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ESTIMATION OF TAG MIXING PERIODS FOR THE 2026 WCPO TUNA STOCK ASSESSMENTS

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Revision 1. With modified tag recapture density plots, and related discussion, in response to comments and requests in the SC22 Online Discussion Forum

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Executive Summary

The integration of tag-recapture data into stock assessments requires that tagged fish become representative of the wider population before their recaptures inform the assessment. In MULTIFAN-CL (MFCL) this is handled through a mixing period, during which recaptures are excluded from the likelihood. The choice is highly influential on assessment outcomes, yet the sparse, spatially unbalanced nature of tuna tagging data makes it difficult to determine directly from observed recaptures.

This paper applies an individual-based simulation approach to estimate mixing periods for release groups in the 2026 WCPO bigeye tuna assessment, updating the method used for the 2022 and 2025 skipjack assessments. Using the Ikamoana model driven by the latest bigeye SEAPODYM reference solution, we simulate the movement of tagged and untagged fish and compare the distributions of fishing pressure they experience, summarised as recapture probability. The dissimilarity between these distributions, measured by a Kolmogorov dissimilarity (K) statistic, provides a continuous measure of mixing for every release group, regardless of how few recaptures it yielded. Critically, mixing is assessed in terms of representativeness of experienced fishing pressure, which is the quantity most affecting tag-informed parameters and stock-status indicators, rather than spatial overlap.

Across bigeye release groups, dissimilarity generally decreased with longer assumed mixing periods, with the median K falling from 0.36 at release to 0.12 after three quarters under a five-region structure. Mixing varied markedly by region: groups where fishing pressure and population distribution overlapped mixed rapidly, while those in regions with spatially heterogeneous pressure mixed slowly, and in some cases showed little improvement even after three quarters. The diagnostics reveal that mixing is not always a simple, monotonic approach to a fully mixed state: directed movement can hold tagged fish in sub-areas of atypical fishing pressure, and movement of the untagged population itself can shift the comparison, so that dissimilarity can remain high or even increase over time. This reframes the operational question from whether a group is "mixed" to how representative it is, and how much representativeness is sufficient for the current stock assessment.

We provide, for each release group, the mixing period implied by a range of K cut-off values, allowing the assessment to select a more or less conservative treatment of tagging data as a structural sensitivity. Under the five-region structure, a conservative cut-off of $K = 0.1$ assigns a two-quarter mixing period to 40% of release groups, while a more liberal cut-off of $K = 0.3$ assigns a one-quarter period to 85% of groups. Combining regions 3 and 4 into a single region (as a four-region sensitivity) produced consistently higher dissimilarity.

The equivalent yellowfin analysis is not presented here: features of the yellowfin SEAPODYM solution at the time of this work drove recapture probabilities toward saturation, reducing the metric's discriminating power. We recommend revisiting it once the reference solution is finalised.

We invite SC22 to:

- Note the results of this analysis of tag mixing for WCPO bigeye tuna, available for use in the 2026 stock assessment, with mixing periods provided across a range of dissimilarity cut-offs to enable their use as a structural uncertainty axis;
- Note the potential to extend the approach to yellowfin tuna, pending a finalised SEAPODYM reference solution for that species;
- Consider the implications of these results for the spatial structure of tuna assessments, and the merit of exploring more spatially explicit, or non-spatial, treatments of tagging data.

1. Introduction

The integration of tag-recapture data into integrated stock assessments rests on the assumption that tagged fish are, after some period, equally vulnerable to capture as the relevant portion of the untagged population. In MULTIFAN-CL (MFCL) this is handled through an explicit *mixing period*: the interval following release during which tag recaptures are excluded from the likelihood, allowing time for tagged fish to distribute themselves such that their estimated demographic parameters can be considered representative of the population. Failure to account for incomplete mixing can substantially bias parameter estimation in mark-recapture experiments (Scutt Phillips et al., 2024, Abadi et al., 2013; Guillemain et al., 2014), when fish are tagged in areas of relatively high fishing effort compared with the wider population. Sensitivity runs in recent WCPO tuna assessments also show that this mixing-period assumption can be highly influential on stock-status indicators driven by fishing mortality, particularly estimated depletion and spawning potential (Day et al., 2023, Magnusson et al., 2023, Teears et al., 2025).

Historically, mixing periods were fixed at a single number of quarters for all quarterly release groups, with an alternative period explored as a sensitivity. Since the 2022 WCPO skipjack assessment (Castillo-Jordan et al., 2022), a per-release-group approach has been used for this species, in which the assigned mixing period depends on a simulated measure of the predicted dissimilarity between the recapture-probability distribution of the tag release group and that of the untagged population in the region of release (Scutt Phillips et al., 2022; Teears et al., 2025). The present paper applies this approach, with several methodological updates, to the 2026 WCPO bigeye and yellowfin tuna assessments.

Two practical constraints motivate such a simulation-based approach. First, true tag releases and recaptures are sparse in space and time. The observational analysis of Kolody and Hoyle (2015) established, using the spatial distribution of recaptures, that tag mixing assumptions are frequently violated in WCPO skipjack tuna assessments, and it remains the benchmark demonstration of the problem. However, the methods developed require recovery-event sample sizes that are unavailable for the large majority of individual release groups, particularly for bigeye, which is tagged in far smaller numbers than skipjack. Their methods are not designed to certify that a sufficient mixing period has been reached, rather they both detect incomplete mixing where data permit. Because MFCL assessments require positive guidance on a mixing period for every release group, an approach is needed that can supply this where the observational data cannot. Kolody and Hoyle (2015) identified mechanistic habitat-based movement models such as SEAPODYM as a promising route to compensate for the unbalanced and sparse tag-release design, and an independent review of the MFCL yellowfin tuna assessment also indicated that such a simulation approach would provide a more defensible basis for assigning mixing periods (Punt et al. 2023).

Second, the spatial structure of MFCL assessments assumes that large regions are internally homogeneous, so that tag mixing is effectively assessed at the regional scale. Scutt Phillips et al. (2024) showed that such an assumption may be impossible to meet, and that defining the relevant untagged reference by the spatial extent of recaptures, rather than by the fixed management region, gives a better measure of the representativeness of a given tag group. However, given the fixed, spatial region structure assumptions of MFCL, the analysis

presented here works within the current regional structure, but its diagnostics make the consequences of that structure visible, a point to which we will return in the discussion.

The approach we take here is deliberately pragmatic. By leveraging many tag release-recapture pairs across time, together with fisheries and environmental data, to estimate movement through SEAPODYM, we simulate the plausible spatial evolution of each release group in the Ikamoana individual-based model (IBM) and record the recapture probability accumulated along all simulated trajectories. Rather than measuring spatial distribution mixing directly, we compare the distribution of *experienced fishing pressure*, calculated as recapture probability, a Lagrangian interpretation of the Baranov catch equation, between the tagged group and an untagged population distributed throughout the domain as predicted by SEAPODYM. Both groups experience exactly the same environmental forcing, spatiotemporally varying fishing effort, and natural mortality, differing only in their initial spatial distribution and hence in the fishing pressure they subsequently experience along their movement trajectories. The dissimilarity between the recapture-probability distributions of the two groups is used as a continuous measure of mixing, where zero corresponds to the two groups being subject to identical probabilities of recapture.

Full spatial mixing, where the tagged group's spatial distribution within the region exactly matches that of the untagged population, is the stronger condition. When it is met, both groups are subject to the identical fishing-mortality field and movement rates, and their experienced recapture-probability distributions are therefore identical by construction. Representativeness of fishing pressure is a weaker condition, but it is related to those quantities that appear most influenced in MFCL estimates from tagging data, namely, depletion and spawning potential. A tag group can therefore be adequately representative for assessment purposes without being fully mixed in space, and it is this weaker condition that our metric targets.

A consequence of working in a spatially explicit, behaviourally driven simulation is that mixing need not increase monotonically with time. The intuition from state-variable assessment models, in which biomass within a region is assumed homogeneous and movement is assumed to be a simple diffusion process, is that tagged fish can only increase their degree of spatial mixing over time. In a system with directed movement and spatially heterogeneous fishing pressure, and for a metric that compares fishing pressure between tagged and untagged groups, this need not be the case. We anticipate at least three mechanisms by which the dissimilarity mixing may depart from the monotonic decline expected under diffusion, failing to decrease, or even increase rather than decrease, over assumed mixing periods. First, *active aggregation*: directed movement toward favourable habitat can hold a tag group in, or draw it into, a sub-area whose fishing pressure differs from the regional background, slowing or preventing convergence on the untagged distribution. This collective, non-random movement can drive poor or non-monotonic diffusion in a way that diffusion cannot represent. Second, *a moving reference*: the untagged population is itself non-stationary, and immigration or emigration of biomass into or out of the region, and into areas of differing fishing pressure, can pull the untagged reference distribution away from a tag group that has not undertaken the same movement. Third, *low-signal noise*: where fishing pressure is very low, both recapture-probability distributions collapse toward zero and the metric compares two nearly degenerate distributions. In this case, small differences produce noisy, non-monotone values. We introduce these mechanisms here because they recur in the results, and because they bear directly on how mixing periods should be interpreted; we explore them further in the Discussion.

Taken together with the finding of Kolody and Hoyle (2015) that mixing may remain incomplete even after six or more quarters, and may likely never be achieved within an assessment region in some cases, these considerations reframe the selection of mixing periods in MFCL assessments. If full mixing is frequently unattainable, then classifying a release group is as simply 'mixed' or 'not mixed' may not adequately represent reality. Here, we instead ask how representative of regional fishing pressure each group becomes, on a continuous scale, and how much representativeness is *good enough* for the purposes of this assessment. Our simulation approach can estimate this quantity for every release group, regardless of the sparsity of its observed recaptures.

2. Methods

2.1 Simulation framework

Simulations were performed using the Ikamoana individual-based simulation model (Scutt Phillips et al., 2018), driven by an ocean-habitat movement model estimated from fisheries, environmental and conventional tagging data through SEAPODYM (Senina et al., 2020). Ikamoana tracks attributes of many individual particles, whose spatial distribution evolves as a group over time according to Lagrangian formulations of the advection–diffusion equation. The attributes tracked here are survival and cumulative recapture probability, computed as functions of natural mortality and of movement through spatiotemporally varying fields of fishing mortality. The equations governing movement, survival and recapture probability are given in full in Scutt Phillips et al. (2018, 2024).

Environmental forcing, natural mortality parameters, and fisheries parameters were taken from the most recent SEAPODYM reference solutions. These updated SEAPODYM reference models are driven by ocean fields from a coupled NEMO–PISCES physical–biogeochemical simulation forced by the JRA55 atmospheric reanalysis, which provides 1958–2022 time series of temperature, currents, dissolved oxygen, and primary production on a $1^\circ \times 1^\circ$ grid (Senina et al. 2026a). These three-dimensional fields were first vertically averaged over three pelagic layers and used to simulate mid-trophic (micronekton) biomass by the SEAPODYM–LMTL sub-model. The physical and biogeochemical fields together with the micronekton biomass then force the population-dynamics models.

2.2 Treatment of fishing effort

Recapture probability in Ikamoana requires an instantaneous fishing mortality at each particle's location and time. For several fisheries, catchability is not directly estimated in SEAPODYM because the catch and effort data do not provide a clear signal. In this Eulerian model framework, the fishing mortality of these fisheries is instead handled by a catch- (or biomass-) removal method, removing the biomass equal to the observed catch in a given month and cell during the historical period. This is not possible in the Lagrangian Ikamoana model, where biomass is not removed but recapture probabilities are accumulated over many individuals. Instead, for these fisheries spatial effort fields are re-computed from the model-predicted catches, which by construction equal the observed catches given the assumed constant catchabilities, and an instantaneous fishing mortality is derived from these corrected effort fields. The cumulative probability of capture is then recorded for each particle as a function of instantaneous fishing and natural mortality as it moves through the domain (Scutt Phillips et al. 2024).

The updated reference model of bigeye tuna was configured and parameterised by fitting to catch, length-frequency, and tagging data over the 1995–2019 window. Maximum-likelihood estimation (MLE) was performed at a coarser spatial ($2^{\circ} \times 2^{\circ}$) and age (quarterly) resolution; the age resolution was then refined, and the refined outputs were validated, showing no deterioration in the statistical scores for the fisheries data. The scores are also stable over the longer window that includes the out-of-sample data (1985–2022) and show a marked improvement over the previous reference model, which used a comparable coupled forcing (ERA-Interim–NEMO–PISCES; see Senina et al., 2026b). The spatiotemporal distributions predicted with the estimated parameters are qualitatively consistent with the observed CPUE in the tropical ocean, although the model may over-estimate abundance in the sub-tropics, which does not affect the present analysis. Note, however, that from 2020 onward the longline data in the fisheries dataset used for the MLE are incomplete. It was not possible to calculate fishing mortality fields post-2019, and so only results from pre-2019 release groups were considered: this excluded all groups from region one from the analysis.

2.3 Changes from the previous (skipjack) analysis

Several methodological updates were made relative to the 2022 and 2025 skipjack mixing analyses:

- The latest bigeye SEAPODYM solution was used, at 2° /monthly resolution with forcing to the end of 2022.
- An updated catchability-over-time function was applied, in-keeping with recent SEAPODYM developments
- An updated natural mortality function was used, with the variable effect of habitat on M now changing with age.
- Metrics were calculated using cohort-structured weighting (Section 2.5), so that the recapture-probability distributions reflect the empirical age composition of each release group on both the tagged and untagged sides.
- The dissimilarity metric was evaluated over the one-month period immediately following the assumed mixing point, rather than as the time-median value over the simulation as in the 2025 analysis, or the end-of-life value as in the 2022 analysis. This focuses the comparison on the fishing pressure experienced at the moment the assessment model begins incorporating recaptures (Hamer 2026 WCPFC-SC22-2026-SA-IP01).

