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A SPATIOTEMPORAL PETERSEN-TYPE MODEL FOR SKIPJACK IN THE EPO

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CONTENTS

1. SUMMARY

A novel spatiotemporal Petersen-type model is presented and applied to tag recapture data for skipjack tuna (SKJ, *Katsuwonus pelamis*) in Eastern Pacific Ocean (EPO). The model provides estimated absolute biomass utilising available tag recapture and catch data as well as movement patterns estimated by a tagging movement model (SAC-13-08, SAC-14 INF-E). Estimated biomass of SKJ in the EPO is between 0.29 and 3.6 million tons. The uncertainty associated with quarterly biomass estimates is generally high but strongly dependent on the number of available tag recaptures. Available data seems to be sufficient for 5 quarters with coefficients of variation (CV) between 0.3-0.6 and with enough time in between to have negligible correlation between the biomass estimates. The results suggest high preference and highest biomass at varying longitudes around the equator.

2. INTRODUCTION

Tag recapture data are a valuable data type that not only allow estimation of important life history parameters such as growth and mortality rates, movement patterns, and stock lineation, but also provide information about the total abundance (Bailey, 1951; Chapman, 1954). For example, the Petersen-type model utilises information from the proportion of recaptured individuals that have tags to estimate total animal abundance (Seber, 1986). While the estimation of total abundance by the Petersen-type model in a non-spatial context is quite straight-forward and only requires tag recapture and catch data, it is more challenging in a spatial context and requires additional information such as transition probabilities. In the case of skipjack tuna (SKJ, *Katsuwonus pelamis*) in the eastern Pacific Ocean (EPO), tag recapture data has been used to estimate growth rates (e.g. Maunder, 2001) and fishing mortality (e.g. Maunder 2012) but has not been used to estimate stock size at time of writing of this report to the knowledge of the authors. Tag recapture data has been used to estimate natural mortality rates in the western and central Pacific Ocean (Peatman et al., 2022) and used in integrated assessments (Castillo Jordan, 2022). This report introduces a spatiotemporal Petersen-type model for the estimation of total abundance based on tag recapture data and describes its application to available tag recapture and catch data for SKJ in the EPO. Required transition probabilities are estimated by the tagging movement model that has been developed to estimate movement patterns for SKJ in the EPO based on available tag recapture data (SAC-13-08, SAC-14 INF-E). The movement is described by a few parameters and flexible functions linking the advection (or taxis) and diffusion to environmental covariates such as water temperature or bathymetry (Thorson et al., 2021). If reliable effort information is not available, the model assumes uniformly distributed effort in space and time without reliable effort information. If reliable effort data is available, this information can be utilised in the estimation of movement patterns and stock biomass.

3. METHODOLODGY

3.1. Spatiotemporal Petersen-inspired model

The spatiotemporal Petersen-type model is inspired by the original Petersen method that assumes complete mixing between a tag-and-release event and a recapture event, and estimates the population size by $N=mC/x$, where N is the population estimate, m is the number of marked individuals, x is the number of recaptures, and C is the total catch. This estimator is derived simply by noting that if complete mixing has occurred then the fraction of tagged fish observed in the recapture event x/C is expected to be the same as the fraction of tagged fish in the population m/N. A natural statistical model, that would lead exactly to the Petersen estimator is: $x \sim Bin(C, m/N)$, where N is the only model parameter to be estimated, as x is the observation and C and m are known covariates. Assuming the catch C is large and the fraction of tags in the population is small, then the binomial model will be approximately equivalent to the Poisson model (Serfling, 1978): $x \sim Pois(Cm/N)$, which again will lead to the same well-known estimator. With multiple observations, we can account for overdispersion (compared to the Poisson distribution), by replacing the Poisson distribution with a negative binomial with the same mean value $\mu=Cm/N$ and an additional overdispersion parameter $\psi > 0$, such that the variance scales with the mean value as $\mu(1+\mu/\psi)$. This will be annotated as: $x \sim Nbin(Cm/N,\psi)$. The statistical modelling approach allows more flexibility in how the tagged population is modelled, including spatial distribution, and the assumptions about sampling.

Complete mixing typically does not occur in tagging experiments of fish populations. Therefore, the spatial distribution of releases and recaptures should be taken into consideration. Here, we describe an approach to take the spatial distribution into consideration within a Petersen estimator context. In this example, the stock area is divided into grid-cells i=1...G by 5x5 degree and the time is divided into quarters t=1...Q. The movement model provides the probability of moving between cells, as a GxG-matrix P_t of transition probabilities between cells at each time-step. This movement pattern is used to calculate the expected number of tagged fish available $T_{i,t,r}$ in each cell (i), at each time (t), from each tagging release event (r). Assuming complete mixing of tagged and untagged fish within each cell this leads to a Petersen inspired model of the recoveries of the tags. Considering the number of tagged fish caught $x_{i,t,r}$ in a specific cell i, at a specific time t, from a specific previous tagging event r. This number can be assumed to follow a binomial distribution: $x_{i,t,r} \sim Bin(C_{i,t}, T_{i,t,r}/N_{i,t})$ and since we know the catch and the expected number of tagged fish available, the only unknown is the population size within the cell. Notice that it is possible to have multiple observations within each cell at the same time if multiple previous release events are available. This Petersen inspired observation model can again be coupled with a spatial model to account for correlations and to provide estimates in cells and at times where no observations are available. The joint model is:

$$\log N \sim \mathbf{N}(\mu, \Sigma)$$

$$x_{t,i,r} \sim \mathrm{Nbin}(C_{t,i}\frac{T_{i,t,r}}{N_{i,t}}, \psi)$$

The covariance matrix Σ of $log(N)=(log(N)_{t,i})_{t=1 \ldots Q,\ i=1 \ldots G}$ is set up to represent the spatial neighborhood structure between the cells and the temporal structure. Such a spatio-temporal model accounts for the correlated nature of the abundance and uses this estimated correlation to provide population size estimates for cells and times without direct measurements (zero recoveries). Finally, the biomass estimate at each point in time is obtained by summing the estimated population sizes in all cells.

There are some important things to note about this Petersen inspired approach. The purpose of the approach is to avoid using effort information, and the post processing is not using the effort information. However, the model used to estimate movement based on the tagging data uses effort to predict recoveries. Fortunately, the estimated movement pattern appears insensitive to different effort assumptions, including uniform effort, so this may not be an issue of practical importance. If the same set of tags are used to estimate the movement pattern as are used in the post processing step, then the tagging information is used twice. The estimated movement pattern is relatively consistent to different sub-setting (using only archival tags or only conventional tags), but to be sure this reuse is not problematic a sensitivity run is included where the movement pattern is estimated only from archival tags and where the post processing is only using the conventional tags. The main issue with the Petersen inspired index of population size is that it reduces the observations used to estimate the index. In periods and areas where no tagging experiments are nearby it leads to indices that are very uncertain. Indices derived by this method are found in Figure 6 and selection to obtain near-independence is in Figure 7.

