SCIENTIFIC COMMITTEE
NINTH REGULAR SESSION

6-14 August 2013
Pohnpei, Federated States of Micronesia

The spatial distribution of striped marlin in the SW Pacific Ocean Estimates from PSAT tagging data

WCPFC-SC9-2013/ SA-IP-09

Chambers M[1], T. Sippel[2], M. Domeier[3] and J. Holdsworth[4]

[1] Department of Agriculture, Fisheries and Forestry, Australian Bureau of Agricultural and Resource Economics and Sciences, GPO Box 1563, Canberra ACT 2601
[2] Fisheries Resource Division, Southwest Fisheries Science Center, National Marine Fisheries Service, 8901 Schaffer Road, La Jolla, CA, USA
[3] Marine Conservation Science Institute, 68-1825 Lina Poepoe Street, Waikoloa, HI 96738, USA
[4] Blue Water Marine Research, PO Box 402081, Tutukaka, NZ

The spatial distribution of striped marlin in the SW Pacific Ocean

Estimates from PSAT tagging data

M. Chambers[1], T. Sippel[2], M. Domeier[3], J. Holdsworth[4]

Information paper SA-IP-09
Ninth Regular Session of the WCPFC Scientific Committee
6–14 August, Pohnpei, Federated States of Micronesia

Abstract: We present graphical summaries of modelled output derived from data provided from satellite telemetry tags attached to 53 striped marlin moving through the southwest Pacific Ocean. Most were tagged with popup satellite archival tags (PSAT), many were also double tagged with satellite-linked radio tags (SLRT), a few only carried SLRT. The marlin were captured and released from recreational vessels fishing off the east coast of Australia, Tasman Sea and the north coast of New Zealand between 2003 and 2008. PSAT derived geopositions were reconstructed with two different algorithms which use time-stamped solar irradiance and sea surface temperature data to estimate geopositions with moderate accuracy (approximate precision: longitude = ±0.5˚ and latitude longitude = ±1.0˚). Accuracy of SLRT position estimates range from approximately ± 150m to greater than ± 1000m. The temporally irregular observations of geoposition typically returned from PSAT and SLRT can complicate interpretation of standardized spatial occupancy (ie. home range, kernel density, etc). To simplify this, a Bayesian state-space model was used estimate movements at regular intervals (daily) while taking geoposition uncertainty into account. Regularized geoposition estimates were estimated by generating samples from posterior distributions of the daily location of striped marlin given individual longitude, latitude and sea surface temperature. Using the regularized estimates, summaries of estimated overall monthly residence of striped marlin in the southwest Pacific Ocean by 1 degree square of latitude and longitude are provided as well as daily posterior medians of longitude and latitude for each of the 53 tagged striped marlin. Model outputs and summaries of monthly habitat provide insights into population structure and can be used further in subsequent analysis of stock structure and movement dynamics.

[1] Department of Agriculture, Fisheries and Forestry, Australian Bureau of Agricultural and Resource Economics and Sciences, GPO Box 1563, Canberra ACT 2601
[2] Fisheries Resource Division, Southwest Fisheries Science Center, National Marine Fisheries Service, 8901 Schaffer Road, La Jolla, CA, USA
[3] Marine Conservation Science Institute, 68-1825 Lina Poepoe Street, Waikoloa, HI 96738, USA
[4] Blue Water Marine Research, PO Box 402081, Tutukaka, NZ

This publication (and any material sourced from it) should be attributed as: Chambers M, Sippel T, Domeier M, Holdsworth J 2013, The spatial distribution of striped marlin in the SW Pacific Ocean – Estimates from PSAT tagging data, WCPFC-SC9-SA-IP-09.

Department of Agriculture, Fisheries and Forestry
Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES)
Postal address GPO Box 1563 Canberra ACT 2601
Switchboard +61 2 6272 2010|
Facsimile +61 2 6272 2001
Email info.abares@daff.gov.au
Web daff.gov.au/abares

Acknowledgements
The New Zealand based tagging was supported by funding from the New Zealand Marine Research Foundation, Enterprise Motor Group, the University of Auckland and the Tagging of Pacific Pelagics program. Special thanks to the New Zealand sport fishing community, in particular the New Zealand Sport Fishing Council and its clubs, boat captains, anglers as well other scientists who contributed their knowledge, technical expertise and their fish. Particular thanks to Barbara Block, Peter Davie and Pete Saul for their contributions and insight. New Zealand based research was approved under permit AEC-R431, issued by the Animal Ethics Committee of University of Auckland School of Biological Sciences.

Tagging carried out by M. Domeier's group was made possible through the assistance of B. Billson, J. Gregory, N. Lucas, P. Offield, C. Offield and J. Pepperell. Major funding was provided by the Offield Family Foundation and the George T. Pfleger Foundation.

Contents

1 Introduction

Stock structure of striped marlin (*Kajikia audax*) in the Pacific Ocean is uncertain (Purcell and Edmands 2011), with population substructure in different regions of the Pacific suggested by different lines of evidence, including genetic analyses (Purcell and Edmands 2011) and electronic tagging analyses (Domeier 2006, Sippel et al., 2011). Within the southwest Pacific Ocean, population substructure is an open question, and was a source of uncertainty in the striped marlin stock assessment of Davies et al. (2012). Separate foraging grounds for striped marlin are thought to exist off the east coast of Australia and the north coast of New Zealand (Domeier 2006, Sippel et al 2011). The extent of mixing between members of these populations is of interest for assessment and management purposes. Existing satellite telemetry data provide an opportunity to investigate population structure and movement within the southwest Pacific Ocean. This paper presents summaries of movement model output aimed at estimating the spatial distribution and movement of striped marlins in the southwest Pacific Ocean.

Electronic tagging data were collected from 53 striped marlin tagged from recreational vessels fishing out of Eastern Australia, the Tasman Sea, and northern New Zealand (Domeier, 2006; Holdsworth, et al., 2009; Sippel et al., 2007; Sippel et al., 2011). Of these, 10 marlin were tagged off the east coast of Australia and 43 off the north coast of New Zealand or within the Tasman Sea. Most were tagged with popup satellite archival tags (PSAT), many were also double tagged with satellite-linked radio tags (SLRT), and a few carried only SLRT.

The temporally irregular observations of geoposition typically returned from PSAT and SLRT can complicate interpretation of standardized habitat usage. To simplify interpretation of spatial habitat utilization derived from temporally irregular and spatially noisy observations of striped marlin location, Bayesian state-space models were fitted to the telemetry data to smooth out excess noise in individual observations of latitude and longitude as well as to provide an objective method of estimating the location of the tagged fish on many days when latitude and/or longitude data were missing. These models were fitted using WinBUGS (Spiegelhalter et al., 2003), and provided an indication of the uncertainty in the location data via posterior distributions for each daily latitude and longitude estimate. It was necessary to fit a range of different models because the different location methods the data were derived from having different degrees of precision. Moreover some of the data were received having already been modelled by Kalman Filters. Model outputs and summaries of monthly habitat provide insights into population structure and can be used in subsequent analysis of stock structure and movement dynamics. Example pseudo-code and WinBUGS code are included in the appendix.

2 Method

PSAT derived geopositions were reconstructed with two different algorithms which use time-stamped solar irradiance and sea surface temperature data to estimate geopositions with moderate accuracy (approximate precision: longitude = ±0.5° and latitude longitude = ±1.0°) (Domeier et al., 2005, Nielsen et al., 2006). Accuracy of SLRT position estimates range from approximately ± 150m to greater than ± 1000m. These data were used as inputs into the Bayesian state-space model described below. Geopositions from the New Zealand based program (both light-level and SLRT) were regularized in a state-space model as described in Sippel et al (2011).

Estimates of striped marlin location summarised in this report are based on the posterior distributions of longitude and latitude from each fish between the day of release and the last day reliable data were received. These posterior estimates of daily striped marlin locations are summarised here in two ways.

1) Ten draws from the posterior distribution of each daily location (a pair of longitude and latitude) from each fish were randomly selected and disecretized to one-degree squares cell of latitude and longitude enabling comparison of the relative frequencies of the probability of striped marlin residence in each cell.

