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# SPECIES-SPECIFIC VERTICAL HABITAT UTILISATION BY TUNAS IN THE TROPICAL WCPO

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## Background

The Pacific Tuna Tagging Programme (PTTP) is a joint research project being implemented by the Oceanic Fisheries Programme (OFP) of the Secretariat of the Pacific Community (SPC), the PNG National Fisheries Authority (NFA) and the members and participating non-members of the Western and Central Pacific Fisheries Commission (WCPFC). The goal of the PTTP is to improve stock assessment and management of skipjack, yellowfin and bigeye tuna in the western and central Pacific Ocean (WCPO). This report specifically addresses objective 4 of the PTTP:

> **"obtain information on species-specific vertical habitat utilisation by tunas in the tropical WCPO, and describe the impacts of FADs on vertical behaviour."**

Vertical habitat utilisation plays a large role in determining vulnerability to all major gear types operating in the fishery. This objective seeks to characterise the effect of FADs (anchored and drifting) on tropical tuna vertical behaviour and habitat utilization. This information will allow better estimation of abundance indices and standardised effort for the main fisheries and possibly contribute directly to the design of management measures for FAD fishing.

Funding support for this objective has been provided by the PNG National Fisheries Authority, New Zealand Agency for International Development, 9th European Development Fund (SciCoFish Project), Republic of Korea, Pelagic Fisheries Research Project, the Institute for Complex Systems Simulation, and the Lenfest Ocean Program.

This document complements the existing reports for this objective:

Leroy, B., D.G. Itano, T. Isu, S.J. Nicol, K.N. Holland and J. Hampton. 2010. Vertical Behavior and the Observation of FAD Effects on Tropical Tuna in the Warm-Pool of the Western Pacific Ocean. *Reviews: Methods and Technologies in Fish Biology and Fisheries* 9: 161-180.

Leroy, B., J. Scutt Phillips, S. Nicol, G.M. Pilling, S. Harley, D. Bromhead, S. Hoyle, S. Caillot, V. Allain, J. Hampton. 2012. A Critique of the Ecosystem Impacts of Drifting and Anchored FADs on Tuna in the Western and Central Pacific Ocean. *Aquatic Living Resources* 26: 49-61.

## Introduction

The study of behavioural ecology presents a number of significant challenges, particularly in the case of free-roaming, marine animals such as tropical tuna that cannot be directly observed. Indeed, there remain many aspects of the behaviour of these animals that are not well understood, including changes in vertical behaviour associated with biological factors, differences in location, and exposure to fishing gears. Assumptions about catchability, thermal-habitat preference, and how these differ across regions, are important components in stock assessment models. Improving our understanding of vertical habitat-use may have implications for scientific advice for the management of industrial fisheries. However, the problems involved in describing observed behavioural patterns objectively, correctly attributing changes in these patterns to appropriate stimuli, and applying statistically rigorous analysis techniques to behavioural time-series, have made such understanding difficult to incorporate into modern stock assessment.

In the case of tropical tuna, movement has important consequences for the susceptibility of these animals to fishing gears. Movement behaviours are manipulated and exploited by both industrial and artisanal fishers through the use of drifting and anchored Fish Aggregation Devices (FADs). This is because tuna, along with other pelagic species, are attracted to and associate with floating objects for reasons that are not fully understood, but may be related to the search for food and social interaction (Leroy et al. 2012). The use of FADs allows coastal fishers to utilise and broaden their pelagic resources (Bell et al. 2009), while for industrial purse seiners it increases the number of school encounters and stabilises catch (Squires & Kirkley 1999). Associated sets have reached 65% of purse seine effort in recent years (Hampton et al. 2012), and FADs are now deployed in such numbers that many thousands are in use at any one time (Moreno et al. 2007). As a result, some areas of the Western and Central Pacific Ocean (WCPO) contain very large changes in FAD density across relatively small spatial scales (Leroy et al. 2012). Such dense areas of floating objects may affect tuna dynamics across larger scales or in a different manner than previously thought.

The information from tuna tagging programmes in the Pacific provide a way to examine both the nature of and influences on these behaviours. In particular, a database now exists from over 130 archival tag returns from bigeye, yellowfin and skipjack tuna in the WCPO. Archival tags are surgically-implanted electronic devices that record data on the light intensity, depth and temperature that an individual fish experiences over a period of time. The time interval between records can be pre-programmed, often as short as 30 seconds, and so consequently, archival tag-release experiments can provide high resolution data for the analysis of vertical movement across many of the factors that may influence tuna behaviours. With this information it is possible to identify how tuna use the vertical water column that makes up their habitat, how physiology and environment affect their movement, and ultimately examine the degree to which FADs may alter this behaviour.

Despite the significant advances in technology and effort that have enabled the collection of large amounts of data on the fine-scale behaviour of tuna in the WCPO and elsewhere, there still exist a number of problems in the analysis and interpretation of these kinds of data.

Firstly, it is not trivial to objectively describe and classify behavioural data. Previous descriptions of behaviour in tuna have been largely qualitative and often related to depth only. Leroy et al. (2010) provided the first analysis of vertical movement of tropical tuna in the WCPO using qualitative descriptions of tuna diving behaviour similar to those attributed to archival tag data in many other studies (e.g. Schaefer and Fuller 2004; 2007; Wilson and Block 2009; Matsumoto et al. 2013a). Tuna behaviours have been classified by using observations such as the proportion of the day spent at certain depths (Schaefer et al. 2007; Matsumoto et al. 2013b), proportion of time spent above or below particular isotherms (Schaefer et al. 2009; Matsumoto et al. 2013a), summary metrics such as mean, maximum and proportional time spent at certain depth bins (Bestley et al. 2009; Walli et al. 2009), number and nature of individual dives (Dagorn et al. 2006; Wilson and Block 2009), the distribution of relative movements through the water column (Humphries et al. 2010) and a combination of these alongside qualitative description of predefined behavioural patterns (Leroy et al. 2010).

Secondly, the behavioural time-series provided by archival tags contain significant autocorrelation. Behaviour observed at one time is often related to behaviour observed previously, a result of the persistence of the underlying processes, such as hunger or resting, which drive these behaviours. This necessitates the use of statistical tools that do not assume independent sampling, and so many of the standard approaches for analysis or statistical modelling are not appropriate.

Finally, although archival tags record high resolution data on movement, the behaviour of these animals is not explicitly observed. Changes in depth and movement patterns are the result of underlying motivational changes in tuna. These motivations may persist or change in relation to environmental or other stimuli. Because these motivations are not directly observed, considerable care must be taken when interpreting the patterns that are observed in the time-series from archival tags. In particular, relating qualitative descriptions of behaviour to some other variable can implicitly incorporate potentially erroneous assumptions, biasing perceived relationships between vertical behaviour and potential covariates.

Here we provide an objective approach to analysing vertical tuna behaviour. We demonstrate a method using hidden Markov models (HMMs) to classify the vertical behaviour of tunas using data derived from archival tags and a number of simulated data sets. This approach has a long history in the field of signal processing, particularly for voice recognition (Gales & Young 2007), and its popularity as a tool for examining ecological data has increased in recent years. In particular, the field of animal behaviour has benefited from the ability to objectively estimate patterns and behavioural states from data in which behaviours may not be explicitly observed. Furthermore, HMMs provide a statistically rigorous framework to include covariate information that may influence the nature of and switching between estimated behavioural states. Examples of such models being applied to ecological problems include the foraging behaviour of mouse lemurs (Schlieche-Diecks et al. 2012), horizontal movement behaviour of Southern Bluefin tuna (Patterson et al. 2009), habitat-use of leatherback turtles (Jonsen et al. 2007) and diving behaviour in Macaroni penguins (Hart et al. 2010). In an ecological context, this approach can objectively identify the nature of observed behavioural patterns, estimate the probability of individuals switching between these behavioural states, and apply model selection criteria to objectively choose the most parsimonious model.

We presume that factors such as environment, ontogenetic development, time of day, and the presence of FADs influence patterns of behaviour in tropical tuna (Robert et al. 2012, Humphries et al. 2010, Maury 2005, Dagorn 2000). Archival tagging data provides neither a complete observation of these species' behaviour, nor the ecological context that drives it. Rather, we assume that the patterns observed in the diving behaviour are linked to latent behavioural states, which may be driven by these external factors. What are currently lacking are tools which can objectively extract behavioural patterns and classify these latent behaviours, whilst explicitly dealing with autocorrelation in the vertical movement time-series. HMMs have been applied to horizontal movement patterns for these very reasons, but are entirely appropriate for application to vertical behaviour.

We apply HMMs to a subset of archival tags from yellowfin and bigeye tuna deployed in the WCPO to examine three hypotheses:

1. Tropical tuna exhibit consistent behavioural patterns in their vertical movement tracks.
2. Individual biology drives differences in these behaviour patterns.
3. Stimuli such as time of day and the presence and density of nearby floating objects affect the transition between these behavioural states in tuna.

## Methods

### *WCPO Archival Tag Database*

The PTTP database stores archival tag returns numbering over 130 individual skipjack, yellowfin and bigeye tuna that in total have spent over 13,000 days at liberty in regions across the WCPO (Figure 1, Appendix 1). Data captured by archival tags includes depth and internal body temperature measurements captured at time intervals ranging from 30 seconds to 5 minutes, with most models also recording water temperature and light intensity.

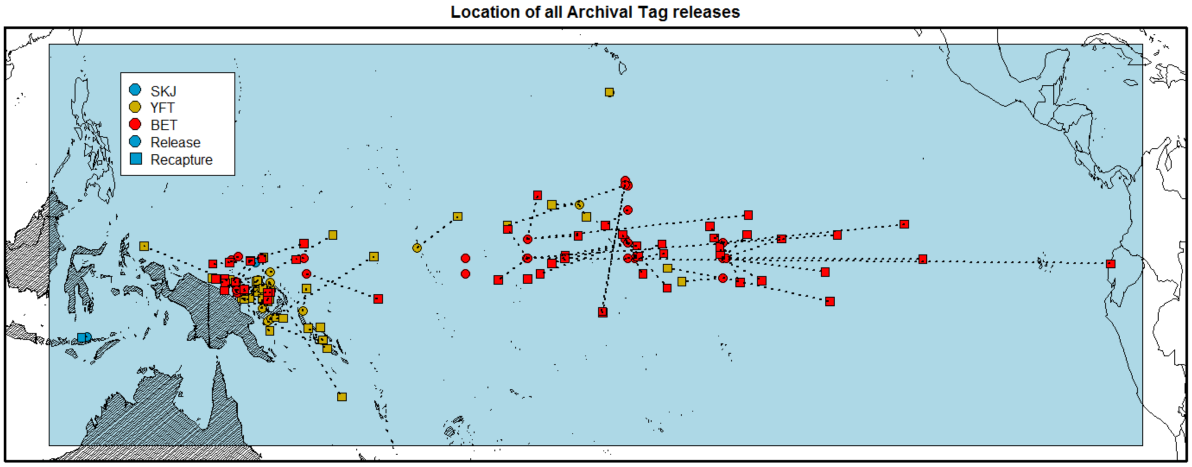

Figure 1. Release and estimated recapture locations for all archival tags in the PTTP database.

### *Data Pre-processing*

HMMs are suited to analyses of autocorrelated time-series, such as those from archival tags. To facilitate examination of persistent behaviours that occur in tuna for time durations longer than a few minutes it was necessary to pre-process the data into summarised units. It was desirable that any data pre-processing did not remove autocorrelation in the archival tag data. The optimal time step for such binning needed to be long enough to capture the range of consistent, composite behaviours that have been described for tuna in previous studies, such as ‘U-shaped diving’ (e.g. Schaefer and Fuller 2005; 2007), whilst also being small enough to capture within-day shifts in behaviour, such as the ‘afternoon diving’ described by Matsumoto et al. (2013b).

