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Broadbill swordfish movements and transition rates across stock assessment spatial regions in the western and central Pacific

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Executive summary

Movement rates between management zones are a key input into spatially disaggregated fisheries assessments, yet often information on the movement of key species of interest is sparce or lacking. While conventional tagging has been useful in understanding directed movement, it does not provide detail on movements between deployment and recapture locations, and in association, detailed movement and exchange across spatial regions of interest. Electronic tagging is a tool which has vastly improved our ability to track the movements of oceanic marine fishes and therefore improve understanding of movements. The most recent stock assessment for swordfish across the western and central Pacific Ocean, conducted in 2017, utilised estimates of diffusive mixing (movement rates) across a spatial boundary at 165°E (currently used to define spatial regions within the stock assessment) derived from deployment of tags on the species. However, these estimates are recognised as being highly uncertain, with uncertainty varying substantially depending on the subset of tagging data included and the method used to estimate movement. Further, the assessment identified that depletion was notably influenced by assumptions on diffusion between spatial regions within the model. In an effort to better resolve the movement rates of swordfish across the spatial boundaries utilised in stock assessments and more broadly across the western and central Pacific Ocean, we used a continuous time Hidden Markov model, informed by data derived from electronic tag deployments and conventional tag releases and recaptures, to describe movement and estimate transition rates for the species under the current spatial structure used in assessments across 165°E. In consultation with stock assessment modelers, we also investigated movement under a scenario where a second spatial boundary was placed at 170°W. This paper outlines the results from these analyses and provides updated information on movement rates that we suggest should be considered for future stock assessments of swordfish in the western and central Pacific Ocean.

Introduction

Fisheries dynamics are influenced by the effects of spatial heterogeneity, which can drive spatial differences in age structure, maturity, growth, movement and stock structure and fleet characteristics (e.g. selectivity and effort, see Cadrin and Secor 2009, Guan et al. 2013). Spatial heterogeneity is particularly relevant to the assessment and management of many pelagic species (e.g. tunas, billfish, sharks), as these species are highly dispersed and capable of large-scale movements and associated fisheries also cover large areas and potentially target a number of stocks or sub-populations (Jardim et al. 2018).

Stock assessments for many large pelagic species attempt to account for some sources of spatial heterogeneity associated population and fishery components (e.g. Fournier et al. 1998). However, stock assessment model boundaries and any internal partitioning are frequently defined on the basis of fishery data available and the political realities of management (e.g. country and regional management jurisdictions), rather than the spatial characteristics of the fish population.

Implementation of spatially explicit models requires information on the movements of individuals from which rates of emigration and immigration can be estimated (e.g. Punt et al. 2000). Observations of movement from conventional tag data may not be sufficient for describing and estimating movement at the spatial and temporal scales required, and may be confounded with mortality, tag reporting rates and the distribution of the fishing fleet. Inappropriate or ill-founded assumptions about spatial structure and movement have the potential to lead to inappropriate advice for fisheries management (Cadrin and Secor 2009).

The development of electronic tagging technologies and associated methods to describe the movement of marine species over extended temporal and spatial scales has provided important insights into the movements, migratory routes and habitats of importance of pelagic species at increasingly finer resolutions (Evans et al. 2008; Patterson et al. 2008; Evans et al. 2014; Patterson et al. 2018). Yet, despite rapid advances in both the technologies and the methods used to detail the movements of pelagic species, direct application of these data into stock assessments or for estimation of fishing parameters is still rare (Eveson et al. 2012).

