Novel methods for quantifying movement behavior
of free-ranging fish from telemetry data

by

Kilian Michael Stehfest

BSc, MRes

This thesis is submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the CSIRO-UTAS PhD Program in Quantitative Marine Science.

Institute for Marine and Antarctic Studies

University of Tasmania, Australia

July 2013
**Statements and declarations**

**Declaration of Originality**
This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

**Authority of Access**
This thesis may be made available for loan and limited copying and communication in accordance with the Copyright Act 1968.

**Statement regarding published work contained in thesis**
The publisher of the paper comprising Chapter 2 holds the copyright for that content, and access to the material should be sought from the journal. The remaining non published content of the thesis may be made available for loan and limited copying and communication in accordance with the Copyright Act 1968.

**Statement of Ethical Conduct**
The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University. All research conducted for this thesis was approved by the University of Tasmania Animal Ethics Committee (Permit No. A0011590).

Kilian Michael Stehfest

Hobart, 3rd of April, 2013
Statement of Co-Authorship

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

- **Kilian Stehfest**, Fisheries Aquaculture and Coasts, Institute for Marine and Antarctic Studies
- **Dr. Toby Patterson**, CSIRO Wealth from Oceans National Research Flagship
- **Dr. Jayson Semmens**, Fisheries Aquaculture and Coasts, Institute for Marine and Antarctic Studies
- **Dr. Laurent Dagorn**, Institut de Recherche pour le Développement
- **Dr. Kim Holland**, Hawaiian Institute of Marine Biology (HIMB), University of Hawaii
- **David Itano**, Hawaiian Institute of Marine Biology (HIMB), University of Hawaii
- **Dr. Adam Barnett**, School of Life and Environmental Sciences, Deakin University

Author details and their roles:

**Paper 1**, Network analysis of acoustic tracking data reveals the structure and stability of fish aggregations in the ocean

*Located in chapter 2*

The candidate was the primary author; Toby Patterson and Jayson Semmens are primary supervisors, providing advice on analytical techniques and manuscript preparation. Laurent Dagorn, Kim Holland and David Itano collected the data analysed in this paper. Laurent Dagorn provided advice on manuscript preparation.

**Paper 2**, Intraspecific differences in movement, dive behavior and vertical habitat preferences of a key marine apex predator

*Located in chapter 3*

The candidate was the primary author; Toby Patterson and Jayson Semmens are primary supervisors, providing advice on analytical techniques and manuscript preparation. Jayson Semmens assisted with data collection, Adam Barnett collected some of the data analysed and provided advice on manuscript preparation.

We the undersigned agree with the above stated “proportion of work undertaken” for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

**Dr. Jayson Semmens**  
Primary Supervisor  
Fisheries, Aquaculture and Coasts  
Institute for Marine and Antarctic Studies  
University of Tasmania

**Prof. Colin Buxton**  
Director  
Fisheries, Aquaculture and Coasts  
Institute for Marine and Antarctic Studies  
University of Tasmania
# Table of Contents

**Chapter 1 - General Introduction** ................................................................. 11  
 1.1 Movement ecology: Concepts and significance .............................................. 11  
 1.2 Fish tracking techniques: a historical overview ........................................... 14  
 1.3 Automated acoustic telemetry: Array designs ............................................. 18  
 1.4 Automated acoustic telemetry: Data analysis .............................................. 20  
 1.5 Network analysis ......................................................................................... 22  
 1.6 Markov chain analysis .................................................................................. 24  
 1.7 Thesis objectives and structure .................................................................... 26  

**Chapter 2 - Network analysis of acoustic tracking data reveals the structure and stability of fish aggregations in the ocean** ................................................................. 29  
 2.1 Introduction ................................................................................................... 29  
 2.2 Materials and methods ................................................................................ 33  
    2.2.1 Data collection ....................................................................................... 33  
    2.2.2 Animal ethics ....................................................................................... 35  
    2.2.3 Association calculations ....................................................................... 36  
    2.2.4 Network analysis .................................................................................. 39  
    2.2.5 Analysis of movement patterns ............................................................. 40  
    2.2.6 Temporal analysis ................................................................................ 41  
 2.3 Results ........................................................................................................ 45  
    2.3.1 Dataset overview .................................................................................. 45  
    2.3.2 Network structure ................................................................................ 46  
    2.3.3 Movement patterns .............................................................................. 47  
    2.3.4 Temporal dynamics ............................................................................. 48  
 2.4 Discussion .................................................................................................... 57  

**Chapter 3 - Intraspecific differences in movement, dive behavior and vertical habitat preferences of a key marine apex predator** ......................................................... 65  
 3.1 Introduction .................................................................................................. 65  
 3.2 Methods ...................................................................................................... 69  
    3.2.1 Tagging of sharks ................................................................................. 69  
    3.2.2 Data analysis ....................................................................................... 70  
 3.3 Results ........................................................................................................ 76  
    3.3.1 Large-scale movement ....................................................................... 76
3.3.2 Temperature preferences ................................................................. 77
3.3.3 Depth preferences ........................................................................ 78
3.4 Discussion ......................................................................................... 88