2) Tracks of individual striped marlin were estimated by posterior medians of daily longitude and latitude.

The relative frequencies of each 1-degree grid cell of striped marlin released in Australia are compared with those of striped marlin released in New Zealand in Appendix A. In Appendix B the cell frequencies are classified by month, or in some cases groups of months, in an attempt to highlight seasonal patterns in the location of striped marlin in the south west Pacific Ocean (Figures 4-10). These summaries include the locations of striped marlins tagged each year from 2003 to 2008. Maps indicating estimated tracks of individual tagged fish are grouped by month of release in Appendix C (Figures 11–19).

3 Results and Discussion

A number of patterns are revealed in the data. Briefly, the striped marlin which were mostly tagged in the late austral summer and autumn migrate north beginning in early autumn (Figure 1). It would appear there is some variation between individuals with regard to the commencement of migration, but by late winter most individuals are estimated to be at latitudes north of 30° south. Sippel et al. (2011) found evidence of possible movement and behaviour biases induced by the initial capture and/or attachment of telemetry tags to striped marlin lasting, on average, 16 days post-release. The interpretation of timing of movements and occupancy of spatial strata should be considered in light of this.

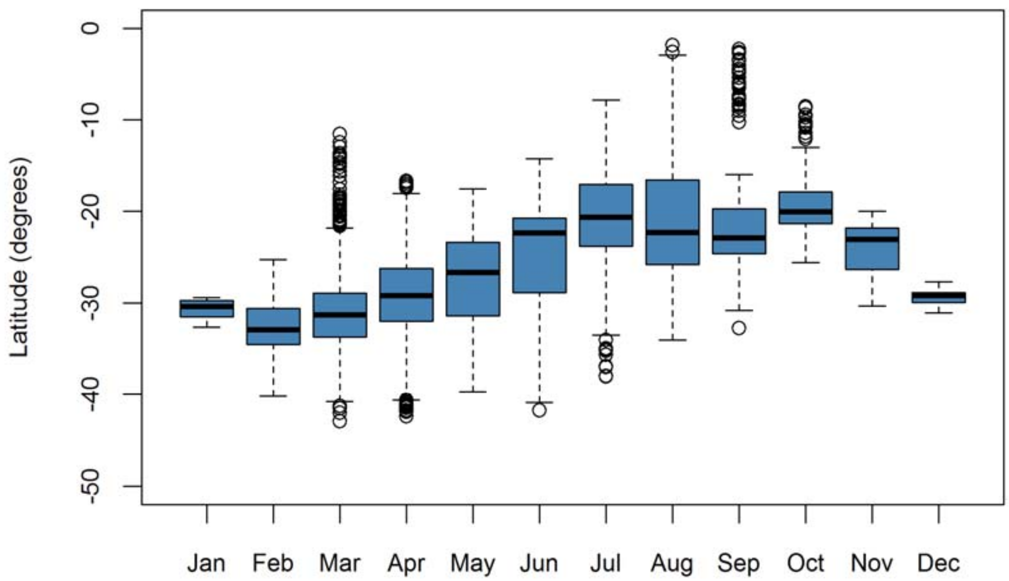

Figure 1: Boxplots of estimated daily latitude by month (all individuals).

The comparison between fish tagged in Australia and those tagged in New Zealand is somewhat limited because of the relatively few fish tagged off Australia. It would seem, however, that whereas the marlin migrating north from New Zealand vary appreciably according to longitude (Figure 3), striped marlin resident off Australia in the summer tended to remain quite close to the coastline during their northward migrations (Figure 2).

The typical pattern of individual striped marlin movement in the south west Pacific Ocean seems to incorporate only moderate or incidental east-west displacement. An appreciable stretch of the Tasman Sea, west of New Zealand at around 160° east is avoided by individuals on either side. The deflection of the East Australian Current at the Lord Howe Rise has been hypothesized as an oceanographic mechanism driving the apparent segregation of striped marlin found east and west of this area (Sippel 2009), and other factors including sea surface temperature and mixed layer depth may be influential as well. A number of individuals tagged east of the Lord Howe Rise moved into the central Pacific Ocean.

These data suggest groups tagged off New Zealand and Australia during summer/autumn mix to some degree on Coral Sea spawning grounds during winter/spring. Since only a minority of the satellite tags remained attached to their host fish long enough to transmit a return from the spawning grounds, these data do not provide much information about fidelity to feeding grounds.

This preliminary analysis of striped marlin movement using electronic tagging data provides some insight about spatial structure in southwest Pacific Ocean. However, sampling of striped marlin was biased, with most observations from the austral summer and autumn and insufficient observations from winter and spring. As previously noted, multiple methods were used to estimate and refine geolocations, and future work with these data should consider standardizing these geolocation methods to ensure continuity of data inputs for the Bayesian state-space model developed here. Furthermore, interpretation of the outputs is provisional and should be carried further with methods of objectively partitioning the data into spatial strata, such as regression trees. Another caveat to consider is that telemetry data such as these are auto-correlated, and this should be accounted for in future analyses.

A comprehensive study of the spatial structure of the striped marlin stock should ideally consider other types of data such as genetic, morphometrics, conventional tagging as well as electronic tagging data.

Appendix A - Comparison of Australian and NZ Releases

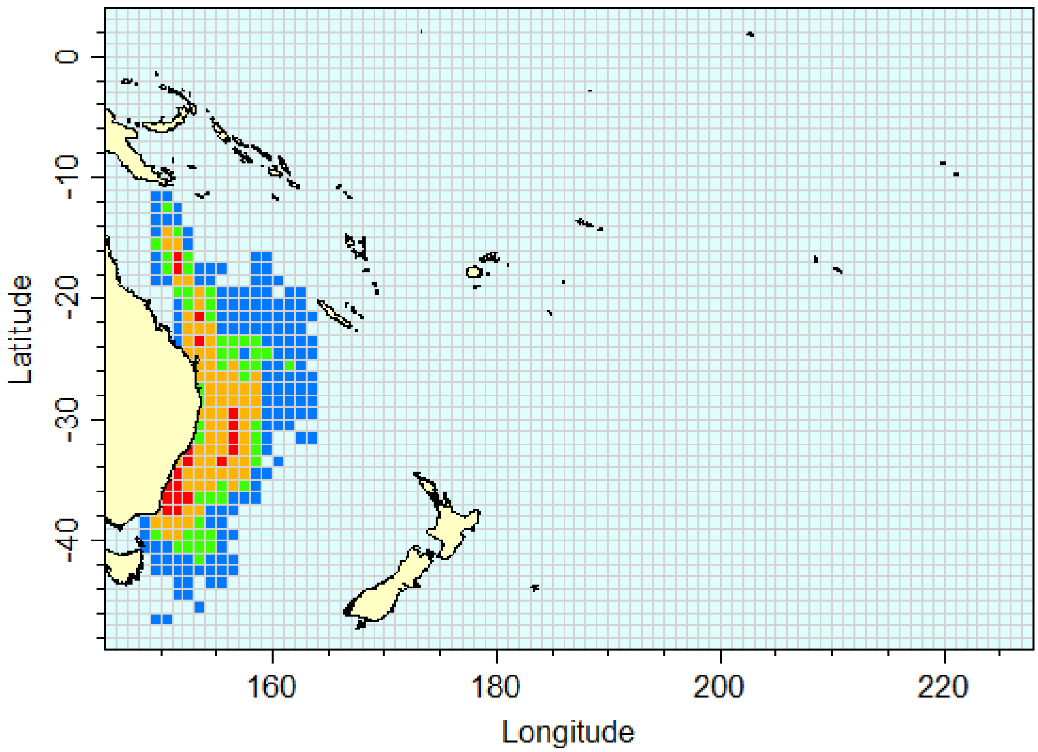

Figure 2: Posterior density of locations of striped marlins released in Australia across all months. Cells shown in red are the highest posterior density regions accounting for 25% of total estimated residence probability. The orange cells accounts for the next 50% of total estimated residence probability. The green, orange and red cells combined account for 90% of the total estimated residence probability. Note that the number of observations varies substantially between months.