Broadbill swordfish (*Xiphias gladius*; hereafter referred to as swordfish) have a widespread geographical distribution throughout temperate, subtropical and tropical regions and are important target and by-catch species for domestic coastal and distant water longline fleets within the western and central Pacific Ocean (WCPO) (Ward 2000; Molony 2005). Distributions of individuals have been observed to vary latitudinally, with the seasonal extension and retraction of warmer waters into higher latitudes and variability in prey distributions (Palko et al. 1981). There also appears to be heterogeneity in the movements of individuals, with fewer males occurring in colder, higher latitudes than females (Palko et al. 1981). Investigations of catch data and molecular material suggest that there is some population structure within swordfish in the Pacific Ocean at the basin-scale, with low levels of mitochondrial gene flow (Reeb et al. 2000). More recent analyses utilising next-generation genomic methods and cutting-edge modelling approaches to investigate the connectivity of swordfish suggest that at least within the Coral Sea/Tasman Sea region, that there is little genetic differentiation between swordfish caught at different locations (Evans et al. 2021). More recent work including an expanded number of sample sites (presented in SC17-SA-IP-12) identifies little evidence of discernable genetic differentiation between samples collected from eastern Australia, Norfolk Island, New Zealand and the Cook Islands.

The most recent stock assessment for swordfish across the WCPO, conducted in 2017 (Takeuchi et al. 2017), was spatially structured into two regions. The delineation of these two regions at 165°E followed earlier assessments and was based on analyses of data derived from electronic tags deployed on the species (Evans et al. 2012). Estimates of diffusive mixing (movement rates) across the spatial boundary at 165°E were incorporated into the assessment model acknowledging that these estimates were highly uncertain at the time of development, with uncertainty varying substantially depending on the subset of tagging data included and the method used to estimate movement. The 2017 assessment further identified that depletion was notably influenced by assumptions on diffusion between spatial regions within the model, with increasing levels of movement implying notably more pessimistic results in terms of depletion and increased levels of fishing mortality.

In an effort to investigate whether the movement rates of swordfish across the spatial boundaries utilised in stock assessments and more broadly across the WCPO could be better resolved, we developed continuous time Hidden Markov models, to estimate quarterly transition rates for swordfish. Using the same electronic tagging dataset and conventional tagging data described in Evans et al. (2012), we re-estimate transition rates across the longitudinal boundary at 165°E used in the 2017 stock assessment. In consultation with stock assessment modelers conducting the stock assessment for swordfish in 2021 (see Ducharme-Barth et al. 2021; SC17-SA-WP-04), we also investigate transition rates under a scenario where a second spatial boundary was placed at 170°W.

Methods

Data

Position estimates derived from Pop-up Satellite Archival (PSAT) tags (N=78) and release and recapture position from conventional tag releases (N=18) as described in Evans et al. 2012, 2014) were included in this analysis.

Conventional tags were released from the Australian Eastern Tuna and Billfish Fishery and from New Zealand, with releases predominantly occurring across the period 2000-2005 (Table 1).

Most of the electronic tagging data is associated with the period 2006-2010 (Table 1) with releases occurring across four spatial zones

1. The Australian Eastern Tuna and Billfish Fishery (ETBF) (N=41)
2. The Cook Islands (N=6)
3. New Zealand (N=11)
4. The southern Western Pacific Ocean (N=10).

Table 1. Number of positions estimates from combined PSAT and conventional tag deployments by month of the year.

Month of year	Year															
	1990	1995	2000	2001	2002	2003	2004	2006	2007	2008	2009	2010	2011	2012	2017	2018
Jan	0	0	0	2	0	0	0	0	42	8	38	20	0	1	0	0
Feb	0	0	0	0	0	0	0	0	57	14	54	19	0	0	0	0
Mar	0	0	0	0	0	0	0	0	46	53	43	36	0	0	0	0
Apr	0	0	0	0	0	0	0	1	22	53	57	20	0	0	0	0
May	1	0	0	0	0	0	0	0	16	68	42	19	1	0	1	0
Jun	0	0	0	0	0	0	0	0	10	79	35	20	0	0	0	1
Jul	0	0	1	0	1	0	1	9	3	101	11	33	0	0	0	0
Aug	0	0	0	0	0	0	0	4	5	124	0	10	0	0	0	0
Sep	1	0	0	0	1	0	1	27	0	104	26	8	0	0	0	0
Oct	0	1	2	0	0	0	2	51	0	69	24	28	0	0	0	0
Nov	0	1	0	1	0	0	2	71	6	74	11	11	0	0	0	0
Dec	0	0	0	0	0	1	3	85	53	45	49	0	0	0	0	0

Spatial Set up

Following the recent stock assessments carried out for swordfish in the Western and Central Pacific Commission (WCPFC) Area, spatial regions were demarcated by meridional divisions.

