UNIVERSITY OF SOUTHAMPTON

FACULTY OF NATURAL EARTH SCIENCES

School of Ocean and Earth Science

On the Movement Behaviours of Tropical Tuna in Modern Commercial Fisheries

by

Joe Scutt Phillips

Thesis for the degree of Doctor of Philosophy

October 2014

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF NATURAL EARTH SCIENCES

Complexity Science

Thesis for the degree of Doctor of Philosophy

ON THE MOVEMENT BEHAVIOURS OF TROPICAL TUNA IN MODERN COMMERCIAL FISHERIES

by Joe Scutt Phillips

Exploitation of tropical tunas in the western and central Pacific Ocean constitutes an industry generating over US$5 billion annually. As concern for the sustainability of fishing operations grows, there is an increasing need to explore the potential effects that small-scale movement behaviours, typically ignored in stock assessment, may have on larger scale population dynamics. In this thesis, I examine a variety of individual movement behaviours exhibited by skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) tuna in the context of their vulnerability to fishers.

A number of simulation models of potential foraging by tuna in their environment were developed. Simulations used alternate habitat-utilisation and prey-field assumptions to test hypotheses regarding emergent behaviour in tuna, in particular examining vulnerability to habitat-specific fishing gears and fish aggregation devices (FADs). In conjunction, vertical movement data from bio-logging experiments on tuna were examined, initially using machine learning classification, but problems of autocorrelated data, lack of objectivity and low statistical power suggested that new analytical methods were needed. In light of this, a new approach to probabilistically classify multivariate bio-logging time-series, using existing methods of hidden Markov modelling, was developed.

The method was applied to vertical movement from 75 yellowfin and bigeye tuna, identifying two clear behavioural states and strong patterns of diurnal state-switching in both species. Evidence for deepening of deep state behaviour in bigeye was found, and high levels of behavioural variability between individuals seen, particularly in the hours following dawn.

The methods developed in this study are an improvement over previous approaches, being more objective and quantitative, and their suggested incorporation into standardisation of catch-per-unit-effort and catchability parameters is discussed. Specifically, they suggest that FADs may not act as ‘ecological traps’ as has previously been hypothesised, and that fluctuations in the prey field are the likely mechanism behind the high variability seen in vertical movement behaviours of tropical tuna.

Table of Contents

List of tables

List of figures

DECLARATION OF AUTHORSHIP

I, Joe Scutt Phillips, declare that this thesis and the work presented in it are my own and have been generated by me as the result of my own original research.

On the Movement Behaviours of Tropical Tuna in Modern Commercial Fisheries ....

....

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Parts of this work have been published as:

   Scutt Phillips J., Patterson T.A., Leroy B., Pilling G.M., Nicol S. (*In Press*) Objective Classification of Latent Behavioural States in Bio-logging Data using Multivariate-normal Hidden Markov Models. *Ecological Applications*. [Parts of Chapter 5]

   Leroy B., Evans K., **Scutt Phillips J.**, Patterson T.A., Caillot S., Usu T., Kumasi B., Davies C., Nicol S., Kumoru L. (2014) Progress report on archival tagging within the Papua New Guinea Tagging Program. *Proc. of the Western and Central Pacific Fisheries Commission Scientific Committee Tenth Regular Session.* Pohnpei, Federated States of Micronesia. [Parts of Chapter 6 and 7]

Scutt Phillips J., Patterson T.A., Pilling G.M., Hoyle S., Leroy B., Nicol S. (2013) Species-specific Vertical Habitat Utilisation by Tunas in the Tropical WCPO. *Proc. of the Western and Central Pacific Fisheries Commission Scientific Committee Ninth Regular Session.* Pohnpei, Federated States of Micronesia. [Parts of Chapter 5]

Leroy B. **Scutt Phillips J.**, Nicol S., Pilling G.M., Harley S., Bromhead D., Hoyle S., Caillot S., Allain V., Hampton J. (2012) A critique of the ecosystem impacts of drifting and anchored FADs use by purse-seine tuna fisheries in the Western and Central Pacific Ocean. *Aquatic Living Resources* **26**(1), 49-61. [Parts of Chapter 2]

Signed: ....

Date: 4th October, 2015 ....

Acknowledgements

The previous four years of work is the result of much support and collaboration, and this thesis would not have been possible without contributions from a great many people. Here, I would like to take this opportunity to thank a small number of those individuals and organisations.

First of all, I would like to thank Professor Seth Bullock at the Institute for Complex Systems and the EPSRC for providing my studentship to undertake this PhD. I am very grateful for being given the opportunity carry out research on my interests in fisheries and marine ecology with such free reign and in such a positive atmosphere. The complexity mindset is one that I will carry forward in all my future work.

I would also like to thank the staff at the Lenfest Ocean Program for their financial support towards the travel and subsistence needed for this project. Without the ability to work with real data, real stakeholders, and alongside such knowledgeable people, this PhD would have been a shadow of what it has become. I am immensely grateful to have had such an incredible opportunity.

Many thanks must go to Dr Clive Trueman at the National Oceanography Centre for accepting to supervise me, despite my work being somewhat outside his normal area of research. I appreciate hugely the guidance you have given me, and the many useful comments you provided in response to rambling documents and emails sent to you in the middle of the night from the other side of the world. Similarly, I would like to express my gratitude to Dr Jason Noble for his supervision regarding the statistics and modelling side of this thesis. I enjoyed our many discussions immensely, and always left your office laughing, quoting Brass Eye, and with a sense of renewed direction for my “fish project”.

I am hugely grateful to Dr Graham Pilling at the Secretariat of the Pacific Community, who’s continued interest in my development still baffles me, but to whom I feel indebted for almost every significant progression in my career. As always, thank you so much for everything. I must also give thanks to Dr Simon Nicol at SPC in New Caledonia for accepting me for such a long and wonderful student placement. I have learnt so much about the ecology of pelagic fish and fisheries, and I was made very much at home as part of the

EMA team. The staff and my colleagues at SPC were so welcoming and made my move to a strange country easy beyond belief. Thank you to the many administrative and technical people who helped me with both work and life during my time in New Caledonia.

The period I spent working on hierarchical modelling at CSIRO in Tasmania was an intense but incredibly useful month, and I would like to thank the institution for hosting me during this time. In particular, thanks go to Dr Toby Patterson, Dr Chris Wilcox, and Dr Marinelle Basson for all the time they gave up to teach me so much and for arranging such a great placement.

Outside of the science, many people helped me get through the ups and downs of this project over the previous four years, and although it would be impossible to thank all of them individually, their support has been beyond value. To my many, many good friends in Nouméa, I would like to say thank for you everything, you have all given me so many wonderful memories and I am forever indebted to you all. Thank you for teaching me to speak French and helping me experience such a beautiful country as much as I could whilst undertaking a PhD.

I would like to thank all of my family, and in particular my mother and father, for always encouraging me and making me feel like I could do whatever it was in life I might set my mind to. They have always been there to listen and provide advice to someone lost in their own work and life. Big shout-outs to the Super SQUAD, and all my friends in Southampton, who helped put everything in perspective over many evenings of laughter and adventures.

Lastly, I would like to give my deepest love and appreciation to Miss Vikitolia Fulilagi. Thank you for everything, I don’t think I could have done this last stage without you. I’m sorry for all the stress and the many ups and downs. Tu m'as rendu la vie plus belle. L’effort dans ces choses valent toujours le coup.

Definitions and Abbreviations

BET	Bigeye Tuna (*Thunnus obsesus*)
AFAD	Anchored Fish Aggregation Device
Catchability	An abstract value representing the fraction of a population that is caught as a result of a given unit of fishing effort
CPUE	Catch-per-unit-effort, a measure of catch (usually by weight) by standard measure of effort. Effort can comprise of a number of alternate metrics, such as days fishing or number of hooks set.
DFAD	Drifting Fish Aggregation Device
FAD	Fish Aggregation Device, a fishing gear
Fork Length FL	A measure of fish size, from the tip of the mouth to the point of forking in the tail
Free School	A school of tuna that is not associated to a floating object or other structure, but are freely moving both horizontally and/or vertically
Prey Field	The local distribution and abundance of species which constitute prey for oceanic top predators
Recruitment Overfishing	A form of overfishing in which very high catches of not-yet-mature fish results in a lack of mature spawning fish in the population at a later time.
SKJ	Skipjack Tuna (*Katsuwonus pelamis*)
WCPFC	The Western and Central Pacific Fisheries Commission
WCPO	The Western and Central Pacific Ocean
YFT	Yellowfin Tuna (*Thunnus albacares*)

Chapter 1: Introduction

1.1 The Exploitation of Tropical Tuna

"Speaking from one of the keepers of the resource, we bring to the gathering stocks that are in good shape. From time immemorial, we have taken our fair share to cater to our needs but we understand the need to share, not only because of the nutritional value of fish but because over 800 million people starve on this planet every year. These are not faceless people in distant lands but fellow travellers in time and space."

– The Honourable Dr Masaso Paunga, Minister for the Kingdom of Tonga, speaking on tuna stocks in the waters around the island nation of Tonga. Taken from the minutes of the second Multilateral, High-Level Conference, Majuro, Republic of the Marshall Islands, 1997.

1.1.1 Tuna and the Pelagic Domain

Long before humans began hunting large pelagic fishes such as tuna to supply their food requirements, these species had evolved complex behaviours related to their own hunt for prey. In the three-dimensional realm of the pelagic domain, ecological concepts such as habitat and resource availability become increasingly dynamic in their semantics. For the most part an environment devoid of permanent features, the open ocean never the less provides transient features across a variety of scales that profoundly influence the behaviour the animals living within this habitat (Levin 1992). These transient features include the large-scale movements of bodies of water, meso-scale eddies and upwelling, and the concentration and availability of schools of prey in the local vicinity (Benoit-Bird and Au 2004; Lehodey and Maury 2010; Rykaczewski and Checkley 2008).

The temporal dynamics of these features also vary considerably, from the scale of hours to entire seasons. In the oligotrophic waters of the tropics, the food web is a complex interconnected system (Ciannelli, Hjermann, and Lehodey 2005). Aggregations of prey can form and disperse over short time-scales and in three-dimensions, creating a prey field which is patchy and heterogeneous (Arnaud Bertrand et al. 2002). The high-performance metabolism of top predators such as tuna and billfish allow high levels of somatic growth (R. Brill 1996), but this can only realised through successful hunting and high levels of feeding. Changing search strategies, exploitation of different layers of water, and identifying patches of prey are likely to play an important part in lives of these species from the individual through to the school and populations.

1.1.2 Modern commercial fisheries

Hunting large pelagic predators in the open ocean has always been considered one of the most challenging pursuits of the fisher. From the romance of recreational big-game fishing to the necessity of small island subsistence fishermen, it holds importance not only for food security and economy but also a cultural significance for many nations (Bell et al. 2009; Meltzoff and LiPuma 1986). Archaeological records suggest that as far back as 42,000 years ago, communities in Indonesia had begun fabricating the fishing and maritime tools required to systematically hunt pelagic species such as tuna (O'Connor, Ono, and Clarkson 2011). Over 150 year ago, fishers from Japan were already developing sophisticated fishing gears that were designed to more efficiently target pelagic species specifically, and many of which form the basis for modern industrial methods (Watson and Kerstetter 2006). Knowledge of these animals' behavioural tendencies was clearly present, and the design of these gears demonstrates just how useful exploiting them was for communities that relied on food from the ocean (Butler 1982; Maggio 2001).

However, it is the large-scale commercial exploitation of pelagic species in the present day that creates a more immediate requirement to understand this ecological system. Modern day tuna fisheries generate many billions of dollars annually, and operate at the subsistence, national and international level. The relatively fast growth, global distribution and strong market value of tuna and tuna-like species has resulted in these fish contributing around 7.5% to worldwide marine capture fisheries production (FAO 2012). At a large-scale, this exploitation can be considered as existing within several regions, which operate across country boundaries and with each nation managing the resources of its own waters. Contributions to global tropical tuna production can be broken down as roughly 10% from the Atlantic Ocean, 20% from the

Indian Ocean, and 70% from the Pacific Ocean. The majority of this catch is focussed on a small group of tropical tuna species. The four principally targeted species of tropical tuna are skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), bigeye (*Thunnus obesus*) and albacore (*Thunnus alalunga*). Each fishery, which is defined as a combination of region and fishing method, targets specific species or size classes, but catch composition can vary and is often a combination of species (Williams and Terawasi 2012). Skipjack tuna are the smallest and fastest growing species, while yellowfin and bigeye are larger and more valuable by weight. Albacore are a mid-sized tuna that are not the main target of the largest principal fisheries. All four species are globally distributed in the tropics.

The Western and Central Pacific Fisheries Commission (WCPFC) oversee the fishing operations in the Western and Central Pacific Ocean (WCPO), governing an industry that generated over US$5.5 billion in 2011. It is by far the most productive fishing region for tuna in the world, providing well over 50% of global tuna catch (Williams and Terawasi 2012). In terms of single species catch, the largest fishery in the region is the purse seine fleet for skipjack, but very high levels of exploitation are present for all species in both the purse seine and long-line fisheries. Trolling and pole-and-line also contribute significant catches in some areas.

The two major fishing techniques of this area are purse seining and longlining. Purse seining is an active fishing method, whereby schools of tuna near the surface are sought and enclosed by a large net that is closed at the bottom by a “purse-string” style arrangement of cables. Skippers search for schools of tuna near the surface using a variety of strategies, making a decision on whether to begin the long process of “setting” the net on the school based on the current behaviour of the fish (Baird 2009). In contrast, longlining is a passive method of fishing, in which many thousands of baited or lured hooks are attached to a typically 30km long line strung between floats. The distance between the floats at the surface determines the depth at which the hooks hang, targeting the thermal habitat of a particular species (Bach 2003). In the case of tropical tuna this is often bigeye, although billfish, opah and oceanic sharks are also targeted (Kitchell et al. 2002). This line is left for several hours to drift before being reeled in and any caught fish collected.

The operational logistics, sizes of the areas managed, and scale of political and economic importance in these fisheries are formidable. Scientific advice plays a key component in the successful management of pelagic resources, and as pressure to provide more fish to the growing global population increases, there is a greater need to understand the dynamics and mechanisms influencing the catch of these species.

1.1.3 Behaviour and Exploitation

It is in the specifics of these fishing methods that understanding the movement behaviours of open ocean animals plays an increasingly important role. While high levels of horizontal movement have the potential to affect the dynamics of a population, the exploitation of some specific behaviours by modern day fishers also requires a deeper comprehension of how tropical tuna utilise their environment both vertically and horizontally. High catches of smaller size classes are increasingly under scrutiny within some fisheries, leading to a further need to quantify how changing behaviours over size may be leading to recruitment overfishing (Morgan 2011). Complex management across multiple scales is now required to ensure the sustainable exploitation of these important marine resources (Langley et al. 2009; Pauly et al. 2002).

Scientific advice is a critical input to fisheries management, principally consisting of stock assessments that provide estimations of abundance and structure of an exploited population. In the WCPO, this is undertaken using the population dynamics model MULTIFAN-CL (Fournier, Hampton, and Sibert 1998), which predicts biomass as a state variable for a number of distinct regions. This model is age-structured, estimated chiefly on fish length-frequency data sampled from a variety of sources, and represents the best understanding currently available of the large scale dynamics of tuna species in the WCPO.

Small-scale movement behaviours are incorporated into this model in two main areas. Horizontal movement is represented via migration parameters of biomass exchange between regions, using the data from mark-recapture tagging experiments as prior information. More than just influencing the distribution of biomass spatially, this mechanism allows dynamics such as source or sink regions to emerge and can have a significant influence on the conclusions drawn from a stock assessment (Langley, Hoyle, and Hampton 2011).

Small-scale behaviour is also partially incorporated into stock assessment through catchability parameters. Catchability is defined as the fraction of a population that is caught as a result of a given unit of fishing effort, for example per 1000 hooks set in a longline. Catchability is not constant across age-class, space or time, and as an abstract variable, aims to capture a number of mechanisms that are important in calculating catch-per-unit-effort (CPUE). These include the density-dependent effects of fishing from a population, changes to gear technology and efficiency over time, and vulnerability of the animals to fishers through behaviour (T. Matsumoto and Bayliff 2011). In MULTIFAN-CL, catchability is a free parameter constrained only by a temporal random walk, allowing some flexibility on accounting for different numbers of fish caught for a given fishing effort year on year (N. Davies et al. 2011).

In addition, certain fisheries exploit very specific behaviours exhibited by tuna. During the past thirty years, the use of man-made floating objects, or fish-aggregation devices (FADs), has increased by an order of magnitude. These floating assemblages appear to attract tuna both horizontally and vertically for reasons that are not fully understood (Moreno et al. 2007), allowing more efficient purse seining on fish exhibiting prolonged shallow water movement around the floating objects. An increased understanding of the mechanisms and effects of this behaviour is critical: associated-sets across all fishing gears accounted for over 63% of catches in the WCPO in 2011 (Williams and Terawasi 2012).

1.2 Thesis Outline

1.2.1 Key Areas of Interest

In Modelling Nature, Sharon E. Kingsland (1995) described ecology as the study of patterns in nature, of how those patterns came to be, and how they change in space and time. Traditionally, identifying those patterns is referred to as descriptive ecology, requiring an appropriate data gathering method to capture and observe the patterns in the system of interest. Understanding how such identified patterns change in space and time is undertaken through analysis, statistical methods and graphical representation. But when it comes to understanding what drives or shapes these patterns, the tool of the ecologist has traditionally been manipulative experimentation. That is, a series of experiments are performed where certain conditions are controlled for, and the effects on those same patterns observed in the natural system are examined. For the ecological study of pelagic animals, the difficulty has always been in conducting this final step (Dagorn, Josse, et al. 2000; Tim Dempster and Taquet 2005). Appropriate manipulations of the environment are simply not possible at the scale in which they occur in the true system. Even when individual tuna have been successfully held in captivity for observation, the biological conclusions alone must be made with the caveat that the environment in the ocean may be very different (Farewell 2001). It is unlikely that the true behavioural patterns of these animals are seen under such conditions.

However, many *in situ* experiments and observations have been made of tropical tuna. Their commercial importance means that a number of potential sources of data exist for examining movement behaviours at a variety of scales, despite a lack of historical manipulative experimentation. These data include historical catch and landings information (Sibert et al. 2006), observations of catch and aggregation events (Lawson 2011; Moreno et al. 2007), large-scale mark-recapture tagging experiments (Hampton 1997; WCPFC Tagging Commitee 2007), and electronic archival data tagging deployments (Schaefer, Fuller, and Block 2007). Some of these data sources have already been incorporated into the scientific advice at the population level through migration parameters and catchability estimates (e.g. Davies et al. 2011; Matsumoto and Bayliff 2011), but there remain many difficulties in informing large-scale and abstract population dynamics models with small- and individual-scale behavioural data (Dagorn et al. 2001; Freon and Misund 1998; Sippel et al. 2014).

1.2.2 The Structure of this Thesis

In this thesis, I will examine the way in which movement behaviours are exhibited by tropical tuna, with particular focus on yellowfin and bigeye tuna's vulnerability to exploitation by purse seine and longline fisheries in the WCPO.

First, I will construct a simple theoretical simulation model of how the individual- and school-scale behaviours of tuna may have the potential to significantly impact critical processes such as growth or vulnerability to fishers. This approach will make a number of assumptions from hypotheses in the literature that have not presently been validated empirically, but a number of key areas that influence these impacts will be identified for further study from the results.

The suite of data available for analysing tuna movement in the WCPO will then be examined for the potential to quantify some of these key areas of behaviour. Preliminary characterisation will be undertaken for a number of these data, before the most pragmatic source is focussed upon for an in-depth empirical analysis.

A new method for quantitatively and probabilistically classifying multivariate behavioural time-series will be developed, using further simulation models and a small subset of real data from tuna to test the approach for effectiveness. This method will then be applied to a large sample of vertical movement data from yellowfin and bigeye tuna in the WCPO, examining the effect of several important factors on the changes seen in behaviour.

Finally, the results of these empirical analyses will be examined in the context of real fisheries stock assessment and alongside other studies of tuna movement, describing how these findings can be used to improve our large-scale understanding of the behaviour of tropical tuna and the influence on their exploitation.

Chapter 2: The Behaviour of Pelagic Predators in Modern Fisheries

2.1 The Pelagic Domain

The pelagic domain is defined as marine or freshwater bodies of open water that lie between the water's surface and the earth's surface, or demersal domain. The marine pelagic environment constitutes 99% of the Earth's biosphere volume, and although there are complex vertical constraints to how much of this three-dimensional area is habitable by pelagic species, it remains the largest realm on the surface of the planet (Game et al. 2009). The water column itself is a habitat that is both seemingly featureless yet heterogeneous in nature. In the open ocean, the dynamic physio-chemical nature of the current and climate system, and its impact on the timing, distribution and availability of prey, shapes the movement and ecology of species across trophic levels (Bost et al. 2009). The water column contains thermal and current structures that are complex in both space and time (Auster and Langton 1999; Dagorn et al. 2001), and both biotic and abiotic environmental variables that are often correlated with the behaviour, distribution and population dynamics of pelagic predators (Torres, Read, and Halpin 2008). These variables include sea surface temperature (e.g. Humston et al. 2000), climate indices (e.g. Rouyer et al. 2008), wind speed (e.g. Cury and Roy 1989), changes in thermocline depth (e.g. Su et al. 2011), and abundance and distribution of prey species (e.g. Bertrand, Bard, and Josse 2002). Here, I briefly summarise some of the key factors linked to the behaviour of top predators in the tropical Pacific Ocean.

2.1.1 Structure and Production in the Water Column

Although absolute depth can vary from region to region, the pelagic water column can never the less be divided into a number of distinct zones (Levinton 1995). The epipelagic layer (also known as the surface layer, mixed layer, or photic zone) is the first zone underneath the surface. In the tropical Pacific, it is characterised by being warm and well mixed, with a strong influence from the sun providing all the primary production in the system. In the western “warm-pool” area of the WCPO, the epipelagic layer generally remains warm and thick year round (Langley, Williams, and Hampton 2008; Lehodey 2001). In contrast, the central equatorial and eastern Pacific contains more seasonal upwelling and higher levels of productivity, with a “cold-tongue” of upwelling that extends through the equatorial region towards the western warm-pool (Andreasen and Ravelo 1997; Lavín et al. 2006). North and south of these equatorial regions lie the less productive oligotrophic gyres where primary production is more nutrient limited (Dufour, Charpy, and Garcia 1999).

The epipelagic layer typically ranges from 100 to 200 metres in depth, and is bounded by the start of the thermocline, the region across which water temperature drops considerably (Andreasen and Ravelo 1997). The thermocline is one of the key features of the pelagic environment, being the boundary between thermally stratified layers of water, and having properties which can vary dramatically over short distances (Arnaud Bertrand et al. 2002). It is caused by differences in water mixing, and in the tropical Pacific shows strong annual and inter-annual variation in nature (Wang, Wu, and Lukas 2000). The depth, compression and strength of the thermocline has significant effects on the structure of this habitat and the aggregation of lower and mid-trophic species in almost all pelagic environments (Bost et al. 2009; Prince and Goodyear 2006).

The layer of water from around 200-1000m is broadly referred to as the mesopelagic zone. The upper mesopelagic layer contains the thermocline and continues to the cooler water immediately below, where a strong depletion of oxygen also occurs (Lan et al. 2011). This leads to the lower mesopelagic layer where the effect of sunlight penetrating the water column increasingly negligible. At 1000m, no sunlight penetrates the water column at all, and this marks the start of the bathybelagic zone (Levinton 1995). Aside from some observed isolated dives to very deep depths, this zone appears to hold little ecological significance to the species of pelagic predators examined in this thesis (Leroy et al. 2010). A diagram of the pelagic water column is given in Figure 2.1.

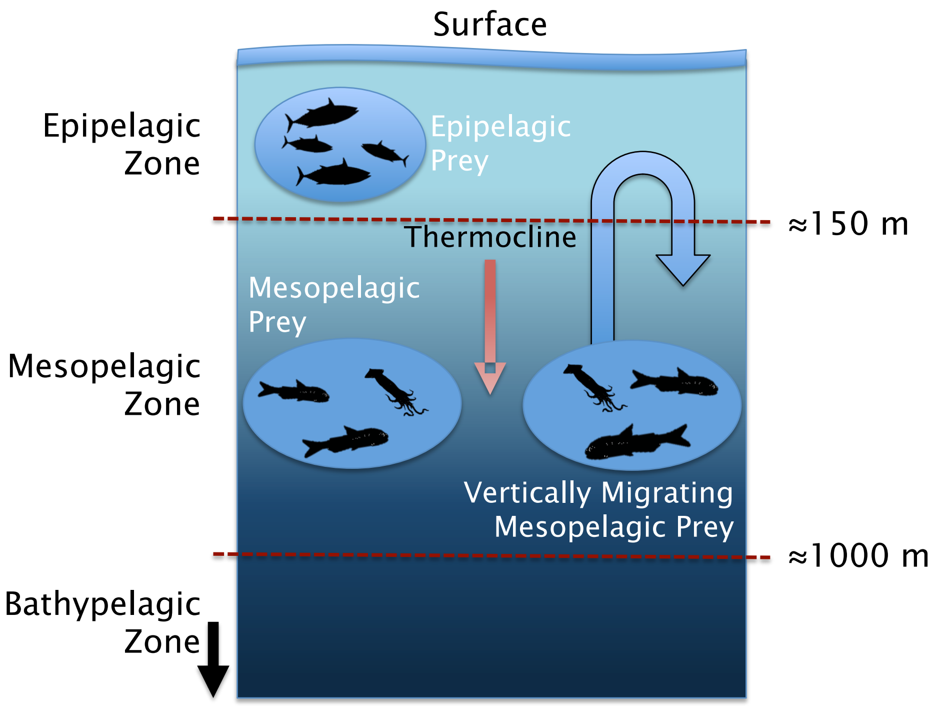

Figure 2.1 Simple representation of the tropical pelagic water column, with components of the prey field shown.

2.1.2 Distribution of Biota

When considering the behaviour of top predators, the distribution and abundance of the species on which they prey must also be considered as a component of the environment, often referred to as the biotic environment or "prey field" (Busch and Johnson 2011; Daewel, Peck, and Schrum 2011; Hazen et al. 2011). In many cases, opportunistic feeding drives the behaviour of top predators in the tropics (Lander et al. 2011; Lehodey, Murtugudde, and Senina 2010), and so the temporal and spatial nature of the prey field in which these species live is crucial to understanding their behavioural patterns. Many oligotrophic regions of the tropics share similar characteristics, where food webs are generally complex but relatively unproductive compared to less nutrient limited regions (Ciannelli, Hjermann, and Lehodey 2005). Despite this relatively low productivity in the open ocean regions of the tropical Pacific, these waters support a considerable food web which underpins the world's largest tuna fishery (Le Borgne et al. 2011). The interacting nature of the biogeochemical ocean structure and the food web can result in highly complex dynamics for top predators that are difficult to predict or study using basic linear conceptual logic (Rouyer et al. 2008). While at a broad basin-scale the productivity of tropical waters may be described as fairly homogeneous, in contrast to other habitats that exhibit highly productive seasonality such as polar regions (e.g. Dalla Rosa et al. 2008), many tropical waters have local-scale prey fields which are continually unpredictable and are driven by short-term dynamics such as storms and eddies (Weimerskirch et al. 2005).

The animals constituting this prey field in the tropical Pacific exhibit considerable spatial and temporal variation in their abundance and distribution, although at present this is not well quantified (Le Borgne et al. 2011; Torres, Read, and Halpin 2008). However, both tropical epipelagic and mesopelagic waters are generally considered to have a non-uniformly distributed or patchy prey field (Barnett 1984; Humphries et al. 2010), with prey fields in shallow epipelagic waters being more dispersed within denser aggregations (Dagorn et al. 2000). In the tropical Pacific the species composition of the epipelagic prey field is highly varied, with species assemblages including anchovies (*Engraulidae spp.*), herrings (*Clupidae spp.*), small mackerels and tunas (*Scombridae spp.*), flying fishes (*Exocoetidae spp.*), the juveniles of reef fish species in coastal waters, squids (*Loliginidae spp.*) and numerous shrimps and krill species (*Euphasidae spp.*) (Allain et al. 2007). Because systematic trawl surveys may not accurately sample the prey field when species' distributions are highly patchy (Marchal and Lebourges 1996), much of the information on the nature of the prey field is inferred from diet studies on predator species (e.g. Jaquemet, Potier, and Ménard 2011; Ménard et al. 2000) or stable-isotope analyses (e.g. Graham et al. 2006; Layman et al. 2012). This necessarily introduces biases due to the differences in ecological niche and foraging behaviours between, not just species, but even different populations and size classes of many pelagic top predators.

Furthermore, in pelagic waters there exists a diel migration of high numbers of these organisms from deep, colder mesopelagic layers of the ocean into the epipelagic layer during the night (Benoit-Bird and Au 2006; Lehodey, Murtugudde, and Senina 2010). In terms of biomass, it may be the single largest migration on Earth (Williamson and Sanders 1996), occurring each and every day. The migration is likely to be an evolutionary adaption to reduce predation pressure during the day, although many predators have coevolved behaviours in response (Dagorn, Menczer, et al. 2000; Lehodey, Murtugudde, and Senina 2010). While this migration certainly floods the epipelagic layer with biomass during the night (Hidaka and Takahashi 2003) there is an even greater uncertainty of the structure and abundance of the micronekton in these deeper layers (Le Borgne et al. 2011). In the tropical Pacific their contribution the total biomass of the prey field may never the less be considerable (Allain et al. 2007; Lehodey, Murtugudde, and Senina 2010), estimated as being over 2 tonnes/km^2 in some studies (Gjøsaeter and Kawaguchi 1980; V. Lam and Pauly 2005). The micronekton species composition in the mesopelagic layer changes from region to region, but in the tropical Pacific consists of myctophid fishes (*Mytophidae spp.)*, squids, and oceanic shrimps (*Euphausidae spp.*) (Hidaka and Takahashi 2003).

2.1.3 Sources of Data on the Biotic and Abiotic Environment

Sophisticated, empirical observations of the abiotic marine environment have been carried out since the 1870s (Lehodey 2006), and there now exist many long term time series of abiotic data. However, the vast three-dimensional size of pelagic habitat, coupled with its dynamic nature, mean that it is very difficult to make observations in the context of a particular animal behaviour. This is even more apparent in the collection of data on the prey field, which is itself dependent on a number of other abiotic environmental forces (Torres, Read, and Halpin 2008).

At the highest scale, easily accessible but abstract climate indices and seasonal environmental observations can be compared to ecological data at similar scales. Measures of fish abundance and distribution have been correlated to these environmental variables with some success (e.g. Cury and Roy 1989; Lehodey 2006; Su et al. 2011), although explanation of the causes for such correlations can be difficult and highly dependent on temporal scale (Rouyer et al. 2008).

Large-scale oceanographic drivers of behaviour, such as sea surface temperature, major currents, and chlorophyll, can be measured through remote sensing (Kerr and Ostrovsky 2003). A number of studies have correlated this type of data with experiments that observe individual-scale behaviour (Lander et al. 2011; Luschi, Hays, and Papi 2003), although this approach has considerable limitations when used in combination with tracking data obtained from nekton that occupy a range of depths in the water column, as geolocation can be subject to considerable uncertainty (Lam, Nielsen, and Sibert 2008; Lehodey and Maury 2010). At a broader scale, ocean models fitted to real world data may provide an indication of the environmental context that could be driving behaviour over similar scales (Lehodey, Senina, and Murtugudde 2008).

Mid-scale observation of mesoscale features known to relate to the distribution of the prey field, such as ocean eddies and upwelling filaments, is also possible using remote sensing and satellite imagery. There is considerable uncertainty in matching these features to behavioural observations of an individual or population of animals (Cotté et al. 2011; Tew Kai et al. 2009). Acoustic surveys allow estimates of abundance, position and depth of aggregating prey species (e.g. Demer et al. 2011; Gerlotto et al. 2004; Hazen et al. 2011), and the use of these surveys in combination with tagging or other behavioural observations provides a more complete picture of the biotic environmental context of behavior in marine animals (Churnside et al. 2009; Dagorn et al. 2001; Josse, Bach, and Dagorn 1998).

At the finest scale, archival data-storage tags attached to pelagic animals usually capture ambient environmental data such as temperature and light-levels experienced by the individual (e.g. Hoolihan et al. 2011; Musyl et al. 2003; Prince and Goodyear 2006). In cases where prey are large enough to themselves be tagged, it is also possible to use archival tags to observe the dynamics of the individuals that make up the prey field (e.g. Davis et al. 2007). As species such as tuna are believed to be opportunistic predators, their diet is reflective of relative of abundance of prey in the area, rather than preferred species (Kirby, Huse, and Lehodey 2003). Some inference of the recent prey field experienced by an individual fish may therefor be made with diet studies that examine stomach contents of individual fish (Arnaud Bertrand, Bard, and Josse 2002; Greenstreet 1998; Rohit, Rao, and Rammohan 2010). Similarly, stable isotope and microchemistry analysis of biological samples allow some inference on the recent environmental and trophic history of an individual (Layman et al. 2012), although a detailed understanding of the background signal of these elements, or “isoscape”, of the region is required (B. S. Graham et al. 2010).

2.2 Foraging Strategies of Top-level Predators

The recent availability of large-scale oceanographic data has meant that the link between physical ocean processes and phytoplankton production has now been observed and modelled for many years (Le Quere and Harrison 2005), and has been examined across a variety of systems. By contrast, the complexities of the phytoplankton-zooplankton relationship are more difficult to observe and model. End-to-end studies linking spatial and temporal variation in primary production to the abundance, distribution and behaviour of top predators that are subject of this thesis, are much more difficult to conduct (Huse and Fiksen 2010; Megrey et al. 2007; Rijnsdorp et al. 2009; Rouyer et al. 2008).

Specific foraging capability and behaviour forms a key emergent property of food webs, even at the zooplankton level (Anderson and Lucas 2008). In many ecological systems with heterogeneously distributed resources, animals search and gather around patchy areas that can be small in both space and time (Bost et al. 2009; Jackson, Holcombe, and Ratnieks 2004; Tew Kai et al. 2009), resulting in emergent population dynamics that can be hard to predict (Provenza et al. 1998, Grimm 1999, Sinerchia et al. 2011). The movement behaviours and distribution of animals in such environments are a product of the underlying dynamics of the prey field (Lander et al. 2011), and when that prey field exists in three dimensions with dynamics that are not well understood, it is difficult to interpret the observed movements of a single free-roaming marine predator (Torres, Read, and Halpin 2008). Furthermore, the scale at which these behaviours are considered is critical when they are to be described (Levin 1992). For some animals, at a basin scale, movements may be focussed on clear foraging grounds or areas, but at the local-scale within these areas, movements may be highly variable in response to environmental or prey field dynamics (Pinaud and Weimerskirch 2005).

As an example of changing movement behaviours, it has been observed that some free-roaming animals change foraging strategies dependent on their environmental context (Sims et al. 2011), although the limitations of observing marine animals make behavioural switching hard to validate. For example, scale-free movements such as Lévy flights have been attributed to the behavioural time-series of animals as diverse as albatross (Viswanathan and

Afanasyev 1996), bumblebees (Reynolds et al. 2007) and blue sharks (Humphries et al. 2010). It has been suggested that these types of search patterns, typified by small intense movements interspersed with less frequent, longer displacements, may be an evolved behaviour to more optimally forage in patchy, heterogeneous environments (Reynolds 2009; Sims et al. 2006), such as the prey field of the tropical Pacific. Furthermore, foraging animals may switch to alternative search behaviours, such a simple random-walk, dependent on the distribution of the prey field currently experienced (Sims et al. 2011). When animals exhibit quantifiable behavioural switching in response to the prey field, analyses focused on identifying the discrete behavioural states could be used to classify movement behaviours and potentially infer the nature of the underlying prey field.

Two main difficulties emerge when attempting to confirm the presence of search strategies in free-roaming animals. Firstly, in marine animals, time-series of movement observations are often restricted to a single, vertical dimension (e.g. Humphries et al. 2010; Sims et al. 2008). This may ignore searching of foraging movements through the horizontal component of the prey field, which is known to be patchy in all three dimensions. This dimensional bias, combined with a number of sampling and transformation procedures usually carried out, can lead to erroneous identification of Lévy flight, or other, behaviour (Codling and Plank 2010; Edwards et al. 2007; Sims, Righton, and Pitchford 2007). The second problem lies in attributing observed movement patterns to a particular behavior, such as an active search strategy. Detailed movement patterns are also observed in a variety of systems, reflecting solely an emergent pattern from underlying dynamics rather than an evolved behaviour. Even seemingly complex behaviours such Lévy flights have been shown to emerge in autonomous gliders attempting to travel in straight distances across ocean currents (Willis and Merckelbach 2011), simulated foragers switching between two random walk behavioural states (Simon Benhamou 2007), and animals that employ simpler movements but reject previously depleted resource patches (Reynolds 2009).

Although hypotheses have been made about the underlying strategies of observed foraging behaviours, there have also been a number of theoretical studies involving simulation models to examine those unobservable but underlying mechanisms that can cause behaviour to emerge (Dagorn, Josse, et al. 2000; Huse and Fiksen 2010; Koehl 1989). The co-evolved vertical foraging strategies of several open ocean species have been simulated given simple assumptions about distribution and movement of animals in a patchy three-dimensional prey field (Dagorn, Menczer, et al. 2000). This individual-based modelling (IBM) approach resulted in evolved neural-networks that mirrored some of the behaviours seen in tropical tunas, billfishes and blue shark, without consideration of any physiological limitations but only the dynamics of maximising interactions between several predators and a shared prey field.

In contrast, (Humston et al. 2000) used a simple particle model to describe the foraging of Atlantic bluefin tuna. Although each particle represents an individual animal, the approach differs from that of an IBM in that the behaviour is limited to movement responses to an inherent awareness of preferred conditions. In this case, particles were attracted to the sea surface temperatures that tuna are observed to aggregate in from aerial surveys. It is hypothesised that these temperature gradients indicate ocean fronts, which constitute rich feeding grounds during the summer months. The simulation results showed very similar distribution patterns to observations, although with less inter-annual variation, attributed to additional, unknown foraging factors. However, if tuna are observed to aggregate with a particular thermal preference at this scale, then it is not surprising that in the absence of other preferences or processes, this model predicts distribution along temperature gradients. The effect of the prey field is ignored by not including the mid-trophic link between temperature-driven regions of production and top predator behaviour in this model, resulting in a potentially tautological description of movement and distribution (Kirby 2001).

In all these methods of examining the dynamics of marine top predators, it is clear that observed movement behaviours are closely linked to the distribution and dynamics of the three-dimensional prey field (Dagorn et al. 2001; Torres, Read, and Halpin 2008). Even if this prey field itself can not be observed of measured, it appears critical that any analysis of movement behaviours in marine top predators must consider the emergence of noise and patterns as a result of many complex interactions between local sources of forage, competition with other predators, and searching for the next patch of prey.

2.3 Tropical Tuna Behaviour

2.3.1 Physiological drivers

In this thesis, I focus specifically on the tropical tunas of the WCPO. In particular, I examine the movement behaviours of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) tuna. These species are globally distributed across tropical waters.

Although tuna spend their entire lives in constant motion, they cannot be said to be faster swimmers than the majority of teleost fish, rather their high performance nature stems from their metabolism (R. Brill 1996). Tropical tunas are capable of relatively very high levels of somatic and gonadic growth, rates of digestion and gastric evacuation, and recovery from exertion (Olson and Mullen 1986). For example, yellowfin tuna can grow to sizes greater than 40kgs by age three (Uchiyama and Struhsaker 1981), and spawn 1-3% of body mass every one to two days once mature (Schaefer 1996).

Although their physiology requires them to spend the majority of their time in warm waters, some tropical tuna species also have adaptions allowing them to spend considerable time foraging in colder and darker layers of the water column. In particular, both yellowfin and bigeye tuna develop swim bladders during their juvenile stages (Bertrand, Josse, and Masse 1999; Magnuson 1973), allowing them to control buoyancy and dive to depths up to 1000m or more (Dagorn, Holland, and Hallier 2006; Schaefer, Fuller, and Block 2009). In addition, tunas are endothermic meaning that they have a physiology which allows both generation of heat from metabolic activity, and retention of that heat via counter-current exchange in their arterial system (Graham and Dickson 2001). Although the ability varies between species, these adaptations allow tuna to effectively thermoregulate and warm the central nervous system in water significantly colder than required by their biology. These traits have likely evolved to enable niche expansion through more effective hunting in deeper layers of water (Block and Finnerty 1994). Other physical factors, such as large body sizes and eyes in bigeye tuna, add to this ability to hunt in deep prey fields through improved thermal inertia and vision, respectively (Schaefer, Fuller, and Block 2009).

Tunas are multiple batch-spawners, and for skipjack, yellowfin and bigeye, spawning can occur more or less constantly throughout the year (Schaefer 2001). Spawning events are usually nocturnal, and apart from a few anomalous observations (e.g. Matsumoto, Skillman, and Dizon 1984; Schaefer and Commission 1998), always occur in surface waters of at least 24°C. These events do not appear to involve a significant migration or protracted shift in behaviours, although pre-dusk courting behaviour between similar size males and females has been observed in captive yellowfin (Margulies et al. 2007).

The energetic demands of constant spawning, high somatic growth and varying levels of physiological regulation are reflected in high standard metabolic rates of 250-400mg of oxygen per hour per kilo (R. Brill 1996), meaning that we might consider foraging, or movement employed to hunt for prey, to be the most significant behaviour in the life history of tropical tuna. In the following, I separate and summarise the observed movement behaviours of tropical tuna as vertical and horizontal.

2.3.2 Vertical movement

Like many diving animals, tropical tunas exhibit strong synchronisation with the movement of the vertically migrating component of the prey field (Hays 2003). This vertical movement is assumed to maximise feeding under the assumptions of optimal foraging and is referred to as vertical habitat-use (Hoolihan et al. 2011; Luo et al. 2006; Schaefer, Fuller, and Block 2007). However, between species of tuna these vertical movement behaviours are diverse and are hypothesised to represent a number of different strategies for exploiting the prey field whilst avoiding competition with other predators (Dagorn, Menczer, et al. 2000; Sharp 2001).

During the night, the influx of deeper prey biomass to the shallow epipelagic layer potentially allows tropical tuna to forage in the warm mixed layer, although the stomachs of many purse-seine caught fish are found to be empty at dawn (Hallier and Gaertner 2008; Ménard et al. 2000). The empty stomach effect may, however, result from association around fish aggregation devices (see below). During the day, when the prey field is more patchily distributed both horizontally and vertically, differences in foraging behaviour between species become more apparent. Skipjack tuna lack the swim bladder and body size necessary to exploit deep prey, although they have been observed to make isolated deep dives (Schaefer, Fuller, and Block 2009), and typically spend the day-time limited to the deepest parts of the epipelagic mixed layer. Yellowfin have more varied behaviour during the day, often spending considerable time within the thermocline and upper mesopelagic layer, but rarely spending continuous periods of time in deep cold water. Bigeye exhibit a wide range of behaviours during the day-time but adults often spend much of the day-time in the cold waters of mesopelagic layer, returning regularly but briefly to the epipelagic zone to thermoregulate (Schaefer, Fuller, and Block 2009).

Qualitative descriptions of tuna diving behaviour have been attributed to data from archival tags in many previous studies. These behavioural patterns are often divided and classified into a number of qualitative groups. A common behavioural pattern in tropical tuna has been defined as time spent deep in cold water, past a particular isotherm that represents the thermocline, with periodic trips back to the surface, also referred to ‘characteristic’, U-shaped, non-associative, or type I behaviour. In contrast, shallow movements within and above the thermocline are referred to as ‘restricted’, associative, or type II behaviour (Leroy et al. 2010; Matsumoto, Kitagawa, and Kimura 2013a; Schaefer, Fuller, and Block 2007; Schaefer and Fuller 2005). Depending on the temporal scale examined, less common patterns are also sometimes identified (Humphries et al. 2010; Matsumoto, Kitagawa, and Kimura 2013b; Schaefer, Fuller, and Block 2009). While at the finest resolution movement through the water column can be highly variable from individual to individual, certain behavioural patterns are common to all tropical tuna, and can persist from just a few hours to an entire 12-hour diel period or longer.

2.3.3 Horizontal movement

Although tropical tuna are classed as highly migratory species in many assessments, the movement of most individual fish has been observed to be fairly limited (Sibert and Hampton 2003), and it may be more appropriate to consider these species as random wanderers that are capable of occasional large scale horizontal movements. The scale of horizontal movement in tropical tuna is highly variable (Leroy et al. 2013), with some individuals moving many degrees of both latitude and longitude within suitable habitat

(Block et al. 2011). Conversely, many individuals also exhibit fairly strong fidelity to the location of their release after tagging (Schaefer, Fuller, and Block 2007; Sibert and Hampton 2003), and schools of yellowfin have been observed to remain in shallow coastal waters around islands in the Pacific warm-pool for many months at a time (B. Leroy *pers comms*). Some consistent west to east movements have been observed in bigeye tuna in the Eastern Pacific, alongside considerable mixing between regions (Schaefer et al. 2015). Whether this is a regular or seasonal phenomenon is not known. Aggregation at horizontally occurring ocean features such as frontal zones, upwelling filaments and mesoscale eddies also occurs (Bestley et al. 2008; Cotté et al. 2011; Rykaczewski and Checkley 2008). Given the influence of the heterogeneous prey field on the movement behaviours of these species, it may be likely that there does not exist one a single migration or other classification of horizontal movement for tropical tuna. Rather, regional populations of fish are likely to reside or migrate in certain areas in response to the prey field dynamics around that location.

2.3.4 Sources of data on the movement of tropical tuna

The chief way of observing individual tuna movement is through the use of surgically implanted archival data storage tags which must be recovered by fishers (e.g. Schaefer et al. 2007), or satellite tags that detach after a period of time and transmit data to the Argos satellite network (e.g. Wilson et al. 2005). These tags store information about the movement of animals, usually in the form of high-resolution depth and temperature recordings and less accurate longitude/latitude estimations made from light levels and length of day. Surgically implanted acoustic tags can also provide movement information within the radius of a fixed receiver station that registers the sonic pings emitted from each individual tag (e.g. Josse et al. 1998, Leroy et al. 2010), usually around 1km.

The depth and temperature information from archival tags provide a means to identify how marine animals utilise their vertical habitat through their movement behaviours. Such data allow functional and numerical relationships between species behaviour and the environment to be quantified (e.g Mori & Boyd 2004; Block 2005; Evans *et al.* 2013), and are increasingly used in ecosystem and population dynamics models for those species providing important economic or cultural ecosystem services (Choquenot and Forsyth 2013; Lehodey, Senina, and Murtugudde 2008; Maury 2010; McLane et al. 2011). However, the integrated assessment models that form the basis for tropical tuna stock assessment in the WCPO have developed somewhat separately from analyses of archival data, and do not currently incorporate their information into parameter estimation (Sipell et al. 2014).

In addition to observations of depth and temperature, many modern electronic tags also record at-depth light levels, which can be used to estimate horizontal movements through daylight-based geolocation. Because an individual tuna is constantly moving to different depths in the water column, these light levels must be corrected to estimate the true light level at the surface (Ekstrom 2004). Once the length of day is determined from these light curves, an estimate of longitude and latitude can be made to provide a track of horizontal movement with associated confidence intervals. In addition, the observed sea surface temperatures from the region can be used to further constrain the possible movements given the water temperatures recorded by the tag (Lam, Nielsen, and Sibert 2008). These kinds of geolocation techniques can prove very effective for examining the horizontal movements of marine animals where individuals undertake large migrations across the ocean, or cross boundaries between regions with distinct environmental profiles (e.g. Block et al. 2011).

While light-based geolocation has great potential for examining horizontal movement behaviours from archival tagging experiments, in tropical tuna at liberty in the WCPO two key issues prevent its robust use. Firstly, for these species the estimated surface light curves are often very poor. This is due to a combination of the prevalent high amplitude movements through the dive profile during the day-time for these animals, and the lack of seasonal change in length of the day near the equator (Lehodey and Maury 2010). Secondly, there is a lack of strong temperature gradients for many regions in the WCPO resulting in little further gains to be made from including sea surface temperature constraints on the geolocation estimates. Subsequently, the uncertainty associated with estimations of horizontal movement for tropical tuna can be very large (Lam, Nielsen, and Sibert 2008). Although broad movement patterns may be examined with some confidence, these same patterns are captured in greater number, and at less expense, in mark-recapture tagging experiments.

Conventional mark-recapture dart tags have been used more broadly, and at considerably lower expensive, to examine larger scale horizontal movements of tropical tuna (Hampton 1997; Hoyle et al. 2014; Kolody and Hoyle 2013), as well as to estimate other biological parameters such as fishing and natural mortality. In the WCPO, tags are released on all three commercial species of tropical tuna, and data on the size of fish, location and behaviour of the school when tagged is captured at the time of release (WCPFC Tagging Commitee 2007). For a subset of the returned tags, those fishers who caught the tagged fish record the same information.

Unfortunately, there exists a large amount of bias in this dataset, including effects from the tagging process itself (Hoyle et al. 2014), inconsistent rates of return (Hampton 1997), recovery of tags from different stages of fishing-market process, and quality of data associated with tag returns (Leroy et al. 2013). Essentially, this tagging method provides only two location points, one accurate at release, and another biased at point of capture by fishers. Data from conventional tagging experiments are used in many different types of analyses to examine broad scale patterns of populations (for a review, see Pine et al. 2003). Mark-recapture analyses generally make the assumptions that tagged individuals are representative of other non-tagged individuals within the same school, the probability of capture of the tagged individual is the same as that of a non-tagged individual (within a region and time-frame), and that tag losses from shedding or non-reporting are negligible or understood (Leroy et al. 2013). Stand-alone analyses using mark-recapture tag data from tropical tuna include the examination of general migrations or source-sink type dynamics (e.g. Schaefer and Fuller 2005; Schaefer et al. 2015), growth and mortality rates (e.g. Hallier, Stequert, and Maury 2005; Hoyle et al. 2014) or examine mixing rates of schools and populations (e.g. Kolody and Hoyle 2013). Mark-recapture data are also typically used to inform the estimation of the migration parameters between regions of age-structured biomass state variables within stock assessment models (Fournier, Hampton, and Sibert 1998; Hoyle et al. 2011), although the temporally and spatially sporadic nature of the tagging programmes prevents the synchronisation of this data with more regularly collected data such as catch.

2.4 Tropical Tuna Fisheries in the Western and Central Pacific Ocean

2.4.1 Economic Importance

At the turn of the millennium, pelagic species such as tunas and mackerels accounted for almost a third of estimated marine catch globally (Pauly et al. 2002), and the conservation status of several of these species are considered as threatened in recent assessments (Collette et al. 2011). Tropical tuna in the WCPO have suffered substantial impacts to abundance from fishing pressure, despite no observable shift in trophic level, and over 2.2 million tonnes were landed from this region alone in the year 2011 (Sibert et al. 2006; Williams and Terawasi 2012). Several recent stock assessments suggest that the bigeye tuna population is currently being overfished in the region (Davies et al. 2011; Harley et al. 2009), with concern that other species may be approaching maximum sustainable yield (Langley, Hoyle, and Hampton 2011). The importance of these species to small-island developing states is considerable, where they provide coastal subsistence fisheries, offshore exploitation and third-party licensing income from foreign, industrial fleets (Bell et al. 2009).

In the Western-Central Pacific region, industrial purse-seine fisheries accounts for over 70% of total catch, with longlining and poll-and-line gears accounting for around 10% each, and the remainder taken by artisanal fisheries (Langley, Williams, and Hampton 2008). The economic input into the region and fishing companies is considerable, with the purse seine and longline tuna catch alone estimated to have delivered around US$4,800 million in 2011 (Williams and Terawasi 2012).

2.4.2 History

Prior to the 1980s, the majority of commercial fishing effort in the WCPO came from longline fleets targeting yellowfin and bigeye in Micronesian countries, the majority of which were Japanese, Taiwanese and Korean distant-water vessels. The start of the 1980s marked the development of purse seine fleets which now account for the majority of the catch in the region, made up of around 70% skipjack and 15-30% yellowfin (Langley et al. 2009). In contrast, longline vessels began increasing effort and targeting bigeye from the mid-1980s through 90s and keeping catches of yellowfin fairly stable (Leroy et al. 2012).

With the expansion of the purse seine fleet, improving the chances of encountering schools within the open ocean became an attractive goal for fishers. During the first two decades of the purse-seine fishery, the use of drifting and anchored Fish Aggregation Devices (FADs) by commercial fishing fleets targeting tropical tuna species increased steadily (Tim Dempster and Taquet 2005; Floyd and Pauly 1984; Guillotreau et al. 2011), replacing the effort made on sets that had previously been around natural floating objects. FADs are man-made devices that vary in design, but generally consist of a collection of floating objects tied together and either moored to the sea floor or left to drift in the open ocean. An immense variety of fauna are known to aggregate or associate under and within floating objects, with tropical tuna showing particularly striking behaviour, appearing attracted to these objects via processes, and for reasons, that are not fully understood (see below).

The present day fishery in the WCPO is dominated by the purse seine fleet, constituting around one third domestic Pacific island nation vessels and the rest made up of distant water vessels from third party nations (Williams and Terawasi 2012). These fleets include many sophisticated vessels, each capable of deploying hundreds of drifting FADs equipped with GPS tracking and acoustic echo-sounding devices (Hampton 2010; Morgan 2011). East of 160˚E, purse seine effort is predominately focussed on sets of associated fish, with effort in the warm-pool more mixed between unassociated, or “free-school”, sets. However, effort changes in response to environmental condition, with strong El Niño events shifting effort towards natural floating object sets due to the natural increase in floating debris experienced in these years (Leroy et al. 2012).

2.4.3 Associated Sets and FADs

Purse-seine sets on FADs, or associated sets as the are known, are a more cost effective method than searching for free-schooling tuna for many skippers and fishing companies. Fishers have exploited the behaviour of tuna around floating objects since the 17th century, but fisheries that use these techniques at an industrial scale impact the marine ecosystem in a number of ways (Bromhead, Foster, and Attard 2003). First, it is clear that the use of purse seining around FADs increases the levels of bycatch of species that also associate with floating objects, which include non-commercial fish species, sea turtles and marine mammals (Filmalter and Dagorn 2011). There are also the polluting and “ghost-fishing” implications of FADs that are not successfully recovered from the ocean (Nakashima and Matsuoka 2005). There are also strong indications that FADs exert a greater influence over juveniles and smaller individuals than large adults (Leroy et al. 2012), altering the species composition in catches, and potentially resulting in recruitment overfishing by fleets that prefer high probabilities of smaller, less valuable catches (Morgan 2011; Squires and Kirkley 1999). These effects are not only confined to the industrial fleets using drifting FADs, but also to other fisheries that utilise anchored devices in coastal areas. The majority of these coastal fisheries have direct bearing on the food security of those people living in Pacific Island nations. These food requirements are increasing, and one way of diversifying the need for protein that is being promoted is to expand these coastal communities ability to benefit from their pelagic resources (Bell et al. 2009; Packard 2009). Near-shore anchored FADs are one of the most cost-effective methods of achieving this.

2.4.4 Sources of data for fisheries activity and catch

The commercial importance of tropical tuna means that there are a variety of data collected from the many monitoring programmes associated with industrial fisheries. Although the scope and quality of such programmes vary from fishery to fishery, in the WCPO a number of data sources exist that are regularly used in scientific advice and stock assessment (Williams 2013), and which may also reflect movement behaviours at broad scales.

While not a direct observation of behaviour, catch information never the less provides an indication of where, when and in what numbers fish are caught. Collecting fisheries-independent catch data via specific scientific surveys is not feasible for tropical tuna in the pacific, due to the size and distribution of the species involved, and so measuring catch from the landings of real fisheries is a rich and heavily used source of data. In the WCPO, the nature and quality of data varies considerably over time. Operational data, that is, information on vessel activity compiled by skippers themselves, has been available for varying periods of time for each fleet. Similarly, landings and port sampling programmes have existed in various forms across the region (Williams 2013), but are usually country specific. Since 1993, there has been partial observer coverage of the purse-seine fleet, with full coverage since 2010. Observer data is highly detailed, describing not simply the times and places fished, but also information on the composition and size of the catch, the behaviour of the school at time of setting, and even when fishing events result in no catch.

Using observer data, it is possible to view the times of days when the majority of purse seine sets are made (Figure 2.2). Fishing with purse seines is not possible during the night, but it is clear that the majority of sets made on floating objects occur at dawn. Associated sets, which are the largest component of the purse seine fishery, are usually made during the hours around and just after dawn, suggesting that FADs may have a more powerful aggregating effect around this time (Dagorn, Josse, et al. 2000; Fréon and Dagorn 2000). In contrast, sets on free schooling and megafauna- or natural log-associated tuna occur relatively equally throughout the day as fishers opportunistically spot these vulnerable schools near the surface.

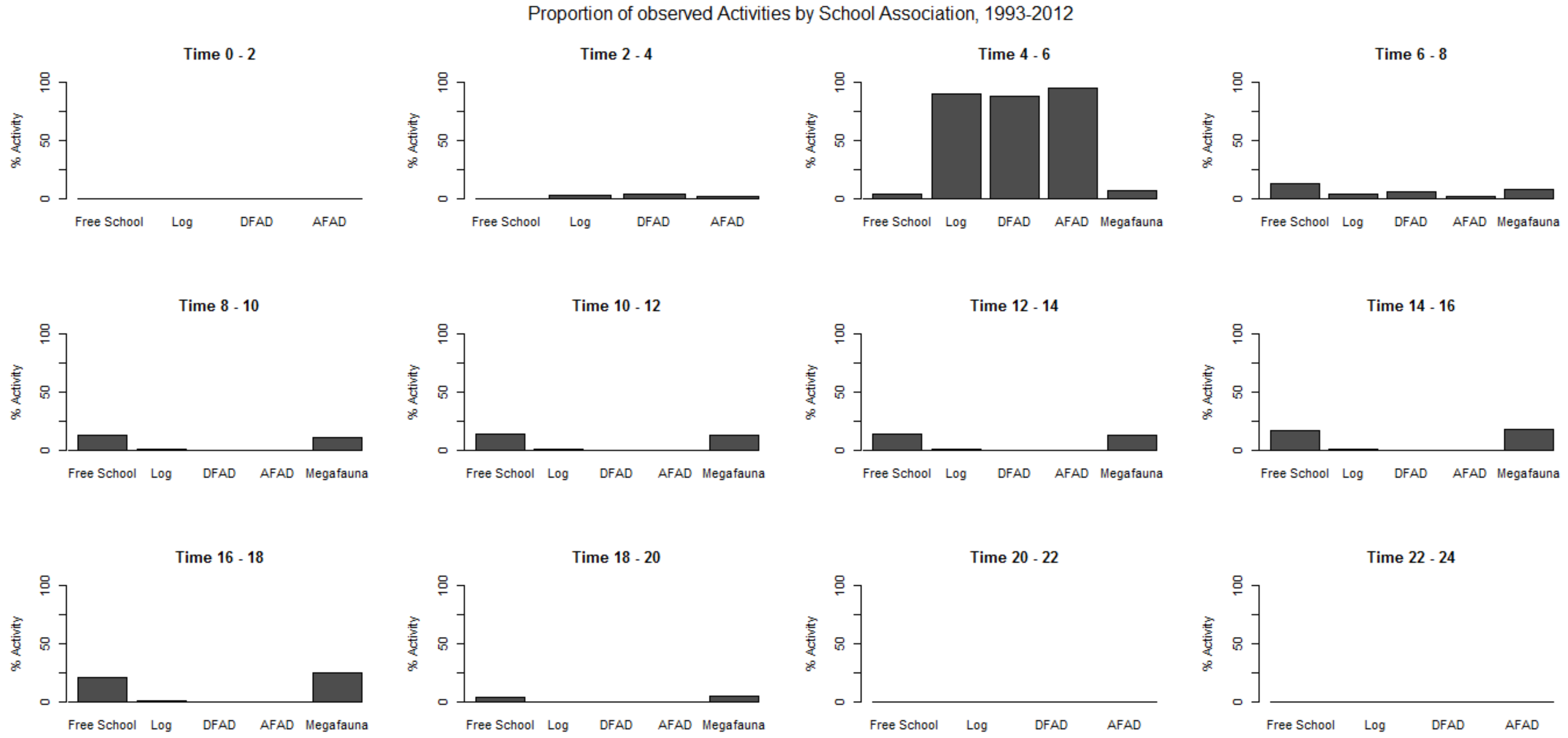

Figure 2.2 All WCPO purse seine setting activities recorded during observer programme from 1993-2012, by time of day. Activities are divided into sets on free schools, natural floating objects (log), drifting FADs, anchored FADs, and megafauna-associated schools.

A major issue with drawing conclusions about true tuna behaviour from fishery-dependent data is that there are many inherent biases. Although there exists observer bias in some of the more specific information collected by purse seine observers, such as the samples of fish chosen for size measuring (e.g. Lawson 2011), the fundamental issue is that these data are biased by the fisheries themselves. Effort is targeted in regions and on species that provide the most economic gain, and so any analyses will not provide a true indication of the underlying dynamics of tuna movement behaviours. As an example, contrary to the time of day sets shown above tuna may be only slight less attracted to floating objects during the period 6am-8am than at dawn, but because it is more efficient to set at dawn, the relative difference between the two times is not represented in the data.

2.4.5 Fisheries management and scientific advice

Governance and management of pelagic resources in the Pacific has consisted of a number of national, sub-regional and regional bodies (Langley et al. 2009). One of these bodies is the Forum Fisheries Agency, formed in 1979 by Pacific island countries to limit vessel numbers across nations and which now coordinates the participation of these countries in the processes and decisions of the region. Management protocols and catch recommendations are now provided by the Western and Central Pacific Fisheries Commission (WCPFC), which was formed in 2005 to combine a number of pre-existing scientific and management arrangements.

Principally, scientific advice is provided through regular species-specific stock assessment reports (e.g. Harley et al. 2009; Langley, Hoyle, and Hampton 2011), which have been conducted for over ten years using an age-structured, single species population dynamics model, MULTIFAN-CL (Fournier, Hampton, and Sibert 1998). This model is spatially structured into six large regions covering the WCPO, and is referred to as an integrated model as it is parameterised using a variety of data sources including bias-corrected port sampling, catch-per-unit-effort analyses, and movement rates from mark-recapture tagging experiments. MULTIFAN-CL assessments are subject to constant improvements, alongside the comparison to new and alternative population dynamics models. The purpose of all these assessment models is principally to estimate stock status, but supplementary analyses including forecasts of tuna responses to future climate scenarios (e.g. Dueri, Bopp, and Maury 2014; Patrick Lehodey et al. 2013) and analyses of fisheries management options (e.g. Sibert et al. 2012) are also regularly undertaken.

One such alternative model that has been developed is the Spatial Ecosystem and Population Dynamics Model (SEAPODYM) (Lehodey, Senina, and Murtugudde 2008), a version of which has been developed for skipjack tuna (Senina, Sibert, and Lehodey 2008). SEAPODYM follows an Advection-Diffusion-Reaction Model (ADRM) approach, representing the movement of physical quantities by a combination of diffusive distribution of density and directed advection based on terms that define gradients for the diffusion. These terms can be driven by dynamic sea surface temperatures, defined migration routes, or a combination of any other temporally or spatially appropriate process. SEAPODYM can be coupled to physical-biogeochemical ocean models, allowing varying environmental drivers to be used for prediction and climate change scenarios, and can utilise a mid-trophic sub-model which provides simulations of tuna prey distribution and the broad scale prey field (Lehodey, Murtugudde, and Senina 2010). Optimisation of the many parameters in this model is on going, but it is difficult to compare simulation output to any real life observations because they simply do not exist at this scale. Subsequently, assessing the accuracy of this model is non-trivial.

However, the purpose of SEAPODYM is to investigate the impact of different fishing management scenarios on stock abundance and spatial distribution, and represents an alternative assessment method to those currently undertaken in MULTIFAN_CL. ADRMs appear suitable for simulating population dynamics at larger spatial and temporal scales, because they allow multiple levels of recruitment, production and prey to be modelled over many underlying environmental projections. By incorporating the key environmental drivers of behaviour, this approach improves on many other models of pelagic predators at this scale. Critically, it allows the prey field itself to be simulated.

However, the underlying parameterisations and mathematical functions still make assumptions about the low trophic level interactions, and these approaches have been criticised for having little biological meaning and simply replicating observed variation without modelling processes (Kirby 2001). The parameter space of the model is so large that, aside from undertaking sensitivity analyses of key parameters, it is difficult to examine the mechanics that lead to the dynamics of the simulated output.

