UC San Diego UC San Diego Electronic Theses and Dissertations

Title

Navigating a seascape: physiological and environmental motivations behind juvenile North Pacific albacore movement patterns

Permalink https://escholarship.org/uc/item/46m1g0sm

Author Snyder, Stephanie M.

Publication Date 2016

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA, SAN DIEGO

Navigating a seascape: physiological and environmental motivations behind juvenile North Pacific albacore movement patterns

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy

in

Marine Biology

by

Stephanie Snyder

Committee in charge:

Peter J.S. Franks, Chair Lin Chao Phil Hastings Suzanne Kohin Brice Semmens Lynne Talley

2016

Copyright

Stephanie Snyder, 2016

All rights reserved.

The Dissertation of Stephanie Snyder is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2016

TABLE OF CONTENTS

Signature Pageii	ii
Table of Contentsiv	v
List of Figures	'n
List of Tablesiz	X
Acknowledgements	X
Vitaxiv	v
Abstract of the Dissertationxv	V
Chapter 1 Introduction	1
References	б
Chapter 2 Quantifying the effects of sensor coatings on body temperature measurement	S ∕I
2 1 Abstract 14	+ 4
2.1 Prostate 1 2.2 Introduction 14	5
2.2 Introduction	7
2.5 Metalods	, 6
2.5 Discussion	8
2.6 Conclusion 3	0
2.7 References	7
Chapter 3 Influence of thermal habitat on thermoregulation in a regional endotherm	l,
albacore tuna (<i>Thunnus alalunga</i>)	1
3.1 Abstract	1
3.2 Introduction	2
3.3 Materials and Methods	4
3.4 Results	0
3.5 Discussion	б
3.6 Conclusion	9
3.7 References	8
Chapter 4 Seasonal habitat suitability along a latitudinal gradient explains variability in	n
migratory behavior of juvenile albacore tuna	2
4.1 Abstract	2

4.2 Introduction	73		
4.3 Materials and Methods	76		
4.4 Results			
4.5 Discussion			
4.6 References			
Chapter 5 Fronts serve as a dual resource: Insights from in situ observations of juvenile			
tuna (Thunnus alalunga) at an open ocean front			
5.1 Summary			
5.2 Introduction, Results, and Discussion			
5.3 Materials and Methods			
5.4 References	117		
Chapter 6 Conclusions			
Appendix Supplementary information for Chapter 3			

LIST OF FIGURES

Figure 2.1 Illustration of the influence of sensor thermal inertia on body temperature measurements. Simulation of a sensor with a coefficient of conductance of 0.81 min⁻¹ (T_s , black) measuring the body temperature (T_b , red) of a 100 g Atlantic sea raven as it shuttles between water temperatures of 10 and 20 °C (T_a , gray) with a duty cycle 33

Figure 2.4 Data and results from Mk9 calibration. **a** Mk9 internal (solid grey line) and external sensors (solid black line) measuring ambient temperature (dashed grey line) during the calibration experiment (entire time series shown in inset). The red and blue lines represent the analytical solutions for the mean internal and external sensor 35

Figure 3.3 Albacore behavioral thermoregulation. (a) Day of observed body temperature (solid red line) and the corresponding modeled body temperature (dashed red line) given dive response to critical upper and lower temperatures, within the context of the observed water temperature (solid blue line) and modeled water temperature.. 64

Figure 3.4 Physiologically set body temperature (a) Histograms of T_{ss} at each of the microhabitats of shuttling and tracking while at the surface and at depth (b) Difference between realized mean body temperature and the physiologically set steady state temperatures, T_{ss} . The boxplots represent the interquartile range about the median 65

Figure 4.2 Migratory destinations and behavior of fish originating (a-b) north and (c-d) south of 40°N. In (a) and (c), the circles blue circles and squares represent outbound origins and inbound destinations, respectively, while the red circles represent the outbound destinations/inbound origins. The compass plots show the *WMV* per fish ...92

Figure 4.5 Fluctuations in (a,d) SST, (b,e) MLD and (c,f) k490 at the outbound origins (in blue), the outbound destinations (red) and at the fish's selected location (in grey). Northern fish are represented in the top panel with southern fish in the bottom panel...96

Figure 5.1 Front Characterization. Maps of (a) chlorophyll and (b) sea surface temperature from satellite imagery on the first day of the study, with the estimated fish locations as white circles. (c) Temperature profiles of the cold (blue) and warm (red) sides of the front derived from the albacore archival tagging data (grey circles) 114

Figure 5.3 Movement at Front. (a) Time series associated with each fish of diving behavior in the top 100 m with colors representing water temperature and the black bars representing nighttime. (b) Distributions of mean percent time at depth at night (shaded background) and day (white background) on either the warm (red) or cold (blue) ... 115

LIST OF TABLES

Table 2.1 Species specific relationships $(k_b = aW^{-b})$ between mass (W, g) and the specific rate of body temperature change (k_b, \min^{-1}) where *a* and *b* are empirically derived constants. Number of organisms used in the experiments is denoted by *n*......32

Table 3.1 Deployment and recovery information for the fish used in this study. Fish inorder of increasing size at tag deployment. Recovery fork lengths in parentheses wereestimated using our mean observed growth rate61	
Table 3.2 Distributions of thermal rates by behavioral mode	
Table 4.1. Juvenile albacore used in this study	
Table 4.2 Migratory behavior of the juvenile albacore tuna 91	
Table 4.3 Habitat characteristics of residence areas and of the migrating fish. *Denotes significance between northern and southern fish to the $p < 0.01$, ^x denotes significance between the origins and destinations, and [*] denotes significant difference between the residence area and the fish	
Table 5.1 Deploy and recovery information on juvenile albacore used in this study116	
Table A1 The effect of window length on the ability to estimate thermal rates	

ix

ACKNOWLEDGEMENTS

First and foremost, I would like to acknowledge my friends and family for their love and support through this weird thing that is a doctorate in philosophy. Even though most of them had no clue what I was doing (or why), they supported me every step of the way. Their belief in me and blind trust that I was doing something worthwhile meant more than they know. I'm so fortunate to have these people in my life: **Maribeth**, **John**, **and Andy Snyder; Mike, Christine, Rick, Carol, April, Jenny, Colin, and Chris Monahan, Megan Krombach, Bridget Carroll, Lauren and John Brewster, Amy Pease, Rosa Runcie, and Moira Igor.**

I would like to acknowledge **Dr. Peter J.S. Franks** for his mentorship and advising throughout this thesis. Peter's scientific insight, perception, and compassion are some of the many aspects of his mentorship that were integral to the completion of this thesis. It is not an exaggeration to say that I would not have gotten to this stage if it wasn't for his guidance and support. I am forever indebted to him and will try to emulate his dedication to others wherever life takes me.

I would also like to thank **Dr. Suzanne Kohin**. Suzy is the reason I made it to Scripps, and her sense of humor, her enthusiasm (and also her cynicism) got me through some of the really tough times at SIO. She has been a great mentor and role model. I have her to thank for really fostering me into the scientific world, and making me feel like I belong there. Suzy not only gave me my first "scientist" job, but she also is the reason I can even start to call myself a scientist. This thesis also could not have been possible if it wasn't for the all the people who have worked to make the Albacore Archival Tagging Program such a success. In particular, I'd like to thank **John Childers** for all his time at sea, tagging albacore, and in his organization of the data. John was great to work in the field with. I admired his ability to not stress out while the fish were flying at our heads as we tried to get tags out. Those were good times.

Many thanks to the members of my committee – **Dr. Lin Chao, Dr. Lynne Talley, Dr. Phil Hastings**, and **Dr. Brice Semmens.** They always had an open door along with enthusiasm and interest in the thesis. It was really refreshing – especially towards the end to be able to discuss the projects with them and to get new insights on things that I'd been staring at for years. For their insights and the boosts of encouragement, I am very grateful.

A big thank you to the current and past members of the Franks lab: **Dr. Christian Briseno, Dr. Fanny Chanillat, Dr. Alain deVerneil, Jessica Garwood, Bryce Inman, Dr. Darcy Taniguchi,** and **Dr. Meg Rippy**. They were a pleasure to work with and could always be counted on for advice and fun.

Another part of my SIO support group were the 2010 Cohort. They were a really fantastic group and I am grateful for all the study sessions, beers, surfs, volleyball games, etc. Out of this group, I'd like to thank the following people in particular: **Noah Ben-Aderet, Raffeala Abbraino, Dr. Amanda Netburn, Rachel Morrison, Doug Krause, Trevor Joyce, Anne Simones, Dr. Charles Perreti, Dr. Shane Hogle,** and **Dr. Michelle Kim**. During my thesis, I had the good fortune of working with the people of the Center for Macroecology, Climate and Evolution at the University of Copenhagen. The researchers there really helped me put my research into a broader perspective. In particular, I'd like to thank: **Dr. Carsten Rahbek, Dr. Kasper Thorup, Kat Snell,**

Lykke Pedersen, Dr. Mikkel Willemoes, Pauliina Ahti, and Dr. Israel Del Toro.

Lastly, I'd like to acknowledge my financial and logistical support. Many thanks to those in the SIO graduate office who assisted in finding money for me throughout my time here for classes or travel, especially **Denise Darling** and **Maureen McCormick**. They made life easier. Many thanks to the National Science Foundation reviewers for deeming me worthy for their Graduate Researcher Fellowship and Graduation Opportunities Worldwide Fellowship. Both of these fellowships have opened up doors that I couldn't have even imagined.

Chapter 2, in full, is a reprint of the material as it appears in *Animal Biotelemetry* 2016. Snyder, Stephanie, Franks; Peter J.S. The dissertation author was the primary investigator and author of this paper.

Chapter 3, in full, is currently being prepared for submission for publication of the material. Snyder, S., Chao, L., Kohin, S., and P.J.S. Franks. The dissertation author was the primary investigator and author of this paper.

Chapter 4, in full, is currently being prepared for submission for publication of the material. Snyder, S., Kohin, S., Rahbek, C., Thorup, K., and P.J.S. Franks. The dissertation author was the primary investigator and author of this paper. Chapter 5, in full, is currently being prepared for submission for publication of the material. Snyder, S., Xu, Y., Talley, L., Kohin, S. and P.J.S. Franks. The dissertation author was the primary investigator and author of this paper.

VITA

2007 Bachelor of Science, Coastal Carolina University

2014 Master of Science, University of California, San Diego

2016 Doctor of Philosophy, University of California, San Diego

PUBLICATIONS

Smith, J., **Snyder, S.**, Berkson, J., Murphy, B.R., and S.L. McMullin (2009) Fisheries Management of Red Snapper in the Gulf of Mexico: A Case Study. Journal of Natural Resources and Life Sciences Education 38: 115-27.

Abbriano, R.M., M.M. Carranza, S.L. Hogle, R.A. Levin, A.N. Netburn, K.L. Seto, **S.M. Snyder**, SIO280, and P.J.S. Franks (**2011**) Deepwater Horizon oil spill: A review of the planktonic response. <u>Oceanography</u> 24 (3): 294–301.

Childers, J., **Snyder, S**., and S. Kohin (**2011**) Migration and behavior of juvenile north Pacific albacore (*Thunnus alalunga*). <u>Fisheries Oceanography</u>. 20(3): 157-173.

Snyder, S., L. E. Nadler, J. S. Bayley, M.B.S. Svendsen, J. L. Johansen, P. Domenici and J. F. Steffensen (**2016**) Effect of closed versus intermittent-flow respirometry on hypoxia tolerance in aquatic breathers. *Journal of Fish Biology*

Snyder, S. and P.J.S. Franks (**2016**) Quantifying the effects of sensor coatings on body temperature measurements. <u>Animal Biotelemetry</u> 4(8). DOI: 10.1186/s40317-016-0100-0

ABSTRACT OF THE DISSERTATION

Navigating a seascape: physiological and environmental motivations behind juvenile North Pacific albacore movement patterns

by

Stephanie Snyder

Doctor of Philosophy in Marine Biology

University of California, San Diego 2016

Professor Peter J.S. Franks, Chair

Characterization of an animal's movement patterns and the motivations behind those movements can allow us to predict their response to changes in the environment or ecosystem. In my thesis, I use biotelemetry data and mechanistic models to investigate the movements of albacore tuna within the context of their thermal biology as they move through a dynamic and heterogeneous thermal environment. My results indicate that albacore have thermal habitat constraints dictated by their inability to maintain a functional body temperature in SST below 11 °C, and high behavioral and physiological costs at SST above 20 °C. I show that albacore migrations are longer and have more consistent phenology and direction when fish are migrating between habitats whose sea surface temperatures trend below 13°C and above 20 °C. Albacore time their migrations with annual changes in the temperatures of their origins and destinations. I also show that thermal fronts serve as a dual resource to albacore. I characterize the movement of four tunas as they utilize sub-mesoscale features associated with a thermal front. For two weeks, the tunas swam between the warmest and coldest available waters, making on average 50 trips across the front per day, with 85% of these occurring during daytime. The use of the warm side of the front resulted in an increase in body temperature, and the strength of the front was directly correlated with foraging success. This work provides the necessary parameters to model albacore movement and a mechanistic understanding of the limits to albacore distribution.

CHAPTER 1

Introduction

Animal movement shapes the ecosystems and biodiversity patterns of our planet. The paths, extents and timings of animal movement influence predator/prey dynamics (Lampert 1989; Abrams 2007; Sims et al. 2005), species distributions (Parmesan et al. 1999), and population dynamics (Fiksen et al. 2007). The vast implications of animal movement have led to a wealth of studies that have provided empirical observations (Payne et al. 2014; Costa, Breed, and Robinson 2012; Rutz and Hays 2009) as well as mathematical and theoretical frameworks (Sainmont, Thygesen, and Visser 2013; Pedersen et al. 2011; McClintock et al. 2012; Singh et al. 2012; Jachowski and Singh 2015; Morales et al. 2004; Nathan et al. 2008; Holyoak et al. 2008; Bauer et al. 2009). In my thesis, I investigate the movement of juvenile albacore tuna within the context of their thermal physiology as they migrate through a heterogeneous and rapidly changing thermal environment.

Albacore tuna (*Thunnus alalunga*) is a globally distributed, temperate tuna species comprising 6 percent of the global tuna catch (FAO, 2016). North Pacific albacore are highly migratory, with migrations spanning the entirety of the North Pacific Ocean throughout their life cycle (Otsu and Uchida 1963; Laurs and Lynn 1977; Childers, Snyder, and Kohin 2011). Their migration patterns are ontogenetically defined, with largest migrations observed in juveniles, ages 2-5 years. Migration routes have been well described (Childers, Snyder and Kohin, 2011; Laurs and Lynn 1977) and their paths have been correlated with the North Pacific transition zone (Zainuddin

et al. 2006). Albacore, like many organisms in the world's marine ecosystems maintain portions of their bodies at temperatures above ambient temperatures (Graham and Dickson 1981). Their thermoregulation is hypothesized to increase swimming speed and efficiency (Altringham and Block 1997; Dewar and Graham 1994; Brill 1996; Bernal et al. 2001), enhanced vision (Fritsches, Brill, and Warrant 2005), increased digestion rates (Newton, Wraith, and Dickson 2015), and larger thermal niches (Dickson and Graham 2014; Block et al. 1993). However, this trait comes at a physiological cost of increased metabolic rate (Dickson and Graham 2014), and has been shown to incur elevated metabolic rates at both low and high temperatures – a metabolic rate curve characteristic of endotherms – in bluefin tuna (Blank et al. 2007). Thus, regional endothermy is a trade-off between the physiological costs of metabolic heat production and the benefits of niche expansion and predatory capabilities.

I examine the influence of the thermal habitat on albacore thermoregulation. Characterizations of thermoregulation can be used to determine habitat availability (Magnuson et al. 1979; Porter and Kearney 2009), behavior (Huey 1974; Angilletta 2009), and vulnerability to climate change (Helmuth, Kingsolver, and Carrington 2005; Huey et al. 2012). Our understanding of thermoregulation relies on accurate measures of body temperature and the rates at which body temperature changes given different thermal environments. There are many challenges to obtaining these measurements (McCafferty, Gallon, and Nord 2015), not the least of which is sensor thermal inertia, i.e. the ability of the sensor to resist changes in temperature. While researchers acknowledge that sensor thermal inertia exists, the significance of its effect on body temperature measurements is under debate (Schaefer and Fuller 2006; Roznik and Alford 2012). In **Chapter 2**, I provide methods to quantify and correct for sensor thermal inertia, and investigate the thermal inertia of the temperature sensors on Wildlife Computer's Mk9 data logger. I characterize the influence of the sensor thermal inertia on simulated and measured body temperature measurements over a range of species and organism size.

In **Chapter 3**, I explore how the thermal environment influences the behavioral and physiological aspects of thermoregulation in juvenile albacore tuna, a regional endotherm. Regional endotherms exhibit a mix of behavioral and physiological strategies to thermoregulate (Holland and Sibert 1994; Holland et al. 1992; Casey, James, and Williard 2014). As exhibited in ectotherms, behavioral thermoregulation can consist of selecting a preferred temperature or shuttling between temperature extremes (Huey 1974). Behavioral thermoregulation in regional endotherms has been demonstrated in their diving behavior – which consists of a trade-off between foraging in cold waters at depth and warming in food-poor waters at the surface (Holland et al. 1992; Dizon and Brill 1979; Casey, James, and Williard 2014). Similar to endotherms, regional endotherms can also physiologically thermoregulate by increasing their metabolic output - as seen in the captive bluefin (Blank et al. 2007) and albacore (Graham and Dickson 1981) tuna – or by decreasing their rates of heat loss to the environment. Bigeye (Holland and Sibert 1994) and yellowfin (Dewar, Graham, and Brill 1994) tuna have been shown to change their rates of heat loss and heat gain depending on the ambient temperature, and bluefin tuna have been shown to alter their rates by season (Teo et al. 2007). I use decades of biotelemetry data coupled with mechanistic models to examine both thermal habitat use and the thermal rates of body temperature change associated with the albacore's level of insulation and metabolic activity. I examine the costs and thermoregulatory outcomes of the tuna that generated these data, using sea surface temperature as an environmental descriptor.

In Chapter 4, I build upon the results of Chapter 3 by examining whether migrations were driven by seasonal changes in habitat suitability. One of the ways to explore the reasons behind movement, and furthermore to understand the adaptability of migration, is to place the variability in observed behavior within a framework of testable hypotheses (Rutz and Hays 2009; Kirby 2001). Biotelemetry data provide measures of the propensity (i.e., the probability to migrate and/or the migratory distances), the residential areas (i.e., the origins and destinations of migration), and the phenology (i.e., the departure and arrival dates) of migration. By coupling this information with large-scale environmental data (e.g., satellite data on abiotic and biotic factors in the environment) and examining the variability among individual behaviors, we can test the importance of different drivers of movement. Chapter 4 uses empirical observations of both albacore movement and their environment to test the hypothesis that habitat suitability drives migration in juvenile albacore tuna. Albacore distributions have been linked to sea surface temperature (Laurs and Lynn 1985; Laurs, Fiedler, and Montgomery 1984; Kimura, Nakai, and Sugimoto 1997) and thermal fronts (Xu et al. 2015). The depth of the thermocline (Childers, Snyder, and Kohin 2011) and the turbidity of the water column (Murphy 1959) have been shown to influence their vertical distributions and foraging capabilities. Thus, I examine both the vertical and the horizontal habitat by assessing the gradients in light and temperature with depth, and sea surface temperature. To test the hypothesis that habitat selection drives migratory behavior, I made the following predictions: (i) the propensity to migrate would be positively correlated with the annual amplitude of environmental fluctuations at the outbound origins, (ii) the phenology of migration aligns with the fluctuations of environmental conditions at the origin of the migratory segments, and (iii) the destinations of migratory segments at the time of migration would have significantly different environmental conditions than the origins, and that these differences will always be in the direction of the median environmental conditions observed across all fish.

In **Chapter 5**, I examine albacore use of thermal fronts. We are at the frontier of understanding the dynamics of how fronts alter pelagic ecosystems, and why organisms accumulate (in the case of drifters) or aggregate (in the case of swimmers) at fronts (Block 2005; Franks 1992; Olson et al. 1994). With increased spatial and temporal sampling of our oceans, we are discovering that sub-mesoscale features (Levy et al. 2012), such as the ones featured here, change the community structure, abundance and distributions of a wide spectrum of organisms including bacteria (Landry et al. 2012; Floodgate et al. 1981), planktonic organisms (Landry et al. 2012; Olson and Backus 1985; Powell and Ohman 2015), the migrating organisms of the deep scattering layer (Landry et al. 2012), and charismatic megafauna such as the tunas (Xu et al. 2015; Sund, Blackburn, and Williams 1981b; Humphries et al. 2010), sharks (Queiroz et al. 2012; Sims and Quayle 1998; Humphries et al. 2010), turtles (Polovina et al. 2000), marine mammals (Baumgartner et al. 2001; Bost et al. 2009), and birds (Hunt, Harrison, and Piatt 1993; Scheffer, Bost, and Trathan 2012; Nel et al. 2001). It is thought that large predators are drawn to these areas to take advantage of the accumulation of prey (Costa, Breed, and Robinson 2012; Block 2005; Olson et al. 1994; Sims and Quayle 1998; Humphries et al. 2010), and that regional endotherms, such as tunas, also take advantage of the warm waters of the front to assist in thermoregulation (Olson et al. 1994; Kirby and Hart 2000; Kirby 2001; Queiroz et al. 2012). Warmer temperatures for these organisms translates into faster swimming speeds, better visual acuity, and increased digestion rates (Dickson and Graham 2014); thus fronts increase foraging performance in addition to prey abundance. Theoretical work has been done to model the optimal behavior at fronts, and to test if this behavior would lead to thermoregulatory advantages, with mixed results (Kirby and Hart 2000). To investigate this 'dual resource' theory, I used *in situ* behavior and environmental sampling from electronic tags deployed on four juvenile albacore tuna and high-resolution remote sensing imagery.

References

- Abrams, Peter A. 2007. "Habitat Choice in Predator-Prey Systems: Spatial Instability due to Interacting Adaptive Movements." *The American Naturalist* 169 (5): 581– 94. doi:10.1086/512688.
- Altringham, J D, and B A Block. 1997. "Why Do Tuna Maintain Elevated Slow Muscle Temperatures? Power Output of Muscle Isolated from Endothermic and Ectothermic Fish." *The Journal of Experimental Biology* 200 (Pt 20): 2617–27.
- Angilletta, M J. 2009. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press.
- Bauer, S, Zoltan B, Bruno J E, G C Hays, J M McNamara, and M Klaassen. 2009. "Animal Migration: Linking Models and Data beyond Taxonomic Limits." *Biology Letters* 5 (4): 433–35. doi:10.1098/rsbl.2009.0324.
- Baumgartner, M F, K D Mullin, L N May, and T D Leming. 2001. "Cetacean Habitats in the Northern Gulf of Mexico." *Fishery Bulletin* 99 (2): 219–39. doi:10.1016/S0967-0637(01)00035-8.