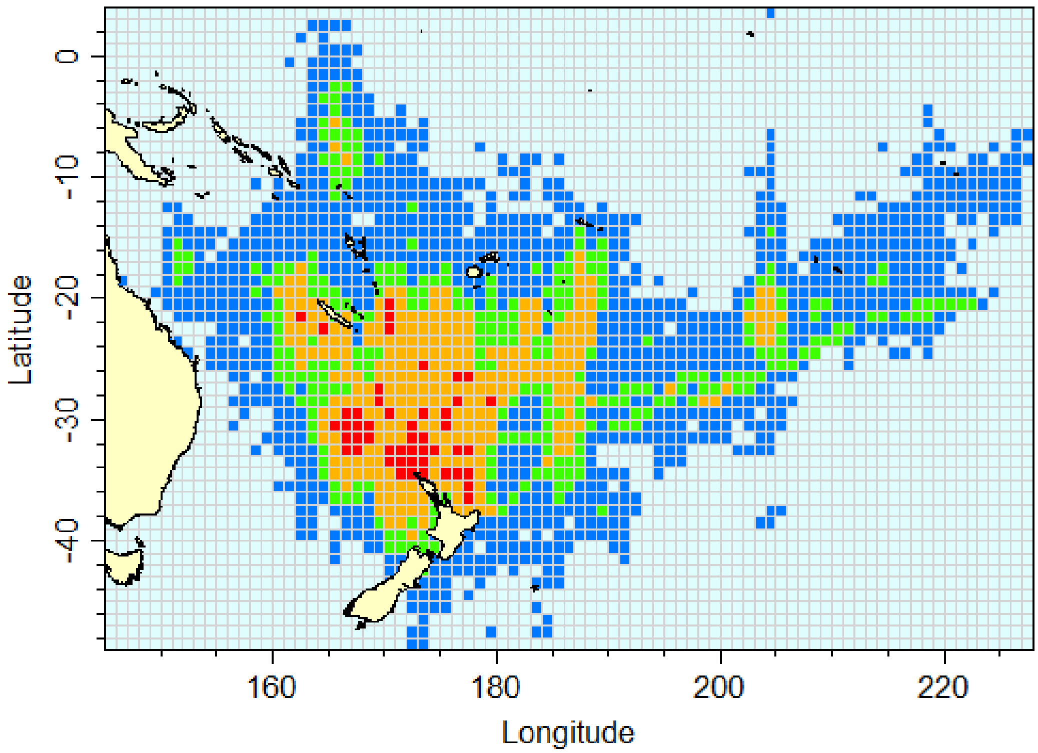

Figure 3: Posterior density of locations of striped marlins released in New Zealand across all months. Cells shown in red are the highest posterior density regions accounting for 25% of total estimated residence probability. The orange cells accounts for the next 50% of total estimated residence probability. The green, orange and red cells combined account for 90% of the total estimated residence probability. Note that the number of observations varies substantially between months.

Appendix B – Estimates of striped marlin residence by month

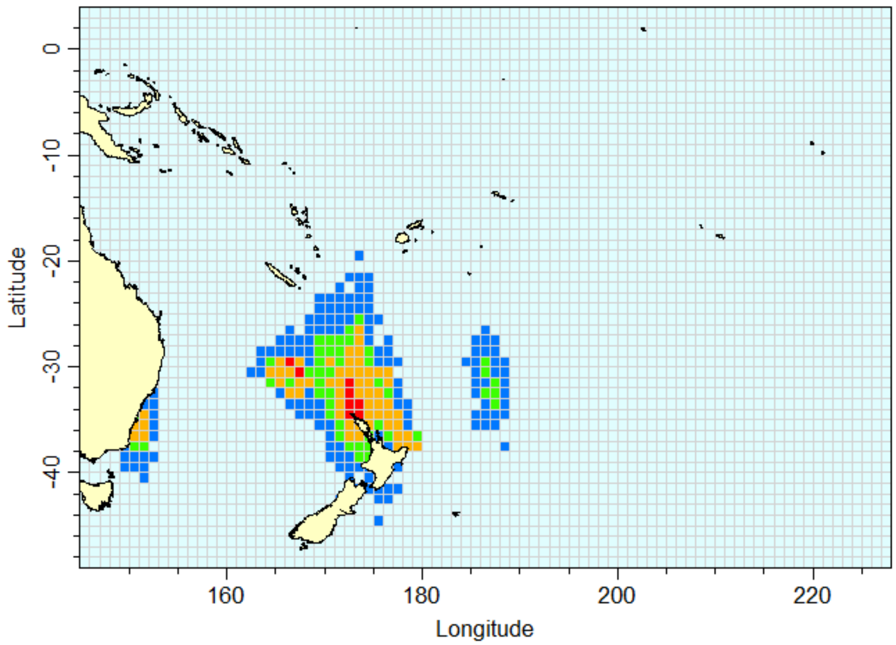

Figure 4: Posterior density of locations of striped marlins between December and February (all years). Cells shown in red are the highest posterior density regions accounting for 25% of total estimated residence probability. The orange cells accounts for the next 50% of total estimated residence probability. The green, orange and red cells combined account for 90% of the total estimated residence probability.

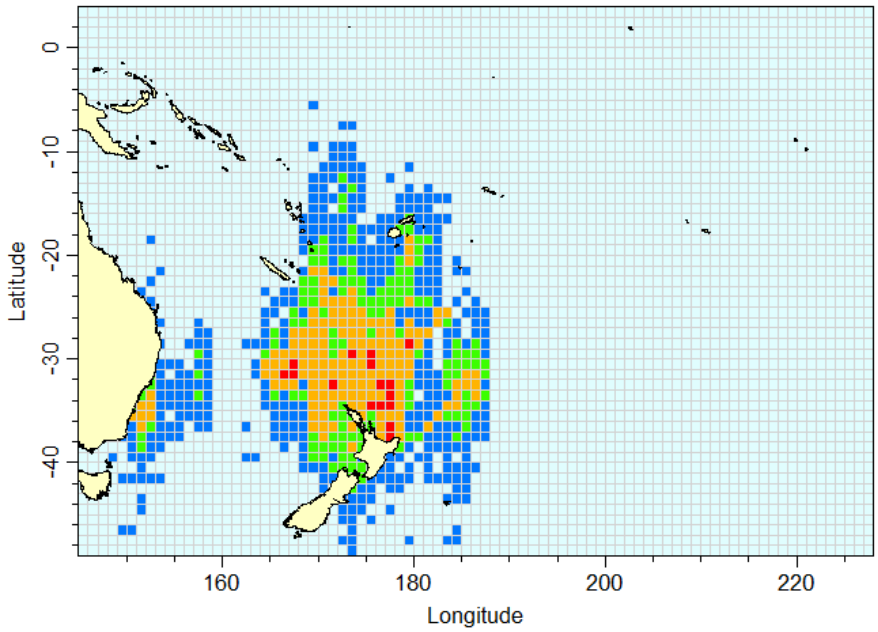

Figure 5: Posterior density of locations of striped marlins in March (all years). Cells shown in red are the highest posterior density regions accounting for 25% of total estimated residence probability. The orange cells accounts for the next 50% of total estimated residence probability. The green, orange and red cells combined account for 90% of the total estimated residence probability.