Raw tag data were divided into sections from which summary metrics were calculated, starting with two initial divisions made at dawn and dusk. Data were divided at these points to avoid metrics being calculated across the time-period when tuna have been previously reported to shift their vertical behaviour.

The first step to identify the average time of day at which these behavioural shifts occur was to use a split-moving window analysis (Ludwig & Cornelius 1987), which was applied to changes in time at depth. This approach has been used elsewhere to divide the vertical behaviour of free-roaming animals into behaviourally consistent sections over longer timescales (e.g. Humphries et al. 2010; Sims et al. 2011). Initially, the depth profiles for each individual were binned into proportion of time spent within 10-meter depth bins during each half-hour time period of the entire dive track. Then a 'virtual' window encompassing 24 time bins (12-hours) was placed at the start of the track, and split into two equal halves. Summing the proportion of time at each depth bin for each window half, the Euclidean distance was then calculated between the split-window. This is a measure of how dissimilar the first window half is from the second, in terms of time spent at different depths. This dissimilarity was recorded for the point in the binned depth profile split by the window, the window then moved on one bin, and the process was repeated for the new window position. In the case of tropical tuna, these measures of dissimilarity are often greatest when the window equally straddles a period of deeper behaviour, typically during the day, and shallower behaviour, such as exhibited during the night, although this was not the case 100% of the time. There was also considerable inter-depth movement that did not correspond to these day/night periods. To identify when the most consistent shifts in movement occurred, the time at depth bins were shuffled 5000 times and the same analysis carried out. When these random dissimilarities failed to exceed those calculated from the originally ordered data at a particular point 95% of the time, we concluded that this represented a significant shift in vertical behaviour, given the variation in the data.

The periodicity of these significant behavioural changes was examined to identify whether there was a consistent, diel pattern in movement; significant changes can be expected to occur more commonly at the the day/night boundaries (crepuscular periods). A histogram of periods during the 24 hours in which significant changes occurred revealed the times at which those changes were most common. A K-means algorithm (MacQueen 1967; Hartigan & Wong 1979) was applied to estimate two clusters from the frequency of times of (a 24 hour) day at which significant changes occur. The centre points of these clusters were selected as the crepuscular boundary periods that divide the dive data between day and night.

Once boundary periods had been identified, the data were further divided into the smaller units between the crepuscular boundary points. Summary metrics were calculated from the raw data for time bins of 1, 2, 3, 4, 6, 12 hours duration. At a time step of 3 hours, a balance was obtained between capturing dynamics such as just diving around crepuscular periods, or periods of 'U-shaped' diving, without the very fine patterns such as thermoregulatory dives being characterised individually in our analyses. Furthermore, such a time scale is appropriate for interpreting behavioural switching driven by underlying motivations that we assume are associated with factors such as FAD-association or periods of feeding or digestion. FAD-association is believed to occur on the scale of hours to months (Bromhead et al. 2003), whilst complete gastric evacuation occurs in tropical tuna at the scale of 5-12 hours (Olsen & Boggs 1986). We noted that at 12 and 6 hour time bins, the details of many shorter term and composite behaviours were also lost in the summary metrics, while noise from large individual dives began to increase at 2 and 1 hour sectioning. Using this 3 hour interval as a guide we then subdivided each crepuscular period into four equally spaced time units. Although each section divided between dawn and dusk was equally spaced, depending on the time chosen for the crepuscular boundary, the day periods and night periods may not always contain exactly the same amount of data.

In this study, we calculated summary metrics from the available tag data across time bins. As the study included tuna from different time periods and areas, we did not use measures of absolute depth which may differ across these factors for behaviours of the same underlying ecological motivation. We used a multivariate assemblage of summary metrics to capture information about both relative movement through the water column and temperature-based habitat use. Water temperature and absolute depth were highly correlated, although non-linearly. We used temperature as measure of habitat use. As individual deep dives and thermoregulatory dives can have a considerable effect on mean temperature metrics, the median water temperature was used. To choose the second summary metric in our multivariate assemblage, a principal component analysis was carried out on all the summary statistics (except those involving absolute depth) calculated from individual fish to examine the ways in which the data may be transformed into orthogonal components. Both the mean and variation in move step lengths consistently provided high loadings in the first principal component. We chose the mean move step length, a measure of vertical movement amplitude, as the movement component of our multivariate normal observation model.

Thus, raw archival data was processed into a time-series containing a two-dimensional, multivariate assemblage of mean move step lengths and medium water temperatures across 3-hour time periods.

## *Study Fish*

We used 8 study fish to examine:

- two species (bigeye and yellowfin);

- two size classes at release (sub 70cm FL fish and ~100cm FL fish). These two size classes were chosen to examine how physiological development of a swim bladder would affect individual behaviour of the smaller class, whilst this development should be complete in the larger individuals (Magnuson 1972);, and
- two release locations distinct in both environment and floating object density. Extensive use of anchored FADs occurs in and around the Bismark Sea (Leroy et al. 2012), whereas in the open ocean locations of the Central Pacific there is a presumed lower density of FADs.

| **Fish** | **Location** | **Species** | **Size at release** | **Days at liberty** | **Date** | **Notes** |
|---|---|---|---|---|---|---|
| Arc294 | Central Pacific | Bigeye | 53cm | 318 | Dec 2011 | |
| Arc272 | Central Pacific | Bigeye | 106cm | 360 | Nov 2010 | |
| Arc217 | Central Pacific | Yellowfin | 68cm | 148 | May 2008 | Fish migrated over 30° West whilst at liberty |
| Arc269 | Central Pacific | Yellowfin | 98cm | 255 | June 2010 | Approx. 240 days data corrupt and removed |
| Arc163 | Bismark Sea | Bigeye | 59 | 174 | Nov 2011 | |
| Arc88 | Bismark Sea | Yellowfin | 50 | 168 | Feb 2007 | Initial 40 days of data corrupt and removed |
| Arc302 | Bismark Sea | Yellowfin | 63 | 280 | Jan 2012 | |
| Arc220 | Bismark Sea | Yellowfin | 98 | 124 | Sept 2007 | |

## *Model*

Hidden Markov models (HMMs) are a group of state-space models which assume that observations depend on a finite number of underlying, unobservable states (Zucchini & MacDonald 2009). In time-series, these observations are assumed to be drawn from separate distributions each corresponding to a 'hidden' state in the same way as an independent or discrete mixture model applied to ecological data (Welsh et al. 1996). However, in an HMM these observations form a Markov chain, with the probability of occupying a given state at a given timestep dependent on the state occupied in the previous timestep. Using this framework, parameters that describe these distributions, the probabilities of transitioning between states, and the relationship between these transitions and other covariates, can all be estimated using numerical estimation of the maximum likelihood for a given dataset (Zucchini & MacDonald 2009, Patterson et al. 2009).

Here, we use the pre-processed dive tracks from our subsample of study fish to estimate the parameters for such a model. We assume that multivariate normal distributions of 3-hour binned mean step move length and median water temperature exist and are arranged in a number of distinct states, and that time series of these data form a Markov chain. Individual tuna switch between exhibiting behaviours drawn from these distributions with transition probabilities based on the behavioural state occupied during the previous three hour time period, and for models that include covariate information, the value of this covariate.

A full description of the HMM model is provided in Appendix 2.

## *Diagnostics and Simulation Experiments*

In order to introduce and examine the effectiveness of the HMM developed in this study, we undertook a number of simulation experiments using artificial data. Consider a theoretical tuna, tagged with an electronic tag that records two metrics over a particular time period. These metrics could relate to the speed the individual moves and the surrounding water temperature, averaged over some time bin. Two-dimensional datasets are generated, corresponding to this idealised individual exhibiting a number of different behaviours, such as remaining in the warm, mixed layer with little change in velocity (sometimes considered 'associative' behaviour), or making repeated dives to deeper, colder layers (as in 'characteristic' bigeye behaviour). We design these behaviours to have varying levels of persistence, and in some cases behavioural switching related to a covariate (perhaps a binary factor relating to day-time or night-time influences). For each simulation, HMMs were constructed and their abilities to correctly estimate true parameter values were examined. 'Pseudo-residuals' were also calculated for each model. As normal residuals do not exist for HMMs, these quantities fulfil a similar role and are explained further in Appendix 3. Each dimension of the multivariate assemblage has an associated set of pseudo-residuals. These become increasingly normally distributed with little structure through time as an HMM becomes more complex.

Three simulation experiments were carried out to assess the accuracy of our method for identifying states in the vertical behaviour of tuna. We generated three sets of artificial data which simulated dive track summary metrics drawn from the following state-dependant mixture of bivariate normal distributions. A full description and results of the simulation experiments are provided in Appendix 3.

The results of the simulation revealed that the HMM was capable of estimating true state distribution parameters and transition probabilities when these multivariate normal distributions were not too similar, although state persistence tended to be underestimated. Relationships between simulated transition probabilities and covariates were also estimated well. However, the AIC as a basis for model selection appeared to consistently select the most complex model despite less complex models being more appropriate. The parameter space in HMMs grows very large with increasing numbers of states, but despite this the AIC does not appear to adequately penalise the improvement in likelihood from these larger models. Examination of 'pseudo-residuals' provided a better, although not completely objective, method of model selection. Pseudo-residuals examined from these simulation experiments showed very little improvement in distribution for models that contained more parameters than the appropriate, 'correct' model. In each case, the simplest model which demonstrated comparable pseudo-residuals to more complex models was selected.

## *Modelling Archival Data Time-series*

For each study fish, HMM parameters were estimated using the method described above for 3-hour mean step length and median temperature summary metrics arranged in a multivariate distribution. The summary metrics from all fish were combined, and the resulting distribution examined to identify an appropriate transformation to normalise the data. A Box-Cox estimate of the ideal transformation exponent, lambda, was made for these two summary metrics, giving 0.11 and 0.19, for mean step length and median temperature, respectively. As both these values were not significantly different from zero, all data were log-transformed prior to the analysis.

Three HMMs were fitted to each study fish, assuming 2, 3 and 4 hidden states. The models estimated a mean and covariance matrix describing behaviour within each state, and a matrix of transition probabilities between the states. For some groups of models, we replaced single transition probabilities with linear functions of covariates. In these cases, we assumed a relationship between the covariate and the probability of switching states, allowing us to examine a number of hypotheses.

Initial conditions for all parameters were formed by scaling the time-series data to a Z-score and using a K-means, unsupervised machine learning algorithm to cluster the data into the same number of groups as estimated states. Using this classification, the centre points and covariance of each group of observations were used as starting values for state distribution parameters. A transition matrix was then calculated based on the K-means clustering of the time-series, and used to create starting values for the transition probabilities. For models that contained coefficient parameters for discrete covariates in the transition matrix (such as day or night), a separate transition matrix was built from a subset of the time series for each value of the covariate, using these K-means classifications. For continuous covariates (such as fish length), the data were divided into two halves and transition matrices constructed for each half based on the K-means classifications. The average value of the covariate in each half was then calculated, and the difference between these values in the two halves, with the corresponding change in transition matrix, was used estimate the value of the slope and intercept for the linear relationship between covariate and probability for each state to state transition. Using these start parameters, models were estimated using the Nelder-Mead algorithm in the R function *optim()* (R Core Team 2013). For each individual, one of the three models was selected as the most appropriate by examination of the pseudo residuals as described above. The number of states in the selected model for each individual is given in Appendix 4.