We considered two spatial configurations:

1. A two region model, as per the current assessment with a boundary at 165°E.
2. A three region model with the existing 165°E but with the addition of another boundary at 170°W

We did not consider north to south movement in this analysis.

Continuous time Hidden Markov Models.

We assume movements are described by a continuous time/discrete space Markov chain, but that we cannot allocate individuals to a given region with complete accuracy due to observation error due to imprecise geolocation data (see Evans and Arnould 2008). This situation requires with use of a Hidden Markov model (HMM) in continuous time (CTHMM).

The rates of movements between regions r are collected into a transition rate or generator matrix $\mathbf{G}$ whose individual elements g_{ij} (for $i \neq j$) give the rate departing from i and arriving at j. The diagonal of $\mathbf{G}$ is defined as:

$$g_{ii} = -\sum_{j \neq i} g_{ij}$$

For the case of two regions (as per the existing stock assessment) then we have:

$$\mathbf{G} = \begin{pmatrix} -\alpha & \alpha \\ \beta & -\beta \end{pmatrix}$$

To form the matrix of probabilities of $i \rightarrow j$ for a given time δt we compute the transition matrix:

$$\mathbf{\Gamma}_{\delta t} = \exp(\mathbf{G}\ \delta t)$$

Note that exp(.) is here the matrix exponential operator. A 2-state model has an analytical solution, however this is difficult to compute in situations with more than 2 states and so numerical techniques are required. Here we used the R library `expm` allowing investigation of a 2 region model (where an internal boundary was set at 165˚E within the stock assessment area) or a 3 region model (where internal boundaries were set at 165˚E and 170˚W within the stock assessment area; see below).

In the above, $\delta t = t_{i+1} - t_i$ is the time between successive observations; G is a generator matrix such that $\sum_i G_{ij} = 0,\ \forall\ i$; in other words the entries in each row of $\mathbf{G}$ sum to zero; and $\mathbf{\Gamma}_{\delta\ t}$ is a row stochastic Markov transition matrix describing the probability of transitions from state i to j over the period $\delta\ t$.

Therefore, in the stationary version of this model, the aim is to estimate the entries in $\mathbf{G}$ from observations in the form of:

$$x_{1:T}^{k} = \left(\{r_{t_1}, r_{t_2}, \delta t_{1,2}\}, \{r_{t_2}, r_{t_3}, \delta t_{2,3}\}, \dots\right)$$

where the notation r_{t_i} is the region the individual occupies at t_i, and $\delta t_{i,j}$ is the time elapsed (in days) between the observations of r_{t_i} and r_{t_j}, for the $k-$th individual's movements.

The log-likelihood for an individual swordfish is given by the algorithms described in standard Hidden Markov model texts (see Zuchinni et al. 2017; Patterson et al. 2017):

$$\log L_{k,T} = \sum_{t=1}^{T} \log\left(\phi_{t-1}\mathbf{\Gamma}(\theta)_{\delta t}\mathbf{P}(x_t^k, V(x_t^k))\right)$$

where $\phi_t = \Pr(S_t = s)$, $\mathbf{P}(x, V)$ is a m-vector of observation probabilities (described in the next section below).

The movement rate parameters are $\theta = \{g_{1,2}, g_{2,1}\}$ for a two region model, and $\theta = \{g_{1,2}, g_{1,3}, g_{2,1}, g_{2,3}, g_{3,1}, g_{3,2}\}$ for the 3 region model, where $g_{1,1} = -g_{1,2} + g_{1,3}$ and so on for the other two diagonal entries in $\mathbf{G}$.