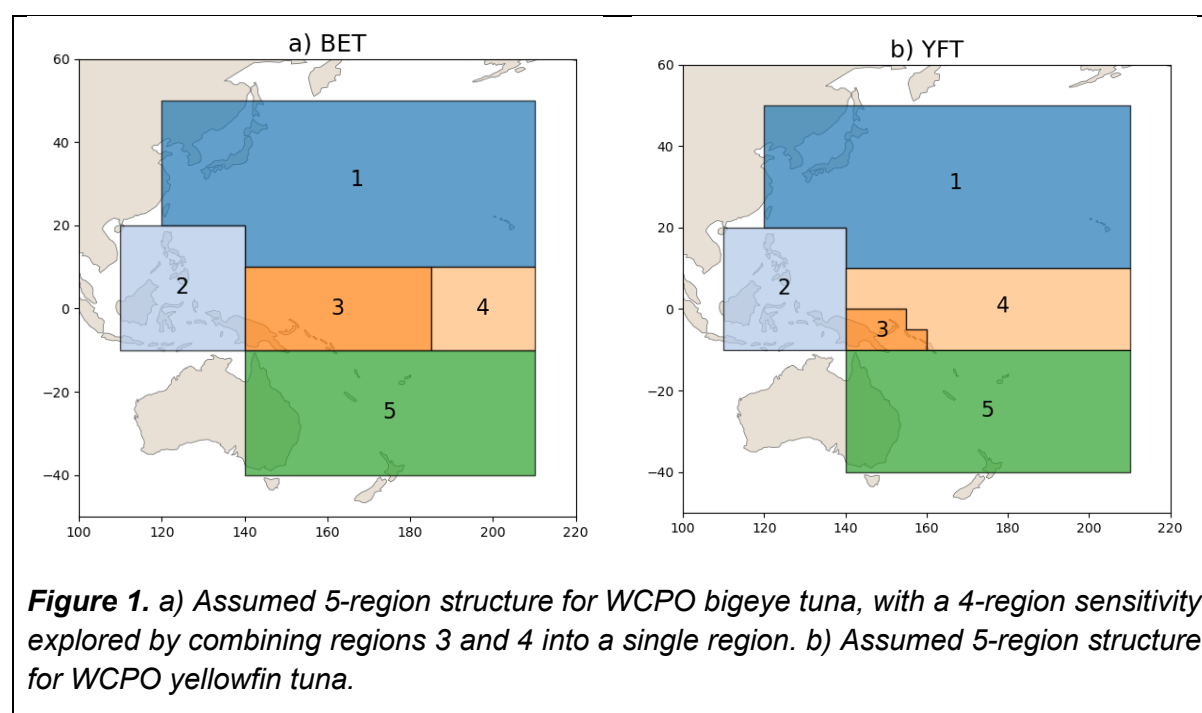
2.4 Data and release groups

Tag-release data were drawn from the Pacific Tuna Tagging Programme (PTTP). Observed releases were aggregated to the mid-point date of their quarter of release, to the two-degree cell of their release location, and to a SEAPODYM monthly age class (assigned by matching observed release length to the mean length-at-age of the SEAPODYM age structure). Aggregated release events with fewer than five or ten observed releases, for bigeye and yellowfin tuna respectively, were removed. The simulated data represent 96% of all PTTP bigeye tags, and 95% of all PTTP yellowfin tags.

For each aggregated release event, 100,000 particles were released evenly throughout the two-degree release cell. In parallel, an untagged 'population' simulation of 3 million particles of the matching age class, with initial spatial distribution as predicted by SEAPODYM, was run

to provide the comparison group. For bigeye tuna, approximately 2,350 release-event simulations and 350 untagged cohort simulations were run, comprising on the order of 1.3 billion particles across 40 to 45 bigeye tag release groups (depending on assumed assessment region structure). For yellowfin tuna, 1,150 release-event simulations and 250 untagged cohort simulations were run, comprising on the order of 865 million particles across roughly 55 release groups.

Assessment region structures followed those decided at the 2026 pre-assessment workshop (Hamer 2026 WCPFC-SC22-2026-SA-IP01), with two region structure sensitivities of 4- or 5- regions for bigeye tuna (figure 1a), and a single, 5-region structure for yellowfin tuna (figure 1b).



2.5 Dissimilarity metric and mixing scenarios

Four mixing scenarios were simulated, in which tagged fish were allowed to disperse from their release location for zero, one, two or three quarters before the comparison was made. In each scenario, comparison between tagged and untagged groups was restricted to particles within the region of interest at the moment of assumed mixing, and the recapture-probability distributions were evaluated one month later, allowing a short, common window of accumulated fishing pressure. As recapture data integrated into MFCL are conditioned on survival up until that point, within Ikamoana, survival is reset at the mixing point under each scenario. Recapture probability compared between scenarios reflects only post-mixing exposure; it does not necessarily decay mechanically with a longer assumed mixing period, and any reduction in recapture probability at longer mixing periods reflects genuine changes in fishing effort, the distribution of fish in relation to that effort, or in age-dependent selectivity as the cohort-structured group ages.

For each release group and mixing scenario, a Kolmogorov dissimilarity (K) statistic was calculated between the cohort-weighted recapture-probability distribution of all tag-release simulations in the group and that of the untagged population in the same region. Both sides

were weighted by the empirical release composition of the group, so that the metric isolates the mixing signal from differences attributable to age-selectivity and cohort-specific movement behaviours. A value of $K = 0$ indicates that the two groups are subject to identical recapture-probability distributions.

2.6 Diagnostics

For each release group, a diagnostic figure was produced with one row per mixing scenario, presenting: (i) mirrored histograms (pseudo-violins) of the tagged and untagged recapture-probability distributions over the one-month post-mixing period, annotated with the weighted K value; (ii) the relative spatial distribution of each group within the region of interest at the moment of assumed mixing; and (iii) the emergent recapture-probability field as a function of survival and the fishing mortalities experienced by the untagged population. This partially exposes the fishing-pressure landscape which drives the comparison behind our dissimilarity metric. A summary of the K trajectory across mixing scenarios is shown alongside. Example figures are presented in the Results; the full set is provided in Appendix A.

In addition, for observed tag-release groups we provide tag recapture-density plots. These show, from single or combined tag release groups, the number of recaptured tags per tonne of catch from purse seine and pole & line fleets, in space and by quarter post-release, following the tag-density approach of Kolody and Hoyle (2015). For each species and region, we constructed pooled recapture-density surfaces, for those regions with the most significant tag releases, to examine whether tag recaptures are systematically elevated near release locations or coastal features, independently of the simulation results.

Density is defined per one-degree cell as the number of recaptured tags divided by any non-zero catch, in tonnes, of purse-seine and pole-and-line fleets in that cell over the relevant quarter. Because most individual release groups yield too few recaptures to characterise any spatial pattern, densities are pooled across release groups: the density is computed separately for each release group and then averaged across the groups that contributed recaptures to a given cell (a mean of per-group ratios, rather than a ratio of summed recaptures over summed catch). This pooling is deliberately conservative, because where fish and fishing co-vary from year to year, averaging per-group densities reduces rather than amplifies apparent structure, so a pattern that persists after pooling is more likely to reflect a real, systematic tendency than an artefact of any single group. A well-mixed release group would be expected to exhibit a spatially uniform number of tags recaptured per unit of catch. As discussed, these observed data are too sparse for most release groups to determine a mixing period by group and are presented as a validation and contextual layer rather than as a determinant of mixing.

Surfaces are such that cells which were fished but returned no tagged fish appear as zeros rather than being absent; only cells that were unfished in the relevant quarter are left blank. Cells with less than one tonne of quarterly catch are excluded, as the ratio is unstable at very small denominators, and apparent densities above the 98th percentile, typically produced by one or two recaptures in a very-low-catch cell, are treated as noise. Recaptures reported from cells with no matched purse-seine or pole-and-line catch (a small proportion of the total and including recaptures by other gears such as longline) cannot be assigned a density and are shown only as raw positions. Cells to which fewer than three release groups contributed data are marked with crosses, to distinguish structure supported by many groups rather than being driven by only one or two.