At present, these stock assessment models principally use large- and mid-scale data sources for parameterisation, such as rates or size of catch and broad movements from mark-recapture tagging experiments. Necessarily, such models are most successful at predicting tuna dynamics at similarly large scales. However, the collection of small- and individual-scale behaviour has largely developed independently from stock assessment models, with little formal incorporation into stock assessment and scientific advice (Sippel et al. 2014). In this thesis I will examine this issue with specific focus on individual-scale movement behaviours.

2.5 Linking Small-scale Movement Behaviours to Fisheries

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 the vulnerability and catchability of these fish to fishers, thermal-habitat preference, and how these differ across regions, are important components in the stock assessment models described above. Understanding the individual and school movement behaviours of tropical tuna, whilst perhaps not traditionally considered when assessing commercial fish stocks, may now be an important factor (Sippel et al. 2014).

Of the links between tuna movement behaviours and vulnerability to fishers considered in this literature review, one of the most obvious is the exploitation of associative behaviours by purse seine fleets deploying FADs. These fleets deploy man-made floating objects in such number that there are now many thousands in use at any one time (Moreno et al. 2007). The uncertainty associated with movement both around FADs and in free-swimming schools is critical, as this behaviour is key to understanding such fish-fishery interactions, as well as how to best mitigate bycatch of other species. Although the position of some anchored FADs is known, and certain areas are known to have more or less purse seining effort and therefore FAD use, the exact temporal and spatial densities of sets made on drifting FADs or natural logs is unclear (ISSF 2012). Modern industrial vessels use radio beacons to track FADs set adrift, and echo sounders attached to the assemblage are employed for sonar observations of the tuna aggregations before net setting. However, at present this information is not publicly available for analysis.

A number of phenomena are known to occur as part of the aggregation of animals around FADs. After deployment in the water and a period of "colonisation", FADs begin to attract and retain tuna segregated into distinct schools of different species or size classes. While there are many uncertain processes that operate in this attraction and retention of tropical tuna, there are also a number of behaviours that are clearly and consistently observed through tagging, acoustic surveys and fishers' experiences (Bertrand, Bard, and Josse 2002; Leroy et al. 2010; Moreno et al. 2007).

In particular, tuna appear to actively target FADs in their horizontal movement, and may be capable of sensing these devices from up to 11km away (Girard, Benhamou, and Dagorn 2004). The sensory mechanism used to locate and orientate towards FADs is unknown, but is unlikely to be chemically driven (Dempster and Kingsford 2003). It has been hypothesised that low-frequency sounds from the anchor chain of moored FADs may help fish to orientate towards them (Leroy et al. 2012), but the sphere of influence for drifting FADs is considered to have a similar range in anecdotal evidence (Moreno et al. 2007). Sound from around an anchored FAD has been characterised as strongest at dusk and during the night, and potentially audible to fish species up to 1km away (Ghazali et al. 2013). It may be that sound and vibration still play an important role in attracting tuna, both from the device itself and the aggregation of other species nearby, creating a positive feedback on colonisation and effectiveness at attracting fish.

There are also apparent patterns in the foraging of FAD-attracted individuals. Stomach contents of FAD-associated tuna are often less full than their free-swimming counterparts (Hallier and Gaertner 2008). There may be considerable differences in foraging impacts between anchored and drifting FADs, with drifting devices correlated to higher frequencies of empty stomachs (Jaquemet, Potier, and Ménard 2011). Inconsistent changes to the diet composition in FAD-associated fish have also been observed, when compared with opportunistic, free-swimming schools (Buckley and Miller 1994; Graham et al. 2006; Ménard et al. 2000).

Several hypotheses have been made to explain the striking behaviour of tuna around FADs. Three of the most acknowledged from Fréon and Dagorn (2000) and Leroy et al. (2012) are summarised here:

Concentration of food: As a large number smaller fish species are known to aggregate around FADs, it has been suggested that floating objects concentrate individuals of prey species on which larger fish can feed. Whilst the search for food is likely to be a driving factor in attracting tuna to FADs, there is no evidence to suggest that sufficient biomass exist at these sites to support an average of 20-40, and some times many more, tonnes of schooling tuna at any one time.

Meeting point: This hypothesis assumes that in the pelagic realm there are very few physical structures, and those that do exist (such as floating objects, islands or seamounts), are used as spatial reference points to increase encounter rates between isolated schools or individuals. These encounters serve to gather fish together to optimum school sizes, and so benefit from the evolutionary advantages of schooling through increased hunting success, genetic diversity, and protection from predators (Parrish 1993; Parrish 1991). This suggests that a positive feedback exists between individuals around FADs, and would explain the 'warm-up' period that is required before tuna begin to aggregate around devices for any extended period. There has been some theoretical (Dagorn and Fréon 1999) and experimental (Soria et al. 2009) evidence to support this process.

Indicator-log: Over evolutionary timescales, the types of naturally occurring floating objects that tuna would have evolved behavioural associations with would have been floating logs, branches, and drifting collections of algae. These objects would have been carried by currents over potentially large distances, eventually aggregating in frontal zones, eddies or upwelling filaments, which are often highly productive areas that can generate and support a high biomass of zooplankton and zooplanktivorous species. This hypothesis assumes that tuna have evolved such an association between these objects and the productive areas that they naturally inhabit, and so whilst the floating objects are not productive themselves, for tuna species they are synonymous with rich patches of ocean. Under this assumption, FADs alter the perception of the prey field by tuna. If true, man-made FADs placed in prey-poor areas may indeed operate as ecological traps (Dagorn et al. 2013; Hallier and Gaertner 2008), retaining tuna in areas that they erroneously associate with high levels of prey biomass. Examining the *in situ* perception of the prey field by a school of tuna in the open ocean is not easy however, making this hypothesis difficult to test.

Clearly, whatever the mechanism behind their attraction to FADs, these devices have the potential to become ecological traps for tropical tuna, but because the processes behind the attraction and association of these species are so unclear, the extent to which this has implications for populations is not an easy question to answer (Dagorn, Holland, and Filmalter 2010; Dagorn et al. 2013). Whether FADs truly are retaining tuna near the surface for long periods before they are caught, or altering significant horizontal displacements that would otherwise occur are critical areas for research. In particular, whether these dynamics are different across species, size or region are important from the point of view of scientific advice given to regional fisheries management organisations.

Although FAD-association is a pressing issue in the study of tropical tuna behaviour, improving our understanding of individual movement behaviour is also related to fisheries management in more fundamental ways. The relationship between one of the relative index of abundance commonly used in stock assessment, catch-per-unit-effort (CPUE), and the effect of the local environment and prey field may be much more complex than previously assumed (Arnaud Bertrand, Bard, and Josse 2002; T. Matsumoto and Bayliff 2011; Maunder et al. 2006). Depth distributions of tuna are clearly linked to the vulnerability and exposure of fish to the separate gear-types (Bigelow, Hampton, and Miyabe 2002), and understanding how these may differ across species, size and region may inform the use of these CPUE indices before they are incorporated in an integrated assessment model.

Fluctuations in historical CPUE can be incorporated into model estimation using the assumption of catchability, or the proportion of the population that is caught from one unit of fishing effort. Catchability is not constant across species, sizes, regions, gears or time, and as such raw CPUE alone cannot be used assess the status of a population (Hampton et al. 2005). A commonly applied method to cope with these factors is to standardise CPUE indices by modelling them in response to the regions, times and fleets that are believed to drive significantly different catchability levels (Maunder et al. 2006). In MULTIFAN-CL, a freely estimated catchability then accounts for further unexplained changes in CPUE. However, with an integrated approach to assessing populations, new insights into the specific behaviours of tropical tuna across these factors could be incorporated through CPUE standardization or informing the prior distributions of estimated model parameters.

Improving our understanding of vertical habitat-use clearly has implications for the scientific advice provided in the management of industrial fisheries. In this literature review I have detailed the problems involved in describing observed behavioural patterns objectively, correctly attributing changes in these patterns to appropriate stimuli, and incorporating movement data into modern stock assessments.

As a pressing example in fisheries management, it is clear that FAD's alter a number of behaviours in tropical tuna, but it is non-trivial to incorporate poorly understood local scale behaviours into large population dynamics models. The most important effects are assumed to be captured through the use of catch data incorporated at a large spatial scale through estimations of CPUE and size-specific catch. Future predictions are made at the same scale: current biomass and the theoretical, 'unexploited' biomass are predicted under a sweep of varying parameters. However, the widespread, and in some areas very dense, use of FADs in the WCPO may have effects on some parameter estimates that may suggest a re-examination of the assumption that these effects are captured through catch data.

2.5.1 Questions Asked in this Thesis

Although there are large gaps in the current understanding of movement behaviours in tropical tuna, there are a number of critical questions that are in place to be examined, given the large amount of data available across a variety of temporal, spatial and ecological scales. This thesis will examine the individual-scale movement behaviours of two species of tropical tuna: yellowfin and bigeye, which are ecologically and economically important species in the modern day fisheries of the WCPO. I will use a combination of theoretical simulations and new empirical analysis techniques to classify and quantify these behaviours at the individual and school scale, in the context of understanding their potential impacts to larger population dynamics.

Specifically, I will examine the following questions:

1. *How are the movement behaviours of tropical tuna best explored and described in the context of interaction with fisheries?*

This literature review has shown that the behaviour of these commercially important species can be examined and described at a number of different scales, from basin and species-level distributions down to the individual interaction between predator and prey. My thesis will focus on the behaviour towards the latter scale, but other data and information will be used if appropriate. For example, a wide variety of dynamics are observed in tuna catches, particularly for associated sets in the purse-seine fleet. Given the potential importance of the interaction between individual tuna, the prey field and FADs, examining which broad behaviours may significantly influence the impact of FADs and exposure to fishing gears should be explored.

Sources of data on individual-scale tuna movement are varied in scale and detail, and so these observed behavioural patterns must be quantitatively and objectively classified. Given the qualitative nature of previous movement behaviour classifications, a more robust approach to describing these data is needed before they can be incorporated into any kind of current stock assessment model or scientific advice. Potential methods that appropriately describe the individual-scale movement data from tropical tuna will be assessed, tested and developed where needed. The aim will be to identify the most appropriate movement patterns, temporal scale and quantitative methodology that should be used to describe the behaviour of these species of tropical tuna.

2. *What causes changes to these behaviours?*

Once an approach to the description of these behaviours has been found, their dynamics in the context of interactions with, and vulnerability to, fishers needs to be explored. Stock assessment models are species-specific, and age or length, and usually spatially, structured. A full analysis of movement behaviour will need to examine as many individuals as possible across these different factors. Not only may there be significant differences in behaviour across biological and spatial factors, but potential changes that occur during time-at-liberty and growth should also be identified. Changes in behaviour around known or assumed periods of association with fish aggregation devices will also be examined in a more quantitative manner than previous studies.

3. *What are the likely implications of these findings on the small-scale movement behaviours of tropical tuna to their larger-scale population dynamics?*

Once critical small-scale movement behaviours and dynamics have been identified and objectively classified, the likely mechanisms and pathways by which they may scale up to affect our understanding of tropical tuna at the larger scale of fisheries must be explored. Given the observed changes to the nature and dynamics of behaviours and the fisheries-specific analyses undertaken in the thesis, the wider implications scientific advice will be discussed and the ways in which quantitative descriptions of movement data can be incorporated in stock assessment components suggested.

In the following chapter, I will begin examining question one and two by using an individual-based modelling approach to test simple hypotheses regarding the perception of FADs by tuna schools. The vertical behaviour of artificial tuna and nature of the prey field will be altered, and the emergent effects on vulnerability to fishing will be quantified.

Chapter 3: A Theoretical Patch of Ocean

3.1 Introduction

In Chapter Two, a broad range of mechanisms and drivers responsible for the movement behaviours of pelagic species was discussed in a fisheries context. One of the key barriers that have been problematic in furthering our understanding of the dynamics of the fisheries-fish behaviour connection is the large size of the three-dimensional area over which they operate. Practically, it is not possible to control mesocosm environments of the appropriate scale to the degree required for true manipulative experimentation.

Empirical observations in natural systems have provided an invaluable way of exploring hypotheses concerned with controls on the behaviour of large pelagic animals (Abascal et al. 2011; Taquet et al. 2007; Tinker et al. 2007). However, due to the limitations in matching together the environmental and prey field context alongside individual behaviour for each observation, such hypothesis testing is severely limited (Dagorn et al. 2001). In these circumstances, thought-experiments can be useful tools in the formation of hypotheses to be tested with empirical data from natural experiments, suggesting the possible mechanisms that may or may not be responsible for the patterns observed in the real system (Bélisle 2005; Wilkinson 2003).

A recent form of thought experiment, simulation modelling, has been used to explore hypotheses within artificial and theoretical substrates. Although simulations have been used to demonstrate potential system dynamics for many years (e.g. Schelling 1971), now computing power and high level programming languages allow such thought-experiments to be easily constructed, experimented upon, and quantified (Grimm 1999; Di Paolo, Noble, and Bullock 2000). They can inform the future design of real-world experimentation, be updated with new information as it becomes available, and used to understand the uncertainty associated with observation (Kirby 2001). If behaviours observed in the real world emerge from simulation models with very simplified underlying mechanics, there is good evidence that these modelled components may be responsible for driving the emergent patterns (Grimm et al. 2005).

3.1.1 Floating Object Association

In this chapter, I describe a simulation model designed to examine some of the unknowns associated with the behaviour of pelagic animals and the implications of observed behaviours for fishing vulnerability. Over the past 30 years, the use of Fish Aggregation Devices (FADs) in tropical tunas fisheries has steadily increased, and now account for around 65% of global landings. These floating devices attract and retain pelagic species through processes that are not fully understood, and are used in tuna fisheries because they offer a number of attractive properties to fishers. Anchored FADs can create new fishing grounds in coastal areas where other habitats are limited or have been damaged (Packard 2009), while for industrial fleets fishing the high seas, using drifting FADs increases the encounter rate of tuna schools (Guillotreau et al. 2011).

Whilst FAD-fishing offers benefits to some fishers, there are also concerns from managers and conservationists regarding the negative impacts of the industrial-scale use of FADs. While the ability of FADs to act as ecological traps is still in dispute (Dagorn et al. 2013; Hallier and Gaertner 2008), it is clear that floating object-associated sets have an altered catch composition biased towards smaller size-classes (Leroy et al. 2012), and in many cases land fish that are of a lower condition (Menard 2000) and which appear to have a different diet composition to their free-swimming counterparts (Buckley and Miller 1994; Fernandez and Allain 2010). The increased number of juvenile fish caught in the FAD-fishery suggests that, given the large fishing effort exerted by purse seine fleets, the potential for considerable recruitment overfishing exists (Morgan 2011). There exists, therefore, a critical need to investigate the processes occurring around FADs that drive this increased vulnerability and retention of smaller size classes (Robert et al. 2012).

The extent to which size-specific effects are linked to the overall mechanism that attracts and retains tuna to FADs is not known. A number of hypotheses have been proposed to explain the attraction and retention of pelagic species to and around floating objects (Castro, Santiago, and Santana-Ortega 2001; Fréon and Dagorn 2000). These vary considerably, are not mutually exclusive by nature, and have been reviewed in detail in previous publications (e.g. Leroy et al. 2012) and in Chapter Two of this thesis. Briefly, hypotheses fall into several categories suggesting that FADs attract fishes by: provision of a protective substrate (Fréon and Dagorn 2000), offering clues about the local prey field (Dagorn, Holland, and Itano 2006), or performing a social function (Robert, Dagorn, Lopez, et al. 2013). Regardless of the mechanism(s) by which FADs operate to increase local fish biomass and/or abundance, it is not clear whether there is an ontogenetic change in behaviour that causes larger fish to be less susceptible to these processes.

The 'indicator-log' hypothesis states that, over evolutionary timescales, predatory fish have learnt to associate floating objects with productive patches of ocean. Naturally occurring floating objects such as logs, branches and algal masses are affected by currents and will spend much of their floating time caught in meso-scale eddies, along the boundaries of different currents, and in estuarine outflow regions. Due to high levels of nutrient influx and mixing in the water column, these small areas tend to produce high levels of primary production and grazing by secondary producers. The associative behaviour of pelagic predators with floating objects has been hypothesised to be due to their role as an indicative clue as to productivity of the local area (Fréon and Dagorn 2000). As FADs are typically deployed irrespective of local productivity, this has raised the question of whether these devices constitute ecological traps, causing tuna and other species to make incorrect decisions about suitable habitat.

3.1.2 Hypotheses Tested with this Model

Evidence for any of the hypotheses explaining FAD attraction is difficult to gather as the scales involved, both spatially and temporarily, are too large to test robustly using manipulative experiments. However, previous analysis of observations (e.g. Gaertner et al. 2008), small scale experiments (e.g. Capello et al. 2004; Dempster and Kingsford 2003) and theoretical studies (e.g. Dagorn, Josse, et al. 2000; Fréon and Dagorn 2000) can provide clues about the processes that may be operating around floating objects. Evidence for the indicator-log hypothesis has been suggested by studies examining the movement of tuna through arrays of FADs (Dagorn, Holland, and Itano 2006), and the observation that changes in oceanographic conditions are often associated with aggregations leaving floating objects (Moreno et al. 2007).

In Dagorn, Josse, et al. (2000), an individual-based simulation model of tuna around virtual FADs was constructed to attempt to replicate some of the movement patterns that are observed around FADs. This study simulated the surface waters of an artificial patch ocean in two dimensions, containing random patches of prey and independent schools of tuna. FADs were made to attract tuna in the absence of real prey, representing the assumptions of the indicator-log hypothesis. The surface layer prey field had random dynamics that tried to replicate the patchiness of the pelagic domain, alongside an influx of biomass during the night from deeper dwelling vertically migrating species of prey. This simulation model replicated a series of qualitative horizontal movement behaviours observed in real tuna, and proportion of tuna associated with the FAD at different times of the day was examined.

Here I use a simulation modelling approach to examine the theoretical role that size-dependent foraging ability plays in the vulnerability of tropical tuna to Fish Aggregation Devices. I use a similar model structure to that in Dagorn, Josse, et al. (2000), but extend the artificial ocean into three dimensions with both tuna schools and prey aggregations individually modelled. Making a number of assumptions:

1. Tuna can perceive the presence and abundance of prey aggregations in their local environment.
2. Tuna can perceive the presence of FADs from a further distance away, although I ignore the mechanism by which they are able to do so.
3. Tuna confuse FADs with areas containing prey aggregations, but only in the absence of locally sensed, 'true' prey aggregations, which they can differentiate from a FAD, representing the indicator-log hypothesis of FAD attraction.
4. Tuna switch between active hunting behaviours in which they search for prey, and resting/digestion behaviour in which they ignore perceived prey aggregations or FADs.
5. Larger size and species-classes are capable of diving to deeper layers of the water column to search for prey aggregations.

Using this framework, I examine the relative difference between the emergent behaviour and condition of artificial tuna in an ocean in which a FAD influences them, and an ocean where they remain free-swimming. Specifically, I resolve the following hypotheses under the assumptions of the model:

1. The emergent condition and diet of the artificial tuna will change when they exist in an ocean containing a FAD compared to a FAD-less ocean.
2. The emergent behaviour and biology of larger size-classes able to dive into deeper layers of the ocean are less impacted by the influence of a FAD.
3. Changes to the distribution of the prey field have major effects on the emergent behavioural and biological impact of the FAD
4. The assumed increased spatial perception of FADs over prey is also critical to strength of FAD impacts.

By altering the variables included in the model structure, changes will be seen in the emergent properties of tuna agents. Indeed, if these variables are the sole mechanisms in the model, then this is to be expected. However, the strength and variability of emergent effects will be compared to previous observations of *in situ* tuna behaviour and biology for evidence of similar and significant changes to condition, diet and vulnerability to FADs. I ask, are the striking patterns in tuna vulnerability and retention around FADs explained by the simple set of assumptions above in a simulated pelagic environment, using a limited number of physiological and environmental variables?

3.2 Materials and Methods

The use of individual-based modelling (IBM) provides a useful tool to examine the emergent system properties from a set of assumptions about the lower level processes, incorporating or removing those physiological and environmental factors that may or may not play a driving role in the mechanisms of interest. As the fundamental unit of an IBM is the individual, it is straightforward to compare these simulated, emergent properties with observed patterns in real world ecological systems (Grimm et al. 2005). Here I describe the IBM developed to test my hypothesis in this study following the standard 'Overview, Design concepts and Details' (ODD) protocol described in Grimm et al. (2006).

The purpose of this model is to examine the role that size-dependent diving ability may play in the vulnerability of tropical tuna to FADs. It is designed to simulate these impacts at the scale of individual fish or schools over short temporal scales, rather than a community or population. This model does not aim to explore social effects between tuna, but rather what the effect of changing prey distribution and a FAD might have on single, idealised pelagic hunters capable of diving to different depths in the water column.

3.2.1 State Variables and Scales

The model comprises of a 3-dimensional, artificial ocean, populated by 'super-individuals' representing schools of prey species or tuna. There are two hierarchical levels to the model: individual school agents and the ocean cells that they move between, and the arrangement of those cells into the complete, 3-dimensional patch of ocean.

The ocean is divided into layers of hexagonal cells, with each ocean cell holding a depth layer coordinate, a 2-d position coordinate within that layer, and a cell-type variable which can be 'free' or 'FAD'. Each cell represents a patch of ocean 1km in diameter, and a depth corresponding to one of three entire ocean layers. Each cell also contains pointers to any prey individuals currently present in that cell.

Prey individuals represent 1000kg 'super-individual' schools of tuna prey species. These individuals are characterised by the variables: type, position and aggregation tendency. Type is categorised into one of five ecological groups: Epipelagic, Migratory Upper-Mesopelagic, Non-migratory Upper-Mesopelagic, Migratory Lower-Mesopelagic, and Non-migratory Lower-Mesopelagic. Aggregation tendency varies with this type, resulting in different prey types having greater or lesser probability of aggregating with other schools of prey in their immediate location. This tendency to aggregate controls the patchiness of the prey field in the artificial ocean. The coordinates of the currently occupied ocean cell are stored in position, and aggregation tendency is represented by a probability. A diagram of a section in the surface layer of the ocean is shown in Figure 3.1.

Tuna individuals represent a single school of tuna, capable of sensing prey and FADs in the artificial ocean. Tuna store the following variables:

position, stomach fullness and current behaviour. Position holds the coordinates of the currently occupied ocean cell, and stomach fullness is represented by a percentage. Current behaviour is one of two states: hunting, or resting. Tuna also have a *maximum dive depth* that they are able to dive to hunt for prey, which is varied between simulation experiments to examine the effect of size-dependent foraging. This results in three classes of tuna, each capable of diving to a successively deeper layer in the water column. These are referred to as skipjack (SKJ), which are limited to the surface, Epipelagic layer; yellowfin (YFT), which can dive to the upper-mesopelagic layer containing the thermocline; and bigeye (BET), which can dive through the thermocline and down to the lower-mesopelagic layer. This species-class labelling is somewhat unrealistic, as diving ability is more of a size-dependent ability in the real world, but I use these simple class names to differentiate between the tuna types used in this simulation.

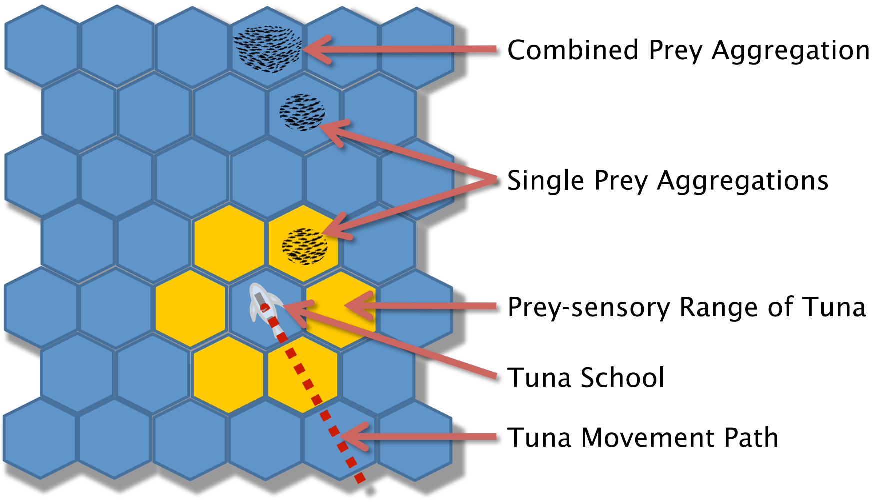

Figure 3.1 Representation of a section of surface layer in the artificial ocean. Prey super-individuals populate the layer, some of which have combined to form denser aggregations.

At the higher level, the ocean is arranged in three layers of ocean cells which do not correspond to absolute depths, but rather dynamic layers. The dimensions of these layers grow and contract in the real pelagic domain and are environmentally distinct both biotically and abiotically. These layers are the Epipelagic layer, the Upper-Mesopelagic layer, and the Lower- Mesopelagic layer, and can be summarised in the following way (see also Chapter Two):

- The Epipelagic layer. The surface layer of warm, mixed water above the thermocline, typically from 0 to ~200m depth
- The Upper-Mesopelagic layer. The layer containing the thermocline and cooler water below, typically 200~400m
- The Lower-Mesopelagic layer. The layer at which the effect of sunlight in the water column is negligible, typically 400m+

The artificial ocean is around 2500 km2 in surface area (50x50 ocean cells), and wrapped around to form a torus. Simulations are run for 6 months of simulated time, with a ten-day spin up period, and under a variety of prey distribution scenarios (see *Initialisation* section). A complete list of parameters is described in Table 3.1.

Table 3.1 Complete parameter list for individual-based model of tuna foraging.

Parameter	**Value**
Artificial Ocean	
Ocean cell diameter (km)	1
Area (cells)	50x50
Depth (cell layers)	3
Daily timesteps	48
Simulation time (timesteps)	10,000
Spin up period (timesteps)	500
No. Epipelagic prey	
-SEAPODYM scenario	825

-Balanced scenario	1321
-ECOPATH scenario	3501
No. Migratory Upper-Mesopelagic prey	
-SEAPODYM scenario	1042
-Balanced scenario	1321
-ECOPATH scenario	1915
No. Non-migratory Upper-Mesopelagic prey	
-SEAPODYM scenario	410
-Balanced scenario	1321
-ECOPATH scenario	330
No. Migratory Lower-Mesopelagic prey	
-SEAPODYM scenario	2430
-Balanced scenario	1321
-ECOPATH scenario	859
No. Non-migratory Lower-Mesopelagic prey	
-SEAPODYM scenario	1898
-Balanced scenario	1321
-ECOPATH scenario	26

Prey

Aggregation tendency (probability)	
-Epipelagic prey	0.8
-All mesopelagic prey	0.4
Sensory range (cells)	1
Tuna	
Diving preference (probability)	0.33
Prey sensory range (cells)	1
FAD sensory range (cells)	10
Meal fullness (%)	5
Resting digestion rate (%)	10
Maximum dive depth (cell layer)	
-SKJ	1
-YFT	2
-BET	3

3.2.2 Process overview and scheduling

The model proceeds in discrete 30-minute time-steps, during which three main processes are scheduled: updating the prey field, simulating the tuna school behaviour, and recording observations from the time step. For all processes involving updating or selection between a number of ocean cells, those cells are determined in a random order.

First, the prey field is updated one ocean cell at a time. This consists of individual schools and aggregations of prey moving in random walks through a single layer of the ocean with a probability that they will favour moving to local cells containing other aggregations of prey. During crepuscular periods, diurnally migrating prey abandon this random walk behaviour and instead move vertically to the corresponding ocean cell above or below their current position, at dusk or dawn respectively. For each ocean cell, all the prey individuals present are given the chance to move in a random order. Each prey individual senses the presence or absence of other prey in each of the seven local cells in the current layer (six surrounding, and the cell already occupied), also in a random order. For each of these encountered cells containing other prey individuals, the current prey makes a stochastic choice based on its aggregation tendency parameter to move to that cell. If no cell is chosen in this way, then a random walk is undertaken. For all prey individuals that have remained in their current cell and form an aggregation of greater than one individual, this large aggregation of multiple prey then also moves in a random walk.

Next, the movement of the tuna school is carried out. A stochastic choice in behavioural mode is made from a probability function driven by the current stomach fullness of the tuna (see *Sub-models*), and tuna subsequently either 'hunt' or 'rest'. When resting, the tuna individual simply ascends if below the Epipelagic layer, or random walks if already there. The current stomach fullness is then reduced by the *resting digestion rate* parameter, here assumed to be a percentage of full, resulting in a linearly decreasing digestion process. The rate of digestion was chosen to match observations of captive yellowfin tuna achieving full gastric evacuation in five hours (Olson and Boggs 1986; Olson and Mullen 1986).

When hunting, the tuna school senses its local, surrounding cell environment first for the presence of prey individuals. This includes cells in layers above and below if the tuna is of a class that is capable of moving to those depths in the water column. I assume that tuna hunt with the same efficiency at all times of the day. The school then moves to the cell containing the densest aggregation of prey individuals, randomly choosing between any equally dense cells. The school then feeds, removing one random prey individual from those present in the cell, which is also then regenerated at a random location in the ocean, keeping the overall prey abundance constant. I assume that all prey types in the artificial ocean contribute equally to tuna stomach contents, specified by *meal fullness,* and that there are no extra metabolic costs from temperature or oxygen limitation of feeding at depth for those classes of artificial tuna capable of doing so.

If no prey aggregations are sensed, then the tuna school sense a much larger local area for the presence of a FAD, given by *FAD sensory range*. The default diameter of this range is set at 10km, consistent with observed distances that tuna actively swim towards or are influenced by floating objects (Girard, Benhamou, and Dagorn 2004; Moreno et al. 2007). However, this value is also reduced to lower values in some alternative simulation experiments (see below). If a FAD is perceived, then the tuna school will move one cell towards it. If the school is already located at the FAD cell, it will simply random walk around the local cells searching for prey, including deeper layers if it is capable of diving. This behaviour represents the perception by pelagic predators of floating objects indicating areas containing prey, as stated under the 'indicator-log' hypothesis of FAD attraction.

If neither prey nor FAD cells are sensed, then tuna move using a random sweeping search-behaviour, with low probability high angled turns. This behaviour is identical to that used for simulated tuna movement in Dagorn, Josse, et al. (2000), with the additional chance of individuals moving vertically between horizontal movement, given by their *diving preference*. Such sweeping searches are suited for optimal searching in patchy environments (S Benhamou 1992).

Finally, the recording of simulated observations is undertaken. Positions of all agents are recorded, along with the internal state of the tuna school and cumulative diet composition from different prey groups. Figure 3.2 depicts the complete schedule of these processes during a single time-step.

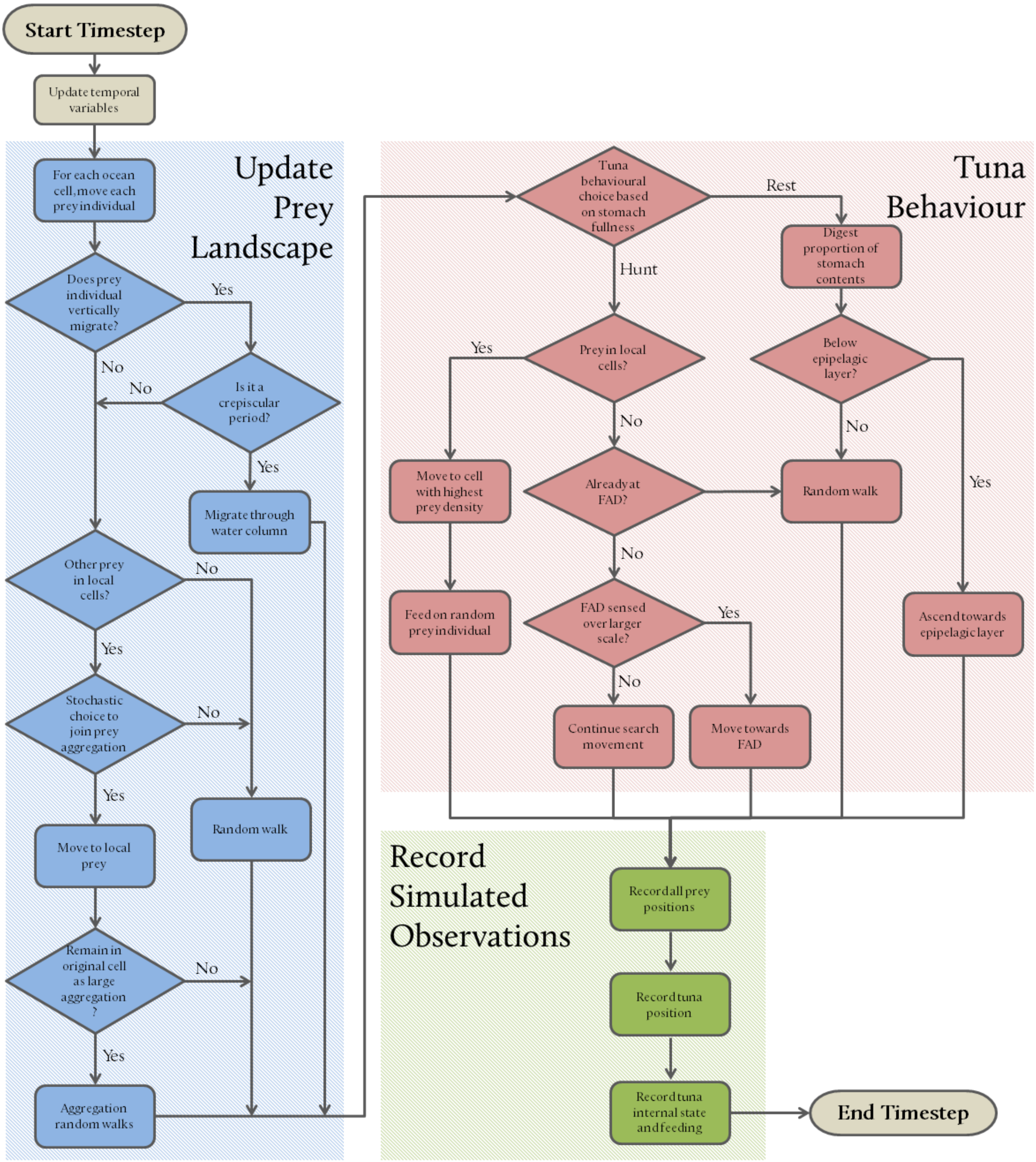

Figure 3.2 Process diagram showing event scheduling during a single time-step of the simulation.

3.2.3 Design concepts

3.2.3.1 Emergence

The emergent properties of interest in this model are the length of time spent near the FAD by simulated tuna, and the internal condition of the tuna (stomach fullness and diet composition), given different parameterisations of the artificial ocean and prey distribution.

3.2.3.2 Fitness

While the timescales of the phenomena investigated by this model do not necessitate the use of evolutionary fitness, fitness seeking by the tuna individuals is indirectly assumed by the desire to search and feed on prey as often as possible.

3.2.3.3 Sensing

Both tuna and prey individuals are assumed to be capable of sensing the presence of other individuals in their local environment, although the specific mechanisms used to do this are ignored here. This is chiefly due to the lack of study into how pelagic fish gain sensory cues from floating objects of the prey field (Dempster and Kingsford 2003; Ghazali et al. 2013). It may be that these species are capable of perceiving dense aggregations of other fish from some considerable distance away using a variety of sensory cues.

3.2.3.4 Interaction

The purpose of this IBM is to investigate the effect of prey field distribution and diving ability in FAD impacts on tuna, and as such only a single tuna school is placed in the artificial ocean in each simulation. I ignore social interactions between individuals or schools of tuna. The prey field is driven by strong interactions between prey schools, and tuna are capable of indirectly influencing this further by depleting prey in areas that they are feeding.

3.2.3.5 Stochasticity

Stochastic events occur throughout this IBM, providing a mechanism of choice for processes that are not understood. In particular, decisions made by individuals regarding directions to move, which aggregations to join or feed on, and whether to hunt or rest, are handled stochastically. Each simulation experiment is replicated 100 times using a different random seed to smooth out the variation caused by these processes.

3.2.3.6 Observation

Variables from each simulation are collected in such a way as to allow qualitative comparison with real-world observations of tuna behaviour and physiology. However, these are collected as from an omniscient observer, rather than from a 'virtual ecologist'. The variety, and in some cases low replication, of in situ observations results in there being no clear choice of virtually sampling these data.

3.2.3.7 Initialisation

All agents are given random positions at the start of each simulation, although prey schools always start at the correct depth for their type. The stomach fullness of the tuna school is given a random value between zero and 100%. When the ocean contains a FAD, the FAD-set cells are always the centre cells of the artificial ocean and at each of the three depth layers, as tuna are known to aggregate across varying depths underneath FADs (Bromhead, Foster, and Attard 2003). The abundance and distribution of prey in the tropical pelagic domain is highly variable through both space and time (Barnett 1984; Arnaud Bertrand et al. 2002). Attempting to bracket this uncertainty, I use three different prey field scenarios to parameterise the artificial ocean in these simulation experiments. Two of these are based on tuna forage species predictions from full ecosystem models, and the third is an arbitrary scenario using a balanced distribution. These scenarios are summarised in Figure 3.3.

A Spatial Ecosystem and Population Dynamics Model (SEAPODYM) has previously been constructed for oceanic top predators (Lehodey, Senina, and Murtugudde 2008). This model uses output from ocean coupled bio-geochemical climate models to predict the biomass of multi-trophic species in the pelagic environment, taking interspecies and environmental interactions into account. Here, I use per km^2 biomass estimates for each of the five ecological prey types included in the model (migratory and highly-migratory lower-mesopelagic prey are grouped together). These estimates are scaled up to the size of the artificial ocean patch and packaged into schools representing 1000kgs of tuna prey species. This SEAPODYM prey scenario is characterised by a large biomass contributions from the deeper dwelling, migratory components of the prey field.

Allain et al. (2007) developed an ECOPATH model for the Western and Central Pacific warm pool pelagic ecosystem, re-balancing the prey estimates from SEAPODYM, other ecological models and observed data using the ECOPATH mass-balance equations. Under this approach, the total abundance estimates for prey species are over six times higher than the SEAPODYM predictions. When incorporated in the IBM of this study, this prey abundance results in tuna being able to feed to an equilibrium point of 50% stomach fullness almost constantly, with no impact from FADs or migration of prey. To address this issue for this alternative prey field scenario, I take the total biomass estimates of the SEAPODYM model but use the distribution across prey groups given by the ECOPATH study of Allain et al. (2007). This prey scenario is characterised by the majority of the biomass being located in the Epipelagic layer, while the rest constitutes almost entirely migratory prey groups in deeper layers.

The third, balanced scenario uses the same total abundance estimates as the other two prey fields but distributes this biomass equally across the five prey groups.

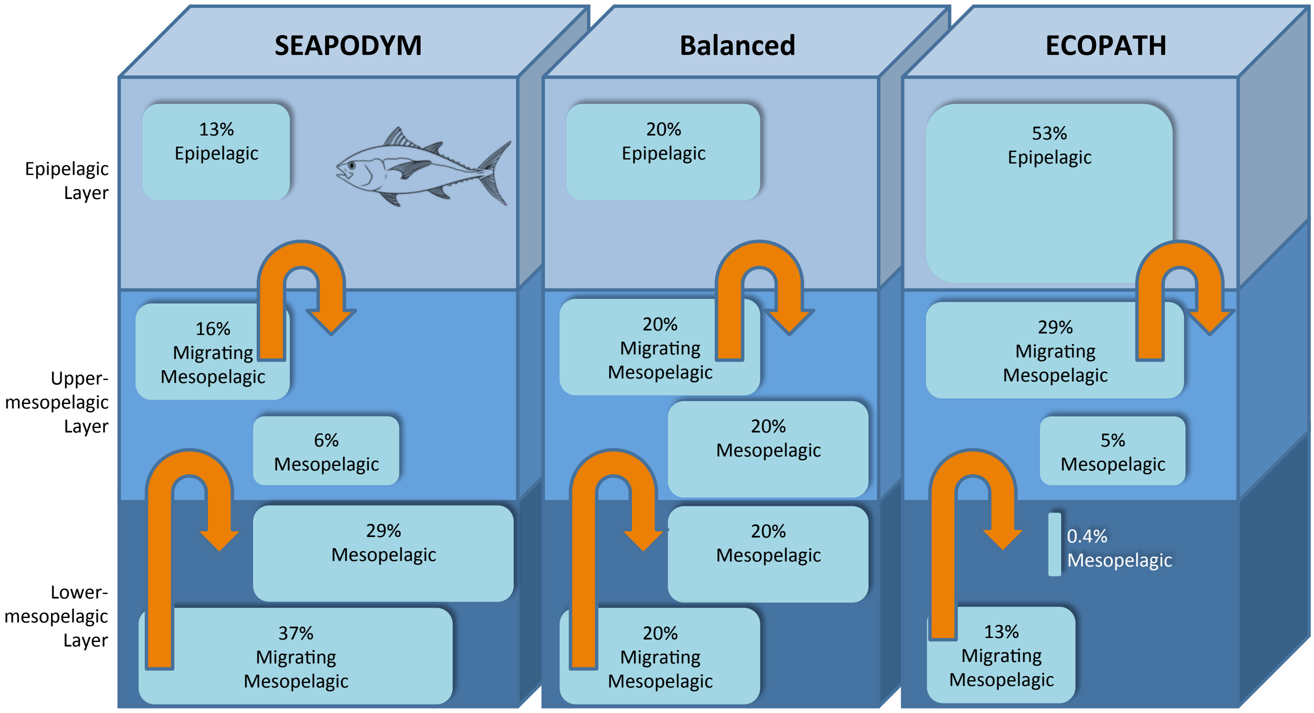

Figure 3.3 Distribution of the prey field in the artificial ocean under each of the three scenarios used in this study.

3.2.3.8 Submodels

The probability with which an artificial tuna school will decide to undertake resting behaviour for a time step is given by a probability function. There is evidence that active hunting by tuna reduces sharply above 50% stomach fullness (Bertrand, Bard, and Josse 2002), with most fish caught on passive gear types such as longlines exhibiting emptier stomachs. At each timestep, tuna randomly choose to rest with probability

$$P(h) = \frac{1}{1 + e^{(4-8f)}}$$

where f is the proportion of stomach fullness and $0 < f < 1$. This function takes the form of a logistic probability function, sharply inflexing at 0.5 stomach fullness. Below this, there is a greater chance that hunting behaviour will be chosen.

3.2.4 Simulation experiments

The chief factor investigated in this study is the different diving ability of the three classes of simulated tuna: SKJ, YFT and BET. All simulations were carried out across these three factors. Simulations consisted of both oceans free of FADs and oceans with a single FAD cell set in the centre, allowing the comparison of impacts to stomach fullness and diet composition between 'free-swimming' and FAD impacted tuna schools. The three prey field scenarios were used to bracket the variability caused by changing availability of prey species.

For simulations containing FAD cells, the emergent retention of tuna around the FAD is measured by continuous residence time (CRT). CRT has been used to quantify FAD strength in a number of studies into fish behaviour around arrays of floating FADs (Capello et al. 2012; Ohta and Kakuma 2004; Robert et al. 2012), and I follow this convention here. This measure is the number of hours spent by an acoustic telemetry tagged tuna within receiver distance of a monitored FAD (around 500-800m), without an absence of greater than 24 hours. In this simulation model, I classify residence as occupying the FAD cell, corresponding to a 500m radius around the virtual FAD.

3.3 Results

The results are presented here with focus given to changes in simulation output across tuna types resulting from their differing abilities to exploit prey at varying depths in the artificial ocean. For each parameterisation, output metrics are averaged across 100 simulation runs to smooth variation from stochastic processes. First, FAD impacts are examined by comparing average stomach fullness and diet between tuna free-swimming in a FAD-less ocean and those affected by a virtual FAD. Then, FAD-specific behaviours are presented through difference in continuous residence times across tuna types and prey field scenarios. Finally, the effect of changing the FAD perception distance by artificial tuna is shown.

3.3.1 Free-swimming versus FAD-impacted tuna

3.3.1.1 Feeding

The simulated impact on tuna foraging efficiency by FADs is indicated by comparing average stomach fullness over the course of a simulation from both oceans free of FADs and those containing a FAD. These results are shown in Figure 3.4 and Figure 3.5 and are also vary across prey field scenario. When a general reduction in stomach fullness occurs, tuna type becomes an important variable, with the smallest and surface-limited tuna class SKJ suffering the greatest impact. The SEAPODYM scenario represents the most “difficult” ocean for all tuna types to survive, with such a large component of the prey field located in the lower-mesopelagic layer. Under this scenario, even the deep diving BET type tuna are negatively affected by the presence of a FAD compared to free-swimming counterparts. When the majority of the prey field is concentrated in the surface layer, little or no FAD-impact to stomach fullness is seen across all three tuna-types.

3.3.1.2 Diet

I also examine impact on diet composition from FADs by comparing the proportion of prey types from each ocean layer that contribute to tuna diet at the end of simulation from both FAD-free and FAD containing oceans. Figure 3.6 illustrates the presence of the altered feeding behaviour caused by FADs, changing the composition of prey groups the tuna are feeding on, although this effect is understandably dependent on prey field scenario. These effects are strongest in SKJ and YFT type tuna, in some cases inversing the feeding ratio of epipelagic to mesopelgaic prey that constitute diet, when under the assumptions of the SEAPODYM prey field scenario. Under this scenario, all tuna-types are impacted by the effect of the FAD, although SKJ type see the largest change from a diet of predominantly epipelagic prey to one that is more balanced between epipelagic and migratory upper-mesopelagic prey components. In contrast, the balanced prey field scenario shows FAD-driven diet impacts only in SKJ type tuna, although these changes are less so than for the SEAPODYM scenario. The ECOPATH scenario, with such a large epipelagic biomass component in the prey field, shows little change in a epipelagic dominated diet across all factors.

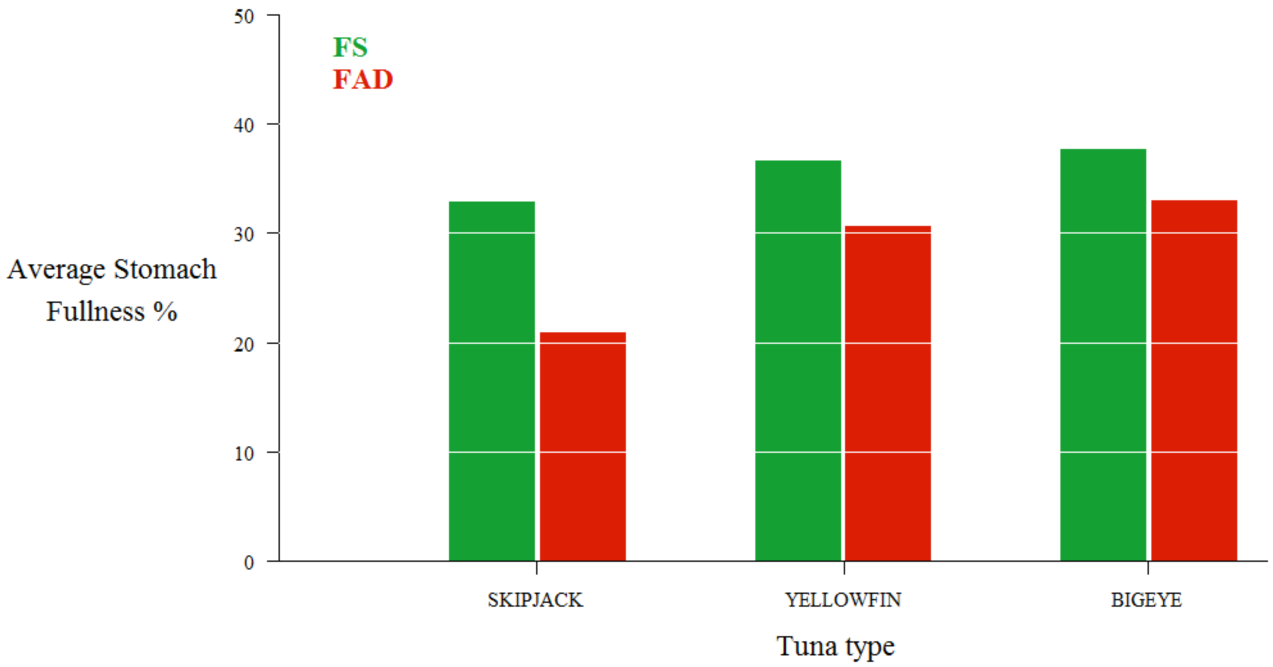

Figure 3.4 Average stomach fullness over the course of all simulations under the SEAPODYM scenario, separated into free-swimming oceans (green) and FAD-containing oceans (red), by tuna-type.

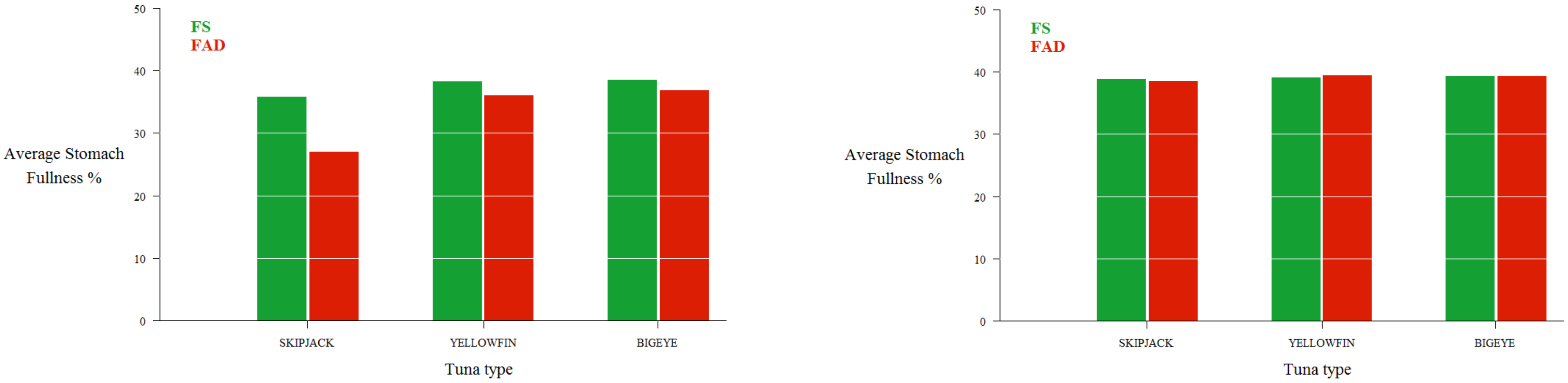

Figure 3.5 Average stomach fullness under Balanced (left) and ECOPATH (right) prey field scenarios

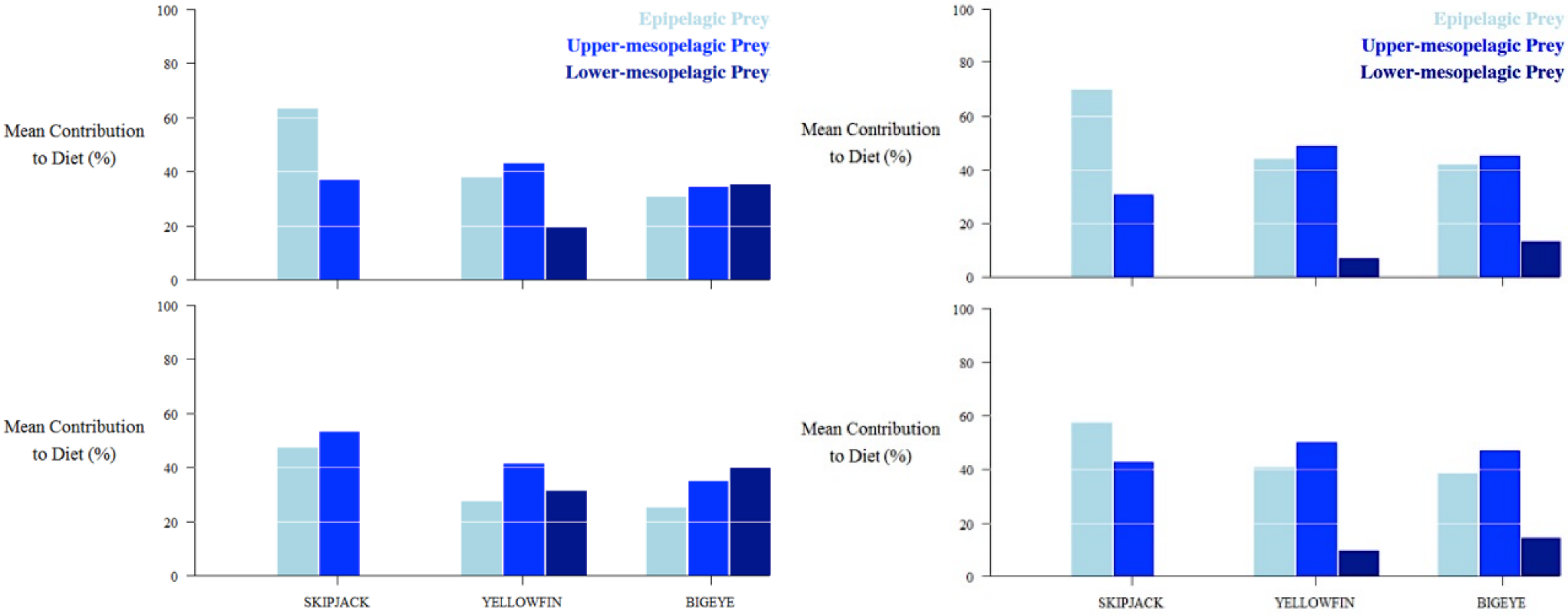

Figure 3.6 Diet composition for SEAPODYM (left) and Balanced (right) scenarios. Upper histograms come from free-swimming tuna, lower are FAD-impacted tuna. Results are separated by tuna-type and prey groups.

3.3.2 FAD-specific Effects

3.3.2.1 Emergent Residence Time Around FADs

In FAD containing oceans, the average continual residence time (CRT, the length of time spent in the FAD cell without absences of greater than 24 hours) is measured across the three tuna types to examine the length of time spent in the FAD vicinity for each prey field parameterisation. These results are summarised in Figure 3.7. SKJ-type tuna clearly spend much more time around the FAD under the balanced and SEAPODYM prey field scenarios, with all fish types spending relatively much more time at the FAD for the SEAPODYM scenario than for any other. When the majority of the prey field is concentrated in the surface layer at all times, as in the ECOPATH scenario, CRTs are an order of magnitude lower, and more equal, for all types of tuna.

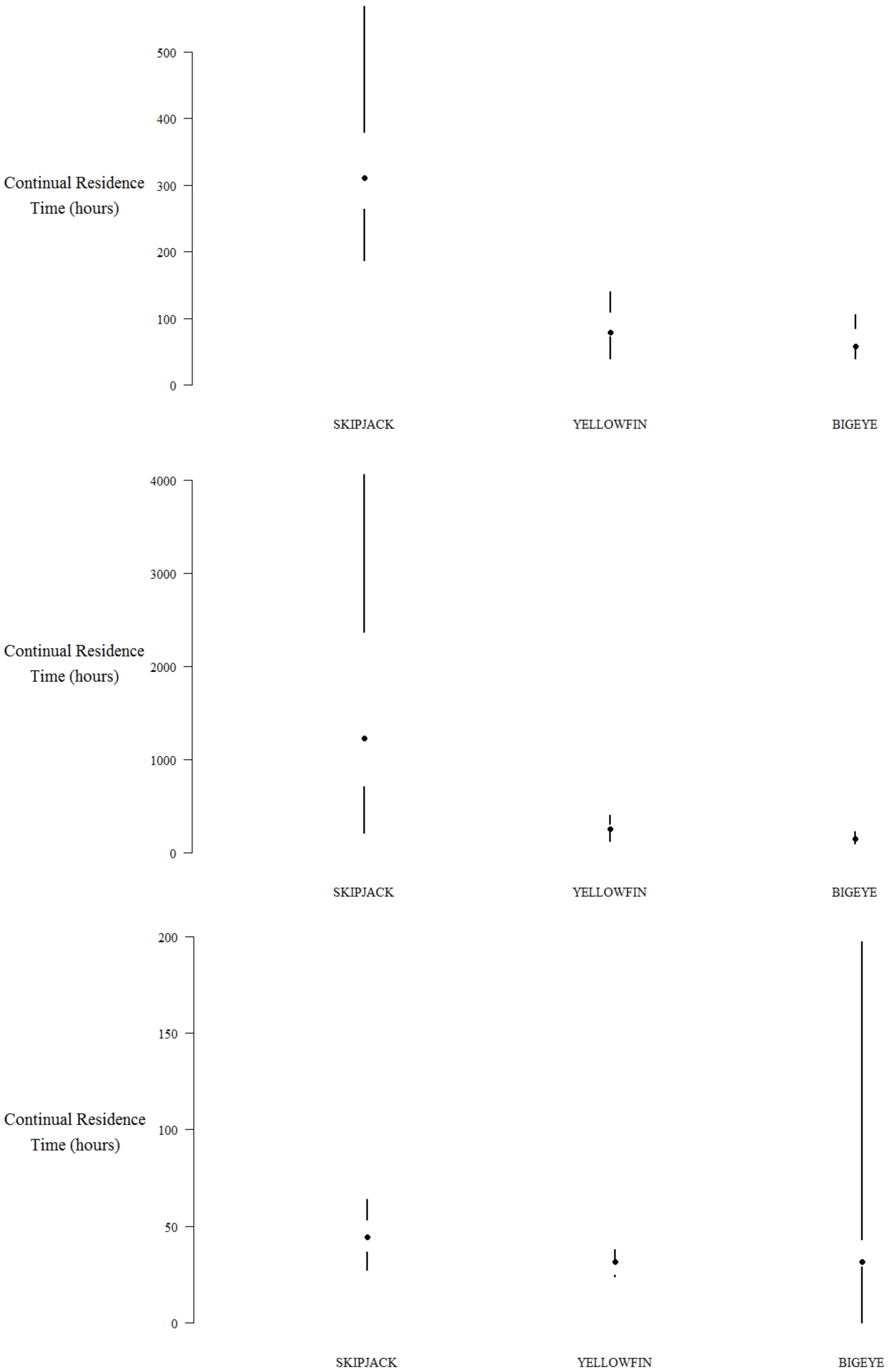

Figure 3.7 Boxplot of continuous residence times by tuna-type under the balanced (top) SEAPODYM (middle) and ECOPATH (bottom) prey field scenarios.

3.3.2.2 Changing FAD Sensory Range

A series of experiments were also performed across a number of FAD sensory perception ranges for the artificial tuna. The change in emergent CRT under the SEAPODYM prey field scenario, which resulted in the largest FAD impacts, are shown across three decreasing FAD perception ranges in Figure 3.8. At 10Km, SKJ type tuna spend an order of magnitude more time than the other tuna types, as shown previously. This difference in CRT between tuna types reduces sharply when FAD sensory range is at 5km, with SKJ type tuna spending an order of magnitude less time at FADs compared to the same class of artificial tuna that senses FADs from 10km away. At 1km, the same sensory range as for prey aggregations, mean CRT drops an order of magnitude again for SKJ-type tuna. At this perception range there is no difference between tuna types in their emergent CRT, with few instances of fish spending longer than 30 hours at the artificial FAD. Similarly, at this low perception range, no impact to stomach fullness or diet is seen when a FAD is introduced to the artificial ocean compared to free-swimming tuna (not shown).

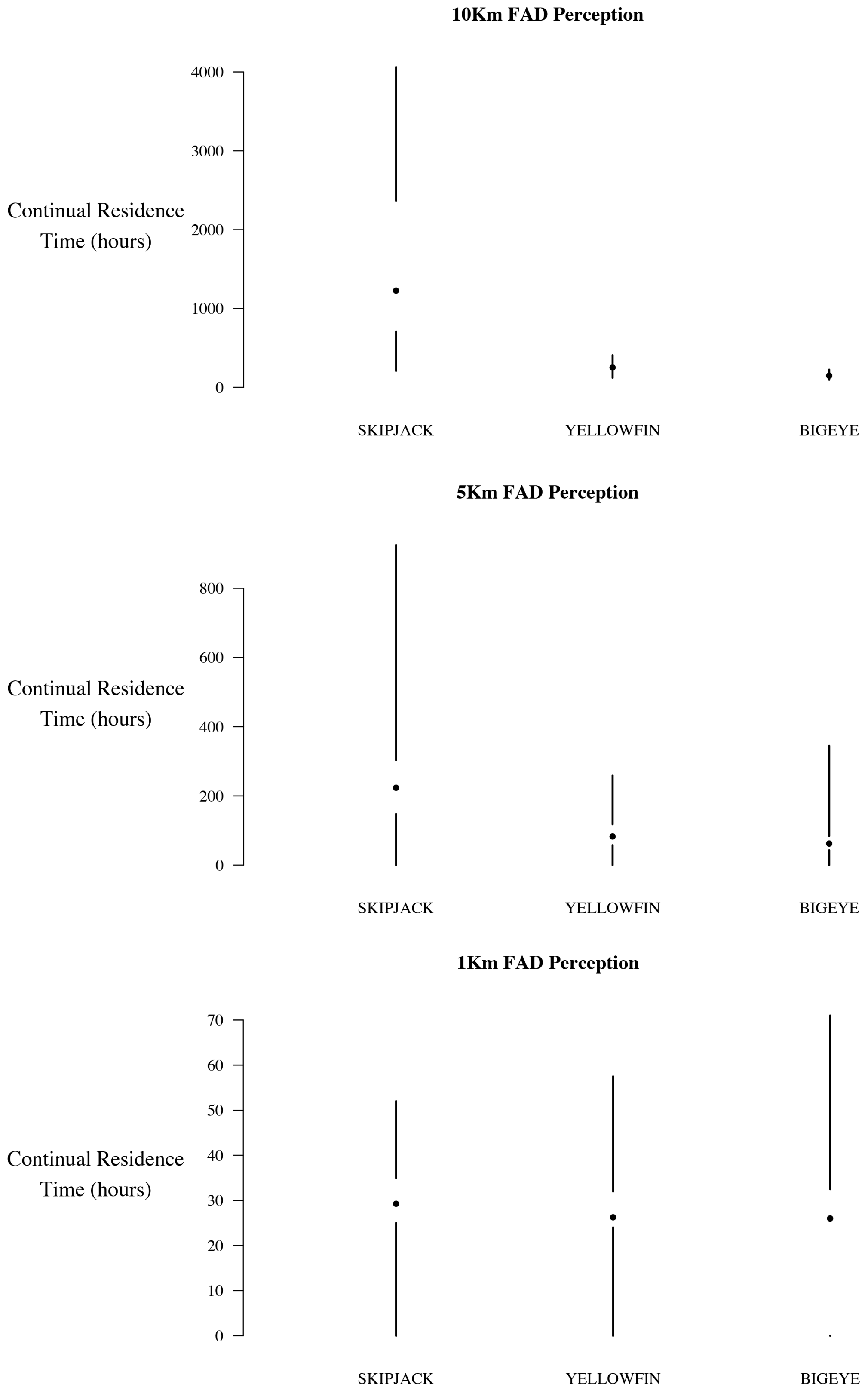

Figure 3.8 Boxplots of continuous residence time by tuna type, across decreasing FAD perception ranges (top to bottom).

3.4 Discussion

In this study I have developed a simple model to explore how tropical tuna foraging may be affected by FADs in the pelagic environment. Under the assumptions of the 'indicator-log' hypothesis of FAD attraction, and using a variety of prey field scenarios, vulnerability to FAD influence differs for different size classes of simulated tuna. There is no behaviour included in this model that explicitly attracts one type of tuna to associate with the FAD more of the time than other tuna; it is merely a result of the same behavioural reaction to the available prey field and physiological diving capability of the individual. When searching an empty ocean, all three tuna types on average spend the same amount of time at the FAD cell. Here, I examine in turn each of the hypotheses stated in the introduction.

3.4.1 FAD-containing oceans negatively impact simulated tuna

Clearly, the addition of an artificial FAD into the ocean results in a number of impacts to both diet and stomach fullness of the simulated tuna, although the strength of this impact is dependent on the prey field and is different for each of the tuna-types examined here (see below). In general, the artificial FAD causes a decrease in the average stomach fullness for all tuna-types during the course of the simulation. The relative diet contributions from each prey-type also shifts towards an increased reliance on deeper dwelling prey groups from the upper- and lower-mesopelagic layers.

The reason that any impact occurs at all is due to the presence of a FAD inhibiting the efficiency of the artificial tuna's hunting strategy. By adding a fixed, false prey item to the ocean, a degree of sub-optimal foraging is imposed on the behaviour of the predator. Rather than searching for true prey aggregation, the tuna school is spending some or all of the time around an arbitrary point that has no interaction with the surrounding prey. Instead of sweeping through empty patches of ocean, tuna random walk around the same area. It is clear that this will have an impact on feeding success, particularly when the prey field is patchily distributed, and is a critical concern if FADs do act as ecological traps in this manner (Bromhead, Foster, and Attard 2003; Dagorn, Holland, et al. 2013).