Chapter 4 - Quantifying coastal shark movement behaviour from acoustic telemetry data: Sex specific differences in space-use of the broadnose sevengill shark .................................. 95

4.1 Introduction ..................................................................................... 95
4.2 Materials and methods ................................................................. 101
  4.2.1 Data collection ........................................................................... 101
  4.2.2 Data processing ........................................................................ 103
  4.2.3 Social network analysis ............................................................. 104
  4.2.4 Spatial network analysis ............................................................. 105
  4.2.5 Empirically derived Markov chain (EDMC) analysis .................... 108
  4.2.6 Pattern oriented modeling (POM) ............................................... 111
4.3 Results .......................................................................................... 115
  4.3.1 Dataset overview ...................................................................... 115
  4.3.2 Social network analysis ............................................................. 116
  4.3.3 Spatial network analysis ............................................................. 117
  4.3.4 Pattern oriented modeling (POM) ............................................... 117
  4.3.5 Comparison of eigenvector ranks ............................................... 119
4.4 Discussion ..................................................................................... 130

Chapter 5 - General discussion ............................................................ 138

5.1 Summary and implications of ecological findings .............................. 139
  5.1.1 Yellowfin tuna (Thunnus albacores) ............................................ 139
  5.1.2 Broadnose sevengill shark (Notorynchus cepedianus) ................... 141
5.2 Methodological advances and future directions ................................ 143
  5.2.1 Network analysis ...................................................................... 143
  5.2.2 Markov chain analysis ............................................................... 145

Chapter 6 - References ....................................................................... 149

Chapter 7 - Appendix I ........................................................................ 183
List of Figures

Figure 2.1 Map of the FAD array around the island of Oahu equipped with automated acoustic receivers.................................................44
Figure 2.2 Sociogram of a) associations between tuna tagged in 2002/2003 and b) associations between tuna tagged in 2005........................................................................................................53
Figure 2.3 Map of the tuna movement network in the FAD array with lines showing between-FAD transitions of tagged tuna for a) 2002/2003 and b) 2005 .................................................................54
Figure 2.4 Plot of lagged association rate (LAR), null association rate (NAR), fitted model of exponential decay in association and survival probability for a) 2002/2003 dataset and b) 2005 dataset. ........................................................................................................55
Figure 2.5 Plot of lagged association rate (LAR), null association rate (NAR), fitted model of exponential decay in association and survival probability for a) small fish and b) medium sized fish tagged in 2005.................................................................56

Figure 3.1 Map of a) PSAT tagging locations in the Derwent Estuary/Norfolk Bay, b) tag pop-up locations, c) most probable tracks estimated using Kalman filtering of raw geolocation data. ................................................75
Figure 3.2 Sea surface temperature (SST) encountered by individual a) male and b) female sharks during the PSAT deployment period. ..........................................................................................................................81
Figure 3.3 Weighted mean swimming depth and interpolated temperature/depth profiles for a) 5 tagged male seven-gill sharks and b) 5 tagged female seven-gill sharks.................................................83
Figure 3.4 Cumulative distribution function of time spent at a) temperature bins and b) spent at depth bins ...........................................................................................................................................................................84
Figure 3.5 Vertical movements for two 10 day periods from a) two male and b) two female broadnose seven-gill sharks............................................................................................................................87
Figure 3.6 Change in power over time for the 6, 12 and 24 hour periodicity in swimming depth for shallow and deep swimming phases........................................................................................................86

Figure 4.1 Map of study area showing acoustic receiver locations and receiver groupings used for data analyses..................................................................................................................................................114
Figure 4.2 Detection and transition frequencies for male and female broadnose seven-gill sharks ........................................................................................................................................................................125
Figure 4.3 Degree centrality and eigenvector centrality ranks for the adjacency matrix and the matrix of between-state transition frequencies for male and female broadnose seven-gill sharks. ..........................................................................................................................126
Figure 4.4 Density distribution of movement range after 30, 60 and 90 days since tagging for observed data and model simulations for male and female broadnose seven-gill sharks. ............127
Figure 4.5 Cumulative empirical distribution functions (CEDFs) for percent of time spent near the shark nursery area boundaries and time taken since tagging to move from the Derwent to Norfolk Bay or vice versa for the observed data and model simulations for male and female broadnose seven-gill sharks......................................................................................128
Figure 4.6 Ranks of spatial states from the dominant eigenvector of the transition probability matrix for the Markov chain model for male and female broadnose seven-gill sharks.............129
List of Tables

Table 2.1 Negative exponential models of association decay over time fitted to the dataset... 43
Table 2.2 Dataset overview .................................................................................................................. 50
Table 2.3 Mean simple ratio index of association (SRI) for each individual, averaged over the dataset as a whole and within tagging cohorts for small and medium sized tuna .................. 51
Table 2.4 Network metrics calculated for the tuna movement networks................................. 51
Table 2.5 Mean number of associates per individual by tagging FAD and number of fish tagged per FAD................................................................................................................................. 51
Table 2.6 Negative exponential models and model parameter values of association decay over time which best fit the 2002/2003 and 2005 datasets.................................................................................................................. 52