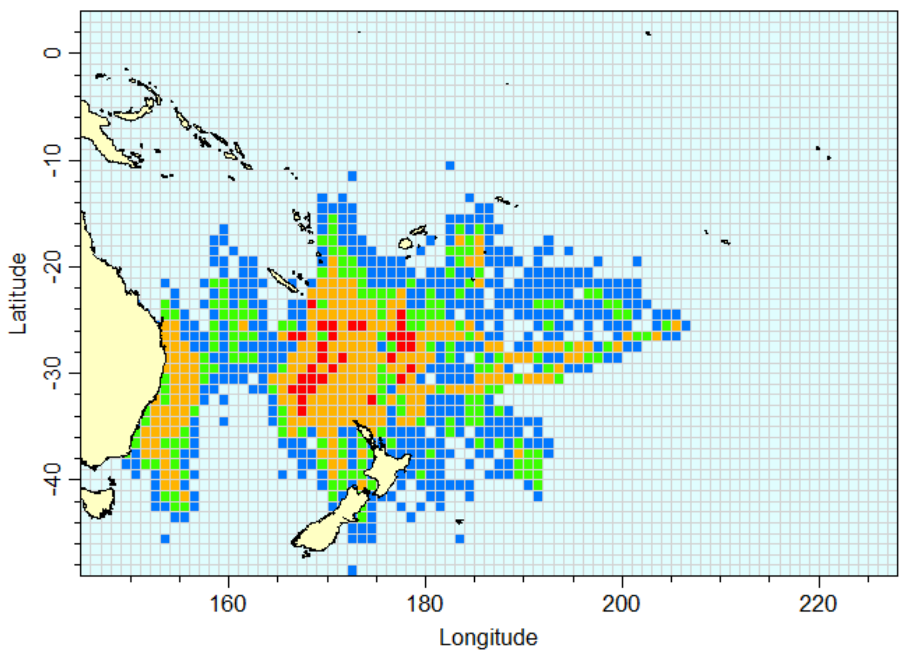

Figure 6: Posterior density of locations of striped marlins in April (all years). Cells shown in red are the highest posterior density regions accounting for 25% of total estimated residence probability. The orange cells accounts for the next 50% of total estimated residence probability. The green, orange and red cells combined account for 90% of the total estimated residence probability.

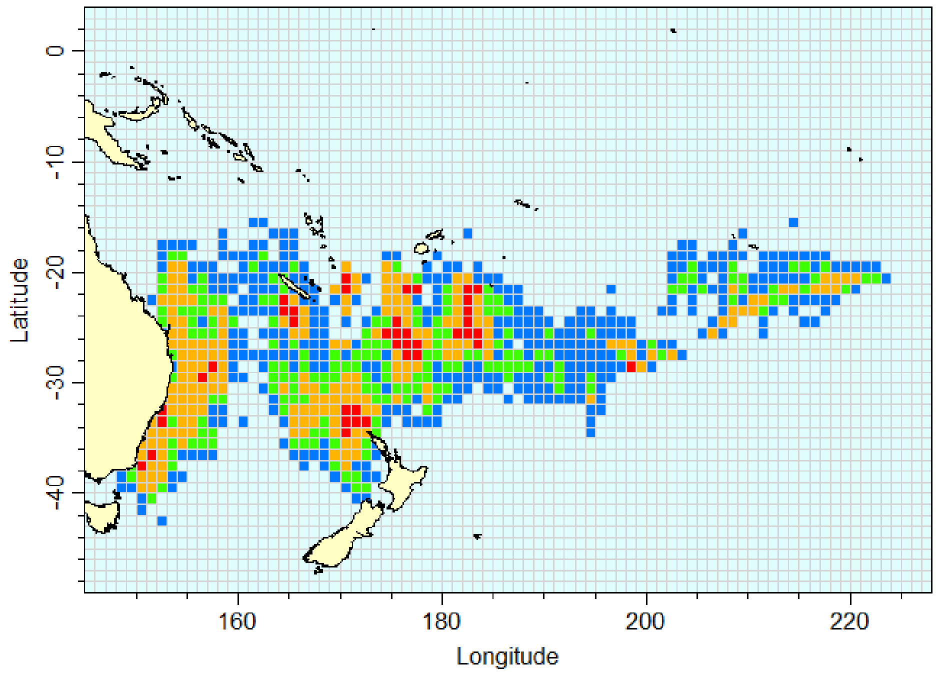

Figure 7: Posterior density of locations of striped marlins in May (all years). Cells shown in red are the highest posterior density regions accounting for 25% of total estimated residence probability. The orange cells accounts for the next 50% of total estimated residence probability. The green, orange and red cells combined account for 90% of the total estimated residence probability.

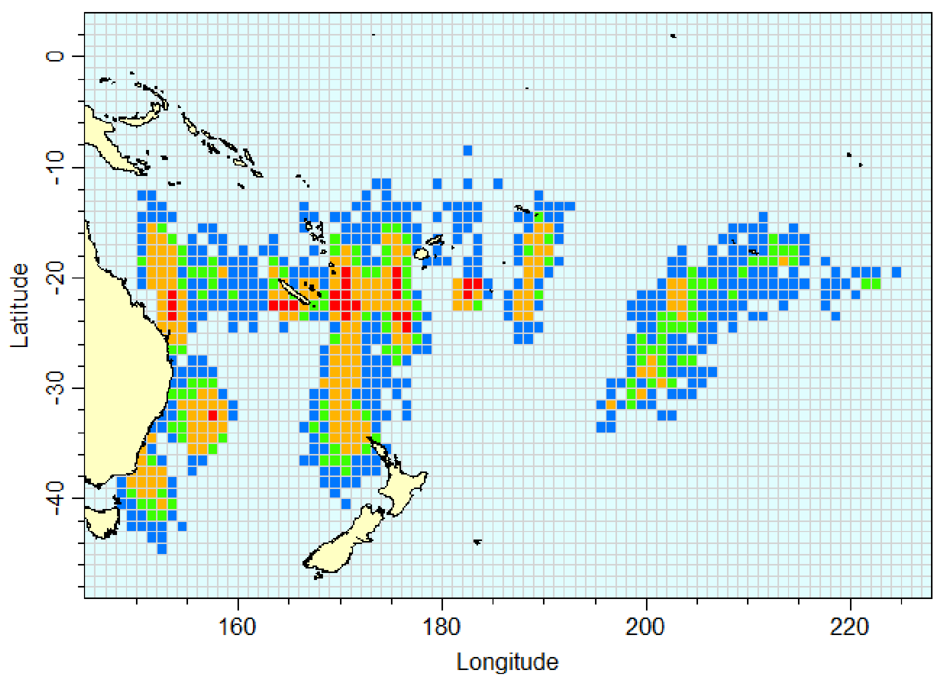

Figure 8: Posterior density of locations of striped marlins in June (all years). Cells shown in red are the highest posterior density regions accounting for 25% of total estimated residence probability. The orange cells accounts for the next 50% of total estimated residence probability. The green, orange and red cells combined account for 90% of the total estimated residence probability.

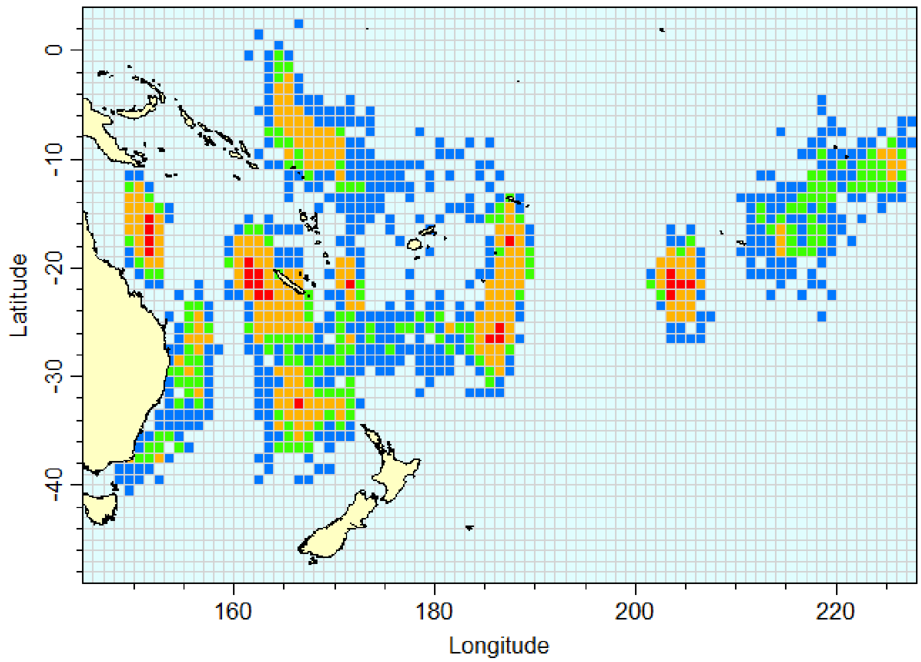

Figure 9: Posterior density of locations of striped marlins in July and August (all years). Cells shown in red are the highest posterior density regions accounting for 25% of total estimated residence probability. The orange cells accounts for the next 50% of total estimated residence probability. The green, orange and red cells combined account for 90% of the total estimated residence probability.