Unbiased observations of contrasting diet in free-swimming and FAD-associated fish are varied and few in the literature, but there exist some broad patterns for comparison. Stomach contents of FAD-caught fish have been observed to be less full than those caught in free-swimming schools (Hallier and Gaertner 2008), and some marked differences in diet between the same groups although these are inconsistent (Fernandez and Allain 2010; Ménard et al. 2000).

3.4.2 Larger size-classes of simulated tuna are less affected by FADs

In this simple representation of the pelagic domain and the indicator-log hypothesis, where FADs provide a false perception of prey to tuna, it is the ability of tuna schools to escape the influence of the floating objects by finding true prey aggregations that reduces FAD vulnerability. In all simulations, the attractive basin of the FAD for the tuna tends to cause periods of association with the FAD cell. This association is most likely to begin during the day, when the prey field is more sparsely spread out over all three ocean layers. At dusk, when the prey field of the shallower layers becomes flooded with vertically migrating individuals, there is a greater chance of tuna finding an “attractive path” away from the influence of FAD to feed.

Once real-world tuna are associated with a FAD, Holland (1996) identified three horizontal movement patterns that characterise the behaviour of tropical tuna caught and released with archival or acoustic tagging equipment. 1) Fish decide to leave the FAD, and do not return over the duration of the experiment. 2) Fish remain associated within a 500 metre radius of the FAD for the entire duration of the tracking. 3) Fish associate tightly with the FAD during the day time, but leave during the night and return to the same or an adjacent FAD the next day. This simulation model, alongside similar previous models, replicates these horizontal movements. In particular, the third type of behaviour occurs when the attraction of prey in the surface waters around the FAD is strongest during the night and tuna leave to feed. At dawn, with the thinning of the surface prey field, fish return to the FAD.

The smallest tuna type, SKJ, consistently suffers the greatest FAD impacts to stomach fullness and diet, as well as spending more time in residence associated at the time. This is particularly noticeable under the deeper species weighted SEAPODYM prey field scenario. In this model, tuna escape the FAD-effect by sensing true prey aggregations that move into the nearby prey field of the FAD. Larger size classes have more chance to escape the influence of the FAD because they have more chance of sensing prey in the deeper layers, particularly at dawn when a lot of the prey biomass migrates into deeper layers. They are capable of following the aggregations down, rather than being left with an empty prey field and the large influence of the FAD. Essentially, fish with the ability to dive into deeper ocean layers simply have greater foraging options and are less susceptible to the false prey signal of the FAD.

Previously observed patterns of tuna residence at FADs are highly variable from one region to another, and even in the same region at two different times. It is subsequently difficult to make direct comparisons with the emergent results of this model and real world phenomena. For example, the observed difference in residence times around FADs between small and larger size classes of tuna is around 2.5 times longer for smaller fish (Robert et al. 2012). The results of this study are certainly of the same order, although greater and lesser differences can be seen dependant on prey scenario.

3.4.3 Prey field scenario affects emergent FAD impacts

All of the metrics used here to indicate vulnerability to FADs are highly dependent on the distribution of prey throughout the artificial ocean. It is clear that the ECOPATH scenario, characterised by large amounts of prey biomass aggregating in the surface layer at all times, yields the lowest FAD impact simulations and the least variation across tuna types. All simulated tuna types, regardless of their ability to exploit deep layers, spend more time at the surface than other layers. This is driven partly by the vertical migration of prey during the night, but also it is a result of individuals ascending above the thermocline during their periods of resting behaviour. When the majority of prey biomass is concentrated in these layers, the search efficiency of the tuna schools is greater and enables more escape routes from the influence of the FAD within this single layer of the ocean.

Empirical observations of both meso-scale changes to the prey field and tuna behaviour or condition around FADs are not available for comparison with these simulation results. However, considerable variation in residence times have been seen between locations that are likely to have different prey fields (Robert et al. 2012) and even at the same FAD array at two different periods with potentially different prey fields (Matsumoto, Kitagawa, and Kimura 2013a).

3.4.4 FAD sensory range affects the strength of impacts

A more distant sensory perception of the FAD magnifies the false prey signal compared to real prey for tuna schools, making the chances of long residence times much larger when there are few prey aggregations in the surface layer. Under the assumptions of the indicator-log hypothesis, the sensory perception of tuna to prey aggregations and floating objects is a key driving force in residence times and therefor vulnerability of tuna to FADs and fishers.

However, when the difference between the false prey signal of the FAD attraction is dampened through reducing the FAD sensory perception range of the simulated tuna, the FAD impacts measured here are reduced considerably. Once the artificial tuna sense the FAD at the same range as the prey, the FAD impacts actually become negligible and residence times around the FAD drop to little more than a day on average. Once the FAD itself exhibits the same basin of attraction as the prey aggregations, its ability to trap simulated tuna schools in a sub-optimal foraging behaviour is completely diminished.

3.4.5 Model Caveats

Here, I have demonstrated that the vulnerability to FADs by smaller size classes of tuna can possibly emerge from solely the reduced ability to exploit deeper layers in the water column in a simple IBM framework. However, a number of caveats must be stressed in the assumptions of the model alongside potential improvements and additions that could be made.

This simulation experiment attempts to examine the effect of differences in the prey field through alternative scenarios, but there are still many dynamics that are not captured. In particular, although at the scale of the artificial tuna school in this model the prey field is highly heterogeneous due to the patchiness of aggregation, at the scale of the patch of ocean itself the prey field is homogenous. That is, the total abundance of prey for each ecological group remains constant throughout the simulation. The size of the artificial ocean here is 2500 km^2, and even patches of ocean this size may experience major changes in prey field due to seasonal or other changes in production. Such changes are likely to affect the ecological groups differently, altering not just the total available prey but also their temporal availability to tunas due to the ratio between vertically migrating and non-migrating species.

Similarly, there are a number of likely density-dependent effects on the prey aggregations that are not incorporated into the model. Aggregation probabilities are likely to change as the number of individuals increase in an aggregation, although the dynamics of this change are not known. For example, there may initially be a positive feedback in the cohesiveness of the aggregation as prey individuals group to benefit from effects of schooling on foraging and predator avoidance (Parrish 1991). There is also likely to be a negative feedback at larger aggregation sizes as competition for resources becomes greater and membership of the aggregation no longer confers the same benefits as at smaller sizes.

Under the assumptions of the indicator-log hypothesis, the attractive sphere of the FAD is clearly critical in determining the time spent associating with the FAD cell. The wider the sphere of attraction compared to that of a school of prey, the more false 'prey signal' there is to schools of tuna from the floating object. It may be that sensory perception of both FADs and prey aggregations is dependent on the density and abundance of biota associated with the object (Ghazali et al. 2013) or present in the aggregation, respectively. This would create a positive feedback mechanism for FAD association, whereby the more individuals were located at the FAD, the more it would become attractive to new schools of tuna. Similarly, the perception range and attraction of aggregation of biota and conspecifics may vary for different species of tropical tuna. In contrast, density-dependent attraction of prey aggregations would likely create a more balancing effect on predation. The more dense a particular prey aggregation, the more it would attract schools of tuna over greater ranges, which would then more rapidly decrease the abundance of prey in the aggregation as more predators arrived to feed. Introducing multiple schools of tuna into the model would allow some of these dynamics to be explored.

Unfortunately, in the absence of manipulative experimentation, it is very unlikely that we will be able to obtain true estimates of fishes' sensory perception of floating objects or prey, even if measures of sound or bio-fouling signals can be made on individual objects (Dempster and Kingsford 2003; Ghazali et al. 2013). However, the majority of FADs occur either in arrays of anchored FADs (Capello et al. 2012; Itano et al. 2004) or deployments of many drifting FADs that move with currents (Dagorn, Holland, and Filmalter 2010; Dagorn, Bez, et al. 2013). Using the model framework described in this chapter, it would be possible to include multiple FADs that had the same dynamics as either drifting or anchored arrays. Under these circumstances, despite a sensory perception equal to that of the prey aggregations, impacts to stomach fullness and diet may still be observed in the artificial environment when multiple FADs are present.

3.4.6 Key Areas for Further Examination

In this chapter, I have shown that changing parameters in a fairly simple representation of tuna and the pelagic ocean can result in varied dynamics in phenomena that are of interest in a fisheries context. However, there are clearly many unknowns associated with the validity of the assumptions and parameterisation of this model, and likely a great many more differences in the real world. Whilst many of the parameters and processes defined in this model have some basis in real data, such as the area of influence of a FAD or the distribution of the prey field, dynamics such as the probability of diving or search strategies are purely assumptions. Despite this, there are a number of areas indicated in this study that are likely to have some significant influence on the movement of tuna around FADs and their vulnerability to fisheries in general.

The diving and search strategies of real world tropical tuna are an area where we are likely to have more success in uncovering new information given the available data. Both the vertical and horizontal behaviours of the artificial tuna in this IBM are essentially guesses, but it is clear that at least diving ability and switching between the different layers of the pelagic domain may have serious effects on the exploitation of the prey field for tuna, and potentially their vulnerability to the effects of FADs.

Similarly, more information on the prey field at a variety of scales would allow a more informed IBM of this kind. Although methods such as acoustic surveys that measure the prey field over wide distances and depths are unlikely to be developed in the near future, more information on the abundance, small-scale distribution and aggregation of these prey species could be used to update the parameters of this model.

In addition, identifying new patterns or observations with which to compare the results of this or similar simulation models with provide an additional way of examining assumptions, without explicitly informing their parameters. More information on the observed dynamics of vertical and horizontal movement around floating objects would provide one source of these patterns. Information on the observed diet of fish would provide another.

There are many ways this theoretical model could be altered, examined further through parameter sweeps, or improved to incorporate some of the missing dynamics described above that may be important in the real movement behaviours of tropical tuna. However, the purpose of this model was to examine the potential for significant impacts to the vulnerability of tropical tuna from changes to two key drivers of behaviour: vertical movement behaviours associated with size class, and the nature of the prey field. In the following chapter, I will summarise a wide variety of the real-world data that is available to us to gain new, useful information on tuna movement behaviours. A number of preliminary analyses will be carried out, and the most pragmatic areas to focus on for further study identified.

Chapter 4: Analysis of Real-world Behavioural Data

In Chapter Three, an expressive but un-fitted theoretical model was used to show how significant changes to important traits in tuna, such as vulnerability to fishing gears, could emerge when behavioural or prey field dynamics are modified. In this chapter, two sources of real world data on the movement of tropical tuna are examined for their potential to better inform the behaviours that were identified as important in the previous chapter. Several preliminary analyses are carried out, and their results and weaknesses briefly discussed.

4.1 Tuna movement data

4.1.1 Mark-recapture data

Mark-recapture tagging programmes have been carried out during several long-term periods and across a number of regions. In particular, the Regional Tuna Tagging Programme (RTTP, 1989-1992) and Pacific Tuna Tagging Program (PTTP, 2006-2014) have established considerable data sets for conventional mark-recapture tags released in the WCPO, now exceeding 70,000 returns (Leroy et al. 2013). Tagging releases consist of capturing many fish individually during a single fishing event, typically several thousand in a day, recording species and size, and attaching a numbered dart tag to the animal (WCPFC Tagging Commitee 2007). Following a period of time-at-liberty, a proportion of these fish are recaptured, and the tag returned alongside information on, ideally, time, location, fishing method and size at capture. Within this data set exist information on changes in horizontal displacement, growth experienced during time-at-liberty, information on school behaviour at release and, in some cases, the same information at recapture.

Mark-recapture tagging provides only a behavioural observation at two moments in time for each individual fish, with everything between those two points hidden from us. Although the observed behaviours at time of release and at time of capture can be assumed to represent at least some of the time of liberty, this may not be the case. For example, it is possible that an individual tagged whilst known to be resident at an anchored FAD actually ceased association the following day, spent several months as part of a free-school, before returning to an anchored FAD and being caught during the first day of association. This is especially true given that, as has been discussed, both fishing and tagging effort is concentrated at FADs.

While these databases represent valuable resources on tuna movement and biological information, mark-recapture tagging data contain many biases. The robustness of the assumption that tagged individuals truly represent the regional population is rarely known fully (Kolody and Hoyle 2013), although some biases can be corrected within certain population modelling approaches (Hampton 2000). Most critically, tag data are not a true measure of movement behaviour because fishing effort is concentrated spatially and temporally (Sibert and Hampton 2003). As tagging effort is often also concentrated in the same areas as fishing, this may result in fish that are naturally resident being caught in greater numbers than fish that may be naturally more migrant, and which subsequently move to areas of lower fishing effort. In addition, concerns regarding the quality of the data have been raised, particularly in relation to recapture locations and events (Leroy et al. 2013). For detailed analyses into movement behaviours, information recorded at recapture would constitute half of the principal observations, and so any conclusions drawn must be interpreted with considerable caution. Using a subset of the data believed to be less prone to error, such as solely using reports from the Japanese fleet that has firm procedures for tag recovery (S. Nicol *pers. comms.*), may alleviate some of these problems. Unfortunately, this would also greatly reduce the number of observations for some species, areas and school-types, as catches across these factors are fleet biased.

The mark-recapture tag database of the PTTP is a great resource for examining the broad movement behaviours of tropical tuna, but using detailed information from recaptures in analyses will always carry the caveats of uncertain quality and bias from the data. These data are inherently fisheries-biased, and assumptions about their ability to accurately represent a population of tuna make analyses problematic.

4.1.2 Electronic tagging

Electronic bio-logging equipment provides much higher resolution data on animal movement behaviours than conventional mark-recapture tags. The behavioural study of wild free-ranging animals has been revolutionised over the last two decades by the development of these types of animal telemetry equipment. High-resolution records of the temporal and spatial behaviour of animals are now available in unprecedented quantities (e.g Block et al. 2011; Hammerschlag, Gallagher, and Lazarre 2011). One form of bio-logging equipment, the electronic archival tag, is a surgically implanted electronic device that records data on the depth and temperature information from an individual fish at scales of seconds to minutes, while that fish is at liberty in the ocean. The PTTP database now contains a number of returns of this type of tag from the WCPO, numbering over 150, mostly from bigeye and yellowfin tuna released in the Bismarck Sea, Solomon Sea and the central equatorial Pacific.

While archival tags provide data on tuna movement that is not fisheries-dependent in the way that conventional mark-recapture data are, there remain a number of problems with analysis. The patterns in time-series of movement behaviours are the result of an animal reacting to its environmental stimulus and its own physiological needs. Unfortunately we observe neither of these things directly from archival tagging data, but can see their effects in some the consistent forms a dive profile takes through time. This results in highly varied and noisy data recorded by bio-logging devices. Describing these data as classified behaviours is problematic because, while sometimes these behaviours are clear, often they occur as a spectrum of patterns. How deep must a bigeye tuna dive before we can say that it is exhibiting “classic” day-time behaviour? What if this behaviour only occurs for half of the day, or includes many noisy movements through the water column? Are movements in shallow water all the same, or are some significantly different in some way to others? Describing vertical movement data requires an approach that can incorporate these spectra of movements, without simply accounting for noisy or bizarre observations by ascribing them to some phenomena that cannot currently be observed.

Often the recent context provides an indication to which group of qualitative patterns a particular series of noisy observations belong, and indeed when the depth and temperature records from archival tags are examined, we see very high levels of autocorrelation in these data. This is the chief cause of another problem in describing behavioural time-series: the data are autocorrelated (Hartmann and Gottman 1980). What is observed over one particular period of time is related to what has occurred during the previous period (and in some cases even earlier), being a result of underlying motivations such as hunger, digestion or predator avoidance. As a result, many standard statistical methods of analysing data cannot be used, as the time-series violate the assumption of independent data (Jassby and Powell 1990).

Considerable investment has been made in the deployment and recovery of these electronic archival tags implanted into tropical tuna in the WCPO, as well as many other species around the world. The time and expense involved in undertaking these kinds of tagging experiments means that the amount of data is several orders of magnitude less than those from mark-recapture tagging programmes, but each tag contains a time series of many thousands of observations for that single individual. While the time-series from archival tags hold good quality information on the vertical movement behaviour of a single fish, from the variety of qualitative patterns used in previous studies, it is clear that there is no standardised method of describing these kinds of behavioural data. When our aim is to assess these behaviours across factors we believe to be significant, or answer questions on how vertical habitat use changes across size classes such as posed in the previous chapter, the lack of appropriate behavioural description is one of the primary problems to overcome. Without quantitative analyses that describe the behavioural information contained in these time-series, it is difficult to incorporate this information into the large-scale population dynamics models used for stock assessment. The integration of this rich source of data into stock assessment analyses is a priority in current fisheries research (Sippel et al. 2014).

4.2 Preliminary Analyses

In light of the potential for examining movement behaviours from archival tag time-series of the PTTP, a preliminary analysis will be carried out to examine real world examples of some of the dynamics either assumed or simulated in Chapter Three. First, summary statistics of vertical movement data from the PTTP archival tag database will be calculated to explore potential changes in vertical habitat use across size classes and regions. Following this, a number of machine learning techniques will be tested for their ability to objectively identify and classify predefined vertical movement patterns from archival tag time-series.

4.2.1 Summary Statistics of Vertical Habitat Use

The data recorded by electronic archival tags are not fisheries-biased in the way mark-recapture tag data are, although the distribution of recapture locations is still necessarily linked to fishing effort. Although a number of problems using data from these tags for horizontal light-based geolocation has already been discussed in Chapter Two, the vertical movement dive profiles recorded are high resolution and contain much information.

A preliminary approach was undertaken to examine basic statistics calculated across the entire length of time-series from the PTTP archival tag database, to ascertain if potential changes in vertical habitat use were seen across factors such as size of fish. I hypothesise that changes in habitat use will be seen across size of individual fish at release, as assumed in the simulation model of Chapter Three.

Mean depth was calculated across the time-series recorded by each tag that did not contain periods of missing or corrupted data longer than 1 hour, and these were compared across individual fork length-at-release. For each species, the mean depth across the whole dive profile is plotted against length-at-release (Figure 4.1) with a simple linear regression overlaid (adjusted R^2 = 0.02, $P < 0.001$ for yellowfin, adjusted R^2 = 0.31m $P < 0.001$ for bigeye). Yellowfin and bigeye share similar mean depths for the smallest size classes, but bigeye quickly begin to inhabit greater mean depths as they increase in size. There appears to be no such change with size at release for yellowfin. No archival tags implanted in skipjack are examined in this thesis, as there are not sufficient numbers of returns in the PTTP for analysis.

Yellowfin and bigeye tuna show distinct diurnal differences in their behaviour, and averaging across these temporal periods potentially results in a composite view of two distinct patterns. A simple way of examining this is to approximate the timing of dawn and dusk in the tropics by dividing the time-series into day and night at 6am and 6pm each day. Clearly this method is a poor estimation, as large horizontal movements and seasonal changes can significantly affect these timings for each individual, but it allows a general separation of likely day and night periods in the data. The correlation between fork length-at-release and mean depth alongside plotted linear regressions, separated into day-time and night-time, are shown in Figure 4.2.

Summarising the regressions, for yellowfin there was little evidence that mean day-time depth varied with release length ($P = 0.227$, adjusted $R^2 = 0.01$), while a slight positive correlation was seen for mean night-time depth ($P < 0.001$, adjusted $R^2 = 0.26$). For bigeye, mean day-time depth decreased with release length ($P < 0.001$, adjusted $R^2 = 0.37$), while no pattern was apparent between night-time depth and length ($P = 0.679$, adjusted $R^2 = 0$). An ontogenetic shift in vertical habitat use in bigeye with size seems clear from mean day-time depth from this simple analysis, with little evidence for a similar change in yellowfin.

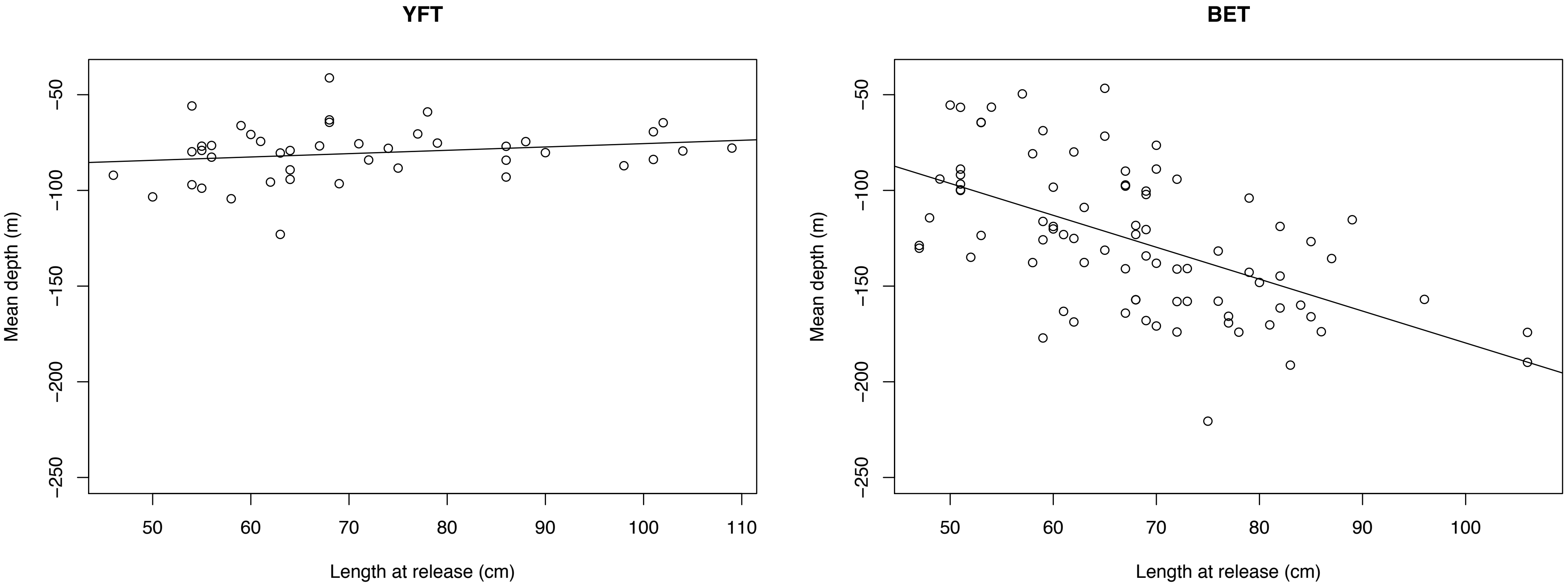

Figure 4.1 Mean depth during archival time-series across length-at-release, alongside linear regression prediction. Results for yellowfin are shown on the left, results for bigeye, on the right.

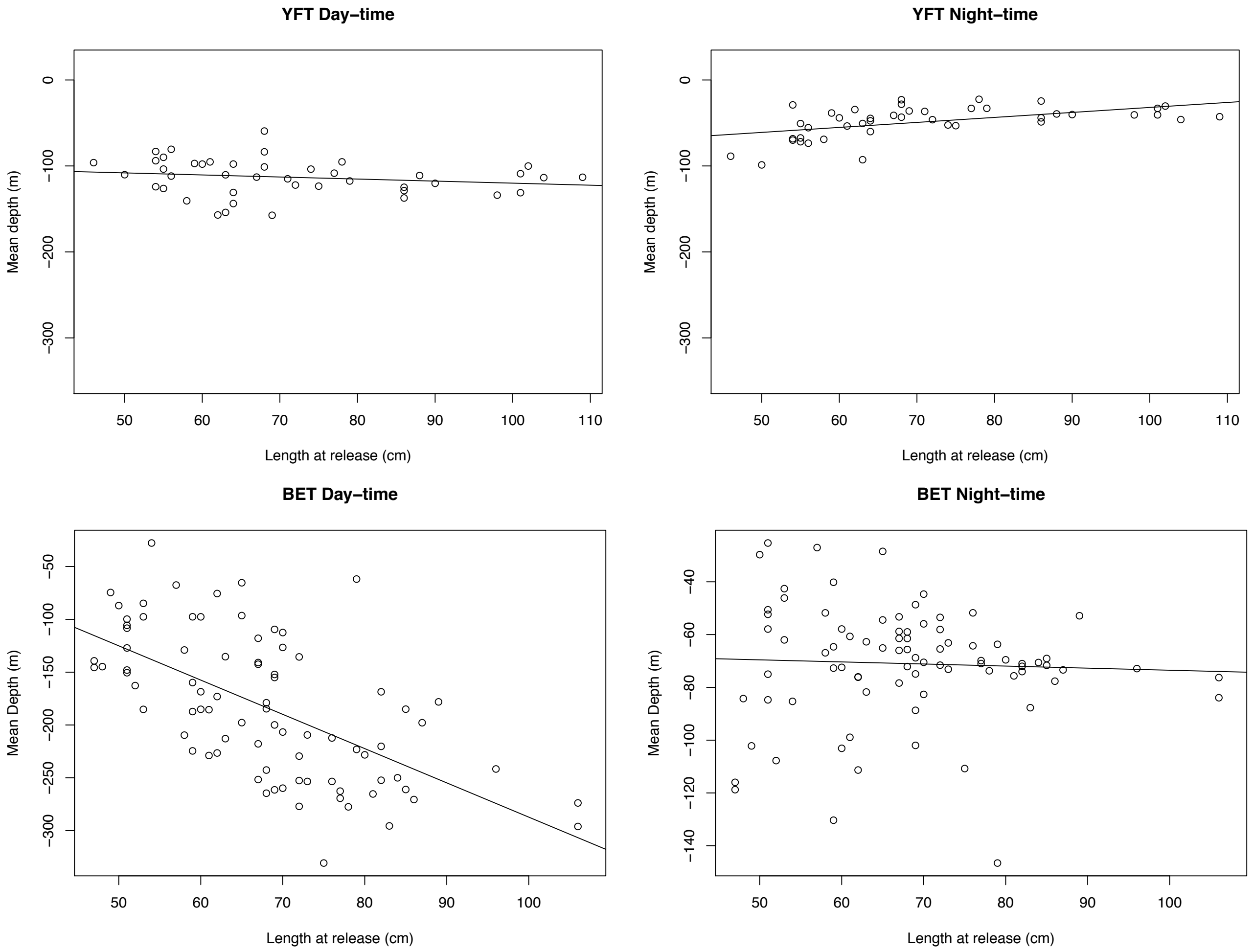

Figure 4.2 Mean depth across length-at-release for yellowfin (top) and bigeye (bottom), and separated into day-time (left) and night-time (right).

While these kind of mean statistics may be useful in identifying some general changes that might occur, there are again a number of fundamental problems in drawing conclusions from them. First, these time-series contain large amounts of data, in some cases many millions of observations. To summarise the time-series using only one summary statistic is to ignore much information and variation contained in this valuable data source. One of the great strengths of archival tag data is its high-resolution nature and subsequent ability to reveal many complex and small-scale patterns. These patterns imply the second problem with such an analysis, namely that what we observe in dive profiles from tropical tuna is assumed to be a composite of a number of discrete behaviours, which cannot be summarised by one number for the entire time-series. As discussed, the patterns in movement through depth and temperature are the result of underlying decisions and motivations of the individual fish, based on reactions to environmental stimuli that occur at a variety of time-scales. It may not be possible to describe these vertical movement patterns in terms of only absolute depth or temperature, and many of the previously identified behaviours in tropical tuna are more complex than a simple measurement of time spent at a certain depth (Matsumoto, Kitagawa, and Kimura 2013a; Schaefer and Fuller 2004).

4.2.2 Classifying Vertical Movement Behaviours

A variety of qualitative descriptions and meanings have been ascribed to the depth- and temperature-time patterns assumed to be common across yellowfin and bigeye. These include foraging dives, thermoregulatory ascents, V-shaped deep dives, and extended periods of association with floating objects at the surface (Bertrand, Bard, and Josse 2002; Dagorn, Holland, and Hallier 2006; Holland et al. 1992; Itano et al. 2004). If such patterns are assumed to be consistent across individuals, then a way to objectively describe and identify these patterns is required, so that the variation in their nature and occurrence can be compared between individuals and across factors of interest.

In order to automatically and objectively identify these patterns, here I apply a variety of machine learning approaches to classify pre-defined behaviours in vertical movement from PTTP archival tags. The hypothesis to be tested is that the frequency of these patterns' occurrence will change over size classes and between regions.

To classify vertical movements it is necessary to compress a time-series to observations that could capture the form and dynamics of various behavioral patterns. The electronic archival tags of the PTTP typically record observations at intervals of between 10 seconds to 5 minutes. Although consideration of the highest resolution observation-to-observation dynamics of the dive track may certainly be useful, here I wish to compare more composite collections of movements through the water column that occur at the scale of hours, rather than seconds. The optimal time-step for such binning needed to be long enough to capture the range of consistent, composite behaviours that have been qualitatively described for tuna in previous studies, such as 'U-shaped diving' (Schaefer and Fuller 2005; Schaefer, Fuller, and Block 2007), whilst also being small enough to capture within-day shifts in behaviour, such as the 'afternoon diving' described by Matsumoto, Kitagawa, and Kimura (2013a). Once each time-series was divided into these suitable time bins, summary metrics could be calculated for each section and used to characterise and quantify the vertical movement pattern for that period.

To divide each time-series into these bins, raw data from the tags were divided into sections from which summary metrics were calculated, starting with two initial divisions made at points that estimated dawn and dusk. Data were divided at these points to minimise the chance of behavioural sections straddling the crepuscular periods during which tuna are known to undertake behavioural switching (Musyl et al. 2003; Ohta and Kakuma 2004). In contrast to arbitrarily choosing the 6am and 6pm time-stamp in the tag data as dawn and dusk, as in the previous analysis, here I estimated these crepuscular points individually for each tag. This was achieved by calculating the average time of day at which large shifts in time-at-depth consistently occur, assuming that this represents dawn and dusk, using a split-moving window analysis (Ludwig and Cornelius 1987). This approach has been used elsewhere to divide the vertical behaviour of free-roaming animals into behaviourally consistent sections over longer timescales (Humphries et al. 2010; Sims et al. 2011). Initially, the depth profiles for each time-series were divided into proportion of time spent within 10-meter 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 distance metric provides a measure of how dissimilar the first window half is from the second, in terms of the time spent by the individual at different depths. Dissimilarity was recorded at the point in the binned depth profile split by the window, the window then moved on one bin. The process was then 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 is not the case 100% of the time. There was also considerable inter-depth movement that did not occur across these crepuscular periods. To identify when the most consistent shifts in movement occurred, the time at depth bins were randomly re-ordered 5000 times and the same analysis carried out. When the dissimilarities from the random time-series failed to exceed those calculated from the originally ordered data for a particular point 95% of the time, it was concluded that this represented a significant shift in vertical behaviour, given the natural variation in the data (an example section of dive track is shown in Figure 4.3).

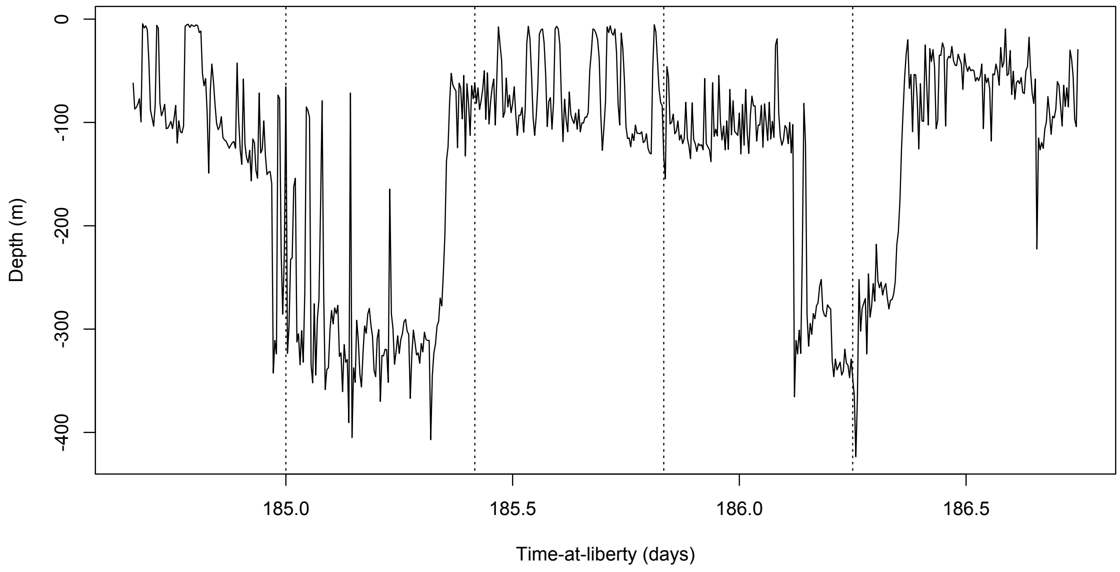

Figure 4.3 Example centre points of significant changes identified between two halves of 12-hour split moving window, shown with vertical dashed lines.

The periodicity of these significant behavioural changes was then examined to identify whether there was a consistent, diel pattern in their occurrence. Significant changes can be expected to occur more commonly at the boundary between day and night. 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 (Hartigan and Wong 1979; MacQueen 1967) 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 for the whole time-series, being the most common times of the day when switches in depth-frequency occurred.

Once boundary periods had been identified, the data were further divided into the smaller time-bins between those crepuscular boundary points. Summary metrics were calculated from the raw data for time bins of 1, 2, 3, 4, 6, 12 hours duration for comparison (an example is given in Figure 4.4). At a time step of 3 hours, a balance was obtained between capturing dynamics such as only diving around crepuscular periods or periods of ‘U-shaped’ diving, without very fine patterns such as lone thermoregulatory ascents being characterised individually in the analysis. Summary metrics were calculated for the data in each 3-hour section. These were: mean of depth and temperature; median of depth and temperature; standard deviation of depth and temperature; interquartile range of depth and temperature; 10th and 90th percentiles of depth and temperature, and range between these values; the mean delta depth and temperature, that is the mean value of successive changes of depth or temperature in one direction, or step length; the standard deviation of depth and temperature step length; temperature variance to depth variance ratio; and standard deviation of velocity, which is the change in depth per time taken between observations recorded by the tag.

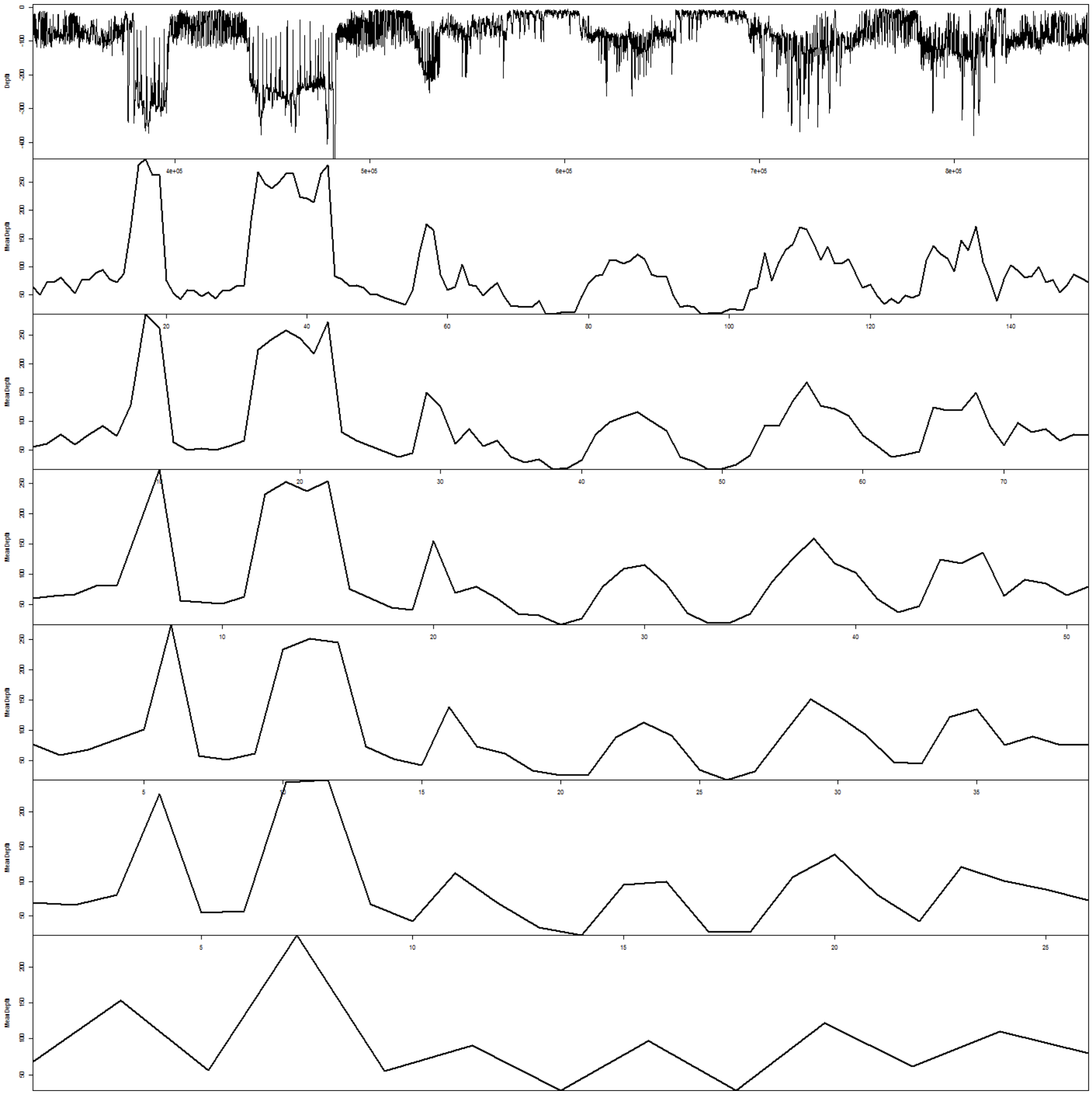

Figure 4.4 Depth from an example section of dive track (top), summarised as a mean value over time-bins of (from top to bottom) one-hour, two-hours, three-hours, four-hours, six-hours, and twelve-hours.

4.2.3 Qualitative descriptions

Rather than assign movement patterns based on their perceived relationship to various factors (i.e. association to floating objects, day/night, 'normal feeding'), here summary metrics are used to quantify four pre-determined qualitative patterns without an implied ecological meaning. This approach allows an examination of the relationship between vertical behaviour and potential covariates such as size or region, without implicitly incorporating assumptions that may be erroneous. Dive profiles are described as a series of these distinct patterns, which have previously been used to classify the typical vertical movement patterns in tropical tuna for persistent periods of 3 to 12 hours. Although qualitative descriptions of behaviour have been ascribed to a variety of temporal scales, here I make the assumption that behavioral patterns exhibited for longer than the three-hour time bin used here are simply continued exhibition of that behaviour, for two more individual three-hour periods.

Four vertical behavioural patterns were defined based on the movement of an individual through the water column, and the thermal-habitat occupied during the behaviour. These patterns were based on consistent behaviours used to describe tropical tuna in previous studies, although their qualitative nature precludes them from being truly objective.

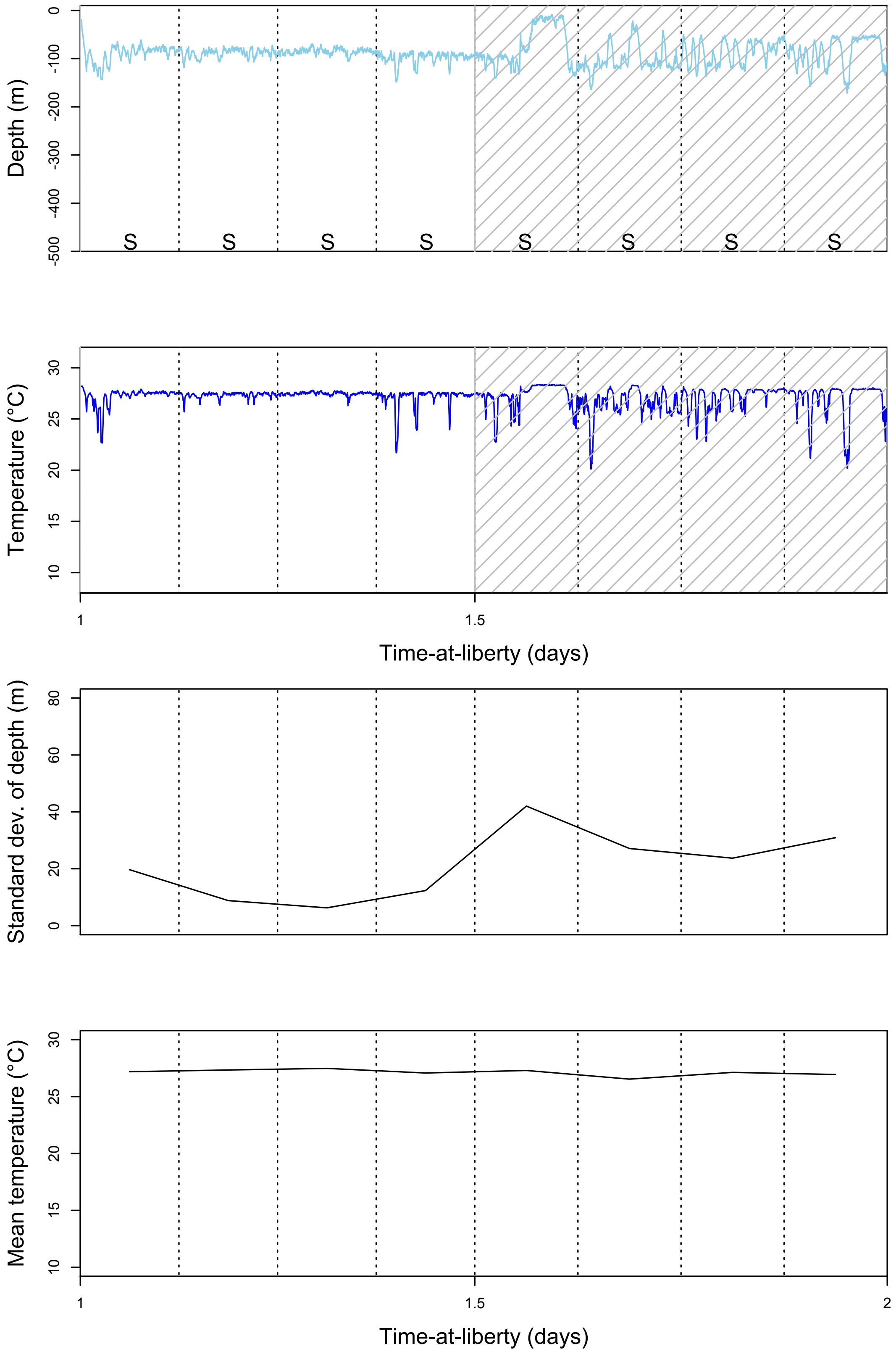

Figure 4.5 Example time-series section of depth and water temperature during typical shallow behaviour. Two example summary metrics, standard deviation of depth and mean water temperature, are shown underneath.

State S – Shallow behaviour

This state is characterised by sustained time in surface epipelagic waters, notably remaining in warmer waters above 25˚C for the majority of the pattern (see Figure 4.5). The fish typically remains in the top 100m of the water column, although the varying depth of the epipelagic layer means this is not always the case. While there may be occasional unconnected dives into the thermocline, these are not particularly deep or sustained, rarely penetrating the 20˚C isotherm. Such behaviours have been identified as shallow or mixed-layer behaviour (Leroy et al. 2010; Matsumoto, Kitagawa, and Kimura 2013a; Schaefer, Fuller, and Block 2007). This classification includes, but is not limited to, surface or floating object association behaviour defined in other previous studies (e.g. Schaefer and Fuller 2013)

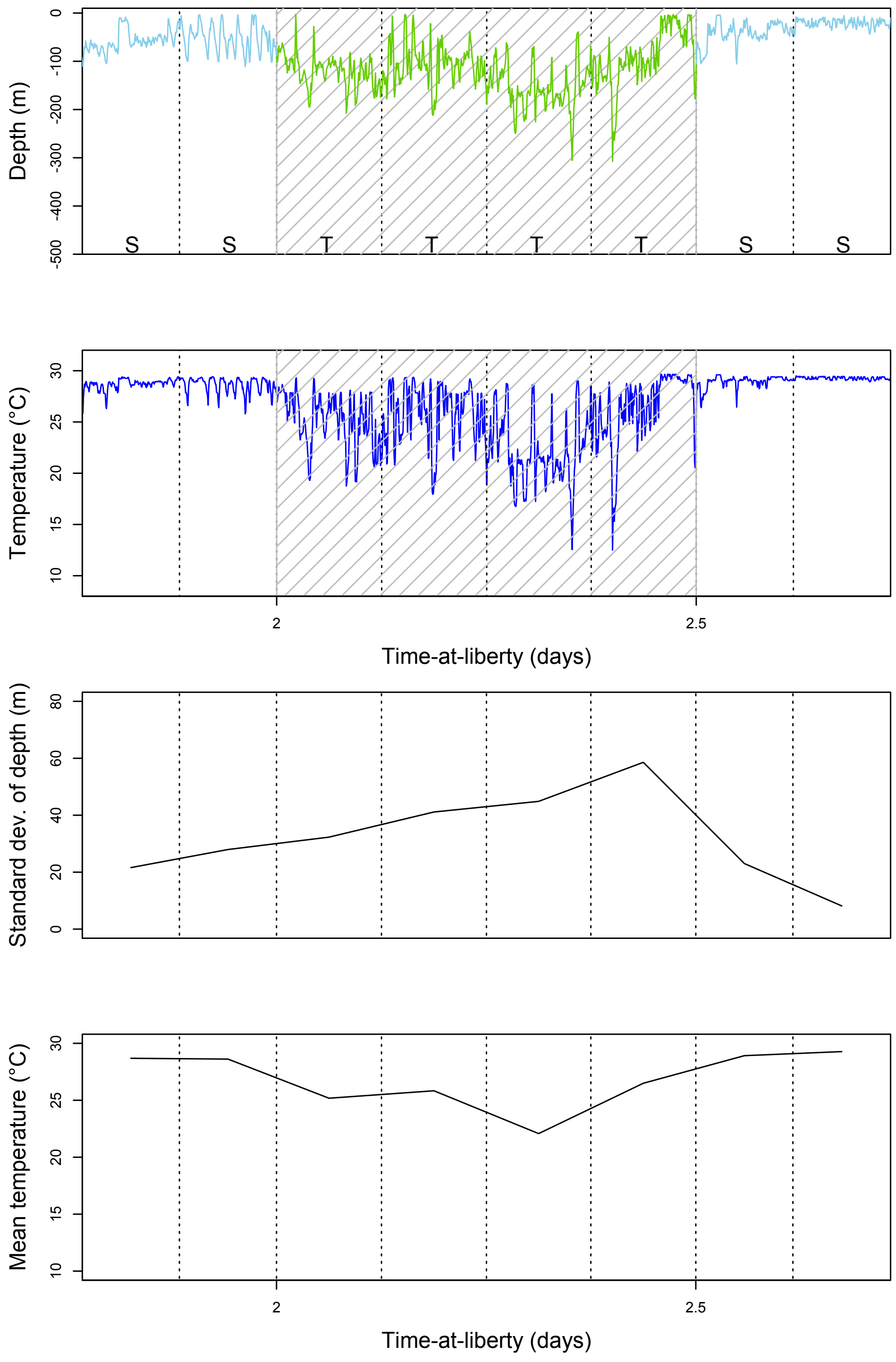

Figure 4.6 Section of dive track showing typical thermocline association behaviour.

State T – Thermocline association

Thermocline association may vary considerably in depth, but all share a general residence within and above the thermocline (see Figure 4.6). This includes sustained movement at depth within this zone where changes in water temperature are very rapid, as well as continued movements in and out of the top of the thermocline. Similar behaviours have been identified in previous studies (Dagorn, Holland, and Itano 2006; Schaefer, Fuller, and Block 2009; Sharp 2001), particularly, although not exclusively, for yellowfin. Thermocline association is rarely sustained at depths lower than the 20°C isotherm, at which point regular ascensions to warmer waters tend to occur (see States U and B below).

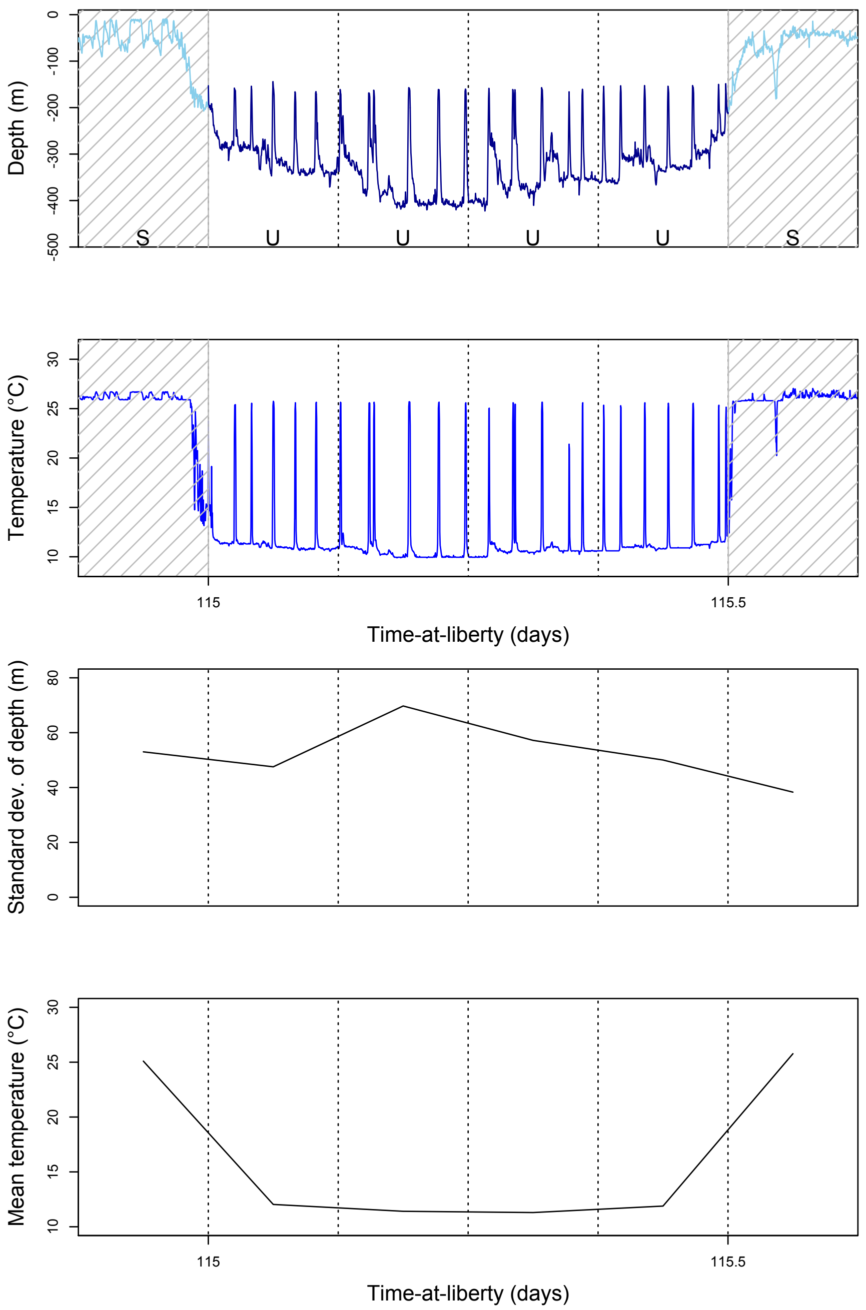

Figure 4.7 Example section of U-shaped diving behaviour with thermoregulatory ascents.

State U – U-shaped diving behaviour

U-shaped patterns consist of clear deep diving movements. These behaviours are typified by high frequency but low amplitude movement at depth below the thermocline in the mesopelagic layer, interspersed with brief ascents to the surface to rewarm (Figure 4.7). Sometimes the maximum depths of the dives will increase during the first half of the day-time, and then decrease until dusk. Occasionally, there are also single, deeper dives undertaken within this behaviour, often marking the end of this pattern. Such behaviour is typical of bigeye tuna, although it is sometimes undertaken by large yellowfin (T. Matsumoto, Kitagawa, and Kimura 2013b; Schaefer, Fuller, and Block 2007; Schaefer and Fuller 2005).

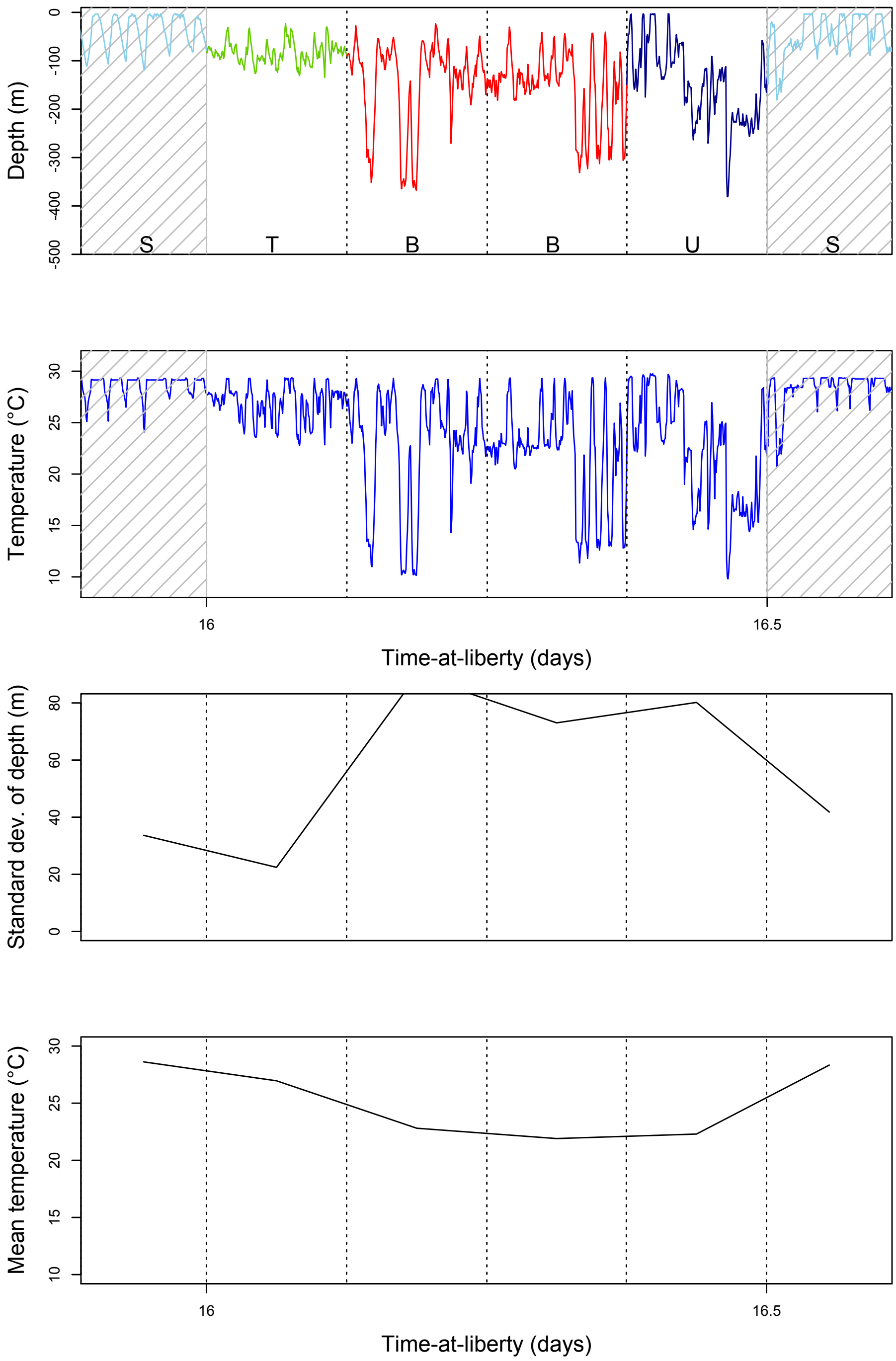

Figure 4.8 Isolated example section of bounce diving behaviour below the thermocline.

State B – Bounce diving behaviour

Bounce diving is typified by fairly continuous movement between the surface and bottom of the thermocline, with little time spent at a particular depth. Although sometimes similar to thermocline association, here I define bounce diving as distinct in that many dives are made to depths colder than seen during thermocline association (Figure 4.8). This kind of bounce diving has been identified for tropical tuna in (Leroy et al. 2010; Schaefer, Fuller, and Block 2009).

4.2.4 Machine learning

Machine learning has a long history in pattern recognition for a variety of fields, but has increasingly been used to solve ecology problems where data are very numerous or abstract (e.g. Mapp et al. 2013; Pontin et al. 2011; Schreer, Hines, and Kovacs 1998). Such approaches provide the benefit of being automated, more objective than human classifiers, and, with modern processing power and software packages, efficient and easily accessible. Here, I initially explore the success of a number of well-known supervised machine learning techniques on their ability to accurately classify yellowfin and bigeye behavioural data from the PTTP.

The time constraints and lack objectivity prevent the manual classification of the near 115,000 three-hour sections of archival dive data present in the PTTP database. Subsequently, the machine learning algorithms were examined for their ability to classify the PTTP archival data based on information captured from a training set of data. This training set consisted of 2000 manually classified three-hour sections from archival tag time-series, with the classification undertaken by four separate experts, each trained in identification of the patterns and carried out in isolation. The sections were taken from 6 separate fish, including yellowfin and bigeye tagged in both the Eastern and Western Pacific regions. Each section of vertical movement data was classified as belonging to one of the four patterns described above by each expert. A canonical training set was then created by assigning the most popular classification amongst the four trainers (by majority vote) to each three-hour section.

Machine learning techniques typically look at the variation or spacing between multi-dimensional datasets, and then group observations based on certain criteria. Unlike statistical modelling, where the aim is usually to find the most parsimonious solution to describing patterns in data, here we are concerned only with successful classification. Subsequently, the more independent ways of quantifying a given pattern are used, the more information is available to an algorithm for classification. Here, I use the summary metrics calculated across the three-hour sections used for manual classification as a quantification of these described behaviours. A pairwise plot of metrics captured from an example bigeye time-series is given in Figure 4.9, showing how each pair of metrics visually correlates to one another.

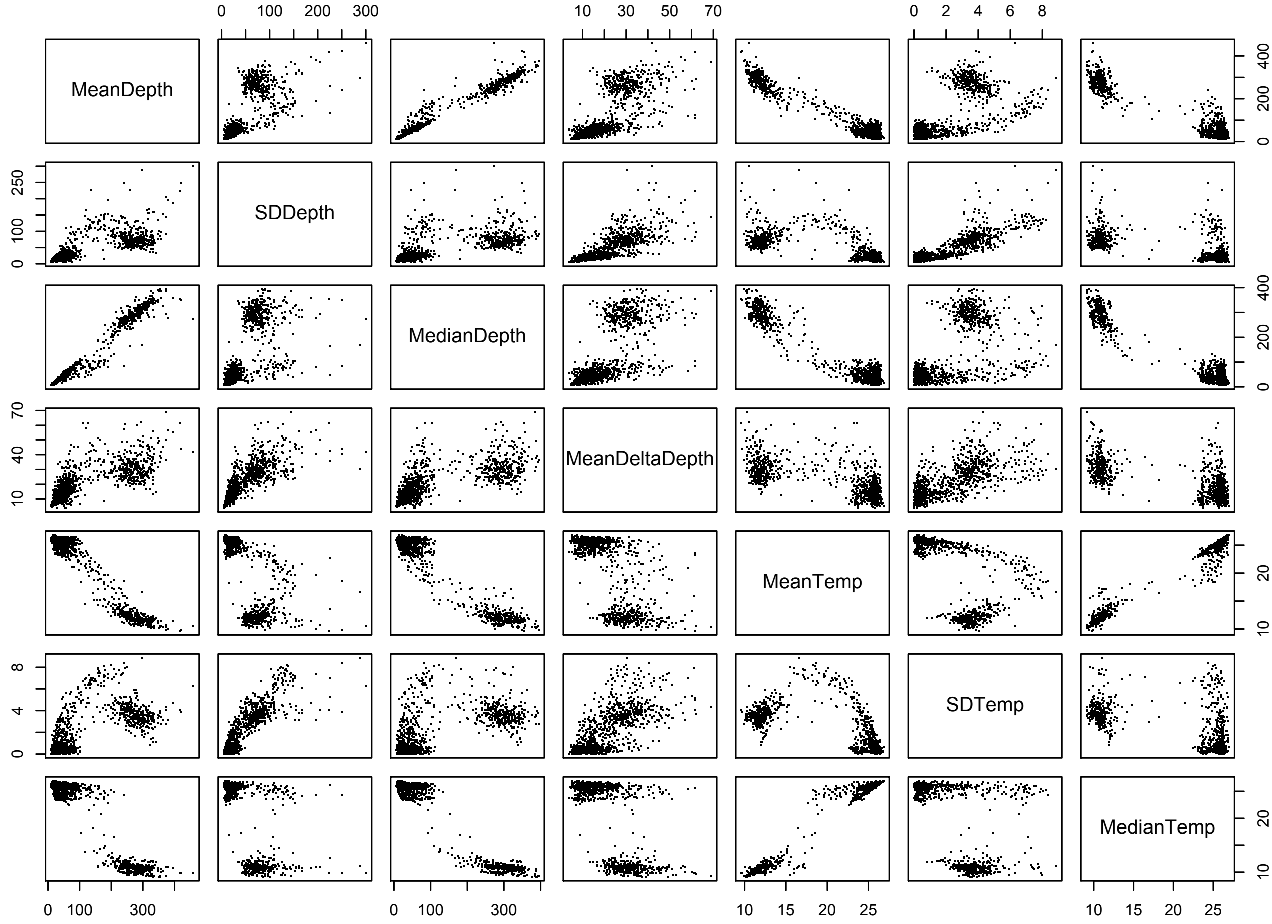

Figure 4.9 Pairwise plots of example summary metrics captured form a single time-series. Rows and columns represent (from top to bottom, left to right): mean depth, standard deviation of depth, median depth, mean depth step-length, mean water temperature, standard deviation of water temperature, and median water temperature.

As these summary metrics occur on different scales, and each has a different distribution, a transformation was necessary before classification. Therefore, all metrics were log transformed and scaled to a Z-score with zero mean and unit variance, ensuring they better resembled normal or a mixture of normal distributions. The data were then randomised, and 20% set aside as an unseen "test set" not used in training the algorithms.

Three alternative machine learning approaches were examined. These were K-nearest neighbour (Fix and Hodges Jr 1951), Nu- Support Vector Machines (Cortes and Vapnik 1995), and Random Forest Classification (Breiman 2001).

K-nearest Neighbour: KNN classification is one of the earliest and simplest machine learning algorithms used for classification. Essentially, a training set of points is used to classify a new unknown point, based on the majority membership of its k-nearest neighbours in the multidimensional space defined by the metrics used for classification. Here, I use the *knn* algorithm in the *class* package (Venables and Ripley 2002) in *R* (R Core Team 2013).

Nu Support Vector Machines: Nu-SVM is a version of the original support vector machines algorithm for classification. As with KNN, this approach uses existing positions of points from a training set to classify new data. In an SVM however, the space is mapped such that each group from the training set is separated by as large a gap as possible by a high-dimensional hyperplane. The most difficult points to classify, i.e. those most alike, bound the margins of this hyperplane and an SVM algorithm maximises this margin to create a large gap between this points, or support vectors. Nu-SVMs take an additional parameter Nu, which sets an upper bound on the training error and lower bound on the number of support vectors. Here, I use the *ksvm* algorithm implemented in the *kernlab* library (Karatzoglou, Smola, and Hornik 2013) in *R*.

Random Forest Classification: Random forest methods combine a high number of weak but efficient decision trees, each created from random subsamples of the data and predictor variables, for classification. This random sampling of predictor variables used for splitting the data helps ensure that trees will be less correlated with each other, particularly if a small number of these variables are very strong predictors. New observations are run down all of the trees in the ensemble, and a majority class membership is calculated, resulting in a process that is computationally relatively fast. For this study I used the algorithm *randomForest* in the R package of the same name (Liaw and Wiener 2002).

A number of parameterisations are possible for each algorithm, requiring at least a minimal parameter sweep to be carried out. A leave-one-out validation was undertaken, in which each individual sample in the training set was classified using an algorithm built on all of the remaining samples. A sweep of some key parameters was done to estimate the best possible values, alongside a cross-validation score (CV). The best parameters and corresponding average CV scores are given in Table 4.1. The most accurate parameterisation was then used to classify the previously unseen 20% test set of data, providing a test score of percentage correct classification for comparison of the three algorithms. Two additional scores were also calculated for each individual behavioural pattern: precision, which is the ability of the algorithm to not to label a particular sample as the behavioural pattern, when it is actually one of the other patterns; and recall, which represents the ability of the classifier to correctly classify a particular sample as not belonging to the behavioural pattern, regardless of what classification was assigned. These scores are summarised in Table 4.2.