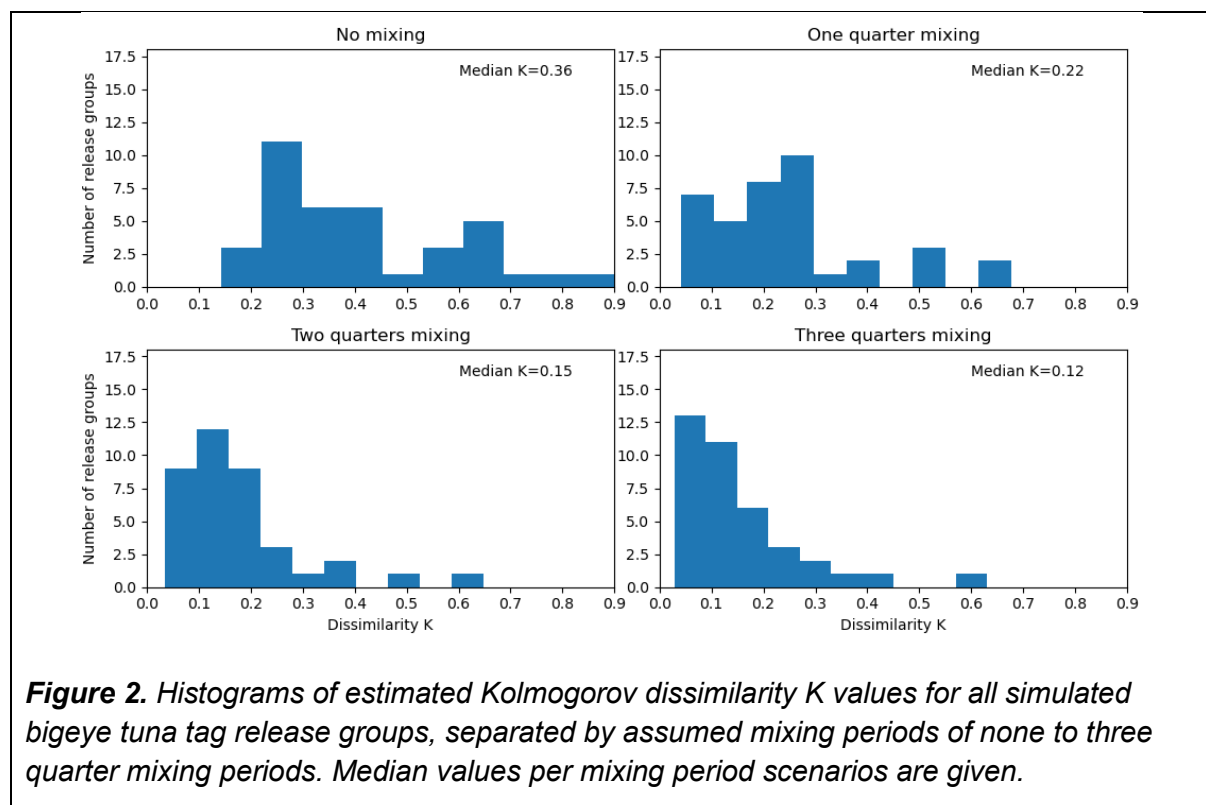
3. Results

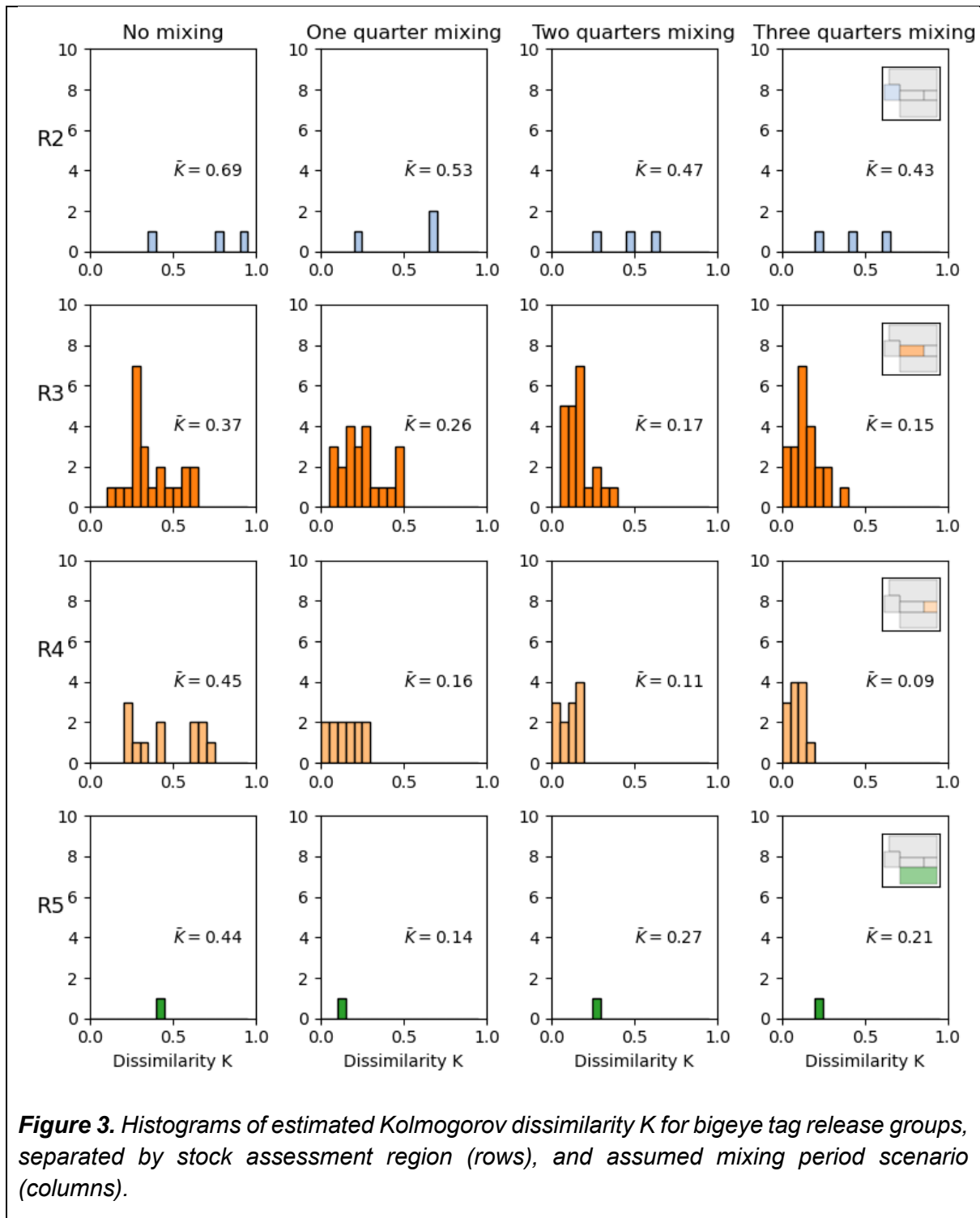
We provide overall distributions of dissimilarity K for all bigeye tuna release groups, then patterns by stock assessment region. Example diagnostics are described to elucidate the mechanisms behind some of these results, and finally, empirical tag-recapture density plots for pooled release groups are provided for comparison. Detailed results for yellowfin tuna are not provided in the results (see section 4.6 of the *Discussion*). However, further diagnostics for both species are given in the appendices.

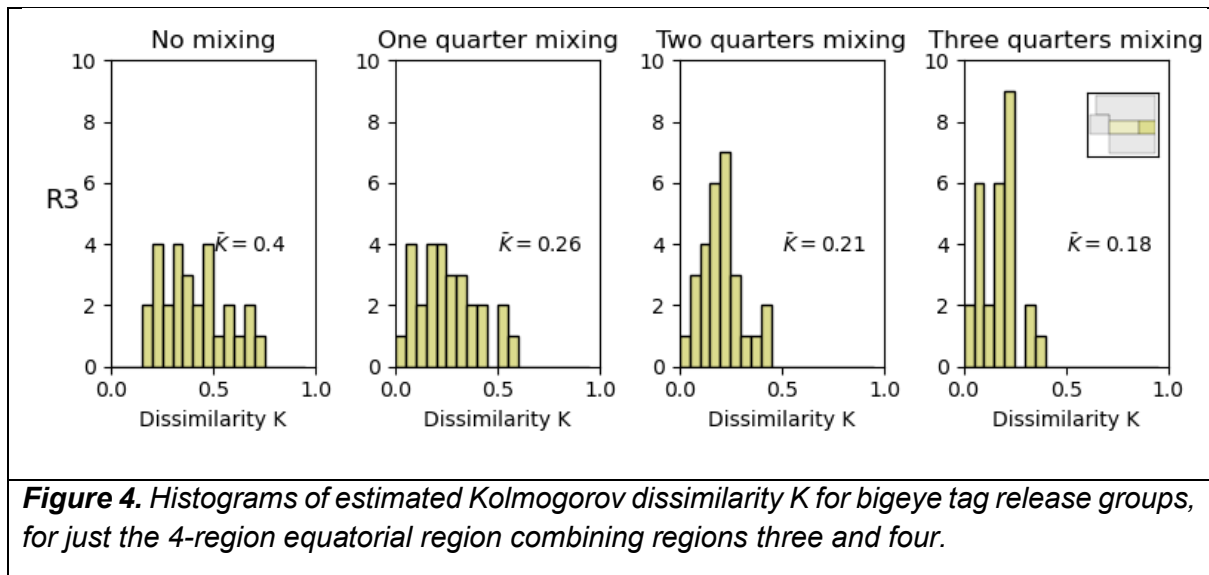
3.1 Mixing by region and mixing period scenario

In general, increasing the assumed mixing period resulted in more bigeye tag release groups exhibiting improved levels of mixing (reduced Kolmogorov dissimilarity K). For the 5-region structure, K decreased from a median value of 0.36 under a no mixing period scenario, to 0.12 when assuming three quarters of mixing (Figure 2).

Examining K shows some distinct patterns by region. Region two, in the far western area of the warm-pool, shows increased mixing during the first and second quarters post-release for one half of release groups, but the other remains very poorly mixing even at three quarters. The equatorial regions three and four showed more consistent levels of increased mixing over time, with the smaller region four showing the same degree of mixing by one quarter, as the larger region three by three quarters. The single release group in the southern region five exhibited improved mixing by one quarter, but then non-monotonic estimations of K in subsequent periods (see section 3.3). Under the 4-region scenario, where regions three and four are combined, while mean K was essentially an average of the two regions under no mixing, higher values were estimated from one quarter (0.26, compared to 0.26 and 0.16), two quarters (0.21, compared to 0.17 and 0.11), and three quarters mixing (0.18 compared to 0.15 and 0.09), than when regions three and four were considered separately (Figure 4).







3.2 Assigned mixing periods and recapture coverage

The use of our K statistic is to supply a continuous value of mixing, from which stock assessment model sensitivities can be chosen by assigning a cutoff value of K to represent a more or less conservative mixing condition to apply to tag release group data. For a given cutoff value of K , and for each release group, the shortest mixing period that provides an estimated K value lower than the cutoff is chosen as the mixing period for that group. If no mixing period explored in the simulation study provides a value below the cutoff, then a default mixing period of 4 quarters is chosen- effectively discarding the vast majority of recapture data for that release group.

Figure 5 shows the distribution of mixing periods assigned to bigeye tag release groups for the 5-region scenario, under a range of cutoff K values, from extremely conservative (0.05) to more liberal (0.30). A table of these values, for each release group explored here, is given in Appendix A. Choosing a more conservative value of 0.1 would result in ~40% of release groups being assigned a two quarter mixing period, the previously fixed period used in assessments of this species. Relaxing the cutoff to 0.3, would result in ~85% of release groups being assigned one quarter, which was the previous assessments mixing period sensitivity analysis.

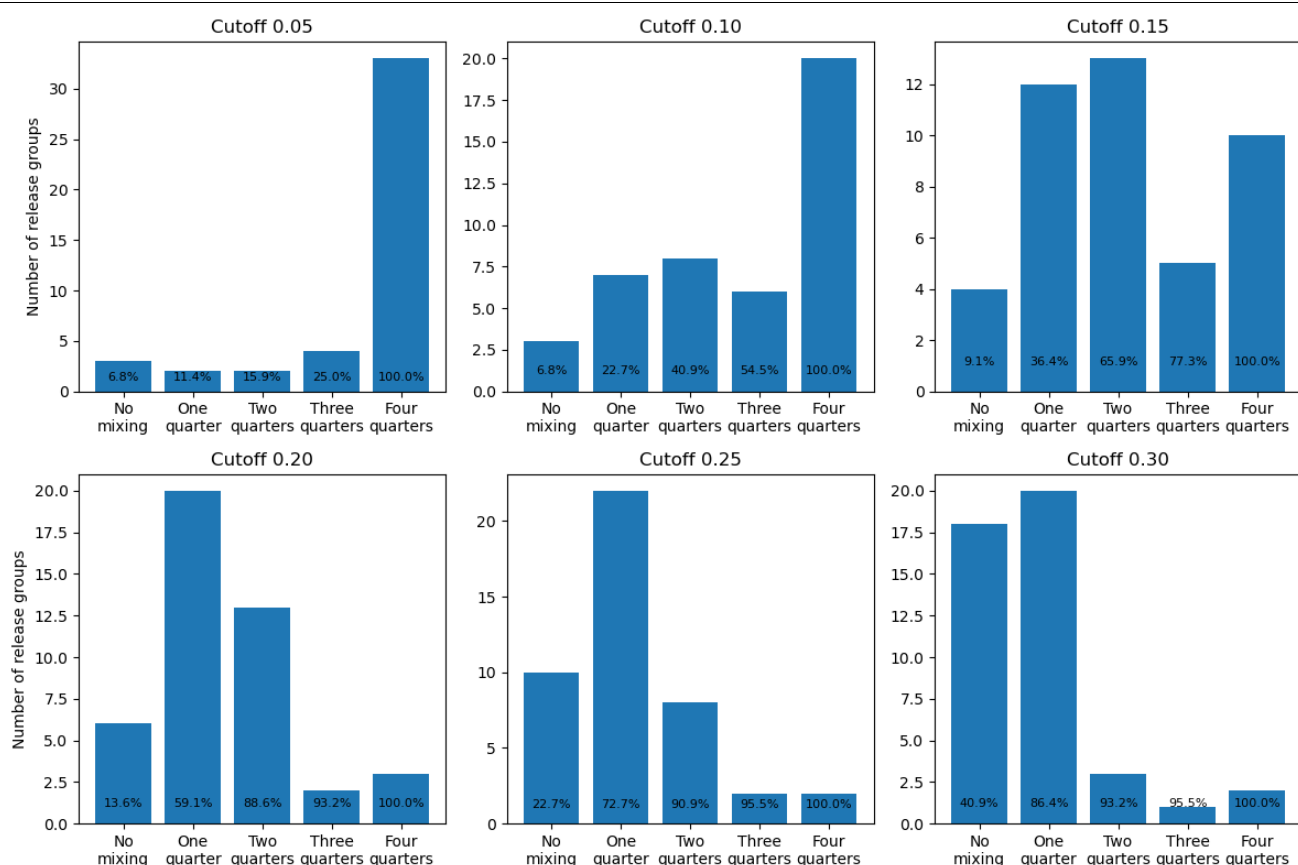
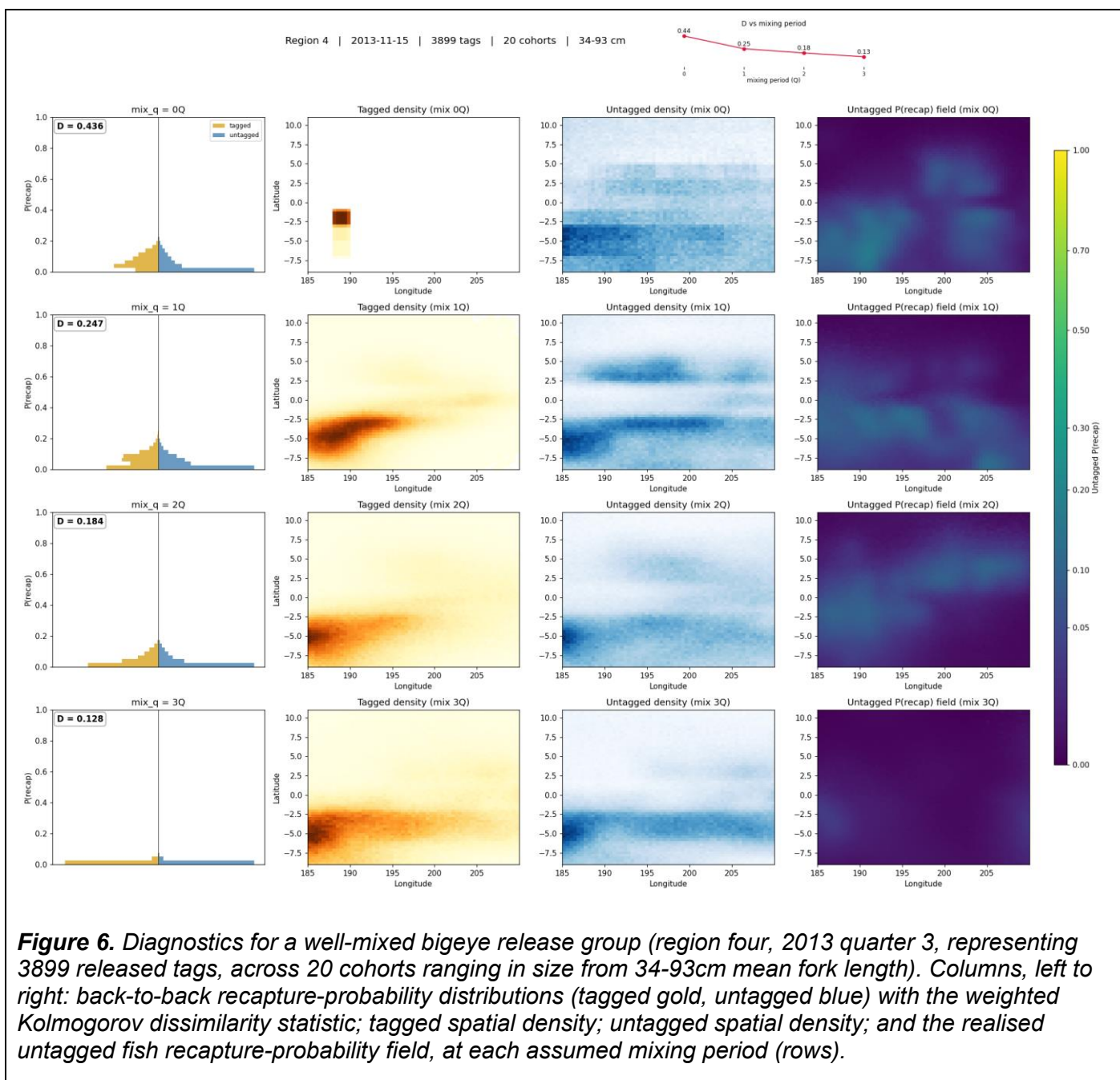