For each group of models estimated, a different assumption was made regarding the relationship between covariates and state switching. First, a set of models were built from all study fish that assumed no relationship between covariate information and switching between behavioural states. Then, we included a binary covariate to each 3-hour section of the time series that described the diel environment, i.e. whether the section data was recorded during the day or night. Day-time was defined if the time of day at the midpoint of the time series section was between 6am and 6pm. A third set of models were built using an estimated length of the individual throughout the time series, projected forward from the length recorded at release. These length estimations were calculated using growth curves from the most recent WCPO stock assessments for yellowfin (Langley et al. 2011) and bigeye (Davies et al. 2011). Finally, model parameters were estimated for two of the study fish at liberty in the Western Pacific, using a binary covariate representing potential movement within the FAD-dense Bismark Sea region. Estimated horizontal movement was available for these individuals based on two different methods of geolocation. For the small bigeye Arc163, the light-level based Trackit package for R (Nielson et al. 2007) was used. Due to high levels of uncertainty in the latitudinal estimates of this method, only estimates of longitude were used to indicate potential time spent within the Bismark Sea. For the large yellowfin Arc220, the most probable track was estimated using the geolocation method described in Royer et al. (2005).The Bismark Sea area was bounded by the box 5°80'S - 2°20'S and 145°50'W - 152°50'W.

## Results

To test the performance of the HMMs and examine our hypotheses, we describe the vertical movement of the study fish using HMMs with no covariate information, with a day-night covariate; and with a length covariate to the 8 study fish. A simple, binary location covariate was applied to two fish. For each archival tag, parameters describing the multivariate normal distributions of the behavioural states were estimated, along with an *m*-by-*m* matrix of transition probabilities, which described the switching between states. These transition probabilities change in relation to covariates, if these data have been included in the model. From this information, the probability of occupying each state at each timestep was calculated from the likelihood contribution of that observation, and used to classify each section of the time-series.

Transition matrices can be difficult to compare across individuals and alternative models. A clearer way of making this comparison is to compare the limiting distributions of the Markov chains they describe, also called the stationary distribution. In this case, the stationary distribution can be thought of as the proportion of time an individual fish would spend in each state, if the time-series ran on infinitely. Thus, each transition matrix can be viewed as a vector of proportions of length *m*, where each value is the proportion of time at the limit spent in each motivational state. A detailed example of estimated parameters and state classification is given in figure 2 for an HMM fitted to data from a small bigeye tuna with two hidden states, and no covariate-informed parameters in the state-transition matrix.

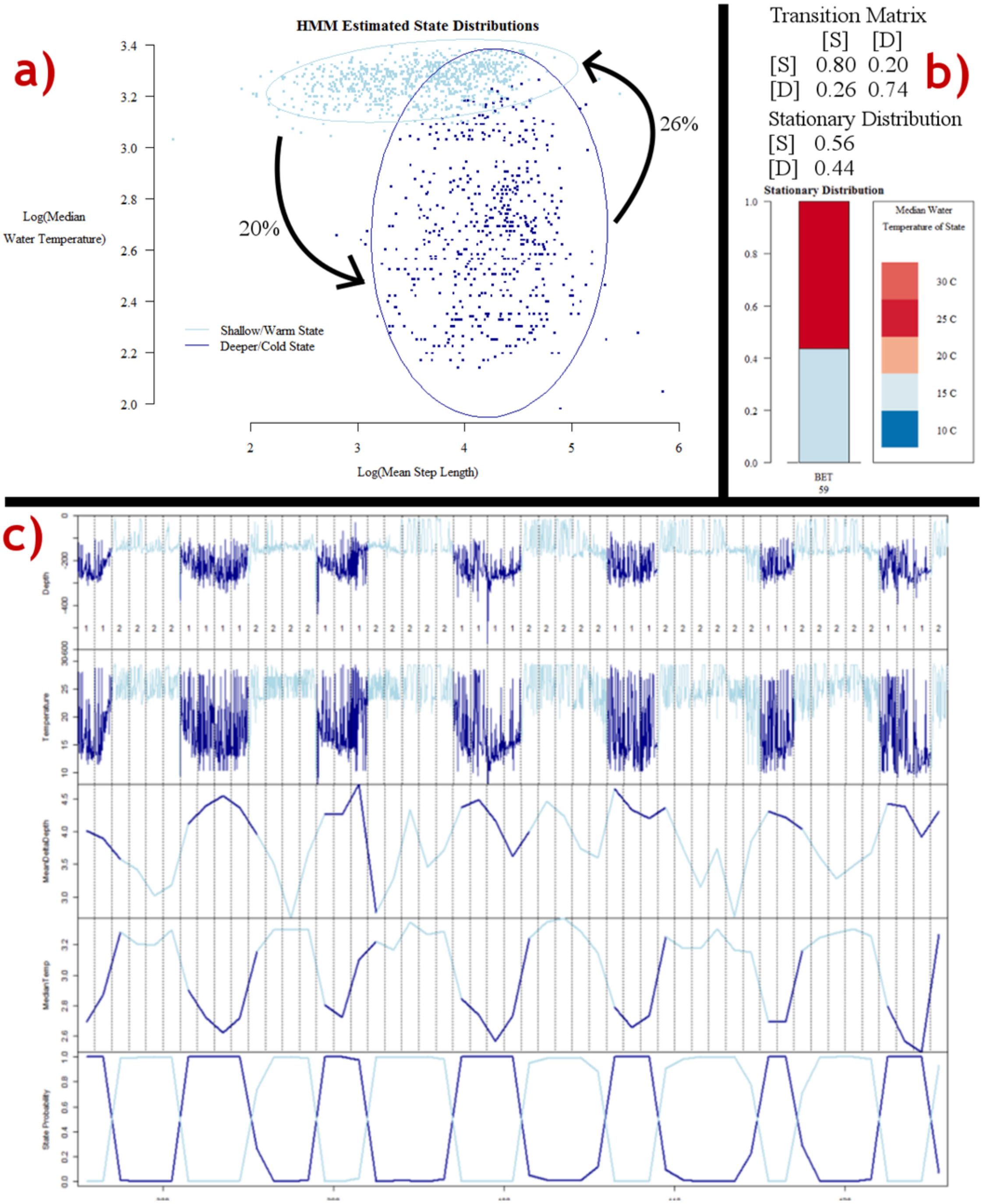

**Figure 2 Example HMM output for Arc163, a bigeye tuna released at 59cm FL in the Western Pacific. This model has two behavioural-state distributions, and includes no covariate information affecting the transition probabilities between those states. Figure a) displays the estimated state distributions of the multivariate summary assemblage shown on a log scale. This fish has two clear states. The shallow state (S) was typified by a large variation in move step lengths (amplitude; x-axis) within a fairly narrow range of thermal habitat in the mixed layer (y-axis). The deep state (D) constituted a looser distribution with larger mean, relative movements through the water column and the fish occupying colder habitats, although there is a high variance in these temperatures. Figure b) shows the estimated transition probabilities and related stationary distributions between these behavioural states. Here, both the shallow and deep states were persistent (80% and 74% respectively), although the shallow state slightly more so. Switching occurred with probability of 0.2 when the individual occupied the shallow state and with probability of just over 0.25 when in the deep state. In the limiting, stationary distribution this resulted in a slightly greater proportion of time spent exhibiting shallow behaviour. Figure c) displays an example section of the time series as classified by the model, showing, from top to bottom, raw depth, raw water temperature, summary mean step move length, summary median water temperature, and the probability of state occupation at each time step.**

The hidden Markov models we have used here provide information on three aspects of tuna behaviour. First, the nature of the most likely observed behavioural-state distributions, given the entire time-series, is estimated. Second, the switching between the underlying motivational states linked to these observed distributions is given by transition probabilities, including the relationship between these probabilities and covariate information, if this information has been used. Finally, these two aspects are used to classify the behavioural time series with a probability of occupying each motivational state at each timestep. We examine each of these aspects for the HMMs fitted to the archival tag data in this study in turn.

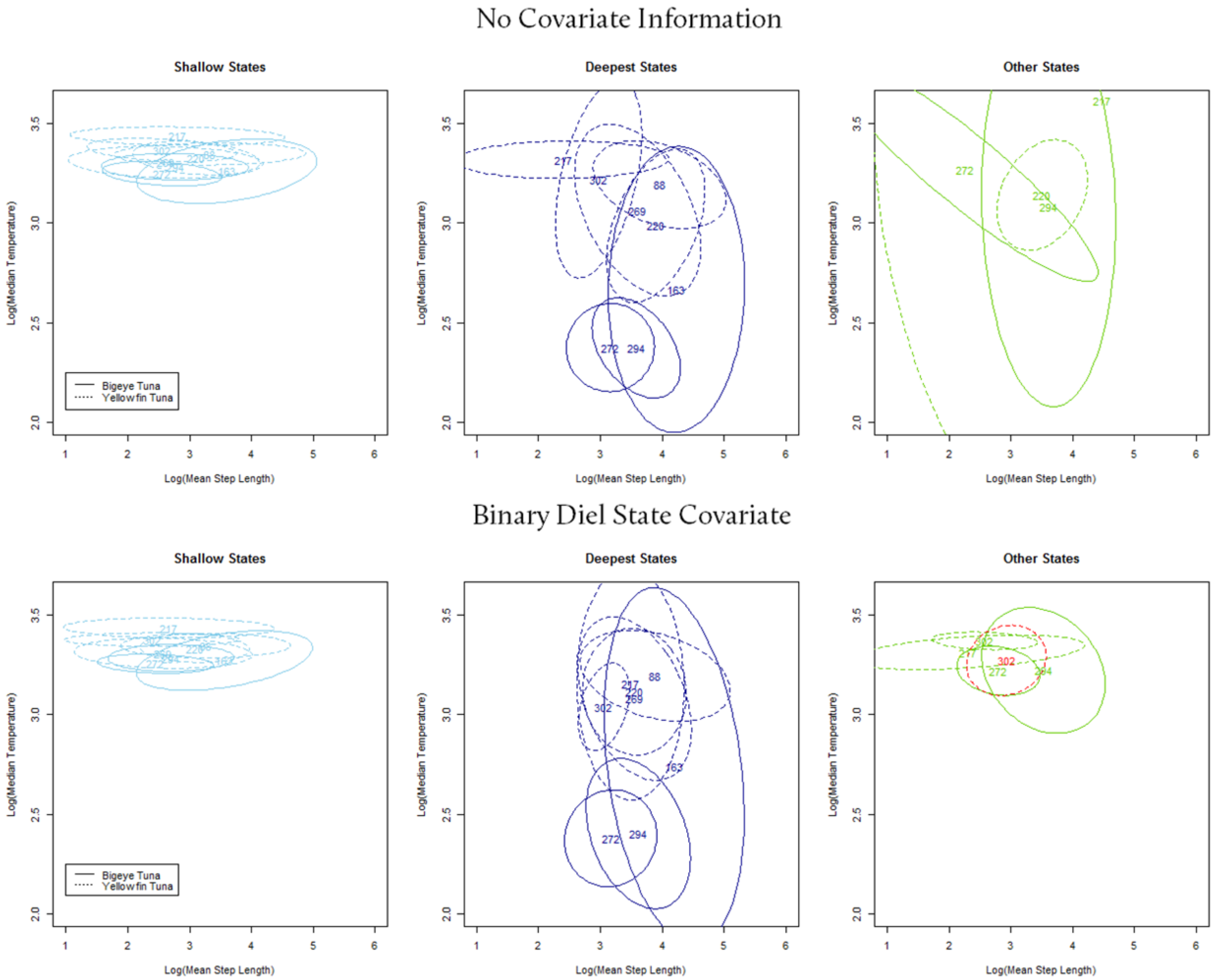

**Figure 3. Estimated state distributions from the selected models for all fish in this analysis, divided into the most shallow, most deep and any other states. For each individual, each state has a separate colour. Top row: results from HMMs with no covariate ~ transition relationship; Bottom row: results from HMMs with a binary covariate for day or night in the transition matrix**

*Observed Behavioural States*

The estimated behavioural states for each individual can be described by a shallow state, where the mean of the multivariate normal distribution in the temperature dimension is highest, a deep state, where this mean is lowest, and, depending on the number of total states in the chosen model, a number of intermediate states. For all HMMs, the most shallow and most deep states were similar for each individual across runs with differing covariate information, indicating that the grouping of summary metric observations is clear enough to estimate the same states across models with differing transition matrices (Figure 2). The shallow state classified in all models was similar across all individuals (Figure 2) with the largest variation in behaviour associated with the mean movement step length rather than the habitat (which constituted a median temperature of between 33 and 25°C, being the epipelagic, mixed layer). In contrast, the nature of the classified 'deepest' states varied between individuals and species (Figure 2) with greater differences in habitat across individuals and less variation in mean movement step length, which was generally of greater amplitude than the shallow states. The deepest states of bigeye tuna were considerably deeper than those of yellowfin.