Table 4.1 Summary of cross-validation scores of most accurate parameterisations for each machine learning algorithm.

Algorithm	**CV Score**
K-nearest neighbour Number of neighbours = 3	0.83
Nu- Support Vector Machines Kernel function = Radial Basis kernel Kernal degree = 2 Inverse kernel width = 0.043 Nu = 0.15	0.91
Random Forest Classification	0.84

Max nodes = 5

Number of variables = 15

Table 4.2 Classification test scores for each behavioural class and overall success.

Algorithm	**Precision**					**Recall**					**Test Score**
	S	T	U	B	Overall	S	T	U	B	Overall	
KNN	.91	.73	.85	.42	0.79	.94	.66	.79	.56	0.78	**0.78**
Nu-SVM	.97	.93	1.0	1.0	0.97	.97	.97	1.0	.89	0.96	**0.96**
Random Forest	.89	.76	.86	.57	0.80	.94	.76	.86	.44	0.81	**0.81**

From these results, it is clear that the Nu-SVM machine learning performs the highest of the three algorithms overall, as well as for each individual behavioural classification. In particular, it appears to identify the bounce diving state much more accurately than the KNN and Random Forest classifiers. Although the 97% classification success on the test set is unlikely to be replicated on a larger unseen set of data, these results are encouraging.

In light of these results, a Nu-SVM classifier was subsequently built using the complete training set, including the previous 20% test set. The classifier was then applied to a subset of the full PTTP archival database consisting of 117 individuals (44 yellowfin and 73 bigeye) constituting around 87000 three-hour sections of data. The classified dive tracks were used to compare the proportion of time spent exhibiting different behaviours, and how these differ across factors of interest. Here, I tested the hypothesis that the proportion of time spent undertaking each of these behaviours varied between species, between size classes and between regions assumed to have differing FAD-density.

4.2.5 Results

The proportion of time spent exhibiting each of the four pre-defined behavioural states was calculated for each time-series. These proportions were divided into day-time, night-time, and all-day subsets.

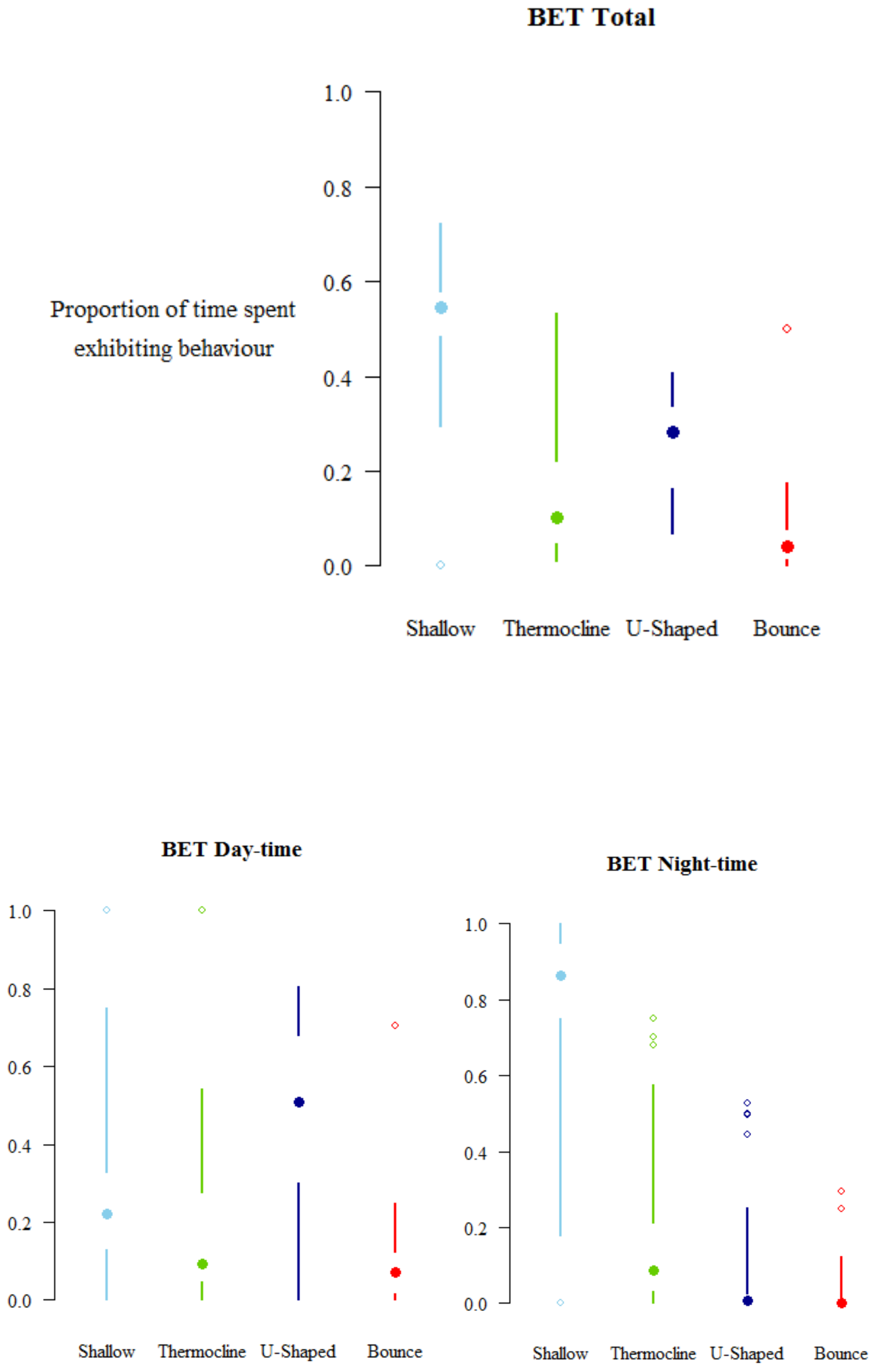

Figure 4.10 Boxplots of time spent exhibit behavioural states for bigeye tuna.

Figure 4.10 shows the proportions of time spent exhibiting each behavioural class across these day-time, night-time and total divisions. Bigeye tuna exhibit fairly consistent switching between undertaking U-shaped diving during the day and, in the majority of cases, shallow behaviour during the night. This conforms to previously described ‘characteristic’ behaviour for bigeye, which are the dominant behaviours observed in other tagging studies (e.g. ≈ 57% in Matsumoto, Kitagawa, and Kimura (2013a); ≈ 52% in Schaefer and Fuller (2010). It appears that there is greater variability between behaviours undertaken during the day, with some individuals spending time associated with the thermocline or the mixed layer, rather than U-shaped diving.

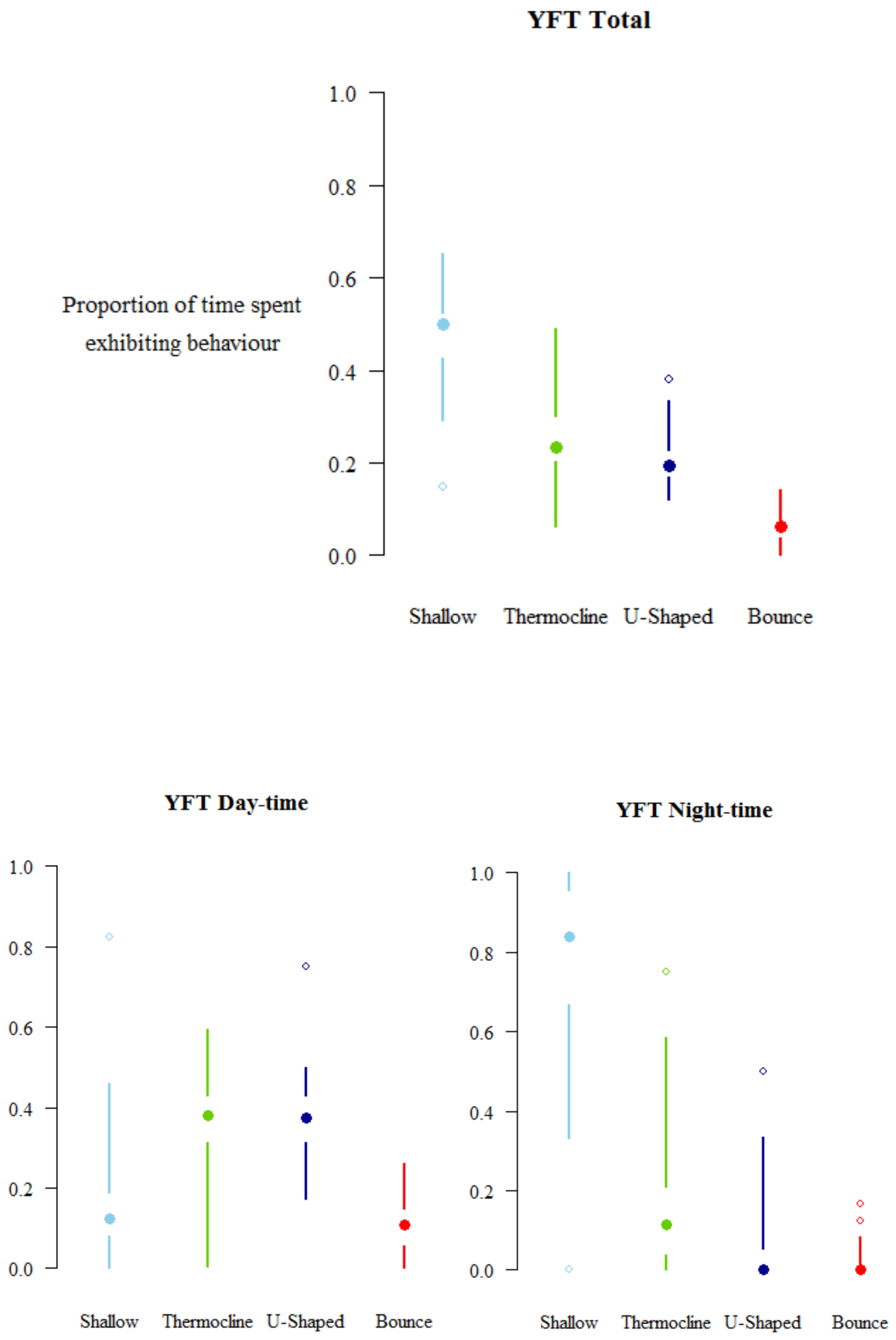

Figure 4.11 Boxplots of time spent exhibit behavioural states for yellowfin tuna.

Figure 4.11 displays behavioural proportion boxplots for yellowfin. Yellowfin tuna exhibit similar behaviours to bigeye during the night-time, spending the majority of these periods in the shallow mixed layer, although like bigeye, they may also associate with the thermocline. Day-time behaviour appears evenly split between U-shaped diving into colder water and time spent in the thermocline, with day-time periods of shallow behaviour less prominent than in bigeye tuna. It is also noted that there is a slightly higher proportion of time spent bounce diving than bigeye tuna, particularly during the day-time.

Changes in an individual’s tendency to undertake certain behaviours may be related to physiological changes in a fish’s ability to dive into colder layers of water, and declining school fidelity. Previously, mean depth over the entire time-series for each individual was used to identify potential changes in behaviour over size at release. Here a similar effect was investigated by visually examining the change in proportion of time spent exhibiting each machine learning classified behaviours over the fork length of fish at time of release. Once again, these results are separated by species and into day/night periods.

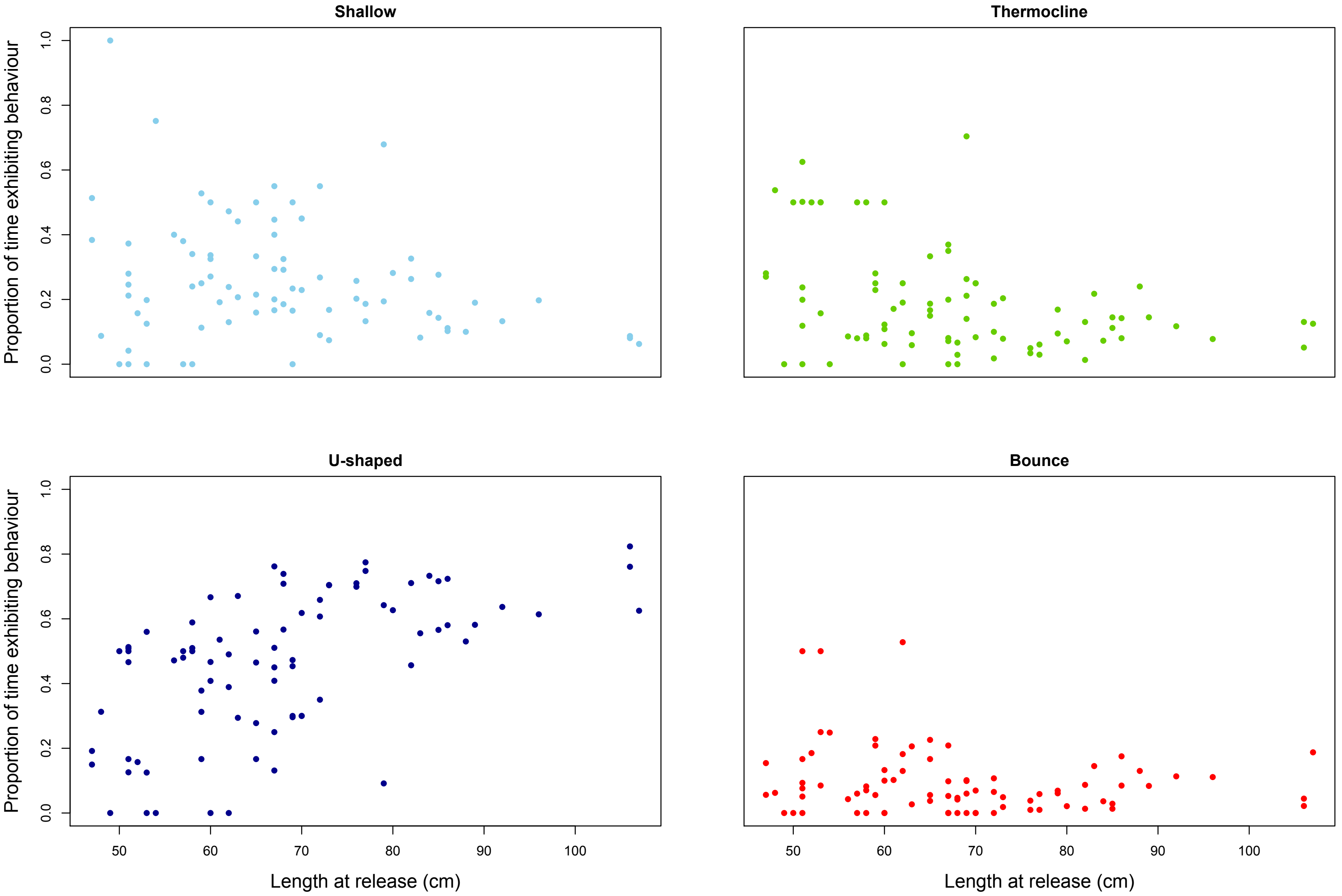

Figure 4.12 Proportion of time spent exhibiting four different behavioural classifications across fork length-at-release for bigeye during the day-time.

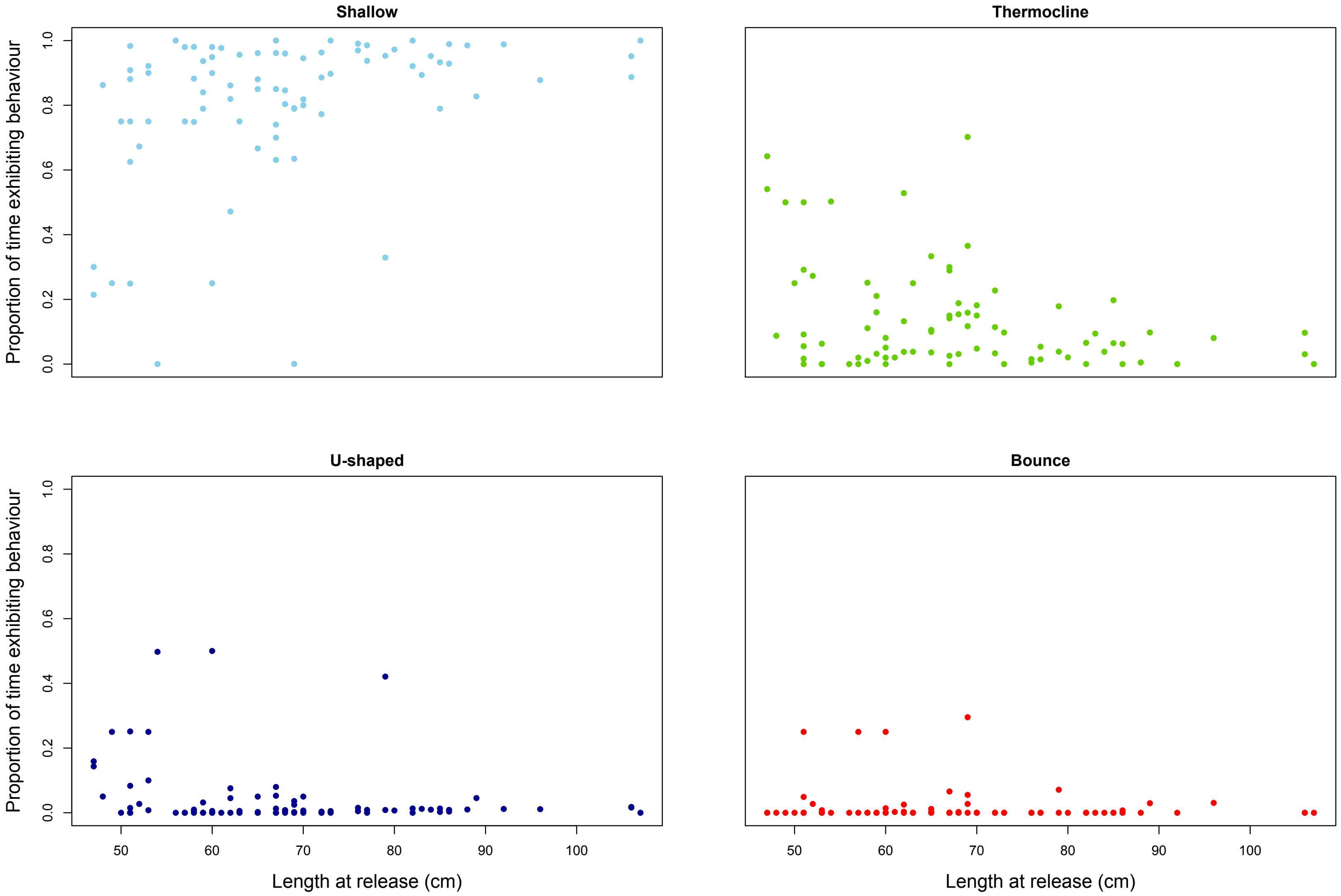

Figure 4.13 Proportion of time spent exhibiting behavioural classifications across fork length-at-release for bigeye during the night-time.

Although there is lots of individual variation in the data, some general patterns are apparent. As they grow larger, bigeye tuna undertake U-shaped diving during the day more consistently, with the largest individuals rarely exhibiting thermocline association. This is likely to be related to the increasing ability to thermoregulate and the increase in the size of the swim bladder, which is well developed in yellowfin by 70cm (Magnuson 1973). The likelihood of uncharacteristically remaining near the surface during the day (such as during FAD-associative behaviour) also appears to decrease. During the night, the propensity for remaining at the surface increases with length, the largest individuals almost exclusively remaining in the surface mixed layer during this time. This may be due to a combination of increased thermal inertia in the warmest layers of water, decreased need to change depths in predatory-avoidance, or a shift to hunting larger size classes of prey inhabiting the surface waters. Bounce diving, during either day or night periods, appears to have no relationship with fish length.

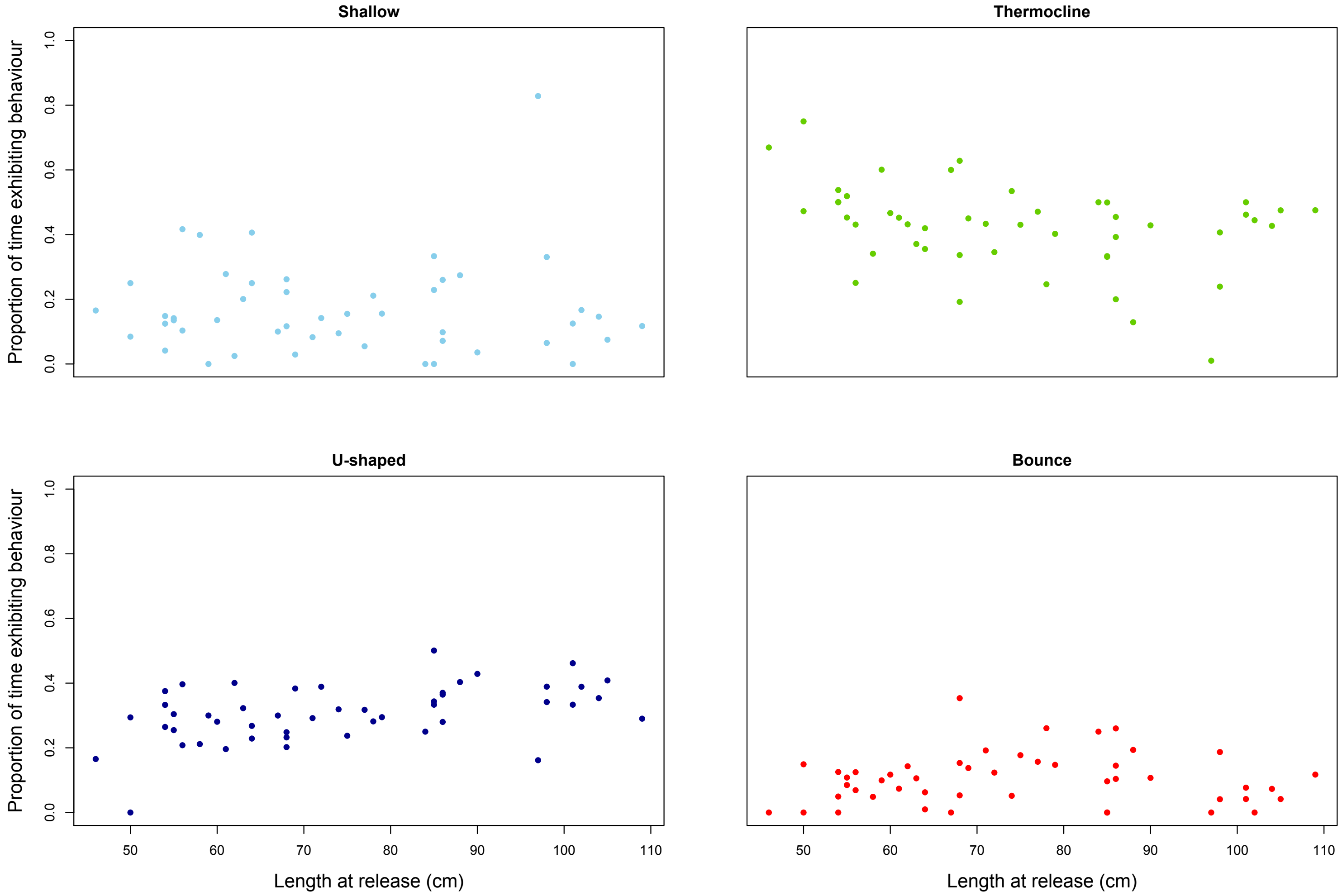

Figure 4.14 Proportion of time spent exhibiting behavioural classifications across fork length-at-release for yellowfin during the day-time.

Figure 4.14 and Figure 4.15 show the proportions time spent in the machine learning classified behavioural classes for yellowfin. During the day-time, a similar pattern to bigeye is observed, although the proportion of time spent associated with the thermocline is still relatively high for large fish. The swim bladder in yellowfin tuna begins to develop between 50-60cm FL, and increases rapidly until around 80cm (Magnuson 1973), which may account for the apparent shift in preference between feeding at the thermocline and deeper in the water column across these lengths. Shallow, 'associative' behaviour during the day-time appears to occur more consistently across all length classes than in bigeye tuna. The behaviour of yellowfin at night is very similar to that of bigeye tuna, with individuals increasingly exhibiting shallow behaviour at the expense of other states as they increase in size.

To begin to examine the possible effect of dense FAD use on behaviour at length, fish were initially divided into two groups: those tagged and released in the Bismarck Sea, an area of dense FAD use (Kumoro 2002), and those released elsewhere. The majority of bigeye released in the Bismarck Sea occupy the same smaller size range, and so there sample size was not high enough to compare these two regions for this species. Here just data from yellowfin during the day-time are examined, and shown in Figure 4.16 and Figure 4.17. Night-time behaviour was comparable across both spatial groups, and so these subsets are also not shown.

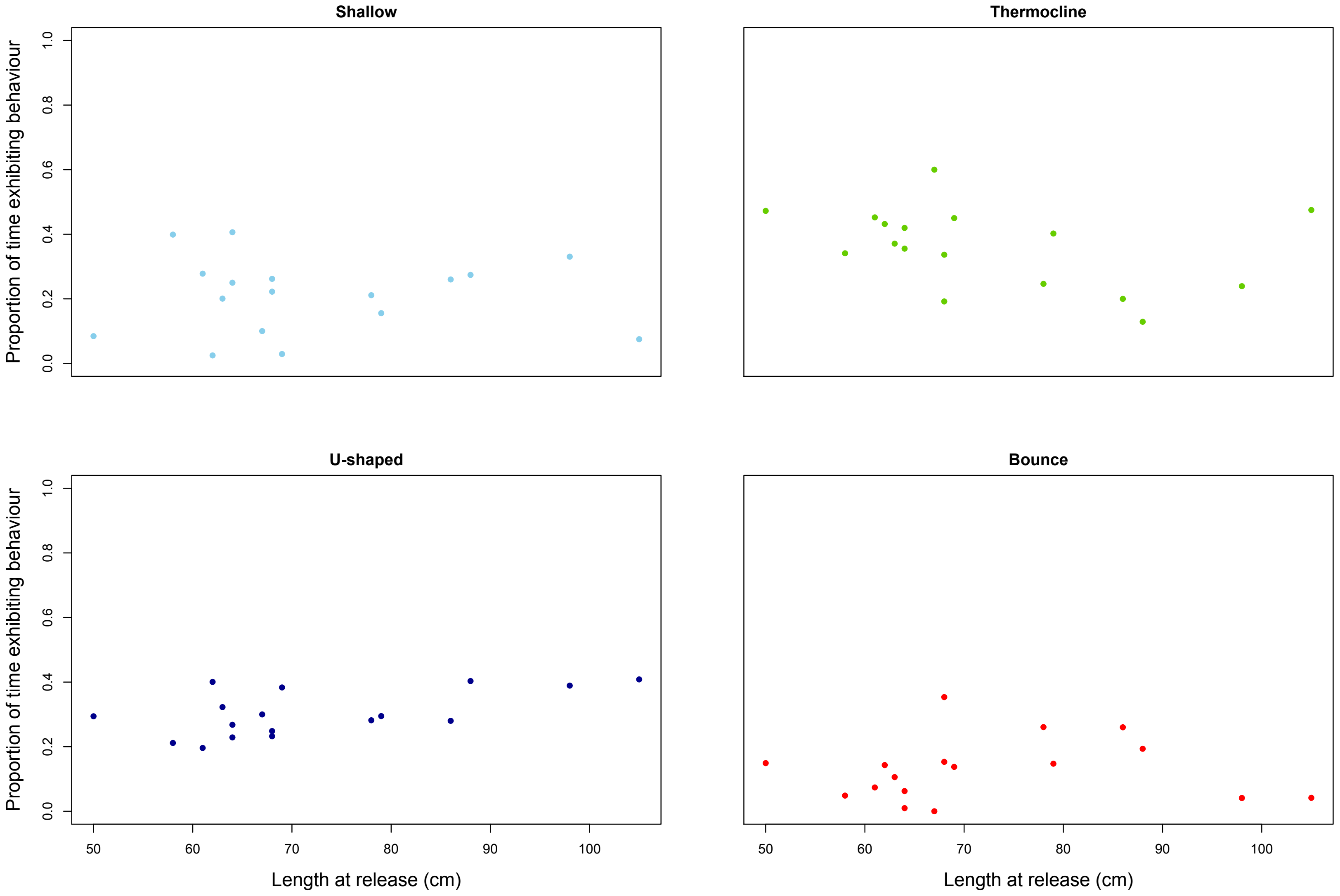

Figure 4.16 Proportion of time spent exhibiting behavioural classifications for yellowfin released outside of the Bismarck Sea area, across fork length-at-release during the day-time.

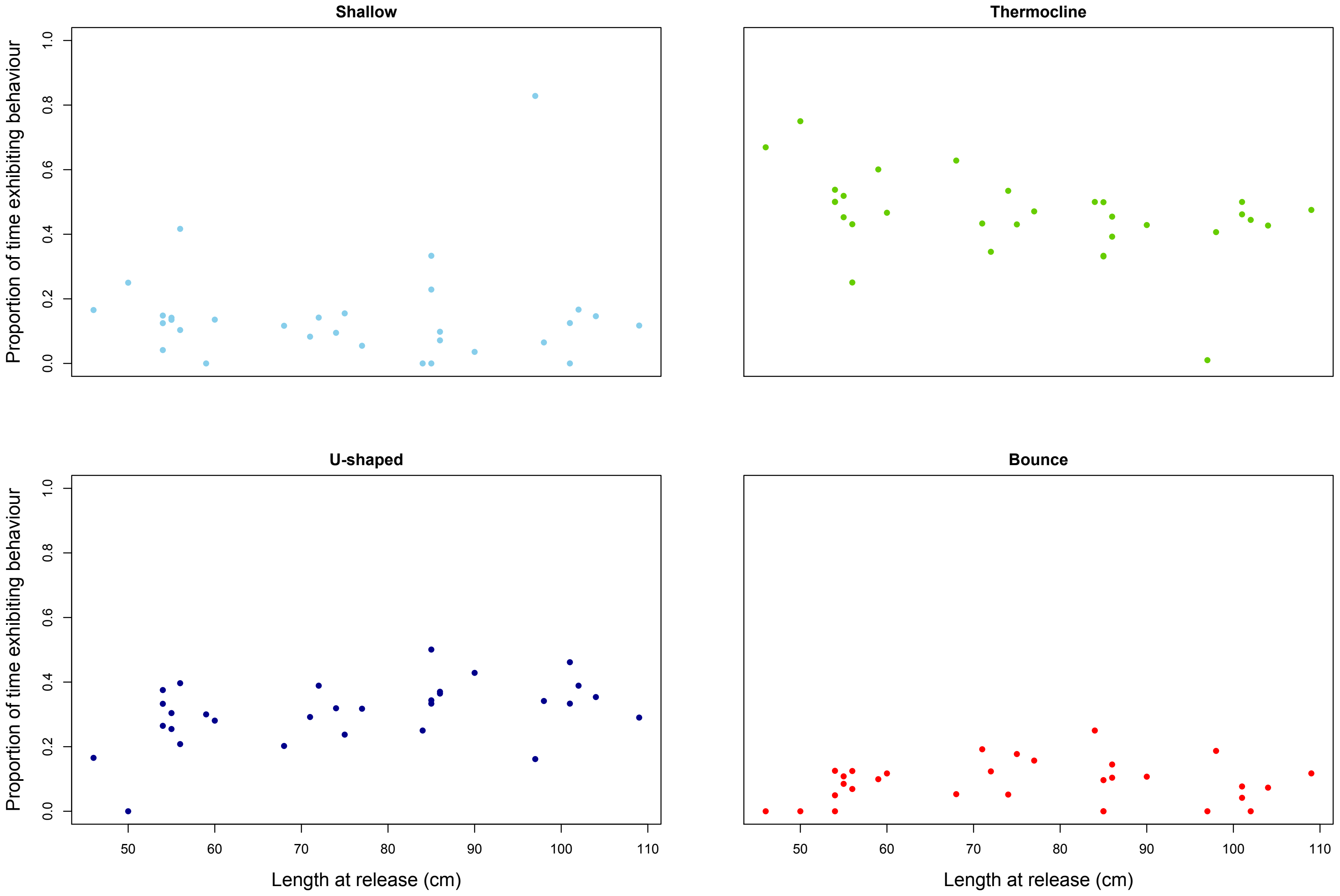

Figure 4.17 Proportion of time spent exhibiting behavioural classifications for yellowfin released within the Bismarck Sea area, across fork length-at-release during the day-time.

Behaviour in both groups shows a consistent pattern of no change in time spent near the surface or bounce-diving as fish increase size. As in the non-spatially divided yellowfin data examined above, fish appear to slightly increase their U-shaped diving and decrease time spent at the thermocline with size. However, there is no clear difference between the two spatially divided groups for any of the machine learning classified behaviours.

4.2.6 Key problems with machine learning

Supervised machine learning provides an automated and objective way of classifying the patterns seen in dive profiles from electronic tags. The analyses here demonstrate how large amounts of data can be processed relatively quickly, allowing analysis of pre-determined behaviours across a population of tags and factors of interest. The preliminary analyses in this chapter confirm behaviours that occur with similar proportions to those that have been previously observed in yellowfin and bigeye, although there is a large amount of variation between individuals. Some changes are also seen which conform to hypotheses about the effects of size and FADs on exhibited behavioural patterns.

However, before detailed interpretations of the results can be made, several significant caveats with this analysis must be discussed. Here, I detail several critical problems with using such an approach to analyse behavioural data.

Accuracy: Although the test scores showed the performance of the Nu-SVM algorithm to be high, the accuracy of out-of-sample classifications can always be called in question. While in many cases behavioural patterns are clear and distinct, in reality there are many instances where behaviours occur on a spectrum. For example, a period of intensive thermocline movement might contain a brief pocket of U-shaped type movement, causing the classifier to associate the pattern with other, clearer U-shaped behaviours. Furthermore, machine learning algorithms such SVMs are binary classifiers, that is, observations are classified as belonging to just one group, without any measure of the probability or likelihood of group membership.

Objectivity: The problem of noisy and composite behaviours causing problems for automated classifiers is actually part of a more critical issue in the description of these data; objectivity. Although machine learning methods are an improvement over purely qualitative descriptions of the data, there are still biases in such a selection. The algorithms themselves are built around a training set that has been selected, interpreted and classified by a human. Such training sets are not truly objective and make a number of assumptions, not least of which is that four distinct behavioural states exist. The patterns seen in dive profiles are actually the result of many underlying motivations and reactions to local stimulus that are unknown to us, the observers. A sound classification technique must take this into account, allowing for variation and noise within the data.

Statistical Power: Machine learning methods do not offer statistical likelihoods or other measures of model appropriateness that allow alternative approaches to be easily compared, other than accuracy in classifying training sets. Similarly, there is no way to incorporate covariate information believed to non-linearly influence the occurrence or nature of behaviours into the classifier itself, such as day or night. Rather, meta-analyses must be carried out on the time series post-classification, as I have done in this chapter, adding another layer of modelling and interpretation to results that must be considered.

Autocorrelation: The behavioural time-series of living organisms are usually autocorrelated (Hartmann and Gottman 1980), meaning that the behaviour exhibited at one time is usually dependent on the behaviour that has recently occurred. Plotting the autocorrelation function of mean temperature summary metrics, calculated over three-hour time bins for an example bigeye from the PTTP, shows that significant auto correlation occurs over diurnal time-scales (Figure 4.18). Ignoring this autocorrelation affects the success of the classification algorithms, as often noisy or less clear sections of behaviour may be more accurately categorised in relation to the context of preceding patterns. Furthermore, traditional statistics carried out on these classifications violate the assumption of independence of observations, and may be unreliable for time-series (Jassby and Powell 1990).

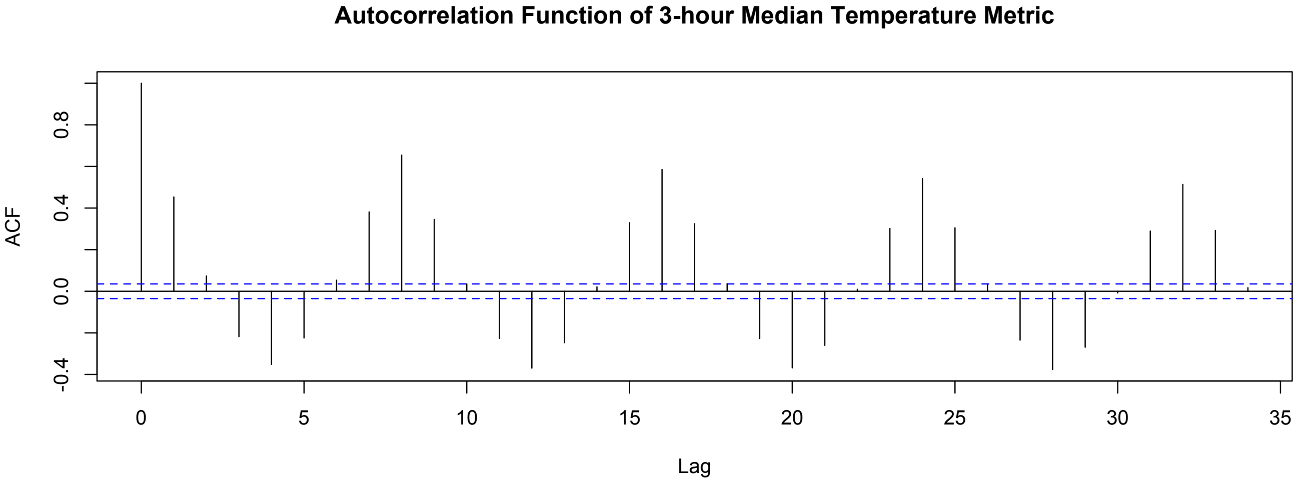

Figure 4.18 Autocorrelation function lag of mean water temperature from a time-series of bigeye tuna behaviour.

Before an interpretation of the vertical movement behaviours from archival tag time-series can be undertaken, data needs to be accurately described and quantified. Only once an appropriate method of description is developed can meta-analyses of changes to movement behaviours across factors such as size or region be carried out with confidence. While the summary statistics and machine learning approaches detailed in this chapter are useful at examining some broad patterns, until the issues listed above can be resolved, alone they are an incomplete solution to the kinds of analyses required to test hypotheses about movement behaviours observed with bio-logging devices. The lack of objectivity in the qualitative descriptions of the data above, and derived machine learning classifications, is of particular concern. Although unsupervised machine learning methods are also available, where data is classified without prior training but simply from the shape of the data themselves, this does not overcome other problems of statistical power and autocorrelation. In the next chapter, I will develop a method that attempts to overcome some of these issues using a hidden Markov-modelling for time-series approach.

Chapter 5: Classifying Continuous Dive Data Using Multivariate-Normal Hidden Markov Models

The potential for electronic bio-logging and archival tagging data to provide new insights into the small-scale behaviour of tropical tuna is clear. As discussed in Chapter Four, before interpretations and conclusions can be drawn from any analysis of these data, an appropriate way to describe and classify the patterns within them needs to be developed. In this chapter, I re-visit some of the key problems with the description of bio-logging data, then detail a method of probabilistic classification using multivariate-normal hidden Markov models. This approach attempts to resolve the issues with the qualitative and machine-learning analyses detailed in Chapter Four. The method is tested on the data from series of simulation experiments, before being applied to a small subset of the PTTP archival tag database of yellowfin and bigeye. These results are examined for accuracy and consistency with previous behavioural studies.

5.1 Introduction

5.1.1 The analysis of bio-logging data

Developing a set of objective tools for quantitative analyses of individual behavioural time-series is now necessary in order for these data to be incorporated into natural resource management models and scientific advice (Morales and Ellner 2002; WCPFC Tagging Commitee 2007). However, quantitative analyses of time-series from bio-logged animals typically involve overcoming a number of problems. Three of these problems are re-iterated here.

First, although bio-loggers can record high-resolution data relating to individual movement, the behaviour of the tagged animal is not explicitly observed. Changes in movement patterns are the likely result of underlying motivational changes in animal behaviour. These motivations may persist or change in relation to environmental or other stimuli, but because these interactions are not directly observed, considerable care must be taken when interpreting time-series data recovered from bio-logging experiments. In particular, relating qualitative descriptions of behaviour to some other variable can implicitly incorporate erroneous assumptions, biasing perceived relationships between movement behaviours and potential drivers (Bélisle 2005).

Second, behavioural time-series data contain significant autocorrelation – i.e. behaviour observed at one time is related to behaviour observed previously. This is the result of persistence of the underlying processes, such as hunger or resting, that motivate the animal's behaviour. The presence of autocorrelation means that traditional statistical tools, based on the assumption of independent observations, may be unreliable (Hartmann and Gottman 1980; Jassby and Powell 1990).

Finally, characterising behavioural states from time-series data requires the analyst to classify and describe distinct patterns, and to identify or smooth noise in the data (Hartmann and Gottman 1980). When undertaken manually, each of these stages can introduce conscious and unconscious biases to the interpretation of this behaviour. Arriving at an objective description, however, is problematic, and care must be taken when choosing the correct temporal and spatial scale to examine inferred behavioural patterns in light of the specific hypotheses being tested (Levin 1992).

Free-roaming marine species such as tropical tuna present a particular challenge in this case. Detailed information on the movements of these animals can be captured with bio-logging equipment, but much of the environmental and ecological context of the behaviour is hidden from us (Kirby 2001). Their movements may be relatively unconstrained both laterally and vertically, their spatial ranges are often large, and behavioural cues are less familiar (Dagorn et al. 2001; Davies et al. 2012). Dynamic environmental boundaries such as ocean fronts constrain or promote spatial behavioural patterns which are often transient and relatively unpredictable (e.g. Bost et al. 2009; Gaspar et al. 2006; Tew Kai et al. 2009). This poverty of information makes the signals observed from tagging experiments on marine animals especially difficult to interpret.

5.1.2 Describing continuous dive data

Continuous dive data can be considered as measurements of depth and temperature captured at the scale of minutes in a single vertical dimension, and which exhibit no consistent behavioural unit of division. In fish species, for example, this vertical movement data is not structured according to any convenient unit of behaviour such as surfacing to breathe, clear individual dives or returns to a nest or colony. The information is typically recorded using sensors that measure time, water depth, internal and external temperature, and light. Such data captured from many bio-logged apex predators (including tunas, billfish, sharks or marine mammals) contain patterns of diving which are hypothesised to be associated with foraging, predator avoidance and physiological regulation (Campana et al. 2011; Hazen et al. 2011; Schaefer, Fuller, and Block 2007). However, since it is near impossible to measure environmental context at depth for free-roaming animals, the behavioural cues driving these patterns remain obscure. To address these challenges, and range of methodologies for the description of bio-logging data have been used.

Categorising vertical movement into behavioural classes has frequently involved assessment by eye, or based on criteria such as time spent within certain depth layers of water at different times of the day (e.g. Chiang et al. 2011; Schaefer, Fuller, and Block 2007; Sims et al. 2009). While behavioural patterns can sometimes be easily recognisable by eye, these patterns may also occur as a spectrum of noisy or composite behaviours, which are difficult to identify objectively.

5.1.3 Hidden Markov models

Hidden Markov models (HMMs) are a form of state-space model that have been increasingly applied to time-series of animal behaviour. HMMs have a long history in the field of signal processing, particularly for voice recognition (Gales and Young 2007), but their popularity as a tool for examining ecological data has increased in recent years. Examples of such models applied to ecological problems include the foraging behaviour of mouse lemurs (Schliehe-Diecks, Kappeler, and Langrock 2012), horizontal movement behaviours of southern bluefin tuna (Patterson et al. 2009), at-sea behaviour of Manx shearwater (Dean et al. 2012), and diving behaviour in macaroni penguins (Hart et al. 2010). HMMs assume observations will depend on a finite number of underlying unobservable states (MacDonald and Zucchini 2009). Accordingly, each individual observation is assumed to be drawn from one of several distributions, each corresponding to a 'hidden' state. In the case of animal behaviour, we might assume an individual has resting and feeding states, each associated with distinct distributions in the data recorded by a bio-logging device. The underlying principle is analogous to an independent or discrete mixture model (Welsh et al. 1996), in which observations are drawn from one of several independent distributions in proportion to a probability for each state. In a HMM, however, the transition between hidden states is assumed to be governed by a Markov chain, where the probability of the animal being in a given state at a given time is dependent on the state it was in during the previously sampled time-step. Thus, if an animal was in a resting state at a given time-step, probabilities are associated with it remaining in this state or switching to each other state defined in the model. Autocorrelation is therefore intrinsically incorporated into the assumptions of the model, albeit with an assumption of first-order Markov dependence. HMMs ability to objectively estimate patterns from data in which behaviour may not be explicitly observed is particularly attractive in studies of *in situ* animal behaviour, where behaviours can only be inferred from indirect observation. HMMs provide a statistically rigorous framework to fit models to data, and can be linked to covariate information by allowing these extra data to further influence the model parameters (MacDonald and Zucchini 2009).

Here I describe a method for processing and describing continuous dive data from free-roaming marine animals using multivariate normal HMMs. The HMMs developed in this study model three aspects of behaviour. First, the most likely parameters describing the state distributions are estimated, indicating the shape of the behavioural states that we assume each observation is drawn from. Second, the parameters that describe the probabilities of switching between these underlying states at any time-step are estimated. Finally, these fully describe the HMM, which can then be used to probabilistically classify the time-series into a behavioural state at each time-step.

The method development is motivated by the need to objectively quantify the behaviour of tropical tuna in light of the poor and un-objective results of described time-series in the previous chapter. Initially I describe and explore the method by simulating data that represent two potential scenarios for the ecology of a theoretical marine animal. HMMs are fitted to these artificial data, and their performance examined. I then undertake the same approach on a small sample of datasets recovered from archival tags implanted in yellowfin and bigeye tuna of the PTTP. The behavioural states and switching estimated by the HMMs on this example subset of real-world time-series are examined for consistency with previous descriptions of tuna behaviour. Finally, the potential for using HMMs fitted to continuous dive data for population dynamics models and providing scientific advice to fisheries are discussed.

5.2 Methods

5.2.1 Multivariate HMM

Detailed mathematical descriptions of HMMs and broader state-space models exist in previous publications (e.g. MacDonald and Zucchini 2009; Patterson et al. 2009), but I outline the basic concepts here. In the context of animal behaviour, a HMM assumes that an observation, X, at a particular time-step (e.g. distance travelled, speed or location) is drawn from a distribution, D, associated with a behavioural or motivational state S. In addition, the time-series of these behavioural states forms a Markov chain that is described by a matrix of probabilities governing the switching between states. The probability of an individual occupying a behavioural state at time t is dependent on the probabilities of occupying each of the states at time $t-1$. Although I do not explore them here, more complex q-order dependence can also be incorporated in a variety of ways, with by including the mixture transition distribution models proposed by Raftery (1985), or expansion of the transition matrix to allow each state to be defined a vector containing the states of the previous q time-steps.

In a HMM the state at each time-step $\boldsymbol{S_t}$ will be one of $\boldsymbol{M}$ states $\boldsymbol{i}$, each associated with a separate probability distribution $\boldsymbol{D}$ with parameters φ_i. The probability of observing $\boldsymbol{x_t}$ is therefor:

$$P(x_t \mid S_t = i) = D(x_t \mid \varphi_i)$$

The hidden process model in a HMM that controls the switching between these states from time $\boldsymbol{t\text{-}1}$ to time $\boldsymbol{t}$ is described by a set of state-to-state transition probabilities grouped in a transition matrix $\boldsymbol{\Gamma}$, which simply arranges the probabilities of switching from the current state to each of the others at each time-step. Each transition from state $\boldsymbol{i}$ to state $\boldsymbol{j}$ is a transition probability, $\boldsymbol{\pi_{ij}}$, collected together in the transition matrix which describes the probability of switching from any state to any other

$$\boldsymbol{\Gamma} = \begin{bmatrix} \boldsymbol{\pi_{11}} & \cdots & \boldsymbol{\pi_{1M}} \\ \vdots & \ddots & \vdots \\ \boldsymbol{\pi_{M1}} & \cdots & \boldsymbol{\pi_{MM}} \end{bmatrix} = \mathbf{P}(\boldsymbol{S_t} = \boldsymbol{j} | \boldsymbol{S_{t-1}} = \boldsymbol{i})$$

Following the law of total probability, each row of this transition matrix describes all possible switching outcomes from a given state, that is $\boldsymbol{\pi_{ij}}$ must sum to 1 across $\boldsymbol{j}$.

In general, the likelihood of a given set of time-series data from $\boldsymbol{t = 1 \ldots T}$ is the joint probability of observing the observation sequence

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

Although the joint probability is the product of each individual observation probability, the sum of the logarithms is usually taken. In a HMM, this joint probability can be decomposed as follows. The state probability, $\boldsymbol{P(S_t)}$, is dependent on the state probabilities at at $\boldsymbol{t\text{-}1}$. Consider the likelihood contribution at time $\boldsymbol{t}$

$$\mathbf{L_t} = \sum_{\boldsymbol{i=1}}^{\boldsymbol{M}} (\mathbf{P}\,(\boldsymbol{x_t} \mid \boldsymbol{S_t} = \boldsymbol{i}) \cdot \mathbf{P}\,(\boldsymbol{S_t} = \boldsymbol{i}))$$

$$= \sum_{\boldsymbol{i=1}}^{\boldsymbol{M}} (\mathbf{P}\,(\boldsymbol{x_t} \mid \boldsymbol{S_t} = \boldsymbol{i}) \cdot \mathbf{P}\,(\boldsymbol{S_t} = \boldsymbol{i} \mid \boldsymbol{S_{t-1}}\,, \boldsymbol{x_{t-1}}))$$

$$= \sum_{i=1}^{M} (\mathbf{P}(x_t \mid S_t = i) \cdot \mathbf{P}(S_t = i \mid S_{t-1}) \cdot \mathbf{P}(S_{t-1} \mid x_{t-1}))$$

The likelihood contribution of each observation is therefore the sum of probabilities of observing this observation for each behavioural state distribution, given the probability that the individual is occupying that state, dependent on the state occupied at the previous time-step. During parameter estimation, the negative log-likelihood was minimised using a multivariate adaptation of the forward filtering recursive algorithm described in Patterson et al. (2009) and MacDonald and Zucchini (2009). The classification probability of each behavioural state at each time-step is undertaken using the state probability backward-smoothing approach detailed in Wikle and Berliner (2007).

It is also possible to include further covariate information in the estimation of these model parameters. A covariate that is assumed to affect the value of a parameter can be included as a coefficient in an equation describing how that parameter changes in relation to the covariate. Here only binary information is included to assume a linear relationship between the covariate and the state switching probabilities. In this case, for each individual transition probability defined in equation 2,

$$\pi_{ij} = \alpha_{ij} + \beta_{ij}\gamma$$

where γ is a continuous or binary covariate, and both α and β are estimated parameters. In the case of the binary covariates I use here, the result is that each state transition probability assumes one of two different values, depending on the value of the covariate. It is also possible to include similar covariate parameters in the state distribution means, allowing the nature of the states themselves to change in relation to covariate information. However, for simplicity of this example application here I assume constant state distribution parameters across the time-series.

For fitting HMMs to behavioural time-series captured from bio-logging devices that record data on water depth and temperature, I use a mixture of multivariate normal distributions to model the multidimensional datasets. Thus this observation model replaces the generic distribution in equation 1, and is a state-dependent multivariate normal distribution of $\boldsymbol{k}$ dimensions, such that we assume for each observation $\boldsymbol{x}_t$,

$$x_t \sim D(\varphi_i) = N(\mu_i, \Sigma_i)$$

where $\boldsymbol{i}$ is the current hidden state, $\boldsymbol{\mu}_i$ is the multivariate mean in $\boldsymbol{k}$ dimensions, and Σ_i the $\boldsymbol{k}$ by $\boldsymbol{k}$ variance-covariance matrix.

5.2.2 Data Pre-processing

For the HMMs in this study, I arranged data into a two-dimensional space where each axis was constructed from a summary metric calculated from dive profiles that have been separated into temporal bins. The method involved three stages of data pre-processing. First, raw dive data is divided and compressed to a time-series of these summary metrics in the same manner as the machine-learning analysis of the previous chapter. Temporal binning and metrics are chosen to capture the variation of patterns in the dive profile, representing relevant dynamics and temporal scale to the behaviours we wish to examine. These summary metrics are then log transformed to approximate a mixed normal distribution, and finally arranged as a multivariate time-series.

It is important to match the temporal scale of observations to the temporal scale of the behaviours that are the focus of the investigation. Working with raw dive data provides many observations, but high levels of variation and short-term behaviours, such as thermoregulatory ascents (Holland et al. 1992). While an examination of these short-term activities using HMMs based on raw high-resolution dive data may certainly be valuable, here I investigate behaviour that occurs within a time frame of hours. Assuming that this is the temporal scale that concerns feeding, digestion and satiation (Olson and Boggs 1986), as well as fishing events (Baird 2009), the continuous raw depth and temperature time-series data were divided into three-hour subsections. This was done by first making divisions each day at dawn and dusk, estimated using a split-moving window analysis (Ludwig and Cornelius 1987) on proportion of time at depth. This approach was described fully in the previous chapter. Three divisions were made between the initial boundaries estimated for dawn and dusk, creating eight subsections of approximately three hours across a twenty-four-hour period. Summarising the dive data across three-hour sections provided variation across many different behavioural patterns, while retaining significant autocorrelation and smoothing some of the noise from those patterns unrelated to this study.

The same summary metrics as in the previous chapter were calculated from each three-hour subsection to form the observations from which the HMM was estimated. Any number of summary metrics can be chosen to form the multivariate arrangement of observations, but here I chose a two-dimensional observation model. The desire was to select a multivariate assemblage of summary metrics that would capture information about relative movement through the water column and temperature-based habitat use, both of which are related to vulnerability to fishing gears. As the study included tuna from different time periods and areas, I did not use measures of absolute depth that may differ across these factors for behaviours of the same underlying ecological motivation. Water temperature and absolute depth were highly correlated, although non-linearly (see Figure 4.9. from the previous chapter). I therefore used temperature as measure of thermal habitat use. As individual deep 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 the multivariate assemblage, a principal component analysis was carried out on all the summary statistics (except absolute depth) calculated from individual fish to examine the ways in which the data may be transformed into orthogonal components. The standard deviation of depth provided consistently high loadings in the first principal component across a range of individual fish. I chose this metric, a measure of vertical movement amplitude across the time bin, as the movement component of this multivariate normal observation model. Although co-varying, these two variables can replicate considerable variation in patterns of raw dive data already classified as different types in previous studies. However, they are also related to the vulnerability of fish to fishing gears, representing both a level in the water column and the strength of association at that depth.

The summary metrics from each time-series were log transformed to better approximate a mixture of normal distributions. These processed data were then arranged as a two-dimensional multivariate assemblage, forming the time-series of observations to be modelled by the HMM.

In addition, each observation was associated with a binary covariate indicating the diel state, either day or night, at the time of observation. All summary metrics were assigned as either day or night dependant on which of the initial twelve hour subdivisions they were taken from. This binary information was used as a coefficient in the estimation of all transition matrix parameters, resulting in HMMs that essentially contained two sets of transition probabilities between states, one each for day and night.

5.2.3 Model Estimation and Selection

For each dataset, a series of HMMs with two to five assumed hidden states was estimated. In addition, a single-state model was estimated consisting of a lone multivariate normal distribution without the transition matrix Markov chain component.

Model parameters were estimated using the numerical estimation of a minimum negative log-likelihood described in Patterson et al. (2009), and using the Nelder-Weald algorithm in the R (R Core Team 2013) function *optim()* (Nelder and Mead 1965), set to a tolerance $1e^{-4}$. Initial values were supplied by using a K-means algorithm (Hartigan and Wong 1979; MacQueen 1967) to cluster the multivariate assemblage into the same number of groups as states assumed in the model. Starting values for multivariate means and variance-covariance parameters were calculated from these clusters, and a transition matrix created from the observed sequence of these classified observations.

A number of techniques can be used to select the most appropriate model from this suite for a given time-series. Using Akaike Information Criteria on independent mixture models has been found to result in over-estimation of the number of states and be an unreliable indicator of model suitability (Celeux and Soromenho 1996; McLachlan and Peel 2004). To avoid similar potential problems selecting the most informative HMM from a suite, I instead examined the estimated negative log-likelihood for a marked change in decrease with increasingly complex models. As the number of pre-determined hidden states increases, the estimated likelihood value tends to also increase due to the model becoming more complex and fitting to the data more tightly. However, a distinct ‘knee-bend’ can be seen in measures of the likelihood across these models as increased numbers of parameters result in smaller improvements in the model fit (Dean et al. 2012; Zhao, Xu, and Franti 2008). Likelihood estimates from models with a greater number of states than occur at this ‘knee-bend’ are likely to be over-fitted.

In addition I used a visual inspection of ‘pseudo-residuals’. MacDonald and Zucchini (2009) introduce these quantities, aiming to fulfil a similar model-checking role as the residuals in conventional statistic models. In a HMM we do not aim to predict the value of a response variable, but rather the nature and probability of observations being a result of the assumed underlying states. As such, there are no residuals in the sense of the difference between predicted and observed values. However, the distribution of pseudo-residuals can be used to examine the appropriateness of a model. A more complete description of pseudo-residuals is given in MacDonald and Zucchini (2009).

5.2.4 Simulation Experiments

Validating the effectiveness of HMMs for identifying true behavioural states from associated indirect measurements is challenging, since it requires *a priori* knowledge of the true behavioural states associated with the time-series data. In the absence of suitable data from animal studies, I also conduct *in silico* simulation experiments to develop and examine the effectiveness of using HMMs to estimate parameters that can then be compared with the true known values. Following this, I apply the method to a small sample of real bio-logging data taken from two species of tropical tuna.

Consider a theoretical free-roaming animal, capable of spending extended periods of time at depth in cold oxygen-depleted layers of water. The feeding ecology of this individual is based on active predation on vertically-migrating prey, which spend the night-time located in a relatively narrow mixed surface layer but which are patchily distributed throughout the water column during the day. When a patch of prey is found the individual will associate with the patch for a period of time, feeding until either it is satiated or the patch disperses. In this scenario, all the phenomena described above occur on the scale of hours. This simplified system is constructed to be analogous to the general dynamics of many large marine predators in oligotrophic waters, such as tunas and billfish (Dagorn, Menczer, et al. 2000).

It is assumed that this individual has been tagged with a bio-logging device capable of recording high resolution data for depth and water temperature at the scale of minutes, and that this information is processed to give summary values for these data at three hour intervals. I simulate two scenarios and estimate HMMs, using replications of each to examine the effectiveness of recovering true parameters:

Scenario One: In the first scenario, the individual alternates between two behavioural states: feeding on prey in a narrow band of warm shallow water, and feeding on prey across a variety of deep cooler water layers. These behaviours are somewhat persistent, as the individual finds patches of prey and associates with them to feed. A conceptual diagram of these behaviours and summary observations is shown in Figure 5.1.

Scenario Two: In the second scenario the individual follows similar behaviour, except that it is now capable of enduring significant time at depth, feeding on patches of prey in very deep cold water. There are also now three behavioural states – two persistent feeding states and a third transitive state, representing movement throughout the water column while searching for patches of prey. Furthermore, switching between these states is linked to a cyclic binary covariate representing a day- and night-time cycle. Feeding in the shallows is more persistent during the night, while feeding at depth is more persistent during the day.

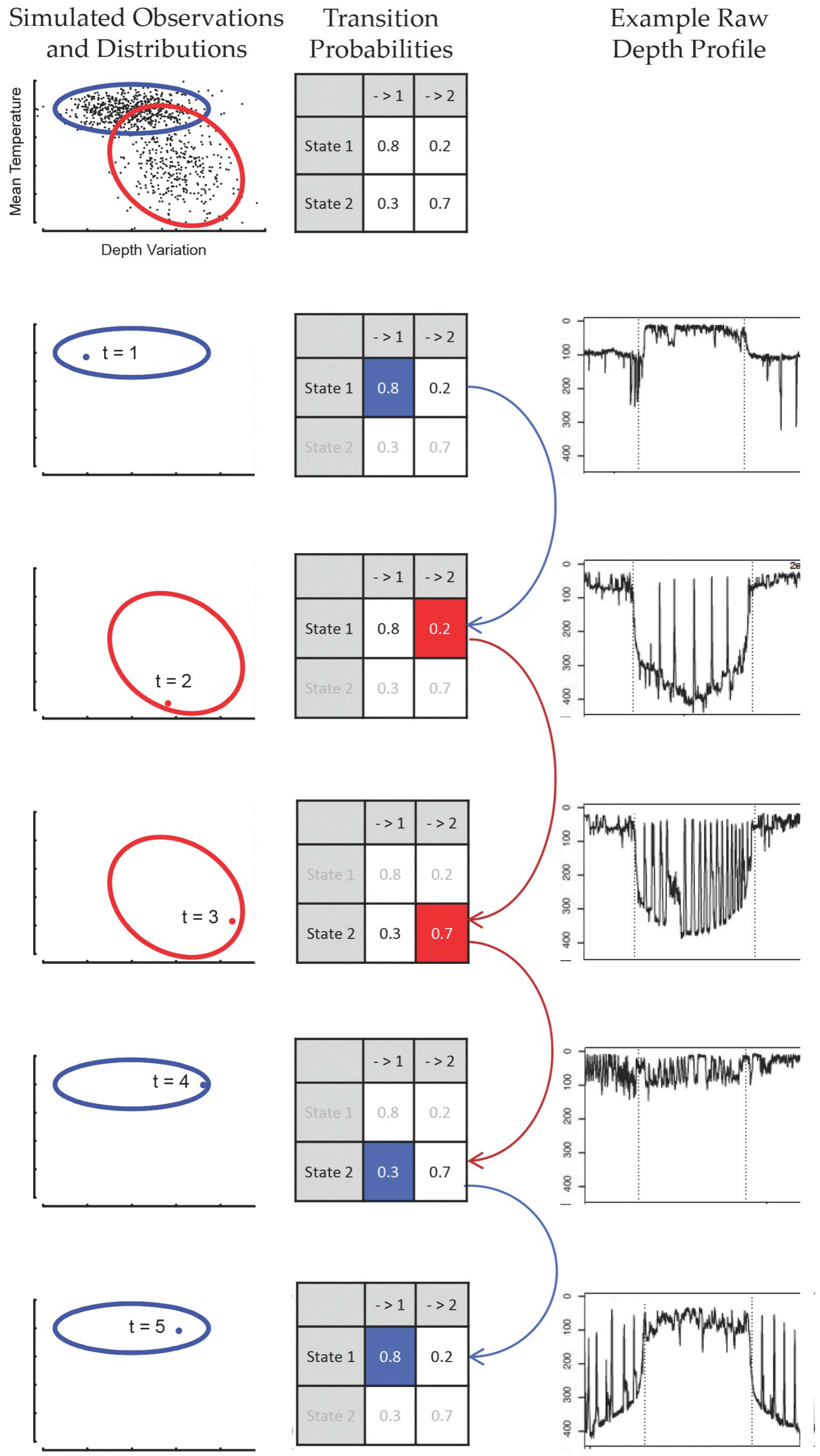

Figure 5.1 Conceptual diagram of a simulation scenario one for the first 5 time-steps. Column one displays the simulated observations and true state distributions they were drawn from. Column two is the true matrix of transition probabilities. Column three gives potential examples of corresponding real patterns from raw time-series of tropical tuna.

I stochastically generated fifty time-series of observations from multivariate normal distributions and transition matrices to create time-series representing the processed data from each of the above scenarios. Each time-series was of length N = 500 observations, which is analogous to over sixty days of data from a bio-logging device assuming a resolution of mean values calculated at three hour intervals. The true multivariate normal distributions, alongside mean estimates from the HMM, are shown in Figure 5.2. A detailed list of the parameters is given Table 5.1 and Table 5.2.

Table 5.1 True multivariate mean, variance-covariance and transition matrix parameters for each state in simulation scenario one.

State	**Multivariate mean σ** ***(depth, temperature)***	**Variance-covariance matrix Σ**	**Transition probabilities**
State 1- *Persistent Shallow State*	4, 10	Depth = 2 Temp = 0.5 Covariance = 0	1->1 = 0.8 1->2 = 0.2
State 2- *Persistent Deep State*	6, 6	Depth = 1.5 Temp = 3 Covariance = -0.5	2->1 = 0.3 2->2 = 0.7

Table 5.2 True multivariate mean, variance-covariance and day/night-time transition matrix parameters for each state in simulation scenario two.