- Bernal, D, K A Dickson, R E Shadwick, and J B Graham. 2001. "Review: Analysis of the Evolutionary Convergence for High Performance Swimming in Lamnid Sharks and Tunas." Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology 129 (2-3): 695–726. doi:10.1016/S1095-6433(01)00333-6.
- Blank, J M, J M Morrissette, C J Farwell, M Price, R J Schallert, and B A Block. 2007.
 "Temperature Effects on Metabolic Rate of Juvenile Pacific Bluefin Tuna Thunnus Orientalis." *The Journal of Experimental Biology* 210 (Pt 23): 4254–61. doi:10.1242/jeb.005835.
- Block, B A. 2005. "Physiological Ecology in the 21st Century: Advancements in Biologging Science." *Integrative and Comparative Biology* 45 (2): 305–20. doi:10.1093/icb/45.2.305.
- Block, B A, J R Finnerty, A F R Stewart, and J Kidd. 1993. "Evolution of Endothermy in Fish: Mapping Physiological Traits on a Molecular Phylogeny." *Science (New York, N.Y.)* 260 (5105): 210–14. doi:10.1126/science.8469974.
- Bost, C A, C Cotté, F Bailleul, Y Cherel, J B Charrassin, C Guinet, D G Ainley, and H Weimerskirch. 2009. "The Importance of Oceanographic Fronts to Marine Birds and Mammals of the Southern Oceans." *Journal of Marine Systems* 78 (3). Elsevier B.V.: 363–76. doi:10.1016/j.jmarsys.2008.11.022.
- Brill, R W. 1996. "Selective Advantages Conferred by the High Performance Physiology of Tunas, Billfishes, and Dolphin Fish." *Comparative Biochemistry* and Physiology - A Physiology 113 (1): 3–15. doi:10.1016/0300-9629(95)02064-0.
- Casey, J P, M C James, and A S Williard. 2014. "Behavioral and Metabolic Contributions to Thermoregulation in Freely Swimming Leatherback Turtles at High Latitudes." *Journal of Experimental Biology* 217 (13): 2331–37. doi:10.1242/jeb.100347.
- Childers, J, S Snyder, and S Kohin. 2011. "Migration and Behavior of Juvenile North Pacific Albacore (*Thunnus Alalunga*)." *Fisheries Oceanography* 20 (March 2010): 157–73. doi:10.1111/j.1365-2419.2011.00575.x.
- Costa, D P, G A Breed, and P W Robinson. 2012. "New Insights into Pelagic Migrations: Implications for Ecology and Conservation," no. August: 73–96. doi:10.1146/annurev-ecolsys-102710-145045.
- Dewar, H, and J Graham. 1994. "Studies of Tropical Tuna Swimming Performance in a Large Water Tunnel - Kinematics." *The Journal of Experimental Biology* 192

(1): 45–59. http://www.ncbi.nlm.nih.gov/pubmed/9317308.

- Dewar, H, J B Graham, and R W. Brill. 1994. "Studies of Tropical Tuna Swimming Performance in a Large Water Tunnel - Thermoregulation." *The Journal of Experimental Biology* 192 (1): 33–44. http://www.ncbi.nlm.nih.gov/pubmed/9317282.
- Dickson, K A, and J B Graham. 2014. "Evolution and Consequences of Endothermy in Fishes." *Physiological and Biochemical Zoology*: *PBZ* 77 (6): 998–1018. doi:10.1086/423743.
- Dizon, A E, and R W Brill. 1979. "Thermoregulation in Tunas." *American Zoologist* 19 (1): 249–65.
- Fiksen, Ø, C Jørgensen, T Kristiansen, F Vikebø, and G Huse. 2007. "Linking Behavioural Ecology and Oceanography: Larval Behaviour Determines Growth, Mortality and Dispersal." *Marine Ecology Progress Series* 347: 195–205. doi:10.3354/meps06978.
- Floodgate, G D, G E Fogg, D A Jones, K Lochte, and C M Turley. 1981. "Microbiological and Zooplankton Activity at a Front in Liverpool Bay." *Nature* 290: 133–36. doi:10.1017/CBO9781107415324.004.
- Franks, P J S. 1992. "Sink or Swim: Accumulation of Biomass at Fronts." *Marine Ecology Progress Series* 82: 1–12. doi:10.3354/meps082001.
- Fritsches, K A, R W Brill, and E J Warrant. 2005. "Warm Eyes Provide Superior Vision in Swordfishes." *Current Biology : CB* 15: 55–58. doi:10.1016/j.
- Graham, J B, and K A Dickson. 1981. "Physiological Thermoregulation in the Albacore *Thunnus Alalunga.*" *Physiological Zoology* 54 (4): 470–86.
- Helmuth, B, J G Kingsolver, and E Carrington. 2005. "Biophysics, Physiological Ecology, and Climate Change: Does Mechanism Matter?" Annual Review of Physiology 67: 177–201. doi:10.1146/annurev.physiol.67.040403.105027.
- Holland, K N, R W Brill, R K Chang, J R Sibert, and D A Fournier. 1992. "Physiological and Behavioural Thermoregulation in Bigeye Tuna (Thunnus Obesus)." *Nature* 358 (6385): 410–12. doi:10.1038/358410a0.
- Holland, K N, and J R Sibert. 1994. "Physiological Thermoregulation in Bigeye Tuna, Thunnus Obesus." *Environmental Biology of Fishes* 40: 319–27.
- Holyoak, M, R Casagrandi, R Nathan, E Revilla, and O Spiegel. 2008. "Trends and Missing Parts in the Study of Movement Ecology."

- Huey, R B, M R Kearney, A Krockenberger, J A M Holtum, M Jess, and S E Williams.
 2012. "Predicting Organismal Vulnerability to Climate Warming: Roles of Behaviour, Physiology and Adaptation." *Philosophical Transactions of the Royal Society B: Biological Sciences* 367 (1596): 1665–79. doi:10.1098/rstb.2012.0005.
- Huey, R B. 1974. "Behavioral Thermoregulation in Lizards: Importance of Associated Costs." *Science*. American Assn for the Advancement of Science.
- Humphries, N E, N Queiroz, J R M Dyer, N G Pade, M K Musyl, K M Schaefer, D W
 Fuller, J M Brunnschweiler, T K Doyle, J D R Houghton, G C Hays, C S Jones, L
 R Noble, V J Wearmouth, E J Southall, and D W Sims. 2010. "Levy and Brownian
 Environmental Context Explains Le Movement Patterns of Marine Predators." *Nature* 465 (7301). Nature Publishing Group: 1066–69. doi:10.1038/nature09116.
- Hunt, G L, N M Harrison, and J F Piatt. 1993. "Foraging Ecology as Related to the Distribution of Plativorous Auklets in the Bering Sea." In *The Status, Ecology, and Conservation of Marine Birds of the North Pacific*, edited by K Vermeer, K.T. Briggs, K.H. Morgan, and D. Siegel-Causey, 18–26. Can. Wildl. Serv. Spec. Publ.
- Jachowski, D S, and N J Singh. 2015. "Themed Issue Article : Conservation Physiology of Animal Migrations Toward a Mechanistic Understanding of Animal Migration : Incorporating Physiological Measurements in the Study of Animal Movement" 3: 1–12. doi:10.1093/conphys/cov035.Introduction.
- Kimura, S, M Nakai, and T Sugimoto. 1997. "Migration of Albacore, *Thunnus alalunga*, in the North Pacific Ocean in Relation to Large Oceanic Phenomena," no. November 1996: 51–57.
- Kirby, D 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*, 407–20.
- Kirby, D S, and P J B Hart. 2000. "A Dynamic Optimisation Model for the Behaviour of Tunas at Ocean Fronts," no. August 1999: 328–42.
- Lampert, W. 1989. "The Adaptive Significance of Diel Vertical Migration of Zooplankton." *British Ecological Society* 3 (1): 21–27.
- Landry, M R, M D Ohman, R Goericke, M R Stukel, K A Barbeau, R Bundy, and M Kahru. 2012. "Pelagic Community Responses to a Deep-Water Front in the California Current Ecosystem: Overview of the A-Front Study." *Journal of Plankton Research* 34 (9): 739–48. doi:10.1093/plankt/fbs025.

- Laurs, M, P C Fiedler, and D R Montgomery. 1984. "Albacore Tuna Catch Distributions Relative to Environmental Features Observed from Satellites" *Deep Sea Research* 31 (9): 1085-1099.
- Laurs, R M, and R J Lynn. 1977. "Seasonal Migration of North Pacific Albacore, *Thunnus alalunga*, into North American Coastal Waters - Distribution, Relative Abundance, and Association with Transition Zone Waters." *Fishery Bulletin* 75 (4): 795–822.
- Laurs, R Michael, and Ronald J Lynn. 1985. "North Pacific Albacore Ecology and Oceanography."
- Levy, M, R Ferrari, P J S Franks, A P Martin, and P Riviere. 2012. "Bringing Physics to Life at the Submesoscale." *Geophysical Research Letters* 39 (14). doi:10.1029/2012GL052756.
- Magnuson, J J, L B Crowder, and P Medvick. 1979. "Temperature as N Ecological Resource." *The American Zoologist*. doi:10.1086/280210.
- McCafferty, D J, S Gallon, and A Nord. 2015. "Challenges of Measuring Body Temperatures of Free-Ranging Birds and Mammals." *Animal Biotelemetry* 3 (1). BioMed Central: 33. doi:10.1186/s40317-015-0075-2.
- McClintock, B T, R King, L Thomas, J Matthiopoulos, B J McConnell, and J M Morales. 2012. "A General Discrete-Time Modeling Framework for Animal Movement Using Multistate Random Walks." *Ecological Monographs* 82 (3): 335–49. doi:10.1890/11-0326.1.
- Morales, J M, D T Haydon, J Frair, K E Holsinger, and J M Fryxell. 2004. "Extracting More out of Relocation Data: Building Movement Models as Mixtures of Random Walks." *Ecology* 85 (9): 2436–45. doi:10.1890/03-0269.
- Murphy, G I 1959. "Effect of Water Clarity on Albacore Catches." *Limnology and Oceanography* 4 (1): 86–93.
- Nathan, R, W M Getz, E Revilla, M Holyoak, R Kadmon, D Saltz, and P E Smouse. 2008. "A Movement Ecology Paradigm for Unifying Organismal Movement Research." *Proceedings of the National Academy of Sciences of the United States* of America 105 (49): 19052–59. doi:10.1073/pnas.0800375105.
- Nel, D C, J R E Lutjeharms, E A Pakhomov, I J Ansorge, P G Ryan, and N T W Klages.
 2001. "Exploitation of Mesoscale Oceanographic Features by Grey-Headed Albatross *Thalassarche chrysostoma* in the Southern Indian Ocean." *Mar Ecol*

Prog Ser 217: 15–26.

- Newton, K C, J Wraith, and K A Dickson. 2015. "Digestive Enzyme Activities Are Higher in the Shortfin Mako Shark, *Isurus oxyrinchus*, than in Ectothermic Sharks as a Result of Visceral Endothermy." *Fish Physiology and Biochemistry* 41 (4). Springer Netherlands: 887–98. doi:10.1007/s10695-015-0055-8.
- Olson, D B, and R H Backus. 1985. "The Concentrating of Organisms at Fronts: A Cold-Water Fish and a Warm-Core Gulf Stream Ring." *Journal of Marine Research* 43 (1): 113–37. doi:10.1357/002224085788437325.
- Olson, D, G Hitchcock, A Mariano, C Ashjian, G Peng, R Nero, and G Podesta. 1994. "Life on the Edge: Marine Life and Fronts." *Oceanography* 7 (2): 52–60. doi:10.5670/oceanog.1994.03.
- Otsu, T, and R N Uchida. 1963. "Model of the Migration of Albacore in the North Pacific Ocean." *Fish. Bull* 63 (1): 33–44.
- Parmesan, C, N Ryrholm, C Stefanescu, J K Hill, C D Thomas, H Descimon, B Huntley, L Kaila, J Kullberg, T Tammaru, W J Tennent, A A Thomas, M Warren. 1999.
 "Poleward Shifts in Geographical Ranges of Butterfly Species Associated with Regional Warming." *Nature* 399 (June): 579–83. doi:10.1038/21181.
- Payne, N L, M D Taylor, Y Y Watanabe, and J M Semmens. 2014. "From Physiology to Physics: Are We Recognizing the Flexibility of Biologging Tools?" *The Journal* of Experimental Biology 217 (Pt 3): 317–22. doi:10.1242/jeb.093922.
- Pedersen, M W, T A Patterson, U H Thygesen, and H Madsen. 2011. "Estimating Animal Behavior and Residency from Movement Data." *Oikos* 120 (9): 1281–90. doi:10.1111/j.1600-0706.2011.19044.x.
- Polovina, J J, D R Kobayashi, D M Parker, M P Seki, and G H Balazs. 2000. "Turtles on the Edge: Movement of Loggerhead Turtles (*Caretta caretta*) along Oceanic Fronts, Spanning Longline Fishing Grounds in the Central North Pacific, 1997-1998." *Fisheries Oceanography* 9 (1): 71–82. doi:10.1046/j.1365-2419.2000.00123.x.
- Porter, W P, and M Kearney. 2009. "Size, Shape, and the Thermal Niche of Endotherms." *Proceedings of the National Academy of Sciences of the United States of America* 106 Suppl : 19666–72. doi:10.1073/pnas.0907321106.
- Powell, J R, and M D Ohman. 2015. "Covariability of Zooplankton Gradients with Glider-Detected Density Fronts in the Southern California Current System." *Deep-*

Sea Research Part II: Topical Studies in Oceanography 112. Elsevier: 79–90. doi:10.1016/j.dsr2.2014.04.002.

- Queiroz, N, N E Humphries, L R Noble, A M Santos, and D W Sims. 2012. "Spatial Dynamics and Expanded Vertical Niche of Blue Sharks in Oceanographic Fronts Reveal Habitat Targets for Conservation." *PLoS ONE* 7 (2). doi:10.1371/journal.pone.0032374.
- Roznik, E A, and R A Alford. 2012. "Does Waterproofing Thermochron iButton Dataloggers Influence Temperature Readings?" *Journal of Thermal Biology* 37 (4). Elsevier: 260–64. doi:10.1016/j.jtherbio.2012.02.004.
- Rutz, C, and G C Hays. 2009. "New Frontiers in Biologging Science." *Biology Letters*, no. February: rsbl.2009.0089. doi:10.1098/rsbl.2009.0089.
- Sainmont, J, U H Thygesen, and A W Visser. 2013. "Diel Vertical Migration Arising in a Habitat Selection Game." *Theoretical Ecology* 6 (2): 241–51. doi:10.1007/s12080-012-0174-0.
- Schaefer, K M, and D W Fuller. 2006. "Comparative Performance of Current-Generation Geolocating Archival Tags." *Marine Technology Society Journal* 40 (1): 15–28. doi:10.4031/002533206787353673.
- Scheffer, A, C A Bost, and P N Trathan. 2012. "Frontal Zones, Temperature Gradient and Depth Characterize the Foraging Habitat of King Penguins at South Georgia." *Marine Ecology Progress Series* 465 (Woehler 1995): 281–97. doi:10.3354/meps09884.
- Sims, D W, and V A Quayle. 1998. "Selective Foraging Behaviour of Basking Sharks on Zooplankton in a Small-Scale Front." *Nature* 393 (June): 460–64. doi:10.1038/30959.
- Sims, D W, E J Southall, G A Tarling, and J D Metcalfe. 2005. "Habitat-Specific Normal and Reverse Diel Vertical Migration in the Plankton-Feeding Basking Shark." *Journal of Animal Ecology* 74 (4): 755–61. doi:10.1111/j.1365-2656.2005.00971.x.
- Singh, N J, L Börger, H Dettki, N Bunnefeld, and G Ericsson. 2012. "From Migration to Nomadism: Movement Variability in a Northern Ungulate across Its Latitudinal Range." *Ecological Applications* 22 (7): 2007–20. doi:10.1890/12-0245.1.
- Sund, P N, M Blackburn, and F Williams. 1981. "Tunas and Their Environment in the Pacific Ocean: A Review." *Oceanography and Marine Biology Annual Review* 19:

443–512.

- Teo, S L H, A Boustany, H Dewar, M J W Stokesbury, K C Weng, S Beemer, A C Seitz, C J Farwell, E D Prince, and B A Block. 2007. "Annual Migrations, Diving Behavior, and Thermal Biology of Atlantic Bluefin Tuna, *Thunnus thynnus*, on Their Gulf of Mexico Breeding Grounds." *Marine Biology* 151 (1): 1–18. doi:10.1007/s00227-006-0447-5.
- Xu, Y, K Nieto, S L H Teo, S McClatchie, and J Holmes. 2015. "Influence of Fronts on the Spatial Distribution of Albacore Tuna (*Thunnus alalunga*) in the Northeast Pacific over the Past 30 Years (1982-2011)." *Progress in Oceanography*, no. February 2016. doi:10.1016/j.pocean.2015.04.013.

CHAPTER 2

Quantifying the effects of sensor coatings on body temperature measurements.

2.1 Abstract

Background: A characterization of an organism's thermoregulatory ability informs our understanding of its physiology, ecology and behavior. Biotelemetry studies on thermoregulation increasingly rely on *in situ* body temperature measurements from surgically implanted data loggers. To protect the organism and the instrument, the electronics and the temperature sensor are often encased in non-conductive materials prior to insertion into the organism. These materials thermally insulate the sensor, thus potentially biasing temperature measurements to suggest a greater degree of thermoregulation than is actually the case. Results: Here we present methodology to quantify and correct for the effect of sensor coatings on temperature measurements by data recording tags. We illustrate these methods using Wildlife Computer's Mk9 archival tag, field data from the peritoneal cavity of a juvenile albacore tuna (Thunnus alalunga) and simulated data of several species of ectotherms (fish: Hemitripterus americanus, Catostomus commersoni and Maxostoma macrolepidotum; reptiles: Macroclemys temminckii, Varanus spp.), ranging in size from 10 to 1000 g. Mk9 tags had rate constants (measures of the sensor's ability to respond to changes in temperature) of $1.79 \pm 0.06 \text{ min}^{-1}$ and $0.81 \pm 0.07 \text{ min}^{-1}$ for the external and internal sensors, respectively. The higher rate constant of the external sensor produced smaller errors than the internal sensor. Yet, both sensors produced instantaneous errors of over 1°C for all species tested, with the exception of *T. alalunga*. Conclusions: The effect of sensor coatings on body temperature measurements is shown to depend on the relative values of the sensor's and the organism's rate constant and the rate of change of environmental temperature. If the sensor's rate constant is lower than that of the organism, the temperature measurements will reflect the thermal properties of the sensor rather than the organism.

2.2 Introduction

Over the past few decades, biotelemetry studies have generated in situ measurements of body temperature response to environmental temperatures (Block 2005; Payne et al. 2014), providing insights into thermoregulatory abilities (Block et al. 2001; Bush, Brown, and Downs 2008), mechanisms (Fitzgerald and Nelson 2011; Hetem et al. 2009) and strategies (Jackson et al. 2009; Dzal and Brigham 2013). Characterizations of thermoregulation can be used to determine habitat availability (Magnuson, J J, Crowder, L B, and Medvick 1979; Porter and Kearney 2009), behavior (Huey 1974; Angilletta 2009), and vulnerability to climate change (Helmuth, Kingsolver, and Carrington 2005; Huey et al. 2012). Our understanding of thermoregulation relies on accurate measures of body temperature and the rates at which body temperature changes given different thermal environments. There are many challenges to obtaining these measurements (McCafferty, Gallon, and Nord 2015), not the least of which is sensor thermal inertia, i.e. the ability of the sensor to resist changes in temperature. While researchers acknowledge that sensor thermal inertia exists, the significance of its effect on body temperature measurements is under debate (Schaefer and Fuller 2006; Roznik and Alford 2012).

Thermal inertia in the absence of radiation (e.g., either in water or in a body cavity) can be estimated as the inverse of its rate constant, which is also referred to as the coefficient of conductance, $k (\min^{-1})$ – at which the object's temperature, T_i (°C), approaches the ambient temperature, T_a (°C, Eq. 1):

$$\frac{dT_i}{dt} = k(T_a - T_i) \tag{1}$$

A large rate constant (low thermal inertia) results in a faster response to a given temperature change. This property holds true for all physical objects, organisms and sensors included. For aquatic ectotherms, organismal rate constants (k_b) decrease exponentially as body size increases, and species-specific relationships have been empirically defined for a number of species (e.g., Stevens and Sutterlin 1976; Spigarelli, Thommes, and Beitinger 1977; Fitzgerald and Nelson 2011). On the other hand, a sensor's rate constant k_s is largely determined by the mass and specific heat of its surrounding.

Virtually every temperature sensor used to study thermoregulation in the field is coated with a material to waterproof the sensor and to protect the organism from infection. The protective coatings vary in composition (e.g., epoxy resin: Boyles, Smit, and McKechnie 2012; Carey, Kanwisher, and Stevens 1984; Coleman and Downs 2010); silicon: (Gilbert et al. 2007; Green et al. 2005; Jackson et al. 2009); paraffin wax: (Downs, Zungu, and Brown 2012; Scantlebury et al. 2012; Zungu, Brown, and Downs 2013); or plastic: (Donaldson et al. 2009; Taylor, DeNardo, and Malawy 2004) and in thickness, as coatings are often applied by the researcher rather than the sensor manufacturer. Because of the diversity of coating materials and thicknesses, each data logger has its own – usually unknown – coefficient of conductance. The thicker and less conductive the material, the lower the sensor's coefficient of conductance, and the slower it will respond to temperature changes.

Because of the inherent variability in organisms (i.e., thermoregulatory ability) and in tag design (i.e., mass and specific heat of protective coatings), it is difficult – if not impossible – to provide a blanket statement on the effect of sensor coatings on body temperature measurements. Herein, we provide researchers the tools to assess whether their sensor is accurately capturing fluctuations in their organism's body temperature, and to correct their time series if necessary. To illustrate our methodology, we use Wildlife computer's Mk9 archival tag along with observed and simulated body temperature time series.

2.3 Methods

2.3.1 Theory

The impact of sensor coatings on body temperature measurements can be explored mathematically. Suppose at time t=0 an organism's temperature (T_b) is at equilibrium with a previously constant ambient temperature, T_0 . If the animal were to move rapidly to a new temperature T_a (e.g., dive below the thermocline), the change of body temperature with time is given by:

$$T_b(t) = T_a + (T_0 - T_a)e^{-k_b t}$$
(2)

This equation indicates that changes in the organism's body temperature result from the difference between the organism's body and ambient temperature and the organism's rate constant k_b , assuming a constant k_b during the time interval 0 to t. The rate constant

defines the time constant (specifically $1/k_b$) over which the organism cools or warms to the ambient temperature: an increase in k_b would be accompanied by a faster rate of body temperature change. Thus, higher rates of body temperature change occur in organisms with higher rate constants or in organisms that encounter a large change in environmental temperature over a short period of time.

Using the same scenario of an organism with a rate constant k_b experiencing a step-function ambient temperature change, we can calculate the effect of measuring the body temperature with a sensor, assuming the sensor is at equilibrium with the ambient temperature T_0 at t=0 and has a rate constant k_s :

$$T_s(t) = T_a + \frac{k_s}{(k_s - k_b)} (T_0 - T_a) e^{-k_b t} + (T_0 - T_a) e^{-k_s t} \left(1 - \frac{k_s}{(k_s - k_b)}\right)$$
(3)

Here we can see that as k_b increases relative to k_s , the influence of k_s on the measurements increases. In essence, both the animal and the sensor act as filters on the changing ambient temperature: the slowest filter (i.e., the smallest k) will determine the measured temperature. If the ambient temperature were to change again before the sensor temperature had equilibrated (i.e., in less than $1/k_s$), the sensor will have a lagged response to the body temperature changes, effectively averaging fluctuations in body temperature (Fig. 2.1). The sensor's thermal inertia will give the impression of a more stable body temperature than is actually the case whenever $k_s < k_b$.

These derivations show that measurement error depends on the relationship between the rate constants of the sensor and the organism as well as the temporal dynamics of the ambient temperature fluctuations. Thus, estimating the sensor's rate constant is a necessary first step in understanding measurement error associated with sensor thermal inertia.

2.3.2 Quantifying and accounting for sensor rate constant

2.3.2.1 Calibration experiment

Prior to deployment, the temperature sensor must be calibrated to calculate its rate constant k_s . The calibration should be completed after the application of protective coating (e.g., potted in epoxy or coated with a layer of epoxy). Calibration data should be collected under the following conditions: (i) the ambient temperature T_a is known and changes at a faster rate than expected in the field, (ii) the physical environment is similar to that encountered during deployment, and (iii) the sensor's sampling rate is faster than the sampling rate used in the study.

Ideally T_a should vary as a step function between the minimum and maximum temperatures expected in the field. This can be achieved by cycling the sensor through two different temperature-controlled treatments (e.g., water baths), noting the time at each transfer. Sensors should be allowed to equilibrate to each ambient temperature. Because the physical environment can change an object's coefficient of conductance by an order of magnitude (Denny 1993), it is essential to test the sensor in the same medium (e.g., air or water) it will encounter in the field. If the sensor will be deployed in the peritoneal cavity of an organism, a calibration experiment in salt water should suffice.