Addition of the diel covariate increased the ability of the HMM in minimising the variance in mean step length between individuals for the deep state behaviour (Figure 2), likely because switching between shallow and deep behaviours was so clearly linked to the time of day that estimated state distributions could become tighter. The variance associated with intermediate third and fourth states for some individuals (where model diagnostics suggested these were the best models) were also smaller on median temperature and mean step length with the inclusion of a covariate (Figure 2).

The estimated state distributions of HMMs fitted with a length covariate in the transition matrix did not differ greatly from the models fitted with no covariate information, with exception of Arc217. This fish undertook a significant horizontal migration during its time at liberty, occupying two locations with different median temperatures in the mixed layer. In this case the inclusion of the length covariate, which increases throughout the time series, increases the likelihood of separating these periods of shallow behaviour into separate state-distributions due to each one only being exhibited in the first half and last half of the time series, respectively.

Similarly, the state distributions for the two models including a Bismark Sea location covariate were very close to the equivalent models using no covariates. The selected models for both these fish were 2-state models.

### *Switching between States*

An examination of stationary distributions for each individual indicated that, across all models, shallow states in the mixed layer were the most dominant behaviour (Figure 4), although the most dominant state was not always the most shallow (as in the case of Arc217). One or more deeper states are exhibited less frequently, where differences between species were evident. The proportion of time spent in shallow or deep states was closer to 50:50 for bigeye than yellowfin. Furthermore, the difference in the nature of these states was also greater for bigeye, the thermal habitat being more different between shallow and deep behaviours (see Figures 3 and 4).

The transition probabilities matrix for the diel HMM demonstrates strong differences in the thermal habitat used by both species between day and night (Figure 5) with occupation of colder median temperature states during diurnal hours which correspond to habitats of the deep state and warmer median temperatures during nocturnal hours which are indicative of the habitats in the shallow state. All three bigeye tuna examined here, and one large yellowfin (Arc220), were the most consistent in switching between their deepest and shallowest behaviours during the day and night, respectively. The large bigeye, Arc272, had almost certain probability of switching to and persisting in deep behaviours during the day. A high proportion of time spent in these shallower, warmer states during the night was more consistent across individuals than spending time in colder, deep states during the day, whereas some individuals still pass considerable time in the mixed layer.

We observed inconsistent trends in the HMMs with the addition of a length covariate. While including the estimated length covariate information in the transition matrix results in some clear relationships between increasing size and behavioural switching for some individuals, for others there appears to be little or no change in relationship to length. Furthermore, a change in the initial conditions used during model optimisation resulted in different estimations of these state-transition parameters, occasionally even suggesting the opposite gradient in the linear relationship. For example, in the case of data from one small bigeye tuna, estimation of transition parameters from initial conditions using an estimate created using K-means clustering, as has been used through this analysis, resulted in increased switching to a deep state as the fish increased in length. In contrast, when no relationship was assumed in the initial conditions, i.e. the fish undertakes the same behavioural switching regardless of size, a slight relationship to the contrary was estimated. Unlike the inclusion of the diel state information, where regardless of initial conditions a similar relationship between change in covariate and transition probabilities was estimated, in the case of length it appears that there is no, or not enough, information in our time-series to interpret such a relationship. Subsequently, we do not present model results for this group of model estimations here.

Conflicting results were observed between the two individuals examined with a Bismark Sea location covariate. For the small bigeye Arc163 (59cm FL at release), persistence of deep behaviour was slightly lower when the fish was within the longitudinal bounds of the Bismark Sea. Persistence of shallow behaviour was comparable both in and out of the Bismark Sea area, resulting in an small overall increase proportion of time spent exhibiting shallow behaviour when inside the bounds of the Bismark Sea (Figure 4). For the larger yellowfin Arc220 (98cm FL at release), there was less evidence to suggest an effect on behavioural switching when inside the Bismark Sea. Similarly to when length was included, different relationships between location and transition probabilities were estimated dependent on the initial conditions used in optimisation. When K-means initial values were used, the estimated relationship was similar to Arc163, i.e. an increase in time spent in the shallow state at the expense of the deep when inside the Bismark Sea. However, using initial start values with no relationship, the final parameters estimated were also very close to this null hypothesis (Figure 4).

### *Classified Timeseries*

An HMM can be used to subsequently classify a time-series by calculating the probability of the individual occupying each state at each timestep using the estimated state distributions and transition matrices. Although this can be applied to a new set of data using a model fitted to a different time-series, he we simply classify each dive track using a model fit to that same time-series. Figure 2c shows a section of classified summary metrics for Arc163, with corresponding sections of raw data also classified. This example classifies the time series into two states, associated with shallow and deep behavioural patterns. Due to the slightly higher persistence of the shallow state, behavioural patterns that may lie somewhere between the two state distributions are more likely to belong to this warmer state, particularly if they occur after other instances of shallow behaviour. An example of this can be seen in the final three days shown in figure 2c, where a high probability of the individual exhibiting its shallow state persists into the first part of the daytime despite a shift to slightly deeper diving patters during some of those mornings.

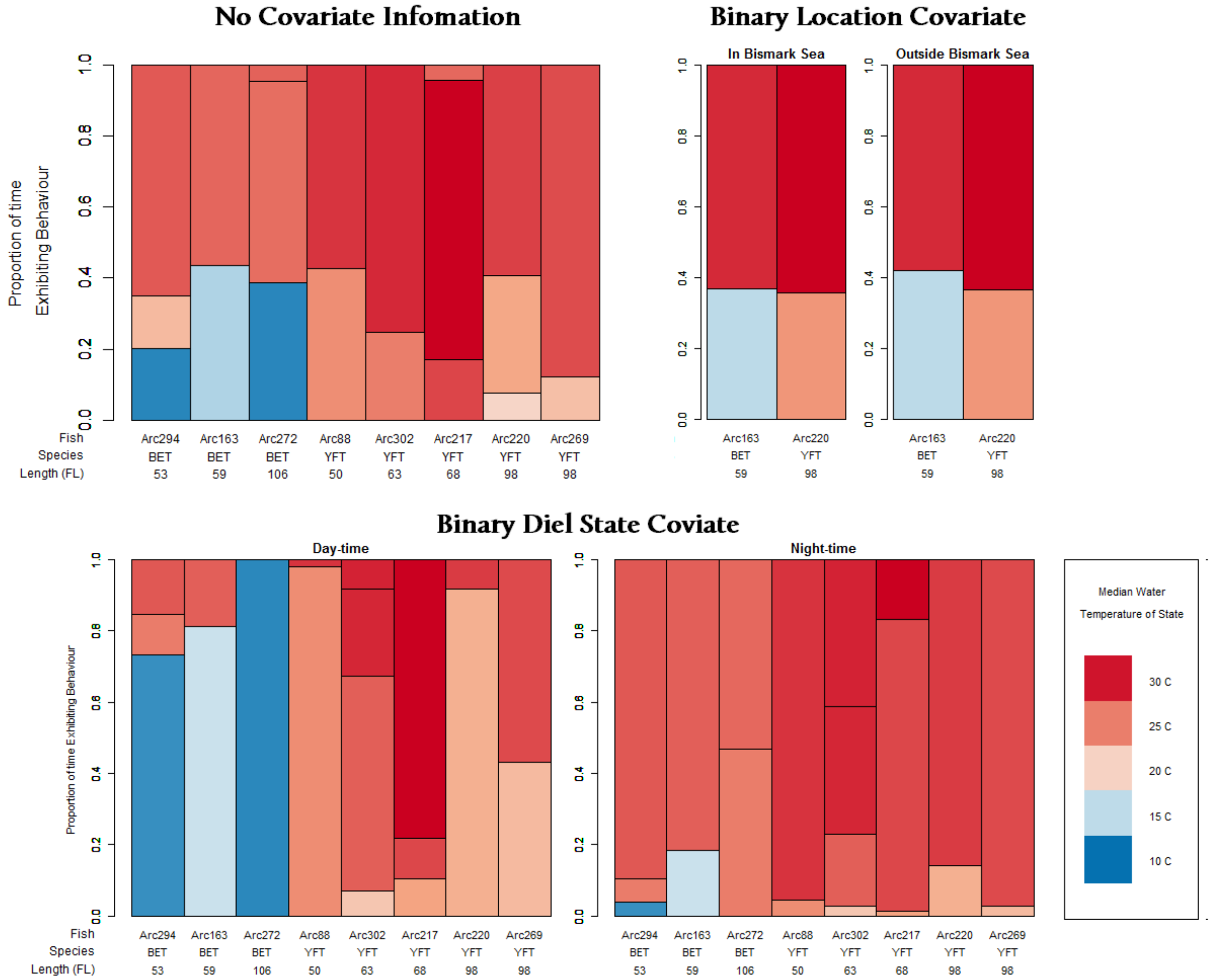

Figure 4 Stationary distributions for selected models and all fish in this analysis, showing the proportion of time spent in each state. The thermal habitat associated with each state is shown by colour, using the multivariate mean value in the median water temperature dimension (back transformed). Top row: results from HMMs with no covariates included in the transition matrix (left), and results from two fish with the potential Bismark Sea residence covariate (right). Bottom row: results from HMMs with a binary covariate for day or night in the transition matrix.

# Discussion

Using HMMs we have demonstrated an approach to objectively describe vertical behaviour in tropical tuna. By summarising raw data into bins at the temporal scale of hours, it is possible to explore the nature of clustered behavioural states, the switching between those states and its relationship to other biological or environmental information, and to classify these time-series using state probabilities at each timestep. The results from the 8 study fish identified patterns of behaviour that are consistent with the literature, although our behavioural conclusions here are tentative in the knowledge that 8 individuals sampled across the size, area, species, and indeed temporal variables may not be representative. Encouragingly, however, the shallow and deep state identified were very similar across all groups of models, suggesting that the grouping of summary metric observations used was sufficient to estimate the same states across models with differing assumptions about transition between those states.

The identification of a similar warm-water, shallow state across individuals and species was consistent with the known biology of tropical tunas which requires them to reside in the warm surfaces waters to thermoregulate. However, tropical tuna have evolved ways to dive and exploit prey in colder layers of water, and it appears there is a greater variety in how these study fish exhibit this behaviour. The shallow states, whilst occupying a narrow range of median temperatures, consist of a large variety of step lengths, which are measures of movement amplitude through the water column. Across all the individuals examined here, there is no evidence of consistently different move step lengths for behaviours within the epipelagic layer. Rather, individuals spent time in the mixed layer exhibiting a continuous range of relative movement from small to large amplitudes. It is likely that this variation is influenced by location factors (e.g. depth and availability of prey) and the addition of continuous horizontal movement covariates would be a useful experiment to test with the complete dataset to better understand the variation in mean step length among individuals. In contrast, for all fish but Arc217, the deeper states have consistently larger, mean step lengths. For the deepest states, such as in Arc272 and Arc294, this is caused by the presence of thermoregulatory ascents during these deeper periods, but it is clear that for the majority of the fish, behaviour in deeper water is associated with larger vertical movements. It is important to note that the results from Arc217 must be interpreted in the knowledge that this yellowfin made a considerable longitudinal migration (over 30° West), and so contains data from two different regions with different mean surface temperatures. Subsequently, these separate sections of the time-series have been classified as distinct states in these HMMs, when in reality they probably fulfil the same behavioural role as one another. Despite the objective nature of our analysis, results must still be interpreted in light of significant shifts in environment that result from seasonality or migration.