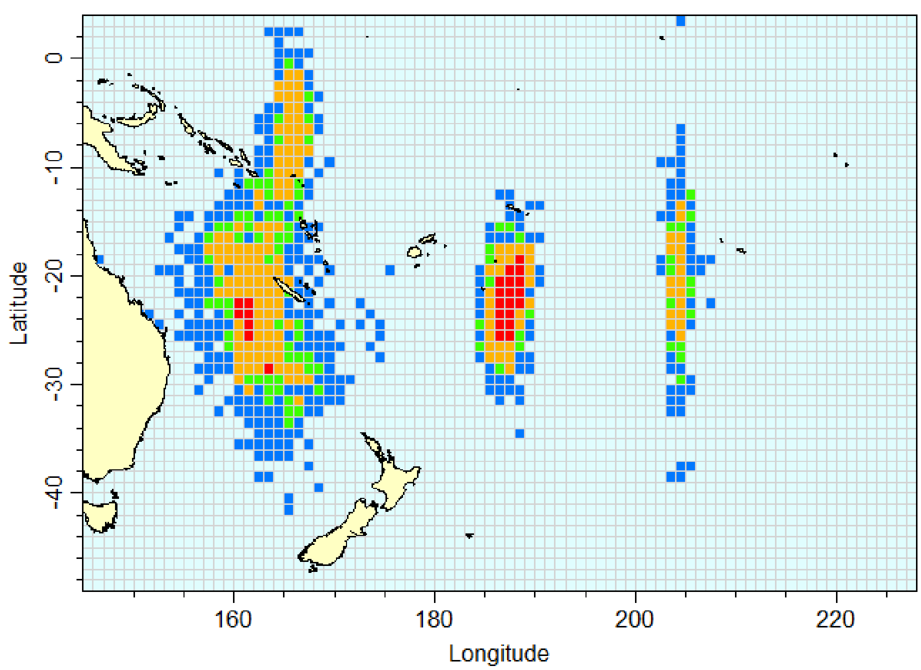

Figure 10: Posterior density of locations of striped marlins between September and November (all years). Cells shown in red are the highest posterior density regions accounting for 25% of total estimated residence probability. The orange cells accounts for the next 50% of total estimated residence probability. The green, orange and red cells combined account for 90% of the total estimated residence probability.

Appendix C - Tracks of individuals by month of release

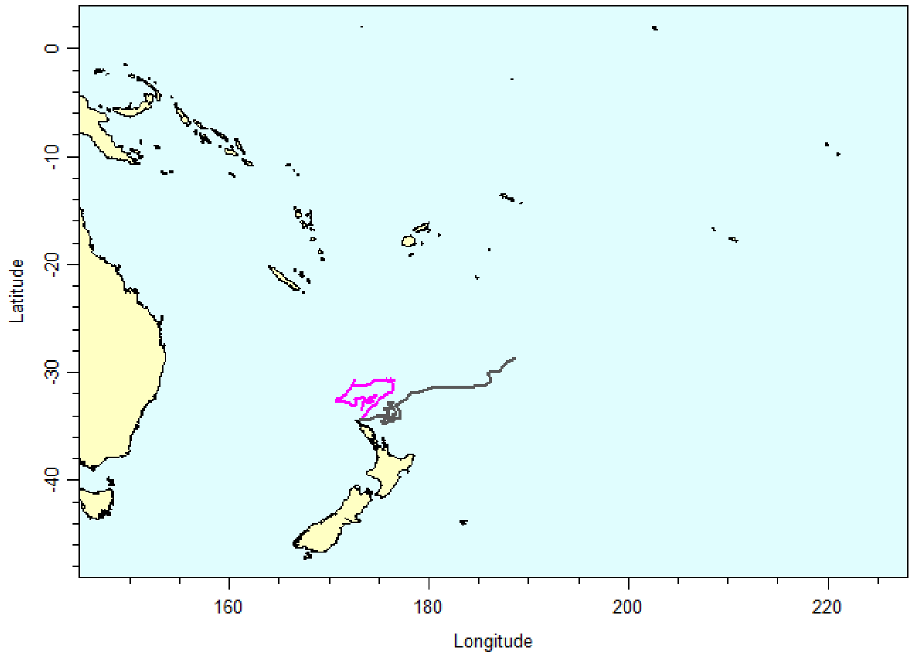

Figure 11: Posterior medians of daily latitude and longitude of striped marlins released in February 2003.

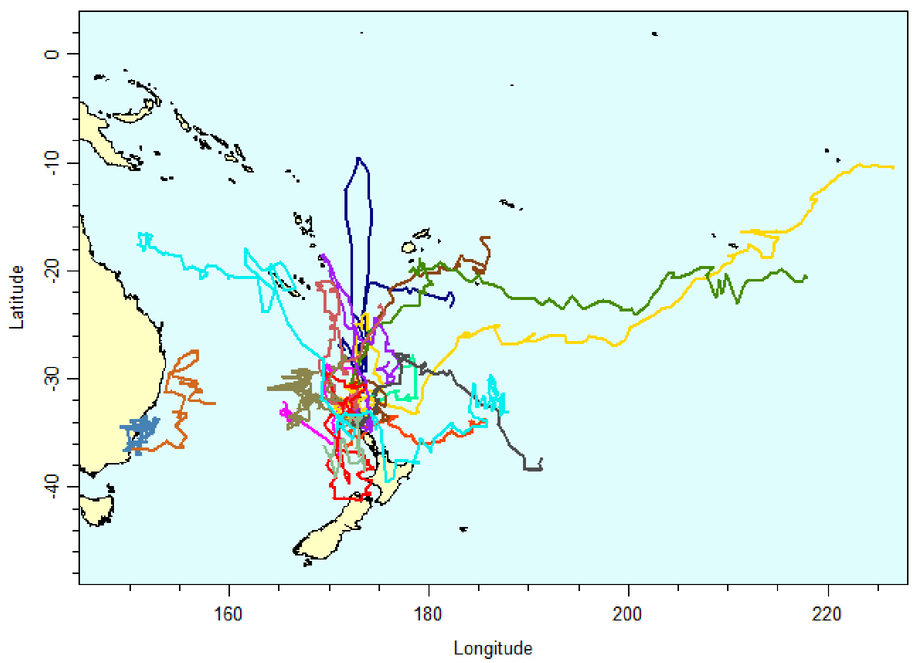

Figure 12: Posterior medians of daily latitude and longitude of striped marlins released in February 2004.

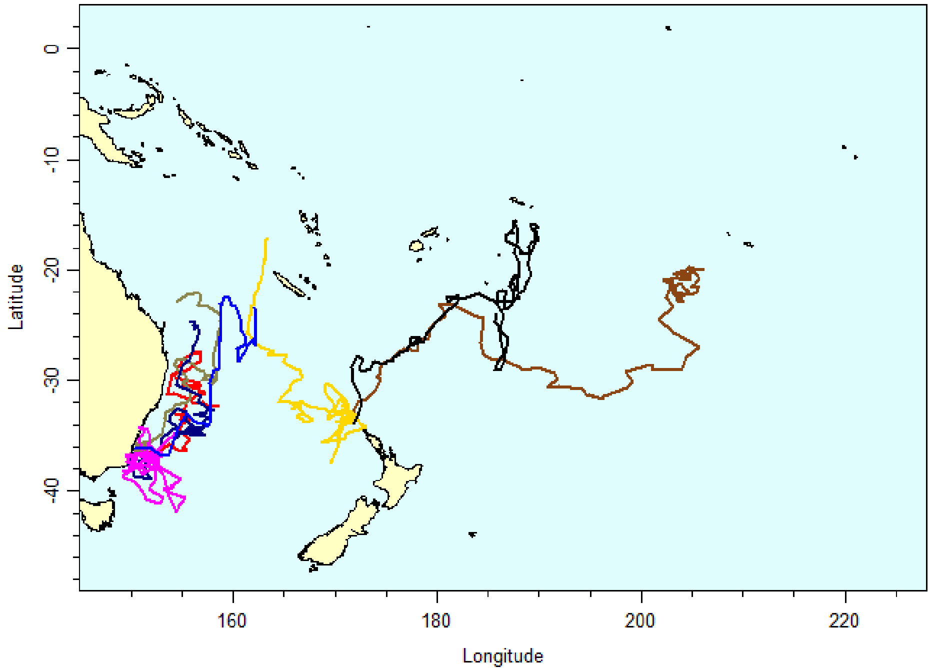

Figure 13: Posterior medians of daily latitude and longitude of striped marlins released in March and April 2004.