With a sampling interval Δt_s , the sampling rate $1/\Delta t_s$ defines the maximum detectable value of k_s . Intuitively, if $k_s > 1/\Delta t_s$, then the sensor temperature T_s should approach the ambient temperature T_a within the time between measurements, Δt_s ,
leaving little to no information for evaluating k_s (see Eqn 2). As k_s is unknown and the *in situ* sampling interval determines the rate at which k_s would be detected in the study, to resolve k_s it is imperative that the calibration be conducted using sampling rates that are faster than the planned *in situ* sampling rate.

2.3.2.2 Calculating sensor rate constant

To calculate the sensor's rate constant (k_s, \min^{-1}) , we make a numerical approximation of Eqn. 1 using the Euler method:

$$\frac{T_s(t) - T_s(t - \Delta t)}{\Delta t} = k_s [T_a(t) - T_s(t - \Delta t)]$$
⁽⁴⁾

This equation models the temperature sensor's rate of change as dependent on the present temperature ($T_s(t)$, °C), its temperature at the previous time ($T_s(t-\Delta t_s)$, °C), the present ambient temperature ($T_a(t)$, °C), and the sensor's rate constant (k_s , min⁻¹). Eqn. 4 gives a first-order solution. The errors associated with this approximation are directly proportional to the time between measurements (the sampling interval, Δt_s).

Eqn. 4 was reformulated to:

$$A = Bk_s \tag{5}$$

(5)

where A is a vector of the sensor temperature's rate of change, and B is a vector of the temperature differences between the current ambient temperature and the sensor temperature at a previous time step:

$$A = \left[\frac{(T_s(t_i) - T_s(t_i - \Delta t_s))}{\Delta t_s}\right]$$
(6)

$$B = [T_a(t_i) - T_s(t_i - \Delta t_s)] \tag{7}$$

where $i = \{2, 3, ..., N\}$ and N is the number of points in a particular window of data. To minimize noise in our estimates of k_s , it is important to only include data from the periods when A and B are not equal to 0 (i.e., from the time when the sensor was placed into the water bath to the time when the sensor approaches equilibrium with the water bath's temperature).

Solutions to Eqn. 5 can be obtained for each cooling or warming period, to generate one estimate for k_s per water bath transfer. Each k_s can then be used to correct the sensor data (see 2.2.3) from all cooling and warming periods throughout the calibration experiment. Although the data from these cooling and warming periods could be used collectively to generate one estimate of k_s , separate estimates of k_s allow the researcher to test the validity of the model using data that was excluded from the original estimation of k_s . The final k_s is defined as the estimate that minimizes the root-mean square error between the corrected temperature time series (T_{corr} , see 2.2.3 Eqn 9) and the water bath temperature time series (T_a):

$$RMSE_{k_s} = \sqrt{\frac{\sum_{t=1}^{N} (T_a(t) - T_{corr}(t))^2}{N}}$$
(8)

where *N* is the length of the time series.

2.3.2.3 Correcting time series

Having obtained a value for k_s it is possible to remove the effects of the sensor's protective coating from the T_s time series and reconstruct the ambient temperature time

(7)

series T_a . Because the ambient temperature in this step is unknown, Eqn. 4 is rearranged to solve for T_a which is now renamed T_{corr} , to denote the corrected sensor time series:

$$T_{corr}(t) = \frac{1}{k_s \Delta t} [T_s(t) - T_s(t - \Delta t)] + T_s(t - \Delta t)$$
⁽⁹⁾

This correction unavoidably enhances the sensor's digitization error. To minimize the sensor's digitization error, the sensor time series T_s should be smoothed over five data points prior to correction using a moving average. To minimize signal loss, any smoothing that results in a change greater than the sensor's digitization error should be reverted back to the raw data.

2.3.3 Case study

Because the impact of the sensor thermal inertia on measurements is dependent on the relative values of the rate constants of the organism and the sensor (Eqn. 3), the significance of the sensor's rate constant will vary by sensor and across and among species. To illustrate this, we estimate the rate constant for two temperature sensors on one model of tag and use these sensors to measure juvenile North Pacific albacore (*Thunnus alalunga*) body and water temperature and to simulate measurements of several ectotherms across a range of sizes.

2.3.3.1 Tag model

We calibrated and calculated the rate constants for 41 Mk9 archival tags (Mk9 Wildlife Computers). This model has been deployed on a variety of taxa (e.g., tunas: (Dagorn et al. 2006); turtles: (Casey, James, and Williard 2014); elephant seals: (Kuhn

et al. 2009); penguins: (Scheffer, Bost, and Trathan 2012)). Mk9s are equipped with two temperature sensors: an internal sensor located within an epoxy housing and an external sensor located at the end of the tag stalk (Fig. 2.2).

The protective coatings on Mk9 sensors are applied by the manufacturer, rather than the individual researcher; thus, the sensor's rate constant should be similar across tags. The tag is capable of measuring temperature every second and storing data for up to years at a time (dependent on sampling rate). The resolution of both temperature sensors is 0.05 °C.

During the calibration experiment of the Mk9s, the sensors were set to sample every 30 s, and were transferred between two saltwater tanks of 11 and 22 °C, for a rate of change in T_a of ~11 °C s⁻¹. Ambient temperature was measured with a thermometer situated in each tank and recorded throughout the experiment.

2.3.3.2 Body temperature data

In situ *measurements*

The *T. alalunga* data used in this study were collected by the Albacore Archival Tagging Program, a collaborative tagging project between the NOAA Southwest Fisheries Science Center and the American Fishermen's Research Foundation (Childers, Snyder, and Kohin 2011). The Mk9 tag was set to sample every 60 s and surgically implanted into the peritoneal cavity of the tuna such that the internal temperature sensor measured the peritoneal cavity temperature while the external sensor measured the surrounding water temperature. The albacore used in the present study was tagged off the coast of Oregon on August 4, 2011. At the time of tagging, the

albacore was considered a juvenile with a measured fork length of 64.5 cm (Otsu and Uchida 1959) and a weight of 5.5 kg (estimated using published length to weight criterion: Uchiyama et al. 2003) at the time of tagging. The tagged fish was at liberty for over a year. The effect of sensor thermal inertia was removed from the *in situ* temperature time series using the algorithm presented above (Eqn. 9) to generate a corrected temperature time series.

Simulated measurements

Empirically derived, species-specific relationships between size and rate constant (k_b) coefficients of conductance were used to simulate body temperature cooling curves of different sized organisms under an ambient temperature change from 20 °C to 10 °C. Organismal coefficients of conductance (k_b , min⁻¹) have been derived in laboratory settings for a variety of taxa and different sized individuals using the following equation:

$$k_b = -\frac{1}{t} \ln[\frac{(T_e - T_b)}{(T_e - T_0)}]$$
(10)

where T_e (°C) is the steady-state body temperature at the experimental ambient temperature, T_0 (°C) is the initial body temperature, and T_b (°C) is the body temperature at *t* minutes into the experiment (Stevens and Sutterlin 1976). These data have been used in the literature to relate k_b and organism size using variants of the following equation:

$$k_b = aW^{-b} \tag{11}$$

where *a* and *b* are empirically derived constants (Table 2.1, Fitzgerald and Nelson 2011, Stevens and Sutterlin 1976, Bartholomew and Tucker 1964, Stevens and Fry 1974).

Eqn. 2 was used to simulate body temperature using the organism specific k_b with T_0 of 20°C and T_e of 10°C.

Sensor measurements of the generated body temperatures were simulated by using two different k_s values (corresponding to the mean coefficient of conductance of the internal and external sensors) and replacing T_a with T_b in Eqn. 4 (Fig. 2.3a). We used a sampling interval of 1 s, and our simulated sensor had no digitization error. The cooling period was defined as the time from when the ambient temperature changed to 10 °C to the time when the body temperature cooled to 10.1 °C. These analyses were carried out for organisms ranging in mass from 10 to 1,000 g for each species listed in Table 2.1.

2.3.3.3 Testing significance

In both the measured and simulated body temperature treatments, the effect of sensor coatings on measurements was determined by looking at (i) overall significance and the instantaneous errors between the body temperature and the sensor temperature time series; and (ii) the differences in known and estimated k_b for the simulated body temperatures. Overall significance was determined using a Student's t-test (P<0.05). This was done over the entire year for the albacore tuna and over the cooling period for the simulated body temperatures. For the measured albacore body temperatures, the error caused by sensor rate constant (E) was calculated as the difference between the smoothed (to reduce digitization error, see above) and corrected sensor temperature time series at time t:

$$E(t) = T_s(t) - T_{corr}(t)$$
⁽¹²⁾

In the case of the simulated body temperatures, T_{corr} was replaced with the known body temperature T_b , and the mean error \overline{E} between the two time series during the cooling period is reported for each species-size (Fig 2.3b).

Additionally, because the k_b in the simulated experiments is known, it was possible to compare an apparent rate constant estimated from the sensor measurements (k_{b-est}, \min^{-1}) to the known k_b . The apparent rate constant was estimated from the sensor cooling curve using Eqn. 10 replacing T_b with T_s . This estimation from the simulated sensor data was then compared to the known rate constant, k_b .

2.4 Results

Mk9 sensor rate constant

Analysis of the calibration data of the Mk9 archival tags gave mean (\pm S.D.) rate constants, k_s , of 1.79 \pm 0.06 min⁻¹ and 0.81 \pm 0.07 min⁻¹ for the external and internal sensors, respectively (Fig. 2.4). Using k_s to correct the sensor measurements significantly reduced the root mean squared error between the sensor measurements and the ambient temperature, *RMSE*_{ks} (Eqn. 8, Table 2.2; t-test: p < 0.001 and p < 0.001 for external and internal sensors, respectively).

Effect of sensor rate constants

In situ measurements

(10)

The external sensor k_s was greater than the *in situ* sampling rate (Δt_s^{-1}) and thus (due to aliasing) the external sensor's thermal inertia was not detectable in the albacore *in situ* time series. Therefore, only the internal sensor measurements were corrected. This correction was done using the internal sensor k_s derived from the calibration data.

Comparison of a year of raw to corrected *in situ* albacore body temperature data from the internal sensor showed no significant difference (t-test, p=0.92). Absolute differences between the raw and corrected body temperatures were within 0.1 °C for 92.4% of the time series. The remaining 7.6% (approximately 28 days of measurements) corresponded to periods when the absolute rates of body temperature change were on average an order of magnitude greater than those observed in the rest of the time series, 0.20 °C min⁻¹ and 0.017 °C min⁻¹ respectively. The maximum error observed during these periods of high rates of body temperature change was 0.2 °C. These errors are minute compared to the overall signal and variability of the juvenile's body temperature, and therefore the sensor's rate constant does not significantly influence measurements of this albacore's body temperature.

Simulated measurements

The level of error associated with sensor coatings differed as a function of both sensor and organism. The external and internal sensor measurements were significantly different from the simulated body temperatures for all the species tested (*Student's t-test; p*<0.001). The level of error varied between sensors and across species and sizes of organisms, with error due to the sensor's rate constant increasing as size decreased across species (Fig. 2.5a-b). Mean error during the cooling period exceeded 1 °C for all

species for the internal and external sensors, respectively. When using the internal sensor, mean error dropped below 1 °C at 60 g (*H. americanus* and *C. commersoni*), 230 g (*M. temminckii*), and 590 g (*Varanus* spp.). The external sensor resulted in less error with mean error dropping below 1°C at 20 g (*H. americanus* and *C. commersoni*) and 80 g (*Varanus* spp. and *M. temminckii*). Using uncorrected measurements from either sensor resulted in an underestimation of the organisms' rate constants, with greater differences between the estimate and the true value as k_b increased (body size decreased, Fig. 2.6).

2.5 Discussion

Sensor thermal inertia has the potential to confound measurements of body temperature, thus impacting our understanding of an organism's thermoregulatory ability. We have shown that the effect of sensor coatings on measurements depends on (i) the sensor's rate constant, (ii) the organism's rate constant, and (iii) the rate of change of environmental temperature. The methods presented here allow researchers to calculate and correct for a sensor's rate constant, and to determine whether the sensor significantly influences body temperature measurements. (The Matlab code for all the analytical methods presented here is available by request.)

All objects have thermal inertia which (in the absence of radiation) can be quantified by a rate constant. As a sensor's rate constant (k_s) decreases relative to that of an organism's (k_b), the sensor will heat or cool more slowly than the organism, thus giving less-accurate estimates of the actual body temperatures. We have shown here that in one model of archival tag (Wildlife computer's Mk9) the two temperature sensors had different rate constants: $1.79 \pm 0.06 \text{ min}^{-1}$ and $0.80 \pm 0.07 \text{ min}^{-1}$ for the external and internal sensors, respectively. The differences in these coefficients of conductance arise from the mass and specific heat of the materials used to coat the sensors. The relatively high rate constant of the external sensor resulted in more accurate estimates of temperatures than observed using the internal sensor.

Variability in the sensors' accuracy depended on differences in the rates of body temperature change, which is largely a result of the organism's rate constant (Eqn. 1-2) and rates of ambient temperature change (Fig. 2.1). Organism size plays a role, as this parameter often influences the organisms' rate constant (Eqn. 11). In our simulations, measurement error and error in estimation of k_b decreased exponentially with size. Furthermore, the juvenile albacore, the largest organism in our study, had the smallest measurement errors. The smaller k_b of larger organisms lessens the influence of ambient temperature fluctuations on body temperature, resulting in a steady or slowly changing body temperature. As steady or slowly changing body temperatures are less susceptible to error from sensor thermal inertia, measurements of temperatures of larger bodied organisms are expected to be less impacted by sensor thermal inertia than those of smaller organisms.

In our observations of the albacore as well as the modeled organisms, measurement error due to sensor rate constants increased with higher rates of body temperature change. For the albacore, periods of rapid diving between cold (deep) and warm (surface) environments had the greatest magnitude of error. In our simulations, measurement error was inversely correlated with size, i.e., sensor rate constants had a greater impact on body temperature measurements of smaller organisms. These observations follow from the general theory of thermal inertia with rate constants (Eqn. 3).

To illustrate the effects of sensor coatings we used a fixed k_b dictated by a species-specific dependence on size. However, organisms have been shown to change their thermal conductance by orders of magnitude in the field (Teo et al. 2007; Holland et al. 1992). This variability, combined with uncertainty in the rates of ambient temperature change, creates the potential for sensor coatings to affect measures of body temperature and estimates biologically relevant rates of heating and cooling in the field, resulting in an overestimation of thermoregulatory ability.

2.6 Conclusions

With today's technology, researchers are able to tag species ranging in size from bumble bees (Hagen, Wikelski, and Kissling 2011) to blue whales (Acevedo-Gutiérrez, Croll, and Tershy 2002). Our ability to measure body temperatures of small organisms (e.g., nanologger: Gandra et al. 2015) must be met with an understanding of how sensor coatings influence those measurements. Though a sensor's rate constant may have little effect on average body temperature estimates, it can affect our understanding of the dynamics of body temperature responses to fluctuations in ambient temperature, as well as our understanding of body temperature ranges (Fig. 2.1). As demonstrated in Eqn. 3, the ability of the sensor to accurately capture the fluctuations of the organism's body temperature depends largely on the relative relationship between the organism's and the sensor's rate constant. Given a sensor with the same rate constant, small organisms encountering a dynamic thermal environment have a greater potential for measurement error than a large organism in a stable thermal environment. Our simulations indicate that thermal inertia alters observed rates of body temperature change in a systematic manner and can generate errors an order of magnitude greater than digitization error. Accounting for these errors is therefore just as important as other experimental considerations, such as sensor placement (McCafferty, Gallon, and Nord 2015).

Due to the inherent uncertainty surrounding rates of body temperature change and sensor thermal rate constants, we recommend that researchers quantify and assess the potential impact of their sensor's rate constant for their organism of interest. Our results indicate that the external and internal sensor of Mk9 tags can accurately capture the water and body temperature fluctuations of similar sized (or larger) albacore tuna. In studies with other organisms or tags, sensor thermal inertia and its associated errors must be quantified, with the exception of cases where (i) the organism does not experience changes in thermal habitat or (ii) the researcher is only interested in average temperatures. Sensor thermal inertia is directly related to the mass and specific heat of the protective coating. Therefore sensor thermal inertia will vary across tags. Researchers can minimize error by applying thinner layers of more thermally conductive materials to reduce the amount of sensor thermal inertia (increase the rate constant, k_s) and therefore its effect on body temperature measurements.

Chapter 2, in full, is a reprint of the material as it appears in *Animal Biotelemetry*. Snyder, S. and P.J.S. Franks, 2016. Quantifying the effects of sensor coatings on body temperature measurements. The dissertation author was the primary investigator and author of this paper.

Species	n	a	b	Range in Mass (g)	Reference
Atlantic sea raven Hemitripterus americanus	24	3.3	0.54	12 - 3,178	(Stevens and Sutterlin 1976)
Alligator snapping turtle Macroclemys temminckii	5	25.0	0.77	700 - 26,000	(Fitzgerald and Nelson 2011)
Australian Varanid Lizards Varanus spp.	12	4.6	0.39	16-4,408	(Bartholomew, G.A. and Tucker 1964)
Sucker Catostomus commersoni Maxostoma macrolepidotum	229	3.7	0.57	.6 – 1,194	(Stevens and Fry 1974)

Table 2.1 Species specific relationships $(k_b = aW^{-b})$ between mass (W, g) and the specific rate of body temperature change (k_b, \min^{-1}) where *a* and *b* are empirically derived constants. Number of organisms used in the experiments is denoted by *n*.

Table 2.2 Mk9 internal and external sensor coefficients of conductance. The mean (\pm S.D.) coefficients of conductance and the *RMSE* between the sensor temperature measurements (pre- and post-correction) and the ambient temperature during the heating and cooling curves of the calibration experiment.

Temperature	Coefficient of Conductance	$RMSE_{k_s}$ (°C)		
Sensor	(k_s, \min^{-1})	Pre-correction	Post-correction	
Internal	0.81 ± 0.07	2.14 ± 0.2	0.52 ± 0.1	
External	1.79 ± 0.06	0.38 ± 0.1	0.18 ± 0.1	



Figure 2.1 Illustration of the influence of sensor thermal inertia on body temperature measurements. Simulation of a sensor with a coefficient of conductance of 0.81 min⁻¹ (T_s , black) measuring the body temperature (T_b , red) of a 100 g Atlantic sea raven as it shuttles between water temperatures of 10 and 20 °C (T_a , gray) with a duty cycle of 5 minutes. The bottom inset shows the error in dashed black line.



Figure 2.2 Photo of Wildlife computers' Mk9 archival tag model.



Figure 2.3 Example of a simulation of an organism's cooling curve and corresponding sensor measurements. **a** A simulation of a 100 g Atlantic sea raven's body temperature (*Hemitripterus americanus*, °C, red line) measured by a sensor with a k_s of 0.81 min⁻¹ (black line) as it responds to a 10 °C decrease in the ambient temperature (°C, gray dashed line). **b** The error observed between the sensor temperature and the body temperature. The mean error (\overline{E}) during the cooling period is reported. In both plots, a double arrow specifies the cooling period.



Figure 2.4 Data and results from Mk9 calibration. **a** Mk9 internal (solid grey line) and external sensors (solid black line) measuring ambient temperature (dashed grey line) during the calibration experiment (entire time series shown in inset). The red and blue lines represent the analytical solutions for the mean internal and external sensor coefficients of conductance, respectively (Eqn. 2). **b** Histogram of the coefficients of conductance k_s calculated for both the internal (grey) and external sensors (black); n = 41 tags.



Figure 2.5 Measurement error as a function of species, size and sensor coefficient of conductance. Mean difference between the simulated body and sensor temperature measurements for the Atlantic sea raven (*H. americanus*), the alligator snapping turtle (*M. temminckii*), lizards (*Varanus* spp.), and sucker fish (*C. commersoni & M. macrolepidotum*) during the cooling period given **a** the average internal sensor coefficient of conductance (0.81 min⁻¹) and **b** the average external sensor coefficient of conductance (1.79 min⁻¹).



Figure 2.6 Comparison of coefficient of conductance estimated from sensor measurements (k_{b-est}) to the actual coefficient of conductance (k_b) for measurements taken using the average internal (white circles) or external (black circles) sensor coefficient of conductance, 0.81 min⁻¹ or 1.79 min⁻¹ respectively.

2.7 References

- Angilletta, M J. 2009. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press.
- Bartholomew G A, and V Tucker. (1964) Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian Varanid lizards. *Physiological Zool.* 37(4):341-354.
- Block, B A, H Dewar, S B Blackwell, T D Williams, E D Prince, C J Farwell, A Boustany, S H Teo, A Seitz, A Walli, D Fudge. 2001. "Migratory Movements, Depth Preferences, and Thermal Biology of Atlantic Bluefin Tuna." *Science (New York, N.Y.)* 293: 1310–14. doi:10.1126/science.1061197.
- Block, B A. 2005. "Physiological Ecology in the 21st Century: Advancements in Biologging Science." *Integrative and Comparative Biology* 45 (2): 305–20. doi:10.1093/icb/45.2.305.
- Boyles, J G, B Smit, and A E McKechnie. 2012. "Variation in Body Temperature Is Related to Ambient Temperature but Not Experimental Manipulation of Insulation in Two Small Endotherms with Different Thermoregulatory Patterns." *Journal of Zoology* 287 (3): 224–32. doi:10.1111/j.1469-7998.2012.00909.x.
- Bush, N G, M Brown, and C T Downs. 2008. "Seasonal Effects on Thermoregulatory Responses of the Rock Kestrel, Falco Rupicolis." *Journal of Thermal Biology* 33 (7): 404–12. doi:10.1016/j.jtherbio.2008.06.005.
- Carey, F G, J W Kanwisher, and E D Stevens. 1984. "Bluefin Tuna Warm Their Viscera during Digestion." *Journal of Experimental Biology* 109: 1–20.
- Casey, J P, M C James, and A S Williard. 2014. "Behavioral and Metabolic Contributions to Thermoregulation in Freely Swimming Leatherback Turtles at High Latitudes." *Journal of Experimental Biology* 217 (13): 2331–37. doi:10.1242/jeb.100347.
- Childers, J, S Snyder, and S Kohin. 2011. "Migration and Behavior of Juvenile North Pacific Albacore (*Thunnus alalunga*)." *Fisheries Oceanography* 20 (3): 157–73.
- Coleman, J C, and C T Downs. 2010. "Daily Rhythms of Body Temperature and Activity in Free-Living Black-Tailed Tree Rats (*Thallomys nigricauda*) along an Aridity Gradient." *Physiology and Behavior* 99 (1). Elsevier Inc.: 22–32. doi:10.1016/j.physbeh.2009.10.006.
- Dagorn, L, K N Holland, J Hallier, M Taquet, G Moreno, G Sancho, D G Itano, R Aumeeruddy, C Girard, J Million, A Fonteneau. 2006. "Deep Diving Behavior Observed in Yellowfin Tuna (*Thunnus albacares*)." Aquatic Living Resources 19

(1): 85–88. doi:10.1051/alr:2006008.