Across all models, shallow states were generally more persistent than deep states. From the small sample of individuals examined here, it appears that yellowfin may be slightly more disparate than bigeye in the time they spend exhibiting shallow and deep behaviours, spending more time in shallow waters. In contrast, bigeye have more even amounts of time spent across their most shallow and deepest states. Once day and night are included as covariates in the transition matrices, a clear relationship between diel period and state switching was evident in all fish. This is consistent with previous descriptions of behaviour, whereby tuna feed on vertically migrating species in the sound-scattering layer (SSL) in the epipelagic layer during the night, and exploit prey in colder layers during the day. In addition, whilst some fish may abandon their deepest behaviours during the day (which has been referred to as ‘floating object association’ by some authors), it is rare that individuals exhibit anything other than their shallow or intermediate states during the night. This is demonstrated in the uniformity of time spent in shallow states during the night across all fish, whereas during the day, time spent across states is more varied. For those fish with intermediate states, these tended to be not only movements in cooler water, but also of greater mean step length than the shallowest states. In the raw archival data, this manifests itself as large amplitude movements into and out of the thermocline, with more time is spent exhibiting these intermediate behaviours during the night than during the daytime.

The relationship between size and behavioural switching is less clear in these results. It is assumed that tropical tuna ontogenetically develop an improved ability to exploit deeper layers of water as they grow through physiological adaptations such as growth of the swim bladder (Magnuson 1972), increased aerobic scope (Korsmeyer & Dewar 2001) and more effective endothermy (Graham et al. 2006). However, from the small subsample of tropical tuna investigated, we saw no clear evidence in consistent changes in behavioural switching across size. It is important to note that absence in size-based behavioural switching does not mean that behaviours are static across size. In this study, behavioural states have been estimated across the entire time-series, defined by distribution parameters that are assumed to be consistent across of the lifetime of the archival tag data. By including length information as a covariate in the transition probabilities between these states, the assumption is made that tuna have a distinct number of states as estimated from the entire time-series, but the switching between this is partially dependent on the size of the fish. However, from a biological perspective this may not occur. Rather, even at sizes where the physiological developments allowing sustained deep diving and foraging have not fully developed, individuals may still exhibit a deep state, albeit at a reduced depth or high movement amplitude, and switch to and from this state with the same probabilities as when they are larger. In this case, the size of the fish affects not the switching between states, but the nature of the states themselves. Such an effect can be incorporated in this approach by including length as covariate in the state-dependent distribution parameters, and is anticipated as a future development of this project. Indeed, this effect can be partially examined in the current analyses by comparing estimated models for the same fish with varying states. In the case of the small bigeye Arc294, a 2-state HMM consists of a fairly tightly distributed shallow state, and deep state that constitutes fairly high amplitude movements over a large range of temperatures. Under this model, the effect of a fish-length covariate on state transitions appears negligible. However, when looking at the results of the same individual using a 3-state model, estimated state distributions consist of similar shallow state to the 2-state model, and two deeper distributions. With these state-dependent distributions, the length effect on state switching suggests an increased proportion of time spent on the deepest, most tightly distributed state at the expense of the shallowest state. Potential evidence for this can be seen by these contrasting plots of rolling mean values of the median water temperature summary metrics for all probable instances of ‘deep’ state behaviour by fish length for a smaller and larger bigeye tuna, respectively (Figure 5.). The median temperatures of an individual tagged at a small size class (59 cm) decreased with estimated growth, whilst for the larger (tagged at 106cm) there is little change in the rolling mean temperature of the deep state.

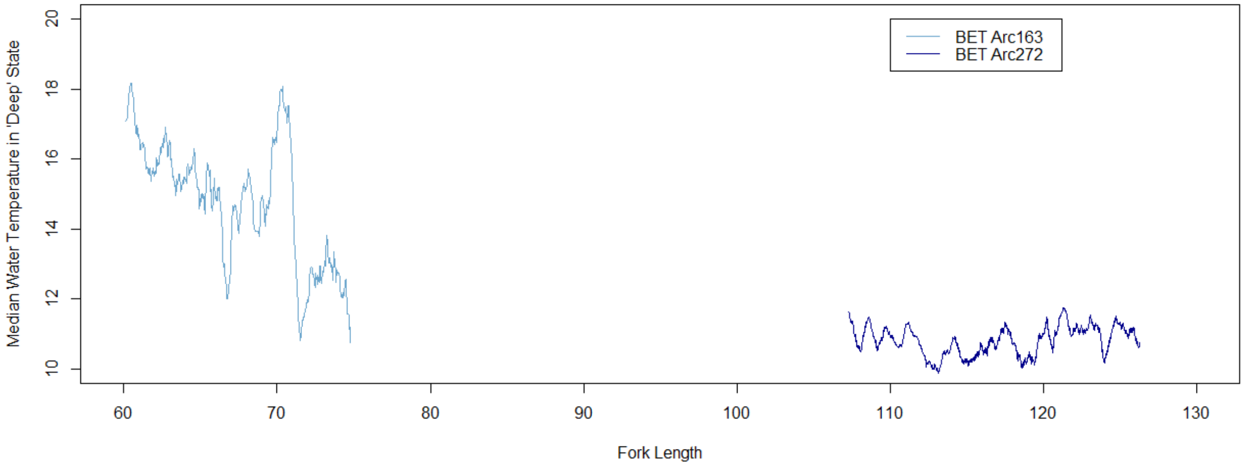

Figure 5. Comparison of the median water temperature observed during bouts of ‘deep’ state behaviour for two bigeye tuna. Observations are plotted as a rolling means of 30 observations.

Our investigation regarding the potential behavioural influence of FAD-dense areas on tropical tuna is far from conclusive, given the uncertainties in the horizontal estimates we have used and our sample size of two. The increased proportion of time spent exhibiting shallow behaviour when in the Bismark Sea by the smaller fish may be due to the increase in ‘associative’ type behaviour, and it is interesting to note that such an effect was less clear, or did not exist, in a larger individual. Some evidence exists for the strength of individual FAD associations being size-dependent (Robert et al. 2012), although there may be stronger location effects in the behaviour of fish across size classes. However, our focus here is on demonstrating the technique of using location covariates for examining questions such as these.

An important issue regarding model selection criteria still remains when using this approach to estimate HMMs for behavioural data such as these. The failure of the AIC to select meaningful or appropriate models is a cause for concern, and whilst use of pseudo-residuals to identify the most appropriate model is clear in some cases, many times it is not. In particular, models with higher numbers of states often increase the likelihood contribution of a small number of outlying observations by a new state distribution accommodating their inclusion, at the expensive of an increasing parameter space. Finding an objective method of model selection to be applied across applications is a key area for improvement.

This issue aside, our evaluation of HMMs for classifying vertical movement suggests that this class of models are potentially extremely useful for modelling the behaviour and ecology of tropical tunas within an objective framework. Our initial work here demonstrates a description of this behaviour that is consistent with previous literature, but that has further statistically incorporated potential covariate information such as time of day and length into this description. Critically, even in the cases where these covariates have not had clear relationships on behavioural switching, this approach provides a framework to assess whether it is the switching between different states, the nature of the behaviour itself, or a combination of the two that changes with these factors. Future developments of this study are anticipated to include an ability to examine covariates in these three ways. Such a framework allows the testing of fisheries management hypotheses on the full archival tag dataset of the PTTP, such as do FAD dense areas influence behaviour switching or the nature of behaviours, or how does vulnerability to fishing gears change temporally (throughout the day, season, with lunar phases etc.). Examining more individual fish that have been double tagged with both electronic and acoustic tags that record proximity to specific FADs would allow a more direct examination of the behaviour changes FAD-association using this approach. Depending on whether consistent behaviour states and/or transition matrices emerge from these fish, it may be possible to use models fitted to individuals with known periods of FAD association to estimate the probability of associative type behavioural patterns in new individuals for which this information is not known. Furthermore, for population dynamics models that contain a thermal component in habitat indices, such as SEAPODYM (Lehodey et al. 2008) which is currently used to inform and assess fisheries in the WCPO, these analyses provide a way to test and improve assumptions about age-based thermal habitat and its effect on the distribution and catchability of tropical tuna.

In this study we have demonstrated a new approach to describing the vertical behaviour in tropical tuna using hidden Markov-models. We identified clear and consistent shallow and deep states across individual fish, and biological factors such as size and species explain some of the differences that we observed. A clear relationship between the diel period and behavioural switching was seen, and this is consistent with previous studies. Although we found no evidence for a change in behavioural switching as fish increase in size, we suggest that increasing size may be responsible for gradual changes in the nature of individual states. This is a recommended area for development in future work. Using simple location covariates we have highlighted a method for examining in detail the effect that dense areas of FADs have on the individual behaviour of tuna, and aim to extend and improve this approach by examining more fish with a variety of more accurate information about proximate FAD-density and association.

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## Appendix 1. Current list of Archival Tags in the PTTP database