3.2. Biomass estimation with effort data

If reliable effort data is available, this information can be used for the estimation of the movement patterns as outlined in SAC-14 INF-E, as well as for the estimation of the index of the population size. Consider again the stock area divided into grid-cells i=1...G by 5x5 degree and the time divided into quarters t=1...Q. Within each cell and quarter, the observed catch $C_{t,i}$ and effort $E_{t,i}$ are known and the natural mortality rate (M) and fishing mortality rates ($F_{t,i}$) can be estimated by the movement model (SAC-14 INF-E). This approach assumes a relationship between E and F that is constant in time and space. Here, we compare three different relationships, (1) F = \lambda * E, where E \in {0,1}, i.e. E is either zero or 1 if effort is larger than 0 (“Binomial effort”), (2) F = \lambda * E (“Proportional effort”), (3) F = (\lambda_1 * I_1 + \lambda_2 * I_2), where I_k is an indicator field for effort in a pre-determined range leading to a flexible relationship between E and F with multiple breakpoints and slopes between the breakpoints (“Flexible effort”). The catch in each cell with positive effort given M and F can then be

$$C_{t,i} \sim Pois\left(\frac{F_{t,i}}{(F_{t,i} + M)}(1 - e^{-F_{t,i}-M})N_{t,i}\right)$$

predicted by the Baranov catch equation, where the biomass in each grid cell and at each time step and $N_{t,i}$ is the only quantity being estimated. A spatio-temporal model is set up to get a combined estimate of the entire area and to account for observation noise. The model is:

$$\log N \sim \mathbf{N}(\mu, \Sigma)$$

$$C_{t,i} \sim \mathrm{Nbin}(\frac{F_{t,i}}{F_{t,i}+M}(1-e^{-F_{t,i}-M})N_{t,i}, \psi)$$

With same assumptions w.r.t. structure of correlations in time and space as the Petersen inspired approach. The downside of this approach is that it is based on effort information, which may not be considered to be a useful predictor of fishing mortality as is the case for catch-per-set of skipjack tuna in the purse seine fishery. Nevertheless, different assumptions regarding the relationship between E and F lead to similar relative abundance trajectories. Indices calculated this way can be found in Figure 10.

The framework is implemented as a software package using the Template Model Builder (TMB; Kristensen et al. 2016) and R 4.0.2 (R Core Team 2020).

4. DATA

The spatiotemporal Petersen-type model requires spatiotemporal tag-recapture data, transition probabilities, spatiotemporal catch data and additional information such as the natural mortality rate and immediate and continuous tag shedding and non-reporting probabilities/rates.

4.1. Transition probabilities

The movement probabilities are based on the spatiotemporal tagging model that describes movement as an advection-diffusion process (SAC-13-08, SAC-14 INF-E). The advection component is based on a habitat preference function that is defined as a smooth function of sea surface temperature (SST) and the kinetic energy of the water (EKE) based on monthly environmental fields and a 5°x5° grid. The results suggest a stronger preference for areas along the equator corresponding to intermediate SST and high EKE (Figure 1A). The resulting advection is towards areas of higher preference (Figure 1B). These results are consistent between a model using both archival and conventional tags and models using only one of these tagging types (Figure 1). Diffusion was estimated as a constant rate in space and time and around 14 degree^2/quarter. In contrast to the consistent advection component, estimated diffusion varied considerably between the models with the different tagging types and ranged from 4 degree^2/quarter (archival data only) to 22 degree^2/quarter (conventional data only).

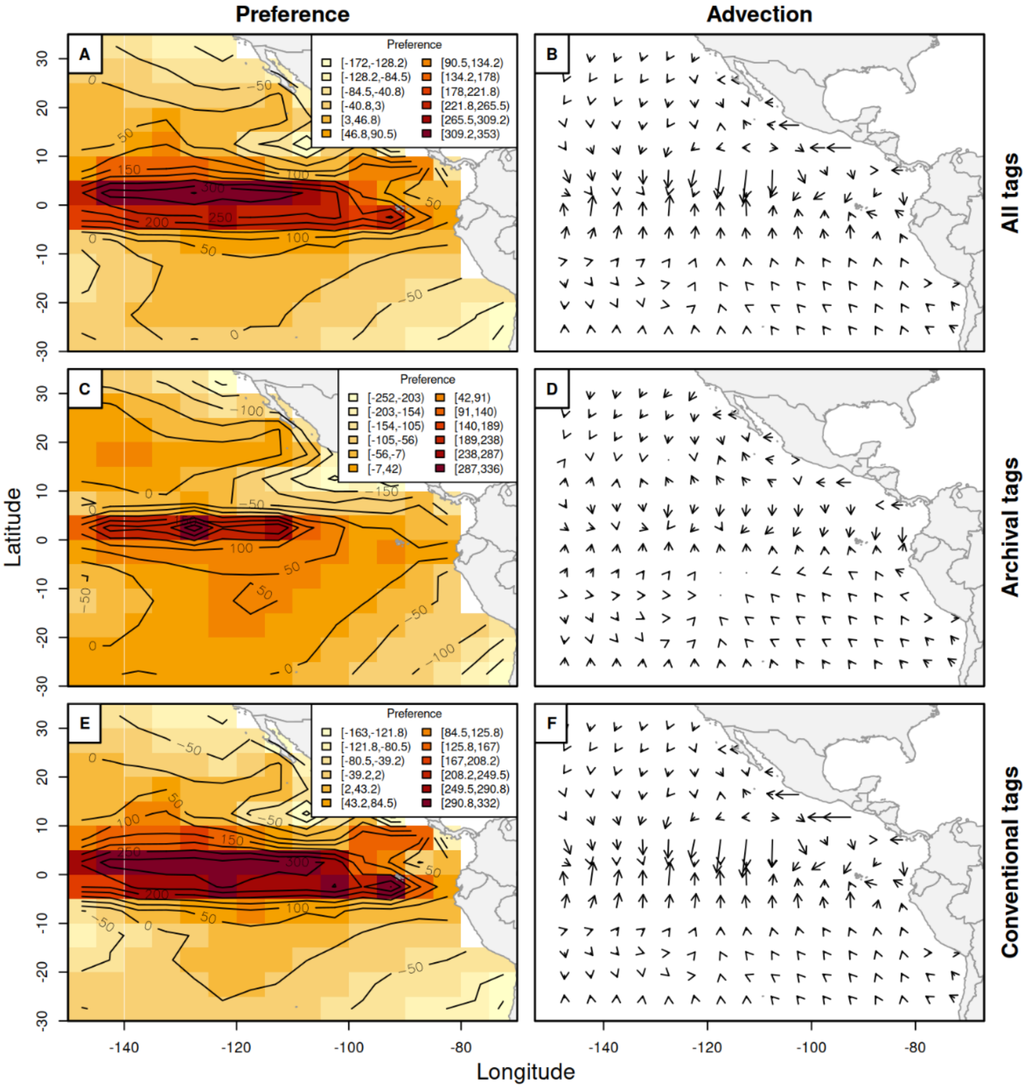


FIGURE 1. Average annual habitat preference and advection in 2022 for the baseline model (A,B) and alternative models using only archival (C,D) or conventional tagging data (E,F).