- Denny, M W. 1993. *Air and Water: The Biology and Physics of Life's Media*. Princeton University Press.
- Donaldson, M R, S J Cooke, D A Patterson, S G Hinch, D Robichaud, K C Hanson, I Olsson, G T Crossin, K K English, and A P Farrell. 2009. "Limited Behavioural Thermoregulation by Adult Upriver-Migrating Sockeye Salmon (Oncorhynchus nerka) in the Lower Fraser River, British Columbia." Canadian Journal of Zoology 87 (6): 480–90. doi:10.1139/Z09-032.
- Downs, C T, M M Zungu, and M Brown. 2012. "Seasonal Effects on Thermoregulatory Abilities of the Wahlberg's Epauletted Fruit Bat (*Epomophorus wahlbergi*) in KwaZulu-Natal, South Africa." *Journal of Thermal Biology* 37 (2). Elsevier: 144– 50. doi:10.1016/j.jtherbio.2011.12.003.
- Dzal, Y A, and R M Brigham. 2013. "The Tradeoff between Torpor Use and Reproduction in Little Brown Bats (*Myotis lucifugus*)." Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 183 (2): 279–88. doi:10.1007/s00360-012-0705-4.
- Fitzgerald, L A, and R E Nelson. 2011. "Thermal Biology and Temperature-Based Habitat Selection in a Large Aquatic Ectotherm, the Alligator Snapping Turtle, *Macroclemys temminckii.*" *Journal of Thermal Biology* 36 (3). Elsevier: 160–66. doi:10.1016/j.jtherbio.2011.01.003.
- Gandra M, Seabra R, Lima F P. 2015. A low-cost, versatile data logging system for ecological applications. *Limnol Oceanogr Methods*. 13(3):115-126. doi:10.1002/lom3.10012
- Gilbert, C, Y L Maho, M Perret, and A Ancel. 2007. "Body Temperature Changes Induced by Huddling in Breeding Male Emperor Penguins." *American Journal of Physiology. Regulatory, Integrative and Comparative Physiology* 292 (1): R176– 85. doi:10.1152/ajpregu.00912.2005.
- Green, J A, I L Boyd, A J Woakes, C J Green, and P J Butler. 2005. "Do Seasonal Changes in Metabolic Rate Facilitate Changes in Diving Behaviour?" *The Journal of Experimental Biology* 208 (Pt 13): 2581–93. doi:10.1242/jeb.01679.
- Helmuth, B, J G Kingsolver, and E Carrington. 2005. "Biophysics, Physiological Ecology, and Climate Change: Does Mechanism Matter?" Annual Review of Physiology 67: 177–201. doi:10.1146/annurev.physiol.67.040403.105027.
- Hetem, R S, B A de Witt, L G Fick, A Fuller, G I H Kerley, L C R Meyer, D Mitchell, and S K Maloney. 2009. "Body Temperature, Thermoregulatory Behaviour and Pelt Characteristics of Three Colour Morphs of Springbok (Antidorcas)

marsupialis)." Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology 152 (3). Elsevier Inc.: 379–88. doi:10.1016/j.cbpa.2008.11.011.

- Huey, R B, M R Kearney, A Krockenberger, J A M. Holtum, M Jess, and S E Williams.
 2012. "Predicting Organismal Vulnerability to Climate Warming: Roles of Behaviour, Physiology and Adaptation." *Philosophical Transactions of the Royal Society B: Biological Sciences* 367 (1596): 1665–79. doi:10.1098/rstb.2012.0005.
- Huey, R B. 1974. "Behavioral Thermoregulation in Lizards: Importance of Associated Costs." *Science*. American Assn for the Advancement of Science.
- Jackson, C R, T H Setsaas, M P Robertson, M Scantlebury, and N C Bennett. 2009. "Insights into Torpor and Behavioural Thermoregulation of the Endangered Juliana's Golden Mole." *Journal of Zoology* 278 (4): 299–307. doi:10.1111/j.1469-7998.2009.00575.x.
- Kuhn, C E, D E Crocker, Y Tremblay, and D P Costa. 2009. "Time to Eat: Measurements of Feeding Behaviour in a Large Marine Predator, the Northern Elephant Seal *Mirounga angustirostris*." *Journal of Animal Ecology* 78 (3): 513– 23. doi:10.1111/j.1365-2656.2008.01509.x.
- Magnuson, J J, And Crowder, L B, and P Medvick. 1979. "Temperature as N Ecological Resource." *The American Zoologist*. doi:10.1086/280210.
- McCafferty, D J, S Gallon, and A Nord. 2015. "Challenges of Measuring Body Temperatures of Free-Ranging Birds and Mammals." *Animal Biotelemetry* 3 (1). BioMed Central: 33. doi:10.1186/s40317-015-0075-2.
- Otsu, T, and R N Uchida. 1959. "Sexual Maturity and Spawning of Albacore in the Pacific ocean." *Fishery Bulletin* 59 (148): 287–305.
- Payne, N L, M D Taylor, Y Y Watanabe, and J M Semmens. 2014. "From Physiology to Physics: Are We Recognizing the Flexibility of Biologging Tools?" *The Journal* of Experimental Biology 217 (Pt 3): 317–22. doi:10.1242/jeb.093922.
- Porter, W P, and M Kearney. 2009. "Size, Shape, and the Thermal Niche of Endotherms." *Proceedings of the National Academy of Sciences of the United States of America* 106 Suppl : 19666–72. doi:10.1073/pnas.0907321106.
- Roznik, E A, and R A Alford. 2012. "Does Waterproofing Thermochron iButton Dataloggers Influence Temperature Readings?" *Journal of Thermal Biology* 37 (4). Elsevier: 260–64. doi:10.1016/j.jtherbio.2012.02.004.
- Scantlebury, M, M Danek-Gontard, P W Bateman, N C Bennett, M B Manjerovic, K E Joubert, and J M Waterman. 2012. "Seasonal Patterns of Body Temperature Daily Rhythms in Group-Living Cape Ground Squirrels Xerus Inauris." *PLoS ONE* 7 (4).

doi:10.1371/journal.pone.0036053.

- Schaefer, K M, and D W Fuller. 2006. "Comparative Performance of Current-Generation Geolocating Archival Tags." *Marine Technology Society Journal* 40 (1): 15–28. doi:10.4031/002533206787353673.
- Scheffer, A, C A Bost, and P N Trathan. 2012. "Frontal Zones, Temperature Gradient and Depth Characterize the Foraging Habitat of King Penguins at South Georgia." *Marine Ecology Progress Series* 465: 281–97. doi:10.3354/meps09884.
- Spigarelli, S A, M M Thommes, and T L Beitinger. 1977. "The Influence of Body Weight on Heating and Cooling of Selected Lake Michigan Fishes." *Comparative Biochemistry and Physiology Part A: Physiology* 56 (1): 51–57. doi:10.1016/0300-9629(77)90441-8.
- Stevens, E D, and A M Sutterlin. 1976. "Heat Transfer between Fish and Ambient Water." *The Journal of Experimental Biology* 65 (1): 131–45.
- Stevens E D, F E Fry. (1974) Heat transfer and body temperatures in nonthermoregulatory teleosts. *Can J Zool*. 52 (9):1137. doi:10.1139/z74-152.
- Taylor, E N, D F DeNardo, and M A Malawy. 2004. "A Comparison between Pointand Semi-Continuous Sampling for Assessing Body Temperature in a Free-Ranging Ectotherm." *Journal of Thermal Biology* 29 (2): 91–96. doi:10.1016/j.jtherbio.2003.11.003.
- Uchiyama, J H, and T K Kazama. 2003. "Updated Weight-on-Length Relationships for Pelagic Fishes Caught in the Central North Pacific Ocean and Bottomfishes from the Northwestern Hawaiian Islands." *Fisheries Science*: 1–34.
- Zungu, M M, M Brown, and C T Downs. 2013. "Seasonal Thermoregulation in the Burrowing Parrot (*Cyanoliseus patagonus*)." *Journal of Thermal Biology* 38 (1). Elsevier: 47–54. doi:10.1016/j.jtherbio.2012.10.001.

CHAPTER 3

Influence of thermal habitat on thermoregulation in a regional endotherm, albacore tuna (*Thunnus alalunga*)

3.1 Abstract

- 1. Unlike most fish, many predatory fishes in the open ocean are regional endotherms, capable of maintaining parts of their bodies at temperatures above those of the surrounding water through both physiological and behavioral mechanisms.
- 2. While this adaptation improves predatory performance and expands thermal niche, we do not understand how thermal habitat influences thermoregulation, or the associated costs and behaviors associated with maintaining body temperature.
- **3.** We examine this question by coupling mechanistic behavioral and physiological models with decades of biotelemetry data on albacore tuna as they inhabit diverse thermal habitats.
- **4.** To understand the influence of thermal habitat on thermoregulation, we quantify behavioral modes, behavioral and physiological costs, as well as thermoregulatory outcomes as functions of sea surface temperature (SST).
- **5.** We observed that albacore either track a specific temperature and incur high physiological costs, or shuttle between two extreme temperatures within their environment with less physiological cost.

- **6.** Our results indicate that albacore have thermal habitat constraints dictated by their avoidance of a critical low body temperature in SSTs below 11 °C, and high behavioral and physiological costs at SST above 20 °C.
- 7. These results suggest that lower and upper thermal thresholds for regional endotherms result from a trade-off between maintaining body temperature within a functional range and the costs associated with thermoregulation.
- **8.** Mechanistic understanding of the limits to predator distributions, such as the one provided here, elucidates the ecological implications of the current trends of increased stratification and warming in the world's oceans.

3.2 Introduction

An organism's ability to perform life's necessary tasks – to grow, forage, reproduce, and avoid predation – depends to some degree on its temperature (Angilletta 2009; Gates 1980; Heinrich 1977). As a result, organisms have evolved a wide range of thermoregulatory abilities and strategies ranging from an ectotherm whose body temperature conforms to its environment and who can function at a wide range of body temperatures, to an endotherm whose body temperature is highly conserved and who has the ability to harness their own metabolic heat (Angilletta et al. 2010). The continuum between the conformer and the homeotherm contains a myriad of thermoregulatory strategies and capabilities (Angilletta 2009; Heinrich 1977). Each strategy has its own trade-offs and ultimately determines the organism's habitat availability and vulnerability to changing environmental temperatures (Huey et al. 2012; Porter & Kearney 2009; Kearney 2006).

Many organisms in the world's marine ecosystems employ an intermediate strategy, termed regional endothermy, in which they maintain portions of their bodies at temperatures above ambient temperatures. These organisms include the tunas (Graham & Dickson 2004; Block & Finnerty 1994), lamnid sharks (Carey & Scott 1972; Reynolds 1979), billfishes (Fritsches et al. 2005; Carey 1982), turtles (Casey et al. 2014; Standora et al. 1982), opah (Runcie et al. 2009; Wegner et al. 2015), and steephead parrotfish (Welsh & Bellwood 2012). The advantages to maintaining higher temperatures are directly related to improving function as predators (Cairns et al. 2008; Dickson & Graham 2014) by increasing swimming speed and efficiency (Altringham & Block 1997; Dewar & Graham 1994; Brill 1996; Bernal et al. 2001), enhancing vision (Fritsches et al. 2005), increasing digestion rates (Newton et al. 2015), and expanding thermal niches (Dickson & Graham 2014; Block et al. 1993). This trait comes at a physiological cost of increased metabolic rate (Dickson & Graham 2014), and has been shown to incur elevated metabolic rates at both low and high temperatures – a metabolic rate curve characteristic of endotherms – in bluefin tuna (Blank et al. 2007). Thus, regional endothermy is a trade-off between the physiological costs of metabolic heat production and the benefits of niche expansion and predatory capabilities.

In light of this trade off, it is not surprising that regional endotherms exhibit a mix of behavioral and physiological strategies to thermoregulate (Holland & Sibert 1994; Holland et al. 1992; Casey et al. 2014). As exhibited in ectotherms, behavioral thermoregulation consists of selecting a preferred ambient temperature or shuttling between temperature microhabitats in the environment (Huey 1974). Behavioral thermoregulation in regional endotherms has been demonstrated as shuttling between

warm surface waters and cold waters at depth – which consists of a trade-off between warming at the surface and foraging at depth (Holland et al. 1992; Dizon & Brill 1979; Casey et al. 2014). Similar to endotherms, regional endotherms can also physiologically thermoregulate by increasing their metabolic input – as seen in the captive bluefin (Blank et al. 2007) and albacore (Graham & Dickson 1981) tuna – or by decreasing their rates of heat loss to the environment – as seen in bigeye (Holland & Sibert 1994) and yellowfin (Dewar et al. 1994) tuna, which change their rates of heat loss and heat gain depending on the ambient temperature.

Interestingly, the influence of the thermal habitat on the thermoregulatory strategy employed by regional endotherms has not yet been examined. Here we explore how the thermal environment influences the behavioral and physiological aspects of thermoregulation in juvenile albacore tuna. We use decades of biotelemetry data coupled with mechanistic models to examine both thermal habitat use and the thermal rates of body temperature change associated with the albacore's level of insulation and metabolic activity. We examine the costs and thermoregulatory outcomes of the tuna that generated these data, using sea surface temperature as an environmental descriptor.

3.3 Materials and Methods

ALBACORE ARCHIVAL TAGGING DATA

We used body and environmental temperature time series collected by the Albacore Archival Tagging Program, a collaborative tagging project between the NOAA Southwest Fisheries Science Center and the American Fishermen's Research Foundation (Childers, Snyder, and Kohin, 2011). Archival tags (Wildlife Computers: Mk9) were surgically implanted into the peritoneal cavities of juvenile North Pacific albacore, *Thunnus alalunga*. The archival tags are equipped with two temperature sensors: an internal sensor located within the epoxy housing and an external sensor located at the end of the tag stalk. The tags were deployed such that the internal temperature sensor measured the peritoneal cavity temperature while the external sensor measured the surrounding water temperature at sampling intervals of 1 minute. The albacore used in this study were tagged in the summer and autumn off the west coast of the United States between the years of 2003 to 2011 (Table 3.1). The first month of data were removed from the analysis to minimize the effect of the tagging procedure on the results. Thermal inertia of the sensor itself was not found to produce significant differences in the body temperature data, and the raw temperature data were used (Snyder and Franks, 2016).

CHARACTERIZATION OF THERMOREGULATION

In situ thermoregulation in tunas results from a combination of physiological and behavioral mechanisms. We broke this process down into 3 parts. First, we examined thermal habitat use within the context of two behavioral modes: (i) tracking, in which the albacore tracked a particular water temperature; or (ii) shuttling, in which the albacore moved between cold and warm water microhabitats. We then quantified the physiologically set thermal rates underlying the observed rates of body temperature change. Lastly, we characterized the extent of thermoregulation and its associated costs. Each component of this study was placed within the context of the fish's thermal environment to understand its influence on albacore thermoregulation.

THERMAL HABITAT USE

To examine thermal habitat use, we binned the data by daylight period – defined as sunrise to sunset, and examined whether the albacore exhibited one of two behaviors: (i) tracking, i.e., following a particular water temperature, or (ii) shuttling, i.e., moving between two thermal extremes. We identified these behaviors by looking at the vertical distribution of daily target temperatures, which we define as temperatures at which the albacore's vertical speeds were less than 1 m min⁻¹. To determine whether target temperatures constituted a distribution about one temperature (corresponding to tracking) or two discrete thermal microhabitats (corresponding to shuttling), we fit a double Gaussian curve (*G*) to the distribution of daily target temperatures (*H*):

$$G = a_1 e^{-\left[\frac{(H-T_{cold})}{c_1}\right]^2} + a_2 e^{-\left[\frac{(H-T_{warm})}{c_2}\right]^2}$$
(1)

where T_{cold} and T_{warm} were the mean temperatures of the cold and warm thermal microhabitats, respectively. The parameters *a* and *c* described the magnitude and width of the peaks of the distribution, respectively. If the probability of the mean microhabitat temperature being in the opposite temperature microhabitat was greater than 1%, then the microhabitats were not considered as separate regions, but rather a continuous distribution about one temperature, and the behavior for that day was regarded as tracking; otherwise the behavior was categorized as shuttling. During days of shuttling, albacore were flagged as being in the cold or warm microhabitat whenever their ambient water temperatures were colder/warmer than the cold/warm microhabitat temperature plus/minus 0.5°C.

For each day, we calculated the tuna's target water temperature(s) and placed these within the context of the daily thermal environment. We calculated the depths of the target temperatures as well as the relationship between the target temperatures and the sea surface temperature (SST), defined as the maximum available temperature for the day. When albacore exhibited tracking behavior, the depth of target temperature was the mode of the daily diving depth; for shuttling days, we calculated the mode depths of both the cold and warm target temperatures. When albacore were tracking, we classified the tracking as either 'Surface' or 'Deep' based on whether the tracking temperature was within or below 1°C of the SST, respectively. We examined the most likely behavior with respect to SST.

For each shuttling day, we tested to see if we could predict the number of dives the albacore would make given the temperatures of the microhabitat (T_{a_micro}), the albacore's microhabitat-specific median thermal rates (k_{micro} and T_{m_micro}), the albacore's maximum body temperature prior to its first dive (T_{b_init}) and a cue of a critical upper (T_{b_low}) or lower limit (T_{b_hi}) body temperature to dive or surface, respectively. To do this, we simulated movement of a fish between cold and warm microhabitats, predicting its body temperature at each time t by:

$$T_B(t) = k_{micro} \Delta t \left(T_{a_{micro}}(t) - T_B(t - \Delta t) \right) + T_B(t - \Delta t) + \dot{T}_{m_micro} \Delta t$$

$$T_B(0) = T_{b\ init}$$
(2)

and assigning the T_{a_micro} at time t to either the warm or cold temperature according to its body temperature in relation to T_{b_low} or T_{b_hi} . We used an unconstrained, nonlinear optimization (*fminsearch*, *Matlab*) to find the T_{b_low} or T_{b_hi} that minimized the following error:

$$E = (d_{obs} - d_{model})^2 \tag{3}$$

where d_{obs} and d_{model} are the number of dives during the daytime for the observation and the model, respectively.

THERMAL RATES

To characterize the physiology underlying rates of body temperature change, we use a simple model (Brill et al., 1994) relating the rate of body temperature change $(\frac{dT_b}{dt}, {}^{\circ}C \min^{-1})$ to a specific rate of temperature decrease or increase (defined as the organism's rate constant, k_b , min⁻¹), the temperature difference between the ambient environment (T_a , ${}^{\circ}C$) and the organism's body (T_b , ${}^{\circ}C$), and the rate of temperature increase due to metabolic processes (T_m^i , ${}^{\circ}C \min^{-1}$):

$$\frac{dT_b}{dt} = k_b(T_a - T_b) + \dot{T_m} \tag{4}$$

We solved this equation using segments (or windows) of data over discrete time periods by performing a matrix inversion of the Euler solution to Eqn 4. As thermal rates are known to vary in time, we used a novel adaptive windowing approach (Supplemental Material) in which we used a series of sliding window lengths (Fig. S1b) to provide a range of solutions (estimates of k_b and \vec{T}_m) for each time point. Window lengths in this study corresponded to [5, 15, 30, 60, ... 720] minutes of data. Each solution was coupled with the ambient temperature time series to produce a modeled body temperature (Supplemental Eqn 8). We chose the thermal rate estimates k_b and \vec{T}_m that minimized the root mean square error between the modeled temperature and the observed body temperatures (Supplement Eqn 9, Fig. S1c).

To explore the adjustment of thermal rates, we examined how the rates varied in time and in ambient temperature conditions. We quantified the distribution of day and nighttime rate values. We also used our time series of thermal rates to estimate physiologically determined steady-state body temperatures (T_{ss} , °C) for a given water temperature (T_a):

$$T_{ss} = T_a + \frac{\dot{T}_m}{k_b} \tag{5}$$

These steady state temperatures (i.e., $\frac{dT_b}{dt} = 0$) were derived within the context of local (i.e., ambient temperature given the fish's position in the water column) and global (i.e., sea surface temperature which we define as the maximum available temperature per day) thermal environment. For temperatures at which the fish spent more than 10 minutes over the day, we calculated the median thermal rates (k_b and T_m) and the steady state body temperature T_{ss} . We compared these rates to the realized body temperature (i.e., the corresponding daily mean body temperature at that ambient temperature). This was done to see whether the measured body temperature matched the "physiologically set" temperature. Comparisons were made using either Mann-Whitney U-tests or Wilcoxon sign rank test depending on whether they were independent or paired comparisons, respectively.

OUTCOMES AND COSTS

We estimated the mode daily body temperature and median daily thermal excess, i.e., the temperature difference between the body temperature and water for each day and examined this within the context of the thermal environment and the costs associated with that environment. We estimated costs by calculating three parameters: (i) the median daily rate of temperature gain due to metabolic processes, (ii) the total vertical distances swum per day, (iii) the percent time per day spent in transit. Vertical distance swum was calculated as the sum of the absolute difference between subsequent depth locations, and percent time in transit was the time spent between microhabitats out of the total day length.

3.4 Results

ALBACORE THERMAL HABITAT USE

The juvenile The juvenile albacore of this study were found in sea surface temperatures (SSTs) between 11.4 °C and 30.9 °C, with a mode SST of 17 °C (Fig. 3.1a). Albacore daily diving behavior was categorized as: (i) temperature tracking, when the albacore remained within one thermal microhabitat (n = 3,157 days) or (ii) shuttling, when the albacore shuttled between two distinct thermal microhabitats (n = 6,646 days). When days were grouped by 1 °C SST bins, shuttling was the most common behavior with the exception of days spent in 11 °C (all tracking) and 26 °C (Fig. 3.1b). While shuttling, albacore spent more time in the warm microhabitat than the cold microhabitat for the majority of the days, spending less time in the warm microhabitat as SST increased (Fig. 3.1c).

On days when the albacore exhibited temperature tracking rather than shuttling, the albacore tracked the same daily mean water temperature 16 °C (IQR: 14.8 to 17.4 °C) whether at the surface or at depth (Mann-Whitney U-Test, p = 0.12). The tracking temperature was significantly colder (Mann-Whitney U-Test, p < 0.01) than the temperature of the warm microhabitat (median 17.2 °C, IQR: 15.8 to 18.6 °C) and significantly warmer (Mann-Whitney U-Test, p < 0.01) than the temperature of the cold microhabitat (median 12.5 °C, IQR: 10.7 to 14.3 °C) during days of shuttling, with a median temperature difference between the warm and cold microhabitats of 4.5 °C (IQR: 3.1 to 6.2 °C). The use of the warm and cold microhabitats during shuttling resulted in an overall daily water temperature of 15.8 °C (IQR: 14.4 to 17.2 °C), which was only slightly colder than the mean daily water temperature experienced during tracking (Mann Whitney U-Test, p < 0.01). Thus under both behavioral modes, albacore utilized their environments in a way that achieved a daily mean water temperature of approximately 16 °C.

However, SST did have an effect on the daily mean water temperatures experienced by the tuna. All daily mean temperatures were positively correlated with SST. During shuttling, the temperature of the warm microhabitats was more strongly correlated with SST than the temperature of the cold microhabitats (p < 0.01, Fig. 3.2a). The positive relationship between "chosen" water temperatures and SST weakens at SST greater than 22 °C for both behavioral modes (p < 0.01, Fig. 3.2a). The different relationships of the microhabitat temperatures and SST resulted in a slight increase in the difference between the microhabitats temperatures with increasing SST (p < 0.01, Fig. 3.2b). This increase in thermal heterogeneity at warmer SST provides the albacore with a greater potential for faster rates of body temperature change when shuttling between the two microhabitats.

During days when albacore exhibited tracking behavior, their median depth was 25 m, with an interquartile range of 10 to 81 m (Fig. 3.2c). On days when they exhibited shuttling behavior, the median depth of the cold microhabitats was 119 m (IQR: 71 to 185 m) and the median depth of the warm microhabitats was 16 m (IQR: 3 to 47 m, Fig. 3.2c). The median vertical distance separating cold and warm microhabitats was 87 m (IQR: 50 to 140 m) with thermal gradients of 0.05 °C m⁻¹ (IQR: 0.03 to 0.09 °C m⁻¹). Microhabitats deepened with SST for all behaviors (p < 0.01, Fig. 3.2c). Vertical distance between microhabitats was directly related to SST, with greater distances at higher SST (p < 0.01, Fig 3.2d). The simultaneous increase in microhabitat vertical separation and microhabitat temperature difference resulted in a weak negative relationship between the temperature gradient between microhabitats and SST (slope = -0.002, p < 0.01).

Shuttling was rarely explained by a response to a critical lower or upper body temperature limit. Our predicted number of dives accounted for 90% of the observed number of daily dives on approximately 10 percent of the days when albacore exhibited shuttling behavior (n = 607 days, Fig. 3.3a). During these days the critical body temperature limits were 17.1 °C (IQR: 16.4 to 18.1 °C) for the upper bound and 14.5 °C (IQR: 13.7 to 15 °C) for the lower bound. The critical upper body temperature increased with SST (p < 0.01), however we found no relationship between the lower critical limit and SST (p = 0.14, Fig. 3.3b). This suggests that, on days when albacore diving can be explained by a critical body temperature rather than other motivators (e.g., foraging),

the lower body temperature limit is universal (14.5 °C) and not influenced by the upper body temperature limit or SST.