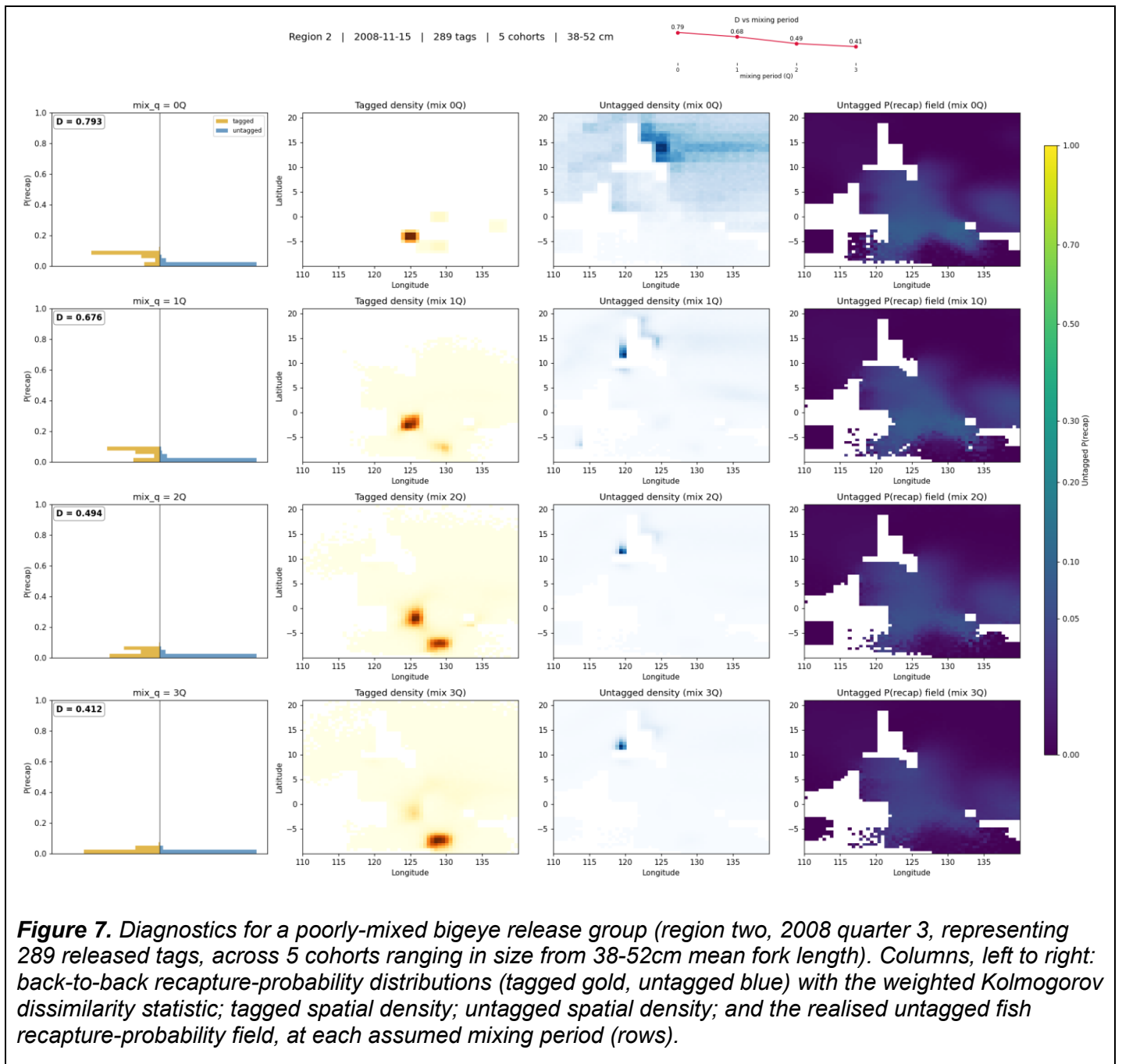
Figure 5. Number of bigeye tuna release groups, under the 5-region structure scenario, which would exhibit each mixing period, under different example cutoff values of Kolmogorov dissimilarity K . The cumulative proportion of groups included into an MFCL assessment, for that cutoff value, is given in each bar.

3.3 Example release group diagnostics

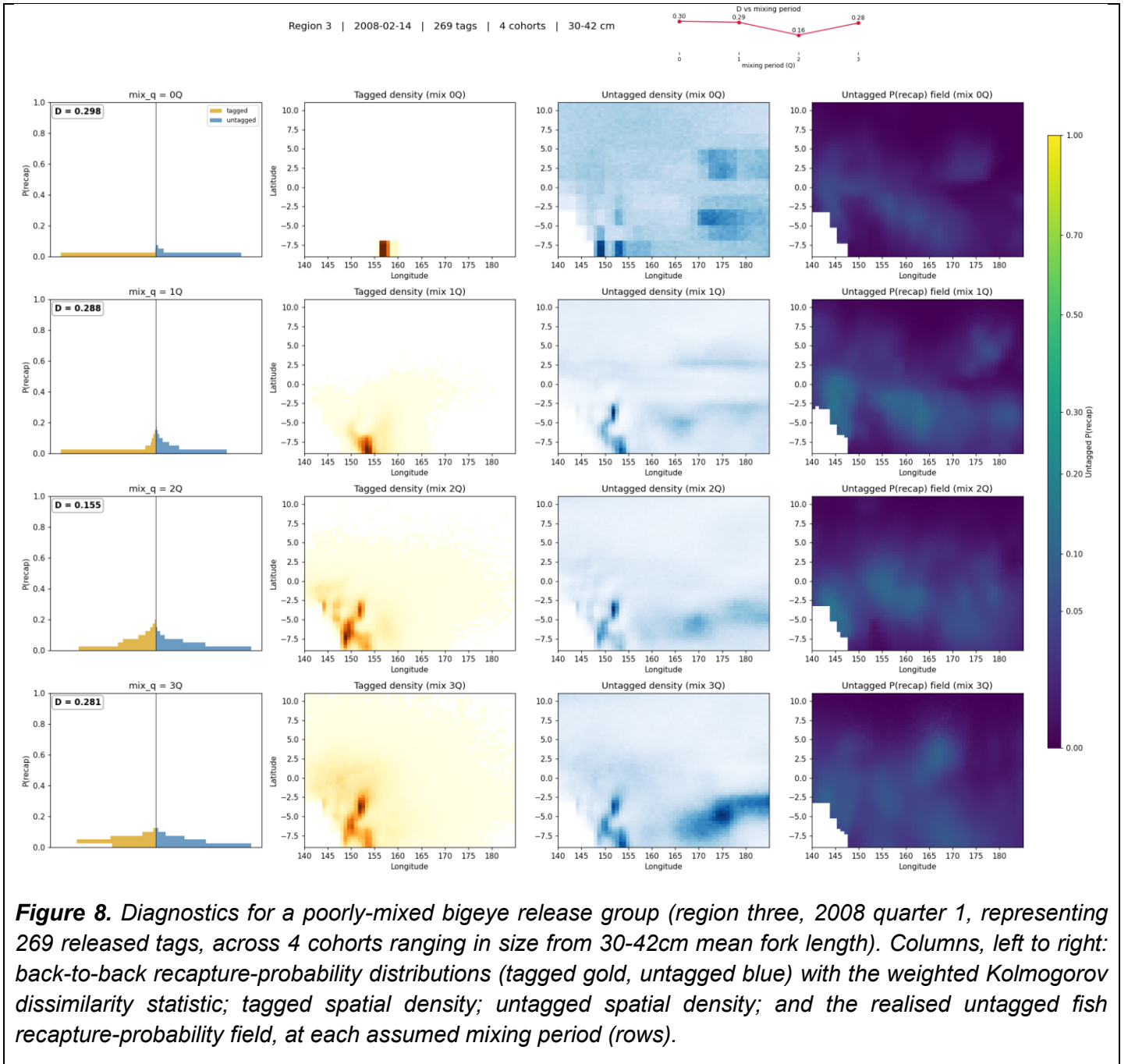
To explore the mixing dynamics of specific release groups, including cases of persistently poor mixing and a case where the dissimilarity metric does not decline monotonically, we here provide three examples of diagnostics to illustrate the range of behaviour, all taken from the 5-region structure scenario. Further simulation diagnostics of those bigeye tag release groups contributing the most releases are included in Appendix B.



A well-mixing group. Figure 6 demonstrates a release group for which dissimilarity declines steadily with assumed mixing period ($K = 0.44, 0.25, 0.18$ and 0.13 for zero to three quarters), as the tag group disperses across the relatively small assessment region four. Initially, the tagged fish remain in the western side of the region close to their area of release, compared to a significant proportion of the untagged density present north of the equator and to east where fishing is occurring. By two quarters, the tagged population's spatial distribution has converged on a corresponding dense area of untagged fish, improving the degree to which their recapture probability distributions are comparable, and therefore driving a lower Kolmogorov dissimilarity. By three quarters mixing, the spatial distribution of the tagged population almost matches that of the untagged distribution, which is now concentrated south of the equator. Combined with a flattening of the fishing pressure across the region over this time-period, the experienced recapture probability distributions of the two groups converge on similar and very low values, providing low value of dissimilarity and thus an indication of good mixing.



Active aggregation. Figure 7 demonstrates a release group in the western region two, for which dissimilarity remains extremely high despite falling over time ($K = 0.79, 0.68, 0.49$ and 0.41). The spatial distribution of tagged fish remains tightly aggregated in the south of the region where fishing pressure is greater, due to the heterogeneous distribution of feeding habitat. The untagged population remains distributed around the land masses in the north of the region, where fishing pressure is also lower. This combination of separate spatial distributions between the groups, combined with separate fishing pressure regimes, results in exceptionally high dissimilarity metrics for all assumed mixing periods explored. It is likely that such a tagged group may never mix at the region level, due to the directed movements predicted in response to environmental forcing: a dynamic that a diffusion-only representation of movement cannot produce.



A moving reference. In figure 8 the tagged group disperses reasonably well to match the spatial distribution of the untagged concentration in the south-west of the equatorial region three, but the dissimilarity rises again at the longest mixing period ($K = 0.30, 0.29, 0.16$, and 0.28). The tagged spatial distribution changes little during this later period; instead, biomass immigrates into the region from the east, which is also represents an area experiencing relatively lower fishing pressure (as seen in the untagged recapture-probability field), pulling the untagged reference distribution away from the largely stationary tag group. This is an example of non-monotonic mixing, due to the non-diffusion only movement of the tagged group, and a moving untagged, reference population.

3.4 Observed recapture density

Individual release group tag recapture density plots were too sparse to reveal any patterns, and so are not included here.

Figure 9 shows pooled, mean recapture density ratios for yellowfin tuna in region 3, where the majority of PTTP releases and recaptures occur. The pooled surfaces for region-3 yellowfin show recapture density elevated in the vicinity of the release area, persisting through roughly one to two quarters at liberty and relaxing thereafter as tags disperse, with a clear tendency to spread eastward out of the archipelago into more oceanic waters at longer times at liberty. In the release area itself this elevation is supported by multiple contributing release groups rather than by individual groups, indicating a systematic near-release tendency rather than a single-group artefact, and some moderately elevated cells persist even at four quarters at liberty. The surfaces do not, however, resolve into a consistent pattern fixed to particular coastlines or recurring locations: the elevated density tracks release location rather than recurring at the same coastal cells across groups. Because essentially every fished cell in the archipelagic region lies close to land, there is no non-coastal fished area within the region against which a distinct proximity-to-land effect could be contrasted. The pattern is therefore consistent with incomplete near-release mixing that relaxes with time at liberty, but neither provides evidence for, nor can it isolate, a specific island- or FAD-driven retention effect.

Figure 10 shows the same recapture density for bigeye release groups in the central Pacific region 4, alongside the mean, estimated Kolmogorov K values from the simulation experiment for this group. This pooled recapture surface is markedly more patchy, even at three quarters at liberty, reflecting the more heterogeneous distribution of fishing effort in this region, evident in the greater number of cells to which fewer than three release groups contributed catch, and few recapture data. As with the yellowfin surfaces, some consistently elevated cells persist at four and, to a lesser extent, five or more quarters at liberty, despite region 4 containing neither archipelagic waters nor dense anchored-FAD networks, suggesting that interpretation of yellowfin near-release persistence as specifically an island- or FAD-driven effect should be taken with caution. We also note a persistent concentration of recapture density in the eastern Pacific. Because recaptures occurring in the EPO are removed from the release group within the assessment, this feature may bear on the treatment of through-time tag recaptures in MF-CL assessments for this species and is worth further consideration.