We estimate shared parameters across N individuals so the objective function is therefore:

$$L(\theta)_{all} = \sum_{k=1}^{N} \log L_{k,T}$$

Incorporation of observation error

Estimation of movement in swordfish using geolocation is notoriously error prone due to individuals predominantly occupying deep waters during the day, with most time spent in surface waters where light can penetrate during the night (see Evans et al. 2014). This results in very little quality light data for the estimation of daily positions. Using position estimates derived from the R package “trackit” (Nielsen and Sibert 2007), longitude estimates were used to allocate an animal to a region within the model at a given time. We input the Kalman filter variance in longitude estimated within trackit, $\sigma_{i,x,t}^2 = \mathrm{Var}_i(x,t)$ into the model to account for geolocation error on the estimation of $x_1 \rightarrow x_2$ movement rates. We also used the estimated trackit variances to parameterize the observation error distribution as described in the following.

Given that the estimates from trackit are Gaussian ellipses, we approximate the error in the longitudinal component only using the cumulative distribution function of the Gaussian $\Phi(b, x_t, \sigma^2) = P(X_t <= b_t, \sigma^2)$, where b is the boundary, x_t is the estimated latitude with associated variance σ^2. This gives the probability that the position was west of a given boundary and so for a two-region model where the boundary was set at 165°E:

$$\mathbf{P}(x_t, V(x_t)) = \begin{cases} 1 - \Phi(b_1, x_t, \sqrt{V(x_t)} & \text{for Region 1} \\ \Phi(b_1, x_t, \sqrt{V(x_t)} & \text{for Region 2} \end{cases}$$

For a three-region model with boundaries set at 165°E and 170°W, b_1, b_2:

$$\mathbf{P}(x_t, V(x_t)) = \begin{cases} \Phi(b_1, x_t, \sqrt{V(x_t)} & \text{for region 1} \\ \Phi(b_2, x_t, \sqrt{V(x_t)} - \Phi(b_1, x_t, \sqrt{V(x_t)} & \text{for region 2} \\ 1 - \left(\Phi(b_1, x_t, \sqrt{V(x_t)} + \Phi(b_2, x_t, \sqrt{V(x_t)}\right) & \text{for region 3} \end{cases}$$

Free parameters were estimated using numerical minimization of the negative log-likelihood in R. The directly estimated parameters of the models are instantaneous rates. However, we require probabilities over a given duration (a quarter of the year). Therefore, to estimate confidence intervals on the quarterly transition probabilities, we used a parametric bootstrap to draw 1000 samples θ^* from:

$$\theta^* \sim \mathcal{N}(\widehat{\boldsymbol{\theta}}, \widehat{\mathbf{H}}^{-1})$$

where $\widehat{\boldsymbol{\theta}} = \{\hat{\alpha}, \hat{\beta}\}$ and $\widehat{\mathbf{H}}^{-1}$ is the negative Hessian matrix of the likelihood. Each of the θ^* was used to form a transition matrix $\boldsymbol{\Gamma}_{\delta t}$ with $dt = 365/4$.

The distributions of the off-diagonal elements were used to estimate the mean transition probabilities and associated 95% CIs.

Results

Tagging data

The time at liberty summary statistics of PSATs within each region is given in Table 2. Figure 1 shows the estimated movements from PSATs and release and recapture points of conventional tags. Also shown are estimates of longitude and latitude through time by region of release.

Table 2. Number of tag deployments from combined PSAT and conventional tag deployment by region of tagging along with median and 5-95% quantiles of the Time at Liberty (TAL) distributions. AU: Australia, CI: Cook Islands, NZ: New Zealand, WPO, southern western Pacific Ocean.