While other environmental fields such as the mixed layer depth or passive advection due to currents might also inform the movement of SKJ in the EPO, the results for these fields were less robust, i.e. showing various habitat preference functions for different model settings. In contrast, models with either only SST or only EKE resulted in overall similar preferences for intermediate SST and high EKE and diffusion (Figure 2G-J). Estimating spatially variable diffusion as a function of SST and EKE affected the habitat preference and predicted similar diffusion in the core area with most data (around the equator) and lower diffusion at extreme latitudes (Figure 2C-F). However, model estimates were considerably more uncertain with spatially variable diffusion. The sensitivity of the biomass estimates on various assumptions regarding the tagging movement model were explored and are presented below.

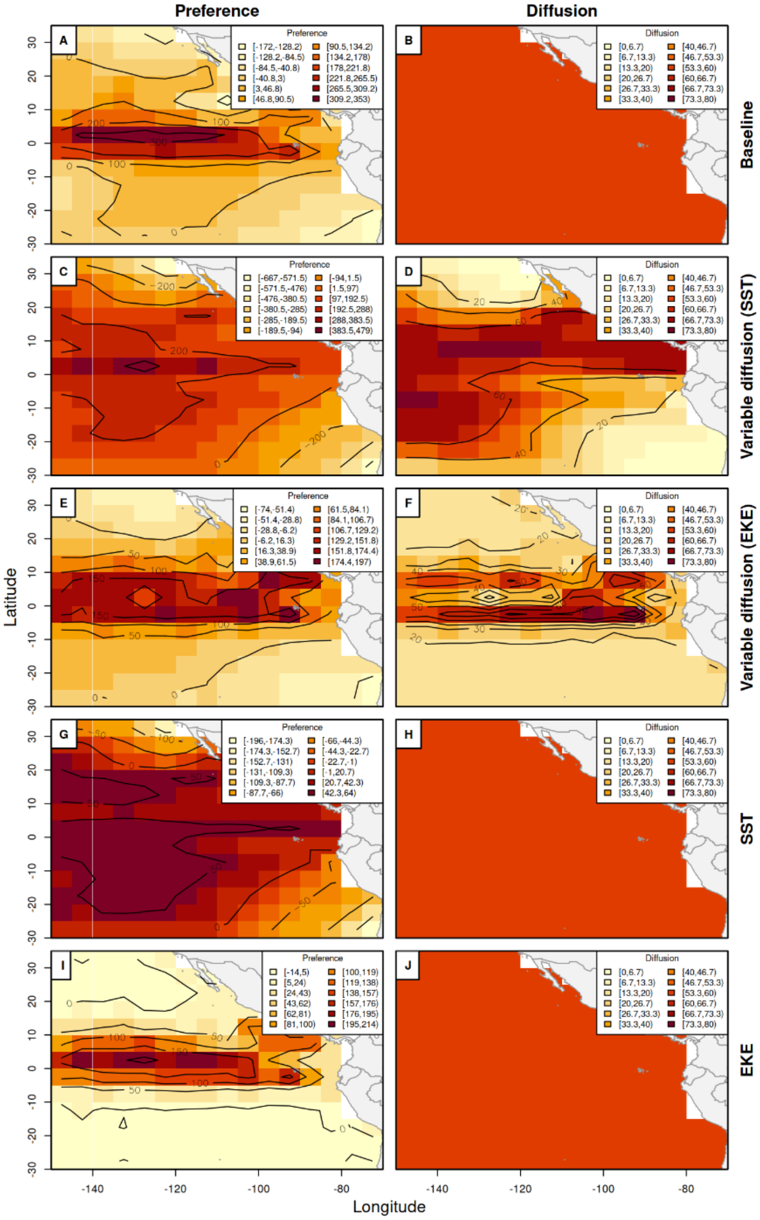


FIGURE 2. Average annual habitat preference and diffusion in 2022 for the baseline model (A,B) and alternative models with variable diffusion as a function of SST (C,D) and as a function of EKE (E,F), as well as a model based on SST only and with constant diffusion (G,H) and based on EKE only with constant diffusion (I,J).

4.2. Tag recapture data

While the tagging movement model with the Kalman filter utilises the tag recovery information in continuous space and time, the observed tag releases and recoveries must be discretised for the tagging biomass model. We discretised the observed tag releases and recoveries for a 5°x5° grid and quarterly time steps.

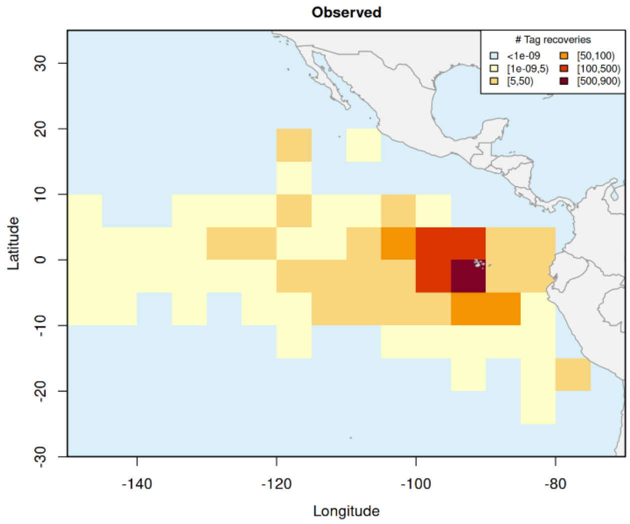


FIGURE 3. Total number of observed number of tag recoveries per 5°x5° grid cell over the whole study period (2000-2022).

The expected number of tag recoveries from a specific tagging event was calculated using estimated transition probabilities and assuming a survival probability. As no information on fishing mortality is available and fishing effort is not considered a useful predictor, we assume survival is only dependent on natural and tagging-related mortality. The natural mortality rate was assumed to be 2.02 year^{-1}, corresponding to the average natural mortality over all age classes assumed in the stock assessment model. Tagging-related mortality is assumed to correspond to a probability of 15%. In addition to the survival probability, tag loss and non-reporting might also affect the expected number of tag recoveries. The values assumed for these immediate probabilities and continuous rates are presented in Table 1. The sensitivity to the assumed natural mortality and shedding and non-reporting rates is presented below.

TABLE 1. Immediate and continuous natural mortality, tag-related mortality, tag loss, and non-reporting probability and rates assumed in the spatiotemporal Petersen-type model.

Type	Time period	Immediate (probability)	Continuous (Rate [year^{-1}])
Natural mortality	2000-2023		2.02
Tag-related mortality	2000-2023	0.15	0
Tag loss	2000-2023	0.01375	0.095
Non-reporting	2000-2018	0.3	
	2019-2023	0.1425	

Given these rates and the transition probabilities, the expected number of tag recoveries can be calculated for the same grid and time step as observed recoveries (Figure 4).