| *Release Date* | *Track Length in Days* | *Species* | *Fork Length* | *Tag Model* |
|---:|---:|:---:|---:|---:|
| 19/05/2005 8:10 | 137.99 | YFT | 77 | L24 |
| 20/05/2005 7:05 | 4.03 | YFT | 85 | L24 |
| 21/05/2005 7:00 | 3.03 | YFT | 84 | L24 |
| 22/05/2005 7:42 | 3.01 | YFT | 85 | L23 |
| 28/08/2006 3:55 | 3.21 | BET | 65 | L24 |
| 28/08/2006 18:05 | 2.60 | BET | 58 | L24 |
| 29/08/2006 10:05 | 204.22 | BET | 65 | L24 |
| 5/09/2006 19:11 | 41.50 | YFT | 104 | MK9 |
| 19/09/2006 18:55 | 81.03 | YFT | 109 | MK9 |
| 19/09/2006 19:05 | 12.54 | BET | 51 | L24 |
| 20/09/2006 3:00 | 12.31 | YFT | 54 | L24 |
| 20/09/2006 5:25 | 60.11 | YFT | 71 | L24 |
| 20/09/2006 5:50 | 12.08 | YFT | 54 | L24 |
| 20/09/2006 6:07 | 15.05 | YFT | 90 | MK9 |
| 20/09/2006 6:30 | 12.17 | YFT | 56 | L24 |
| 20/09/2006 9:15 | 48.20 | YFT | 68 | L24 |
| 20/09/2006 9:35 | 163.18 | YFT | 60 | L24 |
| 21/09/2006 7:45 | 24.99 | BET | 59 | L24 |
| 21/09/2006 8:50 | 11.04 | YFT | 59 | L24 |
| 21/09/2006 9:05 | 53.97 | YFT | 55 | L24 |
| 21/09/2006 19:58 | 13.47 | YFT | 101 | L23 |
| 21/09/2006 20:26 | 12.50 | YFT | 101 | L23 |
| 24/09/2006 18:56 | 9.51 | YFT | 102 | MK9 |
| 24/09/2006 21:07 | 123.75 | YFT | 98 | MK9 |
| 2/10/2006 19:20 | 73.91 | YFT | 97 | L11 |
| 20/10/2006 19:37 | 19.53 | BET | 67 | L11 |
| 20/10/2006 23:29 | 100.38 | BET | 67 | L11 |
| 21/10/2006 3:50 | 238.84 | BET | 62 | L11 |
| 21/10/2006 4:00 | 16.74 | BET | 63 | L24 |
| 3/01/2007 10:00 | 340.00 | YFT | 64 | L24 |
| 27/02/2007 8:20 | 115.74 | YFT | 61 | L24 |
| 27/02/2007 10:05 | 340.40 | YFT | 58 | L24 |
| 27/02/2007 12:25 | 207.22 | YFT | 50 | L24 |
| 13/03/2007 12:40 | 172.49 | YFT | 54 | L24 |
| 16/03/2007 13:05 | 3.76 | YFT | 46 | L24 |
| 16/03/2007 14:35 | 2.71 | YFT | 50 | L24 |
| 17/03/2007 12:47 | 84.11 | YFT | 85 | L23 |
| 26/03/2007 13:15 | 74.76 | YFT | 55 | L24 |
| 27/03/2007 9:38 | 59.01 | YFT | 74 | L23 |
| 27/03/2007 9:46 | 81.47 | YFT | 72 | L23 |
| 12/04/2007 12:21 | 158.43 | YFT | 75 | L23 |
| 15/04/2007 12:07 | 107.30 | YFT | 86 | L23 |
| 15/04/2007 12:48 | 77.84 | YFT | 86 | L23 |
| 27/03/2008 8:24 | 161.97 | YFT | 62 | MK9 |
| 27/03/2008 12:02 | 120.83 | YFT | 69 | MK9 |
| 3/04/2008 6:26 | 6.07 | YFT | 67 | MK9 |
| 10/05/2008 7:48 | 148.01 | YFT | 68 | MK9 |
| 11/05/2008 11:05 | 60.88 | BET | 68 | MK9 |
| 16/05/2008 6:39 | 287.05 | BET | 73 | MK9 |
| 16/05/2008 7:11 | 285.02 | BET | 72 | MK9 |
| 16/05/2008 15:46 | 72.66 | BET | 70 | MK9 |
| 17/05/2008 9:21 | 222.98 | BET | 77 | MK9 |
| 17/05/2008 10:06 | 112.39 | BET | 86 | MK9 |
| 17/05/2008 16:48 | 192.65 | BET | 85 | MK9 |
| 18/05/2008 12:28 | 92.81 | BET | 106 | MK9 |
| 24/05/2008 7:46 | 117.02 | BET | 79 | MK9 |
| 24/05/2008 18:04 | 207.59 | BET | 83 | MK9 |
| 1/06/2008 15:14 | 31.97 | YFT | 88 | MK9 |
| 4/11/2008 13:31 | 4.75 | BET | 51 | L25 |
| 4/11/2008 13:35 | 4.76 | BET | 53 | L25 |
| 5/11/2008 14:32 | 154.81 | BET | 62 | MK9 |
| 8/11/2008 11:56 | 1.82 | BET | 69 | MK9 |
| 8/11/2008 11:59 | 1.81 | BET | 57 | L25 |
| 8/11/2008 12:07 | 1.81 | BET | 51 | L25 |
| 8/11/2008 12:17 | 1.81 | BET | 62 | MK9 |
| 8/11/2008 12:23 | 1.80 | BET | 53 | L25 |
| 8/11/2008 12:27 | 1.80 | BET | 50 | L25 |
| 8/11/2008 12:27 | 173.67 | BET | 59 | L25 |
| 8/11/2008 12:28 | 1.80 | BET | 60 | MK9 |
| 8/11/2008 12:31 | 1.79 | BET | 49 | L25 |
| 8/11/2008 22:07 | 1.82 | BET | 54 | L25 |
| 12/11/2008 5:55 | 14.05 | BET | 47 | L25 |
| 26/03/2009 13:15 | 54.85 | BET | 52 | L25 |

| | | | | |
|---|---|---|---|---|
| 27/03/2009 5:27 | 40.10 | BET | 48 | L25 |
| 27/03/2009 6:35 | 28.09 | BET | 47 | L25 |
| 30/04/2009 8:06 | 61.00 | YFT | 105 | L23 |
| 26/05/2009 8:01 | 152.94 | BET | 58 | MK9 |
| 26/05/2009 8:25 | 24.93 | BET | 60 | MK9 |
| 5/06/2009 19:12 | 25.44 | BET | 57 | L23 |
| 5/06/2009 21:00 | 35.47 | BET | 56 | L23 |
| 5/06/2009 22:34 | 21.64 | BET | 67 | L23 |
| 5/06/2009 23:12 | 180.21 | BET | 60 | L23 |
| 6/06/2009 18:29 | 128.49 | BET | 92 | L23 |
| 6/06/2009 18:44 | 8.49 | BET | 107 | L23 |
| 6/06/2009 21:19 | 100.40 | BET | 88 | L23 |
| 6/06/2009 21:59 | 137.33 | BET | 86 | L23 |
| 31/07/2009 8:27 | 41.34 | SKJ | 49 | L25 |
| 5/08/2009 9:06 | 30.35 | YFT | 56 | L23 |
| 1/09/2009 11:23 | 4.01 | SKJ | 49 | L25 |
| 1/09/2009 11:27 | 11.76 | SKJ | 52 | L25 |
| 10/10/2009 21:15 | 25.30 | YFT | 86 | MK9 |
| 12/10/2009 4:37 | 38.09 | BET | 82 | MK9 |
| 12/10/2009 5:38 | 19.07 | BET | 59 | MK9 |
| 12/10/2009 6:04 | 13.03 | BET | 68 | MK9 |
| 23/10/2009 19:28 | 99.60 | YFT | 68 | L23 |
| 24/10/2009 5:19 | 71.36 | YFT | 78 | L28 |
| 24/10/2009 19:16 | 214.41 | BET | 65 | MK9 |
| 26/10/2009 16:35 | 10.64 | BET | 67 | MK9 |
| 26/10/2009 16:36 | 10.63 | BET | 70 | MK9 |
| 26/10/2009 16:39 | 10.63 | BET | 72 | MK9 |
| 26/10/2009 16:43 | 10.62 | BET | 67 | MK9 |
| 26/10/2009 16:51 | 384.53 | BET | 69 | MK9 |
| 26/10/2009 16:55 | 10.61 | BET | 70 | MK9 |
| 26/10/2009 17:03 | 261.58 | BET | 63 | MK9 |
| 26/10/2009 17:21 | 50.65 | BET | 58 | L23 |
| 27/10/2009 20:41 | 98.72 | BET | 60 | L28 |
| 27/10/2009 21:52 | 196.67 | BET | 61 | L28 |
| 12/05/2010 4:21 | 27.12 | BET | 73 | MK9 |
| 13/05/2010 4:30 | 38.14 | BET | 85 | MK9 |
| 5/06/2010 8:21 | 302.43 | YFT | 79 | MK9 |
| 5/06/2010 8:23 | 487.94 | YFT | 98 | MK9 |
| 23/11/2010 17:20 | 180.46 | BET | 96 | MK9 |
| 24/11/2010 6:26 | 24.06 | BET | 82 | MK9 |
| 24/11/2010 9:07 | 71.89 | BET | 80 | MK9 |
| 24/11/2010 16:39 | 360.57 | BET | 106 | MK9 |
| 26/11/2010 9:21 | 262.86 | BET | 84 | MK9 |
| 11/10/2011 8:29 | 102.97 | BET | 77 | MK9 |
| 12/10/2011 7:16 | 104.00 | BET | 76 | MK9 |
| 14/10/2011 17:04 | 56.58 | BET | 72 | MK9 |
| 19/10/2011 8:17 | 224.94 | BET | 68 | MK9 |
| 22/10/2011 6:43 | 26.00 | BET | 69 | L28 |
| 13/11/2011 20:20 | 153.36 | BET | 67 | MK9 |
| 13/11/2011 20:22 | 131.60 | BET | 76 | MK9 |
| 13/11/2011 20:50 | 246.86 | BET | 79 | MK9 |
| 14/11/2011 20:23 | 291.34 | BET | 69 | L28 |
| 14/11/2011 21:11 | 221.29 | BET | 89 | L28 |
| 5/12/2011 8:56 | 59.96 | BET | 51 | L28 |
| 7/12/2011 19:50 | 236.40 | BET | 51 | L28 |
| 9/12/2011 19:25 | 318.44 | BET | 53 | L28 |
| 10/12/2011 6:44 | 60.15 | BET | 51 | L28 |
| 29/01/2012 12:41 | 279.76 | YFT | 63 | L28 |
| 29/01/2012 12:46 | 56.88 | YFT | 64 | L28 |
| 2/10/2012 7:36 | 10.00 | BET | 65 | MK9 |

## Appendix 2. HMM Model description

The HMM used assumes that observations of the summary metrics were drawn from a number, *m*, of multivariate normal distributions, each with separate parameters depending on the current hidden state. This observational model is identical to a mixture model, except that in an HMM the switching between underlying states forms a Markov-chain. The transition probabilities between these 'hidden' states, $S_1$ to $S_m$, are estimated parameters, i.e. the likelihood of doing something at one time depends on what the fish was doing at the previous timestep, and thus accounts for the autocorrelative nature of these behavioural time-series. These transition probabilities, $\pi_{i\text{-}j}$, between hidden states can be thought of in terms of the transition matrix, Γ, where

$$\Gamma = \begin{array}{c} \\ \mathrm{S}_1 \\ \vdots \\ \mathrm{S}_\mathrm{m} \end{array} \begin{array}{c} \begin{array}{ccc} \mathrm{S}_1 & \cdots & \mathrm{S}_\mathrm{m} \end{array} \\ \begin{bmatrix} \pi_{1-1} & \cdots & \pi_{1-\mathrm{m}} \\ \vdots & \ddots & \vdots \\ \pi_{\mathrm{m}-1} & \cdots & \pi_{\mathrm{m}-\mathrm{m}} \end{bmatrix} \end{array}$$

While some data forms the basis of the observational model, other covariate data can also be included in this transition matrix, capturing the effect that this information may have on the transition probabilities between states. If a linear effect is assumed, then for each transition probability, $\pi_{i\text{-}j}$,

$$\pi = \alpha + \beta\gamma$$

Where γ is a continuous or binary covariate, and both α and β are estimated parameters.

The likelihood of a given set of time-series data from t=1...T is

$$L_T = \Pr(x_1, x_2, x_3 \ldots x_T)$$

Under the assumptions of a mixture model, with *m* underlying distributions,

$$L_T = \prod_T \left\{ \sum_M (\Pr(x_t \mid S_m) \cdot \Pr(x_t \in S_m)) \right\}$$

Here, the contribution to the likelihood at each time-step is the product of the probability of an observation being drawn from a state-dependent distribution and the probability that the observation comes from a time when the system was in that state, summed across all possible states. The total likelihood is the product, or the summed logarithms, of all these likelihood contributions from t = 1 to T.

In an HMM, the observation model remains the same, but now our state probability, which we re-write as $\Pr(S_m)$, is dependent on what we have observed in the system at t-1. Thus

$$\begin{aligned} L_T &= \prod_T \left\{ \sum_M (\Pr(x_t \mid S_m) \cdot \Pr(S_m)) \right\} \\ &= \prod_T \left\{ \sum_M (\Pr(x_t \mid S_m) \cdot \Pr(S_m \mid S_{m-1}\, x_{t-1})) \right\} \\ &= \prod_T \left\{ \sum_M (\Pr(x_t \mid S_m) \cdot \Pr(S_m \mid S_{m-1}) \cdot \Pr(S_{m-1} \mid x_{t-1})) \right\} \end{aligned}$$

In this case, the observation model is a state-dependent multivariate normal distribution, *N*, such that we assume

$$X \in N(\mu, \Sigma)$$

Where $\mu$ is a multivariate mean in *k* dimensions, and $\Sigma$ is a *k* by *k* covariance matrix.