State	**Multivariate mean σ** ***(depth, temperature)***	**Variance-covariance matrix Σ**	**Transition probabilities during day-time**	**Transition probabilities during night-time**
State 1- *Night-time Persistent Shallow State*	4, 10	Depth = 2 Temp = 0.5 Covariance = 0	1->1 = 0.2 1->2 = 0.2 1->3 = 0.6	1->1 = 0.8 1->2 = 0.2 1->3 = 0.0
State 2- *Transitive Searching State*	6, 6	Depth = 2 Temp = 0.5 Covariance = 0.5	2->1 = 0.04 2->2 = 0.48 2->3 = 0.48	2->1 = 0.4 2->2 = 0.58 2->3 = 0.02
State 3- *Day-time Persistent Deep State*	7, 4	Depth = 0.5 Temp = 0.5 Covariance = 0	3->1 = 0.3 3->2 = 0.1 3->3 = 0.6	3->1 = 0.5 3->2 = 0.5 3->3 = 0.0

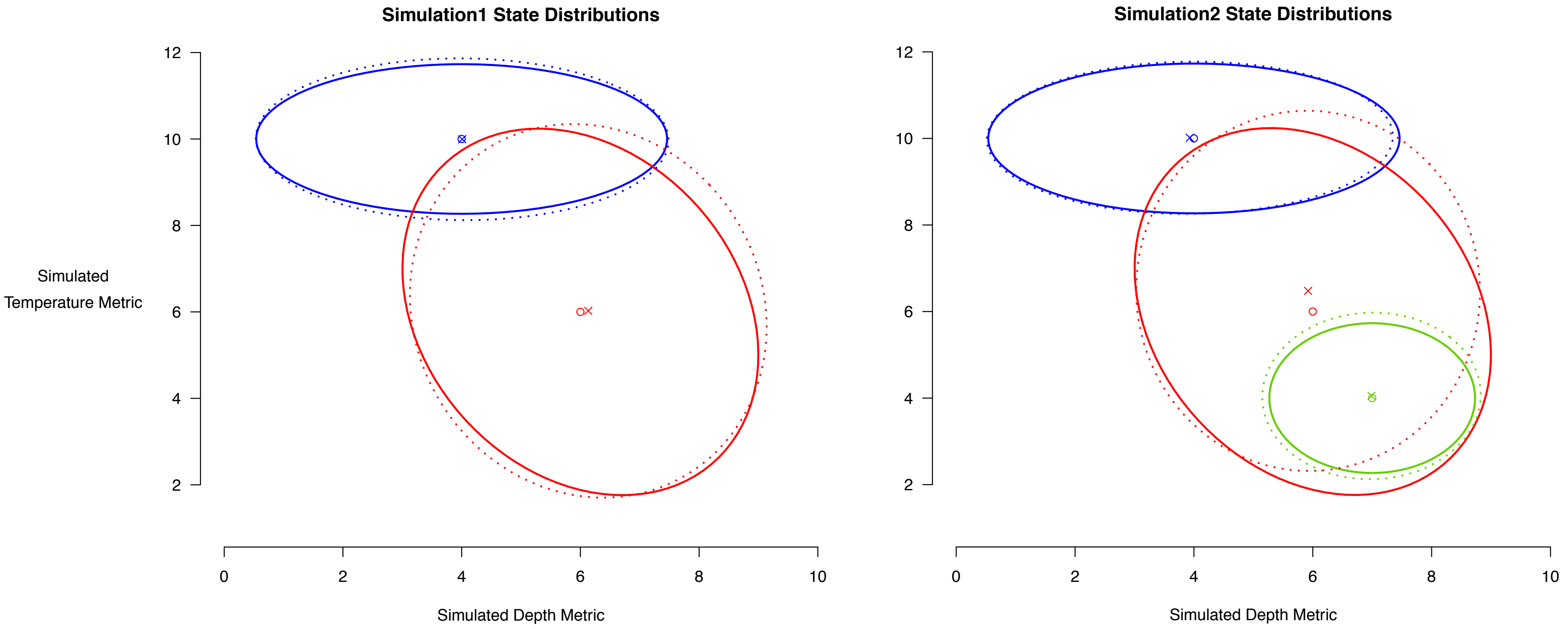

Figure 5.2 True (solid lines) and estimated (dotted lines) state distributions for scenario one (left) and scenario two (right).

5.2.5 Real-world Data

Table 5.3 Time-series from PTTP tags used in this analysis.

Fish	Species	Release Fork length (cm)	Time at liberty (days)	Recording resolution (s)	Date of release	Notes
Arc163	Bigeye	59	174	240	Nov 2011	Lotek Wireless LTD-2510
Arc294	Bigeye	53	318	30	Dec 2011	Lotek Wireless LAT-2810
Arc272	Bigeye	106	360	30	Nov 2010	Wildlife Computers TDR-Mk9
Arc88	Yellowfin	50	168	300	Feb 2007	Lotek Wireless LTD-2410 Initial 40 days of data corrupt and removed
Arc269	Yellowfin	98	255	30	June 2010	Wildlife Computers TDR-Mk9 Approx. 240 days data corrupt and removed
Arc220	Yellowfin	98	124	60	Sept 2007	Wildlife Computers TDR-Mk9

Having examined the success of using multivariate HMMs on simulated time-series, I then applied this method to real-world data. Time-series were chosen from six individuals across two species of tropical tuna – three yellowfin tuna, and three bigeye tuna. The vertical behaviour of these species has been described in numerous previous studies (e.g. Dagorn, Holland, and

Hallier 2006; Ohta and Kakuma 2004; Schaefer, Fuller, and Block 2007), exhibiting some differences in their evolved strategies to exploit prey through the water column (Dagorn, Menczer, et al. 2000).

These behavioural time-series are taken from this PTTP database, and were recorded by archival tags surgically implanted in tropical tuna following the methods outlined in Schaefer, Fuller, and Block (2007). A variety of electronic tag devices were used, and each time-series is summarised in Table 5.3.

5.3 Results

5.3.1 Simulation Results

The results from the two simulation experiments were examined before building HMMs on the time-series data from real bio-loggers. The average negative log-likelihood values from the fifty repetitions across HMMs estimated with a successively greater number of hidden states are shown in Figure 5.3. A visual inspection of these values, alongside pseudo-residuals, showed little improvement for models in which the number of assumed states was greater than the true number used in the two scenarios. These true values were two and three states for scenarios one and two respectively.

The true and average estimated state distributions across the fifty replications of these 'correct' models for each simulation scenario are also shown in Figure 5.2. Quantifying the performance of the HMM estimation is non-trivial. While many common statistical tests exist for comparing sample means to a population mean, for multivariate distributions more complex measures such as Kullbuck-Leibler divergence must be used (Kullback and Leibler 1951). In these simulation experiments however, I simply wish to examine the accuracy of the method for recovering the known parameter values used in the simulation of the data. Furthermore, because of the varying ranges of the parameters estimated in a HMM, limited in some cases to positive numbers for variances and values between zero and one for transition probabilities for example, interpreting accuracy from simply the relative or absolute deviations from a true known parameter is difficult. Here I use parallel coordinate plots (Inselberg 1985) to visually examine the accuracy and variation of the estimated models in these simulation experiments. These plots are used for displaying multidimensional data, with the position of each point marked by a line that passes through each vertical bar at the position of that point in each dimension. The true and estimated values of each set of state distribution parameters alongside transition probabilities for the two scenarios are shown in Figure 5.4 and Figure 5.5.

In general the state distribution parameters were well estimated by the models, with multivariate means estimated more accurately than variance-covariance matrices. Less persistent states, having generally fewer observations, had less accurately estimated parameters. Large, dimension-specific variances were not precisely estimated, although they were normally distributed around the true values. In addition, although covariance values of zero were well recovered, when levels of covariance between dimensions were non-zero, these values were both less precisely and less accurately estimated. Transition parameters were also well estimated, although states with few observations or high overlap with other distributions were naturally less precise. It also appears that there may have been a bias towards underestimation of the most persistent state transitions. In the case of scenario one, the estimated HMMs had a mean classification rate of 97.0% (stand. dev. 0.9%), and for the more complex scenario two, the mean was 90.6% (stand. dev. 3.4%).

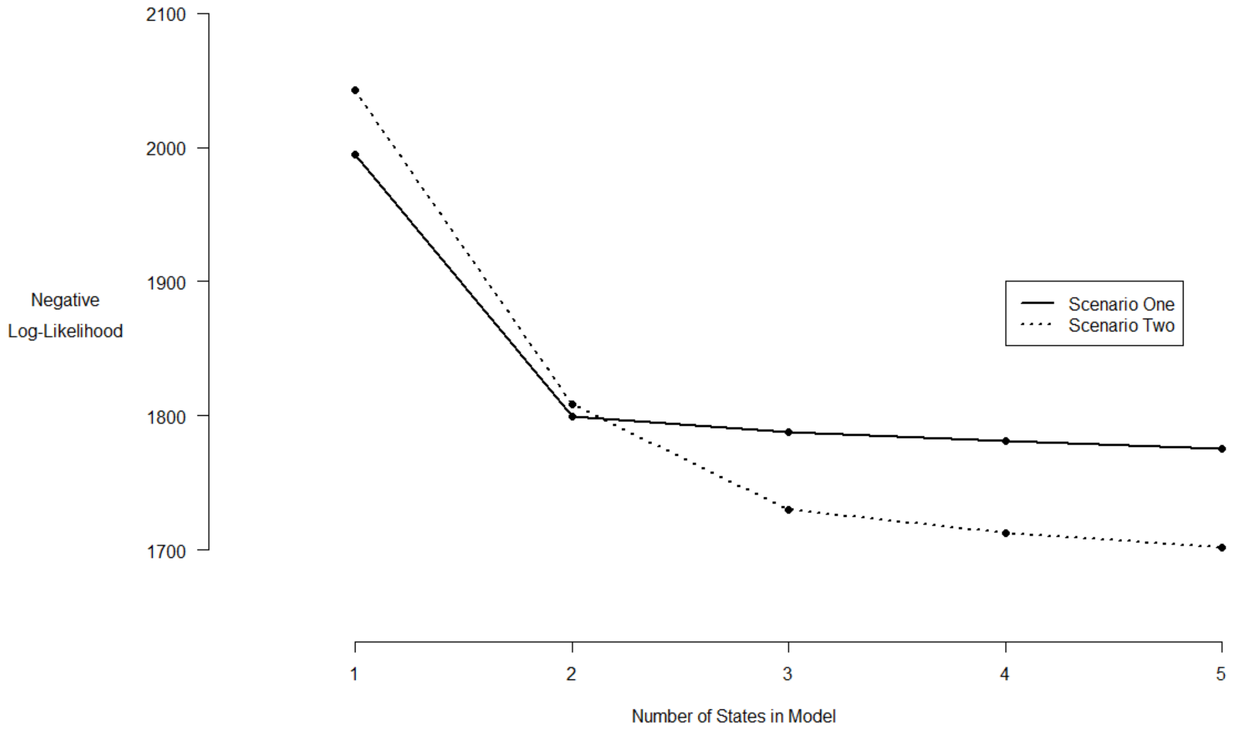

Figure 5.3 Changes in mean estimated negative log-likelihood across number of assumed states for both simulation experiments.

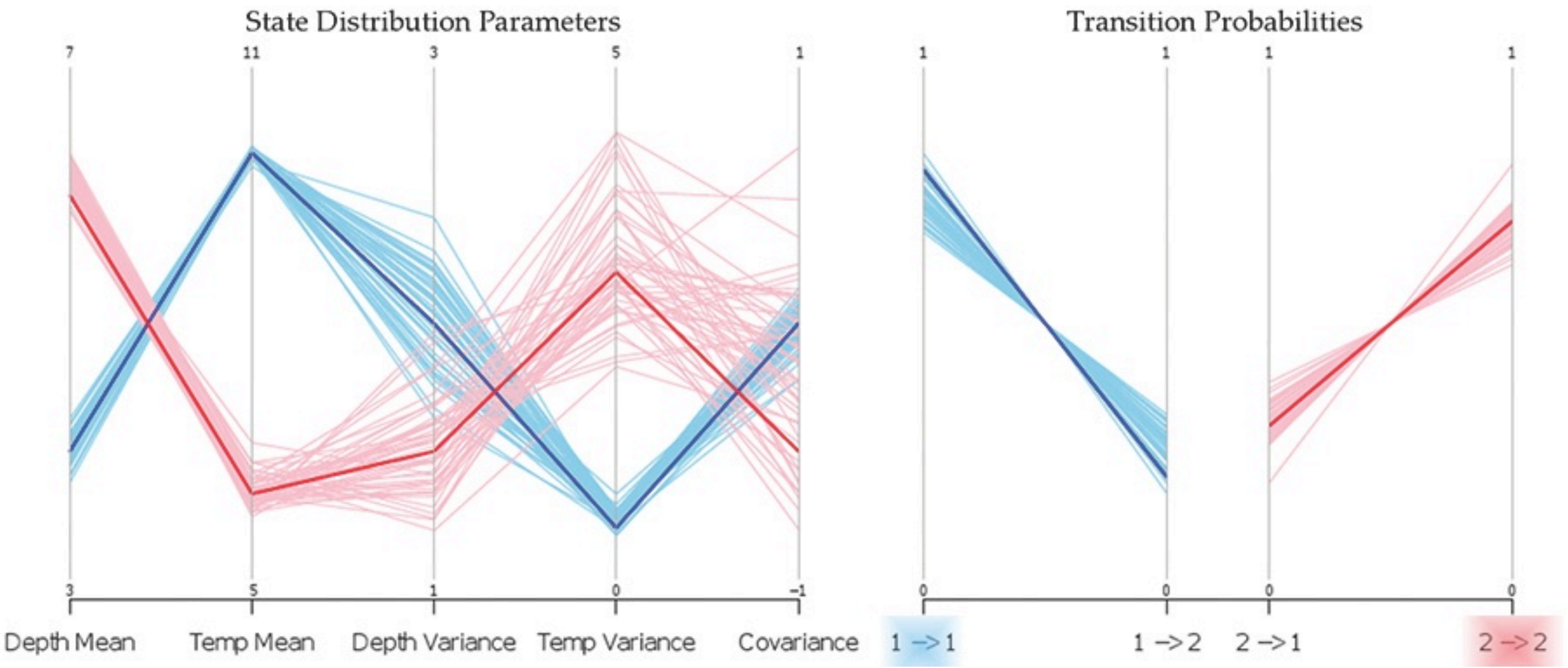

Figure 5.4 Parallel coordinate plots showing true (solid lines) and 50 estimated (faint lines) values for all parameters in scenario one.

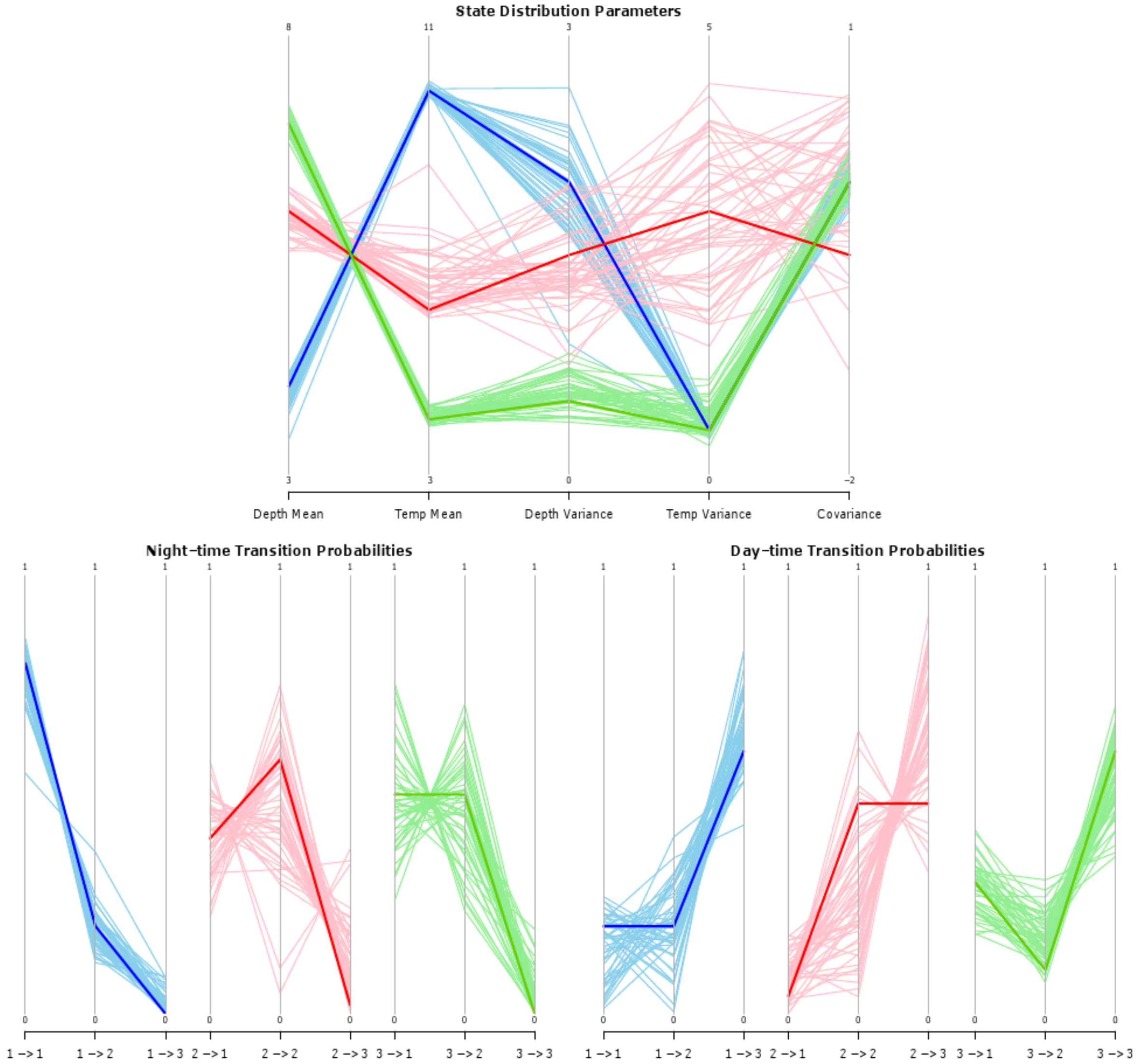

Figure 5.5 Parallel coordinate plots showing true (solid lines) and 50 estimated (faint lines) values for all parameters in scenario two.

5.3.2 Real-world Data

The same model selection criteria of identifying reduced increase in negative log-likelihood across models with an increasing number of states (Figure 5.6), as well as an examination of the pseudo-residuals, was carried out on models of the wild tuna. In all cases the most appropriate HMM was one that assumed two behavioural states. These states can be considered as either warm or cold, dependent on the value of the state distribution mean in the median temperature dimension. Figure 5.7 shows the estimated state distributions for all individuals, divided into these warmer and colder categories.

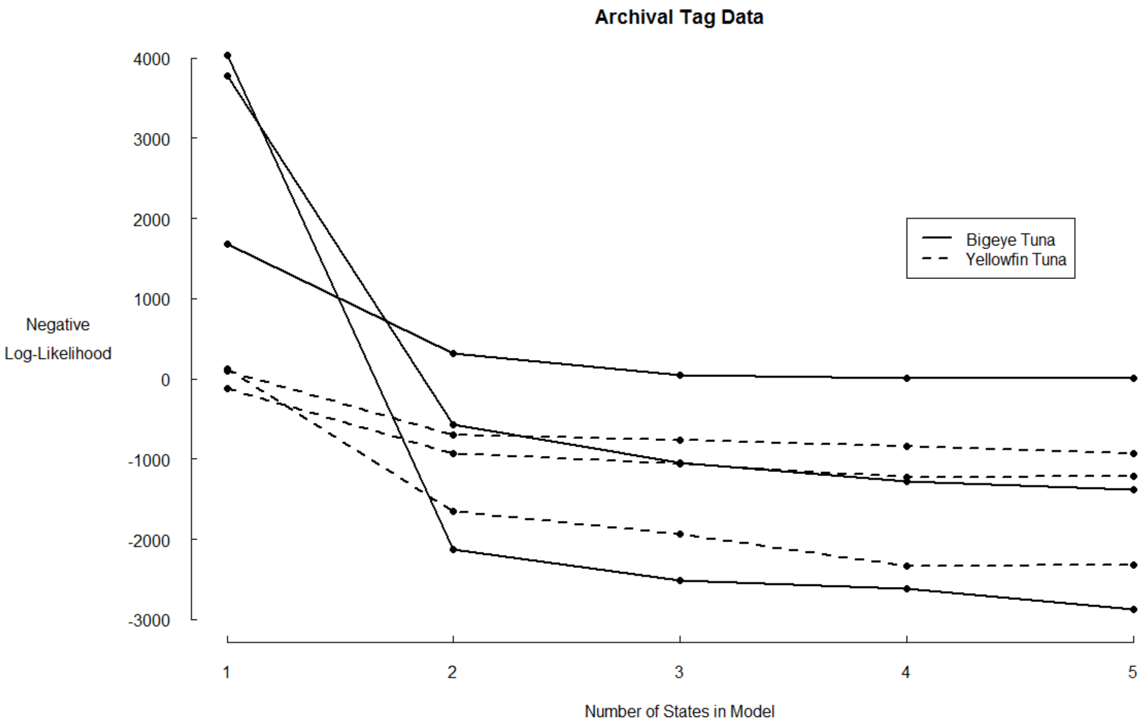

Figure 5.6 Changes in estimated negative log-likelihood across number of assumed states for all tropical tuna time-series examined here.

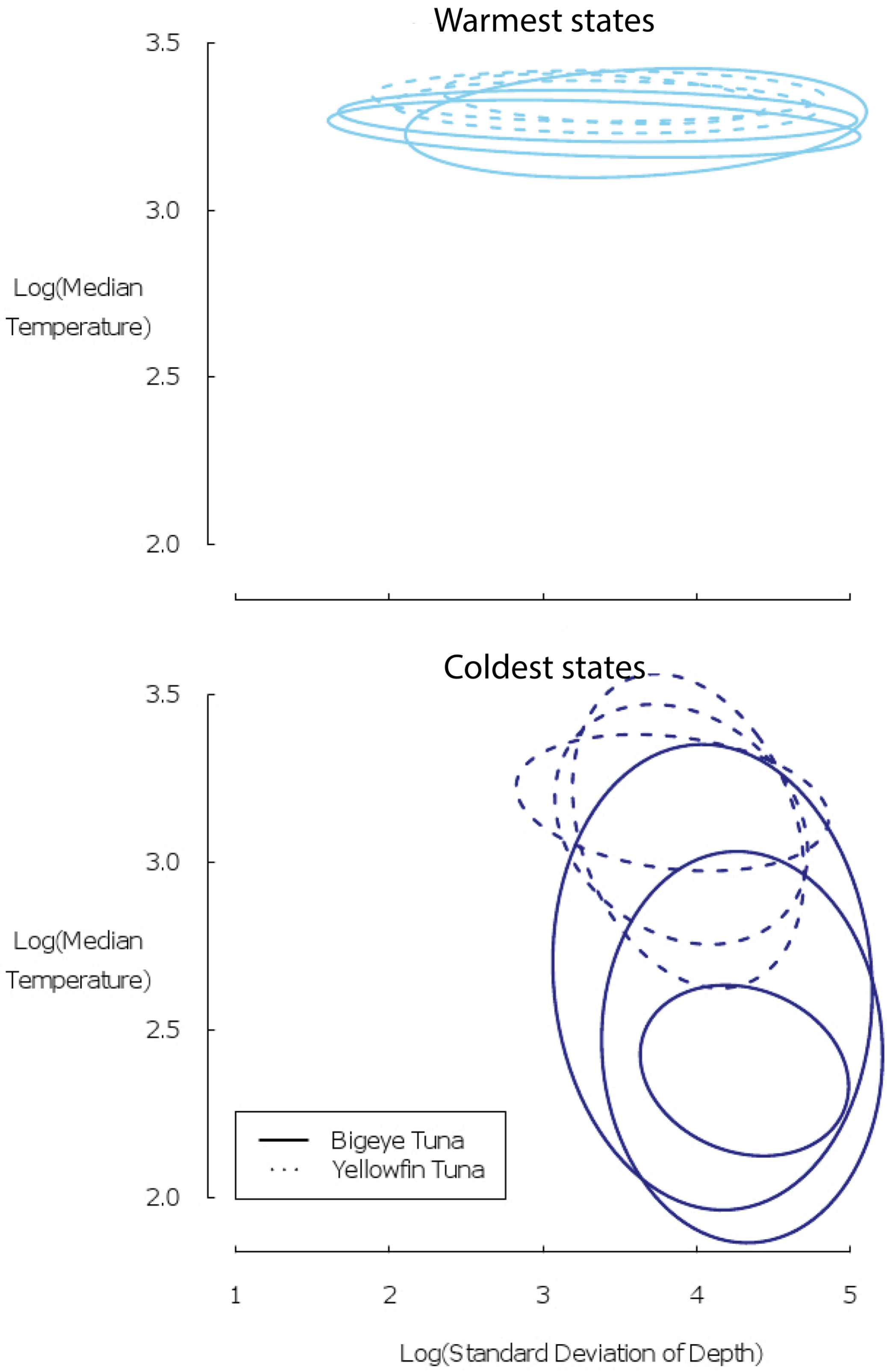

Figure 5.7 Estimated state distributions from two-state HMMs estimated on all tuna time-series examined here.

The estimated warm states were very similar for all individuals, exhibiting a spectrum of depth variation but occupying a similar temperature range. The cold states were more different across individuals, with distributions clearly centred in colder water for the bigeye tuna compared to the yellowfin. In contrast, depth variations were less variable across cold states, and all distributions were centred at a greater standard deviation of depth than in the warm states.

In this example application, I included a covariate representing diel period as part of a linear equation defining the transition probabilities. A concise way to summarise the information in the Markov transition matrix is to calculate its equilibrium state, also called the stationary distribution. In the case of behavioural time-series, the stationary distribution can be thought of as the proportion of time an individual would spend in each state if the time-series continued indefinitely. Thus, a transition matrix can be viewed as a vector, where each value is the proportion of time at the limit spent in each motivational state. It is important to note that these values are distinct from the actual proportion of time spent exhibiting each state in the time-series; rather, they are analogous to a limit cycle or equilibrium point in the dynamics described by the transition matrix. Here, I use stationary distributions to examine estimated transition matrices.

Figure 5.8 shows the two stationary distributions for all fish, one each for day and night. There are clear differences in behavioural switching from day to night in all individuals. All fish, except the yellowfin Arc269, have a large probability of switching to their respective cold states during the day. In contrast, all individuals exhibit an even greater probability of switching to their warm state during the night, with a very small chance of switching back to colder states. In the cases of the bigeye tuna Arc272 during the day and Arc163 during the night, the probability of switching away from these persistent states is actually zero.

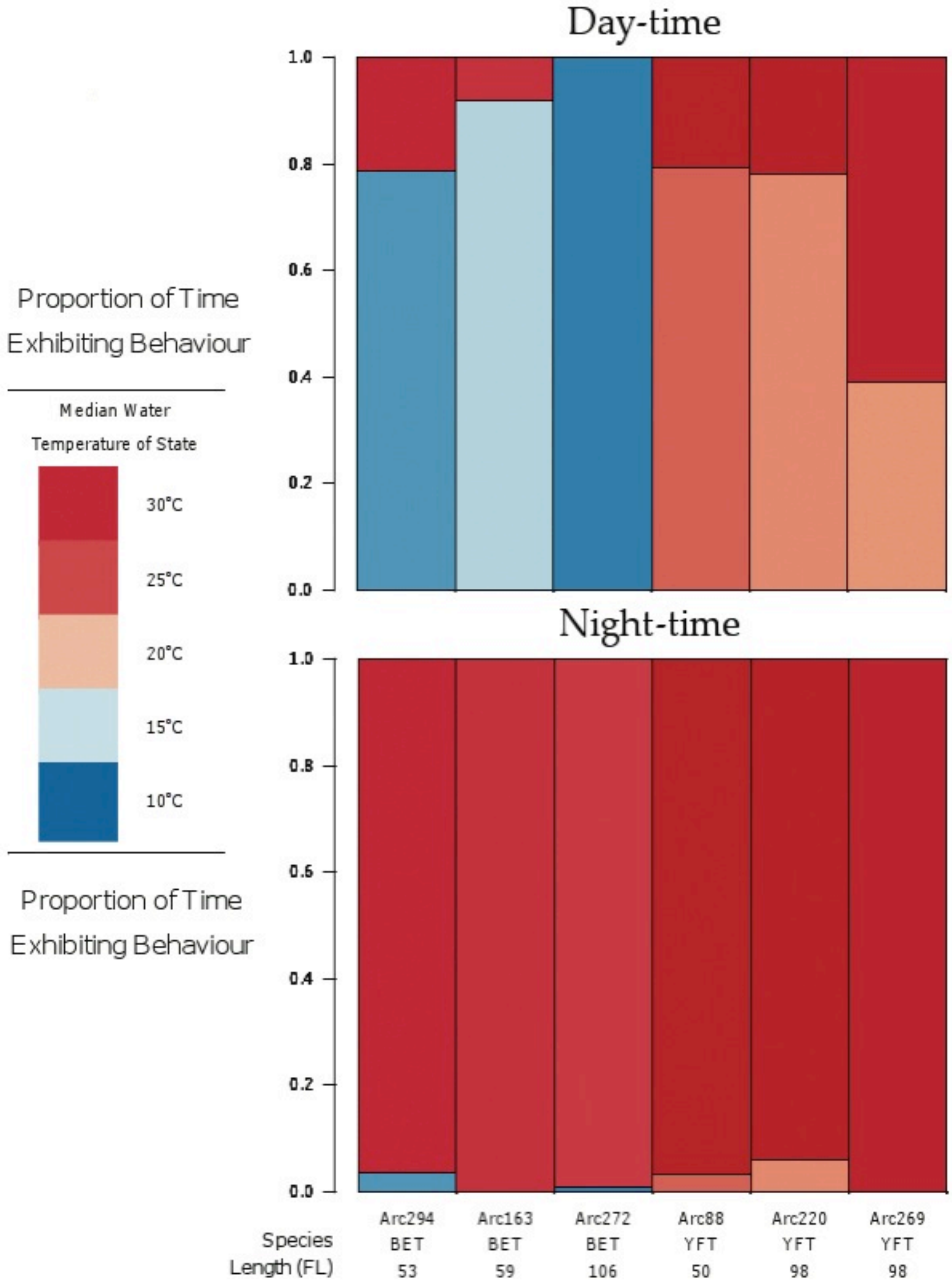

Figure 5.8 Estimated transition matrix stationary distributions during day-time (top) and night-time hours (bottom). Bars represent proportions of time exhibiting behavioural states in the limit for each fish, and are coloured by the back-transformed distribution mean of that state, in the temperature dimension.

Time-series were classified by computing the most likely sequence of states from the given observations using the chosen model parameters as described in MacDonald and Zucchini (2009). Each state is given a probability of occurrence for each observation in the time series, and the largest probability was chosen as the classification of behaviour at each time-step. An example of how these automatic classifications relate to the raw dive data is shown in Figure 5.9. The effect of day and night is clearly seen in the classification, although three-hour sections of warm state behaviour occasionally still occur during the day. Note that the variation in amplitude is much greater for warm state behaviours, exhibiting both tight association at a particular depth and large movements through the water column during a three-hour period. In contrast, the classified cold states are always associated with larger movement through a range of depths.

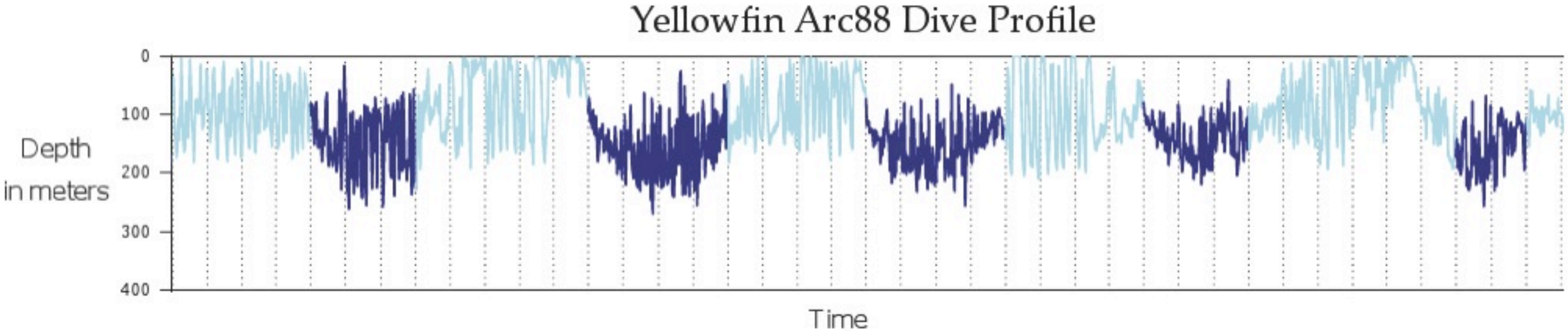

Figure 5.9 Example section of raw dive data from a small yellowfin tuna, Arc88, automatically classified into either warm-state (light blue) or cool-state (dark blue) sections of three-hours using a two-state HMM.

5.4 Discussion

5.4.1 Simulation experiments

The results from the simulation experiments demonstrate the effectiveness of the approach in describing and identifying underlying states from multivariate mixed distributions. The aim of the contrasting simulation scenarios is to examine how successful HMMs are at correctly estimating parameters and classifying states when the true values are known. The two simulation experiments provided both a simple scenario, with well separated states and low levels of complexity in state switching, and a more problematic scenario, containing a higher number of states and less clear switching parameters.

When states are well separated and persistent, identifying a 'knee-bend' in the log-likelihood across increasingly complex models appears to be a clear method for selection of the most appropriate model. However, as in the case of the second scenario in which states are more diffuse in both distribution and persistence, changes in log-likelihood from one state to the next may be more gradual. Given the problems of using AIC and automatic model selection in HMMs, careful consideration and examination of both the estimated state distributions and pseudo-residuals should be undertaken for log-likelihood curves that do not exhibit a sharp bend.

Despite the complexity of the second simulated scenario, which contained significant overlap in distributions and transition parameters incorporating covariate information, the correct classification success rate was still over 90%. State distributions were accurately estimated, with consistently low error for multivariate means in particular. The true value of dimension-specific variance was well recovered by the HMM, but when distributions had non-zero levels of covariance these values were less accurately estimated. Most transition matrix parameters were accurate to within less than 10%, although for less persistent states and transitions the error was greater. This is to be expected, as there are fewer observations in the simulated time-series drawn from these distributions. Subsequently, there is simply less data that can be used for parameter estimation within the likelihood calculation. States estimated with large variance-covariance and low-persistence transition probabilities should be interpreted with particular caution.

5.4.2 Tuna behavioural description and comparison to previous studies

In building a series of HMMs for the small subset of archival tags in this chapter, the aim was not to make statements regarding the behaviour of tropical tuna or vulnerability to fisheries initially. Rather, I sought to examine the way in which real-world continuous dive data can be interpreted using this approach, and if the results are consistent with the known ecology of these species. The choice of summary metrics arranged into state-dependent multivariate distributions represents both an association of an individual fish with a particular layer of water and the strength of the association at that depth, at a three-hour timescale. Consideration of this temporal scale is critical when comparing the results to previous studies on continuous dive data. At this scale we do not identify fine-grained changes in movement (e.g. Humphries et al. 2010; Sims et al. 2008), individual dives (e.g. Dagorn, Holland, and Hallier 2006), or longer-term composite dive profiles (e.g. Schaefer, Fuller, and Block 2007; Wilson and Block 2009). Rather, I aim to describe behaviours that occur at the scale of feeding and fishing events. Such patterns capture changes in diving throughout the course of the day and form the components of multi-day composite behaviours (e.g. Matsumoto, Kitagawa, and Kimura 2013a, 2013b).

In this small sample of tropical tuna, all individuals exhibit behavioural states centred in warm surface waters that are very similar to one another. It is characterised by low variation in temperature but considerable variation in movement through the water column. The thermal biology of tropical tuna requires them to reside predominantly in warm waters. Given that the warm surface layer of the tropical Pacific is well mixed, it is unsurprising that the variation in temperatures is small and similar for all individuals in this warm state. These states were centred between three-hour medians of 25.6˚C and 28.2˚C, comparable to mixed layer behaviours elsewhere described as surface, associated or type I behaviour (Schaefer, Fuller, and Block 2007; Schaefer and Fuller 2010). The distributions of standard deviation in depth were centred between 28m and 36m. However, the variation in this metric was large for all individuals, which suggests that there does not appear to be an association to specific depths; rather, individuals exhibit a continuous range of variation in the depths that they occupy for this state. The bigeye tuna from this sample have warm states that are centred in slightly cooler water than the yellowfin, although this is well within variation that could be due to the temporal and spatial factors present in this small sample.

The behavioural states centred in colder water are more varied across species. In all cases, individuals have a looser association with a particular depth in their cold states than the warm states. Colder state distributions were centred on standard deviations of depth ranging from 46.7m to 73.7m. This is consistent with observations that tropical tuna are required to return to warmer layers of water for thermoregulation (Holland et al. 1992) and possibly to repay oxygen-debt (Prince and Goodyear 2006), but it could also suggest that deep cold behaviour has a generally more depth-transient nature. Tropical tuna have evolved different ways to dive and exploit prey in colder layers of water (Dagorn, Menczer, et al. 2000; Musyl et al. 2003), and it appears that this is reflected in how the two species examined here exhibit deeper behaviour. The cold states of the yellowfin tuna were considerably warmer than those of the bigeye, with the distributions centred on median water temperatures of 22.1˚C to 24˚C. Yellowfin cold states were very similar, with the two larger fish having almost identical distributions. The three bigeye also had colder states that were similar to each other, although distributions were centred between 10.8˚C and 14.3˚C, demonstrating a greater range of median temperatures than for the yellowfin. Only one individual, the largest bigeye tuna Arc272, displayed a deep state that was tightly distributed around both water temperature and standard deviation of depth.

The stationary distributions of the transition matrices show very clear differences in behaviour between day and night. The known foraging ecology of tropical tuna suggests a preference for following diurnally migrating prey species for those individuals that are physiologically capable (Bertrand, Bard, and Josse 2002; Graham et al. 2006), and these results in this regard clearly align with the observations of many previous studies. For the majority of individuals, a strong tendency to switch to warm states during the night and colder states during the day was exhibited. The persistence for warm states during the night is demonstrated by almost an almost zero chance for all fish of switching from these behaviours during this time. In contrast, behavioural states during the day are more varied, particularly for the yellowfin examined here, with only the largest bigeye tuna displaying a complete lack of switching from deep cold states during the day. This does not indicate that this individual will never exhibit its warm state during the day; rather, it suggests that once its behaviour has shifted to the cold state, it will never transition away until dusk.

5.4.3 Method summary

In this study I have demonstrated a technique for objectively characterising continuous dive data, summarising time-series at a temporal scale of interest into a multivariate assemblage. Dimensions are chosen that both represent the variation in qualitative patterns observed in previous studies and relate to drivers of the phenomenon under investigation, allowing straightforward incorporation into a HMM. Classification of the time-series is objective, and provides a simple and easily interpretable way to examine if patterns are observed across factors that can then be re-incorporated as parameters within the transition matrices or state-distributions themselves of an updated HMM. Data from any number of sources can be arranged into an N-dimensional multivariate distribution as the observation model, or another distribution more appropriate to the data can be used (Peel and McLachlan 2000). In addition, information that does not form the behavioural observation model of the animal, but is believed to influence either the switching between these behaviours, the nature of the behaviours themselves, or both, can be included as covariate parameters. While increasing the amount of data used in estimation of the likelihood will improve model fitting, the parameter space of a multivariate HMM will increase non-linearly due to the increasing size of the transition and variance-covariance matrices, so care must be taken when fitting overly complex models. Furthermore, the simulation experiments described above have demonstrated where we might have the most confidence in estimated parameters of a HMM, i.e. the means of multivariate state distributions and the parameters of non-transitory states.

In the context of providing scientific advice to managers, HMM analyses provide easily interpretable models for the objective classification of autocorrelated behavioural data, as well as a framework for examining the nature of, and switching between, behavioural patterns in continuous vertical movement time-series. When considering a particular ecological or management question, the variables used to build the multivariate observation model of these HMMs should be carefully selected. Rather than being an abstract description of an animal's behavioural space, the dimensions on which states are estimated can be chosen such that the quantitative outputs of the HMM can have direct interpretations. In the case of tropical tuna, a large-scale analysis of archival tags would reveal the consistent behavioural states across species or size classes. These behaviours can be described in dimensions that are directly related to questions such as catchability or the exposure of tuna to different fishing gears, and could be quantitatively incorporated into larger natural resource management models that contain specific behavioural components. Subsequently, HMMs containing different covariate information influencing the nature and switching of established states can be compared to examine alternative hypotheses on the mechanisms driving vertical behaviour, and explore the effects that individual-scale behaviour may have at the population level.

5.4.4 Further work

Here, I have shown how using HMMs allows an objective description of behaviour in dimensions relative to the question being asked. Robust and quantitative methods to describe the vertical movement time-series of the PTTP were required before some of the questions of this thesis could be examined. The example subset of individuals examined here provide some evidence of what such quantitative descriptions of behaviour may look like, but a much larger sample of tuna will be required to really examine vertical movement behaviours across factors such as size or species. While quantitative description of behaviour will allow comparison between individual and groups of tuna, the classification of a large number of individuals will also permit a number of meta-analyses on not only parameters from estimated HMMs, but the actual sequence and dynamics of the defined behaviours observed in each time-series. In the next chapter, I will apply this approach to a larger database of tagged individuals and extend the method to explore more covariates that affect behaviour.

Chapter 6: The Vertical Movement Behaviours of Yellowfin and Bigeye Tuna

In the previous chapter, a method was developed allowing a more objective and quantitative approach to classifying and describing the vertical behaviour from bio-logging time-series. A small sample of tropical tuna was used as an example application, examining whether the modelled behaviours were consistent and comparable to previous studies. The strengths and weaknesses of the method were discussed, and suggestions made for expanding the scope and complexity of the HMM analyses. In this chapter I implement a number of the suggested improvements to the method, and apply it to a much larger database of yellowfin and bigeye tuna taken from the PTTP. I describe the apparent vertical movement behaviours at two different temporal scales, and explore the potential effects of growth during time-at-liberty and diurnal light-levels on these behaviours. These results are then discussed for general patterns across species and regions, alongside their implications for advice to fisheries and further work.

6.1 Introduction

Vertical behaviour and archival tag data aim to record behavioural processes such as migration (Campana et al. 2011; Gaspar et al. 2006), foraging (Humphries et al. 2010; Ménard et al. 2005) and physiological regulation (Holland et al. 1992; Prince and Goodyear 2006), which are believed to drive the temporal patterns of depth and temperature recorded from bio-logged pelagic predators. The comparison of the tag-based evidence for behavioural states between groups is further complicated by the wide range of quantitative methods that have been employed to describe them (e.g. Chiang et al. 2011; Schaefer and Fuller 2010; Sims et al. 2011). The method developed during the previous chapter identified clear behavioural patterns in a very small sample of tropical tuna. Some of these behaviours may be exploited during both artisanal and industrial fishing (Bromhead, Foster, and Attard 2003; Matsumoto and Bayliff 2011; Moreno et al. 2007), and their nature and occurrence is therefore necessarily linked to the vulnerability and catchability of these fish in different fisheries.

Quantification of behavioural patterns is also explicitly linked to the analyses used to evaluate the population dynamics of tropical tunas. Habitat preferences that are used to force ecosystem dynamics (Dueri, Bopp, and Maury 2014; Lehodey, Senina, and Murtugudde 2008) are derived from the patterns of behaviour observed in tuna. Behaviour is also incorporated into stock assessment models through estimated catchability parameters and migration coefficients (e.g. Methot Jr and Wetzel 2013). These models are used to forecast tuna responses to future climate scenarios (e.g. Lehodey et al. 2013), analyses of fisheries management options (e.g. Sibert et al. 2012) and estimate stock status (e.g. Harley et al. 2009).

Here, I use the method of describing bio-logging time-series using multivariate HMMs detailed in the previous chapter as the basis for a larger analysis of yellowfin and bigeye tuna archival tag data. These data are taken from the PTTP, which at present contains over 150 returns of electronic tags that have recorded depth, water temperature, and in many cases, light information from skipjack, yellowfin and bigeye from the WCPO. This database represents over 17,500 days of high-resolution data on the vertical movement behaviours of these species. Here, I explore a subset of 75 bigeye and yellowfin tuna. Some improvements over the previous chapter to the data pre-processing stage are described, and I then estimate the different behavioural states exhibited by these individuals, and examine them for consistency across species and region. Both the effect of changing light-level on switches between behavioural states, and how the nature of the behaviours themselves may change with increasing fish size are also explored.

6.2 Methods

6.2.1 Selection of tags

A baseline dataset 75 tags were taken from the PTTP archival tagging database (summarised in Table 6.1), consisting of 30 yellowfin tuna and 45 bigeye tuna. Tags were released across a variety of seasons and areas, but given that fish may have moved considerably during time-at-liberty, here I summarise region as simply being one of either the western warm-pool ("West") or the central equatorial Pacific, east of 180°E ("East"). Each time-series constituted a minimum of 50 days of data from release to avoid short-term deployments and overly significant influence from potential tagging effects. Time-series with sections of missing or corrupted data lasting one hour or more, which could impact the sequence of pre-processed summary metrics, were rejected from the analysis. The subsequent alternate analyses exploring covariate effects and differing assumptions regarding time-scale draw a subset of tags from this dataset.

Table 6.1 All PTTP tag information used in the "baseline" HMM analysis.

Tag	*Species*	*Fork Length-at-release (cm)*	*Time-at-liberty (days)*	*Tag Model*	*Release Date*	*Recording Interval (s)*	*Region*
A0720	BET	51	236	Lotek L28	07/12/2011	30	Central Pacific
A0576	BET	51	60	Lotek L28	04/12/2011	30	Central Pacific
A0738	BET	51	60	Lotek L28	09/12/2011	30	Central Pacific
A482	BET	52	55	Lotek L25	26/03/2009	240	W. Warm-pool
A0694	BET	53	318	Lotek L28	09/12/2011	30	Central Pacific
990115	BET	58	153	Wildlife Computers MK9	25/05/2009	30	Central Pacific
A0281	BET	59	174	Lotek L25	08/11/2008	240	W. Warm-pool
123	BET	59	131	Lotek L28	27/10/2009	60	Central Pacific
132	BET	60	99	Lotek L28	27/10/2009	60	Central Pacific
228	BET	61	197	Lotek L28	27/10/2009	60	Central Pacific
1090337b	BET	61	113	Wildlife Computers MK9	30/09/2012	30	Central Pacific
890209	BET	62	155	Wildlife Computers MK9	05/11/2008	30	W. Warm-pool
990315	BET	63	262	Wildlife Computers MK9	26/10/2009	30	Central Pacific
1190151	BET	67	153	Wildlife Computers MK9	13/11/2011	30	Central Pacific
1190132	BET	67	108	Wildlife Computers MK9	02/10/2012	30	Central Pacific
890002	BET	68	61	Wildlife Computers MK9	11/05/2008	30	Central Pacific
1090429	BET	68	225	Wildlife Computers MK9	18/10/2011	30	Central Pacific
109	BET	68	285	Lotek L28	27/10/2009	60	Central Pacific
990289	BET	69	385	Wildlife Computers MK9	26/10/2009	30	Central Pacific
A0717	BET	69	291	Lotek L28	14/11/2011	30	Central Pacific

1190134	BET	69	371	Wildlife Computers MK9	03/10/2012	30	Central Pacific
890020	BET	70	73	Wildlife Computers MK9	16/05/2008	30	Central Pacific
1190170	BET	70	240	Wildlife Computers MK9	19/10/2011	30	Central Pacific
890010	BET	72	285	Wildlife Computers MK9	15/05/2008	30	Central Pacific
990296	BET	72	161	Wildlife Computers MK9	26/10/2009	30	Central Pacific
1090430	BET	72	57	Wildlife Computers MK9	14/10/2011	30	Central Pacific
890006	BET	73	287	Wildlife Computers MK9	15/05/2008	30	Central Pacific
1190024	BET	76	104	Wildlife Computers MK9	11/10/2011	30	Central Pacific
1190166	BET	76	130	Wildlife Computers MK9	13/11/2011	30	Central Pacific
1090443	BET	77	103	Wildlife Computers MK9	10/10/2011	30	Central Pacific
890031	BET	77	223	Wildlife Computers MK9	16/05/2008	30	Central Pacific
1090470	BET	78	63	Wildlife Computers MK9	11/10/2011	30	Central Pacific
890041	BET	79	117	Wildlife Computers MK9	23/05/2008	30	Central Pacific
1190185	BET	79	247	Wildlife Computers MK9	13/11/2011	30	Central Pacific
1090336	BET	80	72	Wildlife Computers MK9	23/11/2010	30	Central Pacific
1390183	BET	81	56	Wildlife Computers MK9	24/11/2013	30	Central Pacific
890047	BET	83	208	Wildlife Computers MK9	24/05/2008	30	Central Pacific
1090337a	BET	84	263	Wildlife Computers MK9	25/11/2010	30	Central Pacific

890033	BET	85	193	Wildlife Computers MK9	17/05/2008	30	Central Pacific
890032	BET	86	112	Wildlife Computers MK9	17/05/2008	30	Central Pacific
1090094	BET	87	509	Wildlife Computers MK9	26/11/2010	30	Central Pacific
A0721	BET	89	221	Lotek L28	14/11/2011	30	Central Pacific
1090366	BET	96	180	Wildlife Computers MK9	23/11/2010	30	Central Pacific
890035	BET	106	93	Wildlife Computers MK9	18/05/2008	30	Central Pacific
1090198	BET	106	361	Wildlife Computers MK9	24/11/2010	30	Central Pacific
A0589	YFT	51	321	Lotek L28	24/04/2011	10	W. Warm-pool
A13598	YFT	54	172	Lotek L24	13/03/2007	300	W. Warm-pool
A13578	YFT	55	54	Lotek L24	20/09/2006	300	W. Warm-pool
A13632	YFT	55	75	Lotek L24	26/03/2007	300	W. Warm-pool
A0549b	YFT	55	88	Lotek L28	28/05/2011	240	W. Warm-pool
A13555	YFT	60	163	Lotek L24	19/09/2006	300	W. Warm-pool
A13514	YFT	61	116	Lotek L24	26/02/2007	300	W. Warm-pool
A0610	YFT	61	64	Lotek L28	28/01/2012	10	W. Warm-pool
790379	YFT	62	162	Wildlife Computers MK9	26/03/2008	60	W. Warm-pool
A0615	YFT	63	280	Lotek L28	29/01/2012	10	W. Warm-pool
A0623	YFT	63	58	Lotek L28	29/01/2012	10	W. Warm-pool
A0616	YFT	64	57	Lotek L28	29/01/2012	10	W. Warm-pool
A0614	YFT	64	330	Lotek L28	29/01/2012	10	W. Warm-pool
A0613	YFT	64	390	Lotek L28	29/01/2012	10	W. Warm-pool
490597	YFT	68	148	Wildlife Computers MK9	09/05/2008	30	Central Pacific
D0739	YFT	68	100	Lotek L23	23/10/2009	60	Central Pacific
790373	YFT	69	121	Wildlife	27/03/2008	60	W. Warm-pool

				Computers MK9			
A13527	YFT	71	60	Lotek L24	19/09/2006	300	W. Warm-pool
879	YFT	71	246	Lotek L28	20/04/2013	10	W. Warm-pool
D1571	YFT	72	81	Lotek L23	26/03/2007	60	W. Warm-pool
B2645	YFT	74	59	Lotek L23	26/03/2007	60	W. Warm-pool
854	YFT	74	325	Lotek L28	17/04/2013	10	W. Warm-pool
D1572	YFT	75	158	Lotek L23	12/04/2007	60	W. Warm-pool
A12555	YFT	77	138	Lotek L24	18/05/2005	300	W. Warm-pool
121	YFT	78	71	Lotek L28	23/10/2009	60	Central Pacific
1090149	YFT	79	302	Wildlife Computers MK9	04/06/2010	30	Central Pacific
D1621	YFT	86	107	Lotek L23	15/04/2007	60	W. Warm-pool
D1671	YFT	86	78	Lotek L23	15/04/2007	60	W. Warm-pool
390133	YFT	98	124	Wildlife Computers MK9	24/09/2006	60	W. Warm-pool
390127	YFT	109	81	Wildlife Computers MK9	19/09/2006	60	W. Warm-pool

6.2.2 Pre-processing of dive tracks

As before, raw vertical movement data were sectioned and compressed into a bivariate time-series. In the previous chapter, sectioning was initially undertaken by estimating crepuscular periods based re-occurring changes in depth at two points in the day. Tropical tuna are known to exhibit characteristic shallow and deep behaviours, which are generally tightly linked to both night- and day-time, respectively (Matsumoto, Kitagawa, and Kimura 2013a). Using a split-moving window analysis, the two most consistent times-of-day at which strong shifts in vertical behaviour was estimated, and these same times of day were assumed to represent dawn and dusk for every 24-hour period of the time-series. This approach ignores changes to the time of dawn and dusk that may occur during the time-at-liberty of the fish. In this chapter, I use similar marked changes in vertical behaviour throughout a 24-hour day to form the basis of a model for each time-series that estimates how the occurrence of dawn and dusk change over time. This estimation of crepuscular timing is independent of light-at-depth data.

Two processes cause a drift in sunrise and sunset times. First, dependant on latitude, seasonal changes cause day length to increase and decrease throughout the course of the year. Second, horizontal migration by the fish causes a change in both day length (latitudinally) and time of dawn and dusk (longitudinally). To incorporate these two processes, the timing of section bin divisions is represented by a simple linear model, which includes terms for start of the day (dawn) and length of the day-time period. Parameters are included to allow both these values to drift over time, providing a mechanism to incorporate migration and season. These drift parameters operate at a weekly timescale and are limited to additions of ± 0.5 hours, i.e. both the start of dawn and day-time length cannot change by more than half an hour from one week to the next.

The time of the day at which dawn occurs during a given day for week $\boldsymbol{w}$, $\boldsymbol{D_w}$, is

$$D_w = D + \sum_{t=1:w} \Delta D_t$$

where ***D*** is the time of dawn on the first day of the time-series, and ΔD_t is the drift in occurrence of dawn associated with week ***t***.

The day-time length for a given day during week ***w***, L_w, is

$$L_w = L + \sum_{t=1:w} \Delta L_t$$

where ***L*** is the length of the day-time on the first day of the time-series, and ΔL_t is the drift of day length associated with week ***t***. Each day of data during week **w** is binned into two “day” and “night” sections, divided by D_w *and* $D_w + L_w$, representing estimated dawn and dusk periods. Further divisions are made equally between these boundaries to create the desired number of binned sections during a 24-hour period.

Here I compress time-series to sequences of summary metrics over approximately three-hours, with a subset of data used in HMMs estimated at the scale of one-hour time bins for comparison. Given that initial day and night section binning are not necessarily equal due to the estimated times of dawn and dusk, the size of each subsequent smaller time bin may not be exactly three-hours.

Similar to the previous chapter, time-series were arranged as multivariate measures of variation in depth and central tendency of water temperature experienced during each time bin, forming the observation model of behaviour. In this series of analyses, variation in depth was again represented by the standard deviation of depth. Central tendency of water temperature was replaced by simply the mean water temperature, rather than median as in the previous chapter. These two variables capture variation in different patterns of vertical movement. Being a representation of depth (in terms of thermal habitat), and association at the depth, this description is also related to exposure to surface fishing gears (see Chapter Five).

6.2.3 Model assumptions and estimation

Described more fully in the previous chapter, multivariate HMMs are state space models where imperfect observations are represented as discrete states, each defined by a multivariate distribution observation model. The switching between states is governed by a transition matrix giving the probability of switching from any one to state to any other, fundamentally incorporating autocorrelation into the assumptions of the model; that is, the probability of observing something at time t depends on what is observed at time t-1. State distribution and transition parameters can be estimated using a numerical minimisation of a negative log-likelihood (Patterson et al. 2009).

In addition, covariate information that is separate to data used in the observation model can be incorporated into the likelihood estimation by defining state distribution or transition parameters as linear, or other, equations that include the covariates. For example, the probability of switching from one state to another can vary in relation to phenomena separate to the behaviour of the animal, or the multivariate mean of states can be made to change over time in response to covariates. In this set of analyses, parameters that include covariates are expanded into linear equations with coefficients estimated by the same process of minimisation of the negative log-likelihood.

As in the previous chapter, the compressed multivariate time-series were log-transformed to better resemble a mixture of normal distributions. Model parameters were estimated using the *optim* algorithm in R, with initial conditions generated by using k-means machine learning to cluster the data into groups and calculate state distributions and transition probabilities from these classified data. When covariate information was used to influence parameters, the mean value from the maximum and minimum halves of the covariate was used to examine the linear effect on the covariate-containing parameter values, as estimated by the k-means clustering. The coefficients of this linear relationship were then used as start values for the corresponding covariate parameters.

6.2.4 Simulation experiments and tag analyses

As in Chapter Five, a number of simulation experiments were carried out to test the effectiveness of the method to recover true parameter values, using two of the new analyses undertaken in this chapter: changes to state means in relation to a non-linearly increasing covariate (size of fish) and changes to transition probabilities in relation to a continuous, cyclic covariate (estimated changes in surface-light). In the previous chapter, covariates in the transition matrix were simply binary, i.e. day or night. Here, covariate information is continuous. Fifty stochastic repetitions of 500 simulated summary metrics were generated from pre-defined distributions and transition matrices that include influences from covariates in the two ways discussed. HMM parameters are estimated on the data as described above, and the parameters and classifications compared with the true values for consistency. As before, the simulation experiments are based on simple scenarios for the behaviour of a free-swimming marine animal, tagged with a bio-logging device. This device records variation in depth and mean water temperature across three-hour periods, and these are arranged in a multivariate time-series on which to estimate an HMM.

Scenario One- Changing State Means: Consider a marine animal that exhibits behavioural patterns described by a multivariate assemblages of variation in depth and mean temperature captured over a time period of hours. It exhibits two clear states, one of which varies in both temperature and movement through the water column in relation to a continuous covariate. As this covariate increases, the behaviour of the animal becomes centred in colder water with less variation in vertical movement. There is no change to the other state. The covariate increases non-linearly through time, perhaps representing the growth of the animal during the bio-logging deployment. The true state distributions at the minimum and maximum value of this covariate are shown in Figure 6.1.

Scenario Two- Changing Transition Probabilities: An alternative scenario may be that the behaviour exhibited by our theoretical marine animal does not alter in nature, but rather the switching between behavioural states changes over time. In this simulation, it is assumed that a cyclic, continuous covariate influences the transition probabilities between two distinct behavioural states. When the covariate is high, switching to and persistence of the first state is great, with the opposite being true when the covariate is low. The analyses of Chapter Five essentially assumed a discrete version of this scenario, with a binary covariate that switched between one of two values. Here, this covariate can be considered the continuous version of the same information, perhaps representing an external factor that drives change in the position of patches of prey in the water column, forcing the animal to switch foraging strategies. State distributions are the same as in Scenario One, when the covariate information of that scenario was at the minimum value (the most overlap in distributions).

HMMs were estimated on these simulated data in the same way as pre-processed time-series from real archival tags, and the results examined for accuracy in recovering true parameter values.

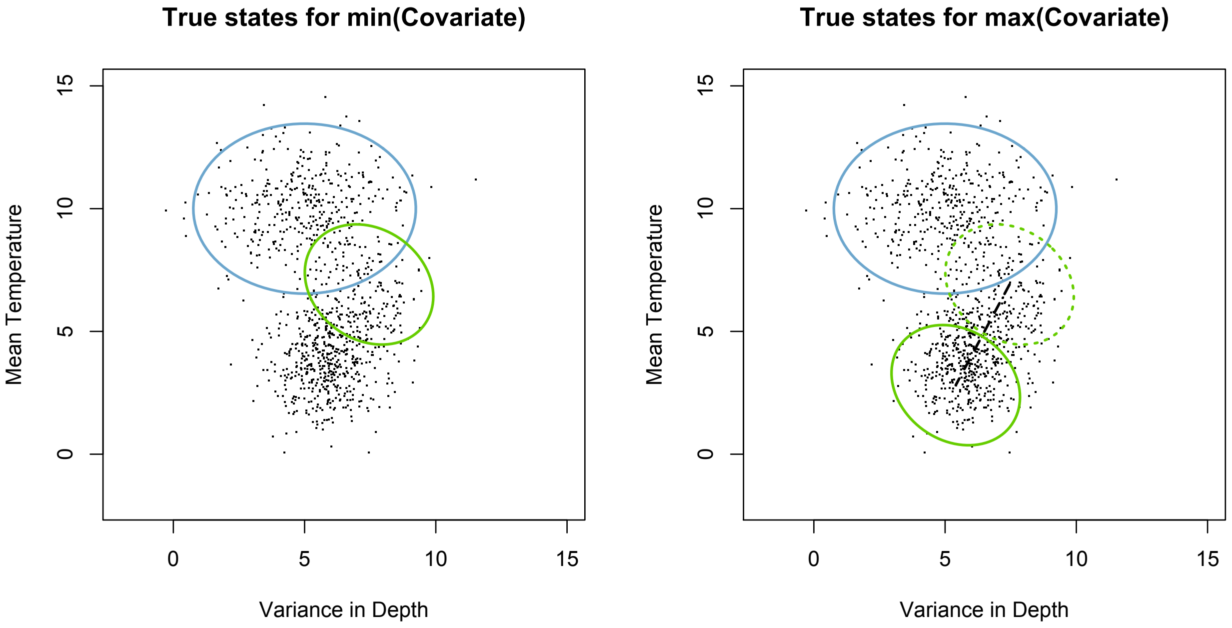

Figure 6.1 True state distributions for simulation scenario one, when the growth covariate was at a minimum value (left) and maximum value (right).

Following these simulation experiments, three groups of analyses on the time-series from the PTTP were carried out. Firstly, a “baseline” set of models were estimated using no covariate information to classify the individual tagging time-series data, summarised at a three-hour timescale, using multivariate HMMs that contained one to four behavioural states. These results were then examined for differences between species, regions, quarter of release, and size of fish. A subset of these tags was used in an alternative set of models, estimated using the same time-series summarised at a one-hour timescale for comparison.

In light of these results, I then estimated more complex HMMs for two further subsets of this baseline dataset. The first examined how behavioural states themselves may change as the individual grows during time-at-liberty, and the second how behavioural switching appears to change in relation to depth-corrected light levels from those tags that contained light-at-depth data.

The first covariate analysis was achieved by including the increasing length of the fish whilst at liberty as a term in a linear equation that described the parameter mean of each state distribution. While length-at-release values are considered accurate, the length at recapture is considered less reliable (Leroy et al. 2012) and was frequently absent from the PTTP tags used here. Therefore the size at a particular time was estimated from length-at-release, projected forward using the Von Bertalanffy growth curves for bigeye and yellowfin tuna used in recent stock assessments (Harley et al. 2009; Langley, Hoyle, and Hampton 2011). Growth increased non-linearly and drove change in the means of all estimated behavioural states during likelihood estimation. These modelled changes in state mean were examined and compared across individuals.

The second covariate analysis used estimated surface light data to affect the switching between behavioural states of a two-state HMM. The light-at-depth data from a subset of tags were transformed to curves estimating the corresponding light level at the surface irrespective of depth, using an existing two-layer depth correction algorithm (Ekstrom 2004). This estimated surface-light information, which cycles diurnally through each 24-hour period, was used as a covariate parameter that changes the probability of state switching in the transition matrix. The general patterns in Markov-chain stationary distributions between species were then compared.

6.3 Results

6.3.1 Simulation Experiments

As in Chapter Five, the success of the HMM method for recovering the known parameter values from the simulation experiments is shown visually with parallel coordinate plots, alongside percentage correct classification rate. As these experiments contain covariate dependent terms, when appropriate, parameters are shown at both the minimum and maximum covariate range.

As before, parameters were accurately, but not always precisely, estimated. In scenario one, state distribution means varied in relation to a non-linearly increasing covariate, but in reality, only one state truly varied in response to this value. Variance-covariance parameters were less accurate than state means, with covariance estimates both more inaccurate and imprecise. State means were well recovered, despite there being changes over time, but estimates were naturally less accurate when distributions were close to each other, as was the case when the covariate value was low. Transition probabilities were well recovered, with some evidence that state persistence is consistently underestimated (Figure 6.2). Mean correct state classification rate was 97%.

For scenario two, the true and estimated parameters are shown in Figure 6.3. In this scenario, state transition probabilities changed in relation to a cyclic covariate. As before, well-separated state means were accurately recovered whilst estimates of larger variance parameters were less precise. The method was less effective at estimating transition probabilities when they changed in response to covariate data, particularly for the less persistent state. Some model estimations even resulted in the most probable transitions for this state being inverted from their true values. Despite inaccuracies, the mean correct state classification rate was still 96%.