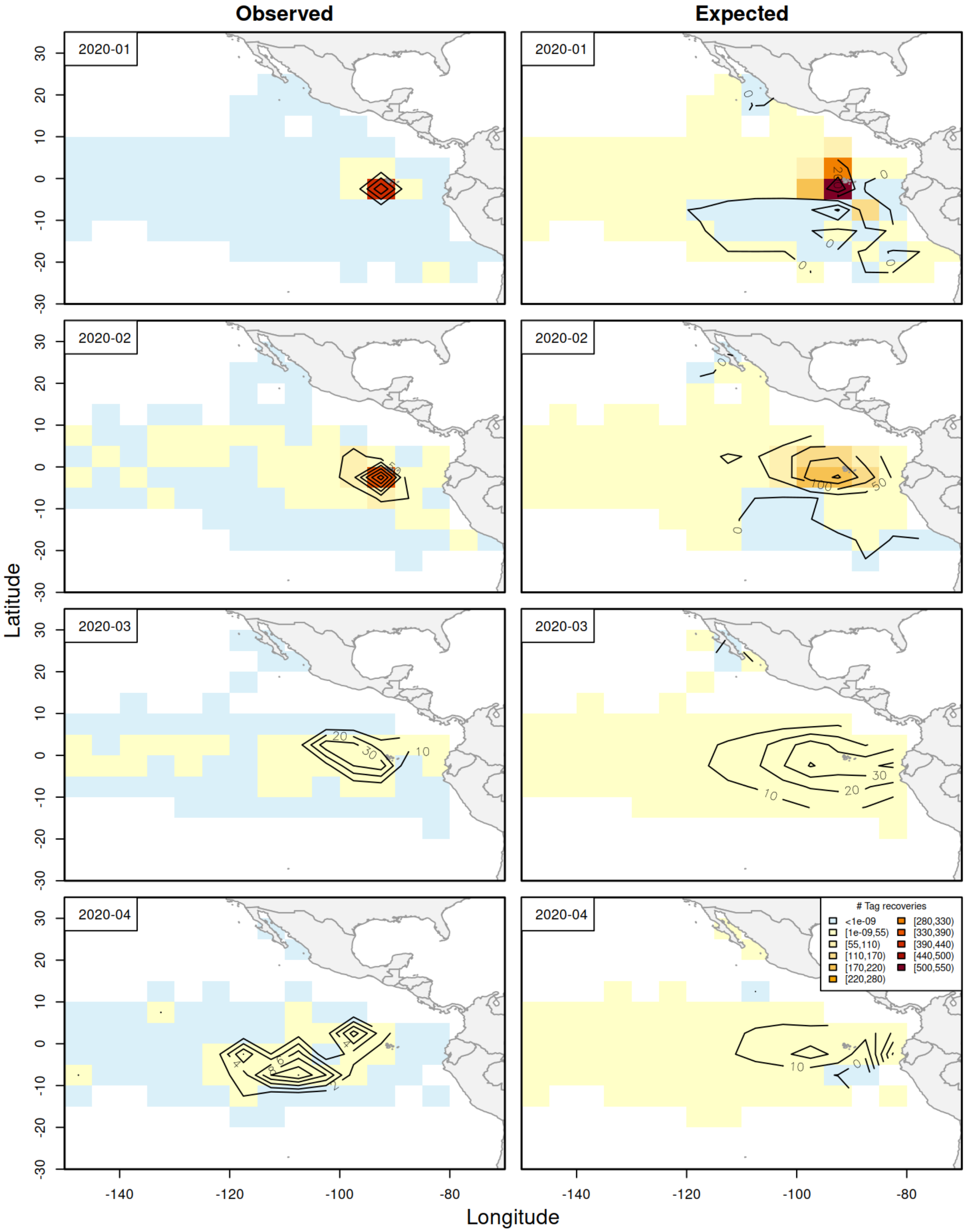


FIGURE 4. Observed and expected number of tag recoveries per 5°x5° grid cell and quarter for 2020.

4.3. Catch data

Catch information of purse seiners was available from 2000 to 2023 as the biomass in metric tons on a fine spatial resolution (1°x1° grid), per day, and fleet (floating object associated sets (OBJ), unassociated sets (NOA), dolphin-associated sets (DEL)), and vessel size (class). For the spatiotemporal Petersen-type model, the catch was aggregated to the total catches on a 5°x5° grid per quarter (Figure 5).

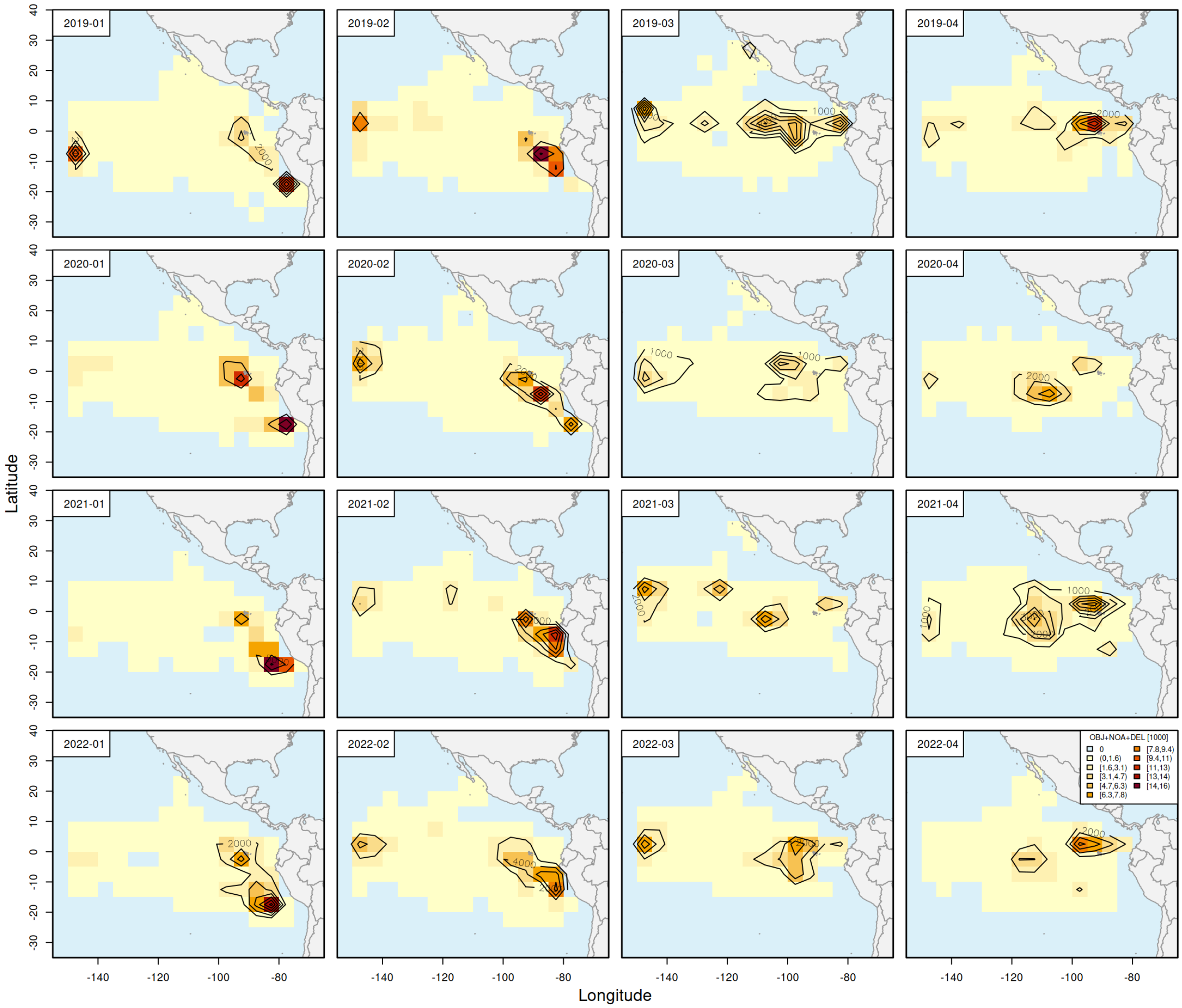


FIGURE 5. Quarterly catches for all purse seine fleets in thousand tons per 5°x5° grid cell from 2019-2023.