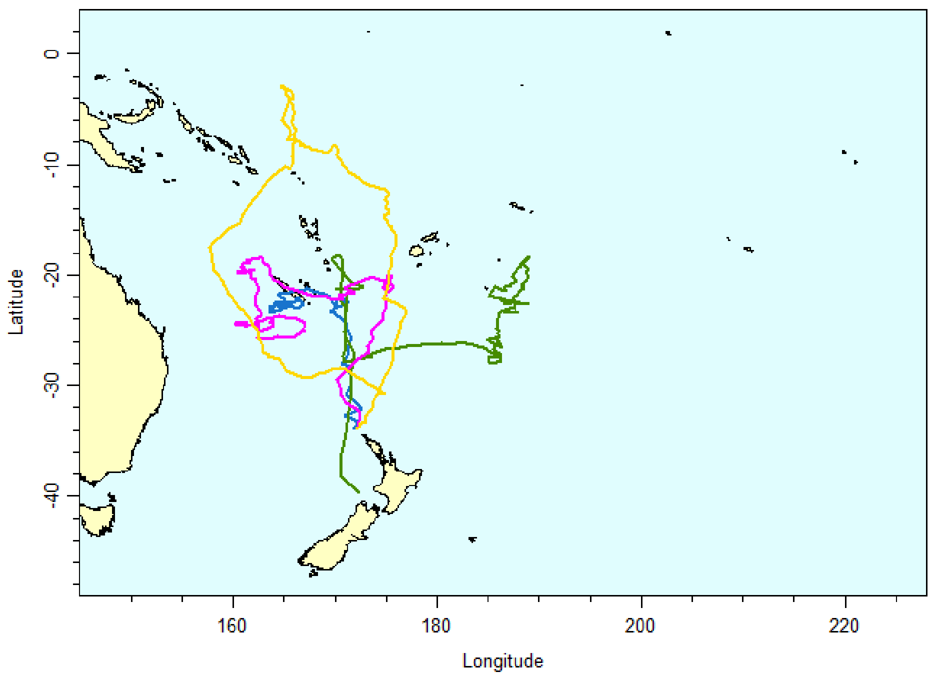

Figure 14: Posterior medians of daily latitude and longitude of striped marlins released in May 2004.

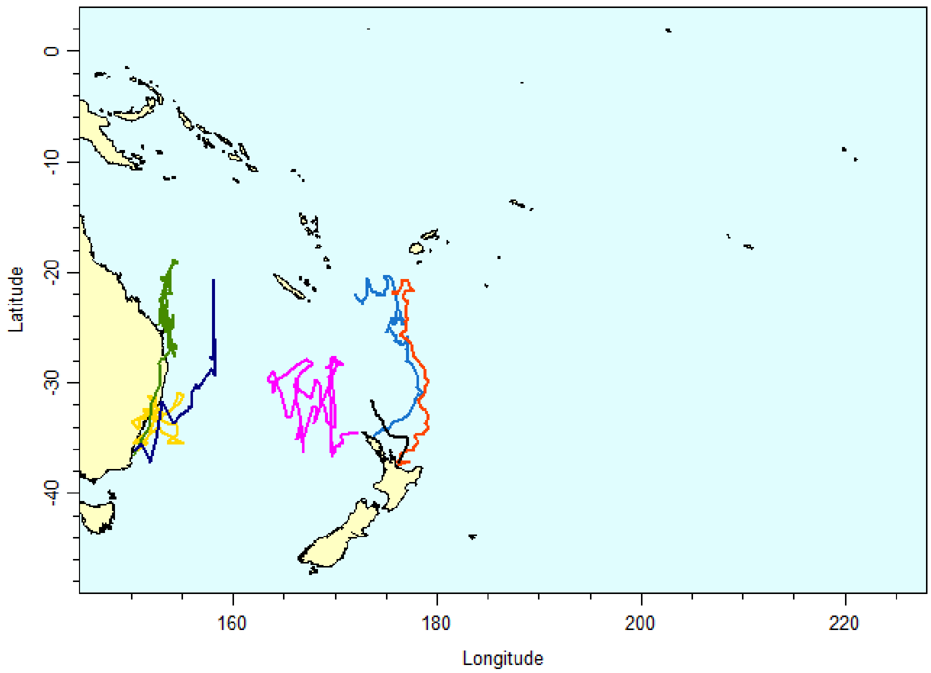

Figure 15: Posterior medians of daily latitude and longitude of striped marlins released between February and April 2005.

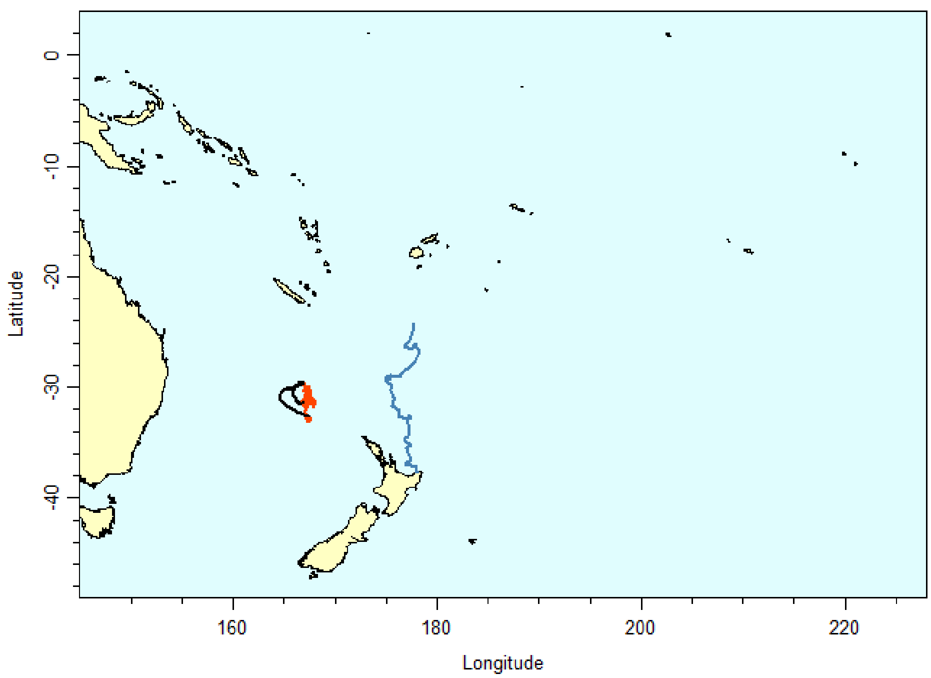

Figure 16: Posterior medians of daily latitude and longitude of striped marlins released in January and February 2006.