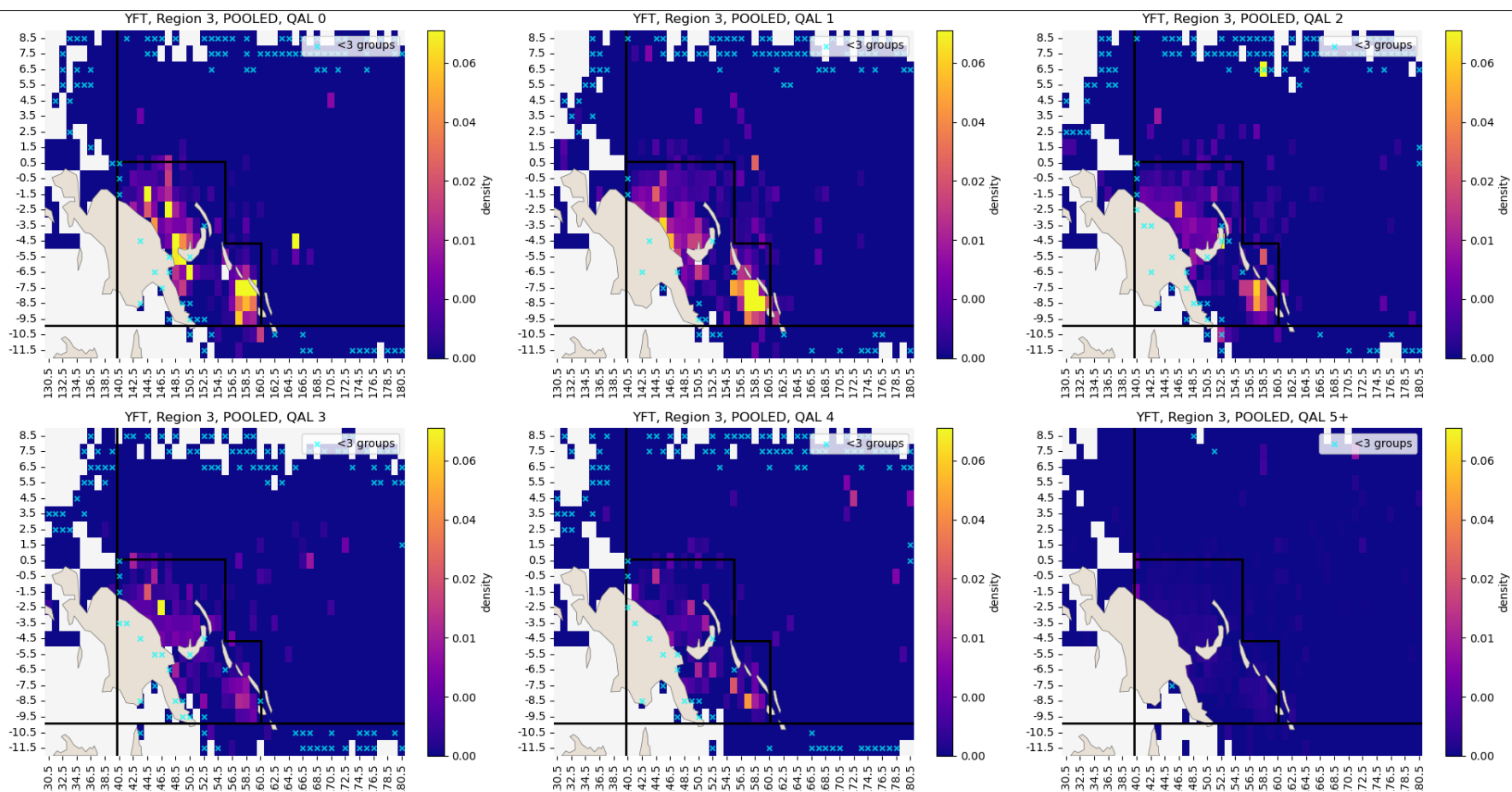


Figure 9. Pooled, spatial recapture density plots for yellowfin tuna release groups, released in region three and separated by quarter-at-liberty (QAL) of zero, one, two, three, four, and five and greater quarters. Data are the mean number of tags caught per tonne of catch from purse seine and pole & line gears, for each contributing release group. X marks designate cells calculated using data from fewer than three release groups.

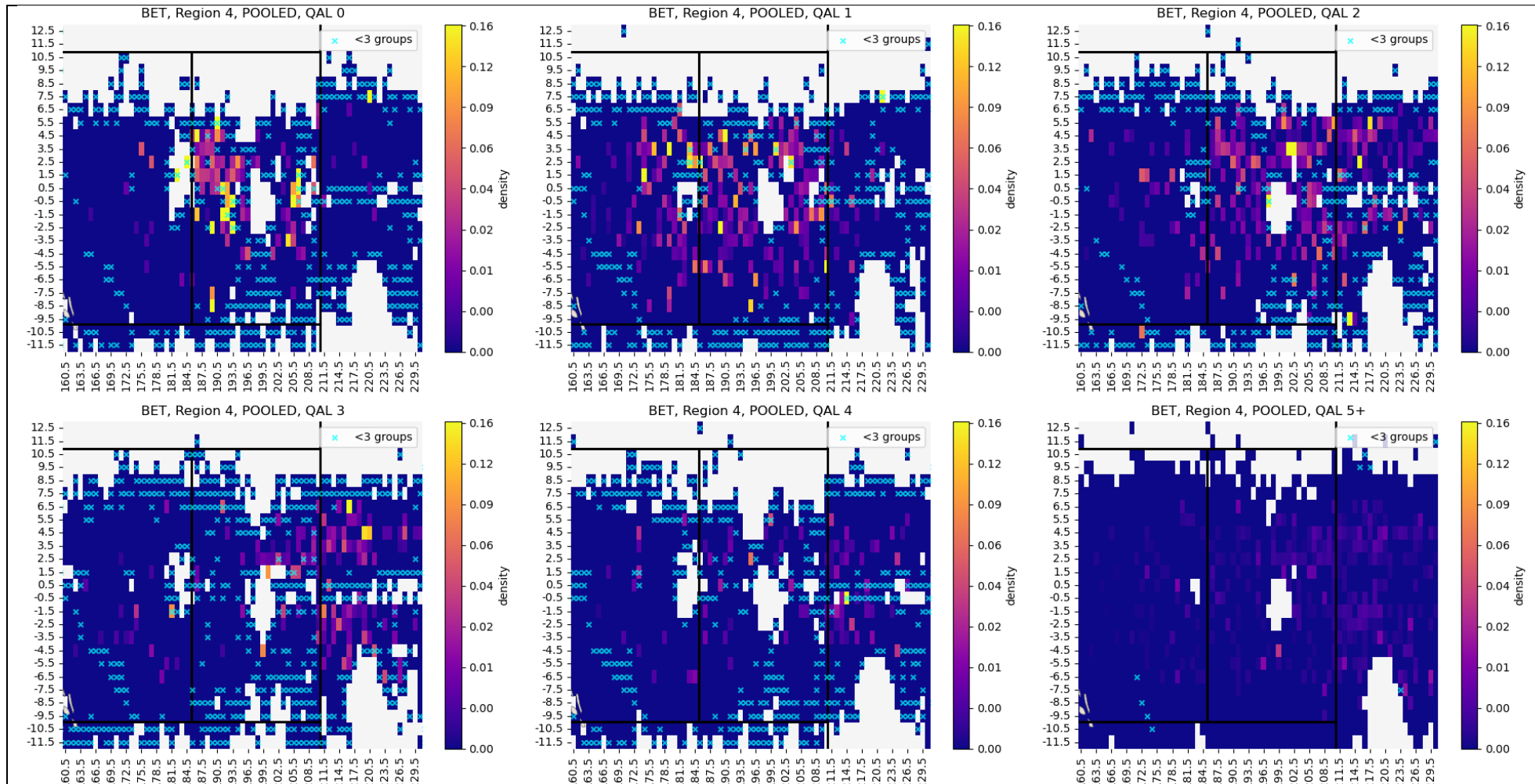


Figure 10. Pooled, spatial recapture density plots for bigeye tuna release groups, released in region four and separated by quarter-at-liberty (QAL) of zero, one, two, three, four, and five and greater quarters. Data are the mean number of tags caught per tonne of catch from purse seine and pole & line gears, for each contributing release group. X marks designate cells calculated using data from fewer than three release groups.

4. Discussion

The results we present here provide, for each bigeye release group, a continuous measure of the representativeness of its experienced fishing pressure relative to the untagged population, and from this an assigned mixing period under a range of dissimilarity cut-offs. The intended use of these results in a MFCL assessment is direct: the K cut-off selected controls how conservative the mixing-period assumption is, and therefore how many tag recaptures are admitted to the MFCL likelihood, with a lower cut-off implying a stricter mixing condition, and typically a longer mixing period and fewer admitted recaptures.

4.1 Representativeness of fishing pressure as the target

The method measures representativeness of experienced fishing pressure rather than spatial mixing. This is a deliberate choice and, we argue, the appropriate one for the assessment. Because spatial mixing also implies well represented fishing pressure by the tagged group, but not the reverse, targeting the weaker condition means the metric responds to exactly the indicators that are most influenced by the tag-informed parameters in MFCL. It does not penalise a tag group for failing to achieve full spatial mixing, which Kolody and Hoyle (2015) indicated may often extend beyond the lifetime of observed recaptures, and where that failure has no consequence for the fishing pressure it experiences. A clear instance is a spatially uniform fishing-mortality field: if fishing pressure is uniform across the region, at any level, including zero, then every fish experiences the same recapture probability regardless of where it is, and representativeness is satisfied by construction, and no spatial mixing is required. The metric correctly reports good mixing in this case because mixing, in terms of fishing mortality estimated in the assessment, is complete, despite a lack of spatial match between the two groups.

This indicates that the method is most informative when fishing pressure is spatially heterogeneous, and least informative at the extremes of the recapture-probability scale. Where pressure is very low everywhere, both distributions collapse toward zero and the metric has little to discriminate; where pressure is very high and recapture probability approaches its asymptote, the distributions are compressed against their upper bound and the metric again loses the ability to resolve genuine spatial differences in pressure, because additional exposure produces diminishing increments in recapture probability. These are not failures of the underlying logic, representativeness genuinely is high when pressure is uniform, but they do mean that the discriminating power of the Kolmogorov dissimilarity statistic is greatest in the intermediate regime that characterises many release groups.

4.2 Mixing is not always monotonic

As anticipated in the Introduction, the dissimilarity metric does not always decline clearly or monotonically with assumed mixing period, and our diagnostics demonstrate the mechanisms that cause this. The examples in Section 3.3 illustrate distinct mechanisms. Active aggregation, in which directed movement holds the tag group in a sub-area of differing fishing pressure, can prevent convergence on the regional reference and sustain high dissimilarity across all mixing periods (Figure 7). A moving untagged reference, in which immigration of biomass shifts the comparison distribution away from a largely stationary tag group, can cause the dissimilarity to rise at longer mixing periods (Figure 8). A third, statistical, driver arises

where recapture probabilities are very low and the metric compares near-degenerate distributions, and small differences produce non-monotone values due to noise.

These dynamics are at odds with the intuition, natural within homogeneous-mixing state-variable models, that fish can only become better mixed over time. That intuition follows from representing movement as diffusion, an entropy-increasing process, but this is not necessarily the case in a spatially explicit system in which fish undertake directed movements and in which the untagged reference is itself non-stationary. The practical implication for the assessment is modest but real: the assigned mixing period is the earliest assumed period at which a group's experienced pressure is sufficiently representative. The existence of later increases in dissimilarity does not undermine that assignment, but it does mean that 'tag mixing' should not be read as a monotone approach to a definitive, fully mixed end-state.

4.3 Region structure and the regional reference

Several release groups mix poorly not because the tag group fails to disperse, but because the regional untagged reference includes biomass in parts of the region that the tag group simply does not reach and where fishing pressure differs. This is the situation diagnosed by Scutt Phillips et al. (2024), who found that defining the untagged reference by the spatial extent of recaptures, rather than by the fixed management region, substantially reduced apparent bias in estimates of fishing mortality in a mark-recapture model. The diagnostics we present here make the effect visible, and the same dynamic is seen in figure 7, where active aggregation confines the tag group to a sub-area the untagged reference does not occupy. Where the tagged and untagged spatial densities occupy different parts of a large region, the dissimilarity often remains elevated regardless of mixing period. While boundary-shift sensitivities in an assessment may improve mixing in some cases, more generally this finding supports finer spatial resolution in regions where effort is concentrated within a sub-area of the management region, and motivates an exploration of alternative ways to influence parameter estimates from the tagged population at more relevant scales (including non-spatial).

4.4 Relationship to observational mixing analyses

The observational methods of Kolody and Hoyle (2015) remain the benchmark for demonstrating, from real recaptures, that mixing assumptions are violated in WCPO tuna assessments. Their analysis showed that, for skipjack, incomplete mixing persisted for at least six quarters and in some regions could not be assessed beyond a few quarters for want of data. It also concluded that adequate mixing might never be achieved, given the existing region definitions. For bigeye, with far fewer tags and recaptures, the data are too sparse to robustly apply these observational tests, and possibly any test based directly on recapture distributions, for the vast majority of release groups. Such tests are designed to detect incomplete mixing rather than to certify a sufficient mixing period.