We use summary metrics calculated from archival tagging data as our multivariate normally drawn observations, and include a range of covariates such as the diel period or size of fish in our estimated transition matrices. Parameters are numerically estimated by conversation of the likelihood to a negative logarithm and minimisation using the *optim* function in R.

## Appendix 3. Simulation Experiments

Three simulation experiments were carried out to assess the accuracy of our method for identifying behaviour states in the vertical behaviour of tuna. We generated three sets of artificial data which simulated dive track summary metrics drawn from the following state-dependant mixture of bivariate normal distributions. Example data from each scenario is given in figure A3-1.

1. Three distributions identical in covariance but well separated by their means. State switching is autocorrelated and governed by a set of transition probabilities which result in highly persistent periods of each state. We expect an HMM to perform very well in such a straight forward scenario with clear distributions and persistent state transitions.
2. Three distributions of differing covariance, with two of those distributions sharing the same mean. State transition probabilities include a binary covariate which switches values regularly every 10 timesteps. States are still persistent, but less so than in scenario 1. This constitutes a much harder task for an HMM, with two very similar states, and more complex, transient state transitions.
3. The same three distributions as in scenario 2 but with no state transition probabilities. State switching is independent, and driven by three different probabilities. In this case, while an HMM should estimate parameters we expect that a mixture model, with no estimated transition matrix, should provide the more parsimonious solution.

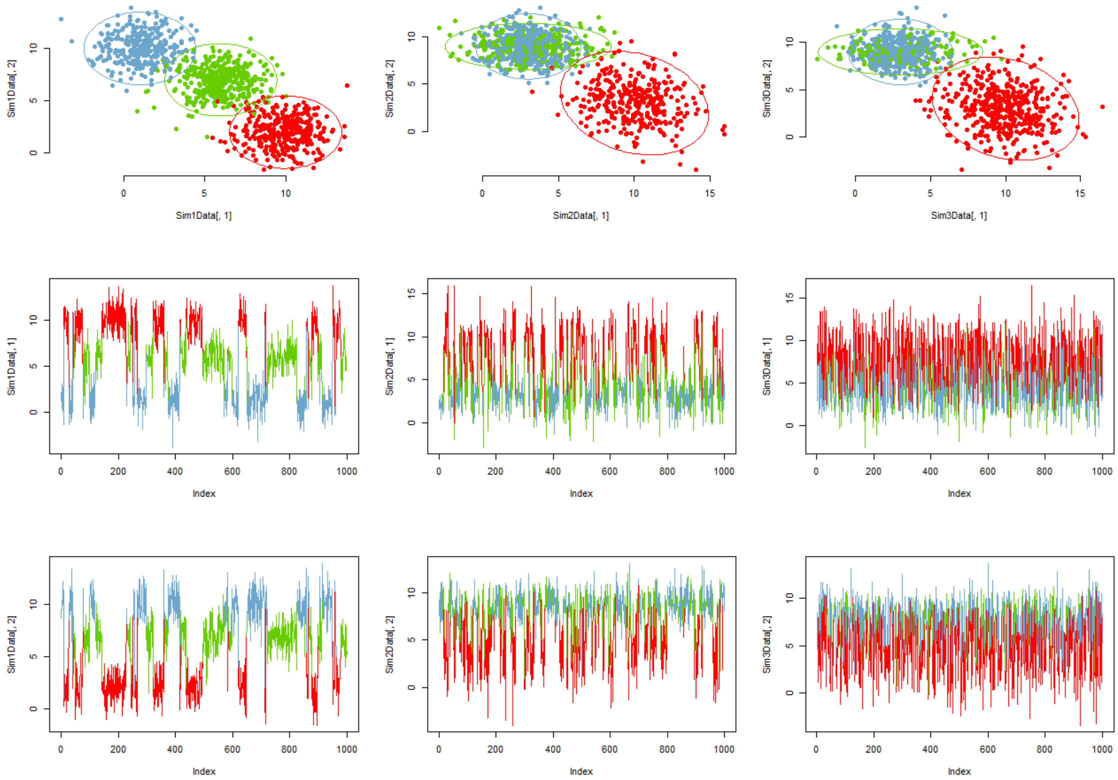

**Figure A3-1 Examples of artificial data generated under each scenario (cols 1-3). Row1: Bivariate data plots, with true state covariances and colours marked. Rows 2-3: Metric 1 and 2 through time, with true states coloured.**

For each scenario, 10 sets of data were generated (N = 1000) and the parameters for both an independent mixture model and a hidden Markov model with two, three and four states were estimated. Mean AICs are given for all these models in Table A3-1. True and estimated parameters from the three-state HMMs are summarised in Table A3-2, and example pseudo residuals are displayed in Figure A3-2. Confusion matrices between the most likely state predictions at each time step and the true, known states are also given for these models.

Table A3-1

| Model | Mean AIC |
|---|---|
| *Scen. 1* | |
| HMM 2-State | 8384.179 |
| HMM 3-State | 7492.038 |
| HMM 4-State | **7451.729** |
| Mixure Model 2-State | 9375.814 |
| Mixure Model 3-State | 9128.736 |
| Mixure Model 4-State | 9119.139 |
| *Scen. 2* | |
| HMM 2-State | 8444.915 |
| HMM 3-State | 8411.69 |
| HMM 4-State | **8328.584** |
| Mixure Model 2-State | 8998.56 |
| Mixure Model 3-State | 8997.167 |
| Mixure Model 4-State | 8999.166 |
| *Scen. 3* | |
| HMM 2-State | 9222.804 |
| HMM 3-State | 9210.701 |
| HMM 4-State | **9193.782** |
| Mixure Model 2-State | 9227.295 |
| Mixure Model 3-State | 9225.498 |
| Mixure Model 4-State | 9227.091 |

Table A3-2

| **Model** | $\mu_1$ | $\mu_2$ | $\mu_3$ | $\Sigma_1$ | $\Sigma_2$ | $\Sigma_3$ | $\pi_1$ | $\pi_2$ | $\pi_3$ |
|---|---|---|---|---|---|---|---|---|---|
| ***Scen. 1 True*** | 10<br>2 | 6<br>7 | 1<br>10 | $\begin{bmatrix}2 & 0\\0 & 2\end{bmatrix}$ | $\begin{bmatrix}2 & 0\\0 & 2\end{bmatrix}$ | $\begin{bmatrix}2 & 0\\0 & 2\end{bmatrix}$ | 0.96<br>0.02<br>0.02 | 0.02<br>0.96<br>0.02 | 0.02<br>0.02<br>0.96 |
| HMM 3-State | 10.025<br>2.014 | 6.031<br>7.021 | 1.035<br>10.025 | $\begin{bmatrix}2.09 & 0.04\\0.04 & 1.99\end{bmatrix}$ | $\begin{bmatrix}2.02 & 0.14\\0.14 & 1.99\end{bmatrix}$ | $\begin{bmatrix}2.08 & 0.15\\0.15 & 2.06\end{bmatrix}$ | 0.919<br>0.041<br>0.040 | 0.040<br>0.920<br>0.039 | 0.035<br>0.041<br>0.924 |
| MM 3-State | 10.053<br>2.029 | 6.078<br>7.056 | 1.059<br>10.051 | $\begin{bmatrix}2.18 & 0.1\\0.1 & 2.09\end{bmatrix}$ | $\begin{bmatrix}2.14 & 0.33\\0.33 & 2.1\end{bmatrix}$ | $\begin{bmatrix}2.13 & 0.19\\0.19 & 2.14\end{bmatrix}$ | 0.346 | 0.366 | 0.289 |
| ***Scen. 2 True*** | 3<br>9 | 3<br>9 | 10<br>3 | $\begin{bmatrix}2 & 0\\0 & 2\end{bmatrix}$ | $\begin{bmatrix}5 & 0\\0 & 1\end{bmatrix}$ | $\begin{bmatrix}4 & -1\\-1 & 5\end{bmatrix}$ | 0.96<br>0.02<br>0.02 | 0.35<br>0.30<br>0.35 | 0.02<br>0.02<br>0.96 |
| HMM 3-State | 3.658<br>8.551 | 5.213<br>7.233 | 9.493<br>3.317 | $\begin{bmatrix}2.81 & 0.01\\0.01 & 1.83\end{bmatrix}$ | $\begin{bmatrix}4.20 & 0.0\\0.0 & 2.41\end{bmatrix}$ | $\begin{bmatrix}3.77 & -0.8\\-0.8 & 4.32\end{bmatrix}$ | 0.590<br>0.279<br>0.131 | 0.383<br>0.292<br>0.325 | 0.160<br>0.111<br>0.730 |
| MM 3-State | 3.66<br>8.500 | 5.329<br>7.204 | 9.567<br>3.410 | $\begin{bmatrix}2.7 & 0.25\\0.25 & 1.65\end{bmatrix}$ | $\begin{bmatrix}3.40 & 0.50\\0.50 & 2.63\end{bmatrix}$ | $\begin{bmatrix}3.64 & -0.5\\-0.5 & 4.18\end{bmatrix}$ | 0.445 | 0.264 | 0.291 |
| ***Scen 3. True*** | 3<br>9 | 3<br>9 | 10<br>3 | $\begin{bmatrix}2 & 0\\0 & 2\end{bmatrix}$ | $\begin{bmatrix}5 & 0\\0 & 1\end{bmatrix}$ | $\begin{bmatrix}4 & -1\\-1 & 5\end{bmatrix}$ | 0.40 | 0.15 | 0.45 |
| HMM 3-State | 4.35<br>8.30 | 6.29<br>6.44 | 8.76<br>4.03 | $\begin{bmatrix}3.24 & -0.0\\-0.0 & 3.20\end{bmatrix}$ | $\begin{bmatrix}4.89 & 0.60\\0.60 & 1.85\end{bmatrix}$ | $\begin{bmatrix}3.87 & -0.6\\-0.6 & 4.09\end{bmatrix}$ | 0.253<br>0.339<br>0.413 | 0.288<br>0.297<br>0.414 | 0.278<br>0.356<br>0.366 |
| MM 3-State | 3.71<br>8.52 | 6.25<br>6.46 | 10.43<br>2.62 | $\begin{bmatrix}2.71 & 0.25\\0.25 & 1.97\end{bmatrix}$ | $\begin{bmatrix}2.9 & 0.30\\0.30 & 2.66\end{bmatrix}$ | $\begin{bmatrix}3.56 & 0\\0 & 3.90\end{bmatrix}$ | 0.442 | 0.256 | 0.302 |