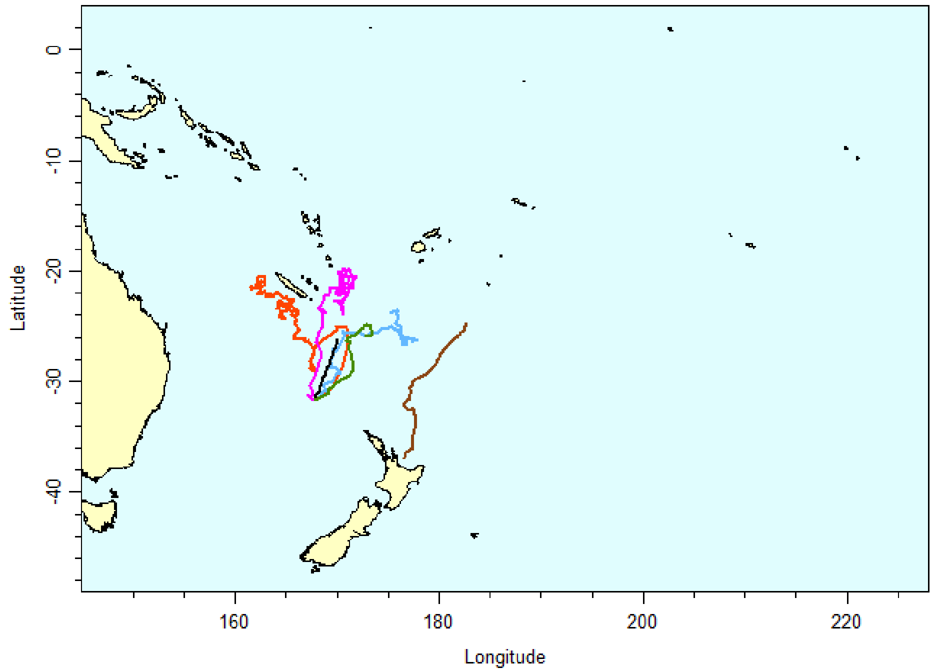

Figure 17: Posterior medians of daily latitude and longitude of striped marlins released in March and April 2006.

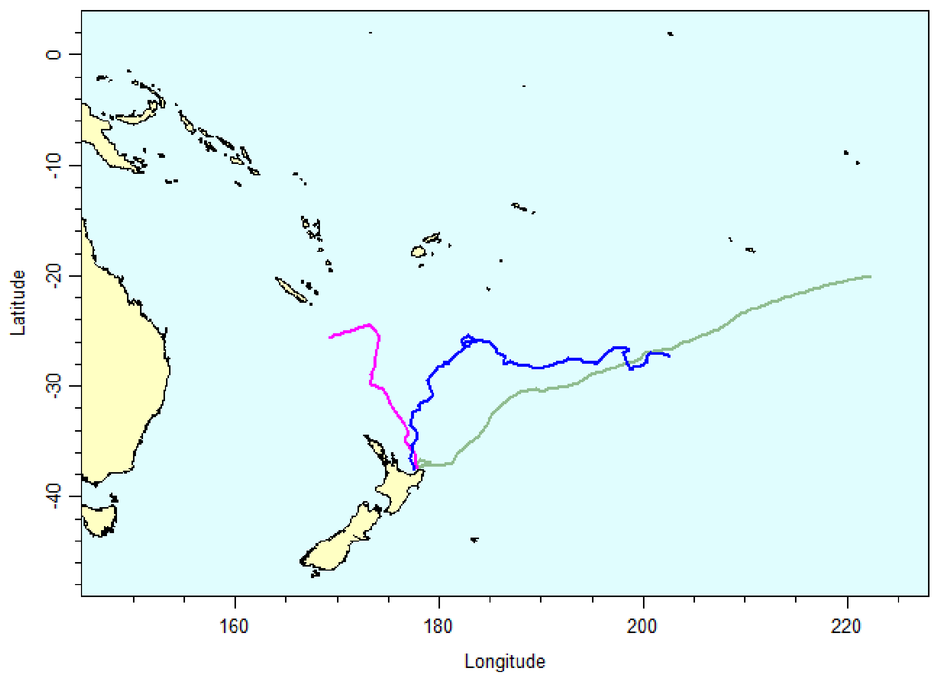

Figure 18: Posterior medians of daily latitude and longitude of striped marlins released in February 2007.

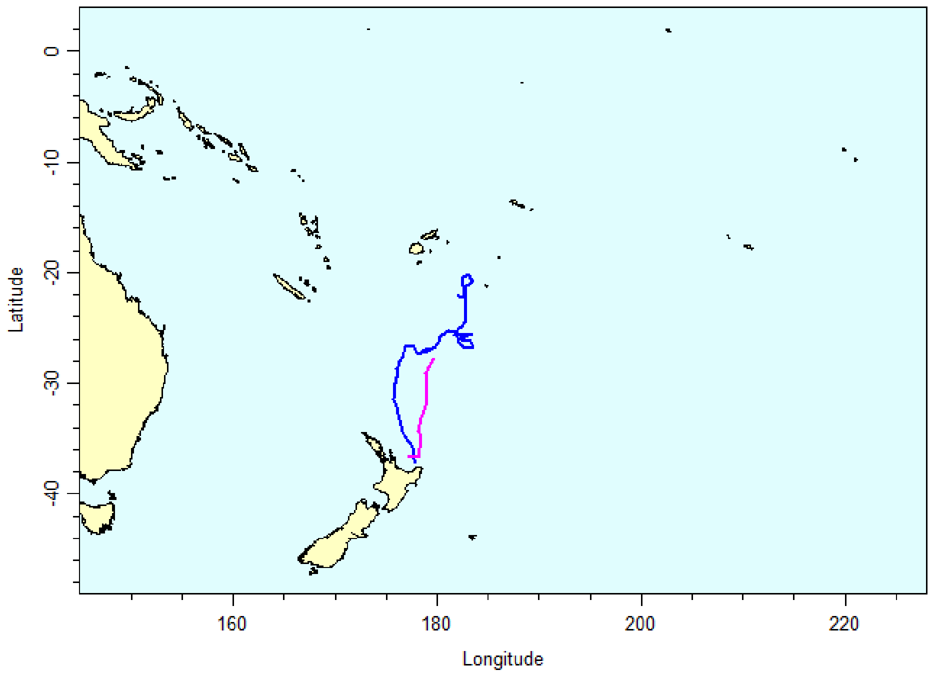

Figure 19: Posterior medians of daily latitude and longitude of striped marlins released in March 2008.

Appendix D - Example of model pseudo-code

1) **Day of Release**

   i. The latitude and longitude of release of each striped marlin is assumed to give the true location of the individual on the day of release.

   ii. If sea surface temperature is missing from the first day this quantity is modelled as an uncertain parameter, otherwise the observed value is assumed to be normally distributed about the true value.

2) **Other Days**

   i. The true longitude of the individual is modelled as its true longitude on the previous day and some positive or negative change in longitude representing a net eastward or westward displacement respectively.

   ii. The true latitude of the individual is modelled as its true latitude on the previous day and some positive or negative change in latitude representing a net northward or southward displacement respectively.

   iii. The observed longitudes and latitudes are assumed normally distributed about their true values as modelled in steps 2.i and 2.ii above (observed values are assumed to include observation error) with modelled precision.

   iv. Separate (lower) precision is allowed for observed latitude around the equinoxes.

   v. For days where observations for latitude and/or longitude are not received from the PSAT tag these are modelled with uncertainty about the estimated true latitude and true longitude on that day.

   vi. Daily changes in longitude are modelled as normally distributed about zero with standard deviation estimated from all data modelled together (typically about 10 individuals).

   vii. Daily changes in latitude are modelled, assumed to be normally distributed about an expected value proportional to the observed change in SST with autocorrelated errors in this relationship.

   viii. For days where SST observations were not received, values are simulated from an expected value which assumes a simple autoregressive structure between daily SST.

Posterior draws of location (jointly modelled 'true longitude' and 'true latitude') are extracted for each fish each day. These are put into 1 degree grid squares of longitude and latitude. These are aggregated across a month or groups of months to give a sort of relative individual × day × posterior_probability for each grid square in each month/group of months considered. Groups of grid squares are then defined such that the groups account for different partitions on a 2D Highest Posterior Density region.