5. RESULTS

Biomass estimates for SKJ in the EPO based on the biomass tagging model range between 290 thousand and 3.6 million tons during the period from 2000 to 2023. Estimates for the core area of commercial fisheries vary between 220 thousand and 2.2 million tons (Figure 6). However, most of these estimates are highly uncertainty and therefore unreliable. Estimates with moderate CVs (<= 0.6) range from 0.22 to 1.44 million tons.

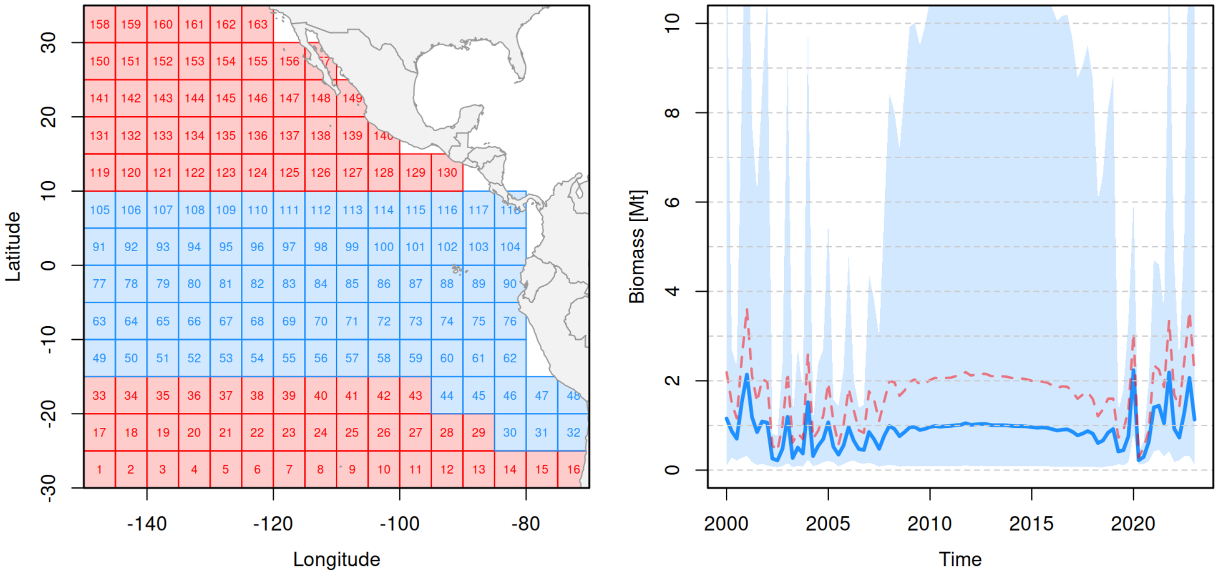
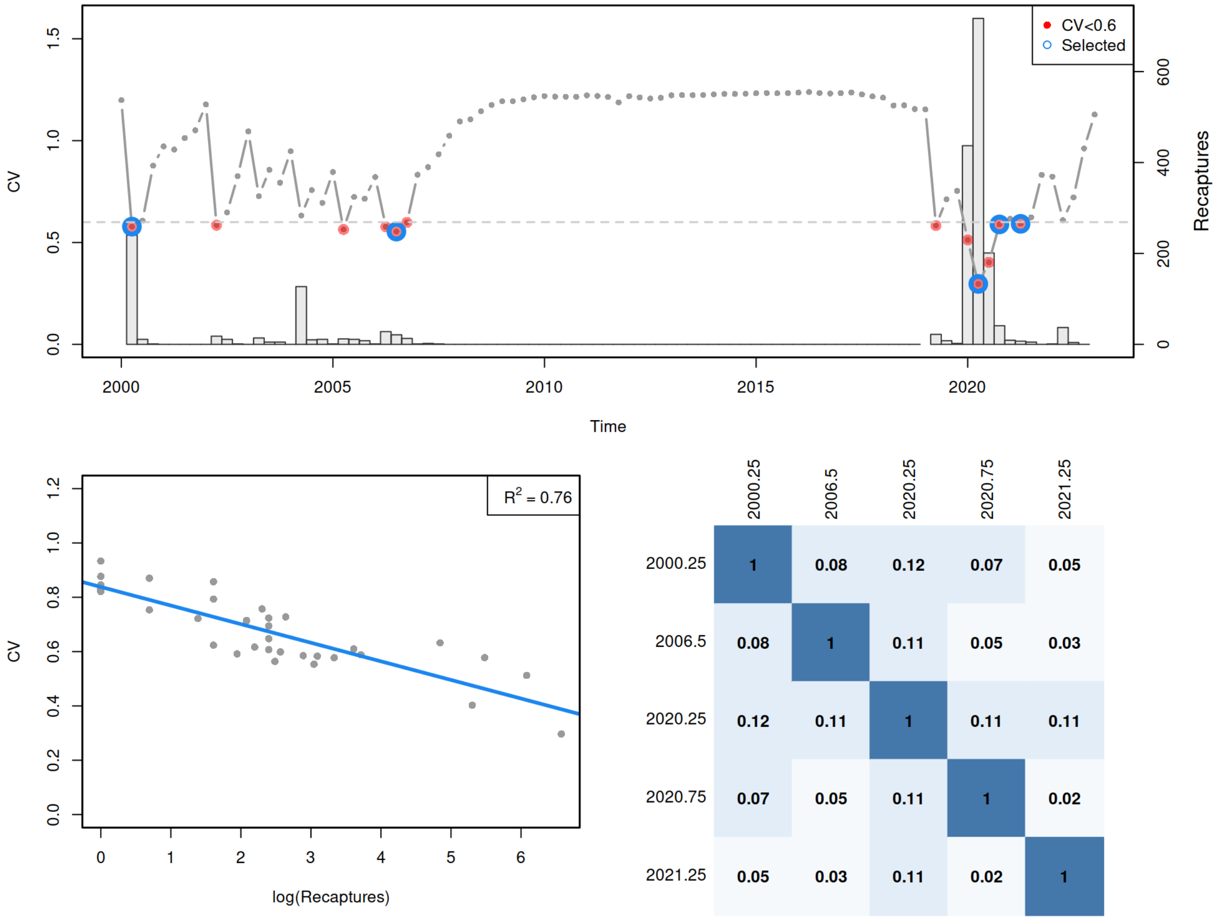


FIGURE 6. Spatial grid for the spatiotemporal Petersen-type model for SKJ in the EPO (A) and estimated total biomass per quarter in million tons (B). The red dashed line corresponds to the biomass summed over the whole grid (red and blue grid cells), while the blue line corresponds to the total biomass in the core area (blue grid cells). The shaded blue area corresponds to the 95% confidence intervals of the biomass in the core area.