PHYSIOLOGICAL THERMOREGULATION

Thermal rates k_b and \dot{T}_m for albacore varied both temporally and with diving behavior. Both thermal rates had significantly different day and night time values (Table 2, Wilcoxon signed rank test, p < 0.01) with higher rates of temperature gain due to metabolic processes, \dot{T}_m , during the day time and higher rate constants k_b at night. Tracking behavior had overall greater thermal rates than shuttling behavior (Mann-Whitney U-Test, p < 0.01, Table 3.2).

Microhabitat temperature did not significantly influence thermal rates. When tracking, thermal rates were significantly different when the tunas were at the surface versus at depth (Mann-Whitney U-test, p < 0.01) with higher k_b and \dot{T}_m when the fish were at depth than at the surface (Table 3.2). However, this difference could not be attributed to ambient temperature, as albacore were found to always track the same temperature (see *Thermal habitat use*). Albacore exhibiting shuttling behavior had significantly higher \dot{T}_m in the warm than the cold microhabitat (Table 3.2, Wilcoxon signed rank test, p < 0.01), and no significant difference was observed with k_b (Table 3.2, Wilcoxon signed rank test, p = 0.85). Thus, while tracking, albacore have higher metabolic temperature output at depth than at the surface, and the reverse while shuttling.

The thermal rate ratio (\dot{T}_m : k_b , units: °C) provides a measure of the thermal excess (i.e., the difference between the body and ambient temperature) when the body

temperature has reached equilibrium. During shuttling, the thermal rate ratio was highest in the warm microhabitats (median 4.8 °C, IQR: 3.0 to 7.2 °C) and lowest in the cold microhabitats (median 3.7 °C, IQR: 2.4 to 5.7 °C). During tracking, thermal rate ratios resembled those in the warm microhabitat during shuttling (median: 4.5 °C, IQR: 2.8 to 6.3 °C). Thermal rate ratios gave steady-state body temperatures (i.e., body temperatures that have reached equilibrium with the ambient temperature) of 2.4 to 6.3 °C above ambient temperature.

When rate ratios were combined with ambient temperature, we could predict the steady-state body temperatures (T_{ss} , Fig. 4a). When tracking, surface behavior had slightly lower T_{ss} than tracking at depth. These differences, although significant, are negligible in practice (Surface: 20.7 °C, IQR: 19 to 22.5; Deep: 20.9 °C, IQR: 19.5 to 22.8; Mann-Whitney U-Test, p = 0.02). On shuttling days, T_{ss} in the cold microhabitat had a median value of 16.7 °C (IQR: 14.1 to 19.7 °C) while T_{ss} in the warm microhabitat had a median value of 22.1 °C (IQR: 19.9 to 25.2 °C).

In pairwise comparisons, realized mean body temperatures were significantly different than T_{ss} for both tracking and shuttling behavior (Wilcoxon sign rank test, p < 0.01), but the T_{ss} during tracking were closer to the realized mean body temperature than during shuttling (Fig. 3.4b). For tracking, realized mean daytime body temperatures (median 20.7 °C, IQR: 19.1 to 22.6 °C) were slightly colder than the T_{ss} (median difference 0.6 °C, Wilcoxon sign rank test, p < 0.01). On shuttling days, realized mean body temperatures (median 19.4 °C, IQR: 17.5 to 21.3 °C) in the cold microhabitat were significantly warmer than T_{ss} in the cold microhabitat (median difference of 1.9 °C, Wilcoxon sign rank test, p < 0.01), while the reverse relationship was true in the warm

microhabitat, with significantly colder realized body temperatures (median 20.1 °C, IQR: 18.4 to 22.1 °C) than T_{ss} (median difference of 2.3 °C, Wilcoxon sign rank test, p < 0.01). Perhaps not surprisingly, body temperatures observed during tracking more closely reflected those of the physiologically set temperatures (i.e., T_{ss}) whereas body temperatures observed during shuttling were significantly colder in the cold microhabitat and significantly warmer in the warm micro-habitat, by about the same amount (~2 °C).

OUTCOMES AND COST

Overall, albacore had daily mode body temperatures of 20 °C (IQR: 18 to 22°C, Fig. 3.5a). Daily mode body temperature was directly correlated with SST at SST lower than 22 °C; however, at SST greater than 22 °C (p < 0.01), mode body temperature became independent of SST (p = 0.27, Fig. 3.5b). Within the same SST, tracking had higher mode body temperatures than shuttling up until SST of 19°C (Fig. 3.5b).

Median thermal excess was 4.0 °C (IQR: 1.5 to 4.2 °C) during tracking. During shuttling it ranged between 2.6 °C while in the warm microhabitat (IQR: 1.5 to 4.2 °C), and 7.5 °C while in the cold microhabitat (IQR: 5.9 to 9.4 °C) (Fig. 3.5c). Thermal excess peaked at SSTs of 15 °C for tracking behavior and 20 °C for shuttling behavior in the cold microhabitat (Fig. 3.5d). The cold microhabitat of shuttling had the highest median thermal excess, followed by tracking. In other words, the tuna were much warmer than the cold waters during shuttling, somewhat warmer than the ambient waters during tracking, and only slightly warmer than the warm waters during shuttling.
Behavioral and physiological costs varied by behavioral mode and thermal habitat. Daily median rates of temperature gain from metabolic processes were significantly higher for periods when albacore tracked a temperature than when albacore shuttled between thermal environments (Table 3.2, Mann-Whitney U-Test, p < 0.01). Overall rates of temperature gain due to metabolic processes were lowest in SSTs between 19 and 23 (Fig. 3.6a).

Shuttling, however, incurred behavioral costs, such as time in transit (45 min d⁻¹, IQR: 18.9 to 83.5 min d⁻¹) and greater vertical distances swum (Shuttle: 6.3 km, IQR: 4.63 to 8.23 km; Track: 4.9 km, IQR: 3.3 to 6.7 km; Mann-Whitney U-Test, p < 0.01). While shuttling, the median number of dives per day was 10.5 with an interquartile range of 5.5 to 19.5 dives at a median vertical speed of 48.2 m min⁻¹ (IQR: 24.2 to 90.6 m min⁻¹). Median transit time between microhabitats was 1.7 minutes (IQR: 0.8 to 3.7 minutes). The number of dives decreased (slope = -0.08, $r^2 = 0.2$) and the mean transit time increased (slope = .05, $r^2 = 0.1$) with greater distance between microhabitats. Because distance between thermal microhabitats increased with SST, higher SST resulted in more time spent in transit during shuttling days (Fig. 3.6b). Under both tracking and shuttling, daily swimming distances increased with SST (Fig. 3.6c).

3.5 Discussion

We have shown that albacore utilize their thermal environment in two general ways: (1) tracking one thermal microhabitat and (2) shuttling between two distinct thermal microhabitats. These behaviors impact the albacore's ambient temperature and depth distributions and incur different physiological and behavioral costs, resulting in

different daily body temperatures. Albacore thermal habitat use shows that they have a preference for an ambient temperature of 16 °C. This temperature corresponded to the chosen temperature in tracking behavior, and the mean water temperature achieved while shuttling between microhabitats of warm and cold temperature. While achieving similar mean temperatures, the depth distributions associated with these behaviors are quite different, with albacore reaching and spending more time in deeper waters while shuttling than while temperature tracking. Associated with increased vertical ranges are higher transport costs, measured by distances swum and time spent in transit. We show that although these behavioral costs are higher in shuttling, the physiological costs, i.e., the rates of temperature gain due to metabolic processes, are higher during tracking. Ultimately, albacore are able to maintain slightly higher body temperatures while tracking than while shuttling, however – as albacore are more often shuttling – this benefit in thermoregulatory ability may be offset by higher physiological cost and/or loss of foraging opportunities.

The vertical structure and maximum temperatures of the available daily thermal habitat influenced the results and costs of the albacore's behavioral and physiological thermoregulation. Albacore were more likely to shuttle between warm, surface and cold, deep microhabitats when SSTs were between 13 and 22 °C. While tracking, they spent less time near the surface as SST increased. The vertical structure of the water column shifted as SST increased, resulting in both a greater temperature difference between the warm and cold microhabitats and a greater distance between microhabitats. This resulted in the albacore experiencing the same vertical gradient in temperature over a greater distance – and thus incurring a greater cost – in warmer sea surface temperatures.

These greater behavioral costs were also met with greater physiological costs: the rate of temperature gain due to metabolic processes \dot{T}_m increased with increasing sea surface temperature above 22 °C. At SST greater than 20 °C, albacore dove to deeper waters in order to avoid body temperatures above 22 °C.

The albacore in this study were found to inhabit waters with SST between 11 and 31 °C, with ninety percent of the days found between SST of 14 and 21 °C. Our results are in agreement with studies of the juvenile albacore distributions in the Atlantic, Pacific and the Indian oceans who have defined SST ranges between 14 and 23 °C (Chen et al. 2005; Laurs et al. 1984; Laurs & Lynn 1991; Sund et al. 1981; Goñi & Arrizabalaga 2005). This SST range does not match the regions where albacore are able to maintain a SST-independent daily body temperature, nor where their physiological costs are lowest.

We have several hypotheses that address this discrepancy. First, we propose that the trade-off between physiological and behavioral costs is important to consider. The most common range in SST experienced by the tunas corresponds to lower behavioral costs than incurred at higher SST and lower physiological costs than incurred at lower SST. It may thus be an optimal temperature range where these two costs are jointly minimized. Second, the benefits of thermal excess may outweigh those of absolute body temperature. It may be that albacore have performance curves, characteristic of stenotherms, that permit high performance across a wide range of body temperatures (Alford & Lutterschmidt 2012). As performance curves are asymmetric, with faster decreases in performance at higher temperatures compared to colder temperatures, errors in thermoregulation around lower body temperatures would have a less detrimental effect on function (Martin & Huey 2008). Thermal excess peaks within the range of SST inhabited by the albacore, and the temperature difference between the albacore and its ectothermic prey may be the most important advantage of thermoregulation. Third, we measured peritoneal temperature rather than red muscle temperature, a common issue in biotelemetry (McCafferty et al. 2015). In the only study of thermoregulation by captive albacore, thermistor placement had an effect on the quantification of thermoregulatory ability (Graham and Dickson, 1981). Thus, it is possible that albacore red muscle is maintained at higher temperatures than those we report here. Lastly, the warmer waters associated with steady body temperatures are also associated with lower food availability. Lower food availability accompanied by higher costs may offset any added benefits of maintaining a constant body temperature.

3.6 Conclusions

Our work demonstrates that juvenile albacore tuna utilize a hybrid approach involving physiological and behavioral thermoregulation to maintain regional endothermy. We find that the available thermal habitat limits albacore distribution, but that the upper and lower boundaries are formed by different constraints. Energy budgets seem to define the upper SST limit while an inability to maintain body temperature above an apparent critical low defines the lower SST limit. This work provides a mechanistic understanding of the behavioral and physiological constraints associated with the vertical and horizontal distributions of regional endotherms. Chapter 3, in full, is currently being prepared for submission for publication of the material. Snyder, S., Chao, L., Kohin, S., and P.J.S. Franks. The dissertation author was the primary investigator and author of this paper.

Fich ID		Deploy			Recover							
F ISII ID	Date	Location	FL (cm)	Date	Location	FL (cm)						
A0396	3-Aug-11	44.9°N, -126.4°E	63.5	16-Jun-13	35.3°N, -214.8°E	84.5						
B2398	1-Jul-04	44.5°N, -125.6°E	64	19-Sep-05	45.9°N, -126.5°E	(74.7)						
1090269	4-Aug-11	44.9°N, -126.3°E	64	26-Jun-13	35.2°N, -216.3°E	(81.1)						
B2605	1-Jul-04	44.5°N, -125.6°E	65	1-Sep-04	45.8°N, -126.2°E	67.3						
B2381	1-Jul-04	44.5°N, -125.6°E	65	1-Sep-05	45.5°N, -126.0°E	73						
1090251	3-Aug-11	44.8°N, -126.4°E	65	24-Aug-13	46.1°N, -126.4°E	(83.1)						
B2393	30-Jun-04	44.7°N, -125.8°E	66	27-May-06	30.3°N, -144.6°E	90						
A0394	3-Aug-11	44.8°N, -126.4°E	68	15-Aug-12	46.8°N, -125.2°E	75.8						
0690078	6-Oct-06	46.1°N, -125.1°E	70	26-Jun-08	13.0°N, -172.0°E	(92.1)						
0690063	7-Aug-06	46.1°N, -124.9°E	70	29-Jun-07	32.0°N, -119.9°E	77.5						
1190241	8-Oct-11	46.5°N, -125.0°E	74.5	7-Aug-14	3.1°N, -169.7°E	103						
A2088	13-Sep-04	45.2°N, -125.2°E	75	10-Aug-05	32.0°N, -118.3°E	(77)						
D1464	6-Aug-06	46.1°N, -125.0°E	75	21-Aug-07	32.4°N, -118.3°E	88.9						
0690065	7-Aug-06	46.1°N, -124.9°E	77	27-May-07	32.5°N, 140.10°E	(84)						
0490306	13-Sep-04	45.0°N, -125.3°E	78	6-Dec-05	33.7°N, -167.8°E	(88.8)						
D1045	6-Aug-06	46.0°N, -125.0°E	80	16-Jun-08	31.2°N, -139.34°E	92						
A1974	7-Nov-03	31.9°N, -119.4°E	81	6-Aug-04	31.4°N, -117.8°E	86.5						
A2082	10-Nov-03	32.0°N, -119.2°E	81.5	20-Aug-04	31.5°N, -117.6°E	(88.3)						
B2942	12-Aug-04	31.2°N, -117.7°E	82.5	5-Jul-05	30.3°N, -117.7°E	89.2						
0390167	25-Jul-03	29.2°N, -117.4°E	84	2-Jul-04	30.0°N, -117.1°E	94						
A1967	7-Nov-03	31.9°N, -119.5°E	86.5	27-Aug-04	31.0°N, -117.7°E	91						
0390191	27-Jul-03	29.3°N, -117.4°E	87	10-Jul-04	29.9°N, -116.7°E	93.5						
A1246	08-Nov-03	31.9°N, -119.3°E	87.5	27-Aug-04	30.9°N, -117.7°E	94						
A1991	8-Nov-03	31.9°N, -119.5°E	87.8	16-Aug-04	31.4°N, -117.4°E	92.5						
A1987	8-Nov-03	31.9°N, -119.4°E	88	21-Aug-04	31.8°N, -118.2°E	(94.9)						
0390173	27-Jul-03	29.3°N, -117.4°E	89	18-Oct-03	32.3°N, -119.2°E	91						
A1973	7-Nov-03	31.9°N, -119.9°E	89.9	30-Aug-04	31.4°N, -117.8°E	97						

Table 3.1 Deployment and recovery information for the fish used in this study. Fish in order of increasing size at tag deployment. Recovery fork lengths in parentheses were estimated using our mean observed growth rate.



Figure 3.1 Albacore behavioral mode by SST. (a) Histogram of days spent at each sea surface temperature, numbers above the bars represent the number of fish that encountered that SST. The mode (black), 5th percentile (blue), and 95th percentile (red) are represented by solid lines. (b) The proportion of days within the SST bin that the albacore spent either shuttling or tracking (c) Percent time spent per day in the cold micro-habitat (blue), warm micro-habitat (red), or in transit (grey) while shuttling.



Figure 3.2 Thermal habitat use by SST. (a) Microhabitat temperatures associated with the behavioral modes at each SST. (b) Temperature difference between the warm and cold microhabitats during shuttling. (c) Depths of microhabitats versus SST. (d) Distance between microhabitats while shuttling as a function of SST. In all plots, red and blue represent the warm and microhabitats of shuttling days, respectively; while gray and black represent tracking days. The circles are the median values at each SST bin with the vertical lines representing the interquartile length. The solid horizontal lines are linear fits of daily points (n = 6,446 days for shuttling, n = 3,157 days for tracking).



Figure 3.3 Albacore behavioral thermoregulation. (a) Day of observed body temperature (solid red line) and the corresponding modeled body temperature (dashed red line) given dive response to critical upper and lower temperatures, within the context of the observed water temperature (solid blue line) and modeled water temperature (dashed blue line) (b) Relationship of the critical upper and lower temperatures with SST. The circles represent median values by SST bin, with the solid vertical lines representing the interquartile range. The solid red line and equation correspond to the linear fit of the daily upper critical body temperature limit with SST (n = 607 days). The relationship of the daily lower critical body temperature limit with SST was not significant.

	k_b (1	10⁻³ min⁻¹)	<i>T_m</i> (10	⁻² °C min ⁻¹)
	Median	IQR	Median	IQR
Overall	6.7	3.3 to 11.2	2.0	.86 to 4.2
Day	6.3	3.7 to 10.3	2.8	1.6 to 4.3
Night	7.0	3.5 to 11.2	1.4	.65 to 3.0
Tracking	7.4	4.0 to 11.5	3.0	1.3 to 5.0
Surface	7.0	3.7 to 11.4	2.8	1.1 to 5.0
Depth	8.0	4.9 to 11.7	3.4	2.0 to 5.1
Shuttling	5.9	3.6 to 9.5	2.7	1.7 to 4.0
Warm	6.0	3.6 to 9.7	2.9	1.7 to 4.3
Cold	6.0	3.5 to 10.0	2.2	1.2 to 3.7

Table 3.2 Distributions of thermal rates by behavioral mode.



Figure 3.4 Physiologically set body temperature. (a) Histograms of T_{ss} at each of the microhabitats of shuttling and tracking while at the surface and at depth (b) Difference between realized mean body temperature and the physiologically set steady state temperatures, T_{ss} . The boxplots represent the interquartile range about the median, and the whiskers represent the most extreme data points, not considered outliers. All three groups in (b) are significantly different from one another (p < 0.01).



Figure 3.5 Thermoregulation by behavior & environment. (a) Histogram of mode daily body temperatures under tracking (black line) and shuttling (grey bars). (b) Daily mode body temperature as a function of SST. (c) Histogram of median daily thermal excess under tracking (black line) and shuttling (grey bars). (d) Daily median thermal excess as a function of SST. In both (b) and (d), the median values of shuttling and tracking per SST bin are represented with grey and black with the lines representing interquartile range.



Figure 3.6 Cost related to thermoregulation by SST. (a) Daily median metabolic output (b) total daily vertical swimming distance, and (c) percent of the day spent in transit as functions of SST. In all plots, median values for shuttling (grey circles) and temperature keeping (black circles) are shown with the corresponding lines representing the IQR.

3.7 References

- Alford, J G, and W I Lutterschmidt. 2012. "Modeling Energetic and Theoretical Costs of Thermoregulatory Strategy." *Journal of Biological Dynamics* 6 (1): 63–79. doi:10.1080/17513758.2011.588342.
- Altringham, J D, and B A Block. 1997. "Why Do Tuna Maintain Elevated Slow Muscle Temperatures? Power Output of Muscle Isolated from Endothermic and Ectothermic Fish." *The Journal of Experimental Biology* 200 (Pt 20): 2617–27.
- Angilletta, M J, B S Cooper, M S Schuler, and J G Boyles. 2010. "The Evolution of Thermal Physiology in Endotherms." *Frontiers in Bioscience (Elite Edition)* 2: 861–81. doi:10.2741/E148.
- Angilletta, M J. 2009. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press.
- Bernal, D, K A Dickson, R E Shadwick, and J B Graham. 2001. "Review: Analysis of the Evolutionary Convergence for High Performance Swimming in Lamnid Sharks and Tunas." Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology 129 (2-3): 695–726. doi:10.1016/S1095-6433(01)00333-6.
- Blank, J M, J M Morrissette, C J Farwell, M Price, R J Schallert, and B A Block. 2007. "Temperature Effects on Metabolic Rate of Juvenile Pacific Bluefin Tuna *Thunnus* orientalis." *The Journal of Experimental Biology* 210 (Pt 23): 4254–61. doi:10.1242/jeb.005835.
- Block, B A, J R Finnerty, A F R Stewart, and J Kidd. 1993. "Evolution of Endothermy in Fish : Mapping Physiological Traits on a Molecular Phylogeny." *Science (New York, N.Y.)* 260: 210–14. doi:10.1126/science.8469974.
- Block, B A, and J R Finnerty. 1994. "Endothermy in Fishes: A Phylogenetic Analysis of Constraints, Predispositions, and Selection Pressures." *Environmental Biology of Fishes* 40 (3): 283–302. doi:10.1007/BF00002518.
- Brill, R W. 1996. "Selective Advantages Conferred by the High Performance Physiology of Tunas, Billfishes, and Dolphin Fish." *Comparative Biochemistry* and Physiology - A Physiology 113 (1): 3–15. doi:10.1016/0300-9629(95)02064-0.
- Cairns, D K, A J Gaston, and F Huettmann. 2008. "Endothermy, Ectothermy and the Global Structure of Marine Vertebrate Communities." *Marine Ecology Progress Series* 356: 239–50. doi:10.3354/meps07286.
- Carey, F G. 1982. "A Brain Heater in the Swordfish." Science (New York, N.Y.) 216 (4552): 1327–29. doi:10.1126/science.7079766.

Carey, G, and D Scott. 1972. "Regulation of brain and eye temperatures by the bluefin

tuna (Thunnus thynnus)" Comparative Biochemistry and Physiology 43: 425-433.

- Casey, J P, M C James, and A S Williard. 2014. "Behavioral and Metabolic Contributions to Thermoregulation in Freely Swimming Leatherback Turtles at High Latitudes." *Journal of Experimental Biology* 217 (13): 2331–37. doi:10.1242/jeb.100347.
- Chen, I, P Lee, and W Tzeng. 2005. "Distribution of Albacore (*Thunnus alalunga*) in the Indian Ocean and Its Relation to Environmental Factors," *Fisheries Oceanography* 14 (1): 71–80.
- Dewar, H, and J Graham. 1994. "Studies of Tropical Tuna Swimming Performance in a Large Water Tunnel - Kinematics." *The Journal of Experimental Biology* 192 (1): 45–59. http://www.ncbi.nlm.nih.gov/pubmed/9317308.
- Dewar, H, J B Graham, and R W Brill. 1994. "Studies of Tropical Tuna Swimming Performance in a Large Water Tunnel - Thermoregulation." *The Journal of Experimental Biology* 192 (1): 33–44. http://www.ncbi.nlm.nih.gov/pubmed/9317308\nhttp://www.ncbi.nlm.nih.gov/pubmed/9317308
- Dickson, K A, and J B Graham. 2014. "Evolution and Consequences of Endothermy in Fishes." *Physiological and Biochemical Zoology : PBZ* 77 (6): 998–1018. doi:10.1086/423743.
- Dizon, A E, and R W Brill. 1979. "Thermoregulation in Tunas." *American Zoologist* 19 (1): 249–65.
- Fritsches, K A, R W Brill, and E J Warrant. 2005. "Warm Eyes Provide Superior Vision in Swordfishes." *Current Biology* : *CB* 15: 55–58. doi:10.1016/j.
- Gates, D M. 1980. Biophysical Ecology. New York : Springer-Verlag.
- Goñi, N, and H Arrizabalaga. 2005. "Analysis of Juvenile North Atlantic Albacore (*Thunnus alalunga*) Catch per Unit Effort by Surface Gears in Relation to Environmental Variables." *ICES Journal of Marine Science* 62 (7): 1475–82. doi:10.1016/j.icesjms.2005.05.014.
- Graham, J B, and K A Dickson. 1981. "Physiological Thermoregulation in the Albacore Thunnus Alalunga." *Physiological Zoology* 54 (4): 470–86.
- Graham, J B, and K A Dickson. 2004. "Tuna Comparative Physiology." *The Journal of Experimental Biology* 207 (Pt 23): 4015–24. doi:10.1242/jeb.01267.
- Heinrich, B. 1977. "Why Have Some Animals Evolved to Regulate a High Body Temperature?" *The American Naturalist* 111: 623–40.
- Holland, K N, R W Brill, R K Chang, J R Sibert, and D A Fournier. 1992. "Physiological and Behavioural Thermoregulation in Bigeye Tuna (*Thunnus*

obesus)." Nature 358: 410-12. doi:10.1038/358410a0.