In light of these results, it appears the dive track compression and multivariate HMM method remains appropriate for these types of more complex analyses. More confidence should be placed in the estimation of state distribution means over the variance-covariance parameters. In addition, results from fast cycling covariate information affecting state switching should be treated with caution, with potentially many replications required before true dynamics can be identified.

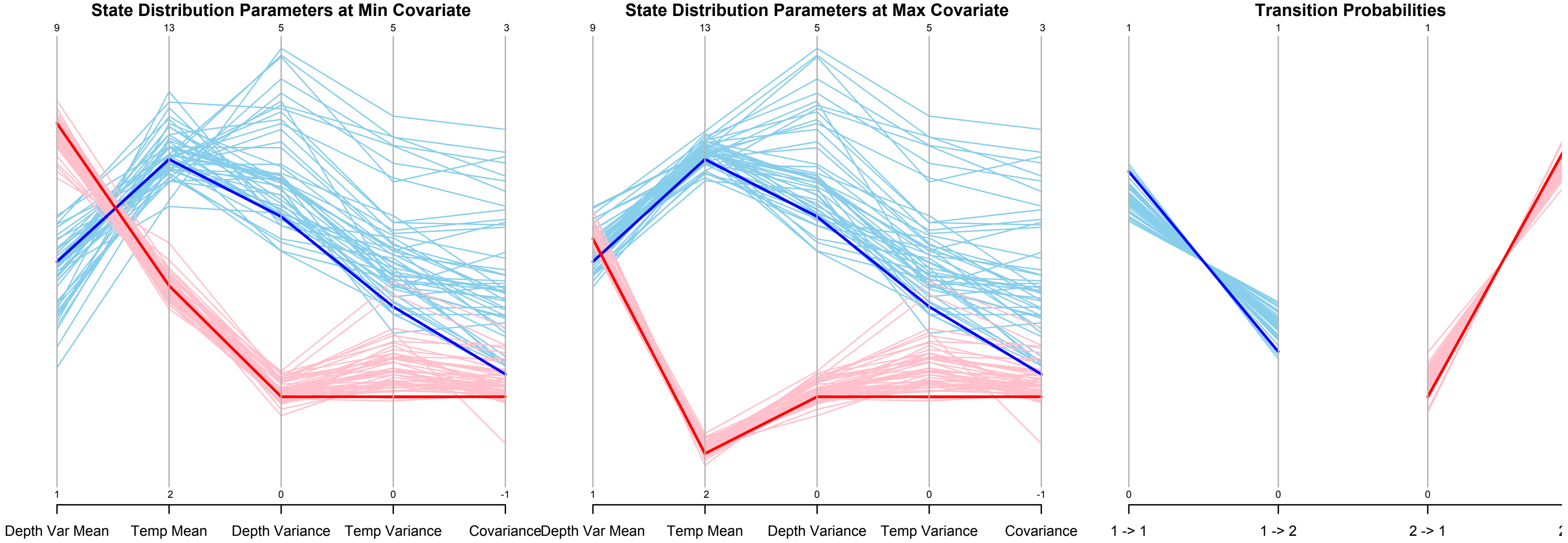

Figure 6.2 Parallel coordinate plots showing the true (dark lines) and estimated (faint lines) parameters for all repetitions of simulation one.

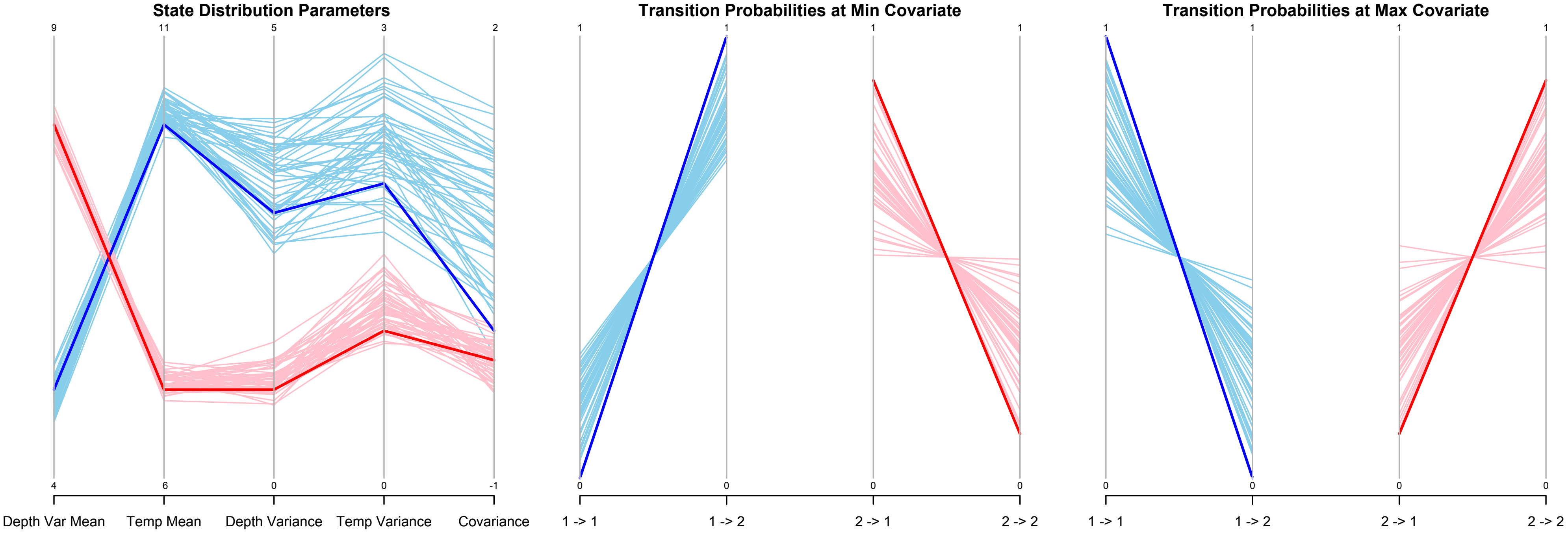

Figure 6.3 Parallel coordinate plots showing the true (dark lines) and estimated (faint lines) parameters for all repetitions of simulation two.

6.3.2 Baseline dataset

HMMs were estimated on the baseline dataset of time-series for models assuming one to four states. As discussed in the previous chapter, there is at present no robust method of parsimonious model selection for HMMs. Moreover, as no model is a true representation of reality, it may be more useful to consider that there is no 'correct' number of behavioural states for a given individual fish. Rather, each estimated model allows consideration of the likely behavioural states, given the assumptions of that particular model structure. While an indication of the most appropriate model can be gained from examining likelihood curves (Dean et al. 2012), pseudo-residuals (MacDonald and Zucchini 2009), and standard model selection criteria such as AIC, these approaches are not truly objective and may be unreliable for HMMs (Peel and McLachlan 2000). The estimated negative log-likelihood curves, as in the previous chapter, display the general pattern of model fit across many individuals (Figure 6.4).

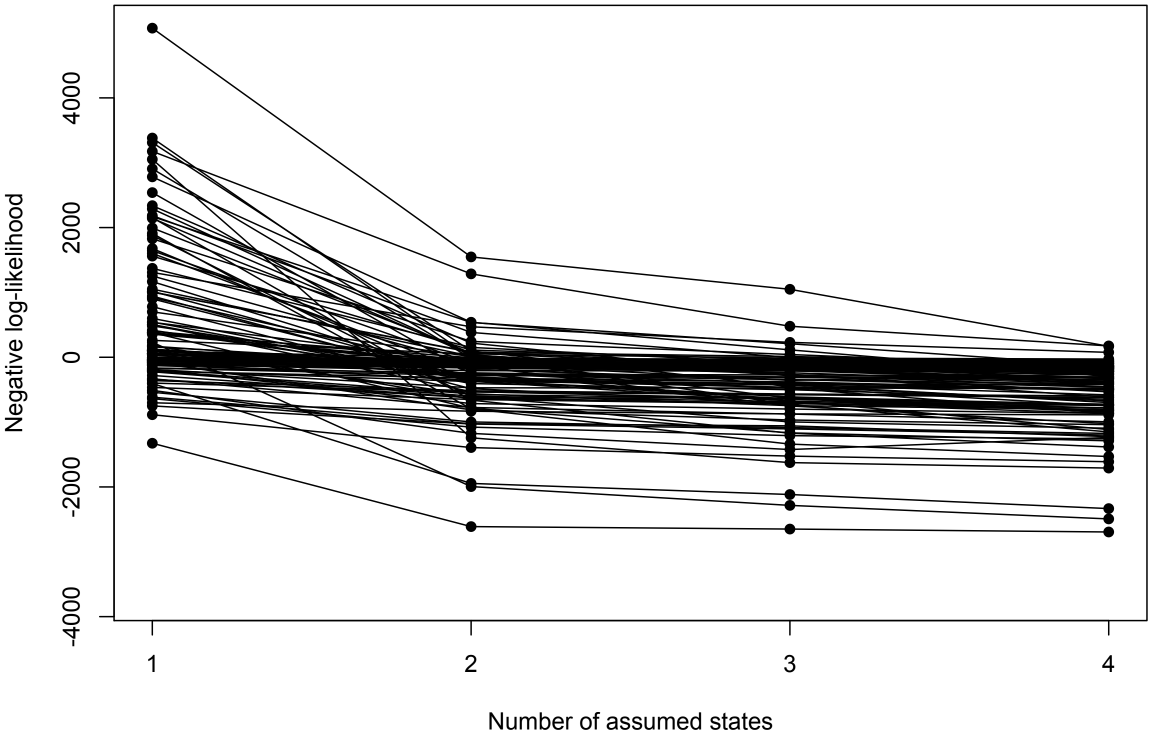

Figure 6.4 Change in HMM estimated negative log-likelihood over increasing number of states, for all tags in the baseline analysis.

Using this approach, the behaviour in the majority of individuals in this analysis is well described by two distinct behavioural states. These states are similar across all the model structures and alternative analyses I subsequently assume in this chapter. The first is based in the shallow mixed-layer of warm water. The amount of variation in vertical movement in this state occurs across a spectrum, including both tight associations with a particular depth as well as large amplitude movements through the water column. The second state is centred in colder water, although the multivariate mean in the temperature dimension is more variable across individuals. This state is linked with larger amplitude movements through the water column.

It may also be appropriate to describe some of the time-series using HMMs assuming either three distinct behaviours, and in some cases, just a single behavioural state. Results under a three-state assumption are described later in the results. The assumption of one behavioural state, where appropriate, corresponds to cases where individuals simply have a single shallow state that is large enough to represent all observations in the time series, and are not shown here. For the remainder of results from the baseline dataset, and subsequent analyses containing covariate observation, I display results from HMMs that assume two behavioural states.

The estimated state distributions for all individuals in the baseline analysis (N = 75) are plotted together in Figure 6.5. When assuming two behavioural states, there are clear differences in the deep state between yellowfin and bigeye. In contrast, this distinction is much smaller between species in the shallow states. The deep states of bigeye tuna are generally much colder and more variable in depth than those of yellowfin, which are more covariant between temperature and movement through the water. This suggests that colder habitat use during deep states in yellowfin is also associated with greater movement through the water column. For bigeye, amplitude in diving remains similar regardless of the thermal habitat experienced for their deepest behaviours. These broad descriptions conform to the *a priori* expectation of the two species' behaviour (Schaefer et al. 2009).

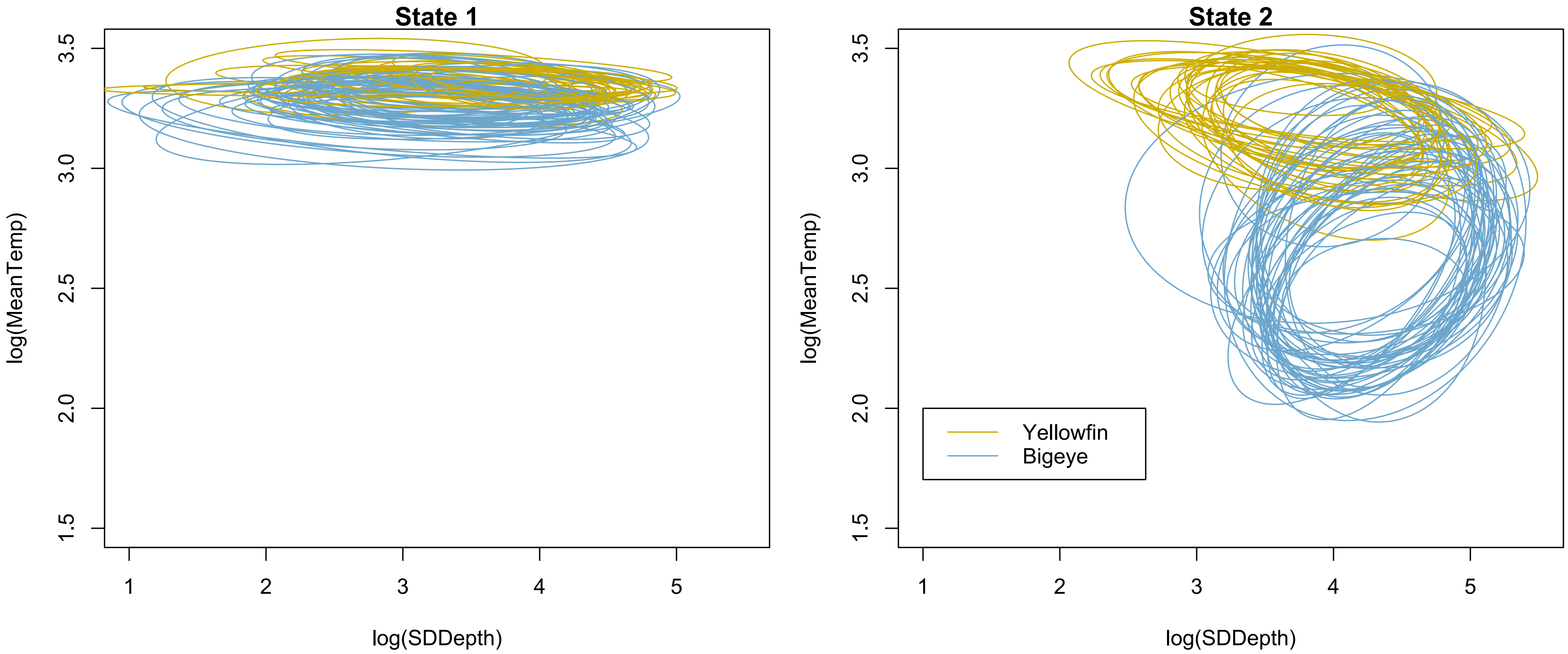

Figure 6.5 Estimated state distributions for all tags in the baseline analysis, under a two-state assumption. States are separated into shallow and warm (left) and deep and cold (right).

Aside from clear differences between species, the individual tropical tuna examined in this analysis also existed at liberty across a wide range of biological, spatial and temporal factors. To statistically examine the effect of these factors on the estimated HMMs, a multivariate analysis of variance (MANOVA) was carried out. For each HMM estimated on an individual time-series, model parameters were arranged into a multivariate vector, comprised of the estimated mean and variance-covariate parameters of each state. Each vector is associated with corresponding factors representing species, year-quarter at release of fish, and eastern (central pacific) or western (warm-pool) region. MANOVA was used on the vector of each behavioural state to test if the null hypothesis, that these factor groups have a common centroid in this dependent variable space, could be rejected and how the variation in parameters of the behavioural model is reduced by membership to these groups. Individual and interaction terms between all factors were included, a model reduction approach was undertaken to obtain a model with only significant terms ($P < 0.05$).

For shallow states, highly significant effects of group membership in species ($F_{1,66} = 9.42$, $P < 0.001$), release region in the western or central Pacific ($F_{1,66} = 9.00$, $P < 0.001$), and year quarter at release ($F_{3,66} = 6.93$, $P < 0.001$) were found. The apparent effect of timing of release is somewhat confounded by the fact that some year quarters only contained releases of one of the two species. Carrying out an ANOVA on individual terms revealed that state means of the standard deviation of depth dimension were significantly affected by species and release-region groups, whilst the mean in the mean temperature dimension was significantly affected by species and release-quarter. Variation in individual variance-covariance parameters was not significantly reduced by membership to any grouping.

For the deep states, highly significant group membership effects were once again seen in species ($F_{1,68} = 120.24$, $P < 0.001$), and release quarter ($F_{3,68} = 8.26$, $P < 0.001$), while region affected parameter variation less than for the shallow states ($F_{1,68} = 3.66$, $P = 0.006$). In addition, an interaction term between species and Pacific region was found to be significant ($F_{1,68} = 6.22$, $P < 0.001$). Analysis of variance on individual terms showed that deep state means in both dimensions were significantly affected by group membership of all terms in the MANOVA analysis (see Figure 6.6). Furthermore, variance in mean temperature and covariance between observations are significantly different across species and release-quarter.

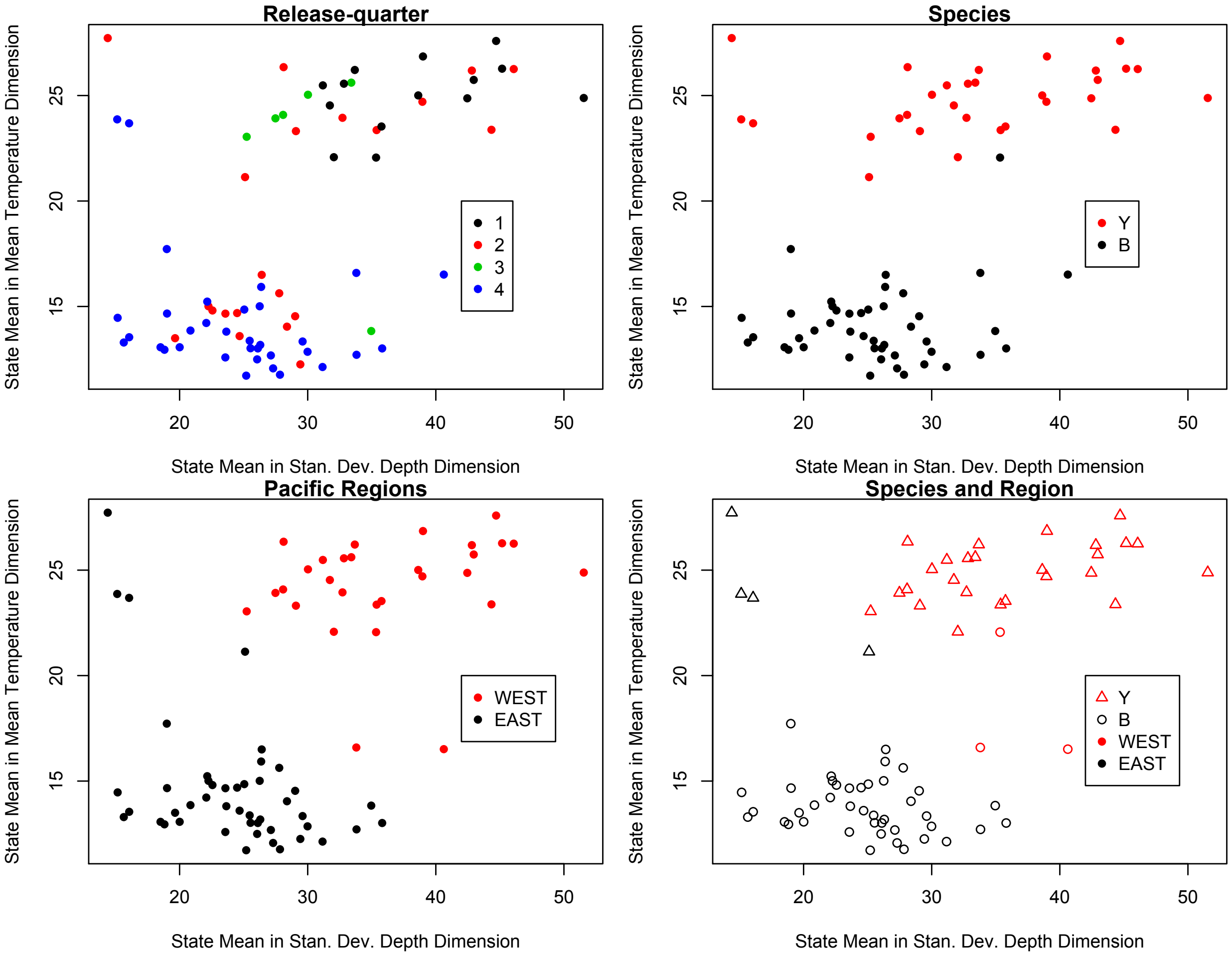

Figure 6.6 Scatterplots showing significant differences in HMM deep state parameters, as indicated by ANOVA, for all tags in the baseline analysis.

The transition matrices that describe the estimated switching between these behavioural states are also estimated in the HMM analysis. Because each model estimates an *m*-by-*m* matrix, comparisons across multiple runs can become complicated, although this is less so for two-state models. As in Chapter Five, I summarise these sets of transitions probabilities using the stationary distribution to reduce each matrix to a vector of length *m*. The stationary distribution is the limiting distribution of the Markov chain described by transition matrix, and represents the portion of time spent in each state, if that particular Markov process were to continue indefinitely.

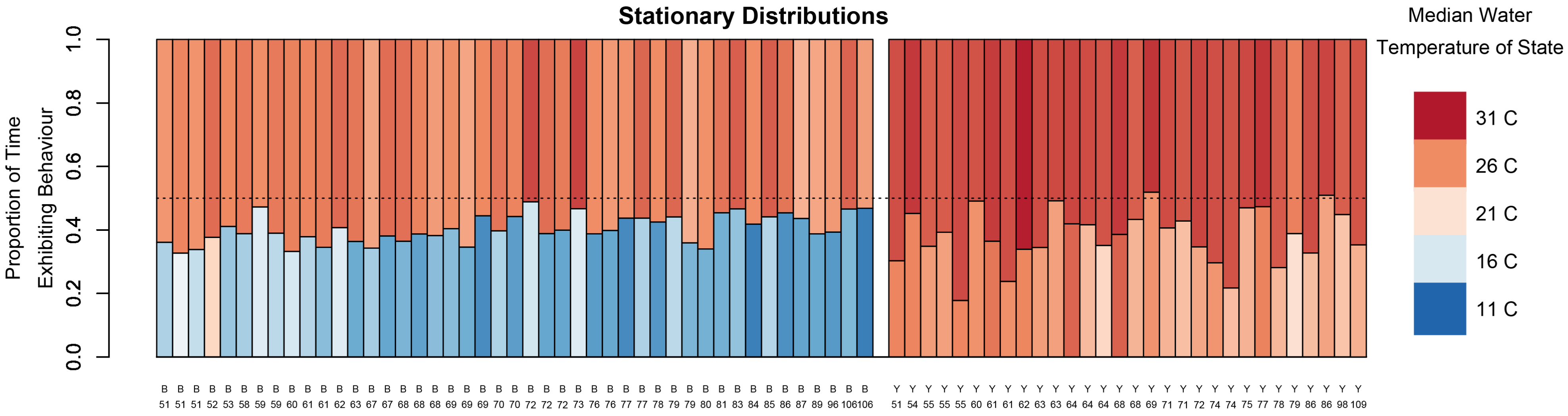

Figure 6.7 All state-switching stationary distributions for tags in the baseline analysis. Bars are separated into time spent exhibiting shallow (top) and deep (bottom) states, coloured by the back-transformed state mean in the mean water temperature dimension. Results for bigeye are on the left, and for yellowfin on the right, with within species tags ordered by increasing length-at-release (left to right).

Figure 6.7 shows the stationary distributions for all individuals from the baseline analysis, ordered first by species and then by fork length-at-release. For the majority of fish, proportion of time spent between the shallow and deep states is roughly equal, with a general tendency to occupy a shallow state more frequently than a relatively deeper one. Although bigeye appear to be more consistent across individuals in time spent between behaviours than yellowfin, a MANOVA analysis revealed that state switching does not change significantly with species (or any other spatial or temporal factors examined here).

6.3.3 States estimated at one-hour intervals

A series of HMMs were also estimated using time-series compressed at one-hour metrics, in order to compare how behavioural states may differ at this temporal scale. These individuals were a subsample of the baseline analysis dataset (N = 68), comprising of time-series of longer than 50 days but with no corrupted or missing data longer than 30 minutes. The same examination of estimated likelihood curves was undertaken to identify if a consistent number of states in the model structure improved the fit to the data (Figure 6.9), across HMMs assuming one to three states.

As with the three-hour scale of compression, the majority of time-series showed a much greater improvement in likelihood increasing from a single state to two. State distributions were fairly similar to those estimated at three hours (Figure 6.10), although all state means in the standard deviation of depth dimension were generally reduced. This was confirmed in a MANOVA analysis on vectors of parameter values that significant differences between both sets of models for all states ($P < 0.001$, for both shallow and deep states). ANOVA on individual terms showed that means were significantly lower in the standard deviation of depth dimensions for both states, which is unsurprising given the reduced capacity for variation in depth across a smaller window of time under one-hour compression.

Stationary distributions were also similar to models estimated at three-hour time-scales, with a slightly greater proportion of time spent in the relative shallow states for the majority of individuals (Figure 6.11). The autocorrelation signal remained similar for both time-series after classification. The autocorrelation function of the time-series of probability of shallow state occupation (deep state necessarily being the compliment) showed a clear diurnal pattern, being a strong positive correlation at a lag of 7 or 23 time-steps, for 3-hour sectioning or 1-hour sectioning, respectively. The general pattern of diurnal state switching is reflected in a negative correlation between classifications at a lag of 4 or 12 time-steps, for 3-hour or 1-hour sectioning, respectively (see Figure 6.8).

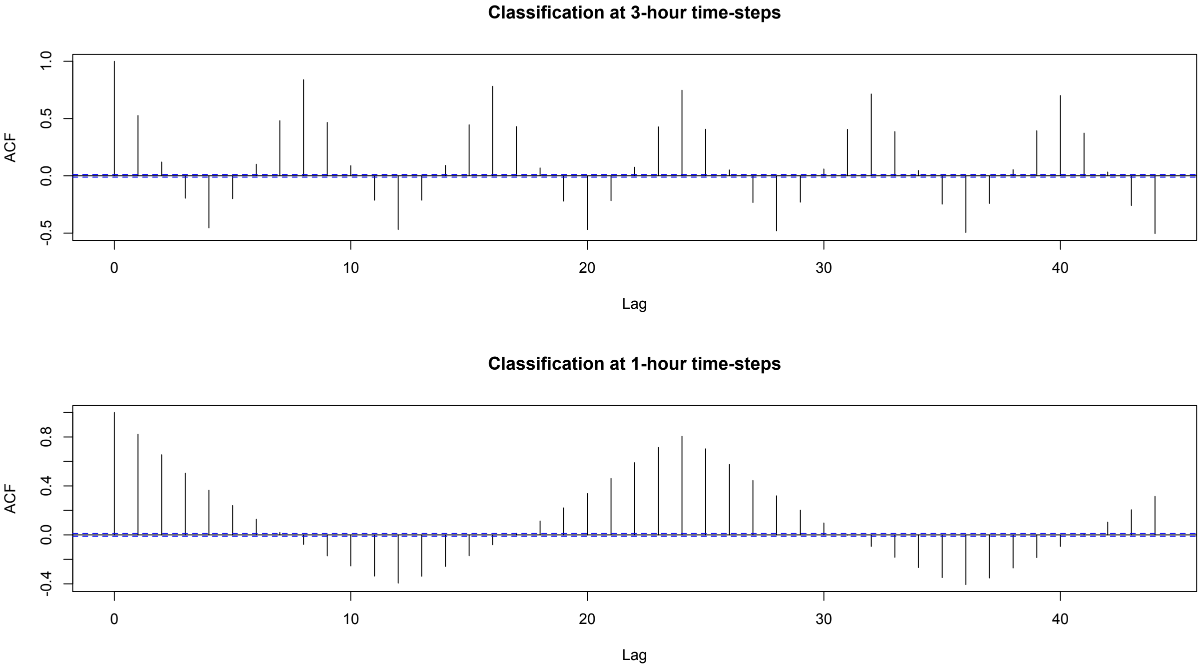

Figure 6.8 Autocorrelation function of an example classified time-series from a bigeye tuna with summary metrics calculated at 3-hour time-bins (top) and 1-hour time-bins (bottom).

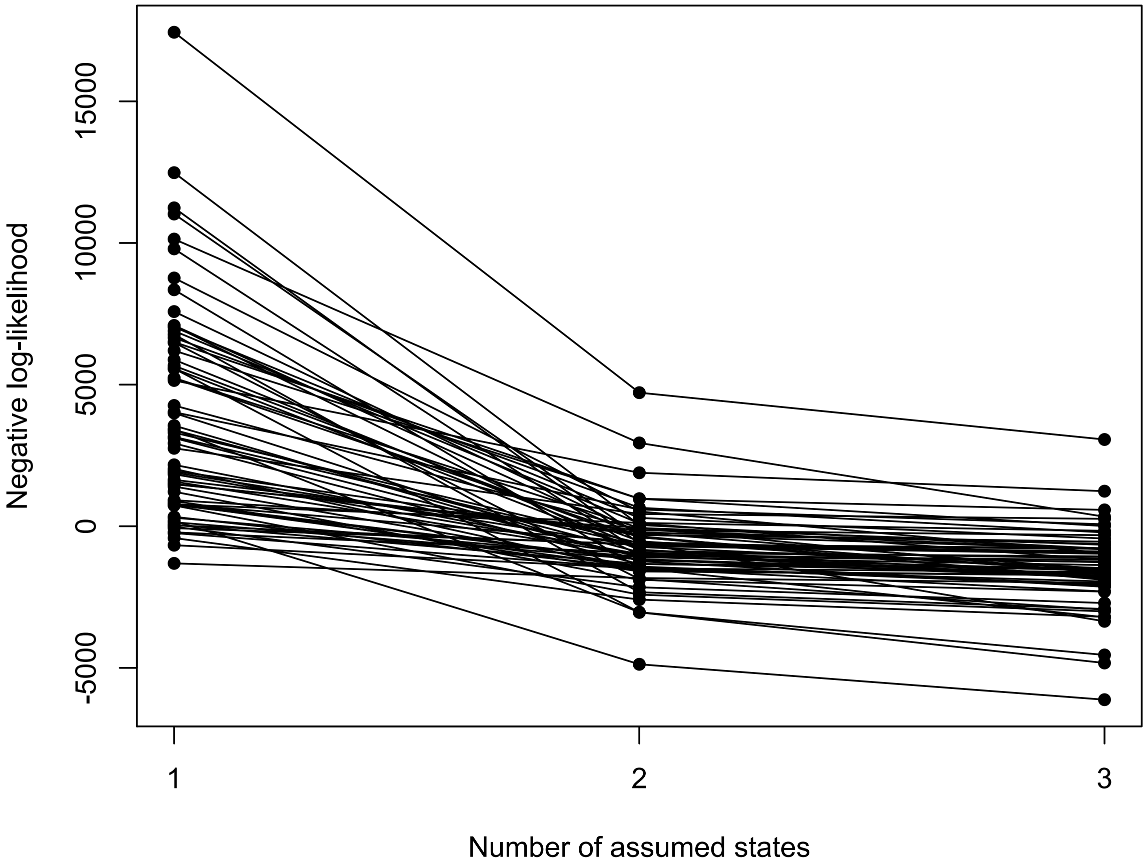

Figure 6.9 Change in estimated negative log-likelihood over increasing assumed HMM states for all tags in the one-hour time-bin analysis.

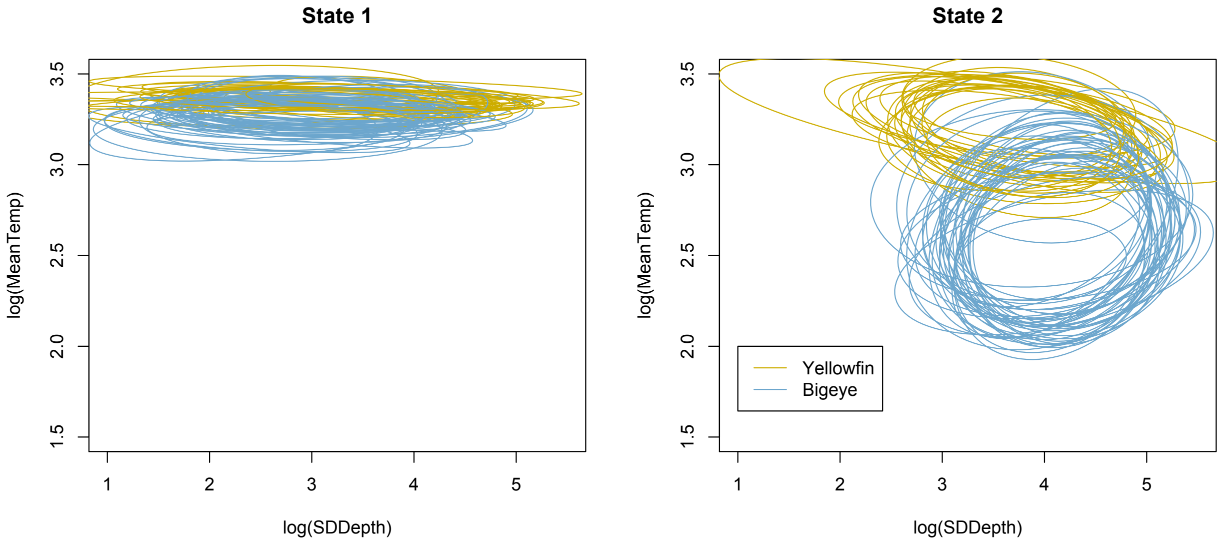

Figure 6.10 Estimated HMM state distributions for all tags in the one-hour time-bin analysis, separated by most shallow state (left) and most deep (right).

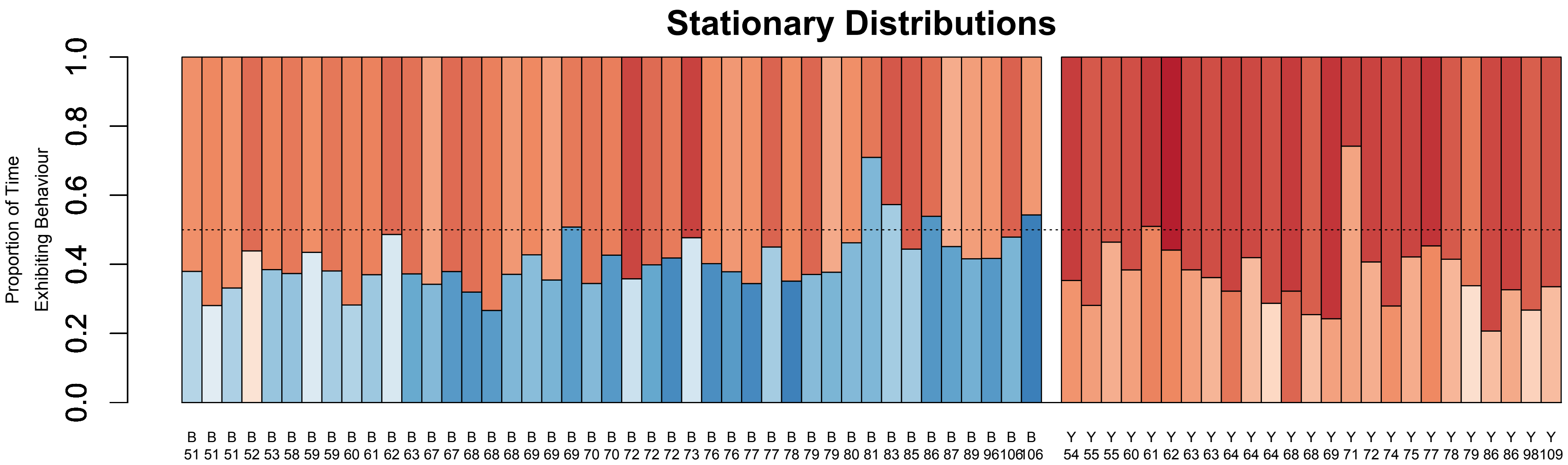

Figure 6.11 All state-switching stationary distributions for tags in the one-hour analysis. Ordering and the back-transformed state mean scale is identical to that in Figure 6.7.

6.3.4 Change in state means with size

A simple examination of the estimated state means over length of fish at release indicates that the temperature dimension of behavioural states may change with size at release (Figure 6.12). This variation of, in particular, the deep state distributions of bigeye tuna lead me to hypothesis that the nature of these classified behavioural states may change as an individual fish grows and undertakes physiological developments that allow it to exploit deeper prey-fields, or perhaps exploit them with greater frequency. To explore this, I initially examined how HMM estimated state means changed with the length of the fish at release. A simple linear regression was fitted to the back-transformed state means of each fish, with fork length-at-release used as a term. Although there seemed to be little indication of a relationship between size of fish at release and the nature of the shallow states, some significant relationships were seen for the deep states, particularly in the mean temperature dimension.

To examine this possibility further, I wished to utilise the fact that there potentially exists more information on changes in behaviour and growth during time-at-liberty within the time-series. Length of fish at release can be thought of as “snapshot” single value giving an indication of the developmental stage of the fish, but during a time-series changes in the behaviour states may occur, as the fish grows during time-at-liberty. Here, I used a covariate parameter in a set of HMM analyses estimated on a subset of the baseline dataset (N = 65), where state means were allowed to vary in relationship to a covariate representing the estimated size of the fish as it changes through time. This is analogous to simulation scenario one of this chapter. As size of fish can only increase through time from release to recapture, the addition of covariate parameters result in state distributions that ‘drift’ linearly through the multivariate behavioural model during the course of the time-series.

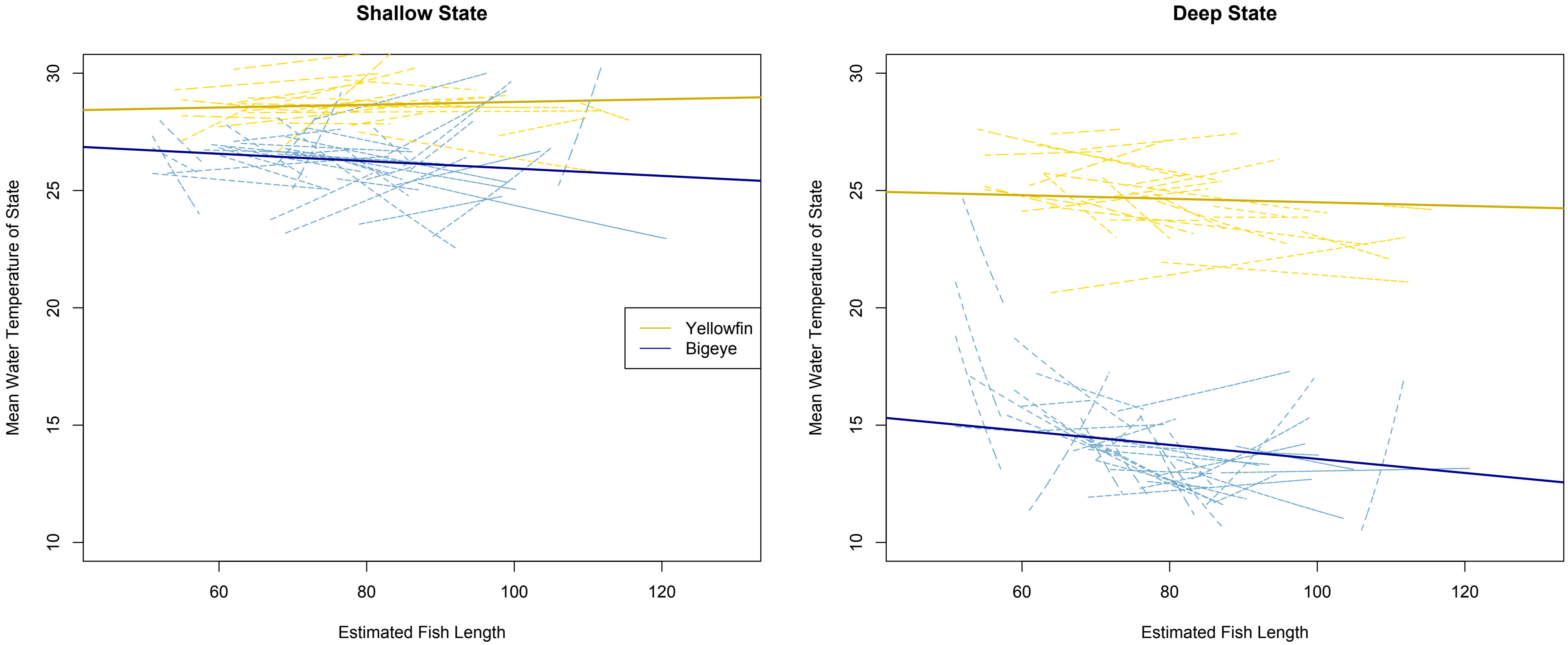

Figure 6.13 HMM estimated relationship between state mean in the mean temperature dimension for each tag in the changing state means analysis, overlaid with mixed-effects linear model showing population-level prediction for the same relationship.

Fundamentally, the description of the estimated shallow and deep states is the same as for the baseline analysis, although mean states cannot be compared to the baseline using MANOVA due to the covariate parameters, but the distributions of these states now change over time. These changes can be compared across all individuals by plotting the length of the fish at each time-step against the corresponded modelled state mean at that same time in a single dimension of the observation model. Modelled change in the mean temperature dimension is shown in Figure 6.13.

Although there is much variation, there appear to be consistent changes in behavioural state means with the length of fish, particularly in the case of deeper states. To summarise the different relationships between size and thermal habitat predicted, and due to the results from each individual fish resulting from the same linear equation, I modelled all HMM predictions of mean temperature for each state using a hierarchical approach. A linear mixed-effects regression model was fitted to all the results from each state and from each species. The predicted state mean temperature, for the projected fish length at each corresponding time-step, was taken as a new observation to be modelled. As these points were naturally grouped together for each separate fish, a random intercept by fish was included, assuming the relationship between length and thermal habitat for all fish share the same slope but differ in intercept. Longer time-series also therefore carried more weight in the model, as they contributed more observations during the mixed-effect model estimation process. The population-level relationship given by the mixed-effects model is overlaid on the HMM estimated relationship for each time-series in Figure 6.13.

The results from bigeye suggest a general deepening of the thermal habitat in both shallow and deep states, although there is considerable variation across individuals. For the shallow state, this gradient is fairly slight, but in the case of the deeper state it is steeper and driven in particular by several of the smallest individuals having consistently steep changes during time-at-liberty. There appears to be less evidence to suggest that the yellowfin in this study exhibit a significant shift in thermal habitat across the size classes of fish examined here.

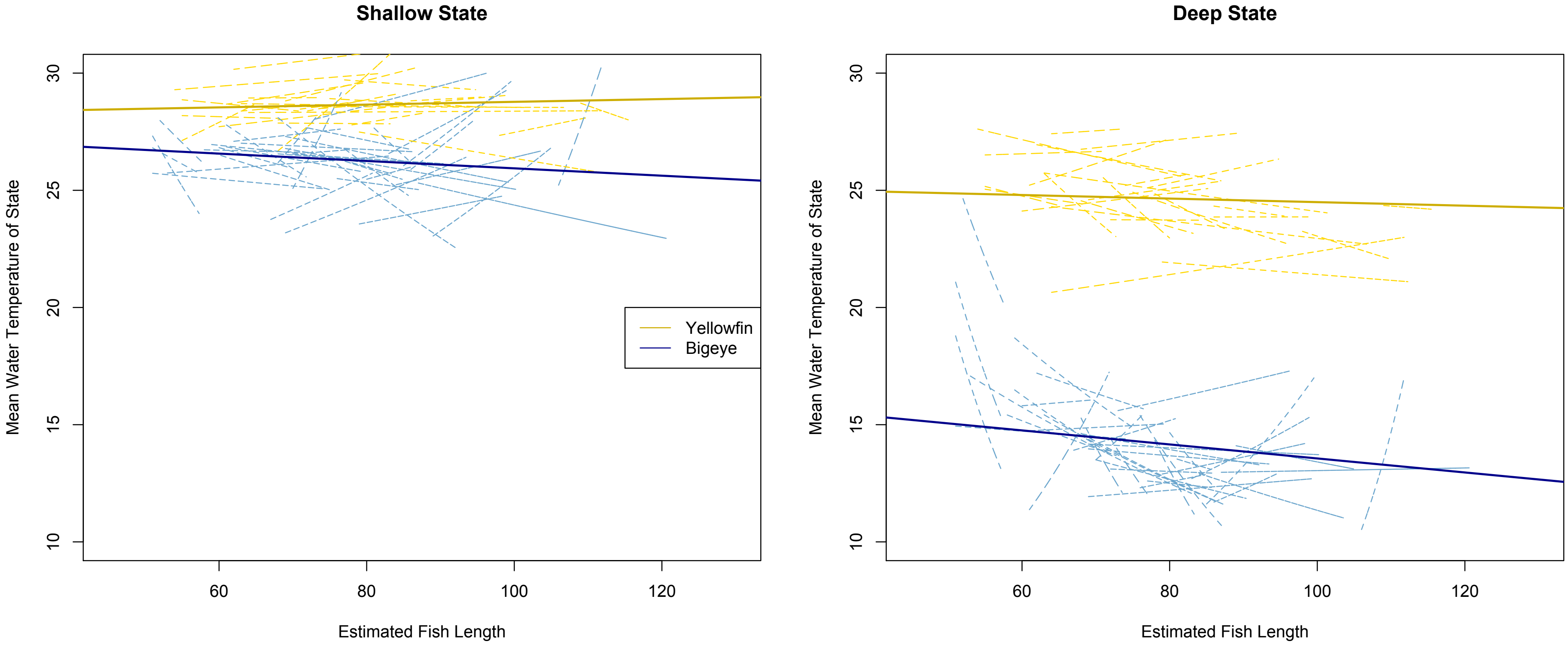

Figure 6.13 HMM estimated relationship between state mean in the mean temperature dimension for each tag in the changing state means analysis, overlaid with mixed-effects linear model showing population-level prediction for the same relationship.

The same hierarchical modelling approach was used to summarise state changes in the standard deviation of the depth dimension, but the results are not shown here. The variation for the deep states of both species is very high with little indication of change over size, but for the shallow states both species shift to slightly less variability in depth as they increase in size, particularly for yellowfin.

6.3.5 State-switching in response to light

A series of HMMs were estimated on a third subset of the baseline analysis tags that recorded light-at-depth information (N = 74). The light-level at the surface of the water for each fish, estimated by a depth-correction algorithm, was included as cyclic covariate term in the transition parameters of two-state HMM models, allowing state switching to change in relation to light.

Estimated state distributions were again similar to those estimated in the baseline analysis (Figure 6.14), with two distinct states differing across two species. A MANOVA analysis of state distribution parameters and group membership to species and model-set membership showed no significant effect between this group of models, and the baseline set ($F_{5,136}$ = 0.104, P = 0.9912 for the shallow state, $F_{5,136}$ = 0.661, P = 0.6539 for the deeper state).

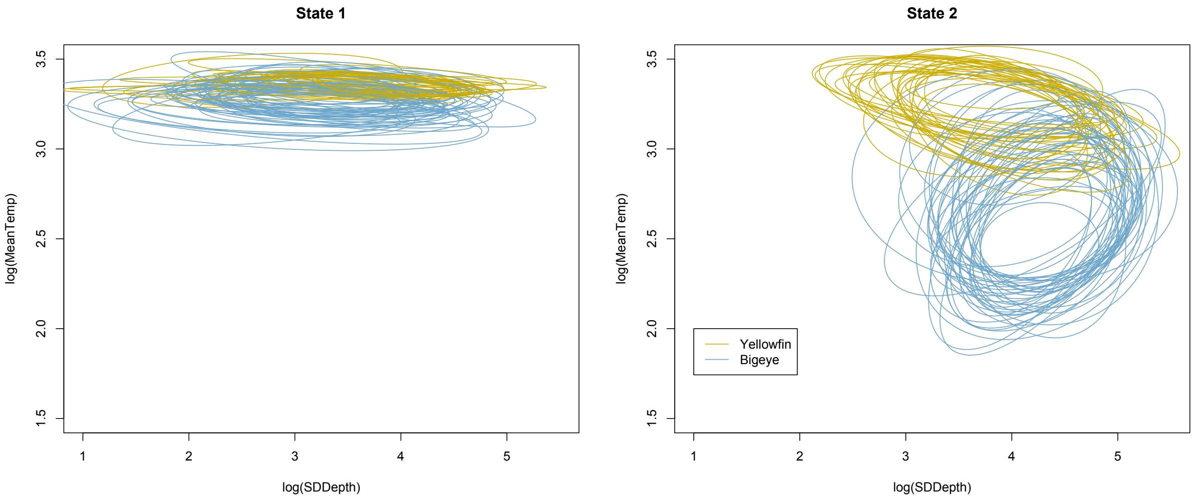

Figure 6.14 Estimated state distributions for the all tags in the light-dependent switching analysis.

State switching can once again be examined by using stationary distributions described by the estimated Markov-chain transition matrix.

Visually displaying the proportion of time spent in each state at the limit, as before, would necessitate multiple plots for different covariate values. Rather, here I plot simply how the proportion of time spent in the shallow state changes with response to light for each individual. As these are two state models, the corresponding time spent in the deep state at any particular light-level is simply the compliment of this value. Light data recorded by the tags of the PTTP occupy a range of values representing different light intensities from different regions and waters, alongside different internal measures and sensitivities across tag models. This makes direct comparison of the absolute depth-corrected surface light estimates between individuals difficult. To account for this, here I use a relative range of light-levels experienced by each individual fish for visual comparison. As the depth-correction stage of processing the light-at-depth can result in occasional extreme values, the range of light values between the 10th and 90th percentiles of the depth-corrected light covariate was used as a relative measure of light that could be compared between individuals. These data were scaled between 0% and 100%, where 0% is the darkest surface light experienced by the individual and 100% is the lightest (within the 10-90th percentile range), and plotted against proportion of time spent in the shallow state for each individual fish (Figure 6.15).

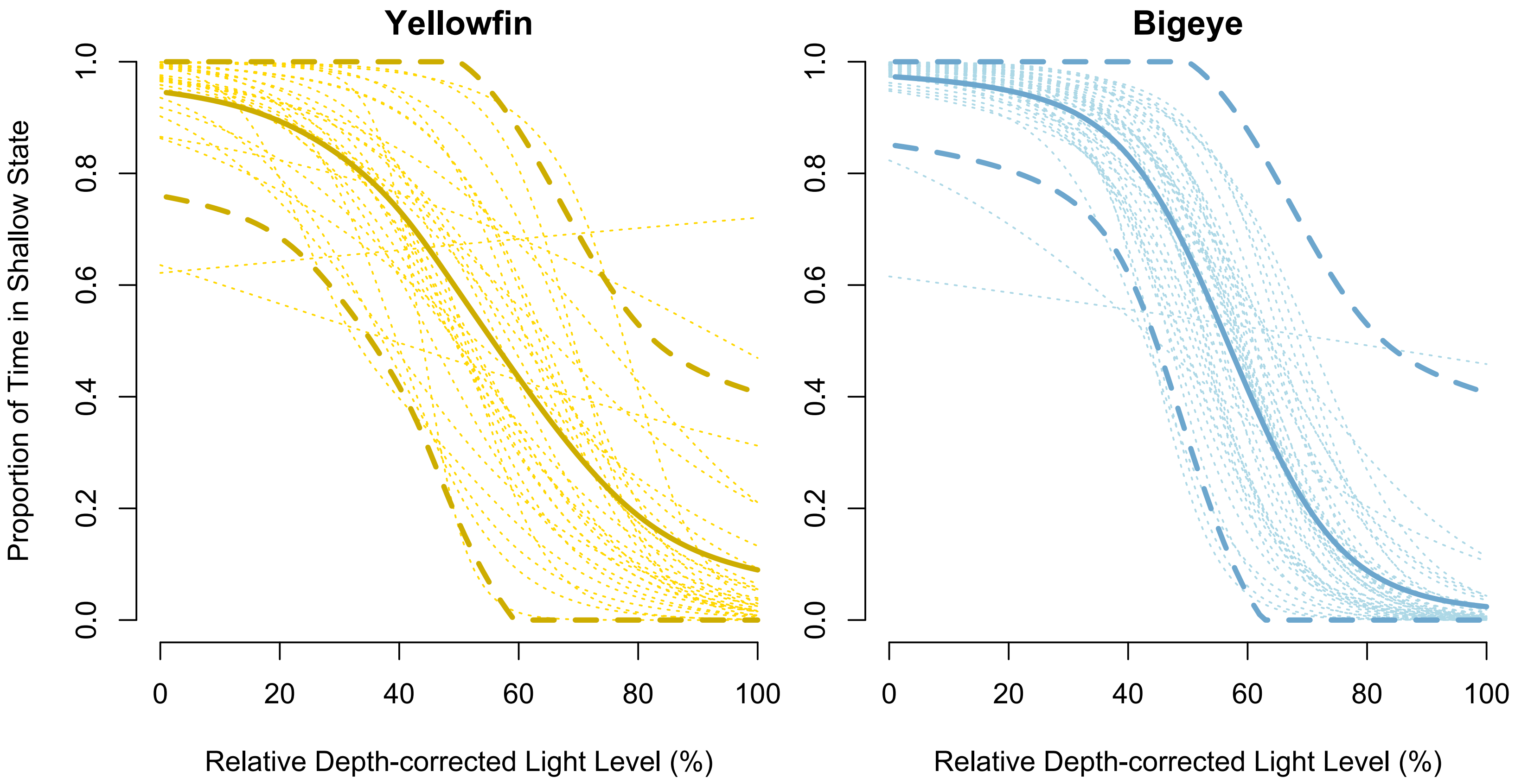

Figure 6.15 Estimated change in proportion of time spent in shallow behavioural states in response to relative light-level for yellowfin (left) and bigeye (right) tuna. Mean proportion of estimated time spent in shallow behavioural states, with 95% confidence intervals, overlaid in bold.

There is a clear link between state switching and ambient light levels in both species of tuna, with stronger light-driven changes in bigeye. While a higher probability of state-occupation is seen at the high and low extremes of surface light in bigeye, greater relative light levels are needed before switching to deep state behaviour than yellowfin. The switching between states in response to light is more linear for yellowfin, although this may be due to the relative shallow and deep behaviours being less distinct in this species. In this case switching will occur more smoothly than in the sharp contrasts between shallow and deep U-shaped diving behaviour seen for bigeye. In contrast to expected diel switching, day-time light levels cause a much lower probability of switching to deep state in a number of bigeye examined here. This could be the result of extended periods at the surface during the day heavily influencing parameter expectation, the result of behaviour typically assigned to floating object-association.

6.3.6 Third and intermediate states

Although the majority of yellowfin and bigeye tuna examined here can be described as having two distinct behavioural states associated with their vertical movement patterns, the case of a three state model can also be considered.

In the case of a three state assumption, for many bigeye the third state is a warmer, less common sub-distribution that is more depth variable than the deep state estimated when assuming two states (see Figure 6.16). In contrast, third states tend to be simply a separation of the shallow state into two for yellowfin tuna. The addition of a third state also affects the distributions of both other states. This is apparent in the significant MANOVA results for model set membership when comparing both shallowest and deepest states against those states estimated in the baseline analysis ($P = 2.397e^{-5}$ and $P = 0.0001$, for the shallow and deep states respectively).

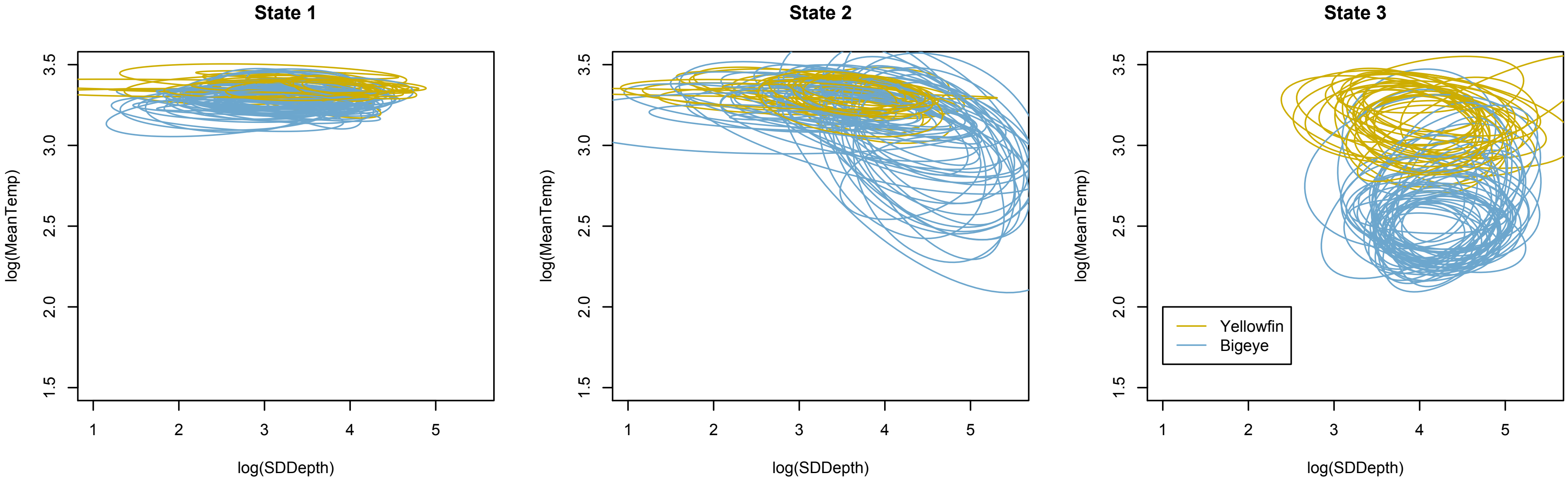

Figure 6.16 Estimated state distributions for all baseline tags, assuming three behavioural states.

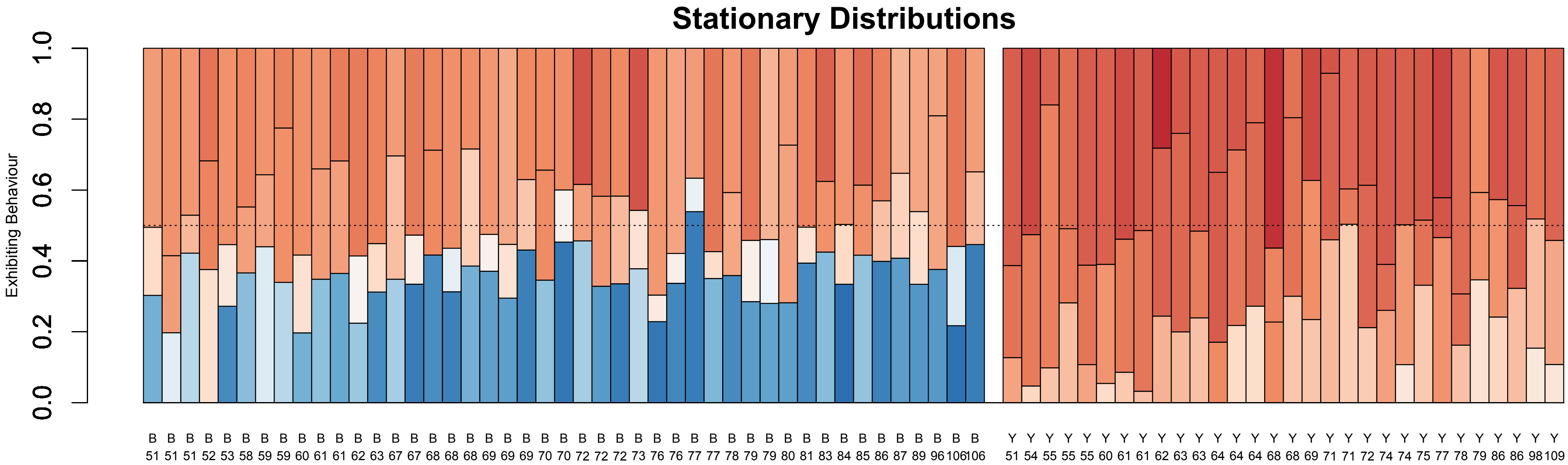

Figure 6.17 Estimated stationary distributions of state switching parameters from all tags in the baseline analysis, assuming three behavioural states. Scales are identical to Figure 6.7.

The stationary distributions reveal more about the nature of third states that lie between previously identified shallow and deep behaviours (Figure 6.17). In yellowfin, the addition of a third behavioural state divides shallow behaviour into two, usually separated by exhibiting higher and lower values of standard deviation of depth. This is also true for some bigeye, although for some individuals this new third state appears distinct. When the mean of the state distribution lies between the shallow and deep state in the temperature dimension, the state occurs only rarely. There is no indication that this intermediary state occurs across factors, other than only occurring in bigeye.

The dynamics around this intermediary state in bigeye can be further examined by looking at the transition probabilities into and out of the state. Taking a subset of those individuals that exhibit an intermediary state defined as centred at a mean temperature between the warmest shallow state and the coldest deep state, but colder than 23˚C, these transitions are shown in Figure 6.18 (N = 22). The majority of these intermediary states are not persistent, and are likely to switch to either the shallow or deep state. Intermediate states are more likely to proceed a period of shallow behaviour than a period of deep.

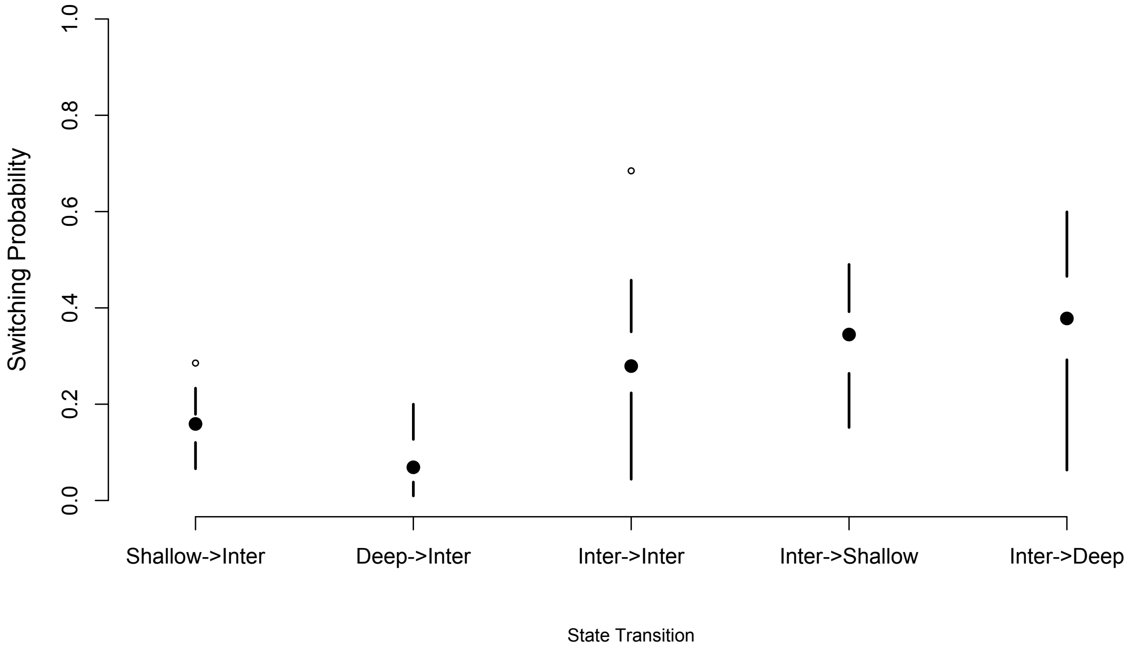

Figure 6.18 Individual transition probabilities for a potential intermediate behavioural state in bigeye tuna.

6.4 Discussion

6.4.1 General description of behaviour

In this analysis, I have expanded the preliminary work of the previous chapter using a fuller dataset of behavioural time-series drawn from the PTTP. Despite increasing the amount of data examined, the results from the baseline dataset maintain that, in general, the vertical movement behaviours of tropical tuna can be well described with two distinct states. These states are relative to each individual, significantly different from each other, and significantly different between species. The two states are associated with separate thermal habitats, and this separation is more distinct in bigeye tuna than in yellowfin. This is similar to the findings of many previous studies (e.g. Josse, Bach, and Dagorn 1998; Musyl et al. 2003; Schaefer, Fuller, and Block 2009), but here these behavioural descriptions are quantified in terms of multivariate state distribution and state transition parameters.

The shallow state is typified by a spectrum of diving amplitudes and a narrow range of warm thermal habitat. From the results of the MANOVA analysis, it appears that this state distribution's multivariate mean is significantly different between species, in both depth variation and temperature. As almost all bigeye tag returns come from the central equatorial Pacific, differences in thermal habitat of shallow states may be due to differing epipelagic temperatures between this region and the western warm-pool, where the majority of yellowfin returns originate. For the yellowfin examined in this chapter, shallow states are centred on a mean temperature of 28.6˚C and a mean standard deviation of depth of 32.6m. For bigeye, the states are cooler, occurring at a mean temperature of 26.3˚C, and being slightly less variable, with a mean standard deviation of depth of 25.0m. Shallow state distribution means were identified as significantly different between the western warm-pool region and the central equatorial Pacific, possibly due to the former region having a thicker and more constant epipelagic layer (Lehodey 2001), through which tuna would move during their shallow state behaviour. Mean standard deviation of depth for all species was 35.7m in the western warm-pool, and 23.6m in the central Pacific region.