The results indicate large uncertainty associated with the biomass estimates up to a CV of 1.4, particularly for biomass estimates in years with limited or no tagging data. For example, the period from 2008 to 2018 is characterised by large uncertainty as no tagging events took place during this period. This is also indicated by the strong correlation between the number of recaptures and the uncertainty of the biomass estimates ($R^2 > 0.7$; Figure 7). Out of twelve data points with a CV below 0.7, we identified five biomass estimates with low CVs (0.3-0.6) and low correlation coefficients (<0.13) allowing to use the biomass estimates as independent biomass estimates in the stock assessment model (Figure 7).



	2000.25	2006.5	2020.25	2020.75	2021.25
2000.25	1	0.08	0.12	0.07	0.05
2006.5	0.08	1	0.11	0.05	0.03
2020.25	0.12	0.11	1	0.11	0.11
2020.75	0.07	0.05	0.11	1	0.02
2021.25	0.05	0.03	0.11	0.02	1

FIGURE 7. Coefficient of variation (CV) for the biomass estimates and the number of tag recoveries per quarter (A), correlation between the uncertainty (CV) and the logarithm of the number of recaptures (B), and the correlation matrix of the selected biomass estimates (C). The red circles indicate the biomass estimates with a CV<0.7 and the blue circles indicate the estimates with lowest CVs and low correlation (<0.13).

The biomass estimates for these quarters show reasonable uncertainty and consistent patterns across a wide range of scenarios (Figure 8). From tested sensitivity scenarios, natural mortality rates were the most influential parameters with 25% larger natural mortality rates leading on average to 34% lower biomass estimates and 25% lower rates leading to 65% larger biomass estimates (Figure 8C).

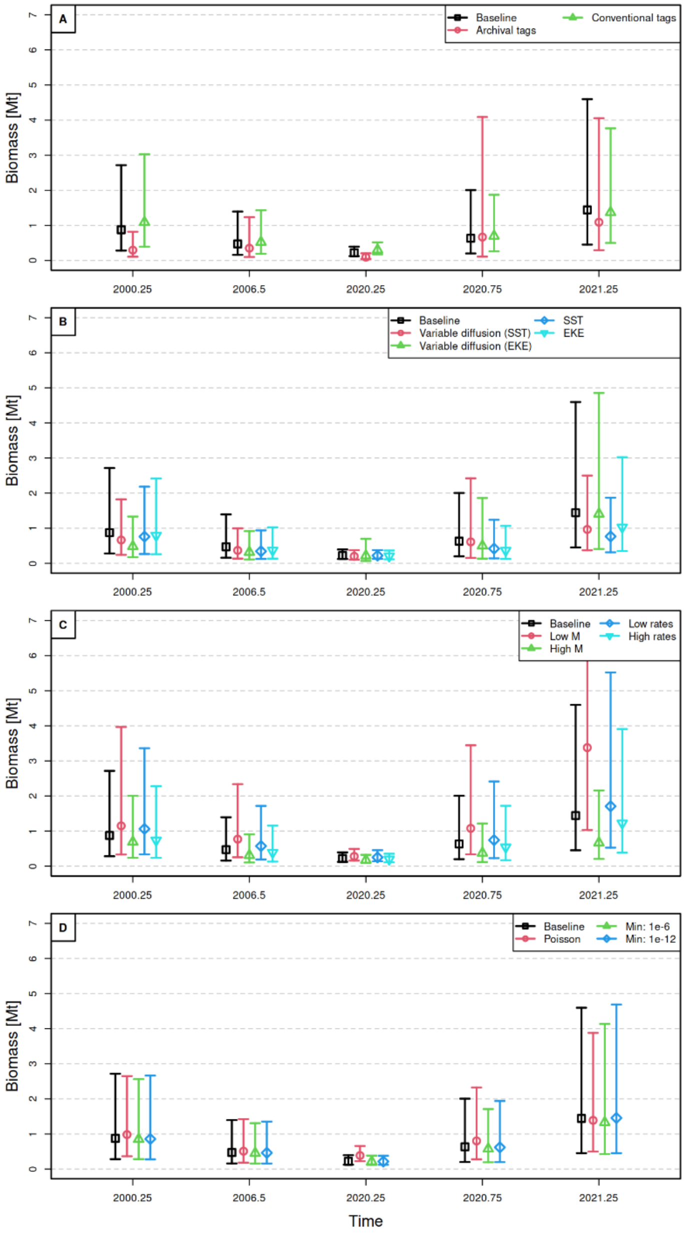


FIGURE 8. Estimated biomass in million tons for the selected quarters and movement probabilities based on archival or conventional tags only (A), with various assumptions regarding the advection and diffusion component (B), different assumptions regarding the natural mortality and shedding and non-reporting probabilities/rates (C), and using the Poisson distribution and smaller and larger cut-offs for the minimum number of expected recoveries (D).

The logarithm of the selected biomass estimates with associated lower and upper 95% confidence intervals (CI) are provided in Table 2.

TABLE 2. Selected biomass estimates for the core distribution area of SKJ in the EPO (Figure 6) based on the spatiotemporal Petersen-type model.

Year	Quarter	log(Biomass)	Lower 95% CI	Upper 95% CI	sd(log(Biomass))
2000	2	13.68	12.55	14.81	0.58
2006	2	13.06	11.98	14.15	0.55
2020	2	12.3	11.72	12.88	0.3
2020	3	13.36	12.2	14.51	0.59
2021	2	14.18	13.02	15.34	0.59

The estimated spatiotemporal distribution shows the highest biomass at varying longitudes around the equator (Figure 10). The uncertainty maps indicate large uncertainty at lower and higher latitudes in line with the spatial distribution of available tagging information (Figure 3).