	N(tags)	Median (TAL)	5%	95%
AU	50	69	0.0590	260
CI	6	150	3.5	340
NZ	11	88	2.8	320
WPO	10	34	0.66	280

Model estimates

2 region model using current assessment regions

Low rates of movement between regions 1 and 2 were estimated by the 2-region CTHMM (Table 3). At a quarterly timescale, the model estimated approximately 3% flow from the greater ETBF (region 1) into the greater western and central Pacific ocean (region 2) and approximately 5% flow westward from region 2 → region 1 (Table 4). The uncertainty on westward flow was substantially higher with the upper confidence interval at 16% (Figure 2). This is likely to be due to the more extensive data size and within-year coverage from tag deployments in the ETBF (region 1).

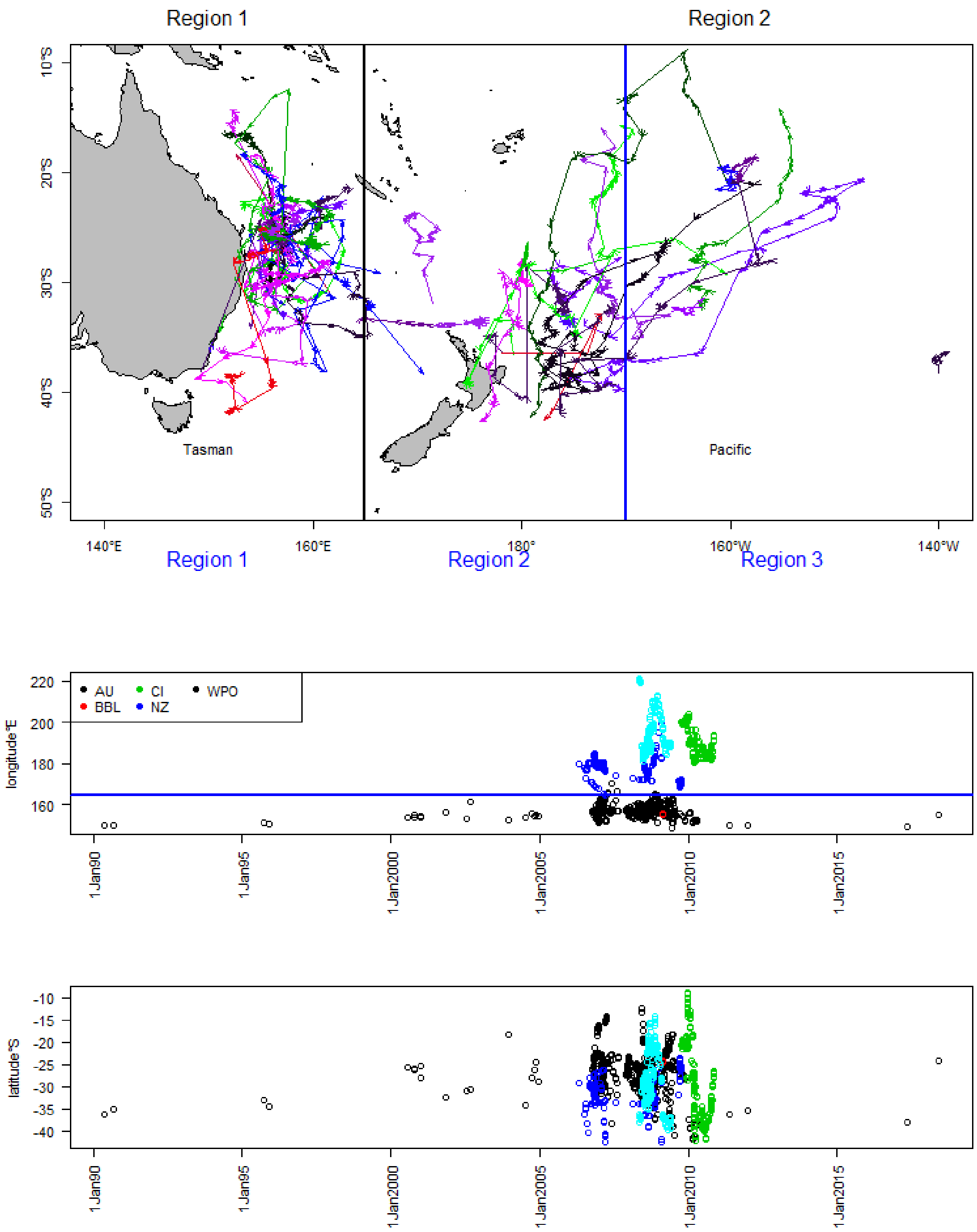

Figure 1 (top) movements from PSAT and conventional tags and spatial zones considered in the analysis. The 2-region model zones are denoted above the plot in black and the 3 -region model zones are below the plot in blue. (middle) estimated longitude by time coloured by release region (bottom) estimated latitude by time coloured by release region.

Table 3. Instantaneous rate parameters from the 2 region CTHMM.

Quantity	value	(SE)
$\ln\hat{\alpha}$	-8.3	0.71
$\ln\hat{\beta}$	-8	0.24

Table 4. Estimated quarterly transfer rates from the 2 region CTHMM.