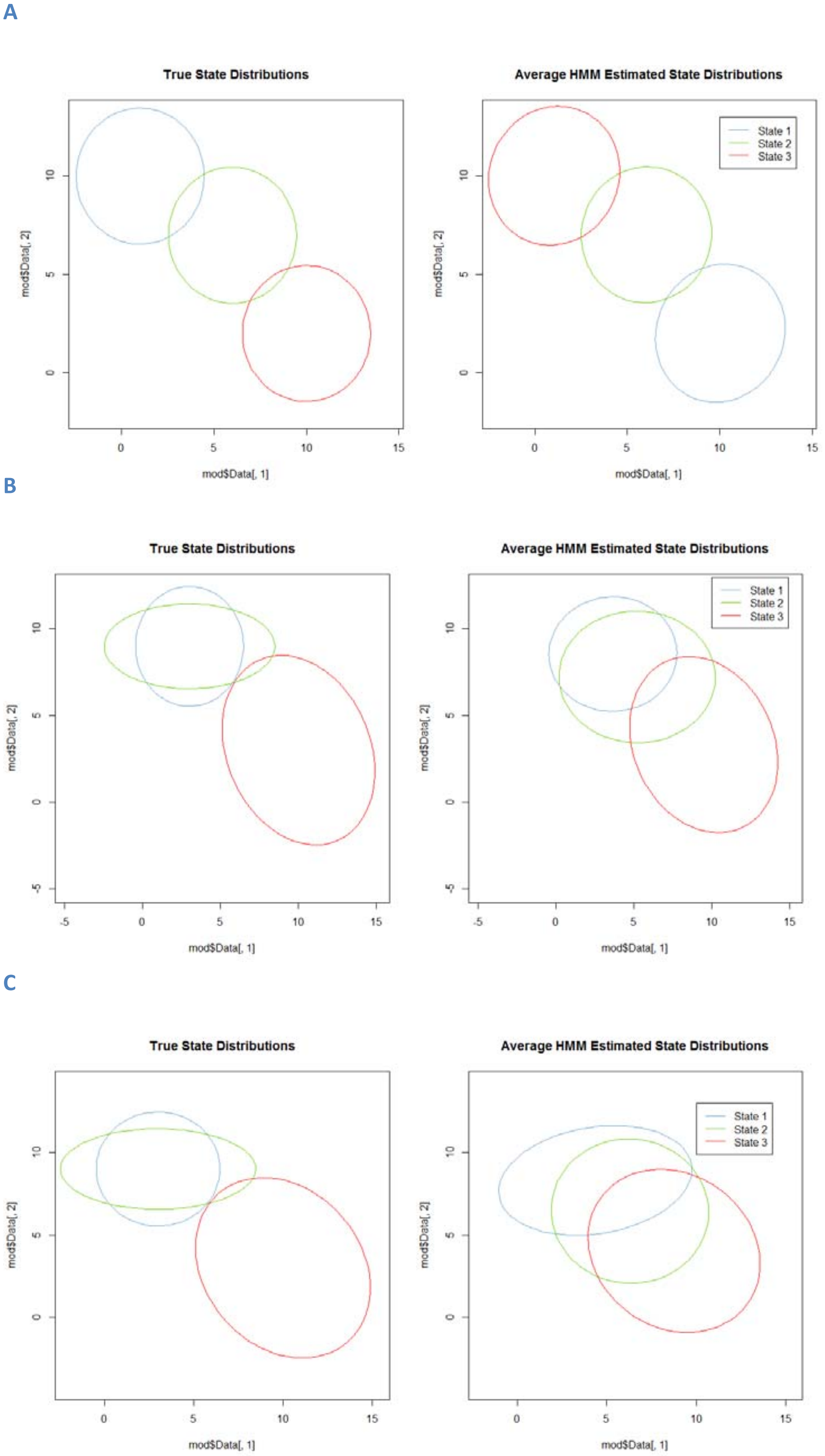

**Figure A3-2. Mean results for 3-state HMMs. A= Scenario 1; B= Scenario 2; C= Scenario 3**

When using linear-regression to model observations of a random variable, the concept of using residuals is a well developed method for assessing the fit and suitability of a particular model. In an HMM we do not aim to predict the value of a response variable, but rather the nature and probability of observations being drawn from underlying states. As such, there are no residuals in the sense of the difference between predicted and observed values. However, Zucchini & MacDonald (2009) introduce quantities called pseudo-residuals which aim to fulfil the same model checking role.

Uniform pseudo-residuals are defined as the probability, assuming the observation distributions and state probabilities of the fitted model, of obtaining an observation less than or equal to each individual observation. For appropriate models, these pseudo-residuals should be uniformly distributed between 0 and 1, with outlier observations generating residuals close to 0 or 1. Similarly, normal pseudo-residuals can be examined by plotting a quantile-quantile plot or histogram of the normal cumulative distribution of the ordinary pseudo-residuals. This allows a clearer view of outliers in the data. Finally, plotting these normal pseudo-residuals through time should reveal little structure in pattern and occurrence if the model is appropriate.

For scenario 1 results, there was a clear improvement in pseudo-residuals between the two- and three-state HMMs (Figure A3-3). Time-dependent structure in residuals decreases significantly with the increase in hidden state, and residuals are also distributed more closely to the expect distributions. The four-state model does not noticeably improve these residuals.

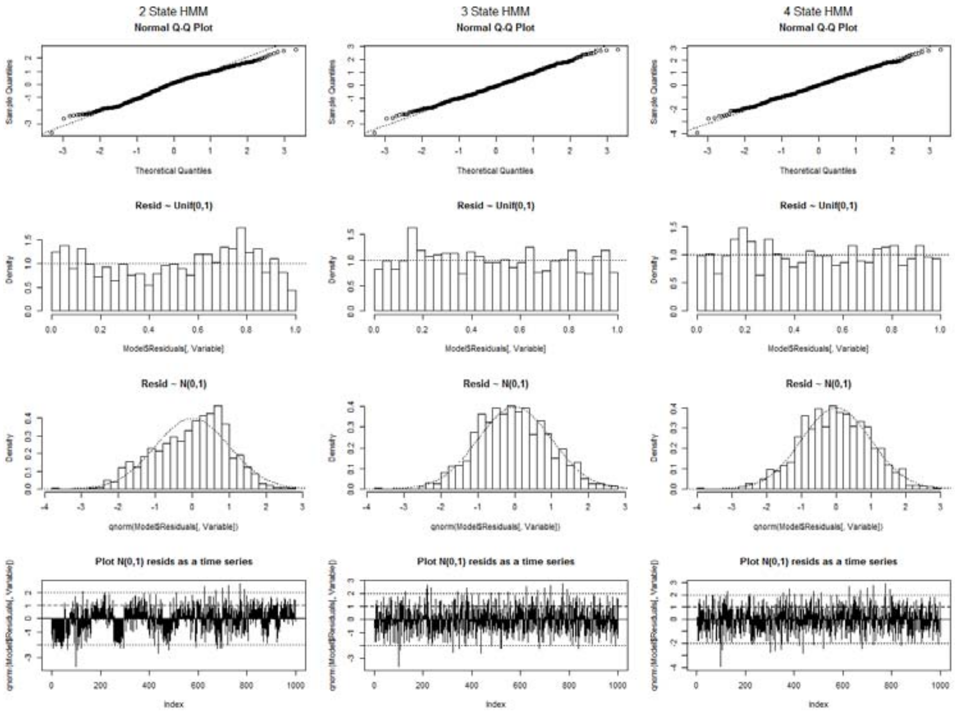

Figure A3-3 Scenario 1 Pseudo-residuals for one dimension of observation data

In scenario 2, the change in pseudo-residuals across models is not clear (Figure A3-4). Although the uniformity of residual distributions appears better for the two-state model, increasing the number of states to three eliminates a number of clear outliers that can be seen in the skew of the Q-Q plot and normal distribution. The increase from three to four states does noticeably improve the distribution or structure of these pseudo-residuals. For scenario 3, where none of the HMMs are an appropriate model, we see very little improvement in pseudo-residual distribution across models of increasing hidden state number (Figure A3-5).

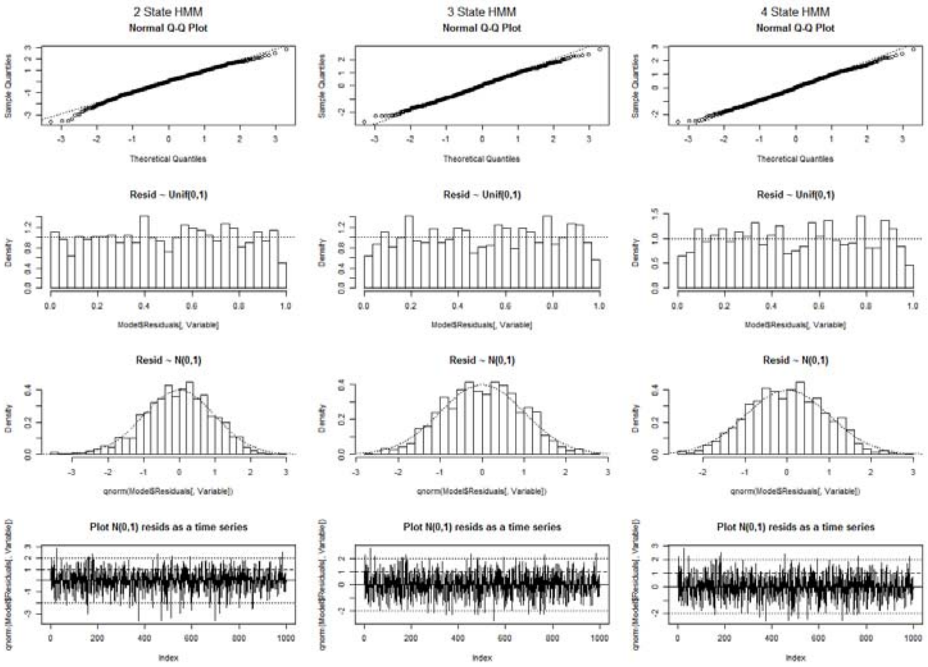

Figure A3-4 Scenario 2 Pseudo-residuals for one dimension of observation data

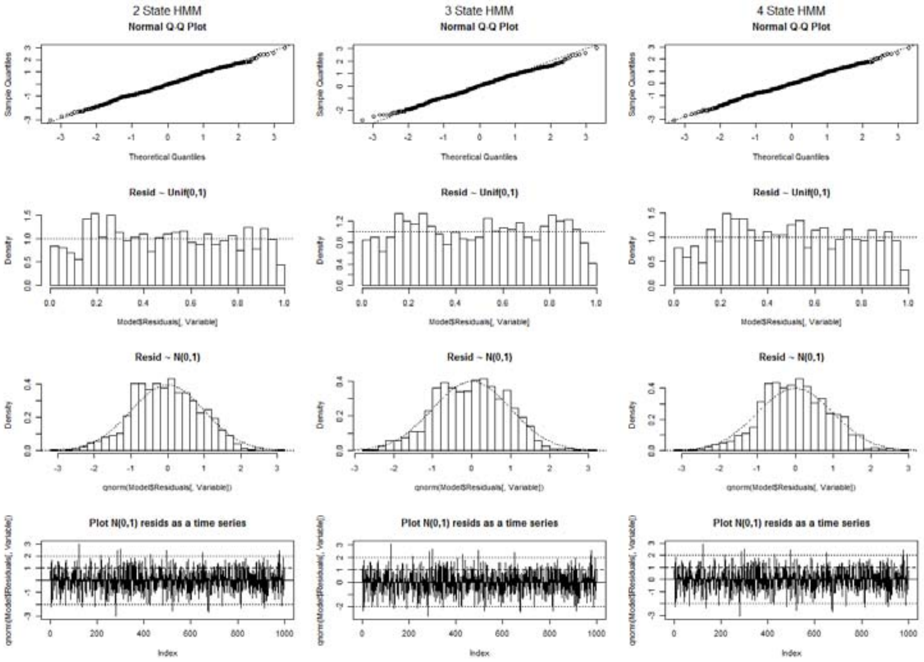

Figure A3-5 Scenario 3 Pseudo-residuals for one dimension of observation data

## Appendix 4. Selected models in full analysis

Table A4-1 Summary of the selected HMM models (2, 3 or 4 state)

| HMM | Arc294 | Arc163 | Arc302 | Arc88 | Arc272 | Arc217 | Arc269 | Arc220 |
|---|---|---|---|---|---|---|---|---|
| No covariate | 3 | 2 | 2 | 2 | 3 | 3 | 2 | 3 |
| Diel | 4 | 2 | 4 | 2 | 3 | 3 | 2 | 2 |
| Length | 3 | 2 | 2 | 2 | 3 | 3 | 2 | 2 |