Compared to the shallow states, the relative deep states of yellowfin and bigeye were typified by higher diving amplitudes and colder thermal habitat. State distribution mean parameters were significantly different between species, region and quarter-of-release. In yellowfin, deep state behaviour was centred on a mean temperature of 24.8˚C and a standard deviation of depth of 46.9m. For bigeye, these values were 14.0˚C and 70.5m, respectively. The high standard deviation of depth in bigeye, representing larger amplitude of movement through the water column during deep state behaviour, is likely to be a result of the characteristic ascents linked to thermoregulation during movement at depth by this species (Holland et al. 1992; Maury 2005).

Behavioural states do not appear fundamentally different when they are examined at the finer-scale of one hour. State distributions have generally smaller variance-covariance matrices, suggesting that when the distributions are more variable under three-hour sectioning, this may be the result of state switching within a single three-hour period.

Behavioural switching between these two states is generally weighted in favour of time spent in shallow states, with the largest bigeye tuna examined here approaching an almost even proportion of time spent in each state. As apparent in the previous chapter, state switching is highly linked to diurnal changes in light across night and day. This light-driven switching is more pronounced in bigeye than in yellowfin, although considerable variation exists between individuals. The apparently sharp change in probability of state switching across light for bigeye should be considered with caution however, as the relative shallow and deep states for each individual are themselves more distinct in this species. Behavioural switching may simply be clearer in bigeye tuna compared to yellowfin, for whom shallow and deep state distributions have greater overlap.

Evidence for cooling thermal habitat with size of fish was seen in the results from HMMs estimated using predicted fork length as a covariate term within state distribution mean parameters. Few consistent patterns were seen in changing shallow state means. In addition, intra- and inter-annual changes in climate affect the temperature of the epipelagic layer, which has the potential to influence apparent changes in the thermal habitat of shallow state behaviours. Seasons experienced during time-at-liberty for each individual must therefore also be considered before interpreting the inconsistent patterns in changing shallow state thermal habitats over time.

Seasonal climate variations affect deeper waters differently, although large-scale climate events can vary the temperature of these layers of water alongside other potentially important drivers of behaviour such as dissolved oxygen (Le Borgne et al. 2011). A cooling of deep state habitat is seen in the results of this chapter for both bigeye and yellowfin. This is more pronounced between fish smaller and larger than around 80cm FL, although some individuals from both species show the opposite correlation in thermal habitat with size. In particular, the smallest sizes of bigeye around 65cm FL examined here may experience a non-linear deepening of thermal habitat. More data from fish at liberty during this period of growth are required to explore this further, but I hypothesis that this change may be driven by the development of the swim bladder and increased thermoregulatory ability with size.

Some of the bigeye tuna examined in this chapter may also exhibit a potentially distinct third behavioural state. This intermediate and transitory state consists of high levels of movement through the water column and variable water temperatures ranging between 15 and 20°C. It is not a persistent behaviour, meaning that the probability of more than a single three-hour observation classified as this state is unlikely. Furthermore, the state is more likely to follow a period of shallow behaviour. Given that shallow state behaviour is associated with the night-time, this state may the first diving behaviour at dawn, or after a morning spent at near the surface (Matsumoto, Kitagawa, and Kimura 2013a). It may represent an initial searching behaviour for patches of prey in the thermocline and mesopelagic layer after extended periods nearer the surface.

Care must be taken in ascribing meaning to this apparent transitory state. Although there appears to be some consistency across individual bigeye in the state’s occurrence, these intermediate states may simply be a composite of shallow and deep state behaviours that occur within a single three-hour time-bin. During the optimisation phase of parameter estimation, those observations that are neither clearly drawn from distinct shallow or deep states distributions may cause a “loose” intermediate state distribution to be estimated, when assuming a three-state model. This intermediate distribution may improve the likelihood estimation because it accounts for otherwise improbable observations. It is interesting to note that when examining the results from three-state HMMs estimated from one-hour binned summary metrics, less evidence for this transitory state was seen in bigeye tuna.

6.4.2 Data requirements and caveats

In this study, region and release-quarter were used as potential factors across which the results from HMM analyses were examined. However, despite the broad variability in tagged tuna within the PTTP database, in actuality this dataset represents a number of separate tagging experiments. Region is highly confounded with species, with most bigeye having been tagged in the central Pacific and most yellowfin in the western warm-pool, and release-quarter is related to these separate tagging events (Leroy et al. 2013). It is likely that a great many more tag returns are required to fully examine spatially and temporally co-varying factors that occur in the real world.

Despite the high temporal and spatial variability in the tag returns examined in this chapter, the similarity in two-state behavioural models for each separate species is clear. Although the addition of more tags will improve the accuracy of these analyses, it is encouraging that identified behaviours are consistent with both previous studies by other authors, and across the species and alternative analyses undertaken in this thesis.

The potential complexity of these models should also be re-iterated here. Although the two-state baseline analysis detailed in this chapter yields two clear behavioural states across individuals of the same species, higher state-number HMMs and analyses incorporating covariates may have complex likelihood surfaces. Results from the simulation experiments described above re-affirm the ability of the approach to recover true parameters when state distributions are clearly separated, but the effect of non-linearly changing covariate parameters can reduce this precision. If results from similar analyses examining these kinds of covariates, or results that specifically utilise estimated variance-covariance parameters, are incorporated into scientific advice, alternative and more robust optimisation algorithms than Nelder-Mead should certainly be explored.

Similarly, a more robust approach to parameter estimation should incorporate alternative methods to providing initial starting values and priors than the k-means based approach used here. HMM analyses incorporating covariate data into parameters in particular should be treated to alternative starting values before optimisation. A sensitivity analysis could then be carried out on an ensemble of model runs using these different prior assumptions, ensuring that the solutions of the optimisation algorithm are consistent and robust.

6.4.3 Fisheries implications and further work

The quantitative description and classification of yellowfin and bigeye tuna vertical movement behaviours undertaken in this chapter provides the means for a number of future analyses and implications for scientific advice to fisheries. Findings of broad importance to fisheries include the apparent differences in thermal habitat between species in both of their relative behavioural states. Although this is already established for deep diving behaviours, i.e. that bigeye occupy a much colder habitat than yellowfin when diving, there may also exist differences between the thermal habitat of yellowfin and bigeye shallow states within the epipelagic layer. Unfortunately, within this analyses there do not exist enough tag returns of each species across the western warm-pool and more eastern central Pacific regions to exclude the possibility of this apparent difference in thermal habitat being spatially driven.

However, quantified measures of thermal habitat have clear significance for catchability across fishing gears, and could also be used in standardisations of catch-per-unit-effort when data on depth of gears are available (Bigelow, Hampton, and Miyabe 2002). In addition, the evidence for size-dependent deepening of thermal habitat in both species has implications for the targeting of size-classes in longlining.

Although diurnal differences in the behaviour of yellowfin and bigeye have been described numerous times previously, the analysis of behavioural switching in response to light-levels given in this chapter provides a more general view of some differences between species. Although there is much variation between individuals, bigeye tuna show fewer tendencies to immediately begin switching behaviours when light-levels begin to increase. These results may suggest a longer period than previously assumed in the epipelagic layer after sunrise for some bigeye. Such behaviour would necessarily be linked to increased vulnerability to purse seine sets on FADs, the majority of which are made at and after dawn. It must be noted however, that light-level is not the same as time-of-day. The low-light levels of dawn may yield a very different pattern of behavioural switching in tuna than the low-light levels of dusk. Despite this, a further analysis of this light-driven behavioural switching over fish-size may reveal it as a potential cause of the recruitment overfishing that may be occurring in associated sets on small bigeye tuna (Bromhead, Foster, and Attard 2003; Morgan 2011).

Aside from the technical caveats with this approach, several improvements and follow-on analyses can now be undertaken. The simplest improvement that can be made is to expand the analysis using more tag returns from the WCPO and elsewhere, improving the modelling of consistent behaviours and providing more statistical strength to explore factors. In particular, examining the change in deep state thermal habitat from fish at liberty over 50-80cm FL would give more insight into potential impacts to surface gear vulnerability for these size classes. Similarly, more individuals at liberty across maturation should be analysed for potential changes in the nature or switching of behavioural states. The length at 50% maturity, L_{50}, is around 115 and 120cm FL, for yellowfin and bigeye respectively (Sun, Wang, and Yeh 2005; Zhu et al. 2011), which correspond to much larger size classes than the majority of tuna used in this analysis.

If new behavioural data become available, classification of new time-series may also now be undertaken with considerably less computational resources than the full model parameter estimations carried out in this chapter. Using the mean parameter estimates from this analysis for either species, or from some other grouping of interest, summary metrics from new data can be classified using the likelihood calculation defined by those parameters. Classified dive profiles would form a new time-series of data that probabilistically describe the observed vertical movement behaviours for an individual, on which meta-analyses can be carried out. These meta-analyses would aim to examine the behaviours actually observed in the time-series, given the assumptions of the HMMs used in classification, for the population of new individuals. The probabilistic nature of the classification allows periods of particular behaviours to be identified alongside a measure of confidence. These behaviours could include likely periods of extended surface behaviour, such as is believed to occur during FAD-association, or the probability of undertaking certain behaviours during the hours around dawn when fish are most vulnerable to purse-seine gears.

Now that a baseline set of described tropical tuna movement behaviours exists, in the next chapter I will return the some of the original questions of this thesis and undertake some of the meta-analyses suggested above. Using the classified time-series, individual-scale patterns of extended surface association and changing vulnerability to gears through the day will be undertaken, and incorporating the specific outputs of these results into analyses of population dynamics discussed.

Chapter 7: Tropical Tuna Behaviour from Small to Large Scales

In this final chapter, I will revisit the questions posed at the beginning of the thesis, and show how they have been answered through example meta-analyses and discussion. These will focus on the fisheries and population dynamics implications of the behaviour description and exploration that I have undertaken in this study. Finally, three avenues for future research that should lead from this work, across increasing time-scales, will be suggested and briefly discussed.

7.1 How are the movement behaviours of tropical tuna best explored and described in the context of interactions with fisheries?

In this PhD thesis, I have discussed some of the ways in which small-scale movement behaviours of tropical tuna can be described. In the literature review of Chapter Two, some mechanisms were identified as potentially important in the context of a pressing question in tuna fisheries, the impacts of fish-aggregation devices, and I presented evidence to suggest that residence behaviour of tuna species around FADs was one of the critical pathways by which these fish are exposed to modern fisheries. The foraging behaviours of schools of tuna upon the animals of the prey field were also shown to be potentially important to quantifying the vulnerability of tuna to fishing gears.

Given the difficulty in real-world behavioural experiments for these species, the use of a simple simulation model of the pelagic environment to explore the emergent behaviours potentially occuring around fish aggregation devices demonstrated how nature of the prey field and vertical movement behaviours can considerably affect simulated residence times and diet impacts given some simple assumptions about foraging. In particular, the ability to exploit more of the prey field through deeper habitat-utilisation, and the sensory dynamics of foraging on schools of prey was shown to greatly affect the vulnerability of tuna to purse-seiners using FADs in this simulation framework.

I then examined a wide range of real-world data on tuna movements, in order to examine which might provide a way to quantify or inform some of the assumptions in this theoretical model. Given the difficulties in measuring the prey field across the range of depths, areas and times that is required for comparison with such a model, I focused on examining the movement behaviours of tropical tuna themselves. After some preliminary analyses with a range of data and methods, I identified the classification and description of the vertical movement patterns contained in data from electronic tags to be an effective way of doing this.

Using real-world data from electronic tagging experiments to explore the dynamics of this vertical habitat-use presents a number of problems of statistical power and objectivity. The approach of compressing data from archival tags to time-series of summary metrics, and then using a multivariate extension of hidden Markov modelling, is a more objective and statistically sound method than has been previously used to classify the behavioural patterns identified in tropical tuna, matching the many probabilistic geolocation methods for describing horizontal movement from bio-logging data (Lam, Nielsen, and Sibert 2008; Patterson et al. 2008; Pedersen et al. 2008). Furthermore, the multivariate observation model can be changed in response to the types of data available and desired classification, and other covariate information can be incorporated into state distribution parameters or transitions. Here, I have focussed on vertical movement behavioural states that are defined in dimensions that relate to thermal habitat and mobility through the water column, because they related to a number of gear interactions that are critical in understanding exposure and catchability in tropical tuna fisheries. Purse seining requires that schools of tuna are located in shallow warm waters generally no deeper than 200m, and that their level of vertical movement is low before nets can set (Baird 2009), and is the dominant fishing gear set on FADs (Williams and Terawesi 2012). FAD-association increases efficiency of purse seine vessels by keeping tuna in exposed locations, both horizontally and vertically (Leroy et al. 2013), while association with particular depths or thermal habitats are related to hook depth and soak times in long-line fisheries (Campbell 2004). In particular, the behavioural space used in the estimation of the HMMs in this thesis can be said to represent a relative exposure to surface fishing gears such as purse seines (See Figure 7.1).

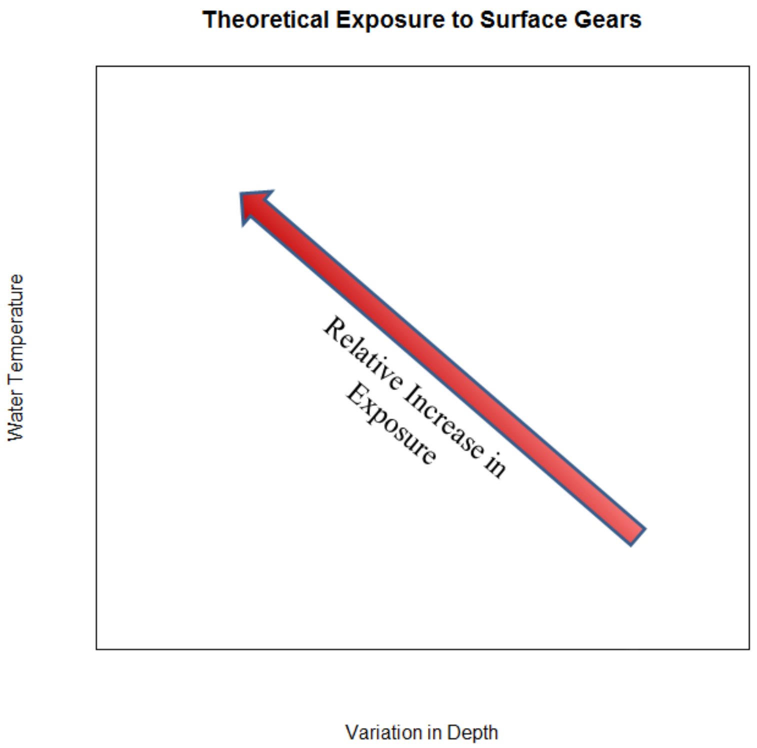

Figure 7.1 Relationship between the observation model used as the basis for behavioural states in thesis, and the assumed effect on relative exposure to surface gears

This same approach could be used for bio-logging data from any species that exhibits noisy and autocorrelated behaviours. For example, if dissolved oxygen data is available and is believed to be an important component in the behaviour of a species, it can be included as one dimension of the observation model. If lung capacity is believed to be a physiologically limiting factor in the diving behaviours of air-breathing animals, then submersion time can be included as a covariate parameter influencing the switching between potential foraging and surfacing states (McIntyre et al. 2011). Animals tagged with multiple bio-logging devices are also particularly well suited to this method. Seabirds equipped GPS and submersion recorders exhibit some clear behavioural patterns and dynamics in a multi-dimensional space that can be classified easily by using multivariate HMMs, for example (Dean et al. 2012; Hart et al. 2010).

For yellowfin and bigeye tuna, I have shown that the nature and switching of the two most prominent states within this two-dimensional behavioural space is remarkably similar within species. The estimated shallow and deep states are broadly consistent with many previous studies on the vertical movement of these species (Schaefer et al. 2015, Schaefer & Fuller 2010, Evans et al. 2008, Schaefer et al. 2007, Maury 2005, Holland et al. 1992). At the time-scale of hours, it appears that there is little evidence for more than two consistent movement patterns described in terms of vertical habitat-use and movement through the water column in these species. Even with only two vertical behaviour modes, the simulation model of Chapter 3 showed that a wide variety of emergent behaviours at longer time-scales were possible, dependent on environment cues such as the presence of FADs and the nature of the prey landscape.

In real tuna, shallow behavioural states centred in the warm epipelagic layer exist with many associated levels of movement through the water column, ranging from both high levels of oscillatory diving through to near constant occupation at a single depth. In contrast, colder behavioural states are always associated with high levels of movement through the water column, particularly in bigeye, which exhibit thermoregulatory ascents. There is no suggestion of a specific FAD-association type vertical behaviour at this scale, rather it is likely to be a continuation of the classified shallow state described by the HMMs built in this thesis (see below). Diurnal state switching is also clearly apparent and has been quantified in terms of both simple estimates of day and night periods, and recorded light levels from the tags themselves. Switching is, again, very similar across all species, and generally weighted in favour of time spent in shallow states.

7.2 What causes changes in these behaviours?

While the nature and switching of hour-scale behavioural states are fairly consistent across individuals, there is considerable variation in the dynamics of these behaviours through time at scales greater than the first order Markov dependence assumed in the behavioural models of this thesis. Beyond clear diurnal switching, the analyses of Chapter 6 have shown much individual variation in changes to deep state behaviours in bigeye during time-at-liberty. There is some evidence that this may be a general deepening of thermal-habitat with growth, but more tags at the edges of the size class limits offered by the PTTP are required to more accurately identify if this is a consistent process.

When the classified time-series are examined, however, we see remarkable variability in the actual occurrence of behaviours in comparison to the theoretical switching modelled by the Markov chain component of the HMMs. This can be explored across individuals by combining the classified behavioural states at different times of the day for all yellowfin and bigeye tuna examined in this thesis. This meta-analysis is distinct from the stationary distributions used to show the theoretical proportion of time spent in each state from the model transition parameters, but rather is simply the distribution of the most probable model classifications as are manifest in each actual time-series.

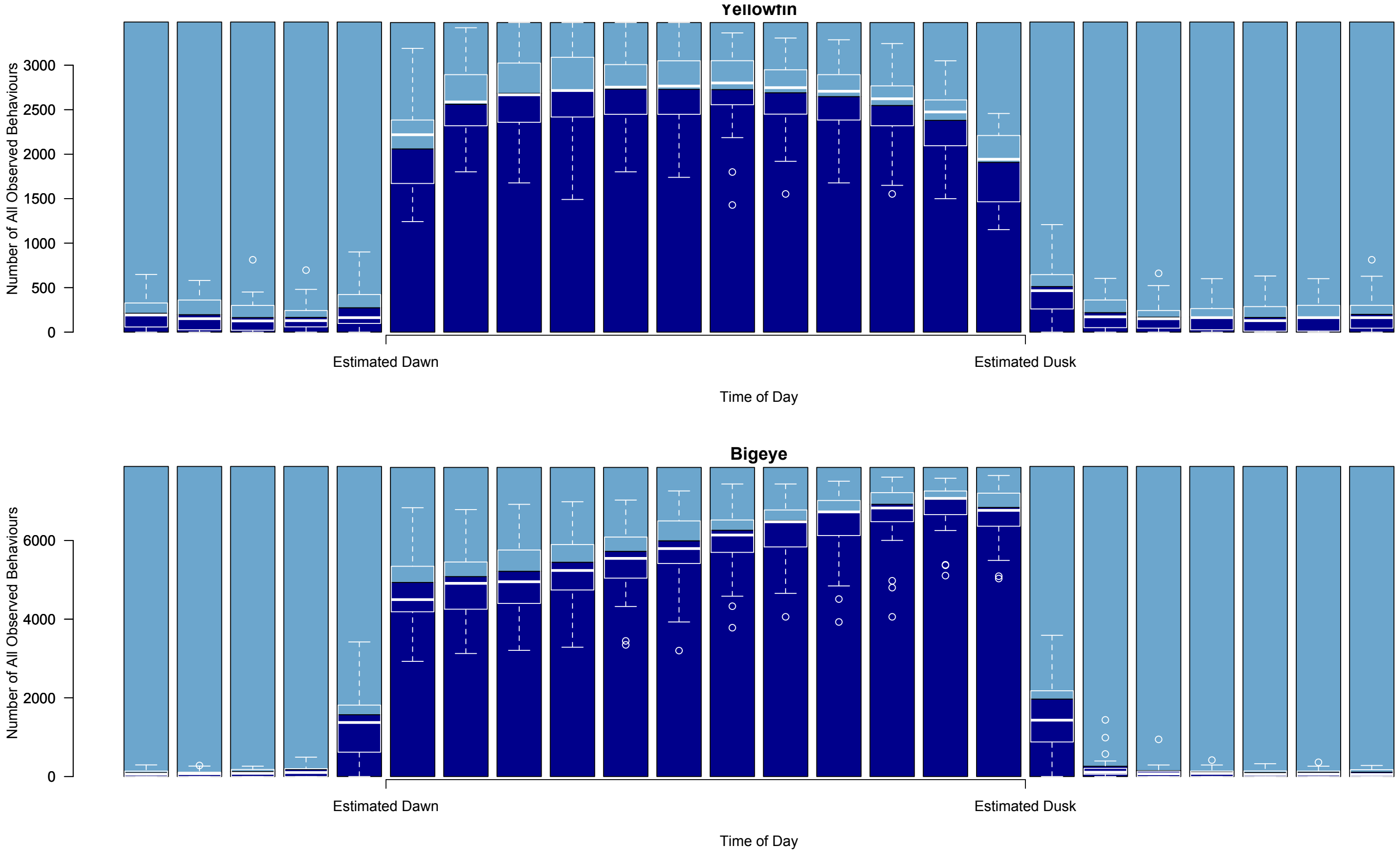

Figure 7.2 Histograms of observed shallow state (light blue) and deep state (dark blue) behaviours classified throughout the day at each one-hour time bins for all yellowfin (top) and all bigeye (bottom) combined. Overlaid are boxplots showing the spread of observed deep states between individuals.

Here I use the two-state HMMs estimated at one-hour intervals (N = 68), as presented in Chapter Six, to provide the observed behavioural states throughout a 24-hour day. At each approximate one-hour section of the day, the most probable state was used as the behavioural classification for that section. The frequencies of these observations were summed across each section of the day for all individuals, separated by species (Figure 7.2).

During the majority of the night, both yellowfin and bigeye tuna almost exclusively exhibited behaviours classified as shallow. The slightly greater number of deep behaviours observed during the night for yellowfin may be due to these deeper behaviours being in truth relatively shallow for some of these fish. Because “shallow” and “deep” are relative behavioural terms for each individual, the deep state of some yellowfin may be equivalent to a thermal habitat centred within the thermocline. Such movement through the thermocline may still occur during night-time hours.

A strong shift for both species occurs after dawn, although this is not surprising given the division of the dive track used in the data pre-processing stage of this method. It must be noted that the two approaches (split-moving window in Chapter Five and optimised dawn/dusk parameters in Chapter Six) used to section the archival time-series in this thesis both use marked changes in average depth to estimate dawn and dusk. These estimated crepuscular periods may not be the true dawn and dusk, but the behavioural dynamics around them provides a useful frame of reference for behaviour.

During the day there is a greater contrast between yellowfin and bigeye behaviours. Although it appears that yellowfin make a more sudden shift to deep-states at dawn, this is due more to the fact that for many yellowfin these behaviours are relatively shallower than for bigeye. It is likely that for bigeye the shift to deep behaviour simply takes more time and consists of more observations that could be considered either shallow or deep in the case of a two-state model, or one of the intermediate states identified in the three-state models of Chapter Six.

As daylight hours continue, bigeye tuna have a greater propensity to exhibit deep state behaviour, with most observations occurring in the hours preceding dusk. This would suggest that any uncharacteristic day-time surface behaviour by bigeye tuna is more likely to occur in the first half of the day than the second, corresponding to the consistent “afternoon diving” behaviour identified in Matsumoto, Kitagawa, and Kimura (2013a). Variation in observed behaviour also decreases as the day-time continues, indicating that this morning shallow behaviour is highly variable between individuals. In contrast, the yellowfin examined here display a more symmetric pattern of behaviour during the day, with the greatest observations of deep behaviour during the middle of the day and a higher chance of remaining uncharacteristically shallow in the hours after dawn and before dusk. Variation remains similar throughout the day-time.

The underlying mechanism for this variation in behavioural switching cannot be known given the available data, but may be a result of individual fish reacting to fluctuations in the local biotic environment such as availability of prey or density of conspecifics. The individual-based model of Chapter 3 demonstrated how stochasticity in predator-prey interactions can lead to large variation in the dynamics of emergent tuna behaviour, within the framework and assumptions of the simulation. Such stochasticity is likely to play a similar role in the intra-individual variability seen in the classified time-series here. Recent acoustic tagging experiments on tuna in FAD arrays also concluded that variability in individual behavioural modes at FADs might be much higher than previously thought (Robert et al. 2013). This greater propensity of shallow behaviour during the morning in bigeye may relate to searching for new aggregations of prey biomass following the descent of vertically migrating mesopelagic animals at dawn. As shown in the individual-based model of Chapter 3, sudden emptying of the prey landscape at dawn drives association to floating objects more strongly than at other times, and this may also be occurring for some of the bigeye tuna from the central equatorial Pacific examined here. The reasons that a similar dynamic is not present for yellowfin is not clear, although given the spatial factors that are different between the majority of the two species groups of these samples, these differences may be related to a different distribution of prey groups between the western warm pool region and the central equatorial Pacific.

Another approach to examining changes to the switching between two behavioural states can be made by identifying sequences of behaviours that are unusual, given the strong diurnal switching estimated in all the HMMs built on tuna data in this thesis. FAD-association itself is believed to cause a change in the dynamics of both horizontal and vertical behaviour of pelagic species. Despite the previously described uncertainties regarding FAD-associative behaviour, the established belief is that floating object association causes tuna to remain near the surface for extended periods of time. No consistent and separate vertical behaviour has been identified by the behavioural modelling I have undertaken in this thesis, and so it appears that FAD-association is typified by changes in state switching over a time-scale longer than hours. This can be examined and compared between individuals by undertaking a second meta-analysis on the HMM classified time-series.

Previous authors have characterised this FAD-association behaviour as an individual remaining shallow during the day-time when it may otherwise be exhibiting characteristically deeper behaviours. This belief has come from the observation of schools of tuna aggregating beneath FADs during the day, and from fish implanted with acoustic tags and therefore known to remain shallow during the day-time in the local vicinity of acoustic receiver-equipped FADS (Leroy et al. 2010; Schaefer and Fuller 2013). In bigeye tuna in the eastern Pacific, this type of associative behaviour has been identified from bio-logging time-series that show extended periods of shallow behaviour, which do not include the characteristic U-shaped day-time diving of this species. Periods of time where fish exhibit associative behaviour can be manually identified from these unusual day-time behaviours. Alternatively, classification can be quantified by selecting periods of time when an individual spends more than a particular proportion of the day above a given isotherm (Schaefer, Fuller, and Block 2009; Schaefer and Fuller 2010).

Here, a similar meta-analysis of the dynamics in tuna behaviour through time can be undertaken using the baseline two-state HMM classifications from the previous chapter (which contained no covariate information affecting the nature or switching between behavioural states, and assumed a three-hour timescale for behavioural description) in relation to these “surface-association” behaviours with floating objects. This approach is different to previous studies in the dynamics of surface-type behaviours in two key ways. First, the identification of associative periods is objective and automatic, using the HMM classified time-series. Second, here the degree to which an individual fish exhibits surface-association behaviour is defined as the rolling mean across 8 time-steps (24-hours, at three-hour time-steps) of shallow state probability. If a fish were undertaking “characteristic” diurnal switching, remaining relatively deeper during the daytime than at night, we would expect this surface-association probability to remain around 0.5. If behaviour switched to that typically assigned to association with a floating object, with the fish remaining in the epipelagic layer throughout both day and night, the probability of surface-association would be close to 1. Varying strengths of surface-association behaviour are therefore represented by values between 1 and 0.5 (and example is given in Figure 7.3). Continual deeper states, such as 24-hours spent exhibiting thermocline-centred behaviours in yellowfin, are represented by values less than 0.5.

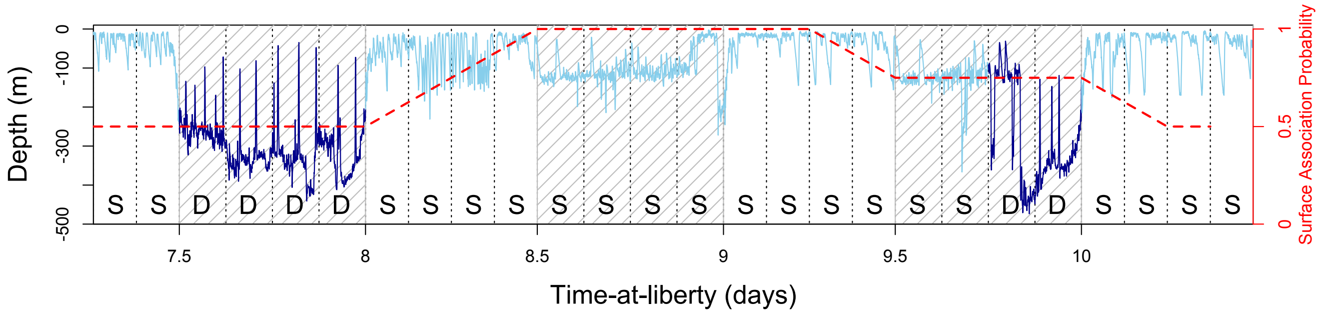

Figure 7.3 Example dive track, with individual three-hour sections classified into either shallow or deep state behaviours and coloured differently. The rolling 24-hour probability defining surface-association is shown in red through time.

A period of surface-association can therefore be classified for points in the time-series at which the probability exceeds a given threshold. To examine the occurrence of surface-associations across a range of threshold values, summary statistics were calculated from each time-series, assuming threshold probabilities of 0.95, 0.9, 0.85, 0.8, 0.75 and 0.7. Where data allowed, I also calculated surface-association summary metrics in relation to known events at release and recapture. Estimated surface-association events at release were defined as surface-association probabilities that rose above a threshold beginning within the first 24 hours after tagging and release, and then continued for some period of time. Estimated surface-association events at recapture were similarly defined as events that finished rising above a threshold within the final 24-hour rolling mean window before capture. The length of such events was compared across individuals. Finally, the mean surface-association probability during the first and last 24-hours of the time-series was compared to the mean for the entire time-series. The surface-association probability through time, alongside any known school behaviour at release and recapture, is shown for all fish in Figure 7.4. Summary metrics across assumed threshold probabilities are given as linear boxplots for all bigeye and yellowfin (Figure 7.5).

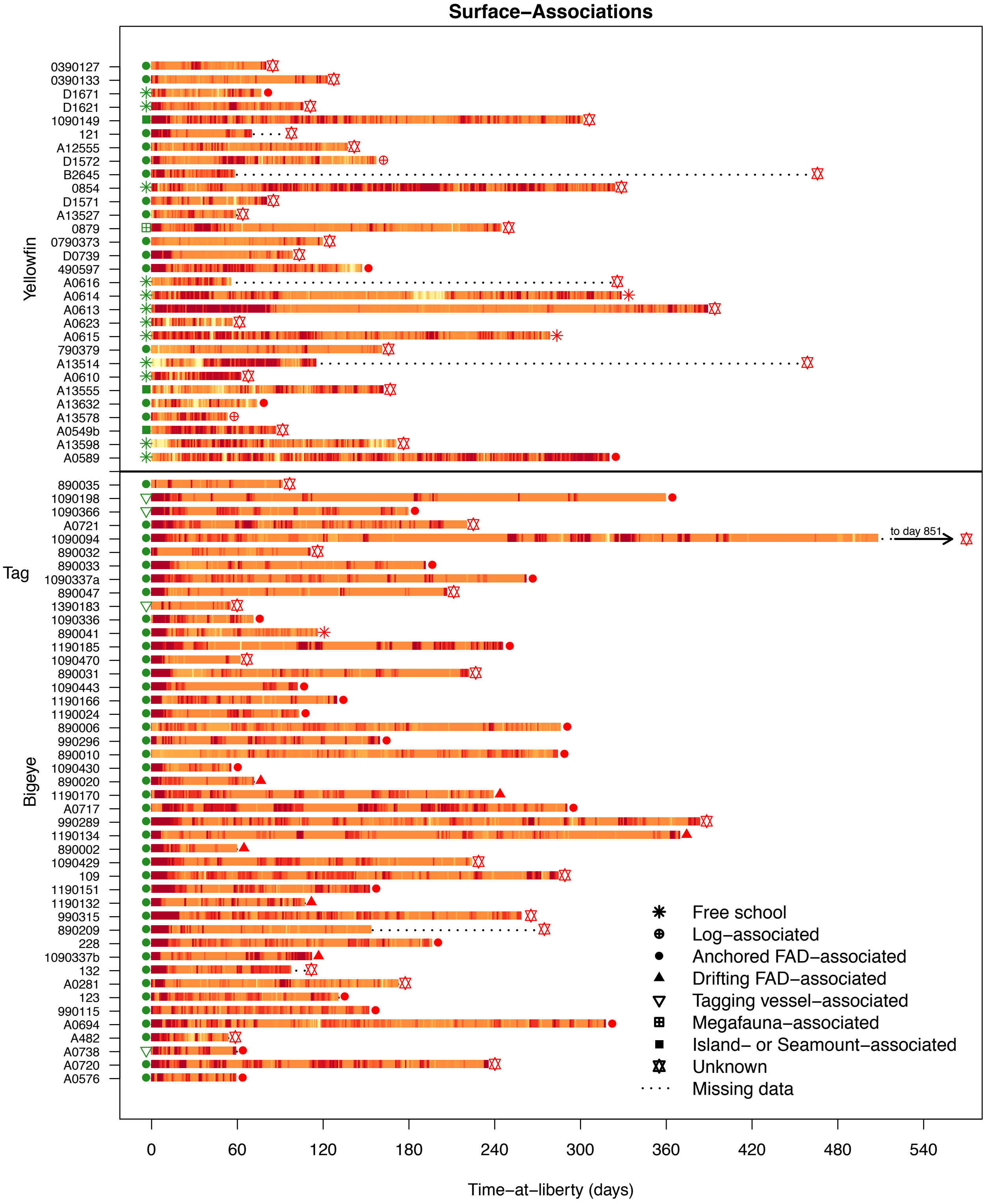

Figure 7.4 Surface-association probabilities for all fish, ordered by species and length-at-release (bottom to top). Dark red periods indicate high surface-association probability (≈1), orange showing probability of more characteristic switching behaviour (≈0.5).

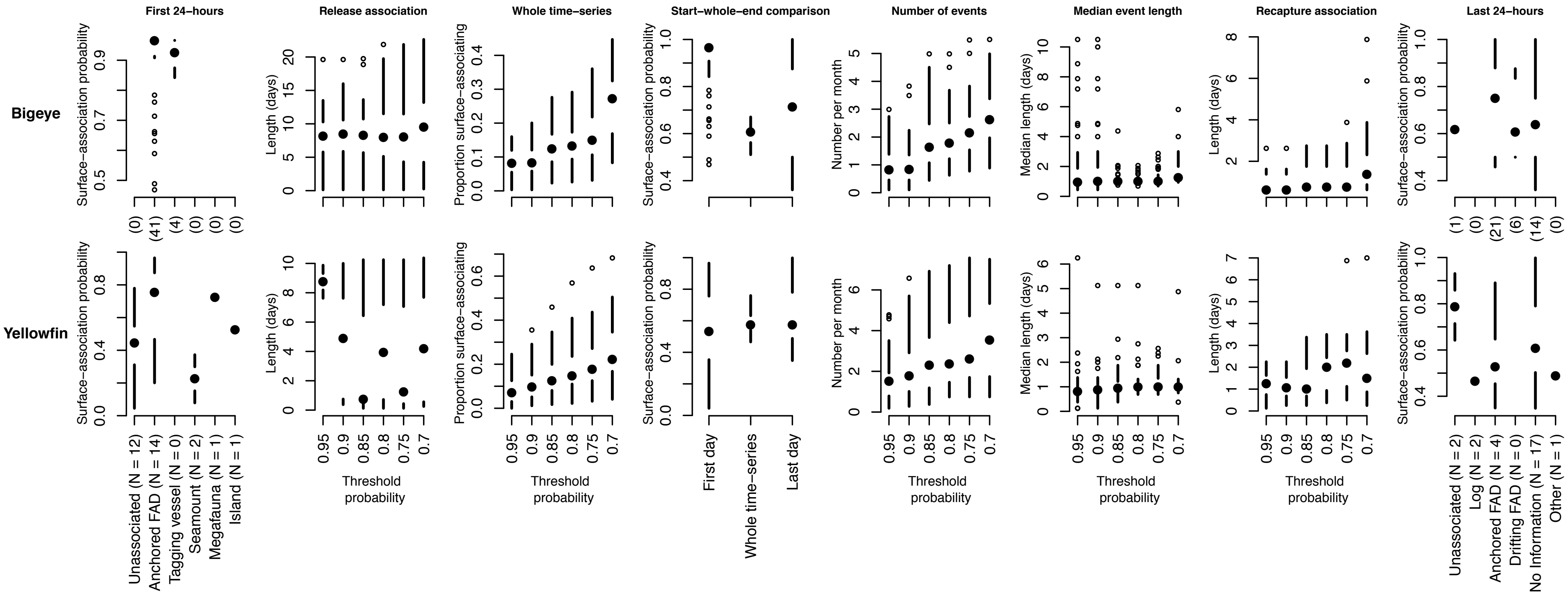

Figure 7.5 Summary metric boxplots of surface-association occurrence for bigeye and yellowfin. From left to right: surface-association probability during the first 24 hours by school behaviour at release; length of the release association for those fish that exhibited one across threshold probability used for classification; proportion of whole time-series spent surface-associating across threshold probability; surface-association probability comparison between first 24-hours, the entire time-series, and the final 24-hours before capture; the number of separate surface-association events across threshold probability; the median surface-association event length for each fish across threshold probability; the length of capture associations for those fish that exhibited one, across threshold probability; and the surface-association probability during the final 24-hours across school behaviour at capture.

Consistent and often long periods of surface-association were present at the start of the time-series for the majority of central Pacific bigeye tuna, all of which were released at anchored Tropical Atmosphere Ocean (TAO) buoys or while associated with the tagging vessel. The first 24-hours after release showed very high levels of surface-association for the majority of bigeye individuals, compared to the mean value for the entire time-series. Some yellowfin tuna released in the western warm pool also showed long periods of surface-association near the beginning of their time-at-liberty, despite being released into schools displaying a wider variety of behaviours. Of particular note is YFT A0613, which was released into a free school south of New Britain in Papua New Guinea. Despite this region being of low FAD density, this individual exhibited over 80 days of near continuous surface-association beginning around three days after release. The mean probability of surface-association during the first 24-hours after release was comparable to the mean probability during the whole time-series.

For the actual surface-association events that occurred immediately following release (release associations), there were differences between the two species of tuna. Assuming a 75% threshold probability, 38 of the 45 bigeye examined here had release associations, and for 29 fish this event was the longest surface-association observed during their entire time-at-liberty. The mean time of these associations for bigeye was 8.6 days, with a standard deviation of 5.8 days, when assuming an 75% threshold probability. The length of release associations did not change significantly across different threshold probabilities. Although the true length of the association period is unknown, as it also includes time before tagging, these first association events are far longer than the median event length and among the longest recorded in the time-series for many fish. For 38 of the 45 bigeye examined in this thesis, tagging and release occurred at anchored TAO buoys that have been in place for many years, and appear to exert a strong association effect that was clear. These results are similar to the initial release FAD-residence reported for bigeye in Matsumoto et al. (2013a) (mean residence time = 8.3 days, 8.6 days here).

Release associations in yellowfin were much more varied across different values of threshold probability. 11 fish exhibited surface-associations immediately prior to release, assuming a threshold probability of 75%, and this release association was the longest in the time-series for 4 of these individuals. The mean length of this release association was 3.9 days, with a standard deviation also of 3.9 days, although the data were much more positively skewed at this threshold. In contrast, the range of association behaviours at release were much more varied in this sample of yellowfin, and this was reflected in less consistently strong surface-association events at release with known floating object locations. Furthermore, although some individuals exhibited a long surface-association after being released at anchored FADs in the western warm pool, for many of these FAD-associated fish this event was short or even non-existent following release. The strong spatial bias in this sample of fish prevents us from drawing definite conclusions about this being a species-level effect. However, given that any anchored FADs of the Bismarck Sea and coastal Solomon Islands are unlikely to have been deployed for the same amount of time as the TAO buoys in the equatorial Pacific, and also reside in a region of much greater anchored FAD density dominated by archipelagic waters and seamounts, it may be that this habitat causes a more diffusive effect on floating object associations. The mix of surface-association behaviour exhibited by those yellowfin released into free schools suggests that at least some of these surface-association events may not be the result of floating-object association. The release location of several of these free schooling yellowfin, the coastal region of south of New Britain, is an area with few known anchored FADs arrays, and yet these fish still exhibit clear, and in some cases extended, surface-associations.

7.2.1 Surface-association throughout time-at-liberty

During time-at-liberty, a wide variety of patterns in behaviour were seen between all individuals. Many central Pacific bigeye exhibited clear surface-association events interspersed between sustained periods of characteristic diurnal shallow-deep switching behaviour. For some individuals, several short surface-associations occurred in groups (e.g. BET 89006), and few individuals exhibited extended periods of surface-association that were more interspersed between characteristic behaviour (e.g. BET 990115).

The distinction between surface-association and other behaviour was less clear in yellowfin from the warm pool. For the majority of these fish, periods of surface-association occurred as many brief events interspersed with more characteristic diurnal switching behaviour. For a small number of yellowfin the opposite was true, as they exhibited very long periods of surface-association broken up with very brief periods of switching behaviour (e.g. YFT 0854).

For the actual length of separate surface-association events, the distribution varied for each individual, and was positively skewed in most cases. Most events for each individual were short, with a smaller number of long, consistent surface-associations also occurring. When grouping the medians event length for all individuals, the distribution of these medians was also slightly positively skewed for both species, although the there was not much variation for the majority of individuals. The median of grouped median event lengths was 1 day for both species, assuming a threshold of 75% for surface-association classification.

7.2.2 Surface-association events at recapture

The period of time immediately preceding capture was also varied between individuals. Surface-associations existed prior to capture for some fish (capture associations), although these were rarely as long as those exhibited at release. Many individuals showed no signs of surface-association prior to capture. When they did occur, capture associations were very different to release associations. The mean probability of surface-association during the 24-hours prior to capture was varied. For many bigeye, this probability was higher than the mean during time-at-liberty. For yellowfin, the final 24-hours at liberty were comparable to the mean during the entire time-series.

Due to the low quality of school-association behaviour at recapture, comparisons between tag-derived surface-associations and the school-association observed at capture were difficult. For 21 bigeye believed to have been caught at anchored FADs, surface-association probability during the final 24-hours at liberty was varied, but generally higher than the mean during time at liberty. The 6 bigeye believed to have been caught at drifting FADs, this probability was comparable to the mean during time-at-liberty. Information on school behaviour at recapture for yellowfin was so poor that I refrain from describing the patterns in surface-association probability here.

7.2.3 Implications

While the behaviour typically assumed to be linked to FAD-association is a clear and sustained residence near the surface, this meta-analysis has shown that exhibition of a more broadly defined surface-association behaviour is highly variable across individual fish. Despite the great many spatial and temporal differences in local stimulus likely experienced by each fish, the proportion of time spent exhibiting surface-association behaviours were very similar between yellowfin tuna released predominantly in the western warm pool, and bigeye tuna released in the central equatorial Pacific. When compared to proportion of time spent exhibiting associative behaviour in previous acoustic tagging experiments of yellowfin tuna at liberty within arrays of anchored FADs, the times of the events that I describe here were much shorter. Even assuming the less conservative threshold probability of 75%, the yellowfin examined here spent only 18% of their time exhibiting surface-associations, which is considerably shorter than the proportions of 60% reported by Ohta and Kakuma (2004) and 64% reported by Robert et al. (2012). Our results for both species are closer to the proportion of time exhibiting association behaviour reported by Matsumoto et al. (2013a) for bigeye in the north-western Pacific (13%), Schaefer and Fuller (2010) for bigeye in the equatorial eastern Pacific (9%-19%), and Schaefer et al. (2009) for yellowfin (10%) and bigeye (16%), also in the equatorial eastern Pacific.

The number and length of events was different between the two groups of tuna, with yellowfin in the western warm pool region generally having a greater number of short surface-association events and bigeye having a slightly lower number of longer events. However, despite the greater plasticity in switching to surface-behaviours in yellowfin, the highly skewed distribution in the length of individual surface-association periods within the majority of time-series indicates that there may be two different behavioural modes for both species: a more common short association with the epipelagic layer, and a less common extended association. Previous acoustic telemetry experiments have suggested that tropical tuna known to be associated with receiver equipped FADs have multiple modes of differing residence time (Robert, Dagorn, Filmalter, et al. 2013), and residence times and number of known FAD-association events have varied greatly across previous studies, even for the same region (Robert et al. 2012). Although an inappropriate assumption, if the surface-associations that have been identified in this chapter are taken as representing association with drifting or anchored floating objects, the residence times are considerably shorter than many older studies (Ohta and Kakuma 2004; Dagorn et al. 2007), and even slightly shorter than more recent studies that have suggested assumed residence times should be re-considered (Schaefer et al. 2010; Robert et al. 2012; Schaefer et al. 2013). In actuality, it is possible that some of these short surface-associations may represent other behaviours such as periods of active horizontal relocation (Schaefer et al. 2015), spawning (Evans et al. 2008), opportunistic feeding (Fernandez & Allain 2010) or some other unknown behaviour.

Although this analysis of surface-association behaviours reveals great variation in vertical movement behaviours, it remains impossible to say which surface-association events identified here are related to FAD use by tuna, outside of identified FAD-associations at release and capture. From these known release and capture events, and from the increase in surface-association behaviours in yellowfin in the Bismarck Sea region, it can be said that at least a moderate proportion of these surface-association events represent likely FAD-associations. The long residence periods at the beginning of bigeye tuna time-series released at TAO buoys are typical of the types of known FAD-associations observed in previous studies (e.g. Ohta and Kakuma 2004, median residence time = 7 days, 8.1 days here). However, the short duration of many surface-association events suggests that this may not be such a common form of FAD-association. Fish briefly visiting FADs, travelling between FADs in an array, or associating non-continuously with frequent excursions away which are coupled to more characteristic vertical movement behaviours, appears much more typical, particularly for the yellowfin from the western warm pool examined here. This type of FAD-use by tropical tuna has also been suggested in a number of previous studies that have described associative behaviour in tuna within FAD arrays near island masses (Holland 1996; Dagorn et al. 2007; Leroy et al. 2010). In addition, some of the prolonged surface-associations in yellowfin observed here are clearly linked to time spent in archipelagic and neritic regions. Such a coastal effect has potential implications for the many acoustic telemetry experiments that have studied FAD-association behaviours of yellowfin and bigeye tuna within coastal arrays of anchored FADs (Ohta and Kakuma 2004; Dagorn et al. 2007). It may be hypothesised that, while floating objects may concentrate tuna horizontally at local scales, the island effect on changes to vertical behaviour may be present at larger spatial scales, regardless of the density of floating objects in the region.

7.3 What are the likely implications of these findings on the small-scale movement behaviours of tropical tuna to their larger-scale population dynamics?

The quantitative methods of description and classification of yellowfin and bigeye tuna vertical movement behaviours developed in this thesis provides the basis for a number of future analyses and implications for scientific advice to fisheries. Findings of broad importance to fisheries include the apparent differences in thermal habitat between species in both of their relative behavioural states. Although this is already established for deep diving behaviours, i.e. that bigeye occupy a much colder habitat than yellowfin when diving, there may also exist differences between the thermal habitat of yellowfin and bigeye shallow states within the epipelagic layer. Unfortunately, within this analysis there are insufficient tag returns from each species across the western warm pool and more eastern central Pacific regions for us to exclude the possibility that this apparent difference in thermal habitat is driven by spatial differences in the temperature of the epipelagic layer (Evans et al. 2008).

However, quantified measures of thermal habitat have clear significance for catchability across fishing gears, and could be used in standardisations of catch-per-unit-effort when data on depth of gears are available (Bigelow, Hampton, and Miyabe 2002), or to improve habitat indices in spatial models of distribution (Lehodey et al. 2008). In addition, the evidence for the size-dependent variability of thermal habitat in both species has potential implications for the targeting of size-classes in longlining. CPUE is often used as a relative index of population abundance in both simple and integrated stock assessment models, assuming the proportion of the population caught by a single unit of fishing effort, the catchability, remains constant. This assumption is rarely the case, and so CPUE is usually standardised using a number of explanatory variables that are believed to have affected catchability throughout the time-series (Campbell 2004; ISSF 2012). These variables typically include size- or age-classes of the caught fish, different fleets, periods of time between significant changes in gear technologies, and regions or habitat indices. Also included in some CPUE standardisations are environmental variables or more detailed gear and fishing information (Campbell 2012; Maunder et al. 2006), both of which aim to capture some assumed effect on the exposure of fish to fishers.

The vertical movement behaviours of tropical tuna necessarily have a direct relationship with their exposure to fishing gears (Bigelow, Hampton, and Miyabe 2002). The quantification of these behaviours across factors such as size allows incorporation of previously qualitative behavioural notions into these types of analyses. For example, it would now be possible to use the HMM-estimated distributions of thermal habitat in different behavioural states as variables to explain variation in longline CPUE, structured by fish size-class. Similarly, the distribution of observed behaviours during the course of a 24-hour day given earlier in this chapter could be used alongside time of fishing for the same purpose.

The estimated parameters from the HMM models estimated by this work can also be used to inform other mechanistic models that predict or examine a system at higher ecological scales. In this context, mechanistic models assume that processes at the organismal level, or equivalent, are important at governing the emergent behaviour of the ecological system. This is in contrast to phenomenological models, which seek to predict future observations of a system by correlation with some explanatory variables, assumed to adequately sample the causal pattern of interest (Koehl 1989).

In fisheries, mechanistic models can relate to stock assessment, but they can also be simple models which aim to increase our understanding of how a system works (Schoener 1986). For example, in Chapter Three an expressive but un-fitted individual-based model was constructed to examine the effect of diving ability on emergent residence time at FADs, as well as other factors such as diet. While this model broadly replicated some patterns seen in association with FADs by tuna, many of the parameters had little basis in quantitative observation. In particular, the division of the ocean into distinct layers and the dive probabilities of the artificial tuna appear particularly suited to updated parameterisation from the results of this thesis.

From the tropical tuna examined here, it appears that the division of the ocean into three distinct habitats is as a sound assumption. The thermal habitats of the estimated behavioural states in Chapter Six suggest that both yellowfin and bigeye occupy a very similar range of habitat in the epipelagic layer, but separate out into two distinct groups when these species exhibit their deepest behaviours. This thermal habitat appears more varied for yellowfin, although due to the depth being focused within the thermocline where the temperature change is greater per meter moved, this is not surprising. Probabilities of switching between these thermal habitats can be directly incorporated from the parameters of the HMMs.

The analysis of change in state distribution means by size (also in Chapter Six), suggested that the smaller class bigeye might have deep state thermal habitats that are similar to those of yellowfin. If bigeye of these size-classes are as yet unable to exploit deeper layers of water, it may leave them more vulnerable to the influence of floating objects, under the assumption that FADs act as potentially false indicators of productivity. This was demonstrated in the theoretical model of Chapter Three, and the resulting potential for recruitment overfishing for this stock is a critical concern in current fisheries management (Davies et al. 2011; Morgan 2011). Similarly, the surface-association behaviour defined and identified from extended and high probability surface behaviour shows that diel shifts in depth and periods of deep state behaviour can still occur during these events. These surface-associations provide an alternative source of patterns than acoustically tagging fish, with which to compare potential FAD-association or other extended surface periods from the IBM of Chapter Three.

Other, more complex mechanistic models also exist for use in providing scientific advice. APECOSM (Apex Predators ECOSystem Model, Maury 2010), is a community structured, dynamic energy budget model that aims to incorporate a number of functional relationships that impact marine populations. Organisms in the model are divided into trophic groups that occupy different layers of the water column and in some cases are capable of vertical migration. The vertical behaviour of key predator species, in this case tropical tuna, are modelled by distinct equations that govern switching between different feeding behaviours on the biomass of these functional prey groups, based on simulated energy and physiological requirements. Simulations have successfully replicated a number of broad behavioural patterns in bigeye tuna, including day/night changes in behaviour and thermoregulatory ascents (Maury 2005).

Such models of vertical behaviour are of course driven by mechanisms that are not included in the models estimated in this thesis. However, aside from potentially constraining the parameterisation or structure of mechanistic models, the approach of estimating HMMs on multivariate time-series provides a way to generate relevant behavioural observations that can be compared to those models that provide output at a similar scale. As an example, if depth, water temperature and internal body temperature are the key inputs in the physiologically-driven behavioural model of APECOSM, a three-dimensional multivariate HMM can be built on these data from real tuna at the same time-scale. The nature and switching of different states within this behavioural space can be used to fit or evaluate the parameters of the mechanistic model.

Another recent model used for scientific advice to tuna fisheries is the SEAPODYM model (Lehodey, Senina, and Murtugudde 2008). This model simulates population dynamics of tuna-like species via bottom-up, ocean bio-geochemical forcing, and can be fit to a variety of assimilated fisheries data. In this sense, it is a phenomenological model in its predictions, but contains a number of mechanistic components drawn from the current understanding of tuna behaviour. These include both vertical and horizontal habitat preferences, based on the believed physiological capability of different species and the abundance and distribution of lower trophic level prey. In the case of vertical thermal-habitat preferences, these are defined by a normal distribution with a mean that decreases linearly with length and a standard deviation that increases linearly with weight (see Figure 7.6). This mechanism is based on the assumption that tuna will search for an optimum intrinsic temperature regardless of age, but that as size increases, they will require residence in colder water due to a higher steady state temperature and will be capable of greater changes in vertical habitat due to the thermal inertia (Holland et al. 1992).

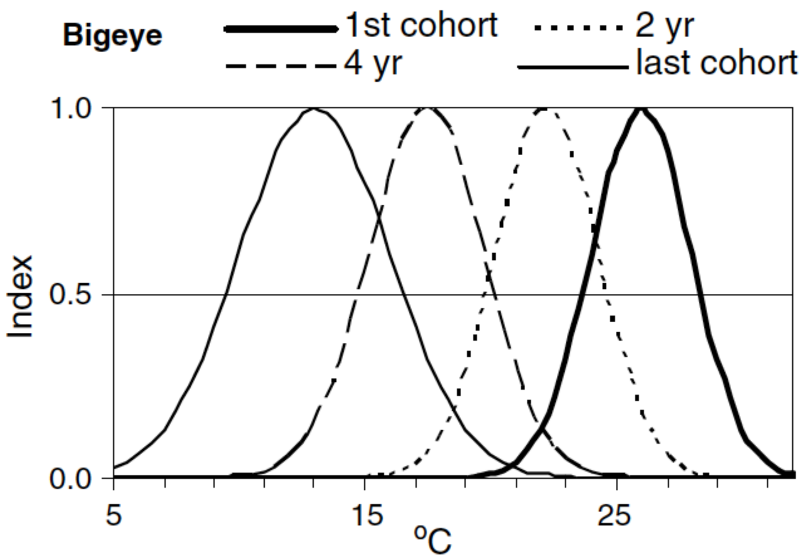

Figure 7.6 Example of changes in thermal-habitat indices for different age-classes of bigeye tuna, taken from Lehodey et al. (2008).

From the results of this thesis, vertical movement is clearly much more complex than this mechanism. It includes dynamics such behavioural switching, non-constant patterns over time, and potentially non-linear relationships between these behaviours and size. Many of the parameters estimated in multivariate HMMs of bio-logging time-series can directly inform this component of SEAPODYM. The behavioural state distributions have estimated means and variances in the water temperature dimension, and in Chapter Six a relationship to describe how these state means vary with size of the fish was calculated, showing some evidence that it may be non-linear. Alternatively, multiple behaviours and transition probabilities could replace this simple model of habitat preference altogether, incorporating probability and variation of switching between thermal-habitats directly.

The degree to which FAD-association affects tuna vulnerability to fishing, and more broadly if they constitute an ecological trap, has been discussed many times in this thesis and elsewhere (Bromhead et al. 2003; Hallier & Gaertner 2008; Dagorn et al. 2013). Although we cannot make definitive statements about when during archival tag time-series FADs may have influenced the individual tuna in this work, the high variability both within individual time-series and between individual fish indicates that these surface-association periods are likely to be driven by number of local influences that include factors other than floating objects. Throughout the work of this thesis, the importance of the local-scale environment and prey field on the movement behaviours of tropical tuna has been stressed. The simulation model of Chapter Three showed how relatively minor changes to the prey field can result in very different emergent system properties at other scales (such as time spent around a FAD). Furthermore, while fairly consistent behavioural states were estimated with the quantitative methods developed in chapters five and six, it is clear that temporal dynamics are highly variable. Recent acoustic tagging experiments on tuna in FAD arrays also concluded that variability in individual behavioural modes at FADs might be much higher than previously thought (Robert, Dagorn, Filmalter, et al. 2013). This stochasticity is likely due to reactions by the individual or school to local stimulus.

Given the high variability in exhibited surface-association behaviours, alongside the likelihood that small-scale interactions with the prey field play an important role in determining the motivational states, it may be concluded that at least some of this stochasticity may be due to fluctuations in the prey field. The diet of tropical tuna is highly varied and based on opportunistic predation (Bestley et al. 2010; Bromhead, Foster, and Attard 2003). This makes it difficult to form a link between the apparent stochasticity in observed behaviours, and any potential data on changes in prey adundance. However, the variability in observed surface-associations at known points of FAD-association (i.e. release and capture) still precludes us from identifying a single, definitive FAD-driven surface-association behaviour. If FADs act as ecological traps, it is by modifying the perceived habitat selection process in tuna and other pelagic animals, causing them to remain in potentially unfavourable areas that they may otherwise have left (Hallier & Gaertner 2008, Dagorn et al. 2010). It is impossible to truly test this hypothesis here, due to knowledge gaps in the local environment experienced by this sample of fish, but the results of this thesis do have implications for our understanding of FAD-gear interactions for these tuna. There is a horizontal component and vertical component in the aggregative effect of FADs, both of which influence the potential vulnerability to surface fishing gears. To varying extents, floating objects appear to bring tuna to a locality in horizontal space and then aggregate them near the surface for longer than normal periods of time, where they become more vulnerable to purse seine capture. Here, I have focussed on the vertical component of this behavioural impact and the surface-association events I have identified in this chapter vary greatly, both at the inter- and intra-individual level. Some events are prolonged and result in capture, but the large majority do not. Although examination of these behaviours over a greater range of size-classes is required before any potential ontogenetic propensity for surface-association can be dismissed, it appears that there are few patterns to this behaviour in bigeye and yellowfin tuna. At a general level, exhibition of this behaviour occurs for a very similar proportion of time for all the fish examined here (around 15%), which were at liberty across a wide range of seasons, geographic locations and regions of FAD-density. Therefor, I suggest that there is little evidence to suggest that the use of FADs greatly increases the vertical component of vulnerability to purse seine capture. Furthermore, if FAD-association is assumed to always involve surface-association (although the opposite appears not to be true), then it appears that in oceanic environments sustained FAD-association is not common.

If the vertical component of FAD-association is not regularly retaining tuna for long periods of time near the surface, then it is the concentration of fish in the horizontal plane that is driving an increased efficiency for purse seine vessels in locating schools. Here I have shown that similar behaviours occur in archipelagic waters where interactions between fish and natural floating objects or coastal regions are likely to be common. Management measures that seek to limit the other impacts linked with FAD-associated sets, such as altered catch composition or bycatch, should therefor seek to control overall fishing effort on floating objects. Banning the use of FADs for particular regions or seasons simply results in shifting effort from one place or time to another with little impact on the catch or the number of sets made (Pilling et al. 2013), and if the large majority of residences at floating objects by tuna are moderately short then there is little evidence to suggest that their biology, movement behaviours or entrainment to a region are being significantly affected by an increased density of FADs (Dagorn et al. 2013).

7.4 Future Research

The findings of this thesis suggest a number of further avenues of research in understanding the movement behaviours of tropical tunas in the context of Pacific fisheries. Here, I briefly discuss three areas in which future effort should be made across increasingly large time-scales, from pressing analytical studies which could be carried out immediately, to the development of new large-scale models and implementation of region-wide conservation measures.

7.4.1 Extended and Population Level Analyses

In the future, the number and quality of bio-logging experiments is going to increase. Not only are current WCPO tagging programmes going to result in increasing returns of archival tags similar to those I have examined in this thesis, but many other tagging programmes exist for tropical tuna species in other parts of the Pacific (e.g. Block et al. 2003; Schaefer et al. 2015). New and cheaper bio-logging technologies are becoming available, such as geomagnetic sensors that aid in horizontal geolocation and pop-up dart-tags that allow a single accurate GPS location to be registered alongside implanted archival tag data. Bio-loggers are becoming smaller, meaning that smaller individuals can be tagged to fill the gap in our understanding of the behaviour of these size classes.

Given the likely increase in data that will occur, and the vertical movement time-series of tropical tuna species that already exist outside of the PTTP, the description and classification analyses of Chapters Five and Six should be continued with data from more tags. Although there have been a wide variety of release locations for tags in the PTTP, they can generally be divided into three regions: the open-ocean central Pacific, the archipelagic waters of the Solomon Sea, and the anchored FAD-dense Bismarck Sea. However, many other electronic tagging experiments have been carried out in regions such as the Hawaiian Islands (Brill et al. 1999; Musyl et al. 2003), south-western Japan (Matsumoto, Kitagawa, and Kimura 2013a, 2013b), and the eastern equatorial Pacific (Schaefer and Fuller 2004, 2010). If these tags could be combined with the data used in this thesis, a clearer description of species level behaviour would be attained. In particular, the analysis of size-dependent differences in deeper state behaviours would benefit from more individuals.

The meta-analyses of this chapter should also be continued and expanded as more data becomes available. The stark differences in surface-associations between individuals should be examined further as a priority. Although it is impossible to know whether these events are true floating object associations or not, we do know the school behaviour at time of release and, in many cases, recapture. Patterns of surface-association during these known periods of free-schooling, anchored FAD-association and drifting FAD-association should be explored. Similarly, the dynamics surround surface-association events should analysed to identify if these periods of behaviour occur and cease suddenly, or whether they gradually develop over a period of time.

Despite the general poor quality of light-based geolocation at low-latitudes (as discussed in Chapter Two), an investigation of combining classified vertical behaviours using the approach of this thesis alongside the best track estimates and error margins of current geolocation methods should be undertaken. Not only would this provide estimates of where a fish is when surface-associations or other vertical behavioural patterns are occurring, but also potentially general shifts in these behaviours associated with movement in and out of particular regions. Furthermore, improved classification of vertical behaviour could provide additional constraints on the actual estimation process of horizontal movement tracks when these two data are combined.

7.4.2 Tagging Simulation

In Chapter Three, I developed an individual-based simulation model to examine the effect of changing a small number of assumptions on very specific phenomena surrounding FADs and tuna behaviour. Despite the simplicity of the model, many broad patterns were replicated using this approach and number of strong changes in simulated residence times and diet were seen when behaviours or the environment were altered. The empirical analyses of chapters five and six provide quantitative outputs that can be used to inform this model, and the multivariate HMM method was tested on some simple simulated datasets to ensure that the method effectively recovered values of known parameters. However, these simulated data were generated from distributions and transition parameters that assumed certain theoretical behaviours (e.g. foraging at depth with thermoregulatory ascents) would manifest as multivariate normal distributed observations in the behavioural space most suited to this analysis. In order to better test if vertical movement behaviours can truly be described in a meaningful way by the HMM approach, it is necessary to adapt the simulation model of Chapter Three to a higher temporal and depth resolution. Using this structure, the virtual individuals or schools of tuna in the model can be virtually "tagged", and their high resolution behaviour under a number of assumptions be analysed by the same multivariate HMM approach used on real fish from the PTTP in this thesis. This could potentially shed light on what some of the behaviours estimated by an HMM on real tuna may represent *in situ*.