Estimate	Value	CI
$\Pr(Region\ 1 \rightarrow Region\ 2)$	0.028	0.007 –0.072
$\Pr(Region\ 2 \rightarrow Region\ 1)$	0.047	0.0061 –0.15

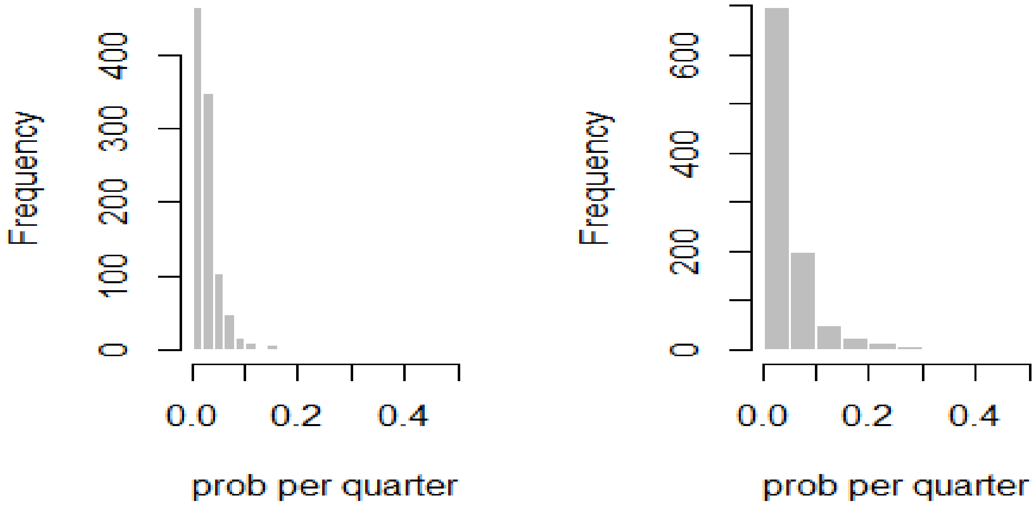

Figure 2. Distribution of quarterly transfer rates for the 2 region model (left: West / region 1 to East /Region 2; right: East / region 2 to West/region 1).

3 region model using an additional spatial boundary at 170˚W

Rates of transition in the 3 region model are shown in Table 5. Estimated quarterly transitions across the regions 1 → 1 and 2 → 1 were very similar to those estimated by the 2-region model. With the inclusion of a second boundary at 170˚W, the model estimated considerable movement across regions 2 → 3 (0.31) and very little movement across regions 2 → 1 (0.03). The estimated movements across regions 3 → 3 (0.51) and 3 → 2 (0.48) were relatively similar. This might indicate that swordfish in regions 2 and 3 are relatively well mixed, although it should be noted that these transition rates are calculated from much smaller numbers of tags than those across regions 1 and 2 and as a result have higher uncertainty (Table 6). Over the time period of a quarter, rates of movement between non-adjacent regions (i.e. region 1 → 3 and vice versa) was estimated to be very low (<0.01).