Appendix E – Example of WinBUGS code

The following code models the location of 11 individuals for a total of 1261 days.

```
model
{
for (t in 1:11)
{
True.Long[First[t]] <- Long[First[t]]
True.Lat[First[t]] <- Lat[First[t]]
                    SST[First[t]] ~ dnorm(Mean.SST[First[t]],tau.SST)
Mean.SST[First[t]] ~ dnorm(SST.Mean,0.1)
delta.Lat[First[t]] <- 0
D.Lat[First[t]] <- 0
}
for (i in 1:1250)
{
Long[Oth[i]] ~ dnorm(True.Long[Oth[i]],tau.Long)
Lat[Oth[i]] ~  dnorm(True.Lat[Oth[i]],tau.Lat[LatVar[Oth[i]]])
True.Long[Oth[i]] <- True.Long[Oth[i]-1] + delta.Long[Oth[i]]
True.Lat[Oth[i]] <- True.Lat[Oth[i]-1] + delta.Lat[Oth[i]]
D.Lat.ar[Oth[i]] <-  D.Lat[Oth[i]] +gamma*(delta.Lat[Oth[i] - 1] - D.Lat[Oth[i] - 1])
delta.Lat[Oth[i]] ~ dnorm(D.Lat.ar[Oth[i]],delta.Lat.tau)I(-10,10)
delta.Long[Oth[i]] ~ dnorm(0,delta.Long.tau)
D.Lat[Oth[i]] <- theta*delta.T[Oth[i]]
SST[Oth[i]] ~ dnorm(Mean.SST[Oth[i]],tau.SST)
delta.T[Oth[i]] <- SST[Oth[i]] - SST[Oth[i]-1]
Mean.SST[Oth[i]] <- SST.Mean + gammaT*(SST[Oth[i] - 1]  - SST.Mean)
}
SST.Mean <- 22.2 + rand.part
rand.part ~ dnorm(0,0.5)
gamma ~ dbeta(1,1)
gammaT ~ dbeta(1,1)
theta ~ dnorm(0,0.00001)
sd.SST ~ dunif(0,3)
tau.SST <-  1/(sd.SST*sd.SST)
tau.Lat[1] <- 1/(sd.Lat[1]*sd.Lat[1])
tau.Lat[2] <- 1/(sd.Lat[2]*sd.Lat[2])
sd.Lat[1] ~ dunif(0,20)
sd.Lat[2] ~ dunif(sd.Lat[1],100)
tau.Long <- 1/(sd.Long*sd.Long)
sd.Long ~ dunif(0,20)
delta.Long.tau <- 1/(delta.Long.sd * delta.Long.sd)
delta.Long.sd ~ dunif(0,10)
delta.Lat.tau  <- 1/(delta.Lat.sd * delta.Lat.sd)
delta.Lat.sd ~ dunif(0,20)
}
```

Model Parameters

The input variables, **Lat**, **Long** and **SST** are all modelled (stochastic) for days when these values are missing.

The variables **True.Lat** and **True.Long** are defined for each fish every day. This allows for observation error to be estimated in latitude and longitude data received from the PSAT tags and also allows for imputation of these values for days when data aren't received.

Mean.SST this value is fixed to a value given by the overall mean of **SST** from days when **SST** is received. Effectively the expected **SST** on a given day is modelled as an autoregressive process allowing separate estimation of expected **SST** each day.

delta.Lat is the estimated change in latitude between day $i-1$ and day i.

D.Lat.AR is the expected value of **delta.Lat** on a given day and is proportional to the observed (or modelled) difference in **SST**, but with autocorrelated errors.

D.Lat is the change in latitude expected between day $i-1$ and day i given the observed or modelled difference in **SST**.

gamma is the estimated autocorrelation in errors of the observed (or modelled) change in **Lat**.

delta.T is simply the difference in temperature between day i and day $i-1$. If PSAT values for **SST** were returned for days i and $i-1$, then **delta.T** is a fixed value. Otherwise **delta.T** is wholly determined by the realised values of **SST** on days i and $i-1$.

theta is the estimated constant of proportionality between the change in temperature, **delta.T,** and the expected change in latitude, **D.Lat**.

gamma.T is the estimated autocorrelation (between days) in observed **SST**.

tau.Long is the estimated precision in observed or modelled **Lon** (inverse of longitude observation error variance).

sd.Long is the estimated standard deviation in longitude observation error.

tau.Lat is the estimated precision in observed or modelled **Lat** (inverse of latitude observation error variance).

sd.Lat is the estimated standard deviation in latitude observation error.

tau.SST is the precision of the mean of **SST** as an estimator of observed or modelled **SST**.

delta.Lat.tau is the precision of predicted changes in **Lat** given by **delta.Lat.AR**, between day $i-1$ and day i. Equal to the inverse square of **delta.Lat.sd**.

delta.Lat.sd is the estimated standard deviation of daily changes in observed or modelled **Lat**.

delta.Long.tau is the precision of zero as an estimator of change in **Long** between day $i-1$ and day i. Equal to the inverse square of **delta.Long.sd**.

delta.Long.sd is the estimated standard deviation of daily changes in observed or modelled **Long**.

In addition to these, quantities **First** and **Other** defined to index observations.

First is a vector defining the observations corresponding to the day of release of an individual striped marlin.

Other is a (redundant) vector defining observations corresponding to days other than the day of release for the striped marlin in question.

References

Davies, N., Hoyle, S., Hampton, J. (2012) Stock assessment of striped marlin (Kajikia audax) in the southwest Pacific Ocean. Western and Central Pacific Fisheries Commission - Scientific Committee Meeting WCPFC-SC8-2012/SA-WP-05:84

Domeier M, Kiefer D, Nasby-Lucas N, Wagshchal A, O'Brien F (2005) Tracking Pacific bluefin tuna (Thunnus thynnus orientalis) in the northeastern Pacific with an automated algorithm that estimates latitude by matching sea-surface temperature data from satellites with temperature from tags on fish. Fishery Bulletin 103:292–306

Domeier, M. L. 2006, 'An analysis of Pacific striped marlin (*Tetrapturus audax*) horizontal movement patterns using pop-up satellite archival tags', *Bulletin of Marine Science*, Vol. 79, pp. 811-825

Holdsworth, J. C., Sippel, T. J., Block, B. A. 2009, 'Near real time satellite tracking of striped marlin (*Kajikia audax*) movements in the Pacific Ocean', *Marine Biology*, Vol. 156, pp. 505-514.

Nielsen A, Bigelow KA, Musyl MK, Sibert JR (2006) Improving light-based geolocation by including sea surface temperature. Fisheries Oceanography 15:314–325

Purcell CM, Edmands S (2011) Resolving the genetic structure of striped marlin, Kajikia audax, in the Pacific Ocean through spatial and temporal sampling of adult and immature fish. Canadian Journal of Fisheries and Aquatic Sciences 68:1861–1875

Sippel, T. J., Davie, P. S., Holdsworth, J. C. & Block, B. A. 2007, 'Striped marlin (*Tetrapturus audax*) movements and habitat utilization during a summer and autumn in the Southwest Pacific Ocean', *Fisheries Oceanography*, Vol. 16, pp. 459-472.

Sippel T, Davie P, Holdsworth J, Block B (2007) Striped marlin (Tetrapturus audax) movements and habitat utilization during a summer and autumn in the Southwest Pacific Ocean. Fisheries Oceanography 16:459–472

Sippel T (2009) Tracking of striped marlin (Kajikia audax) in the southwest Pacific Ocean: environmental influences on movement and behaviour. PhD thesis, University of Auckland, Auckland

Sippel, T., Holdsworth, J., Dennis, T. & Montgomery, J. 2011, 'Investigating Behaviour and Population Dynamics of Striped Marlin (*Kajikia audax*) from the Southwest Pacific Ocean with Satellite Tags', PLoS ONE 6(6): e21087. doi: 10.1371/ journal.pone.0021087

Spiegelhalter, D., Thomas, A., Best, N. & Lunn, D. 2003, *WinBUGS User Manual*, Version 1.4, MRC Biostatistics Unit, Institute of and Department of Epidemiology and Public Health, Imperial College School of Medicine, UK, available at http://www.mrc-bsu.cam.ac.uk/bugs.