- Holland, K N, and J R Sibert. 1994. "Physiological Thermoregulation in Bigeye Tuna, *Thunnus obesus.*" *Environmental Biology of Fishes* 40: 319–27.
- Huey, R B, M R Kearney, A Krockenberger, J A M Holtum, M Jess, and S E Williams.
 2012. "Predicting Organismal Vulnerability to Climate Warming: Roles of Behaviour, Physiology and Adaptation." *Philosophical Transactions of the Royal Society B: Biological Sciences* 367: 1665–79. doi:10.1098/rstb.2012.0005.
- Huey, R B. 1974. "Behavioral Thermoregulation in Lizards: Importance of Associated Costs." *Science*. American Assn for the Advancement of Science.
- Laurs, M, P C Fiedler, and D R Montgomery. 1984. "Albacore Tuna Catch Distributions Relative to Environmental Features Observed from Satellites." *Deep Sea Research* 31 (9): 1085–99.
- Laurs, R M, and R J Lynn. 1985. "North Pacific Albacore Ecology and Oceanography."
- Martin, T L, and R B Huey. 2008. "Why 'Suboptimal' Is Optimal: Jensen's Inequality and Ectotherm Thermal Preferences." *The American Naturalist* 171 (3): 102–18. doi:10.1086/527502.
- Newton, K C, J Wraith, and K A Dickson. 2015. "Digestive Enzyme Activities Are Higher in the Shortfin Mako Shark, *Isurus oxyrinchus*, than in Ectothermic Sharks as a Result of Visceral Endothermy." *Fish Physiology and Biochemistry* 41 (4). Springer Netherlands: 887–98. doi:10.1007/s10695-015-0055-8.
- Porter, W P, and M Kearney. 2009. "Size, Shape, and the Thermal Niche of Endotherms." *Proceedings of the National Academy of Sciences of the United States of America* 106: 19666–72. doi:10.1073/pnas.0907321106.
- Reynolds, W. 1979. "Shark Thermoregulation." Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 64: 451–53.
- Runcie, R M, H Dewar, D R Hawn, L R Frank, and K A Dickson. 2009. "Evidence for Cranial Endothermy in the Opah (*Lampris guttatus*)." *The Journal of Experimental Biology* 212: 461–70. doi:10.1242/jeb.022814.
- Standora, E A, J R Spotila, and R E Foley. 1982. "Regional Endothermy in the Sea Turtle, *Chelonia mydas*." *J Thermo Biol* 7: 159–65.
- Sund, P N, M Blackburn, and F Williams. 1981. "Tunas and Their Environment in the Pacific Ocean: A Review." Oceanography and Marine Biology An Annual Review 19: 443–512.
- Teo, S L H, A Boustany, H Dewar, M J W Stokesbury, K C Weng, S Beemer, A C Seitz, C J Farwell, E D Prince, and B A Block. 2007. "Annual Migrations, Diving Behavior, and Thermal Biology of Atlantic Bluefin Tuna, *Thunnus thynnus*, on

Their Gulf of Mexico Breeding Grounds." *Marine Biology* 151 (1): 1–18. doi:10.1007/s00227-006-0447-5.

- Wegner, N C, O E Snodgrass, H Dewar, and J R Hyde. 2015. "Whole-Body Endothermy in a Mesopelagic Fish, the Opah, *Lampris guttatus*." *Science* 348: 786–90. doi:10.1126/science.aaa8902.
- Welsh, J Q, and D R Bellwood. 2012. "Regional Endothermy in a Coral Reef Fish?" *PLoS ONE* 7 (3): 3–7. doi:10.1371/journal.pone.0033187.

CHAPTER 4

Seasonal habitat suitability along a latitudinal gradient explains variability in migratory behavior of juvenile albacore tuna

4.1 Abstract

Characterization of an animal's movement patterns and the motivations behind those movements allow us to predict their response to changes in the environment or ecosystem. Biotelemetry studies alongside remote sensing technologies provide a wealth of information to test established hypotheses behind the question of why animals move. We use archival tagging data and satellite imagery on temperature and turbidity to test the hypothesis that seasonal changes in habitat suitability drive the migrations of juvenile albacore tuna. Migratory behavior differed between fish departing from locations north versus south of 40 °N. We find that the northern fish had longer and more consistent phenology and direction. Migration distance was found to correlate with latitudinal gradient in sea surface temperature at the outbound origin rather than those at the destination. The phenology of the northern fish's migrations corresponded with annual changes in the temperatures of their origins and destinations, which was reflected in changes in their body temperatures. Northern fish began migrations offshore when their weekly mean body temperatures were approximately 17 °C, a temperature rarely seen in the southern fish. Our work suggests that the variability in migratory behavior of juvenile albacore can be explained by a physiological motivation to avoid seasonally cold waters. Herein, we provide the necessary parameters to model albacore movement in the context of changing ocean temperatures and to predict future albacore distributions.

Keywords: albacore tuna, migration, habitat suitability, biotelemetry.

4.2 Introduction

Animal movement shapes the ecosystems and biodiversity patterns of our planet. The paths, extents and timings of animal movement influence predator/prey dynamics (Lampert 1989; Abrams 2007; Sims et al. 2005), species distributions (Parmesan et al. 1999), and population dynamics (Fiksen et al. 2007). The vast implications of animal movement have led to a wealth of studies that have provided empirical observations (Payne et al. 2014; Costa, Breed, and Robinson 2012; Rutz and Hays 2009) as well as mathematical and theoretical frameworks (Sainmont, Thygesen, and Visser 2013; Pedersen et al. 2011; McClintock et al. 2012; Singh et al. 2012; Jachowski and Singh 2015; Morales et al. 2004; Nathan et al. 2008; Holyoak et al. 2008; Bauer et al. 2009). Yet for many organisms the impetus behind their movements is still a mystery.

An animal may move to gain refuge from predators (Skov et al., 2013) or inhospitable environments (Gibbons 1986), to reproduce (Hoar 1953), or to find food (Fryxell and Sinclair 1988; Whitlock et al. 2015). An animal's migratory behavior can vary in distance, duration, and timing (Singh et al. 2012). A successful migration is a feat that requires a wealth of information on habitat, direction, and time, as well as the capability to move in response to this information (Bowlin et al. 2010). Decisions on whether or not to migrate and how far to go can be set by genetics (Berthold 1991) or social learning (Andersen 1991), or adaptable based on current physiological, environmental or ecological conditions (Parmesan et al. 1999). Whether learned or inherited, the animal's impetus to move and the map it uses to navigate can lead the animal astray if it is not adaptable to current conditions or ecosystems (Andersen 1991; Wilcove and Wikelski 2008; Bowler and Benton 2005).

One of the ways to explore the reasons behind movement, and furthermore to understand the adaptability of migration, is to place the variability in observed behavior within a framework of testable hypotheses (Rutz and Hays 2009; Kirby 2001). Biotelemetry data provide measures of the propensity (i.e., the probability to migrate and/or the migratory distances), the residential areas (i.e., the origins and destinations of migration), and the phenology (i.e., the departure and arrival dates) of migration. By coupling this information with large-scale environmental data (e.g., satellite data on abiotic and biotic factors in the environment) and examining the variability among individual behaviors, we can test different drivers of movement. Our study uses empirical observations of both albacore movement and their environment to test the hypothesis that habitat suitability drives migration in juvenile albacore tuna.

Albacore tuna (*Thunnus alalunga*) is a globally distributed, temperate tuna comprising 6 percent of the global tuna catch (FAO, 2016). North Pacific albacore are highly migratory, with migrations spanning the entirety of the North Pacific Ocean throughout their life cycle (Otsu and Uchida 1963; Laurs and Lynn 1977; Childers, Snyder, and Kohin 2011). Their migration patterns are ontogenically defined, with largest migrations observed in juveniles, ages 2-5 years. Migration routes have been well described (Childers Snyder, and Kohin, 2011; Laurs and Lynn, 1977) and their

paths have been correlated with the North Pacific transition zone (Zainuddin et al., 2006). Although the hypothesis of habitat suitability as the driver of this movement was put forth in 1977 (Laurs and Lynn, 1977), the motivation for this behavior has yet to be tested.

Our study quantifies the migratory behavior of juvenile albacore and places this behavior within the context of the seasonal cycles in the oceanography of residential habitats. We test the hypothesis that habitat suitability drives the migratory behavior of albacore tuna. Albacore distributions have been linked to sea surface temperature (Laurs and Lynn 1991; Laurs, Fiedler, and Montgomery 1984; Kimura, Nakai, and Sugimoto 1997) and thermal fronts (Xu et al. 2015). The depth of the thermocline (Childers, Snyder, and Kohin 2011) and the turbidity of the water column (Murphy 1959) have been shown to influence their vertical distributions and foraging capabilities. Herein, we examine both the horiztonal and vertical habitat by assessing the annual trends in sea surface temperature and gradients in light and temperature with depth. To test the hypothesis that habitat selection drives migratory behavior, we made the following predictions: (i) the propensity to migrate would be positively correlated with environmental fluctuations at the outbound origins, (ii) the phenology of migration aligns with the fluctuations of environmental conditions at the origin of the migratory segments, and (iii) the destinations of migratory segments at the time of migration would have significantly different environmental conditions than the origins, and that these differences will always be in the direction of the median environmental conditions observed across all fish.

4.3 Materials and Methods

Albacore locations

Tagging data from juvenile North Pacific albacore were collected through the Albacore Archival Tagging Program, a collaborative effort between the National Marine Fisheries Service and the American Fishermen's Research Foundation. The 24 individuals represented in our study were tagged along the west coast of North America in two sites: Southern (off Baja California) and Northern (off Oregon). We surgically implanted one of three models of archival tag (Wildlife Computers: Mk9, Lotek: Lat2310 and LTD2310) into the peritoneal cavity of the albacore tuna. Daily locations were estimated using the UKFSST method – an unscented Kalman filter that incorporates light information and refines locations by matching the tag's measured sea surface temperature with satellite sea surface temperature data (Lam, Nielsen, and Sibert 2008). All individuals in this study were at liberty for over 200 days, with an average time at liberty of 370 days (Table 4.1).

Migratory Behavior

Each migration route was simplified into net square displacement (NSD) from the tagging location. Net square displacement is defined as the square of the Euclidian distance at a given time from the tagging location (Borger and Fryxell 2012). Timing of migration and migration distance were determined by fitting the following model to the NSD data (Singh et al., 2012):

$$NSD(t) = \frac{\delta_{out}}{\left[1 + \exp\left(\frac{(\theta_{out} - t)}{\phi_{out}}\right)\right]} + \frac{-\delta_{in}}{\left[1 + \exp\left(\frac{(\theta_{in} - t)}{\phi_{in}}\right)\right]} \quad (1)$$

where t is days past tagging, δ_{out} and δ_{in} are the net square displacement distances (km²) during the outbound (i.e., when the fish moved away from its original location) and inbound (i.e., when the fish moved back towards its original location) migrations respectively, θ_{out} and θ_{in} are measures of the beginning (days) of the outbound and inbound migrations respectively, and finally ϕ_{out} and ϕ_{in} provide measures of the duration of migration (days).

To assess the precision and accuracy of the fit, the concordance criterion (CC) – also known as the concordance coefficient – was used (Huang et al., 2009):

$$CC = \frac{\sum_{i=1}^{n} (y_i - \hat{y}_i)}{\sum_{i=1}^{n} (y_i - \bar{y})^2 + \sum_{i=1}^{n} (\hat{y}_i - \bar{\hat{y}})^2 + n(\bar{y} - \bar{\hat{y}})^2}$$
(2)

 $-1 \leq CC \leq 1$

where *n* is the number of samples, *y* is the NSD observation data and \hat{y} is the modeled data. The concordance criterion is the product of Pearson's correlation coefficient (which measures precision) and coefficient of accuracy (which as its name suggests is a measure of accuracy). CC values less than 0 indicate a lack of fit, and a value of 1 represents a perfect agreement between the data and the model.

Using these parameters, it was possible to objectively define the timing as well as the origins and destinations of each fish's seasonal migration. We defined the beginning and ending points of migratory behavior as when the fish had moved 1% (t_1) and 99% (t_{99}) of the migration distance, respectively. These could be calculated using the following equations:

$$t_1 = \theta - \ln(98) \phi \tag{3}$$
$$t_{99} = \theta + \ln(98) \phi$$

where θ and ϕ are parameters from the model fit described above (Eqn 1; Fig. 4.1). These parameters (t_1 and t_{99}) provide the days since tagging. To be able to compare across tags, we added these values to the Julian day of the fish's tagging date. This was done for each migratory segment, i.e., the outbound and inbound migrations. Origins and destinations of migratory segments (i.e., the residence areas) were determined by averaging the locations that occurred prior to or after migratory behavior, or – in the case of the outbound destination – the locations that occurred between the outbound and the inbound migration segments (Fig. 4.1). Inbound locations were only calculated for those fish whose tracks continued at least 7 days after the inbound migration ended (i.e., $t_{99} + 7$).

To differentiate between fish that migrated, dispersed or exhibited home range behavior, the NSD data were also fit to the dispersal model, which is simply the outbound portion of the migration model (Singh et al., 2012):

$$NSD(t) = \frac{\delta}{\left[1 + \exp\left(\frac{(\theta - t)}{\phi}\right)\right]}$$
(4)

And the home range model (Singh et al., 2012):

$$NSD(t) = \varphi_1[1 - \exp(\varphi_2 t)]$$
 (5)

where φ_1 is representative of the distance about the tagging location in which the tuna remains and φ_2 is the rate at which the tuna approaches that distance. If the fit for the dispersal or home range model produced a higher CC than the migration model, the fish was classified as dispersing or non-migrating, respectively.

As we are examining seasonal migrations, tracks longer than 365 days were separated into two time series: (i) the first full year and (ii) the remaining days. If the second time series was longer than 200 days, the migration model was applied to the track and reported as a separate migration. If shorter than 200 days, the second time series was discarded from the analysis.

For fish that migrated or dispersed, we examined the maximum migration distance, phenology, average speed and direction of their migratory journeys as well as their final distance from their outbound origin. Circular statistics were used to examine consistency in migratory orientation and phenology among fish. Weighted mean vectors (WMV) were estimated for each migratory segment and compared across fish using the CircStat package in Matlab (Berens 2009). The WMV was calculated using daily direction (the bearing between subsequent locations) weighted by step length (the Euclidean distance between subsequent locations). Circular variance in WMV (S_{dir}) was calculated as 1 - R, where R is the resultant vector length (Berens 2009). To examine variance in timing, day of year was scaled to radians, and circular variance in timing (S_{time}) was estimated in the same manner as described for the variance in distance. For fish that exhibited an inbound migration as well as an outbound migration, the average migration speeds were compared with a paired t-test. To assess accuracy in return to original outbound location, we calculated the Euclidean distance between the outbound origin and the inbound destination.

Habitat Characterization

We examined 3 environmental variables (sea surface temperature, SST; turbidity, k490; and mixed layer depth, MLD) that have been hypothesized to influence albacore habitat suitability. To quantify habitat selection (i.e., movement away or towards a particular environment), it was essential to examine the oceanographic conditions at residence areas throughout the fish's time at liberty – not only when the fish was residing in those areas. Thus, we relied on satellite data for characterizing temperature and light conditions.

Satellite data SST data used in this study were obtained from the NOAA highresolution (0.25°x0.25°) blended analysis of daily SST and Ice (OISSTv2, Reynolds et al., 2007). The mixed layer depth climatology used in this study was a monthly compilation of *in situ* temperature profile data from autonomous profiling floats, known as Argo (Holte et al., 2010). The mixed layer depth was calculated from these profiles using a hybrid method that incorporates both gradient and threshold models of calculating mixed layer depth (Holte and Talley 2009). As temperature is known to influence tuna vertical distributions (Childers, Snyder, and Kohin 2011), we used the mixed layer depth climatology generated from gradient and threshold temperatures rather than density. The MLD climatology had a spatial resolution of 1°. Lastly, we compiled turbidity (k490, the diffuse attenuation coefficient at 490 nm) estimates derived from 8-day composites of satellite ocean color measurements at a spatial resolution of 9 km (NASA Ocean Biology, 2016). These satellite data were sampled and compiled within a 2° grid of the fish's location and residence areas throughout each fish's time at liberty. This provided a habitat characterization of the residence areas to compare to the fish's selected habitat.

Habitat Selection

We defined the propensity to migrate as both the proportion of fish that migrated and the distances traveled, as a function of the range in environmental fluctuations at the residence sites. To examine the proportions of migratory fish, we grouped the fish by annual amplitude of SST, light attenuation and MLD at the outbound origin. We then qualitatively compared the type of migratory movement observed (i.e., home range, dispersal or migration) in each group. We also regressed the distances traveled against the annual amplitude of environmental fluctuations at the outbound origins. Departure dates were compared with the time at which the conditions of the migration origin's environment trended above and below the annual mean at that location. For each migration, we did a pairwise comparison of the conditions at the origin and the destination from the time of departure through the period of residence in the destination. This was done for both the outbound and inbound journeys. We used a Mann-Whitney U-test to detect significant differences between the origin and destination environments. Lastly, we calculated the direction of this difference relative to the median environmental conditions across all fish in the study.

4.4 Results

All fish in this study either dispersed or migrated; however migratory behavior varied markedly between those fish with outbound origins north of 40° (n = 13 migrations and 2 dispersals) and those fish departing from more southern locations (n =

12 migrations and 1 dispersal) herein referred to as northern and southern fish, respectively (Table 4.2). Northern fish had significantly greater migration distances $(4,567 \pm 1,308 \text{ km}, \text{mean} \pm \text{std})$ than the southern fish $(1,273 \pm 578 \text{ km}, \text{mean} \pm \text{std}; t$ *test*, $p = 1 \cdot 10^{-9}$) to their outbound destinations. Yet, for fish that made a return journey, northern fish had the same degree of accuracy in returning to their outbound origins as the less-traveled southern fish (median: 297 km, inter-quartile range: 456 km, n=26 fish; Mann-Whitney U-test, p = 0.82).

While all northern fish exhibited an east-west migration with similar outbound and inbound departure dates, the migration routes of southern fish varied in timing and direction. All northern individuals began their outbound migration between September 27 and November 22 (average departure date: October 25, $S_{time} = 0.04$), and their inbound migration between March 8 and the May 25 (average departure date: April 11, $S_{time} = 0.23$). For southern fish, the outbound migration occurred anywhere from September 14 to May 18 (average departure date: March 2, $S_{time} = 0.70$), and the inbound migration from April 11 to June 21 (mean day of year: April 30, $S_{time} = 0.23$). Similarly, while all the fish departing from the north migrated towards destinations in a southwest direction ($WMV = 199^\circ$, $S_{dir} = 0.01$; Fig. 4.2a-b), outbound migrations in the south varied widely in direction ranging from northwest to southeast ($WMV = 202.4^\circ$, $S_{dir} = 0.52$; Fig. 4.2c-d). Inbound migrations were also similar among the northern fish, which all traveled in a northward direction ($WMV = 6.15^\circ$, $S_{dir} = 0.02$; Figure 2a-b), while the southern fish were found to move in any direction ($WMV = 33.2^\circ$, $S_{dir} = 0.48$; Figure 4.2c-d).

Outbound migration speeds were not significantly different between the northern and southern groups and averaged 54 ± 16 km d⁻¹ (t-test, p = 0.12). However inbound migration speeds were significantly faster in the north $(100 \pm 19$ km d⁻¹) than in the south $(64 \pm 24$ km d⁻¹, $p = 1 \cdot 10^{-4}$). In both groups, inbound migrations were faster than outbound migrations (paired t-test, $p = 1 \cdot 10^{-5}$). The lower variability in northern fish behavior versus the southern fish occurred despite northern fish departing from origins spanning a larger distance (2,253 versus 1,719 km) over a longer time period (7 versus 3 years).

As behavior differed along a latitudinal gradient, we examined how the environment varied with latitude at the outbound origins and destinations. Median sea surface temperatures at the residence areas (i.e., the outbound origins and the outbound destinations) ranged from 9 to 23 °C and decreased with increasing latitude at a rate of 0.48 °C °N⁻¹ (Fig. 4.3a). However, the range in SST did not show significant relationships with latitude (Fig. 4.3b). Vertical habitat did not show significant differences in the mixed layer depth across the latitudinal gradient (Fig. 4.3c-d) or in turbidity (Fig. 4.3e-f).

Comparisons between northern and southern residence areas, and pairwise comparisons of the residence areas showed significant differences in available habitat. Northern fish had significantly colder outbound origins Table 4.3) but statistically similar outbound destinations compared to those of the southern fish (Table 4.3). This led to greater absolute differences in mean SST between the origin and destination for northern migrations ($8.0 \pm 2.3^{\circ}$ C) than for southern migrations ($3.4 \pm 3.2^{\circ}$ C, t-test, p <0.01). The annual range in SST was greater at both the origins and destinations of northern fish compared to the origins and destinations (Table 4.3) of southern fish. Mixed layer depth at the outbound origin was significantly deeper and had a greater annual range in the north than in the south (Table 4.3) for all fish. At the outbound destinations, mean annual mixed layer depth was not significantly different (Table 4.3), but the annual range was significantly greater in the north than in the south (Table 4.3). We did not observe significant differences in water clarity between the resident sites of northern and southern fish. Pairwise comparisons of outbound origins versus outbound destinations revealed differences in temperature and water clarity. Outbound origins had greater annual mean SST than outbound destinations (Table 4.3). The extent of the mixed layer was shallower at the origins than at the destinations (Table 4.3). Lastly, the outbound destinations had clearer water than outbound origins (Table 4.3).

In moving between the residence areas, albacore experienced median sea surface temperatures significantly greater than that of their origins and significantly less than that of their outbound destinations (Table 4.3). The mixed layer depths that the fish encountered were significantly more variable than those at either residence area, but were only significantly deeper than the mixed layer depths found at the origin (Table 4.3). Interestingly, albacore inhabited on average murkier waters than the annual averages at the residence areas (Table 4.3). The waters the albacore inhabited also had a significantly larger range than those of either residence area (Table 4.3). Northern fish inhabited significantly more variable thermal habitats that were on average colder with deeper mixed layers, but inhabited waters of approximately the same turbidity (Table 4.3).

We examined migration distance within the context of those habitat characteristics that had significant differences at the residence sites of northern versus southern fish. Migration distances were found to indirectly correlate with mean annual SST of the outbound origins, but not with the mean annual SST of the outbound destinations (Fig. 4.4). Migration distance did not correlate with mean mixed layer depth (Fig 4.4) or with variability in either SST or MLD.

The trends in SST at the outbound origins and outbound destinations were similar across years, producing predictable seasonal cycles of temperature at the outbound and inbound sites. In the northern region, the phenology of migration was correlated with these seasonal fluctuations of SST such that the fish migrated from their outbound origin as sea surface temperatures began to decrease, and departed the outbound destination when the temperatures there began to increase (Fig. 4.5a). Persistent seasonal cycles were also seen in mixed layer depth and k490. Again as northern fish had consistent timing, their departure from and arrival at the outbound origin were correlated with the deepening of the thermocline in the outbound destination and the shoaling of the thermocline in the outbound origin, respectively (Fig. 4.5b). Lastly, the timing of migration also coincided with a seasonal decrease in turbidity (Fig. 4.5c). For the southern fish, there was a less-pronounced seasonal cycle in all the environmental indicators, but more high-frequency variability; the timings of the individual migrations could not be correlated with these fluctuations (Fig. 4.5d-f).

Timing of outbound movements in the north corresponded with steep declines in body temperature (Fig. 4.6a). The mode body temperature at time of outbound departure was 17 °C in the north. Body temperatures of the southern fish were mostly above 18°C with only 2 fish with weekly body temperatures dropping below 17 °C (Fig 4.6b). In both cases, the fish moved towards warmer waters following these weeks.