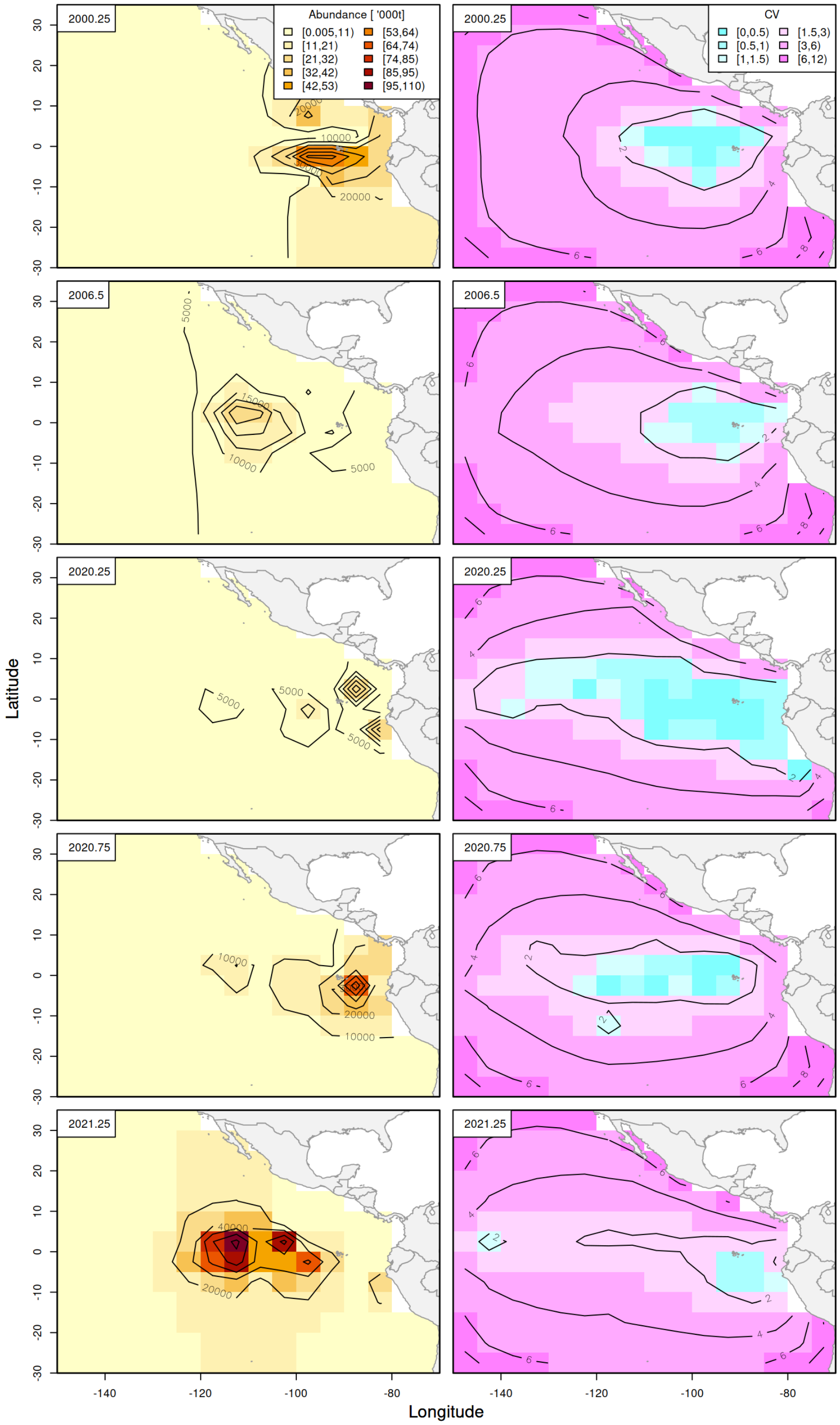


FIGURE 9. Estimated biomass per grid cell in thousand tons (first column) and the coefficient of variation (CV) per grid cell (second column) for the selected years.

6. DISCUSSION

This report introduces a spatiotemporal Petersen-inspired method that estimates fish abundance in space and time. Moderately reliable estimates of biomass for SKJ in the EPO are between 0.29 and 3.6 million tons. Most estimates are characterised by large uncertainty that is strongly correlated with the number of recaptures. Nevertheless, the biomass estimates in five quarters had acceptable uncertainty and correlation. The CV of the biomass estimates in the selected quarters ranges between 0.3 and 0.6 and the correlation is below 0.13, a commonly used threshold for almost independence of observations in spatial contexts (Lindgren et al., 2011). The estimates are relatively robust to a range of assumptions regarding the estimation of transition probabilities by the tagging movement model such as spatially variable diffusion or different environmental covariates informing the habitat preference. By contrast, the results revealed that the biomass estimates are sensitive to the assumed natural and tagging-related mortality rates and immediate and continuous shedding and non-reporting probabilities/rates. The probabilities and rates used here correspond to the best currently available information and to the values used in the stock assessment model for SKJ. The temporal trend over the whole period is likely less reliable given the large uncertainty in some quarters and the nature of the spatiotemporal Petersen-type model assuming the spatiotemporal average biomass in areas or periods without tag recaptures. The estimated biomass is likely most representative of the vulnerable stock biomass, i.e. the length classes that are caught by the purse seine fleets and thus represented in the catch and tagging data. The overall length distribution of purse seine catches and archival and conventional tags ranges from 25 cm to 80 cm with two distinct peaks at lengths around 45-50cm and 65-70cm for the tag recapture data and a wide length distribution with highest density around 40-50 cm for the purse seine catches (Supplementary Figure S1).

The approach presented here utilises the conventional tagging data multiple times: For the estimation of the natural mortality rate and shedding/non-reporting probabilities/rates, for the estimation of the transition probabilities, and the estimation of the biomass. However, the results highlight that the transition probabilities and biomass estimated based on the movement tagging model with archival tags only are comparable to the results based on the archival and conventional tags combined. The main difference is a lower diffusion estimate for the model with archival tags only. As described above, using available effort data allows us to estimate fishing mortality and, thus, a more certain biomass estimate over the spatial domain and time period. However, the absolute biomass becomes then dependent on the reliability of the effort information and assumed/estimated relationship between E and F (Figure 10A). Nevertheless, regardless of the assumptions of the E~F relationship, estimated biomass with and without effort information spans similar ranges. Moreover, the relative biomass trend is almost identical across a wide range of assumed E~F relationships (Figure 10B). The relative biomass (mean 1) estimates of the biomass model with the flexible effort model are provided in Supplementary Table S1.

There are several avenues for future development of the model. The Petersen model assumes that only natural and tagging mortality influence the tagged population. This is because effort data is not used to represent fishing mortality. However, fishing mortality is an important component of the tag dynamics. Since the spatiotemporal numbers are directly modelled and spatiotemporal catch data is available, then this can be used to represent the spatiotemporal fishing mortality for both the movement and biomass estimation, which could be estimated simultaneously. It is not clear if using the estimated numbers for fishing mortality would use information needed for estimating abundance or movement, but use of archival tagging data to inform movement might overcome this possible issue. Another improvement of the model would be to stratify the model by size to account for size specific fishing mortality and growth.