The simulation approach used here is complementary. It supplies, through a mechanistic movement model, the statistical power and per-release group coverage that the sparse observational data cannot, and it does so for every release group for which environmental and fisheries data exist. Where observed recaptures are sufficient, observational analyses provide some empirical indication of the apparent dynamics; where they are not, the simulation extends guidance to those groups that would otherwise have none. We note that the observation of full mixing being frequently unattainable reframes the problem in a way that

favours a continuous, 'how representative' measure over a binary 'mixed or not' verdict. If a fully and spatially mixed state is often never reached, the operationally relevant question is how much representativeness is sufficient for the assessment's purposes. This is the question that our analysis is designed to answer.

4.5 Observed recapture density

The tag recapture-density diagnostics show true observations and connect directly to the established tag-density framework of Kolody and Hoyle (2015). Consistent with the sample-size limitations noted in that work, however, they are too sparse for the large majority of individual bigeye or yellowfin release groups to determine a mixing period: most groups have only single-digit recaptures distributed across a handful of cells, which is insufficient to characterise whether the spatial gradient is approaching uniformity.

Examined together, the pooled recapture-density surfaces do not provide clear evidence that localised effects such as island or anchored-FAD retention can be identified from the observed tagging data. Any near-release or near-coastal signal is confounded by three factors that cannot be separated with the data available: release location itself, since releases are clustered in the same coastal and archipelagic waters where any retention effect would be expected; the local environment, which co-varies with those same areas and independently drives movement; and spatial variation in reporting rate, which is both higher and more uncertain in archipelagic waters owing to small-scale and artisanal catch. A further, structural limitation is the absence of comparable areas, i.e. regions sharing a similarly high density of islands and anchored FADs but differing in their environmental setting, against which these tagging data could be contrasted to isolate a local effect from an environmental one. We therefore consider that, while the pooled surfaces are a useful observational complement to the simulation results, the question of whether local features measurably bias tag mixing is unlikely to be resolvable from recapture data alone at the scale and resolution of the current assessment, and would be better pursued through dedicated fine-scale study than through further aggregation of these data

4.6 Yellowfin tuna analysis

The equivalent tag mixing analysis was performed for yellowfin tuna but is not presented here. At the time of undertaking simulations, the SEAPODYM solution for this species exhibited fishing-mortality fields in which, for many strata, the effort-correction step described in Section 2.2 implied catches that approached the entire available biomass within large areas. Specifically, such a dynamic drives recapture probability of the cohort-weighted groups toward saturation across much of the domain, which as noted in Section 4.1, results in the dissimilarity metric losing ability to resolve genuine spatial differences in fishing pressure between the two groups. Progress toward the final reference SEAPODYM solution will bring more confidence in levels of available biomass, notably through the refinement of fisheries selectivities estimation, and should result in more pertinent estimates of recapture probabilities. The specific issues associated with the current SEAPODYM solution and how they will be addressed in the final reference solution are described in Bonin et al. (2026, SC22-SA-IP-07). Yellowfin results were not considered sufficiently robust for the timely inclusion into the assessment but we recommend revisiting them at a later date.

4.7 Limitations

There are a number of important caveats and limitations to our approach, which should be noted. First, all results are conditional on the SEAPODYM movement and mortality parameterisation; alternative behavioural hypotheses (for example a simple random walk, or different habitat responses) were not explored here and may be worthwhile sensitivity analyses.

Release events are aggregated to a single mid-quarter date and a two-degree release cell, for computational efficiency purposes. In particular, the temporal aggregation degrades the potential to capture important movement and fishing pressure dynamics that may have occurred for the true, tagged fish. Similarly, fine-scale processes, such as localised aggregation around floating objects or coastlines immediately after release, are not captured and may affect recapture rates during periods immediately following release. We are not aware of any movement model estimated on real data that does capture such processes, although simulation modelling studies have suggested that this may have only marginal impact on fishing mortality at higher spatial scales (Nooteboom et al. 2023)

While our simulations assume 100% reporting of recaptures, actual reporting rates vary across space, time and fleets. Reporting rates are estimated within MFCL assessments, where they are highly influential on those parameters informed by tagging data, and so for the purposes of our analysis, this impact is considered negligible.

Finally, the mixing period scenarios we have examined are restricted to integer quarters (zero to three), consistent with the MFCL time-step, but longer mixing periods were not simulated for computational reasons. However, as increasingly long mixing periods result in the discard of increasing proportions of the recapture data, this trade-off was considered acceptable.

4.8 Recommendations

We invite SC22 to:

- Note the results of this analysis of tag mixing for WCPO bigeye tuna, available for use in the 2026 stock assessment, with mixing periods provided across a range of dissimilarity cut-offs to enable their use as a structural uncertainty axis;
- Note the potential to extend the approach to yellowfin tuna, pending a finalised SEAPODYM reference solution for that species;
- Consider the implications of these results for the spatial structure of tuna assessments, and the merit of exploring more spatially explicit, or non-spatial, treatments of tagging data.

Declaration of generative AI use

During the preparation of this work the authors used Claude Opus 4.8 for the purposes of methodological development, code development and writing. All analysis was undertaken by the authors. Any AI-generated output were reviewed and further edited by the authors as needed and, they take full responsibility for the content and scientific findings of the paper.

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References

- Abadi, F., Botha, A., and Altwegg, R. (2013). Revisiting the Effect of Capture Heterogeneity on Survival Estimates in Capture-Mark-Recapture Studies: Does It Matter? *PLoS One* 8. doi: 10.1371/journal.pone.0062636
- Bonin, L., Senina, I., Forestier, R., Lengaigne, M., Temple-Boyer, J., Guihou, K. et al. (2026). Progress towards a new SEAPODYM reference model of yellowfin tuna (*Thunnus albacares*) in the Pacific Ocean (WCPFC-SC22-2026/SA-IP07). Twenty-second regular session of the Scientific Committee of the Western and Central Pacific Fisheries Commission.
- Castillo-Jordan, C., Teears, T., Hampton, J., Davies, N., Scutt Phillips, J., Macdonald, J., et al. (2022). Stock assessment of skipjack tuna in the western and central Pacific Ocean: 2022., (SC18-SAWP-01). Eighteenth Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission
- Day, J., Magnusson, A., Teears, T., Hampton, J., Davies, N., Castillo Jordán, C. et al. (2023). Stock assessment of bigeye tuna in the western and central Pacific Ocean: 2023 (WCPFC-SC19-2023/SA-WP-05). Nineteenth regular session of the Scientific Committee of the Western and Central Pacific Fisheries Commission.
- Guillemain, M., Pradel, R., Devineau, O., Simon, G., and Gauthier-Clerc, M. (2014). Demographic heterogeneity among individuals can explain the discrepancy between capture-mark-recapture and waterfowl count results. *Condor* 116. doi: 10.1650/CONDOR-13-148.1
- Kolody, D., and Hoyle, S. (2015). Evaluation of tag mixing assumptions in western Pacific Ocean skipjack tuna stock assessment models. *Fish Res* 163, 127–140.
- Magnusson, A., Day, J., Teears, T., Hampton, J., Davies, N., Castillo Jordán, C., et al. (2023). Stock assessment of yellowfin tuna in the western and central Pacific Ocean: 2023 (WCPFC-SC19-2023/SA-WP-04). Nineteenth regular session of the Scientific Committee of the Western and Central Pacific Fisheries Commission.
- Nooteboom, P. D., Scutt Phillips, J., Senina, I., van Sebille, E., & Nicol, S. (2023). Individual-based model simulations indicate a non-linear catch equation of drifting Fish Aggregating Device-associated tuna. *ICES Journal of Marine Science*, 80(6), 1746-1757.
- Punt, A.E., Maunder, M.N., and Ianelli, J.N. (2023) Independent Review of Recent WCPO Yellowfin Tuna Assessment (WCPFC-SC19-2023/SA-WP-01). Nineteenth regular session of the Scientific Committee of the Western and Central Pacific Fisheries Commission.
- Scutt Phillips, J., Sen Gupta, A., Senina, I., van Sebille, E., Lange, M., Lehodey, P., et al. (2018). An individual-based model of skipjack tuna (*Katsuwonus pelamis*) movement in the tropical Pacific ocean. *Prog Oceanogr* 164. doi: 10.1016/j.pocean.2018.04.007
- Scutt Phillips, J., Lehodey, J., Hampton, J., Hamer, P., Senina, I., and Nicol, S. (2022). Quantifying Rates of Mixing in Tagged, WCPO Skipjack Tuna. Technical Report WCPFC-SC18-2022/SA-WP-04
- Scutt Phillips, J., Lehodey, J., Senina, I., Barker, R., Peatman, T., Schofield, M., ... & Nicol, S. (2024). Optimising the design and analysis of capture-mark-recapture experiments using individual-based models. *Frontiers in Marine Science*, 11, 1497812.
- Senina, I., Lehodey, P., Sibert, J., and Hampton, J. (2020). Integrating tagging and fisheries data into a spatial population dynamics model to improve its predictive skills. *Canadian Journal of Fisheries and Aquatic Sciences* 77, 576–593.
- Senina, I., Bonnin, L., Forestier R., and Nicol, S. (2026a). Advancing the SEAPODYM modelling framework: methodology, validation, and analyses. Twenty-second Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission, WCPFC-SC22-2026/EB-WP-01

Senina, I., Bonin, L., Forestier, R., Lengaigne, M., Temple-Boyer, J., Guihou, K. and S. Nicol (2026b). SEAPODYM applications to Pacific tuna species. Twenty-second Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission, WCPFC-SC22-2026/EB-IP-03

Teears, T., Ghergariu, M., Peatman, T., Pohl, B., Scutt Phillips, J., and Hampton, J. (2025). Background Analyses and Data Inputs for the 2025 WCPO skipjack tuna Stock Assessment., (SC21-SA-IP-03). Twenty-first regular session of the Scientific Committee of the Western and Central Pacific Fisheries Commission.

Appendix A. Mixing Period Selection by KS Dissimilarity Cutoff

We here provide the selected mixing period in quarters for all bigeye tuna PTPP release groups, under a range of cutoff values for the Kolmogorov dissimilarity metric. Mixing periods under the 4-region scenario, which aggregates region three and four alongside the selected mixing period assuming mean values of the metric for each region, are provided at the bottom.

Region	Date	0.05	0.1	0.15	0.2	0.25	0.3	0.35	0.4	0.45
3	15/08/2006	4	4	4	1	1	1	1	1	1
3	15/11/2006	4	4	3	3	3	2	2	2	1
3	14/02/2007	4	1	1	1	1	0	0	0	0
3	15/11/2007	4	2	2	1	1	0	0	0	0
3	14/02/2008	4	4	4	2	2	0	0	0	0
3	15/05/2008	4	2	2	2	1	1	0	0	0
4	15/05/2008	1	1	1	1	1	1	0	0	0
2	15/08/2008	4	4	4	4	1	1	1	0	0
3	15/08/2008	3	1	1	1	1	1	0	0	0
2	15/11/2008	4	4	4	4	4	4	4	4	3
3	15/11/2008	4	4	4	2	2	1	1	1	1
3	14/02/2009	4	4	2	2	2	0	0	0	0
5	14/02/2009	4	4	1	1	1	1	1	1	0
3	15/05/2009	3	3	1	1	1	1	1	1	0
4	15/05/2009	4	1	1	1	0	0	0	0	0
2	15/08/2009	4	4	4	4	4	4	4	4	4
3	15/08/2009	4	4	2	2	2	2	2	2	2
3	15/11/2009	4	3	2	1	1	0	0	0	0
4	15/11/2009	4	3	2	2	2	1	1	1	1
4	15/05/2010	2	2	1	1	1	1	1	1	1
3	15/11/2010	4	4	4	2	1	1	0	0	0
4	15/11/2010	1	1	1	1	1	1	1	1	0
3	15/05/2011	4	4	2	2	2	2	2	2	0
3	15/08/2011	3	2	1	1	1	1	1	1	1
3	15/11/2011	4	2	2	1	1	0	0	0	0
4	15/11/2011	4	4	2	1	0	0	0	0	0
3	14/02/2012	4	1	1	1	0	0	0	0	0
4	15/08/2012	3	1	1	1	1	1	1	1	1
4	15/11/2012	2	2	1	1	1	0	0	0	0
3	15/05/2013	4	4	4	2	2	0	0	0	0
3	15/11/2013	4	4	4	3	3	3	2	2	2
4	15/11/2013	4	4	3	2	1	1	1	1	0
4	15/08/2014	4	4	2	2	1	1	1	1	1
4	15/08/2015	4	3	3	1	0	0	0	0	0
4	15/11/2015	4	4	4	2	2	1	1	1	1
3	15/08/2016	4	4	3	0	0	0	0	0	0
3	15/11/2016	4	3	3	2	1	1	1	0	0
3	15/08/2018	4	4	0	0	0	0	0	0	0
2	Mean	4	4	4	4	4	4	4	4	3
3	Mean	4	4	3	2	2	1	1	0	0
4	Mean	4	3	2	1	1	1	1	1	1
5	Mean	4	4	1	1	1	1	1	1	0