While such a tagging simulator could be based on some simple assumptions about the environment or prey field as was done in the IBM of Chapter Three, driving forces could also be input from a number of other sources that already exist. For example, SEAPODYM can already project spatial and temporal abundance of mid-trophic forage species (Lehodey, Murtugudde, and Senina 2010) based on physical-biogeochemical forcing. These projections could be used to parameterise the prey field of an individual-based tagging simulator under a variety of different climate or other scenarios through time. Similarly, many spatially explicit approaches to modelling fisher and fleet behaviour already exist (e.g. (Abernethy et al. 2007; Dreyfus-León 1999; Gillis, Peterman, and Pikitch 1995), which could be incorporated into the simulator to examine the effort effects of actual tag return distributions across regions.

More broadly, a true tagging simulator would provide a means to test a wide variety of important assumptions about tuna behaviour that are critical to scientific advice. The biases in conventional and electronic tagging discussed in Chapter Four, which include the many uncertainties of estimating position using light-based geolocation, to errors in return-rates of dart tags due to fishing effort or reporting, are considerable. While many population dynamics and other models exist that aim to simulate the movement of tuna biomass both vertically and horizontally, this thesis has shown that while the some behavioural states appear consistent across tuna, their temporal occurrence is highly variable. Small-scale effects and stochasticity appear important. Using a computationally efficient individual-based, or similar, modelling approach would allow many replications of simulated tag releases to be run with stochastic effects incorporated. The distribution of virtual tag movements, behaviours, and returns could then be compared with those in the WCPO to test a wide range of hypotheses. Huge financial and scientific investments have been made in tagging programmes in the WCPO and other regions. Not only should the valuable information gained from these experiments be maximised by a better understanding of biases through simulation, but also much hypothesis testing of the behavioural assumptions used in population dynamics models could be undertaken. The design of future tagging experiments and monitoring programmes would be well guided by the development of such tagging simulation experiments.

7.4.3 Smart-FADs

The difficulty with understanding the dynamics of tuna around floating objects remains the fact that we do not know the local-scale environmental and prey field changes occurring around them. This has been a re-occurring problem in the interpretation of empirical analysis results in this thesis. In the previous chapter, it was shown that higher-level behavioural dynamics, such as surface-associations, are highly variable across individuals. This suggests that tropical tunas may undertake these periods of extended surface behaviours for a variety of reasons. Data on the dynamics of aggregations of tuna in relation to the nature the prey field are scarce. It is likely that interactions between both conspecifics and prey drive, not just aggregation around floating objects, but also much of the unexplained variation that remains in the quantitative observations of vertical behaviour revealed in this thesis.

In Chapter Two, some of the available sources of real world environmental data at this scale were briefly discussed, but nothing exists across the spatial and temporal ranges required to truly understand what is causing this variability of behaviour from one individual to another. Although satellite imagery provides an appropriate horizontal coverage of primary production, the distribution and abundance of the prey field for tropical tuna can only be characterised by acoustic surveys (Churnside et al. 2009; Josse, Bach, and Dagorn 1998), which do not exist in high enough resolution for analysis.

Future networks of autonomous oceanographic stations or gliders have been suggested as a potential ways to capture this kind of information (Rudnick et al. 2004), but their deployment across the vast and often remote regions of the Pacific would be a costly and difficult undertaking. Furthermore, we do not know the abundance, locations and movements of the majority of the many thousands of FADs deployed in the WCPO. These two gaps in knowledge prevent definitive statements being made about the observed changes in small-scale tuna behaviour in relation to their use of floating objects.

However, many such autonomous collectors of this oceanographic and biotic data already exist in FAD-fished regions. Modern day drifting, and some anchored, FADs already make use of sophisticated GPS and echo-sounding technologies for the benefits of fishers. This data captures much of the information on aggregation dynamics and prey field contexts that would be beneficial in understanding why some associative periods in tuna are consistent and others are diffuse. While some modifications or additions would be required to maximise the capture of this information, the cost of these “Smart-FADS” would not be astronomical (Itano et al. 2004).

The preliminary analysis on surface-associations presented in this chapter does not suggest that all FADs can be considered to drive a negative impact on the vulnerability of yellowfin and bigeye. Indeed, it raises some evidence against the “ecological trap” theory of man-made floating objects. Three-month bans on FAD-setting have already been implemented in recent years with little impact on catch as fishing effort is simply moved around these closure periods. Indeed, despite these closures a record high number of FAD-sets was made in 2011 (Pilling et al. 2013). Given the fact that FADs constitute a large and economically important component of modern day fisheries in the Pacific, the recommendation of a basin- or even region-wide ban on their use is unlikely to be viewed favourably by fisheries commissions or their stakeholders. It is still unclear as to which regions or types of FADs are “negative”, despite the sophisticated technologies and methodologies now available to us to study the behaviour of tuna.

Alternatively, the enforcement of a proportion of deployed FADs being Smart-FADs, whose recorded data is available to the fisheries commission and its member countries, would allow a much greater characterisation of the effects of FADs on not only the behaviour of fish, but also on the placement and effectiveness of these devices. Capturing more information on the small-scale environmental contexts that are important for the behaviours and vulnerability of tunas would allow more sophisticated advice on how to control FAD-fishing effort, for the goal of supporting true sustainable exploitation of tropical tuna species into the future.

List of References

Abascal, Francisco J., Manuel Quintans, Ana Ramos-Cartelle, and Jaime Mejuto. 2011. “Movements and Environmental Preferences of the Shortfin Mako, Isurus Oxyrinchus, in the Southeastern Pacific Ocean.” *Marine Biology* 158(5): 1175–84.

Abernethy, Kirsten E., Edward H. Allison, Philip P. Molloy, and Isabelle M. Côté. 2007. “Why Do Fishers Fish Where They Fish? Using the Ideal Free Distribution to Understand the Behaviour of Artisanal Reef Fishers.” *Canadian Journal of Fisheries and Aquatic Sciences* 64(11): 1595–1604.

Allain, Valerie, Simon Nicol, Tim Essington, and Tom Okey. 2007. *An Ecopath with Ecosim Model of the Western and Central Pacific Ocean Warm Pool Pelagic Ecosystem*. Honolulu.

Anderson, T.R., and M.I. Lucas. 2008. “Upwelling Ecosystems.” In *Encyclopedia of Ecology*, eds. S.E. Jorgensen and B. Fath. New York, USA, Elsevier Science, 3651–61.

Andreasen, D J, and A C Ravelo. 1997. “Tropical Pacific Ocean Thermocline Depth Reconstructions for the Last Glacial Maximum.” *Paleoceanography* 12(3): 395–413.

Auster, P.J., and R.W. Langton. 1999. “The Effects of Fishing on Fish Habitat.” In *American Fisheries Society Symposium*,.

Bach, P. 2003. “Acoustic Telemetry versus Monitored Longline Fishing for Studying the Vertical Distribution of Pelagic Fish: Bigeye Tuna (Thunnus Obesus) in French Polynesia.” *Fisheries Research* 60(2-3): 281–92.

Baird, S J. 2009. “Characterisation of Pelagic Fisheries Using Observer Data.” *New Zealand Fisheries Assessment Report* 6(February): 58.

Barnett, M A. 1984. “Mesopelagic Fish Zoogeography in the Central Tropical and Subtropical Pacific Ocean: Species Composition and Structure at Representative Locations in Three Ecosystems.” *Marine Biology* 82(2): 199–208.

Bélisle, M. 2005. “Measuring Landscape Connectivity: The Challenge of Behavioral Landscape Ecology.” *Ecology* 86(8): 1988–95.

Bell, Johann D. et al. 2009. “Planning the Use of Fish for Food Security in the Pacific.” *Marine Policy* 33(1): 64–76.

Benhamou, S. 1992. “Efficiency of Area-Concentrated Searching Behaviour in a Continuous Patchy Environment.” *Journal of Theoretical Biology* 159(1): 67–81.

Benhamou, Simon. 2007. “How Many Animals Really Do the Levy Walk?” *Ecology* 88(8): 1962–69.

Benoit-Bird, Kelly J., and W. W. L. Au. 2006. "Extreme Diel Horizontal Migrations by a Tropical Nearshore Resident Micronekton Community." *Marine Ecology Progress Series* 319: 1–14.

Benoit-Bird, Kelly J., and Whitlow W.L. Au. 2004. "Diel Migration Dynamics of an Island-Associated Sound-Scattering Layer." *Deep Sea Research Part I: Oceanographic Research Papers* 51(5): 707–19.

Bertrand, A, Erwan Josse, and J Massé. 1999. "In Situ Acoustic Target-Strength Measurement of Bigeye (Thunnus Obesus) and Yellowfin Tuna (Thunnus Albacares) by Coupling Split-Beam Echosounder Observations." *ICES Journal of Marine Science: Journal du Conseil* 56(1): 51–60.

Bertrand, Arnaud et al. 2002. "Hydrological and Trophic Characteristics of Tuna Habitat: Consequences on Tuna Distribution and Longline Catchability." *Canadian journal of fisheries and aquatic sciences* 59(6): 1002–13.

Bertrand, Arnaud, F-X Bard, and Erwan Josse. 2002. "Tuna Food Habits Related to the Micronekton Distribution in French Polynesia." *Marine Biology* 140(5): 1023–37.

Bestley, Sophie, Toby A Patterson, Mark A Hindell, and John S Gunn. 2008. "Feeding Ecology of Wild Migratory Tunas Revealed by Archival Tag Records of Visceral Warming." *The Journal of animal ecology* 77(6): 1223–33.

———. 2010. "Predicting Feeding Success in a Migratory Predator: Integrating Telemetry, Environment, and Modeling Techniques." *Ecology* 91(8): 2373–84.

Bigelow, KA, John Hampton, and N Miyabe. 2002. "Application of a Habitat□ based Model to Estimate Effective Longline Fishing Effort and Relative Abundance of Pacific Bigeye Tuna (Thunnus Obesus)." *Fisheries Oceanography* (July 2001): 143–55.

Block, Barbara A. 2005. "Physiological Ecology in the 21st Century: Advancements in Biologging Science." *Integrative and comparative biology* 45(2): 305–20.

———. 2011. "Tracking Apex Marine Predator Movements in a Dynamic Ocean." *Nature* 475(7354): 86–90.

Block, Barbara A., Daniel P Costa, George W Boehlert, and Randy E Kochevar. 2003. "Revealing Pelagic Habitat Use : The Tagging of Pacific Pelagics Program Idées Sur L ' Utilisation de L ' Habitat Pélagique : Le Programme de Marquage de Pélagiques Dans Le Pacifique." *Oceanologica Acta* 25: 255–66.

Block, Barbara A., and John R. Finnerty. 1994. "Endothermy in Fishes: A Phylogenetic Analysis of Constraints, Predispositions, and Selection Pressures." *Environmental Biology of Fishes* 40(3): 283–302.

Le Borgne, Robert et al. 2011. “Vulnerability of Open Ocean Food Webs in the Tropical Pacific to Climate Change.” In *Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change*, eds. Johann D. Bell, Johanna E. Johnson, and Alistair J. Hobday. Noumea, New Caledonia: Secretariat of the Pacific Community, 189–250.

Bost, C.A. et al. 2009. “The Importance of Oceanographic Fronts to Marine Birds and Mammals of the Southern Oceans.” *Journal of Marine Systems* 78(3): 363–76.

Breiman, Leo. 2001. “Random Forests.” *Machine learning* 45(1): 5–32.

Brill, R. 1996. “Selective Advantages Conferred by the High Performance Physiology of Tunas, Billfishes, and Dolphin Fish.” *Comparative Biochemistry and Physiology Part A: Physiology* 113(1): 3–15.

Brill, R. W. et al. 1999. “Horizontal Movements and Depth Distribution of Large Adult Yellowfin Tuna (Thunnus Albacares) near the Hawaiian Islands, Recorded Using Ultrasonic Telemetry: Implications for the Physiological Ecology of Pelagic Fishes.” *Marine Biology* 133(3): 395–408.

Bromhead, Don, Jennifer Foster, and Rachel Attard. 2003. … report to the Fisheries … *A Review of the Impacts of Fish Aggregating Devices (FADs) on Tuna Fisheries.*

Buckley, T.W., and B.S. Miller. 1994. “Feeding Habits of Yellowfin Tuna Associated with Fish Aggregation Devices in American Samoa.” *Bulletin of Marine Science, 55* 2(3): 445–59.

Busch, Susan, and BM Johnson. 2011. “Energetic Costs and Benefits of Cyclic Habitat Switching: A Bioenergetics Model Analysis of Diel Vertical Migration in Coregonids.” *Canadian Journal of Fisheries and Aquatic Sciences* 68(4): 706–17.

Butler, Michael J A. 1982. “Plight of the Bluefin Tuna.” *National Geographic* 162(2): 220–39.

Campana, Steven E et al. 2011. “Migration Pathways, Behavioural Thermoregulation and Overwintering Grounds of Blue Sharks in the Northwest Atlantic.” *PloS one* 6(2): e16854.

Campbell, Robert A. 2004. “CPUE Standardisation and the Construction of Indices of Stock Abundance in a Spatially Varying Fishery Using General Linear Models.” *Fisheries Research* 70(2): 209–27.

———. 2012. *Aggregate and Size-Based Standardised CPUE Indices for Longline Target Species Caught within the South-West Pacific*. WCPFC-SC8-2012/SA-IP-13.

Capello, M, M Soria, P Cotel, and G Potin. 2012. “The Heterogeneous Spatial and Temporal Patterns of Behavior of Small Pelagic Fish in an Array of Fish Aggregating Devices (FADs).” *Journal of Experimental Marine Biology and Ecology* 430: 56–62.

Castro, J.J., J.A. Santiago, and A.T. Santana-Ortega. 2001. “A General Theory on Fish Aggregation to Floating Objects: An Alternative to the Meeting Point Hypothesis.” *Reviews in fish biology and fisheries* 11(3): 255–77.

Celeux, Gilles, and Gilda Soromenho. 1996. “An Entropy Criterion for Assessing the Number of Clusters in a Mixture Model.” *Journal of classification* 13(2): 195–212.

Chiang, Wei-Chuan et al. 2011. “Vertical and Horizontal Movements of Sailfish (Istiophorus Platypterus) near Taiwan Determined Using Pop-up Satellite Tags.” *Journal of Experimental Marine Biology and Ecology* 397(2): 129–35.

Choquenot, David, and David M. Forsyth. 2013. “Exploitation Ecosystems and Trophic Cascades in Non-Equilibrium Systems: Pasture - Red Kangaroo - Dingo Interactions in Arid Australia.” *Oikos* 122(9): 1292–1306.

Churnside, James et al. 2009. “Combining Techniques for Remotely Assessing Pelagic Nekton : Getting the Whole Picture.” In *The Future of Fisheries Science in North America. Springer Netherlands*, Springer Netherlands, 345–56.

Ciannelli, L., D. Ø. Hjermann, and P. Lehodey. 2005. “Climate Forcing, Food Web Structure and Community Dynamics in Pelagic Marine Ecosystems.” In *Aquatic Food Webs: An Ecosystem Approach*, Oxford: Oxford University Press, 143–69.

Codling, Edward A., and Michael J. Plank. 2010. “Turn Designation, Sampling Rate and the Misidentification of Power Laws in Movement Path Data Using Maximum Likelihood Estimates.” *Theoretical Ecology* 4(3): 397–406.

Collette, B B et al. 2011. “High Value and Long Life—Double Jeopardy for Tunas and Billfishes.” *Science* 333(6040): 291–92.

Cortes, Corinna, and Vladimir Vapnik. 1995. “Support-Vector Networks.” *Machine learning* 20(3): 273–97.

Cotté, Cédric et al. 2011. “Scale-Dependent Interactions of Mediterranean Whales with Marine Dynamics.” *Limnology and Oceanography* 56(1): 219–32.

Cury, P, and C Roy. 1989. “Optimal Environmental Window and Pelagic Fish Recruitment Success in Upwelling Areas.” *Canadian Journal of Fisheries and Aquatic Sciences* 46: 670–80.

Daewel, Ute, Myron a. Peck, and Corinna Schrum. 2011. “Life History Strategy and Impacts of Environmental Variability on Early Life Stages of Two Marine Fishes in the North Sea: An Individual-Based Modelling Approach.” *Canadian Journal of Fisheries and Aquatic Sciences* 68(3): 426–43.

Dagorn, Laurent et al. 2001. “Improving Our Understanding of Tropical Tuna Movements from Small to Large Scales.” In *Electronic Tagging and Tracking in Marine Fisheries: Proceedings of the Symposium on Tagging* *and Tracking Marine Fish with Electronic Devices*, Kluwer Academic Pub, 385–405.

Dagorn, Laurent, Nicolas Bez, Thomas Fauvel, and Emily Walker. 2013. "How Much Do Fish Aggregating Devices (FADs) Modify the Floating Object Environment in the Ocean?" *Fisheries Oceanography* 22(3): 147–53.

Dagorn, Laurent, and Pierre Fréon. 1999. "Tropical Tuna Associated with Floating Objects: A Simulation Study of the Meeting Point Hypothesis." *Canadian Journal of Fisheries and Aquatic Sciences* 56(6): 984–93.

Dagorn, Laurent, Kim N Holland, and John Filmalter. 2010. "Are Drifting FADs Essential for Testing the Ecological Trap Hypothesis ?" *Fisheries Research* 106(1): 60–63.

Dagorn, Laurent, Kim N Holland, Victor Restrepo, and Gala Moreno. 2013. "Is It Good or Bad to Fish with FADs? What Are the Real Impacts of the Use of Drifting FADs on Pelagic Marine Ecosystems?" *Fish and Fisheries* 14(3): 391–415.

Dagorn, Laurent, Kim N. Holland, and David G. Itano. 2006. "Behavior of Yellowfin (Thunnus Albacares) and Bigeye (T. Obesus) Tuna in a Network of Fish Aggregating Devices (FADs)." *Marine Biology* 151(2): 595–606.

Dagorn, Laurent, KN Holland, and JP Hallier. 2006. "Deep Diving Behavior Observed in Yellowfin Tuna (Thunnus Albacares)." *Aquatic Living* 88: 85-88.

Dagorn, Laurent, Erwan Josse, Pascal Bach, and Arnaud Bertrand. 2000. "Modeling Tuna Behaviour near Floating Objects: From Individuals to Aggregations." *Aquatic living resources* 13: 203–11.

Dagorn, Laurent, Filippo Menczer, Pascal Bach, and Robert J Olson. 2000. "Co-Evolution of Movement Behaviours by Tropical Pelagic Predatory Fishes in Response to Prey Environment: A Simulation Model." *Ecological Modelling* 134(2-3): 325–41.

Dalla Rosa, L. et al. 2008. "Movements of Satellite-Monitored Humpback Whales on Their Feeding Ground along the Antarctic Peninsula." *Polar Biology* 31(7): 771–81.

Davies, Nick et al. 2011. 15 *Stock Assessment of Bigeye Tuna in the Western and Central Pacific Ocean*. Pohnpei State.

Davies, Tim K. et al. 2012. *A Review of the Conservation Benefits of Marine Protected Areas for Pelagic Species Associated with Fisheries*. McLean, Virginia, USA.

Davis, R W et al. 2007. "Diving Behavior of Sperm Whales in Relation to Behavior of a Major Prey Species, the Jumbo Squid, in the Gulf of California, Mexico." *Marine Ecology Progress Series* 333: 291–302.

Dean, Ben et al. 2012. “Behavioural Mapping of a Pelagic Seabird: Combining Multiple Sensors and a Hidden Markov Model Reveals the Distribution of at-Sea Behaviour.” *Journal of the Royal Society, Interface / the Royal Society*: rsif20120570.

Demer, David A et al. 2011. 2 *Acoustic-Trawl Surveys of Pacific Sardine (Sardinops Sagax) and Other Pelagic Fishes in the California Current Ecosystem : Part 1 , Methods and an Example Application*. La Jolla, California, USA.

Dempster, T, and Mj Kingsford. 2003. “Homing of Pelagic Fish to Fish Aggregation Devices (FADs): The Role of Sensory Cues.” *Marine Ecology Progress Series* 258: 213–22.

Dempster, Tim, and Marc Taquet. 2005. “Fish Aggregation Device (FAD) Research: Gaps in Current Knowledge and Future Directions for Ecological Studies.” *Reviews in Fish Biology and Fisheries* 14(1): 21–42.

Dreyfus-León, Michel Jules. 1999. “Individual-Based Modelling of Fishermen Search Behaviour with Neural Networks and Reinforcement Learning.” *Ecological Modelling* 120(2–3): 287–97.

Dueri, Sibylle, Laurent Bopp, and Olivier Maury. 2014. “Projecting the Impacts of Climate Change on Skipjack Tuna Abundance and Spatial Distribution.” *Global Change Biology* 20(3): 742–53.

Dufour, Philippe, Loic Charpy, and Nicole Garcia. 1999. “Phytoplankton Nutrient Control in the Oligotrophic South Pacific Subtropical Gyre (Tuamotu Archipelago).” 179(1962): 285–90.

Edwards, Andrew M et al. 2007. “Revisiting Lévy Flight Search Patterns of Wandering Albatrosses, Bumblebees and Deer.” *Nature* 449(7165): 1044–48.

Ekstrom, Philip A. 2004. “An Advance in Geolocation by Light.” *Memoirs of the National Institute of Polar Research* 58: 210–26.

Evans, K., M. A. Lea, and T. A. Patterson. 2013. “Recent Advances in Bio-Logging Science: Technologies and Methods for Understanding Animal Behaviour and Physiology and Their Environments.” *Deep Sea Research Part II: Topical Studies in Oceanography* 88-89: 1–6.

Evans, Karen et al. 2008. “Behaviour and Habitat Preferences of Bigeye Tuna (Thunnus Obesus) and Their Influence on Longline Fishery Catches in the Western Coral Sea.” *Canadian Journal of Fisheries and Aquatic Sciences* 65(11): 2427–43.

FAO. 2012. *The State of World Fisheries and Aquaculture 2012*. Rome.

Farewell, Charles J. 2001. “Tunas in Captivity.” In *Tuna: Physiology, Ecology, and Evolution, Vol. 19*, eds. Barbara Ann Block and Ernest Donald Stevens. Gulf Professional Publishing., 391–413.

Fernandez, Emilie, and Valérie Allain. 2010. “Importance of Reef Prey in the Diet of Tunas and Other Large Pelagic Species in the Western and Central Pacific Ocean.” *SPC Fisheries Newsletter* 133: 35–39.

Filmalter, JD, and L Dagorn. 2011. “First Descriptions of the Behavior of Silky Sharks, Carcharhinus Falciformis, around Drifting Fish Aggregating Devices in the Indian Ocean.” *Bulletin of Marine Science* 87(3): 325–37.

Fix, Evelyn, and Joseph L Hodges Jr. 1951. *Discriminatory Analysis-Nonparametric Discrimination: Consistency Properties*. DTIC Document.

Floyd, JM, and D Pauly. 1984. “Smaller Size Tuna around the Philippines - Can Fish Aggregating Devices Be Blamed?” *Infofish Marketing Digest* 5(84): 25–27.

Fournier, DA, J Hampton, and JR Sibert. 1998. “MULTIFAN-CL: A Length-Based, Age-Structured Model for Fisheries Stock Assessment, with Application to South Pacific Albacore, Thunnus Alalunga.” *Canadian Journal of Fisheries and Aquatic Sciences* 55(9): 2105–16.

Fréon, P., and Laurent Dagorn. 2000. “Review of Fish Associative Behaviour: Toward a Generalisation of the Meeting Point Hypothesis.” *Reviews in Fish Biology and Fisheries* 10(2): 183–207.

Freon, P., and OA. Misund. 1998. *Dynamics of Pelagic Fish Distribution and Behaviour: Effects on Fisheries and Stock Assessment*. London: Blackwell Science, Oxford (UK). Fishing News Books. Blackwell Science Ltd,.

Gaertner, Jc et al. 2008. “Visual Censuses around Drifting Fish Aggregating Devices (FADs): A New Approach for Assessing the Diversity of Fish in Open-Ocean Waters.” *Marine Ecology Progress Series* 366: 175–86.

Gales, Mark, and Steve Young. 2007. “The Application of Hidden Markov Models in Speech Recognition.” *Foundations and Trends in Signal Processing* 1(3): 195–304.

Game, Edward T et al. 2009. “Pelagic Protected Areas: The Missing Dimension in Ocean Conservation.” *Trends in ecology & evolution* 24(7): 360–69.

Gaspar, Philippe et al. 2006. “Marine Animal Behaviour: Neglecting Ocean Currents Can Lead Us up the Wrong Track.” *Proceedings. Biological sciences / The Royal Society* 273(1602): 2697–2702.

Gerlotto, F, and J Castillo. 2004. “Three-Dimensional Structure and Avoidance Behaviour of Anchovy and Common Sardine Schools in Central Southern Chile.” *CES Journal of Marine Science: Journal du Conseil* 61(7): 1120–26.

Ghazali, S.M. et al. 2013. “The Diel Variation and Spatial Extent of the Underwater Sound around a Fish Aggregation Device (FAD).” *Fisheries Research* 148: 9–17.

Gillis, Darren M, Randall M Peterman, and Ellen K Pikitch. 1995. “Implications of Trip Regulations for High-Grading; a Model of the Behavior of Fishermen.” *Canadian Journal of Fisheries and Aquatic Sciences* 52(2): 402–15.

Girard, Charlotte, Simon Benhamou, and Laurent Dagorn. 2004. “FAD: Fish Aggregating Device or Fish Attracting Device? A New Analysis of Yellowfin Tuna Movements around Floating Objects.” *Animal Behaviour* 67(2): 319–26.

Gjøsaeter, J, and Kōichi Kawaguchi. 1980. *A Review of the World Resources of Mesopelagic Fish*. Food & Agriculture Org.

Graham, Brittany S et al. 2010. “Using Isoscapes to Trace the Movements and Foraging Behavior of Top Predators in Oceanic Ecosystems.” In *Isoscapes*, eds. Jason B. West, Gabriel J. Bowen, Todd E. Dawson, and Kevin P. Tu. Dordrecht: Springer Netherlands, 299–318.

Graham, Brittany S., Dean Grubbs, Kim Holland, and Brian N. Popp. 2006. “A Rapid Ontogenetic Shift in the Diet of Juvenile Yellowfin Tuna from Hawaii.” *Marine Biology* 150(4): 647–58.

Graham, Jeffery B, and Kathryn A Dickson. 2001. “Anatomical and Physiological Specializations For Endothermy.” In *Tuna: Physiology, Ecology, and Evolution, Vol. 19*, eds. Barbara Ann Block and Ernest Donald Stevens. Gulf Professional Publishing., 121–66.

Greenstreet, S. 1998. “Seasonal Variation in the Importance of Pelagic Fish in the Diet of Piscivorous Fish in the Moray Firth, NE Scotland: A Response to Variation in Prey Abundance?” *ICES Journal of Marine Science* 55(1): 121–33.

Grimm, Volker. 1999. “Ten Years of Individual-Based Modelling in Ecology: What Have We Learned and What Could We Learn in the Future?” *Ecological Modelling* 115(2-3): 129–48.

———. 2005. “Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology.” *Science* 310(5750): 987–91.

———. 2006. “A Standard Protocol for Describing Individual-Based and Agent-Based Models.” *Ecological Modelling* 198(1-2): 115–26.

Guillotreau, Patrice, Frédéric Salladarré, Patrice Dewals, and Laurent Dagorn. 2011. “Fishing Tuna around Fish Aggregating Devices (FADs) vs Free Swimming Schools: Skipper Decision and Other Determining Factors.” *Fisheries Research* 109(2-3): 234–42.

Hallier, Jean-Pierre, and D Gaertner. 2008. “Drifting Fish Aggregation Devices Could Act as an Ecological Trap for Tropical Tuna Species.” *Marine Ecology Progress Series* 353: 255–64.

Hallier, Jean-Pierre, Bernard Stequert, Olivier Maury, and FX Bard. 2005. “Growth of Bigeye Tuna (Thunnus Obesus) in the Eastern Atlantic Ocean from Tagging-Recapture Data and Otolith Readings.” *Collect. Vol. Sci. Pap. ICCAT* 57(1): 181–94.

Hammerschlag, N., A.J. Gallagher, and D.M. Lazarre. 2011. “A Review of Shark Satellite Tagging Studies.” *Journal of Experimental Marine Biology and Ecology* 398(1-2): 1–8.

Hampton, John. 1997. “Estimates of Tag-Reporting and Tag-Shedding Rates in a Large-Scale Tuna Tagging Experiment in the Western Tropical Pacific Ocean.” *Fishery Bulletin* 95: 68–79.

———. 2000. “Natural Mortality Rates in Tropical Tunas: Size Really Does Matter.” *Canadian Journal of Fisheries and Aquatic Sciences* 57(5): 1002–10.

———. 2005. “Fisheries: Decline of Pacific Tuna Populations Exaggerated?” *Nature* 434(7037): 1–2.

———. 2010. *Tuna Fisheries Status and Management in the Western and Central Pacific Ocean*. Noumea, New Caledonia.

Harley, Shelton J et al. 2009. “Stock Assessment of Bigeye Tuna in the Western and Central Pacific Ocean.” In *Western and Central Pacific Fisheries Commission Scientific Committee, Fifth Regular Session*, Pohnpei, 1–98.

Hart, Tom et al. 2010. “Behavioural Switching in a Central Place Forager: Patterns of Diving Behaviour in the Macaroni Penguin (Eudyptes Chrysolophus).” *Marine Biology* 157(7): 1543–53.

Hartigan, John A, and Manchek A Wong. 1979. “Algorithm AS 136: A K-Means Clustering Algorithm.” *Journal of the Royal Statistical Society. Series C (Applied Statistics)* 28(1): 100–108.

Hartmann, DP, and JM Gottman. 1980. “Interrupted Time□series Analysis and Its Application to Behavioral Data.” *Journal of Applied Behavior Analysis* 4(4): 543–59.

Hays, Graeme C. 2003. “A Review of the Adaptive Significance and Ecosystem Consequences of Zooplankton Diel Vertical Migrations.” *Hydrobiologia* 503(1-3): 163–70.

Hazen, Elliott L. et al. 2011. “The Relationship among Oceanography, Prey Fields, and Beaked Whale Foraging Habitat in the Tongue of the Ocean” ed. Howard Browman. *PLoS ONE* 6(4): e19269.

Hidaka, Kiyotaka, and M I O Takahashi. 2003. “Biomass and Taxonomic Composition of Micronekton in the Western Tropical – Subtropical Pacific.” *Fisheries Oceanography* 12: 112–25.

Holland, Kim N et al. 1992. “Physiological and Behavioural Thermoregulation in Bigeye Tuna (Thunnus Obesus).” *Nature Letters* 358: 410–12.

———. 1996. “Biological Aspects of the Association of Tunas with FADs.” *SPC Fish Aggregating Device Inf. Bull.* (November): 2–7.

Hoolihan, John P. et al. 2011. “Vertical Habitat Use of Sailfish (Istiophorus Platypterus) in the Atlantic and Eastern Pacific, Derived from Pop-up Satellite Archival Tag Data.” *Fisheries Oceanography* 20(3): 192–205.

Hoyle, Simon D, N Davies, A D Langley, and J Hampton. 2011. *Stock Assessment of Skipjack Tuna in the Western and Central Pacific Ocean*. Pohnpei.

Hoyle, Simon D., Bruno M. Leroy, Simon J. Nicol, and W. John Hampton. 2014. “Covariates of Release Mortality and Tag Loss in Large-Scale Tuna Tagging Experiments.” *Fisheries Research*: 1–13.

Humphries, Nicolas E et al. 2010. “Environmental Context Explains Lévy and Brownian Movement Patterns of Marine Predators.” *Nature* 465(7301): 1066–69.

Humston, Robert, Jerald S. Ault, Molly Lutcavage, and Donald B. Olson. 2000. “Schooling and Migration of Large Pelagic Fishes Relative to Environmental Cues.” *Fisheries Oceanography* 9(2): 136–46.

Huse, Geir, and Ø. Fiksen. 2010. “Modelling Encounter Rates and Distribution of Mobile Predators and Prey.” *Progress In Oceanography* 84(1-2): 93–104.

Inselberg, Alfred. 1985. “The Plane with Parallel Coordinates.” *The Visual Computer* 1(2): 69–91.

ISSF. 2012. *Understanding Purse Seine CPUE*. Rome.

Itano, D. et al. 2004. “Monitoring Movement Patterns, Residence Times and Feeding Ecology of Tuna, Billfish and Oceanic Sharks within a Network of Anchored FADs.” In *17th Meeting of the Standing Committee on Tuna and Billfish*, Majuro, Marshall Islands.

Jackson, Duncan, Mike Holcombe, and Francis Ratnieks. 2004. “Coupled Computational Simulation and Empirical Research into the Foraging System of Pharaoh’s Ant (Monomorium Pharaonis).” *Bio Systems* 76(1-3): 101–12.

Jaquemet, S., M. Potier, and F. Ménard. 2011. “Do Drifting and Anchored Fish Aggregating Devices (FADs) Similarly Influence Tuna Feeding Habits? A Case Study from the Western Indian Ocean.” *Fisheries Research* 107(1-3): 283–90.

Jassby, AD, and TM Powell. 1990. “Detecting Changes in Ecological Time Series.” *Ecology* 71(6): 2044–52.

Josse, Erwan, Pascal Bach, and Laurent Dagorn. 1998. “Simultaneous Observations of Tuna Movements and Their Prey by Sonic Tracking and Acoustic Surveys.” *Hydrobiologia* 371: 61–69.

Karatzoglou, Alexandros, Alex Smola, and Kurt Hornik. 2013. “Kernlab: Kernel-Based Machine Learning Lab.”

Kerr, Jeremy T., and Marsha Ostrovsky. 2003. “From Space to Species: Ecological Applications for Remote Sensing.” *Trends in Ecology & Evolution* 18(6): 299–305.

Kingsland, Sharon E. 1995. *Modeling Nature*. University of Chicago Press.

Kirby, David S. 2001. “On the Integrated Study of Tuna Behaviour and Spatial Dynamics: Tagging and Modelling as Complementary Tools.” In *Electronic Tagging and Tracking in Marine Fisheries: Proceedings of the Symposium on Tagging and Tracking Marine Fish with Electronic Devices*, Dordrecht: Kluwer Academic Publishers, 407–20.

Kirby, David S., Geir Huse, and Patrick Lehodey. 2003. “An Individual-Based Model for the Spatial Population Dynamics of Pacific Skipjack Tuna.” *Fisheries Research* (June).

Kitchell, James F. et al. 2002. “The Role of Sharks and Longline Fisheries in a Pelagic Ecosystem of the Central Pacific.” *Ecosystems* 5(2): 202–16.

Koehl, M A R. 1989. “Discussion: From Individuals to Populations.” In *Perspectives in Ecological Theory*, Princeton, New Jersey, USA: Princeton University Press, 39–53.

Kolody, Dale, and Simon Hoyle. 2013. “Evaluation of Tag Mixing Assumptions in Western Pacific Ocean Skipjack Tuna Stock Assessment Models.” *Fisheries Research*.

Kullback, S, and RA Leibler. 1951. “On Information and Sufficiency.” *The Annals of Mathematical Statistics*: 79–86. http://www.jstor.org/stable/10.2307/2236703 (January 19, 2014).

Kumoro, L. 2002. “Notes on the Use of FADs in the Papua New Guinea Purse Seine Fishery.” In *Fishing Technology Working Group at the 176th Meeting of the Standing Committee on Tuna and Billfish, Mooloolaba, Australia,*.

Lam, Chi H, Anders Nielsen, and John R Sibert. 2008. “Improving Light and Temperature Based Geolocation by Unscented Kalman Filtering.” *Fisheries Research* 91(1): 15–25.

Lam, V, and Daniel Pauly. 2005. “Mapping the Global Biomass of Mesopelagic Fishes.” *The Sea Around Us Project Newsletter, July/August*.

Lan, K.-W. et al. 2011. “Ocean Variations Associated with Fishing Conditions for Yellowfin Tuna (Thunnus Albacares) in the Equatorial Atlantic Ocean.” *ICES Journal of Marine Science* 68(6): 1063–71.

Lander, Michelle E, Miles L Logsdon, Thomas R Loughlin, and Glenn R Van Blaricom. 2011. “Spatial Patterns and Scaling Behaviors of Steller Sea Lion

(Eumetopias Jubatus) Distributions and Their Environment." *Journal of theoretical biology*: 1–10.

Langley, Adam et al. 2009. "Slow Steps towards Management of the World's Largest Tuna Fishery." *Marine Policy* 33(2): 271–79.

Langley, Adam, Simon Hoyle, and John Hampton. 2011. 03 *Stock Assessment of Yellowfin Tuna in the Western and Central Pacific Ocean*. Pohnpei State.

Langley, Adam, P.G. Williams, and John Hampton. 2008. *The Western and Central Pacific Tuna Fishery: 2006 Overview and Status of Stocks. Tuna Fisheries Assessment*. Noumea, New Caledonia: Secretariat of the Pacific Community.

Lavín, M.F. et al. 2006. "A Review of Eastern Tropical Pacific Oceanography: Summary." *Progress in Oceanography* 69(2-4): 391–98.

Lawson, Timothy. 2011. "Purse-Seine Length Frequencies Corrected for Selectivity Bias in Grab Samples Collected by Observers." In *Western and Central Pacific Fisheries Commission Scientific Committee, Ninth Regular Session*, Pohnpei, 8.

Layman, Craig A et al. 2012. "Applying Stable Isotopes to Examine Food-Web Structure: An Overview of Analytical Tools." *Biological reviews of the Cambridge Philosophical Society* 87(3): 545–62.

Lehodey, Patrick. 2001. "The Pelagic Ecosystem of the Tropical Pacific Ocean: Dynamic Spatial Modelling and Biological Consequences of ENSO." *Progress In Oceanography* 49(1-4): 439–68.

———. 2006. "Climate Variability, Fish, and Fisheries." *Journal of Climate* 44(20): 17–5030.

———. 2013. "Modelling the Impact of Climate Change on Pacific Skipjack Tuna Population and Fisheries." *Climatic change* 119(1): 95–109.

Lehodey, Patrick, and Olivier Maury. 2010. "CLimate Impacts on Oceanic TOp Predators (CLIOTOP): Introduction to the Special Issue of the CLIOTOP International Symposium." *Progress In Oceanography* 86(1-2): 1–7.

Lehodey, Patrick, Raghu Murtugudde, and Inna Senina. 2010. "Bridging the Gap from Ocean Models to Population Dynamics of Large Marine Predators: A Model of Mid-Trophic Functional Groups." *Progress In Oceanography* 84(1-2): 69–84.

Lehodey, Patrick, I Senina, and R Murtugudde. 2008. "A Spatial Ecosystem and Populations Dynamics Model (SEAPODYM) – Modeling of Tuna and Tuna-like Populations." *Progress In Oceanography* 78(4): 304–18.

Leroy, Bruno M. et al. 2010. "Vertical Behavior and the Observation of FAD Effects on Tropical Tuna in the Warm-Pool of the Western Pacific Ocean." In

Western and Central Pacific Fisheries Commission Scientific Committee, Sixth Regular Session, Pohnpei, 21.

———. 2012. “A Critique of the Ecosystem Impacts of Drifting and Anchored FADs Use by Purse-Seine Tuna Fisheries in the Western and Central Pacific Ocean.” *Aquatic Living Resources* 26(1): 49–61.

———. 2013. “Lessons Learned from Implementing Three, Large-Scale Tuna Tagging Programmes in the Western and Central Pacific Ocean.” *Fisheries Research*: 1–11.

Levin, S.A. 1992. “The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture.” *Ecology* 73(6): 1943–67.

Levinton, J S. 1995. *Marine Biology: Function, Biodiversity, Ecology*. Oxford University Press.

Liaw, Andy, and Matthew Wiener. 2002. “Classification and Regression by randomForest.” *R news* 2(3): 18–22.

Ludwig, John A, and Joe M Cornelius. 1987. “Locating Discontinuities along Ecological Gradients.” *Ecology* 68(2): 448–50.

Luo, J. et al. 2006. “Vertical Habitat Utilization by Large Pelagic Animals: A Quantitative Framework and Numerical Method for Use with Pop-up Satellite Tag Data.” *Fisheries Oceanography* 15(3): 208–29.

Luschi, Paolo, Graeme C. Hays, and Floriano Papi. 2003. “A Review of Long-Distance Movements by Marine Turtles, and the Possible Role of Ocean Currents.” *Oikos* 103(2): 293–302.

MacDonald, I L, and W Zucchini. 2009. *Hidden Markov Models for Time Series: An Introduction Using R*. Chapman & Hall/CRC.

MacQueen, James. 1967. “Some Methods for Classification and Analysis of Multivariate Observations.” In *Proceedings of the Fifth Berkeley Symposium on Mathematical Statistics and Probability*, , 281–97.

Maggio, Teri. 2001. *Mattanza: The Ancient Sicilian Ritual of Bluefin Tuna Fishing*. Penguin Books.

Magnuson, JJ. 1973. “Comparative Study of Adaptations for Continuous Swimming and Hydrostatic Equilibrium of Scombroid and Xiphoid Fishes.” *Fishery Bulletin Bull* 71(2).

Mapp, James et al. 2013. “Clupea Harengus: Intraspecies Distinction Using Curvature Scale Space and Shapelets-Classification of North-Sea and Thames Herring Using Boundary Contour of Sagittal Otoliths.” In *ICPRAM*, , 138–43.

Marchal, Emile, and Anne Lebourges. 1996. “Acoustic Evidence for Unusual Diel Behaviour of a Mesopelagic Fish (Vinciguerria Nimbaria) Exploited by Tuna.” : 443–47.

Margulies, Daniel et al. 2007. “Spawning and Early Development of Captive Yellowfin Tuna (Thunnus Albacares).” *Fishery Bulletin* 105(2): 249–65.

Matsumoto, Takayuki, and William H. Bayliff. 2011. 24 *A Review of the Japanese Longline Fishery for Tunas and Billfishes in the Eastern Pacific Ocean, 1998-2003*. La Jolla, California, USA.

Matsumoto, Takayuki, Takashi Kitagawa, and Shingo Kimura. 2013a. “Vertical Behavior of Bigeye Tuna (Thunnus Obesus) in the Northwestern Pacific Ocean Based on Archival Tag Data.” *Fisheries Oceanography* 22(3): 234–46.

———. 2013b. “Vertical Behavior of Juvenile Yellowfin Tuna Thunnus Albacares in the Southwestern Part of Japan Based on Archival Tagging.” *Fisheries Science* 79(3): 417–24.

Matsumoto, Walter M, Robert A Skillman, and Andrew E Dizon. 1984. “Synopsis of Biological Data on Skipjack Tuna, Katsuwonus Pelamis.” *FAO Fisheries Synopsis (FAO)*.

Maunder, M et al. 2006. “Interpreting Catch per Unit Effort Data to Assess the Status of Individual Stocks and Communities.” *ICES Journal of Marine Science* 63(8): 1373–85.

Maury, Olivier. 2005. “How to Model the Size-Dependent Vertical Behaviour of Bigeye (Thunnus Obesus) Tuna in Its Environment.” *Collect. Vol. Sci. Pap, ICCAT* 57(2): 115–26.

———. 2010. “An Overview of APECOSM, a Spatialized Mass Balanced ‘Apex Predators ECOSystem Model’ to Study Physiologically Structured Tuna Population Dynamics in Their Ecosystem.” *Progress in Oceanography* 84(1): 113–17.

McIntyre, Trevor et al. 2011. “Water Column Use and Forage Strategies of Female Southern Elephant Seals from Marion Island.” *Marine Biology* 158(9): 2125–39.

McLachlan, Geoffrey, and David Peel. 2004. *Finite Mixture Models*. John Wiley & Sons.

McLane, Adam J., Christina Semeniuk, Gregory J. McDermid, and Danielle J. Marceau. 2011. “The Role of Agent-Based Models in Wildlife Ecology and Management.” *Ecological Modelling* 222(8): 1544–56.

Megrey, B et al. 2007. “A Bioenergetics-Based Population Dynamics Model of Pacific Herring (Clupea Harengus Pallasi) Coupled to a Lower Trophic Level Nutrient–phytoplankton–zooplankton Model: Description, Calibration, and Sensitivity Analysis.” *Ecological Modelling* 202(1-2): 144–64.

Meltzoff, Sarah Keene, and Edward LiPuma. 1986. “Hunting for Tuna and Cash in the Solomons: A Rebirth of Artisanal Fishing in Malaita.” *Human organization* 45(1): 53–62.

Ménard et al. 2000. “Food Consumption of Tuna in the Equatorial Atlantic Ocean: FAD-Associated versus Unassociated Schools Frédéric.” *Aquatic Living Resources* 13(3): 233–40.

Menard, F. 2000. “Exploitation of Small Tunas by a Purse-Seine Fishery with Fish Aggregating Devices and Their Feeding Ecology in an Eastern Tropical Atlantic Ecosystem.” *ICES Journal of Marine Science* 57(3): 525–30.

Ménard, F et al. 2005. *Acoustic Characterization of Tropical Tuna Prey in the Western Indian Ocean in Relation with Environmental Conditions*.

Methot Jr, Richard D, and Chantell R Wetzel. 2013. “Stock Synthesis: A Biological and Statistical Framework for Fish Stock Assessment and Fishery Management.” *Fisheries Research* 142: 86–99.

Morales, JM, and SP Ellner. 2002. “Scaling up Animal Movements in Heterogeneous Landscapes: The Importance of Behavior.” *Ecology* 83(8): 2240–47.

Moreno, Gala, Laurent Dagorn, Gorka Sancho, and David Itano. 2007. “Fish Behaviour from Fishers’ Knowledge: The Case Study of Tropical Tuna around Drifting Fish Aggregating Devices (DFADs).” *Canadian Journal of Fisheries and Aquatic Sciences* 64(11): 1517–28.

Morgan, A.C. 2011. *Fish Aggregating Devices (FADs) and Tuna Impacts and Management Options*. Washington DC, USA.

Mori, Yoshihisa, and IL Boyd. 2004. “The Behavioral Basis for Nonlinear Functional Responses and Optimal Foraging in Antarctic Fur Seals.” *Ecology* 85(2): 398–410.

Musyl, Michael K. et al. 2003. “Vertical Movements of Bigeye Tuna (Thunnus Obesus) Associated with Islands, Buoys, and Seamounts near the Main Hawaiian Islands from Archival Tagging Data.” *Fisheries Oceanography* 12(3): 152–69.

Nakashima, Toshiko, and Tatsuro Matsuoka. 2005. “Ghost-Fishing Mortality and Fish Aggregation by Lost Bottom-Gillnet Tangled around Fish Aggregation Device.” *Nippon Suisan Gakkaishi* 71(2): 178–87.

Nelder, J A, and R Mead. 1965. “A Simplex Method for Function Minimization.” *The Computer Journal* 7(4): 308–13.

O’Connor, Sue, Rintaro Ono, and Chris Clarkson. 2011. “Pelagic Fishing at 42,000 Years before the Present and the Maritime Skills of Modern Humans.” *Science* 334(6059): 1117–21.

Ohta, I., and S. Kakuma. 2004. “Periodic Behavior and Residence Time of Yellowfin and Bigeye Tuna Associated with Fish Aggregating Devices around Okinawa Islands, as Identified with Automated Listening Stations.” *Marine Biology* 146(3): 581–94.

Olson, Robert J, and Christofer H Boggs. 1986. “Apex Predation by Yellowfin Tuna (Thunnus Albacares): Independent Estimates from Gastric Evacuation and Stomach Contents, Bioenergetics, and Cesium Concentrations.” *Canadian Journal of Fisheries and Aquatic Sciences* 43(9): 1760–75.

Olson, Robert J., and Ashley J. Mullen. 1986. “Recent Developments for Making Gastric Evacuation and Daily Ration Determinations.” *Environmental Biology of Fishes* 16(1-3): 183–91.

Packard, Lucille. 2009. “Nearshore Fish Aggregating Devices : A Means of Habitat Protection and Food Security in Post-Disaster Solomon Islands.” *Fisheries (Bethesda)* (April 2007): 19–20.

Di Paolo, EA, J Noble, and S Bullock. 2000. *Simulation Models as Opaque Thought Experiments.*

Parrish, J K. 1993. “Comparison of the Hunting Behavior of Four Piscine Predators Attacking Schooling Prey.” *Ethology Berlin* 95(3): 233–46.

Parrish, J.K. 1991. “Do Predators’ Shape'fish Schools: Interactions between Predators and Their Schooling Prey.” *Netherlands Journal of Zoology, 42* 2(3): 358–70.

Patterson, Toby a et al. 2008. “State-Space Models of Individual Animal Movement.” *Trends in ecology & evolution* 23(2): 87–94. http://www.ncbi.nlm.nih.gov/pubmed/18191283 (November 3, 2012).

Patterson, Toby a, Marinelle Basson, Mark V Bravington, and John S Gunn. 2009. “Classifying Movement Behaviour in Relation to Environmental Conditions Using Hidden Markov Models.” *The Journal of animal ecology* 78(6): 1113–23.

Pauly, Daniel, Villy Christensen, Sylvie Guénette, and TJ Pitcher. 2002. “Towards Sustainability in World Fisheries.” *Nature* 418(August): 689–95.

Pedersen, M. W. et al. 2008. “Geolocation of North Sea Cod (Gadus Morhua) Using Hidden Markov Models and Behavioural Switching.” *Canadian Journal of Fisheries and Aquatic Sciences* 65(11): 2367–77. http://www.nrcresearchpress.com/doi/abs/10.1139/F08-144 (November 2, 2012).

Peel, D, and G J McLachlan. 2000. “Robust Mixture Modelling Using the T Distribution.” *Statistics and Computing* 10(4): 339–48.

Pilling, Graham, Peter Williams, John Hampton, and Shelton Harley. 2013. “Analysis of the Implementation and Effectiveness of Key Management Measures for Tropical Tunas.” *Western and Central Pacific Fisheries Commission Scientific Committee, Ninth Regular Session* (August): 1–24.

Pinaud, David, and Henri Weimerskirch. 2005. “Scale-Dependent Habitat Use in a Long-Ranging Central Place Predator.” *Journal of Animal Ecology* 74(5): 852–63.

Pine, WE et al. 2003. “A Review of Tagging Methods for Estimating Fish Population Size and Components of Mortality.” *Fisheries* 28(10).

Pontin, D.R., S. Schliebs, S.P. Worner, and M.J. Watts. 2011. “Determining Factors That Influence the Dispersal of a Pelagic Species: A Comparison between Artificial Neural Networks and Evolutionary Algorithms.” *Ecological Modelling* 222(10): 1657–65.

Prince, Eric D., and C. Phillip Goodyear. 2006. “Hypoxia-Based Habitat Compression of Tropical Pelagic Fishes.” *Fisheries Oceanography* 15(6): 451–64.

Le Quere, CL, and SP Harrison. 2005. “Ecosystem Dynamics Based on Plankton Functional Types for Global Ocean Biogeochemistry Models.” *Global Change Biology* 11(11): 2016–40.

R Core Team. 2013. “R: A Language and Environment for Statistical Computing.” http://www.r-project.org/.

Raftery, Adrian E. 1985. “A Model for High-Order Markov Chains.” *Journal of the Royal Statistical Society. Series B (Methodological)*: 528–39.

Reynolds, Andrew M et al. 2007. “Honeybees Perform Optimal Scale-Free Searching Flights When Attempting to Locate a Food Source.” *The Journal of experimental biology* 210(21): 3763–70.

———. 2009. “Scale-Free Animal Movement Patterns: Lévy Walks Outperform Fractional Brownian Motions and Fractional Lévy Motions in Random Search Scenarios.” *Journal of Physics A: Mathematical and Theoretical* 42(43): 434006.

Rijnsdorp, A. D. et al. 2009. “Resolving the Effect of Climate Change on Fish Populations.” *ICES Journal of Marine Science* 66(7): 1570–83.

Robert, Marianne et al. 2012. “Size-Dependent Behavior of Tuna in an Array of Fish Aggregating Devices (FADs).” *Marine Biology* 159(4): 907–14.

Robert, Marianne, Laurent Dagorn, Jon Lopez, et al. 2013. “Does Social Behavior Influence the Dynamics of Aggregations Formed by Tropical Tunas around Floating Objects? An Experimental Approach.” *Journal of Experimental Marine Biology and Ecology* 440: 238–43.

Robert, Marianne, L Dagorn, Jd Filmalter, et al. 2013. “Intra-Individual Behavioral Variability Displayed by Tuna at Fish Aggregating Devices (FADs).” *Marine Ecology Progress Series* 484: 239–47.

Rohit, Prathibha, G Syda Rao, and K Rammohan. 2010. “Feeding Strategies and Diet Composition of Yellowfin Tuna Thunnus Albacares (Bonnaterre , 1788) Caught along Andhra Pradesh , East Coast of India.” *Fisheries Research* 57(4): 13–19.

Rouyer, T et al. 2008. “Complex Interplays among Population Dynamics, Environmental Forcing, and Exploitation in Fisheries.” *Proceedings of the National Academy of Sciences of the United States of America* 105(14): 5420–25.

Rudnick, Daniel L et al. 2004. “Underwater Gliders for Ocean Research.” *Marine Technology Society Journal* 38(2): 73–84.

Rykaczewski, Ryan R, and David M Checkley. 2008. “Influence of Ocean Winds on the Pelagic Ecosystem in Upwelling Regions.” *Proceedings of the National Academy of Sciences of the United States of America* 105(6): 1965–70.

Schaefer, Kurt M. 1996. “Spawning Time, Frequency, and Batch Fecundity of Yellowfin Tuna, Thunnus Albacares, near Clipperton.” *Fishery Bulletin* 94(1): 98–113.

———. 1998. *Reproductive Biology of Yellowfin Tuna (Thunnus Albacares) in the Eastern Pacific Ocean*. Inter-American Tropical Tuna Commission.

———. 2001. “Reproductive Biology of Tunas.” In *Tuna: Physiology, Ecology, and Evolution, Vol. 19*, eds. Barbara Ann Block and Ernest Donald Stevens. Gulf Professional Publishing., 225–71.

———. 2015. “Movements, Dispersion, and Mixing of Bigeye Tuna (Thunnus Obesus) Tagged and Released in the Equatorial Central Pacific Ocean, with Conventional and Archival Tags.” *Fisheries Research* 161(0): 336–55.

Schaefer, Kurt M., and D. W. Fuller. 2004. “Behavior of Bigeye (Thunnus Obesus) and Skipjack (Katsuwonus Pelamis) Tunas within Aggregations Associated with Floating Objects in the Equatorial Eastern Pacific.” *Marine Biology* 146(4): 781–92.

Schaefer, Kurt M., and Daniel W Fuller. 2005. “Conventional and Archival Tagging of Bigeye Tuna (Thunnus Obesus) in the Eastern Equatorial Pacific Ocean.” *Collect. Vol. Sci. Pap, ICCAT* 57(2): 67–84.

Schaefer, Kurt M., Daniel W Fuller, and Barbara A Block. 2009. “Vertical Movements and Habitat Utilization of Skipjack (Katsuwonus Pelamis), Yellowfin (Thunnus Albacares), and Bigeye (Thunnus Obesus) Tunas in the Equatorial Eastern Pacific Ocean, Ascertained Through Archival Tag Data.” In *Tagging and Tracking of Marine Animals with Electronic Devices*, Reviews: Methods and Technologies in Fish Biology and Fisheries, eds. Jennifer L. Nielsen et al. Dordrecht: Springer Netherlands, 121–44.

Schaefer, Kurt M., and Daniel W. Fuller. 2010. “Vertical Movements, Behavior, and Habitat of Bigeye Tuna (Thunnus Obesus) in the Equatorial Eastern Pacific Ocean, Ascertained from Archival Tag Data.” *Marine Biology* 157(12): 2625–42.

———. 2013. “Simultaneous Behavior of Skipjack (Katsuwonus Pelamis), Bigeye (Thunnus Obsesus), and Yellowfin (T. Albacares) Tunas, within Large Multi-Species Aggregations Associated with Drifting Fish Aggregating Devices (FADs) in the Equatorial Eastern Pacific Ocean.” *Marine Biology* 160(11): 3005–14.

Schaefer, Kurt M., Daniel W. Fuller, and Barbara A. Block. 2007. “Movements, Behavior, and Habitat Utilization of Yellowfin Tuna (Thunnus Albacares) in the Northeastern Pacific Ocean, Ascertained through Archival Tag Data.” *Marine Biology* 152(3): 503–25.

Schelling, TC. 1971. “Dynamic Models of Segregation.” *Journal of mathematical sociology* 1(2): 143–86.

Schliehe-Diecks, S., P. M. Kappeler, and R. Langrock. 2012. “On the Application of Mixed Hidden Markov Models to Multiple Behavioural Time Series.” *Interface Focus* 2(2): 180–89.

Schoener, Thomas W. 1986. “Mechanistic Approaches to Community Ecology: A New Reductionism.” *American Zoologist* 26(1): 81–106.

Schreer, Jason F JF, RJOH J O’Hara Hines, and KM Kit M Kovacs. 1998. “Classification of Dive Profiles: A Comparison of Statistical Clustering Techniques and Unsupervised Artifical Neural Networks.” *Journal of Agricultural, Biological, and Environmental Statistics*: 383–404.

Senina, I, J Sibert, and P Lehodey. 2008. “Parameter Estimation for Basin-Scale Ecosystem-Linked Population Models of Large Pelagic Predators: Application to Skipjack Tuna.” *Progress In Oceanography* 78(4): 319–35.

Sharp, Gary D. 2001. “Tuna Oceanography- An Applied Science.” In *Tuna: Physiology, Ecology, and Evolution, Vol. 19*, eds. Barbara Ann Block and Ernest Donald Stevens. Gulf Professional Publishing., 345–90.

Sibert, John, and John Hampton. 2003. “Mobility of Tropical Tunas and the Implications for Fisheries Management.” *Marine Policy* 27(1): 87–95.

Sibert, John, John Hampton, Pierre Kleiber, and Mark Maunder. 2006. “Biomass, Size, and Trophic Status of Top Predators in the Pacific Ocean.” *Science* 314(5806): 1773–76.

Sibert, John, Inna Senina, Patrick Lehodey, and John Hampton. 2012. “Shifting from Marine Reserves to Maritime Zoning for Conservation of Pacific Bigeye Tuna (Thunnus Obesus).” *Proceedings of the National Academy of Sciences* 109(44): 18221–25.

Sims, David W et al. 2006. “Encounter Success of Free-Ranging Marine Predator Movements across a Dynamic Prey Landscape.” *Proceedings. Biological sciences / The Royal Society* 273(1591): 1195–1201.

———. 2008. “Scaling Laws of Marine Predator Search Behaviour.” *Nature* 451(7182): 1098–1102.

Sims, David W, David Righton, and Jonathan W Pitchford. 2007. "Minimizing Errors in Identifying Lévy Flight Behaviour of Organisms." *The Journal of animal ecology* 76(2): 222–29.

Sims, David W. et al. 2009. "Satellite Tracking of the World's Largest Bony Fish, the Ocean Sunfish (Mola Mola L.) in the North East Atlantic." *Journal of Experimental Marine Biology and Ecology* 370(1-2): 127–33.

Sims, David W., Nicolas E. Humphries, Russell W. Bradford, and Barry D. Bruce. 2011. "Lévy Flight and Brownian Search Patterns of a Free-Ranging Predator Reflect Different Prey Field Characteristics." *Journal of Animal Ecology* 81(2): 432–42.

Sippel, Tim et al. 2014. "Using Movement Data from Electronic Tags in Fisheries Stock Assessment: A Review of Models, Technology and Experimental Design." *Fisheries Research*.

Soria, Marc, Laurent Dagorn, Gaël Potin, and Pierre Fréon. 2009. "First Field-Based Experiment Supporting the Meeting Point Hypothesis for Schooling in Pelagic Fish." *Animal Behaviour* 78(6): 1441–46.

Squires, Dale, and James Kirkley. 1999. "Skipper Skill and Panel Data in Fishing Industries." *Canadian Journal of Fisheries and Aquatic Sciences* 56(11): 2011–18.

Su, N.-J. et al. 2011. "Modelling the Impacts of Environmental Variation on the Distribution of Blue Marlin, Makaira Nigricans, in the Pacific Ocean." *ICES Journal of Marine Science* 68(6): 1072–80.

Sun, C L, Wei-Ren Wang, and Suzan Yeh. 2005. "Reproductive Biology of Yellowfin Tuna in the Central and Western Pacific Ocean." In *Western and Central Pacific Fisheries Commission Scientific Committee, First Regular Session*,.

Taquet, Marc et al. 2007. "Behavior of Dolphinfish (Coryphaena Hippurus) around Drifting FADs as Observed from Automated Acoustic Receivers." *Aquatic Living Resources* 20(4): 323–30.

Tew Kai, Emilie et al. 2009. "Top Marine Predators Track Lagrangian Coherent Structures." *Proceedings of the National Academy of Sciences of the United States of America* 106(20): 8245–50.

Tinker, M.T., D.P. Costa, J.a. Estes, and N. Wieringa. 2007. "Individual Dietary Specialization and Dive Behaviour in the California Sea Otter: Using Archival Time–depth Data to Detect Alternative Foraging Strategies." *Deep Sea Research Part II: Topical Studies in Oceanography* 54(3-4): 330–42.

Torres, LG, AJ Read, and P Halpin. 2008. "Fine-Scale Habitat Modeling of a Top Marine Predator: Do Prey Data Improve Predictive Capacity." *Ecological Applications* 18(7): 1702–17.

Uchiyama, J H, and P Struhsaker. 1981. "Age and Growth of Skipjack Tuna, Katsuwonus-Pelamis, and Yellowfin Tuna, Tunnus-Albacares, as Indiciated by Daily Growth Increments of Sagittae." *Fishery Bulletin* 79(1): 151–62.

Venables, W N, and B D Ripley. 2002. *Modern Applied Statistics with S*. Springer.

Viswanathan, GM, and V Afanasyev. 1996. "Lévy Flight Search Patterns of Wandering Albatrosses." *Nature*.

Wang, Bin, Renguang Wu, and Roger Lukas. 2000. "Annual Adjustment of the Thermocline in the Tropical Pacific Ocean." *Journal of Climate* 13(3): 596–616.

Watson, J W, and D W Kerstetter. 2006. "Pelagic Longline Fishing Gear: A Brief History and Review of Research Efforts to Improve Selectivity." *Marine Technology Society Journal* 40(3): 6–11.

WCPFC Tagging Commitee. 2007. *Pacific Tuna Tagging Programme - Phase 2: Western and Central Pacific*. Pohnpei State.

Weimerskirch, Henri, Matthieu Le Corre, Sébastien Jaquemet, and Francis Marsac. 2005. "Foraging Strategy of a Tropical Seabird, the Red-Footed Booby, in a Dynamic Marine Environment." *Marine Ecology Progress Series* 288: 251–61.

Welsh, Alan H, Ross B Cunningham, C F Donnelly, and David B Lindenmayer. 1996. "Modelling the Abundance of Rare Species: Statistical Models for Counts with Extra Zeros." *Ecological Modelling* 88(1): 297–308.

Wikle, Christopher K, and L Mark Berliner. 2007. "A Bayesian Tutorial for Data Assimilation." *Physica D: Nonlinear Phenomena* 230(1): 1–16.

Wilkinson, David M. 2003. "The Fundamental Processes in Ecology: A Thought Experiment on Extraterrestrial Biospheres." *Biological Reviews of the Cambridge Philosophical Society* 78(2): 171–79.

Williams, Peter. 2013. "Scientific Data Available to the Western and Central Pacific Fisheries Commission." *Western and Central Pacific Fisheries Commission Scientific Committee, Ninth Regular Session* (August): 1–35.

Williams, Peter, and Peter Terawasi. 2012. *Overview of Tuna Fisheries in the Western and Central Pacific Ocean Including Economic Conditions 2011*. Pohnpei.

Williamson, CE, and RW Sanders. 1996. "Utilization of Subsurface Food Resources for Zooplankton Reproduction: Implications for Diel Vertical Migration Theory." *Limnology and Oceanography* 41(2): 224–33.

Willis, Jay, and Lucas Merckelbach. 2011. "Lévy Flights Are Not Evolved Behaviour." *Nature Precedings* 6564(1): 1–7.

Wilson, Steven G., and Barbara A. Block. 2009. “Habitat Use in Atlantic Bluefin Tuna Thunnus Thynnus Inferred from Diving Behavior.” *Endangered Species Research* 10: 355–67.

Zhao, Qinpei, Mantao Xu, and P Franti. 2008. “Knee Point Detection on Bayesian Information Criterion.” In *Tools with Artificial Intelligence, 2008. ICTAI’08. 20th IEEE International Conference on*, , 431–38.

Zhu, G, X Dai, Li Ming Song, and L Xu. 2011. “Size at Sexual Maturity of Bigeye Tuna Thunnus Obesus (Perciformes: Scombridae) in the Tropical Waters: A Comparative Analysis.” *Turkish Journal of Fisheries and Aquatic Sciences* 11: 149–56.