Table 5 Estimated quarterly transition rate for 3-region model. See figure 1A for regional boundaries.

	Region 1	Region 2	Region 3
Region 1	0.98	0.02	0.00
Region 2	0.03	0.66	0.31
Region 3	0.01	0.48	0.51

Table 6 Median and 95% CIs on connectivity between regions in the 3-region model. See figure 1A for regional boundaries.

	lower CI	median	upper CI
1→ 2	0.01	0.02	0.30
1→ 3	0.00	0.00	0.48
2→ 1	0.00	0.05	0.22
2→ 3	0.13	0.28	0.41
3→ 1	0.00	0.02	0.58
3→ 2	0.20	0.49	0.69

While these results are generally plausible, numerical instability encountered during the parametric bootstrap highlighted large uncertainties and that there is insufficient data to inform the model estimates of transitions between regions 2 and 3. As a result, the results of the 3 region model should be regarded as preliminary and requiring further investigation.

Discussion

On the basis of the 2 region model investigated here, quarterly transition rates between the two regions are lower than those currently used in the reference case model in the most recent swordfish stock assessment (Takeuchi et al. 2017). The use of alternative models where the population rapidly mixes as used in sensitivity analyses are not supported by the estimates calculated here.

Some care should be taken in interpreting or using these estimates as they are however highly uncertain for two main reasons:

1. The sample sizes of tags from which transition rates are estimated is fairly small. In particular, conventional tag recapture rates for swordfish are notoriously low. Further, there are well documented issues with PSAT retention (see Evans 2010) that result in biases in the length of time at liberty to short deployments. Although, in this data set, 52.5% of tags were of longer duration than 1 quarter of a year. Also, it is important to note that the spatial configuration of the releases is generally biased toward the western regions of the fishery (i.e. the ETBF). While deployments of PSATs in the ETBF were well spread through the year, this is not true for other deployment regions. This thereby limits any detection of intra-annual migration schedules from deployments outside of the ETBF. Better resolution of movements across spatial areas could be facilitated through further deployments of tags with both the spatial and temporal aspects of deployments needing to be carefully considered.

2. The process models developed here are very simple. While they mirror the structure of the current assessment, there is no accounting for size, intra-annual movement schedules or any other factors within the models. However, it is not clear that a more complex model would be estimable from the current data. This remains to be investigated in future analysis.

Our investigation of a scenario where an additional spatial boundary was added at 170°W(the three-region model) showed generally plausible results that suggest very little mixing between regions 1 and 3 (0% across regions 1 → 3 and 1% across regions 3 → 1. Again, however, there is considerable uncertainty in these estimates. Two potential contributors to this uncertainty are:

1. The limited amount of long-term data informing the eastern regions of the model and the general lack of widespread movement. This makes estimates of connectivity from non-adjacent regions over a quarter very hard to estimate.
2. In association, and as identified with the 2-region model, most of the data informing these models is biased to region 1 (55% of positions/ N=1073 positions). When the remaining 44% (N=867 positions) is then considered in relation to the boundaries included in the 3-region model, only 13% (N=255 positions) were contained in the eastern most region (region 3).

The observed difficulties in estimating variances in the 3-region model are also likely linked to the relatively low data coverage in region 3. These estimation issues and the high degree of uncertainty this implies, illustrate the need for further data collection across regions 2 and 3 and in particular, region 3.

Despite the issues noted above, the method we have demonstrated are able to combine conventional and PSAT data to estimate connectivity between assessment regions and provides an alternative approach to estimating transition rates between spatial sub-regions within stock assessments for swordfish. These methods could be re-applied if and when further movement data becomes available. They are also applicable to other species where tag data might be used to inform connectivity rates used in spatial assessment models. We would therefore invite the WCPFC Scientific Committee to consider the updated information on movement rates and the methods presented here in future stock assessments of swordfish in the western and central Pacific Ocean.

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