of Guadalcanal in the Solomon Islands, improves the rate of tag mixing of these release groups considerably. Using the same mixing criteria of D = 0.1 as above, this scenario leads to 26% of groups being included assuming a zero quarter mixing period, and 32% assuming one quarter. In this example, the inclusion of all tagging data from the former groups using zero mixing period would equate to the integration of nearly 55,000, informative tag releases into the assessment model. We propose that such hypothesis testing be carried out when considering assessment spatial structure and maximising the information obtainable from large-scale tagging data.

Similarly, the interrogative use of Ikamoana tagging simulations could improve the design of future tagging experiments. Highlighting the most efficient spread in both space and length classes could help guide the planning of cruises, where logistically possible. Moreover, here we have forced our model using a parameterisation from SEAPODYM, as it assimilates data on Pacific skipjack and is currently our best, sub-regional model of tuna dynamics, but alternative behavioural hypotheses could easily be tested. Simple random walks, ocean flow, or future fishing effort scenarios could be incorporated to examine the robustness of mixing or other tagging experiment objectives to these processes.

This analysis represents the first attempt to quantify mixing rates for a large proportion of tagged WCPO skipjack tuna in what we propose be an iterative process, as several improvements could still be made. Trivially, additional simulations representing those tag releases which were filtered due to low numbers could be undertaken, as well excluding the rounding of true release event dates to the mid-quarter. Similarly, once downscaled forcings are available, the time-series of simulated tags could be extended to cover older tag releases from the JPTP, RTTP and SSAP. To improve the actual quantification of mixing, simulated release events should also be weighted by the number of actual releases they represent. In the current approach, all simulated release events are treated equally when comparing their experienced fishing pressure with the untagged population, and are undertaken using 100,000 particles to effectively sample the range of possible trajectories that fish may take. In reality, one location and age class combination of tagged fish may consist of very few tags, whereas another may constitute many thousands. This will impact the comparison with the untagged population, which consists of all age classes which are present in the release group. To account for this when quantifying the degree of mixing of a historical release group, Monte Carlo sampling of simulated trajectories could be undertaken to more accurately account for the non-uniformity of release numbers.

This approach to quantifying mixing in WCPO skipjack using the individual-based Ikamoana model rests on many assumptions regarding the movement behaviours and mortality of the species, as they are estimated from real fisheries, tagging and environmental data within SEAPODYM. However, it represents a more informed method to the uniformly applied and arbitrary choice of mixing period previously used and provides stock assessment scientists with more quantitative tools with which to test sensitivity to mixing in population dynamics models. Tagging data can be extremely informative for exploited populations, but their interpretation and integration into population dynamics models must be undertaken appropriately so as to extract the maximum value from their collection. As our understanding of the environmentally driven behaviour and fisheries interactions of tuna improves, we recommend that the simulation tools we have employed in this study be further developed for similar hypothesis testing and interrogation of past and future data collection.

Recommendations

- Note the use of tag mixing estimates developed here in the 2022 skipjack tuna assessment
- Adopt the use of the method for selection of mixing periods within assessment model grids
- Support the development of the individual-based model Ikamoana, for hypothesis testing and analysis of tuna data in the WCPO
- Note the utility of the approach for informing future tagging cruises and assessment model spatial structures

Acknowledgements

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