4.5 Discussion

We have shown that migratory behavior of albacore differs for juvenile albacore tuna leaving the coast north and south of 40°N. Northern fish exhibited longer and more precisely timed migrations compared to southern fish. We found direct correlations between the annual mean SST at the outbound origins and migration distance. In both the northern and the southern fish, migration resulted in fish experiencing higher annual mean temperatures than had they stayed at the outbound origin and lower annual mean temperatures than the outbound destination. Overall, albacore experienced on average murkier waters with deeper mixed layer depths than if they had stayed in their residence sites.

For the northern fish, the drop in SST at the destination site resulted in steep declines in body temperature which were not present in the southern fish. Migration timing in the north coincided with weekly mean body temperatures dropping below 17 °C, a body temperature rarely seen in the southern fish. This suggests that fish in the southern region were not forced by seasonally inhospitable habitats, whereas fish in the north were forced to move to maintain higher body temperatures. This is further supported by a lower precision in timing of the southern fish and shorter distances, which coincided with smaller fluctuations in their sea surface temperature environments.

There has been a long debate about whether albacore north of 40°N and albacore south of 40°N are separate populations (Barr 2009). This debate is partly based on a slower growth rate in the northern fish versus the southern fish (Barr 2009). Our work shows that northern fish must undergo extensive seasonal migrations, significantly longer than those of southern fish. It is possible that the energetic demands of this migration contribute to a lower growth rate. Furthermore, our work shows a direct relationship between the mean SST at the origin and the migration distance, suggesting that the migration distances are based more on the habitat rather than a pre-programmed migration route. To understand the fine-scale movements of the southern fish, more data on prey and predator distributions as well as fine spatial and temporal scale data on the prevalence of mesoscale features are needed. Advancements in measuring foraging success of tagged fish can provide a much better understanding of how ecosystem dynamics influence migration (Whitlock et al. 2015).

Analysis of migratory behavior in the context of oceanographic conditions can provide useful tools for modeling movement under variable conditions to predict population level changes in distribution. This type of information is critical to marine conservation and the management of fisheries. For albacore, this type of information may help elucidate the reasons behind the temporal shifts observed in the troll and line fishery of the west coast (Phillips et al. 2014) as well as assist in understanding population structure. Our analysis provides the necessary information to parameterize albacore movement in response to dynamic sea surface temperature conditions and predict albacore availability to the west coast fishery. Chapter 4, in full, is currently being prepared for submission for publication of the material Snyder, S., Kohin, S., Rahbek, C., Thorup, K., and P.J.S. Franks. The dissertation author was the primary investigator and author of this paper.

Fish ID	Days at Liberty	Tagging Fork Length (cm)	Tagging Date	Tagging Location	Recovery Location
0390167	343	84	25-Jul-03	29.2°N, -117.4°E	30.0°N, -117.1°E
0390191	348	87	27-Jul-03	29.3°N, -117.4°E	29.9°N, -116.7°E
B2942	308	82.5	12-Aug-04	31.2°N, -117.7°E	30.3°N, -117.7°E
A1974	273	81	7-Nov-03	31.9°N, -119.4°E	31.4°N, -117.8°E
A1967	294	86.5	7-Nov-03	31.9°N, -119.5°E	31.0°N, -117.7°E
A1973	281	89.9	7-Nov-03	31.9°N, -119.9°E	31.4°N, -117.8°E
A1246	293	87.5	08-Nov-03	31.9°N, -119.3°E	30.9°N, -117.7°E
A1987	287	88	8-Nov-03	31.9°N, -119.4°E	31.8°N, -118.2°E
A1991	282	87.8	8-Nov-03	31.9°N, -119.5°E	31.4°N, -117.4°E
A2082	283	81.5	10-Nov-03	32.0°N, -119.2°E	31.5°N, -117.6°E
B2393	695	66	30-Jun-04	44.7°N, -125.8°E	30.3°N, -144.6°E
B2398	445	64	1-Jul-04	44.5°N, -125.6°E	45.9°N, -126.5°E
B2381	427	65	1-Jul-04	44.5°N, -125.6°E	45.5°N, -126.0°E
0490306	448	78	13-Sep-04	45.0°N, -125.3°E	33.7°N, -167.8°E
A2088	330	75	13-Sep-04	45.2°N, -125.2°E	32.0°N, -118.3°E
D1045	680	80	6-Aug-06	46.0°N, -125.0°E	31.2°N, -139.34°E
D1464	380	75	6-Aug-06	46.1°N, -125.0°E	32.4°N, -118.3°E
0690065	292	77	7-Aug-06	46.1°N, -124.9°E	32.5°N, 140.10°E
0690063	326	70	7-Aug-06	46.1°N, -124.9°E	32.0°N, -119.9°E
A0394	378	68	3-Aug-11	44.8°N, -126.4°E	46.8°N, -125.2°E
1090251	752	65	3-Aug-11	44.8°N, -126.4°E	46.1°N, -126.4°E
A0396	518	63.5	3-Aug-11	44.9°N, -126.4°E	35.3°N, 145.2°E
690078	629	70	6-Oct-06	46.1°N, -125.1°E	13.0°N, -172.0°E
1090269	692	64	4-Aug-11	44.9°N126.3°E	35.2°N, 143.7°E

 Table 4.1 Juvenile albacore used in this study.



Figure 4.1 Quantifying migration phenology and destinations. Net square displacement of an albacore from its starting location (black dots) with the migration model fit (blue line, CC = 0.99) and the starting and end times of migratory journeys (blue circles). Map inset shows the fish's track (black line) with the outbound origin (which doubles as the inbound destination; open circle), outbound destination (open square), outbound path (black circles) calculated using the model fit parameters.

Table 4.2 Migratory behavior of the juvenile albacore tuna in this study.

CC (Mig/Disp/HR)	0.98/0.54/0.00	0.99/0.95/0.00	0.95/0.96/0.00	0.94/0.39/0.00	00.0/66.0/26.0	0.97/0.21/0.07	0.96/0.73/0.00	0.98/0.46/0.00	0.98/0.20/0.00	0.98/0.06/0.00	0.97/0.53/0.00	0.97/0.89/0.00	0.95/0.44/0.00	0.94/0.48/0.00	0.77/0.40/0.00	0.90/0.89/0.00	0.90/0.44/0.00	0.90/0.62/0.00	0.96/0.80/0.02	0.99/0.59/0.01	0.95/0.70/0.04	0.98/0.66/0.01	0.95/0.07/0.08	0.92/0.38/0.04	0.99/0.70/0.01	0.98/0.72/0.01	0.67/0.02/0.09	0.47/0.51/0.28
Inbound Destination	45.9 °N, -126.3 °E	I	I	43.3 °N, -129.6 °E		43.3 °N, -128.3 °E	30.5 °N, -128.2 °E	49.4 °N, -131.6 °E	44.6 °N, -127.7 °E	42.9 °N, -126.4 °E	44.8 °N, -129.0 °E		44.3 °N, -125.0 °E	46.9 °N, -126.6 °E	40.8 °N, -128.7 °E	30.9 °N, -118.2 °E	44.2 °N, -126.4 °E	30.5 °N, -120.2 °E	29.4 °N, -117.1 °E	29.9 °N, -118.3 °E	29.1 °N, -117.35 °E	32.8 °N, -117.8 °E	29.7 °N, -117.4 °E	30.5 °N, -117.7 °E	31.7 °N, -118.0 °E	31.2 °N, -117.8 °E	30.3 °N, -117.4 °E	I
Inbound Departure Date	12-May-13	5-Apr-06	ļ	6-Apr-05	I	8-Mar-07	15-Apr-07	22-Apr-12	5-Apr-05	30-Mar-05	25-May-12	9-May-08	30-Apr-07	18-May-12	6-May-12	11-Apr-07	27-Mar-05	19-Apr-05	27-Apr-04	25-Mar-05	5-May-04	14-Jun-04	9-May-04	23-Apr-04	21-Jun-04	21-Jun-04	12-May-04	ı
Outbound Destination	36.2 °N, 169.5 °E	33.4 °N, -169.6 °E	34.3 °N, 155.6 °E	31.6 °N, -178.5 °E	33.2 °N, 141.6 °E	28.1 °N, 179.7 °E	38.2 °N, -163.1 °E	38.0 °N, 177.9 °E	32.6 °N, -174.4 °E	30.6 °N, -156.0 °E	35.5 °N, 163.8 °E	35.1 °N, -160.4 °E	33.7 °N, -164.4 °E	35.9 °N, 164.3 °E	31.9°N, -175.6 °E	29.1 °N, -135.5 °E	32.7 °N, -152.9 °E	19.7 °N, -128.7 °E	26.6 °N, -114.7 °E	30.1 °N, -138.0 °E	25.7 °N, -113.9 °E	28.4 °N, -135.2 °E	32.3 °N, -121.7 °E	25.4 °N, -113.9 °E	27.8 °N, -134.1 °E	26.6 °N, -132.8 °E	32.6 °N, -122.2 °E	31.3 °N, -118.0 °E
Outbound Departure Date	4-Oct-12	7-Oct-05	10-0ct-12	27-Sept-04	5-Nov-06	14-Oct-06	17-Oct-06	28-Oct-11	12-Nov-04	6-Nov-04	7-Nov-11	20-Oct-07	11-Nov-06	22-Nov-11	17-Nov-11	11-Dec-06	14-Sept-04	11-Mar-05	13-Oct-03	27-Nov-04	16-Oct-03	26-Mar-04	17-Apr-04	15-Feb-04	20-Mar-04	19-Apr-04	8-Apr-04	18-May-04
Outbound Origin	51.0 °N, -134.5 °E	48.6 °N, -130.3 °E	47.8 °N, -129.7 °E	46.9 °N, -127.9 °E	45.5 °N, -127.0 °E	45.0 °N, -127.8 °E	44.8 °N, -126.9 °E	44.3 °N, -129.3 °E	44.2 °N, -129.0 °E	43.8 °N, -128.7 °E	43.5 °N, -128.4 °E	42.8 °N, -124.7 °E	41.8 °N, -125.5 °E	41.5 °N, -128.5 °E	40.7 °N, -127.2 °E	39.5 °N, -127.5 °E	38.6 °N, -127.7 °E	35.1 °N, -132.5 °E	34.7 °N, -121.9 °E	33.6 °N, -121.1 °E	32.8 °N, -120.3 °E	31.5 °N, -118.4 °E	29.6 °N, -116.4 °E	29.3 °N, -117.6 °E	29.3 °N, -116.6 °E	28.8 °N, -117.0 °E	28.4 °N, -116.3 °E	27.6 °N, -115.6 °E
Max NSD (10 ⁵ km ²)	286.96	131.45	503.98	223.53	601.89	333.57	125.81	294.96	180.79	91.18	381.61	123.07	117.83	386.68	197.68	56.79	77.53	57.34	12.24	32.98	9.04	34.87	4.10	6.40	40.34	27.89	5.48	2.30
Fish ID	1090251	B2393	1090269	B2393	0690065	690078	0690063	1090251	B2398	0490306	1090269	D1045	D1045	A0396	A0394	D1464	B2381	A2088	0390191	B2942	0390167	A1987	A1974	A1967	A2082	A1991	A1973	A1246


Figure 4.2 Migratory destinations and behavior of fish originating (a-b) north and (c-d) south of 40° N. In (a) and (c), the circles blue circles and squares represent outbound origins and inbound destinations, respectively, while the red circles represent the outbound destinations/inbound origins. The compass plots show the *WMV* per fish for the outbound (circles) and inbound (squares) journeys with the average of the outbound and inbound journeys of all fish shown in red and blue, respectively. The contour lines on the compass represent 50, 100, and 150 km day⁻¹.



Figure 4.3 Latitudinal gradients in (a) mean annual SST, (b) annual range in SST, (c) mean annual MLD, (d) annual range in MLD, (e) mean annual k490, and (f) annual range in k490. In all plots, the outbound origins are represented as white circles and the outbound destinations are represented as black squares.

Table 4.3 Habitat characteristics of residence areas and of the migrating fish. *Denotes significance between northern and southern fish to the p < 0.01, ^xdenotes significance between the origins and destinations, and ^{*}denotes significant difference between the residence area and the fish.

	Ori	gin	Destir	ation	Fi	sh
	Annual Mean	Annual Range	Annual Mean	Annual Range	Annual Mean	Annual Range
SST	$13.7\pm2.8~^\circ C^{x*}$	$8.0\pm1.4~^{\circ}C^{x}$	$19.5\pm2.2~^\circ C^{x*}$	$9.4\pm2.7~^{\circ}C^{x*}$	$16.5 \pm 1.0 \ ^{\circ}\text{C}^{*}$	$7.64 \pm 2.1 \ ^{\circ}C^{*}$
Northern	$11.5 \pm 1.1 \ ^{\circ}C^{*}$	8.9 ± 0.9 °C*	19.4 ± 2.2 °C	11.4 ± 1.4 °C*	$15.8\pm0.6~^\circ\text{C}*$	8.9 ± 1.7 °C*
Southern	$16.3 \pm 1.6 ^{\circ}\text{C}^{*}$	6.8 ± 0.9 °C*	19.6 ± 2.3 °C	7.0 ± 1.8 °C*	$17.3 \pm 0.6 \ ^{\circ}C^{*}$	$6.2\pm1.6~^{\circ}\mathrm{C}^{*}$
MLD	$37.7\pm6.4\ m^{x*}$	$45.1\pm 10.8\ m^{x*}$	48.4 ± 13.7^{x}	$74.0 \pm 32.7 \ m^{x*}$	$46.7 \pm 10.2 \ m^*$	$99.2\pm36.1~m^*$
Northern	$41.0\pm5.4\ m^*$	$51.8 \pm 8.3 \text{ m}^*$	$51.6 \pm 8.1 \text{ m}$	$91.8\pm20.5\ m^*$	$52.8\pm7.3\ m^*$	$121.2 \pm 19.0 \ m^{*}$
Southern	$33.8\pm5.4\ m^*$	$37.4 \pm 7.6 \text{ m}^*$	$44.7 \pm 17.8 \text{ m}$	$53.5 \pm 32.5 \text{ m}^*$	$39.6\pm8.4~m^*$	$73.8 \pm 34.8 \text{ m}^*$
ln k490	$-3.5 \pm 0.8 \ m^{-1x}$	$-2.8\pm0.8\ m^{-1x^*}$	$-4.2 \pm 0.7 \ m^{-1x*}$	$-3.5\pm0.7\ m^{-1x*}$	$-2.9\pm0.2\ m^{-1*}$	$\text{-1.5}\pm0.8\ \text{m}^{\text{-1}*}$
Northern	$-3.6 \pm 0.5 \ m^{-1}$	$-2.9 \pm 0.5 \ m^{-1}$	$-4.0 \pm 0.4 \ m^{-1}$	$-3.4 \pm 0.4 \text{ m}^{-1}$	$-2.9 \pm 0.2 \text{ m}^{-1}$	$-1.3 \pm 0.9 \text{ m}^{-1}$
Southern	$-3.3 \pm 1.0 \text{ m}^{-1}$	$-2.6 \pm 1.0 \ m^{-1}$	$-4.4 \pm 0.9 \ m^{-1}$	$-3.7 \pm 0.9 \text{ m}^{-1}$	$-3.0 \pm 0.2 \ m^{-1}$	$-1.7 \pm 0.6 \ m^{-1}$



Figure 4.4 Migration distance as a function of (a) mean annual SST, (b) annual range in SST, (c) mean annual MLD, and (d) annual range in MLD. In all plots, outbound origins and destinations are represented by open circles and closed squares, respectively.





Figure 4.5 Fluctuations in (a,d) SST, (b,e) MLD and (c,f) k490 at the outbound origins (in blue), the outbound destinations (red) and at the fish's selected location (in grey). Northern fish are represented in the top panel with southern fish in the bottom panel. The E and W in plots (a-c) represent the median inbound and outbound departure dates, respectively.



Figure 4.6 Physiological motivation behind movement. Weekly average body temperature over a year cycle for (a) northern and (b) southern fish. Individual fish are shown in gray lines with the average as a solid blue (northern) and red (southern) line. Dashed lines in (a) represent the timing of migration back to the origin (day of year 117) and outbound to the destination (day of year 287).

4.6 References

- Abrams, Peter A. 2007. "Habitat Choice in Predator-Prey Systems: Spatial Instability due to Interacting Adaptive Movements." *The American Naturalist* 169 (5): 581–94. doi:10.1086/512688.
- Andersen, R. 1991. "Habitat Deterioration and the Migratory Behaviour of Moose (Alces Alces L .) in Norway." *Journal of Applied Ecology* 28 (1): 102–8. doi:10.2307/2404117.
- Barr, C M. 2009. Are There Two Subgroups of Albacore, Thunnus alalunga, in the North Pacific? Evidence from Variability in Catch, Seasonal Mgirations, and Length Composition for Two Subgroups in the Coastal Fishery of North America. Vol. 1. doi:10.1017/CBO9781107415324.004.
- Bauer, S, Z Barta, B J Ens, G C Hays, J M McNamara, and M Klaassen. 2009. "Animal Migration: Linking Models and Data beyond Taxonomic Limits." *Biology Letters* 5 (4): 433–35. doi:10.1098/rsbl.2009.0324.
- Berens, P. 2009. "CircStat: A MATLAB Toolbox for Circular Statistics." *Journal of Statistical Software* 31 (10): 1–21. doi:10.1002/wics.10.
- Berthold, P. 1991. "Genetic Control of Migratory Behaviour in Birds." *Trends in Ecology and Evolution* 6 (8): 254–57. doi:10.1016/0169-5347(91)90072-6.
- Borger, L, and J Fryxell. 2012. "Quantifying Individual Differences in Dispersal Using Net Squared Displacement." In *Dispersal Ecology and Evolution*, 222–30. doi:10.1093/acprof.
- Bowler, D E, and T G Benton. 2005. "Causes and Consequences of Animal Dispersal Strategies: Relating Individual Behaviour to Spatial Dynamics." *Biological Reviews* 80: 205–25.
- Bowlin, M S, I Bisson, J Shamoun-baranes, J D Reichard, N Sapir, P P Marra, T H Kunz, D S Wilcove, A Hendenstrom, N Sapir, P P Marra, T H Kunz, D S Wilcove, A Hedenstrom, C G Guglielmo, S Akesson, M Ramenofsky, and M Wikelski. 2010. "Grand Challenges in Migration Biology" 50 (3): 261–79. doi:10.1093/icb/icq013.
- Childers, J, S Snyder, and S Kohin. 2011. "Migration and Behavior of Juvenile North Pacific Albacore (*Thunnus alalunga*)." *Fisheries Oceanography* 20 (March 2010): 157–73. doi:10.1111/j.1365-2419.2011.00575.x.
- Costa, D P, G A Breed, and P W Robinson. 2012. "New Insights into Pelagic Migrations: Implications for Ecology and Conservation," Annual Review of Ecology, Evolution and Systematics 43: 73–96. doi:10.1146/annurev-ecolsys-102710-145045.

- Fiksen, Ø, C Jørgensen, T Kristiansen, F Vikebø, and G Huse. 2007. "Linking Behavioural Ecology and Oceanography: Larval Behaviour Determines Growth, Mortality and Dispersal." *Marine Ecology Progress Series* 347: 195–205. doi:10.3354/meps06978.
- Fryxell, M, and A R E Sinclair. 1988. "Causes and Consequences of Migration by Large Herbivores" *Trends in Ecology and Evolution* 3 (9).
- Gibbons, J W 1986. "Movement Patterns among Turtle Populations: Applicability to Management of the Desert Tortoise" *Herpetologica* 42 (1): 104–13.
- Hoar, B Y W S. 1953. "Control and timing of fish migration," *Biological reviews* 28: 437 452.
- Holte, J, and L Talley. 2009. "A New Algorithm for Finding Mixed Layer Depths with Applications to Argo Data and Subantarctic Mode Water Formation." *Journal of Atmospheric and Oceanic Technology* 26 (9): 1920–39. doi:10.1175/2009JTECHO543.1.
- Holyoak, M, R Casagrandi, R Nathan, E Revilla, and O Spiegel. 2008. "Trends and Missing Parts in the Study of Movement Ecology." *Proceedings of the National Academy of Sciences* 205 (49): 19060-19065.
- Jachowski, D S, and N J Singh. 2015. "Themed Issue Article : Conservation Physiology of Animal Migrations Toward a Mechanistic Understanding of Animal Migration : Incorporating Physiological Measurements in the Study of Animal Movement" *Conservation Physiology* 3: 1–12. doi:10.1093/conphys/cov035.Introduction.
- Kimura, S, M Nakai, and T Sugimoto. 1997. "Migration of Albacore, *Thunnus alalunga*, in the North Pacific Ocean in Relation to Large Oceanic Phenomena," *Fisheries Oceanography* 6(2): 51–57.
- Kirby, D 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*, 407–20.
- Lam, C H, A Nielsen, and J R Sibert. 2008. "Improving Light and Temperature Based Geolocation by Unscented Kalman Filtering." *Fisheries Research* 91 (1): 15–25. doi:10.1016/j.fishres.2007.11.002.
- Lampert, W. 1989. "The Adaptive Significance of Diel Vertical Migration of Zooplankton." *British Ecological Society* 3 (1): 21–27.
- Laurs, M, P C Fiedler, and D R Montgomery. 1984. "Albacore Tuna Catch Distributions Relative to Environmental Features Observed from Satellites." *Deep Sea Research* 31 (9): 1085–99.

Laurs, R M, and R J Lynn. 1977. "Seasonal Migration of North Pacific Albacore,

Thunnus alalunga, into North American Coastal Waters - Distribution, Relative Abundance, and Association with Transition Zone Waters." *Fishery Bulletin* 75 (4): 795–822. <Go to ISI>://WOS:A1977EH44200008.

- Laurs, R M, and R J Lynn. 1991. "North Pacific Albacore Ecology and Oceanography." NOAA Technical report 105: 69-87
- McClintock, B T, R King, L Thomas, J Matthiopoulos, B J McConnell, and J M Morales. 2012. "A General Discrete-Time Modeling Framework for Animal Movement Using Multistate Random Walks." *Ecological Monographs* 82 (3): 335–49. doi:10.1890/11-0326.1.
- Morales, J Manuel, D T Haydon, J Frair, K E Holsinger, and J M Fryxell. 2004. "Extracting More out of Relocation Data: Building Movement Models as Mixtures of Random Walks." *Ecology* 85 (9): 2436–45. doi:10.1890/03-0269.
- Murphy, G I. 1959. "Effect of Water Clarity on Albacore Catches." *Limnology and Oceanography* 4 (1): 86–93.
- Nathan, R, W M Getz, E Revilla, M Holyoak, R Kadmon, D Saltz, and P E Smouse. 2008. "A Movement Ecology Paradigm for Unifying Organismal Movement Research." *Proceedings of the National Academy of Sciences of the United States* of America 105 (49): 19052–59. doi:10.1073/pnas.0800375105.
- Otsu, T, and R N Uchida. 1963. "Model of the Migration of Albacore in the North Pacific Ocean." *Fish. Bull* 63 (1): 33–44.
- Parmesan, C, N Ryrholm, C Stefanescu, J K Hill, C D Thomas, H Descimon, B Huntley, L Kaila, J Kullberg, T Tammaru, W J Tennent, J A Thomas, M Warren. 1999.
 "Poleward Shifts in Geographical Ranges of Butterfly Species Associated with Regional Warming." *Nature* 399: 579–83. doi:10.1038/21181.
- Payne, N L, M D Taylor, Y Y Watanabe, and J M Semmens. 2014. "From Physiology to Physics: Are We Recognizing the Flexibility of Biologging Tools?" *The Journal* of Experimental Biology 217 (Pt 3): 317–22. doi:10.1242/jeb.093922.
- Pedersen, M W, T A Patterson, U H Thygesen, and H Madsen. 2011. "Estimating Animal Behavior and Residency from Movement Data." *Oikos* 120 (9): 1281–90. doi:10.1111/j.1600-0706.2011.19044.x.
- Phillips, A J, L Ciannelli, R D Brodeur, W G Pearcy, and J Childers. 2014. "Spatio-Temporal Associations of Albacore CPUEs in the Northeastern Pacific with Regional SST and Climate Environmental Variables." *ICES Journal of Marine Science* 71 (7): 1717–27. doi:10.1093/icesjms/fst176.
- Reynolds, R W, T M Smith, C Liu, D B Chelton, K S Casey, and M G Schlax. 2007. "Daily High-Resolution-Blended Analyses for Sea Surface Temperature." *Journal of Climate* 20 (22): 5473–96. doi:10.1175/2007JCLI1824.1.