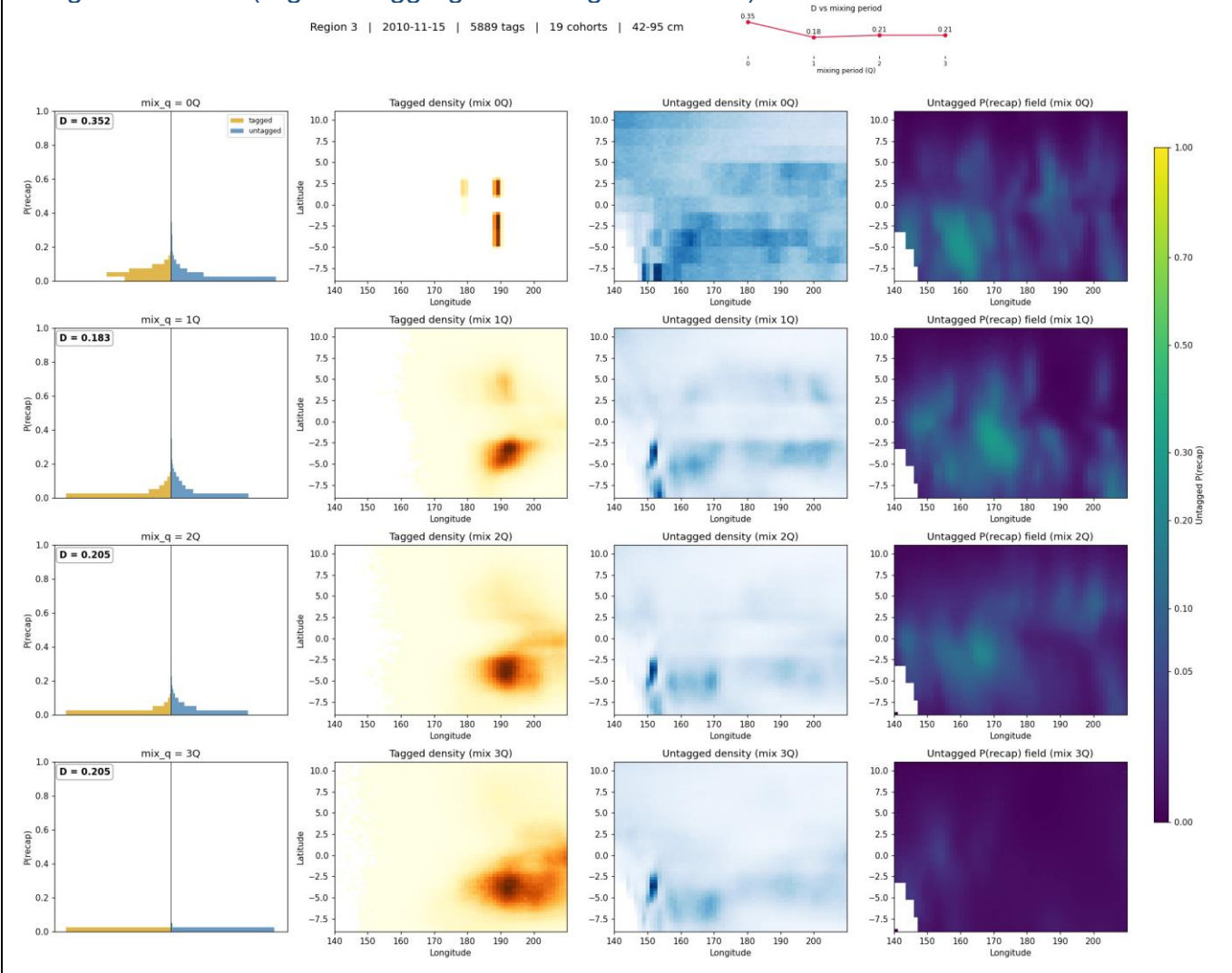
Region	Date	0.05	0.1	0.15	0.2	0.25	0.3	0.35	0.4	0.45
3+4	15/08/2006	4	4	4	4	4	4	4	1	1
3+4	15/11/2006	4	4	4	4	3	3	3	3	2
3+4	14/02/2007	4	4	4	1	1	1	0	0	0
3+4	15/11/2007	4	4	4	4	1	1	0	0	0
3+4	14/02/2008	4	4	4	4	2	1	0	0	0
3+4	15/05/2008	4	1	1	1	1	1	1	0	0
3+4	15/08/2008	4	1	1	1	1	1	1	0	0
3+4	15/11/2008	4	4	4	4	4	1	1	1	1
3+4	14/02/2009	4	4	4	3	2	0	0	0	0
3+4	15/05/2009	4	3	2	0	0	0	0	0	0
3+4	15/08/2009	4	3	3	2	2	2	2	2	2
3+4	15/11/2009	3	2	2	2	1	1	1	1	1
3+4	15/05/2010	4	4	4	2	2	2	2	1	1
3+4	15/11/2010	4	4	4	1	1	1	1	0	0
3+4	15/05/2011	4	4	4	3	2	2	2	2	0
3+4	15/08/2011	4	3	1	1	1	1	1	1	1
3+4	15/11/2011	2	2	1	1	0	0	0	0	0
3+4	14/02/2012	1	1	1	1	0	0	0	0	0
3+4	15/08/2012	4	1	1	1	1	1	1	1	1
3+4	15/11/2012	4	4	4	1	1	0	0	0	0
3+4	15/05/2013	4	4	4	2	0	0	0	0	0
3+4	15/11/2013	3	3	3	3	2	2	1	1	1
3+4	15/08/2014	4	4	2	2	2	1	1	1	1
3+4	15/08/2015	4	1	1	0	0	0	0	0	0
3+4	15/11/2015	4	4	4	4	1	1	1	1	1
3+4	15/08/2016	4	3	3	2	2	2	1	1	0
3+4	15/11/2016	4	4	4	3	1	1	0	0	0
3+4	15/08/2018	4	4	2	2	0	0	0	0	0
3+4	Mean	4	4	4	3	2	1	1	1	0

Appendix B. Simulation Diagnostic Plots

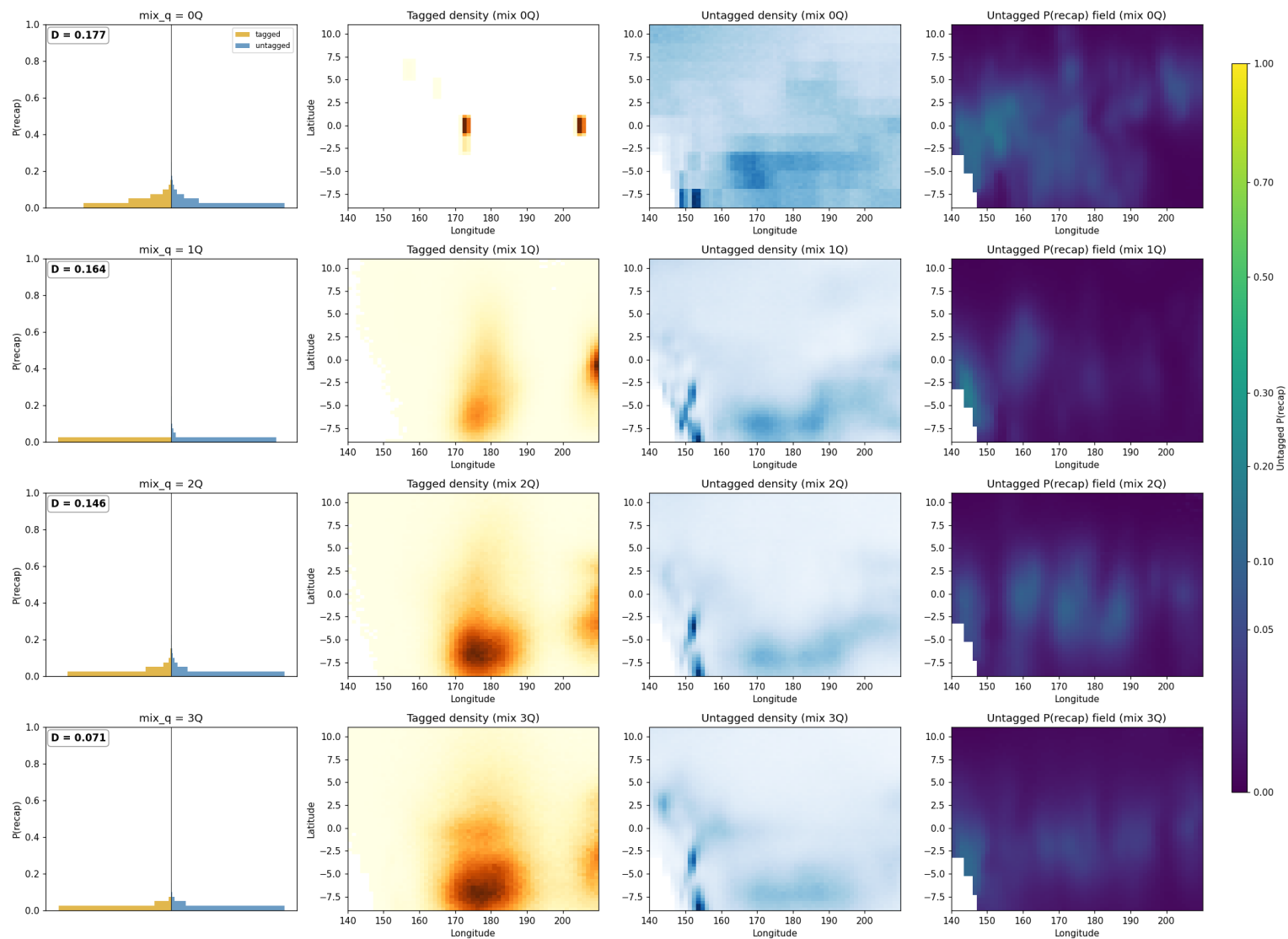
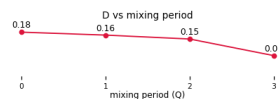
Selected simulation diagnostics from the tag release groups contributing significant numbers of releases across different regions, for integration into the WCPO bigeye tuna stock assessment, excluding those already provided in the main text. Diagnostics are separated into groups from the 4-region assumed spatial structure (regions three and four combined), and then release groups released in regions under the 5-region scenario.

Date	Region	Releases	Recaptures
15/11/2010	3+4	5889	1927
15/05/2009	3+4	4540	812

4-region structure (region 3 aggregated to region 3 and 4)