Table 3.1 Dataset overview. .............................................................................................................. 73
Table 3.2 Data collection and summary set-up of the pop-up satellite archival tags (PSATs)..... 74

Table 4.1 Dataset overview ............................................................................................................... 120
Table 4.2 Comparison of proportion of SRI elements of value zero, mean SRI and coefficient of variation (C.V.) of the SRI for the real and permuted association data ..................................... 121
Table 4.3 Results for pattern-oriented modeling of 5 pertinent ecological indices of space-use for male sharks....................................................................................................................................... 122
Table 4.4 Results for pattern-oriented modeling of 5 pertinent ecological indices of space-use for female sharks. ......................................................................................................................... 123
Table 4.5 Proportion of male and female sharks moving between the Derwent and Norfolk Bay for the observed data and model simulations.................................................................................. 124
Abstract

In recent decades, technological progress in the field of biotelemetry has allowed the collection of vast amounts of data on the movement of free-ranging marine animals and recently there have been great advances in analysing data from tags that allow the observation of complete animal tracks. One of the most common and low-cost tools for tracking marine animals, however, are automated acoustic arrays, which often do not record complete tracks but provide presence/absence data for tagged animals at fixed locations. The development of quantitative methods for analysing these data has lagged behind the technological advances in the field.

This thesis applies novel methods for quantifying the movement behaviour of highly mobile free-ranging teleosts and elasmobranchs using automated acoustic tracking data and answers ecological questions of management relevance for tropical tuna (Yellowfin tuna *Thunnus albacares*) and a temperate shark species (Broadnose sevengill shark *Notorynchus cepedianus*). Additionally, pop-up satellite archival tag (PSAT) data are analysed for the temperate shark species, to put the findings of the acoustic tracking data analysis into the context of the animals’ large-scale movement behaviour.

The two acoustic datasets represent two different types of common receiver array designs: For the tuna study, individual receivers were deployed at ecologically significant locations (fish aggregating devices, FADs) to determine the residency at and movement between these
locations. For the shark study, receivers were deployed as multiple curtains between opposite shorelines to detect passes of animals through the curtains and determine general movement patterns within a coastal area.

Network analysis methods were applied to both datasets to quantify the co-occurrence of individuals at a given location and to determine the relative importance of each location to the animals. For the former, we adapted association indices from social network analysis to quantify temporally explicit joint occurrences of individuals. For the latter we treated the number of transitions between locations as a measure of the connectivity between them. The network analysis approach to the acoustic tracking data was well suited to the type of array used in the tuna study and was a considerable improvement over traditional measures of co-occurrence which often only include either the spatial or the temporal dimension, not both. It provided new insight into the temporal dynamics of tuna aggregations at FADs and how they may be linked to between-FAD movement. We observed large interannual variation in movement rates of tuna between FADs, and corresponding interannual variability in the mean number of spatio-temporal associates for each individual as well as the temporal stability of associations. When movement rates were high, associations within FAD aggregations decayed to randomness three times faster than when movement rates were lower. This raises the possibility that if FADs are sufficiently close for fish to perform frequent between-FAD movements, school mixing may be increased and cohesion reduced.
For the shark data, we compared results from the network analysis to a Markovian movement model estimated from counts of observed transitions. Specifically, we tested the suitability of the two methods for determining whether the differences in large-scale movement behaviour between males and females we established from the PSAT data are mirrored in their space-use during their coastal summer residency. Both spatial network analysis and Markov chain analysis showed differences in space-use between male and female broadnose sevengill sharks, however, rankings of the relative importance of geographic areas differed between the two approaches. This indicated that not only transitions but also residency periods, which are not accounted for by spatial network analysis, were important for identifying priority areas for the sharks.

Determining how animals interact and move within their environment has been a relatively understudied area, lacking in quantitative analytical methods. This thesis has applied various novel approaches which quantify both how individuals interact and use space, deepening our understanding of the two and the link between them.
Acknowledgements

First and foremost, I would like to thank my two supervisors Toby Patterson and Jayson Semmens for their tireless motivation, guidance and support throughout this PhD. It wouldn’t have been possible without them.

I would also like to thank Stewart Frusher and Mark Hindell for their support in the initial stage of my PhD and for making me feel welcome when I first arrived in Tasmania.

I would furthermore like to thank Laurent Dagorn for his collaboration and for making highly productive and enjoyable trips to the Seychelles and Azores possible.

Many thanks go out to Adam Barnett, Laurent Dagorn, Kim Holland and David Itano for letting me play with their data and Jaime McAllister and Russ Bradford for helping me collect my own.

I would also like to extend my gratitude to Bill Holsworth and the Holsworth Wildlife Research Endowment for their generous financial support over the course of my PhD.

Last but not least, I am deeply grateful to my friends and family for all their love and support and to all my partners in crime at TAFI and CSIRO, who managed to make 4 years of sitting in an office a lot of fun.