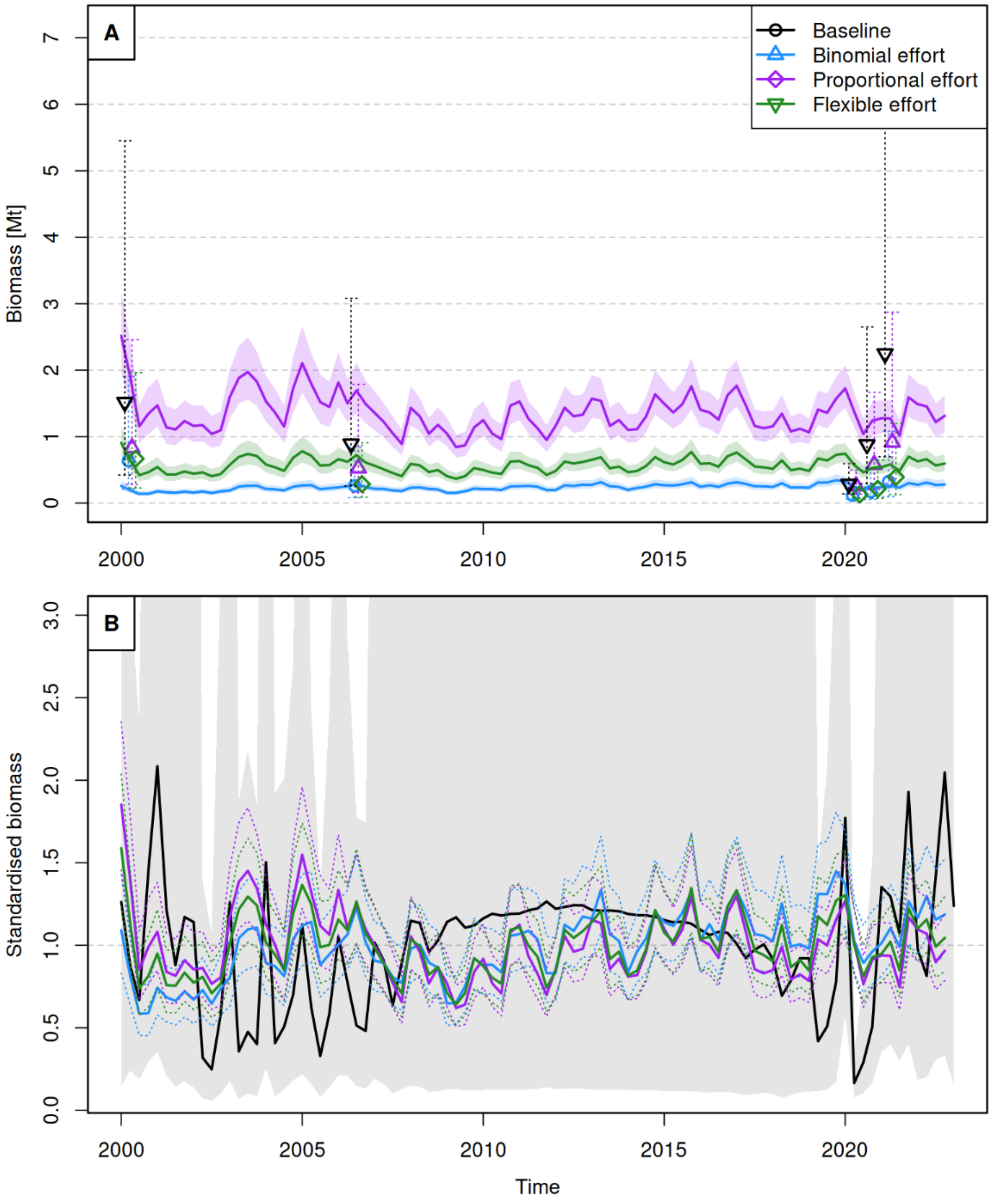


FIGURE 10. Estimated absolute biomass in million tons for the selected years with and without using effort information for the whole spatial domain (B) and standardised biomass without effort and various assumptions regarding the effort~fishing mortality relationship (A). While the lines in A are biomass estimates based on the biomass model using various effort assumptions, the plotting symbols are based on the Petersen-type model and the transition probabilities and natural mortality estimated by the tagging movement model utilising effort information.

7. ACKNOWLEDGMENTS

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9. SUPPLEMENTARY MATERIAL

TABLE S1. Relative biomass estimates (mean 1) per year and quarter for SKJ in the EPO based on tagging biomass model using flexible effort assumption.

Year	Q1	Q2	Q3	Q4
2000	1.59	1.13	0.74	0.81
2001	0.95	0.76	0.75	0.83
2002	0.77	0.81	0.71	0.77
2003	1.01	1.22	1.3	1.24
2004	1.02	0.94	0.85	1.19
2005	1.37	1.25	0.99	1
2006	1.16	1.09	1.27	1.07
2007	0.99	0.89	0.8	0.71
2008	1.04	0.99	0.82	0.87
2009	0.71	0.64	0.71	0.92
2010	0.87	0.8	0.77	1.09
2011	1.11	1	0.93	0.74
2012	0.85	1.09	1.04	1.09
2013	1.14	1.21	0.92	0.96
2014	0.82	0.85	0.98	1.21
2015	1.08	1.02	1.14	1.35
2016	1.04	1.05	0.96	1.23
2017	1.33	1.15	0.97	0.94
2018	0.9	1.12	0.87	0.91
2019	0.85	1.18	1.12	1.27
2020	1.3	1	0.81	0.93
2021	0.95	1.02	0.85	1.23
2022	1.1	1.16	0.99	1.04

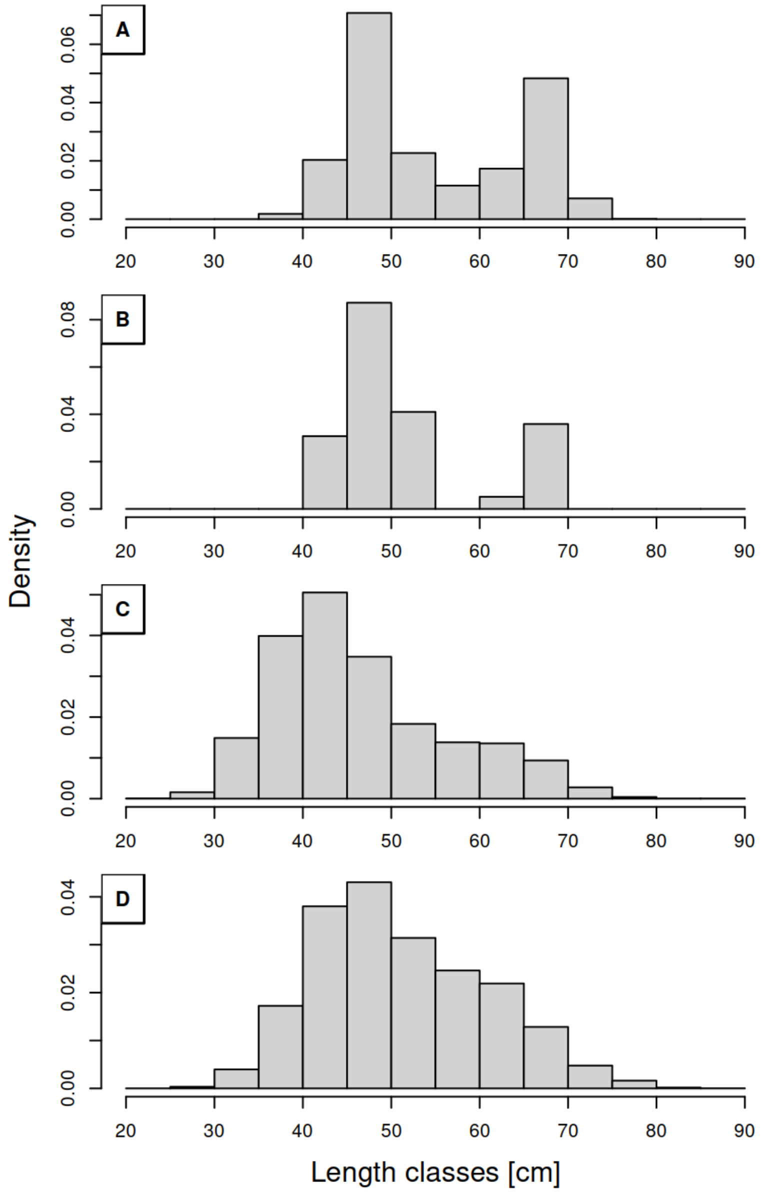

FIGURE S1. Length distribution of conventional tags (at time of release, A), of archival tags (at time of release, B), of NOA catches (C), of OBJ catches (D).