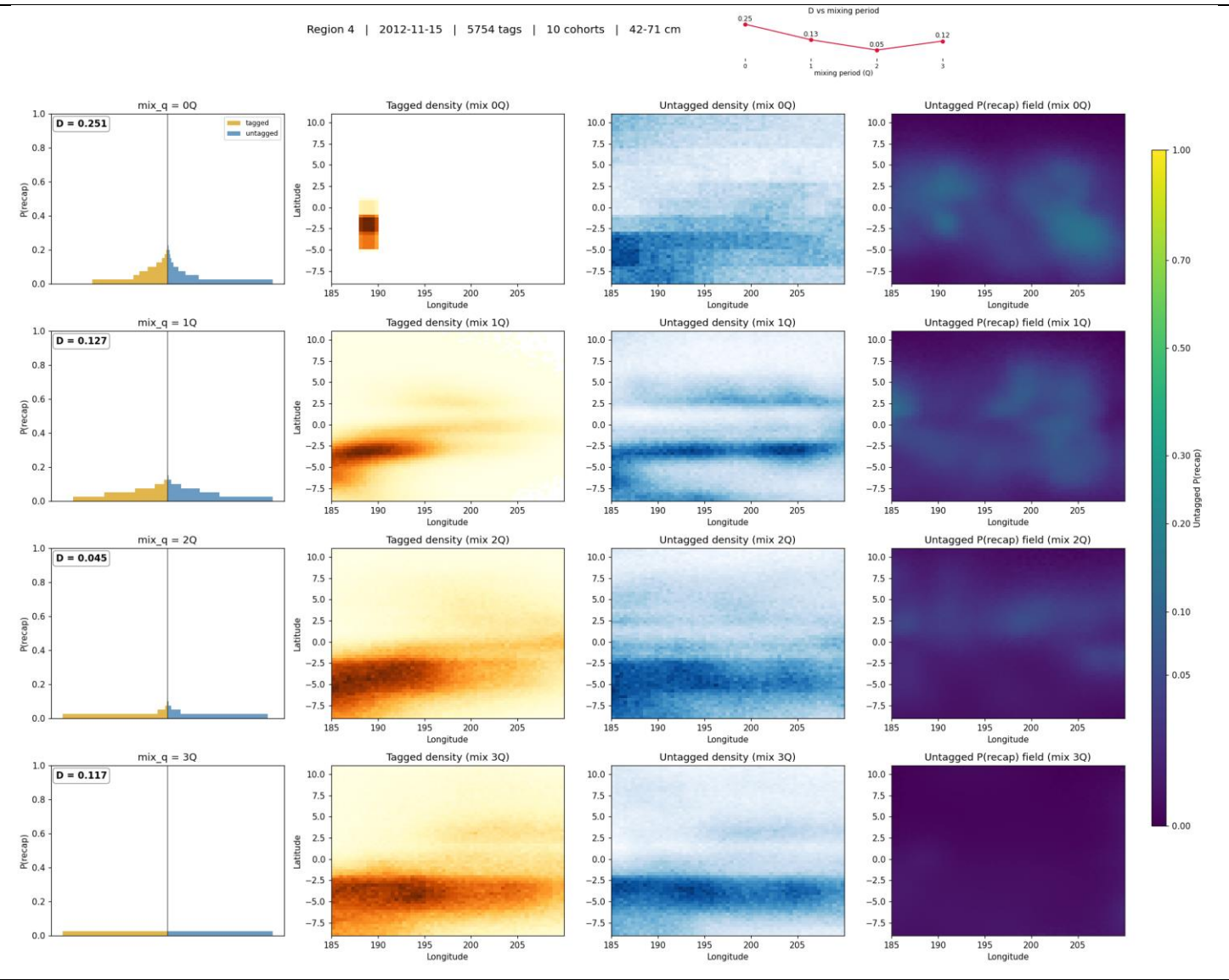


Region 3 | 2009-05-15 | 4540 tags | 20 cohorts | 38-95 cm

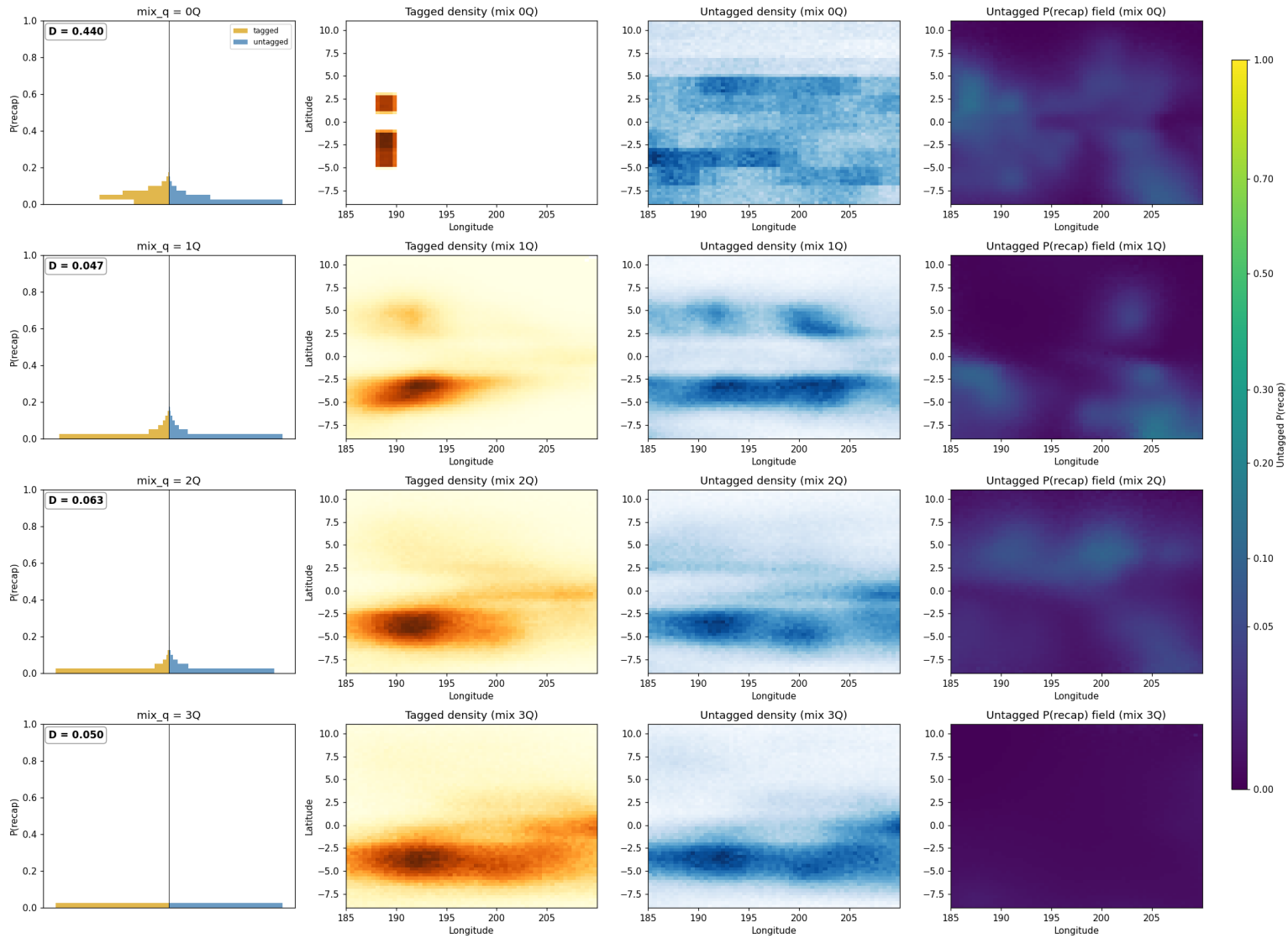
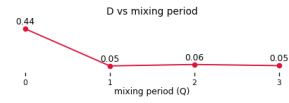


5-region structure (region 3 and 4 separated)

Date	Region	Releases	Recaptures
15/11/2012	4	5754	2219
15/11/2010	4	5320	1755
15/11/2011	4	2636	749
15/05/2009	3	2530	330
14/02/2012	3	1922	503
15/11/2011	3	1188	291
15/08/2009	2	139	49
15/08/2008	2	37	2



Region 4 | 2010-11-15 | 5320 tags | 19 cohorts | 42-95 cm



Mixing period (h)	D (m²/s)
0	0.22
1	0.17
2	0.10
3	0.11

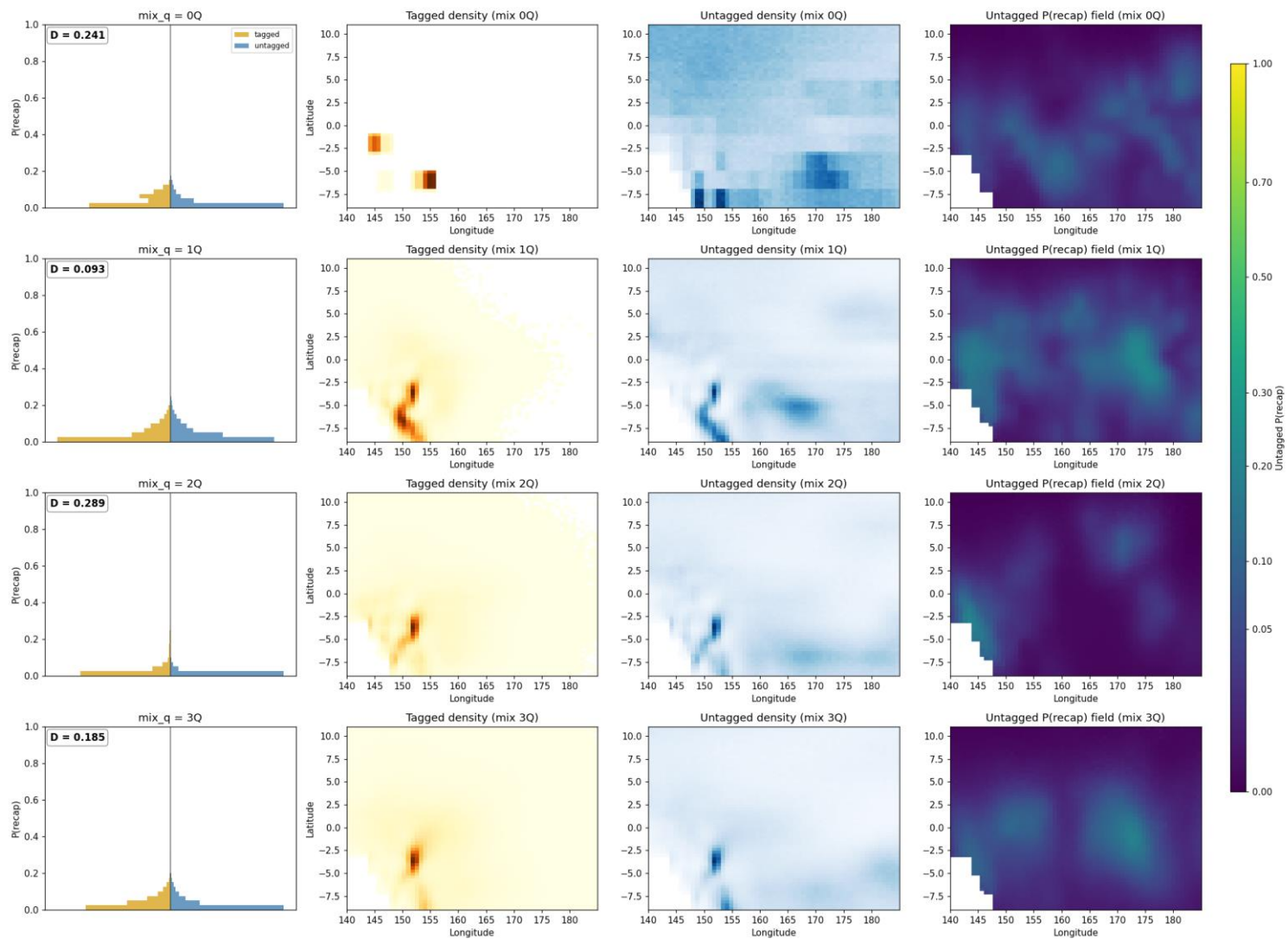
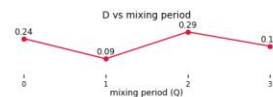


D vs mixing period

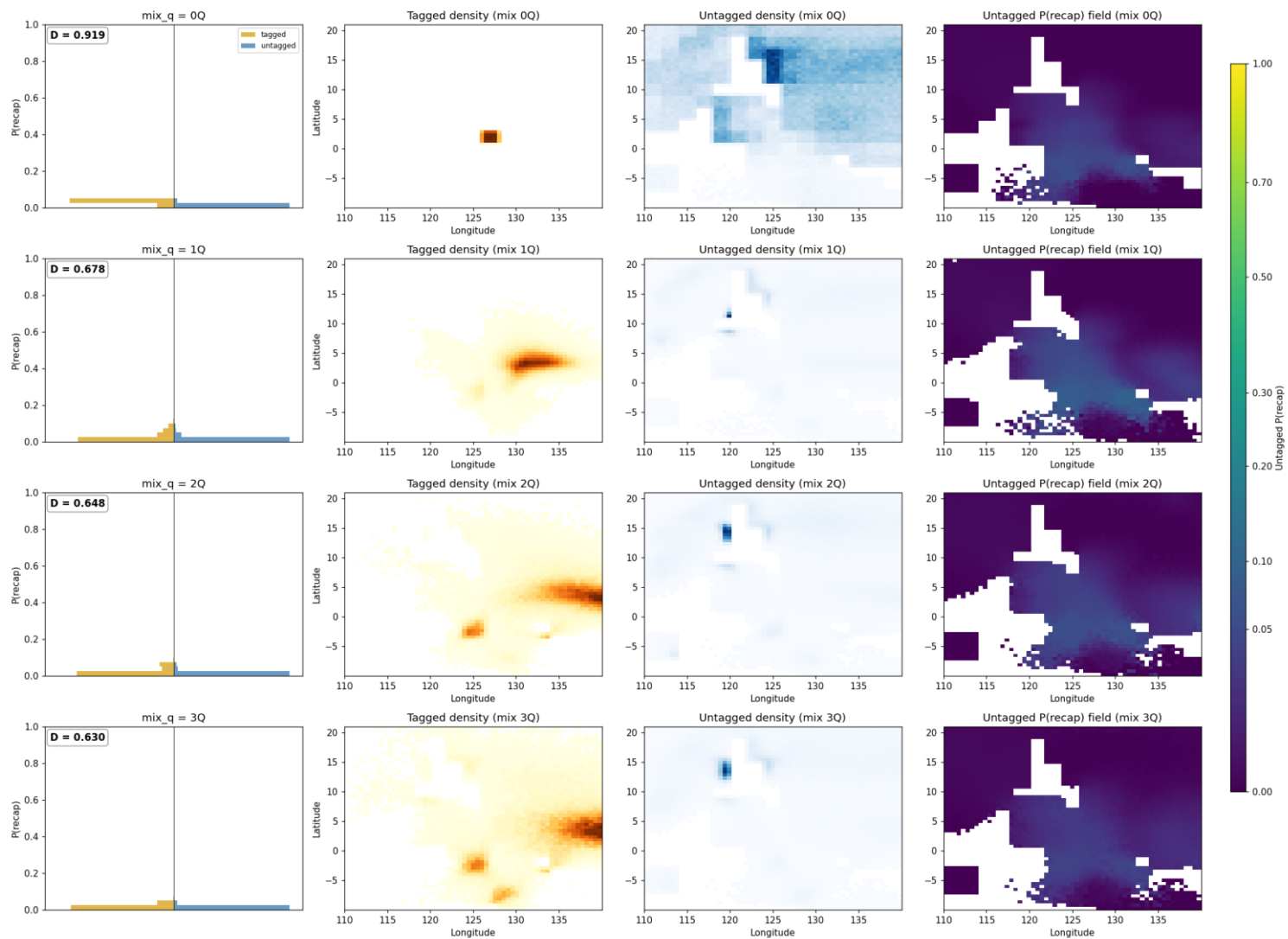
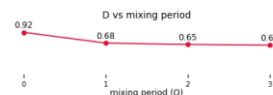
mixing period (Q)	D
0	0.42
1	0.11
2	0.14
3	0.04



Region 3 | 2012-02-14 | 1922 tags | 11 cohorts | 30-65 cm



Region 2 | 2009-08-15 | 139 tags | 2 cohorts | 30-34 cm



Region 2 | 2008-08-15 | 37 tags | 2 cohorts | 30-34 cm