- Rutz, C, and G C Hays. 2009. "New Frontiers in Biologging Science." *Biology Letters*. rsbl.2009.0089. doi:10.1098/rsbl.2009.0089.
- Sainmont, J, U Thygesen, and A W Visser. 2013. "Diel Vertical Migration Arising in a Habitat Selection Game." *Theoretical Ecology* 6 (2): 241–51. doi:10.1007/s12080-012-0174-0.
- Sims, D W, E J Southall, G A Tarling, and J D Metcalfe. 2005. "Habitat-Specific Normal and Reverse Diel Vertical Migration in the Plankton-Feeding Basking Shark." *Journal of Animal Ecology* 74 (4): 755–61. doi:10.1111/j.1365-2656.2005.00971.x.
- Singh, N J, L Börger, H Dettki, N Bunnefeld, and G Ericsson. 2012. "From Migration to Nomadism: Movement Variability in a Northern Ungulate across Its Latitudinal Range." *Ecological Applications* 22 (7): 2007–20. doi:10.1890/12-0245.1.
- Skov, C, B B Chapman, H Baktoft, J Brodersen, C Brönmark, L Hansson, K Hulthén, and P A Nilsson. 2013. "Migration Confers Survival Benefits against Avian Predators for Partially Migratory Freshwater Fish." *Biology Letters* 9 (2): 20121178. doi:10.1098/rsbl.2012.1178.
- Whitlock, R E, E L Hazen, A Walli, C Farwell, S J Bograd, D G Foley, M Castleton, and B A Block. 2015. "Direct Quantification of Energy Intake in an Apex Marine Predator Suggests Physiology Is a Key Driver of Migrations." *Science Advances* 1 (8): e1400270–e1400270. doi:10.1126/sciadv.1400270.
- Wilcove, D S, and M Wikelski. 2008. "Going, Going, Gone: Is Animal Migration Disappearing?" PLoS Biology 6 (7): 1361–64. doi:10.1371/journal.pbio.0060188.
- Xu, Y, K Nieto, S L H Teo, S McClatchie, and J Holmes. 2015. "Influence of Fronts on the Spatial Distribution of Albacore Tuna (*Thunnus alalunga*) in the Northeast Pacific over the Past 30 Years (1982-2011)." *Progress in Oceanography*. doi:10.1016/j.pocean.2015.04.013.

CHAPTER 5

Fronts serve as a dual resource: Insights from *in situ* observations of juvenile tuna (*Thunnus alalunga*) at an open ocean front

5.1 Summary

Organisms – ranging in trophic level from phytoplankton to sharks – amass at the boundaries between water masses known as fronts (Olson et al. 1994; Acha et al. 2015; Scales et al. 2014). Fronts are ubiquitous in our oceans, and shape the habitats of endangered sea birds (Scheffer, Bost, and Trathan 2012; Nel et al. 2001; Russell et al. 1992) and whales (Baumgartner et al. 2001; Bost et al. 2009) as well as economically valuable tunas (Sund, Blackburn, and Williams 1981; Xu et al. 2015; Zainuddin et al. 2006; Fiedler and Bernard 1987; Laurs and Lynn 1991), however we have yet to observe how these animals utilize fronts. Here we document the first observation of predator utilization of a thermal front. Using biotelemetry data and oceanographic information, we show the behavior of four juvenile albacore tunas as they forage at a front in the waters off Baja California, Mexico. For 2 weeks, the tunas utilize sub-mesoscale features associated with the front, swimming between the warmest and coldest available waters, making on average 50 trips across the front per day, with 85% of these occurring during daytime. Use of the warm side of the front resulted in increased body temperature, and the strength of the front was directly correlated with foraging success. Our work supports theory that fronts act as a dual resource (Kirby and Hart 2000; Olson et al. 1994), providing both temperature and food resources to pelagic predators.

5.2 Introduction, Results and Discussion

We are at the frontier of understanding the dynamics of how fronts alter pelagic ecosystems, and why organisms accumulate (in the case of drifters) or aggregate (in the case of swimmers) at fronts (Block 2005; Franks 1992; Olson et al. 1994). With increased spatial and temporal sampling of our oceans, we are discovering that submesoscale features associated with oceanic fronts change the community structure, abundance and distributions of a wide spectrum of organisms including bacteria (Landry et al. 2012; Floodgate et al. 1981), planktonic organisms (Landry et al. 2012; Olson and Backus 1985; Powell and Ohman 2015), the migrating organisms of the deep scattering layer (Landry et al. 2012), and charismatic megafauna such as the tunas (Xu et al. 2015; Sund, Blackburn, and Williams 1981; Humphries et al. 2010), sharks (Queiroz et al. 2012; Sims and Quayle 1998; Humphries et al. 2010), turtles (Polovina et al. 2000), marine mammals (Baumgartner et al. 2001; Bost et al. 2009), and birds (Hunt, Harrison, and Piatt 1993; Scheffer, Bost, and Trathan 2012; Nel et al. 2001). While individual behavior of these organisms has yet to be documented, many studies have documented the accumulation of plankton (Olson & Backus, 1985; Powell & Ohman, 2015) and the increased abundance of forage fish (Tseng et al. 2014) at fronts. Increases in abundance of plankton are hypothesized to result from local vertical mixing and currents – creating both gradients in temperature as well as an influx of nutrients for phytoplankton growth (Acha et al. 2015; Olson et al. 1994), or the dynamics of local hydrography – shoaling isotherms causing an increase of nutrients and phytoplankton in the euphotic zone (Olson et al. 1994; Franks 1992).

Dual resource hypothesis It is thought that large predators are drawn to fronts to take advantage of accumulations of prey (Costa, Breed, and Robinson 2012; Block 2005; Olson et al. 1994; Sims and Quayle 1998; Humphries et al. 2010), and that regional endotherms, such as tunas, also take advantage of the warm waters of the front to assist in thermoregulation (Olson et al. 1994; Kirby and Hart 2000; Kirby 2001; Queiroz et al. 2012). Warmer temperatures for these organisms translates into faster swimming speeds, better visual acuity, and increased digestion rates (Dickson and Graham 2014); thus fronts increase foraging performance in addition to prev abundance. Theoretical work modeling the optimal behavior at fronts, and testing whether this behavior would lead to thermoregulatory advantages, has had mixed results (Kirby and Hart 2000). To investigate this 'dual resource' theory, we used in situ behavior and environmental sampling from electronic tags deployed on four juvenile albacore tuna and high-resolution remote sensing imagery (see Methods). The albacore tuna were within the location measurement error (approximately 300 km) of a thermal front over the two-week period from February 25th to March 9th, 2004. We defined this area by a 2° grid, bounded by 25°N to the south, 27°N to the north, 244.6°E to the west and 246.6°E to the east. During this period, the tags on the albacore recorded water temperature, depth, and diving behavior of the tunas every minute.

Front characterization The tags and the satellite imagery captured an upwelling event that brought deep, cold, nutrient-rich waters to the surface along the coast of Baja California, with a subsequent increase in chlorophyll concentrations (Fig. 5.1a-b). Drawing from the temperature at depth measurements from the fish during this twoweek period, we defined the profiles of the warm and cold regions of the front to have surface temperatures of 16.4 and 17.9 °C respectively, with the top of their thermoclines at approximately 55 and 75 m (Fig. 5.1c, Methods). The temperature differences between the two profiles were greater than 1 °C across each 1 m depth bin to depths up to approximately 200 m (Fig. 5.1c). We investigated behavior at the front by quantifying albacore distribution and movement within and among four frontal regions: cold, surface (CS); cold, deep (CD); warm, surface (WS); and warm, deep (WD, Fig. 5.1d). These regions were defined by the temperature at depth being either warmer (warm side) or colder (cold side) than 0.25 °C around the midpoint between the warm and cold temperature. Surface regions (CS and WS) and deep regions (CD and WD) were defined as shallower or deeper than 5 m above/below the top of the thermocline in the corresponding frontal waters. Using the satellite imagery and the locations of the cold and warm surface waters, we found that over the two weeks, a histogram of the daily 10th percentile of the nearest-neighbor distances gave across-frontal distances (median 3.1 km; IQR: 2.2 to 4.9 km) near the limit of the satellite resolution (~1 km) indicating that the distances between these water masses is found at the sub-mesoscale, and therefore undetectable by the satellite imagery (Fig. 5.1d - inset). During the period of time at the front, the 10th percentile of the across-front distances increased and on March 10th after two of the four fish departed, the detectable distances had a 10th percentile of 6.6 km (Fig. 5.2). This increasing cross-frontal distance suggests that the front was weakening and decaying, presumably with a coincident decrease in the biological signatures at the front.

Albacore movement During the two-week period, albacore were actively utilizing waters on both sides of the front (Fig. 5.3a). The juvenile tunas exhibited a

characteristic diurnal pattern in diving behavior, with more diving during the daytime (vertical distance traveled: $6,703 \pm 8.0$ m) than at night (vertical distance traveled: 2,376 \pm 6.4 m). At night, albacore spent the majority of their time within the WS waters (88.3 $\pm 10.6\%$), while during the day albacore split their time mainly between the WS waters $(49.6 \pm 19.3\%)$ and the CD waters $(30.6 \pm 14.2\%)$, Fig. 5.3b). We observed 4,237 movements between frontal regions over the 14-day period. A majority of these movements occurred during the day (3,719 movements) rather than at night (500 movements), with the remainder occurring at either sunrise or sunset. For ninety percent of the movements between regions, the fish spent less than 3 minutes in transit. This resulted in 110.5 \pm 32 min of time in transit during the day, almost twice the time in transit observed at night (63.1 ± 37.6 min). Of the transits between frontal regions, 66%were across-front movements, mainly comprised of movements between the WS and CD waters (1,711 of the 2,778 across front movements, Fig. 5.3c). Movements across the front resulted in almost twice the absolute temperature change with depth (median: 0.11 °C m⁻¹; IQR: 0.05 to 0.16 °C m⁻¹) than movements within either the cold (CS-CD, median: 0.07 °C m⁻¹; IQR: 0.06 to 0.09 °C m⁻¹) or warm (WS-WD, median: 0.06 °C m⁻¹ ¹; IQR: 0.04 to 0.08 \pm °C m⁻¹) sides of the front. During the day, residence times (i.e., time spent per trip within a given region) were greatest in the CS (median: 7 min; IQR: 3 to 17 min) and WS (median: 9 min; IQR: 3 to 23 min) regions versus those in the CD (median: 5 min; IQR 3 to 17 min) and WD waters (median: 5 min; IQR 3 to 9 min).

Temperature resource Our observations of distribution and movement suggest preferential use of the WS versus the CS. If the dual resource hypothesis is correct, we would expect that the albacore behave in this manner in order to receive some

thermoregulatory benefit from the WS that is lacking in the CS waters. Daytime body temperatures of albacore diving from the WS waters to the CD waters (median: 19.2 °C; IQR: 18.5 to 20.0 °C) were about 2 °C warmer than albacore diving from the CS waters to CD (median 17.0 °C; IQR: 16.3 to 18.0 °C, Mann-Whitney U-Test, $p < 10^{-10}$). This difference resulted in albacore arriving from the WS waters to the CD waters having around a 50% increase in thermal excess - i.e., the temperature difference between their body temperature and water temperature – (median: $1.65 \,^{\circ}$ C; IQR: 0.9 to 2.3 °C) than when arriving to the CD from the CS (median: 1.06 °C; IQR: 0.5 to 1.9°C, Mann-Whitney U-Test, $p < 10^{-7}$). Qualitatively, an increase in muscle temperature results in ability to swim faster (Dickson and Graham 2014; Brill 1996). This gives regional endothermic predators faster swimming speeds than their ectothermic prey (Cairns, Gaston, and Huettmann 2008; Brill 1996). Thus, while at the front, albacore coming from the warm, surface waters have a greater advantage than those coming from the cold, surface waters, and that this advantage is greatest the cold, deep waters rather than in the warm, deep waters.

Foraging resource Without information on the prey field or information on where foraging is taking place, we have relied on a qualitative comparison of the increases in body temperature after sunset that is often termed the heat increment of feeding (HIF) associated with specific dynamic action (Whitlock et al. 2013). By integrating the temperature surplus between the body temperature and the nighttime steady-state body temperature (see *Methods*), we were able to estimate relative foraging success as a function of the albacore's utilization of the front and the strength of the front. As the magnitudes of these values can vary based on forage items, sea surface

temperature, and differences among individuals, we are only comparing values within an individual during their time at the front (Whitlock et al. 2013). In doing so, we assume that the tunas are foraging on similar prey throughout their time at the front. We found that as the distance between the WS and CS waters of the front increased, the relative foraging success decreased (slope = -75 °C km, p=0.008, Fig 5.4).

Predator behavior at fronts Here we presented the first *in situ* observations of a pelagic predator utilizing a front. The association of the tuna with this front coincided with an upwelling event, which enhanced productivity of the region and strengthened the horizontal gradients in sea surface temperature. Our observations of albacore behavior at the front support the 'dual resource' theory, suggesting that the front acts as both a temperature and a food resource. At night, albacore diving activity was reduced and their distribution was mostly restricted to the warmest available waters, whereas during the day the albacore mostly cycled between the WS and the CD. Albacore body temperatures were significantly higher in the WS compared to the CS, providing evidence that these waters provide a physiological benefit to the albacore. Qualitative comparisons of HIF calculations also suggest that foraging success is influenced by the strength of the front. Our results suggest that large, pelagic predators could be using fronts not only to access high concentrations of food, but to also improve their 'hunting' abilities by using the adjacent, accessible warm waters to maintain higher body temperatures.

Future directions The combination of biotelemetry datasets and high-resolution oceanographic data provide a unique window into how pelagic predators utilize the open ocean. The methods we present here can be used to extract behavior at fronts for a wide

range of predators. While observations such as those presented here provide valuable insights into the behavior of tunas at fronts, the lack of information on the prey field and horizontal scaling for the temperature front restrict our ability to quantify the benefit of prey capture or to calculate distances and speeds across the front. While our qualitative analyses do not refute the dual resource hypothesis, *in situ* data collection on the prey field and the horizontal scale of the front would provide a more quantitative understanding of the enhanced concentration of food at the front and the swimming costs associated with exploiting the front (Metcalfe et al. 2015). With the increased availability of high-resolution in situ datasets from moorings, long term ecological monitoring, and biotelemetry studies, there exists great potential for understanding how the physical environment structures pelagic ecosystems (Block 2005; Costa, Breed, and Robinson 2012). By incorporating this information across temporal and spatial scales, we can begin to understand how the observed associations with vertical and horizontal gradients in temperature, light, and oxygen shape distributions and movement patterns of pelagic organisms (Levin 1992).

5.3 Materials and Methods

Biotelemetry & Satellite Data

The albacore tagging data were collected by the Albacore Archival Tagging Program, an ongoing collaborative effort between the Southwest Fisheries Science Center and American Fisherman's Research Foundation. The fish used in this study were tagged in July and November of 2004 as juveniles with fork lengths at time of deployment of less than 90 cm (Table 5.1). Two tag models were used (Wildlife computers Mk9 and Lotek ltd2310), and consisted of a tag body (housing a pressure and temperature sensor) and a stalk (housing a light and temperature sensor). The tag body was surgically implanted into the peritoneal cavity of the fish with the stalk protruded out into the water column. The tags were programmed to record depth, water temperature, body temperature, and light every minute. Daily horizontal locations of each fish were derived using light curves, and then refined using the UKFSST algorithm (Lam et al., 2008). On average these locations produced tracks with errors on the order of 300 km. Of note, three of the four fish were tagged on the same trip and then recovered within days of each other.

Our study area was defined by a 2° grid, bounded by 25°N to the south, 27°N to the north, 244.6°E to the east and 246.6°E to the west. We coupled this data with satellite imagery on both sea surface temperature and chlorophyll. We chose the highest spatial resolutions (~1 km) available for this study period. To examine productivity, we chose to use 3-day high-resolution chlorophyll-a SeaWiFS product from the National Oceanic and Atmospheric Administration's CoastWatch program (Siegel et al. 1998). To examine the sea surface temperature field, we chose the Jet Propulsion Laboratory's Multi-scale ultra-high resolution sea surface temperature product (JPL MUR MEaSUREs Project 2010).

Front Characterization

The front was chosen based on a period when all four fish were found in the same 300 km radius and when the temperature of the water within a 1 m depth bin varied by more than 1 °C horizontally. Among the possible fronts evident in the data, this front

was chosen because the fish stayed at the front for 2 weeks. The combination of the duration at the front and the number of fish at the front ensured that the front was highly sampled both horizontally and vertically by the fish.

To estimate the physical features of the front, the front was assumed to be stable while the fish were in proximity to the front. We then used the vertical sampling from the fish to define temperature depth profiles for the warm and cold sides of the front. For the two weeks while the fish were in proximity to one another, we took all the data and binned it into 2 m depth bins. We then calculated frequency distributions of the temperatures within each 2 m bin. We then fit a double Gaussian curve to the data:

$$G = a_1 e^{-\left[\frac{(H-T_{cold})}{c_1}\right]^2} + a_2 e^{-\left[\frac{(H-T_{warm})}{c_2}\right]^2}$$
(1)

where T_{cold} and T_{warm} were the estimates of the temperatures of the warm and cold sides of the front at that depth bin. The data were then smoothed over 5 m and interpolated linearly such that a temperature was assigned to each 0.1 m. The depth of the top of the thermocline was also estimated for each side of the front. This depth was defined as the depth at which the temperature fell below 1 °C of the maximum temperature.

The horizontal location of the front was dynamic throughout the fish's time at the front. To understand the length scale of the horizontal distance between the warm and the cold surface waters, we estimated the nearest-neighbor distance between each point corresponding to the sea surface temperature on the warm side (derived from the tagging profiles) to the sea surface temperature on the cold side. Then for each day, we calculated the 10th percentile of these distances. This allowed us to quantify an approximate distance across the front throughout the time the fish were in residence.

Albacore Movement

Because of the poor temporal and spatial resolution of the tag-derived locations, the horizontal location relative to the front was estimated using the fish's watertemperature-at-depth information coupled with the characterization of the front. We examined the fish's use of four distinct areas of the front: the surface and deep waters of the warm side of the front (WS and WD, respectively) and the cold side of the front (CS and CD). Fish were flagged in a region if their temperature at a given depth was above or below 0.25°C of the middle temperature between the cold and warm profiles. The surface was defined as waters 5 m above the top of the thermocline, and the deep was flagged as 5 m below the top of the thermocline.

To examine movement and distribution, we examined both the movement paths between the different regions as well as the time each albacore spent in each of the frontal regions. We counted the movements between the different regions, noting the time of day, time spent in transit, and the origin and destination of those movements. We also calculated the overall depth distribution for the cold versus warm side of the front at night and during the daytime.

Front as a dual resource

To test whether the front served to both enhance the albacore's ability to maintain elevated body temperature and foraging success, we examined aspects of the albacore's thermoregulation and foraging during the albacore's two weeks at the front. We compared the albacore's median body temperature and thermal excess (i.e., temperature difference between the albacore's body and water temperature) during the residence time in the CD region after coming from the WS waters and the CS waters using a Mann-Whitney U-Test. To examine the contribution of the front to foraging, we calculated the area under the heating increment of feeding (HIF) curve observed following sunset using a Whitlock et al. (2015)'s model:

$$HIF = \int_{t_{start}}^{t_{end}} (T_b(t) - T_{ss})$$
(2)

where t_{start} and t_{end} are the start and end times of the HIF, T_b is the body temperature at time t and T_{ss} is the nighttime steady state body temperature.

We modified some of Whitlock and colleagues' criteria to suit our study system and *in situ* data. We used only nighttime data, as heating during the day could be caused by diving or increased activity (Snyder et al., *in prep*), and smoothed the data over two hours to remove any effect of perturbations in the sea surface temperature or short excursions to other temperatures. Similar to Whitlock et al., we excluded start and end times that gave HIF periods less than 2 hours (compared to their 4 hour cut-off). We defined steady-state body temperature as the mode of the nighttime body temperatures, rounded to 0.1 °C. The start and end of the HIF event were defined as the first time the albacore's temperature rose above the steady-state temperature and had a positive derivative with time with the end as the last time the albacore's temperature was above the steady-state temperature and had a negative derivative with time. We performed a linear regression analysis between the time series of HIF and the 10th percentile of the across frontal distance to assess whether HIF correlated with frontal strength. Chapter 5, in full, is currently being prepared for submission for publication of the material. Snyder, S., Xu, Y., Talley, L., Kohin, S. and P.J.S. Franks. The dissertation author was the primary investigator and author of this paper.



Figure 5.1 Front Characterization. Maps of (a) chlorophyll and (b) sea surface temperature from satellite imagery on the first day of the study, with the estimated fish locations as white circles. (c) Temperature profiles of the cold (blue) and warm (red) sides of the front derived from the albacore archival tagging data (grey circles) with temperature difference at each depth bin represented by the black line in the inset. The dashed line of the inset represents a temperature difference of 1 °C. (d) An approximate transect of the front based on a linear interpolation of the cold and warm profiles across the pdf of distances from the surface cold and warm regions of the front over the fish's time at the front. The boundaries of the four thermal regions are outlined in white.



Figure 5.2 Shortest available distance between the warm surface waters and cold surface waters within the 2° grid study area over the residence time of the tunas at the front.



Figure 5.3 Movement at Front. (a) Distributions of mean percent time at depth at night (shaded background) and day (white background) on either the warm (red) or cold (blue) side of the front. Shaded area denotes standard deviation among fish. (b) Movement paths between the different frontal regions (n = 4,075 transits between regions).

Etah ID	Deploy			Recover		
F ISH ID	Date	Location	FL (cm)	Date	Location	FL (cm)
0390167	25-Jul-03	29.2°N, -117.4°E	84	2-Jul-04	30.0°N, -117.1°E	94
A1967	7-Nov-03	31.9°N, -119.5°E	86.5	27-Aug-04	31.0°N, -117.7°E	91
A1246	08-Nov-03	31.9°N, -119.3°E	87.5	27-Aug-04	30.9°N, -117.7°E	94
A1973	7-Nov-03	31.9°N, -119.9°E	89.9	30-Aug-04	31.4°N, -117.8°E	97

Table 5.1 Deploy and recovery information on juvenile albacore used in this study.

2000 \bigtriangleup 1500 HIF (°C) \bigtriangleup 1000 \triangle * 500 0 ð A ≝⊮ Ø * 00 杲 0 3 4 5 6 7 2 10th Percentile Across Front Distance (km)

Figure 5.4 Heat increment of feeding as a function of across front distance.

5.4 References

- Acha, E M, A Piola, O Iribarne, and H Mianzan. 2015. "Ecological Processes at Marine Fronts." Summarizes Relevant Studies on Biological Oceanography and Ecology of Marine Fronts, 5–12. doi:10.1007/978-3-319-15479-4.
- Baumgartner, M F, K D Mullin, L N May, and T D Leming. 2001. "Cetacean Habitats in the Northern Gulf of Mexico." *Fishery Bulletin* 99 (2): 219–39. doi:10.1016/S0967-0637(01)00035-8.
- Block, B A 2005. "Physiological Ecology in the 21st Century: Advancements in Biologging Science." *Integrative and Comparative Biology* 45 (2): 305–20. doi:10.1093/icb/45.2.305.
- Bost, C A, C Cotté, F Bailleul, Y Cherel, J B Charrassin, C Guinet, D G Ainley, and H Weimerskirch. 2009. "The Importance of Oceanographic Fronts to Marine Birds and Mammals of the Southern Oceans." *Journal of Marine Systems* 78 (3). Elsevier B.V.: 363–76. doi:10.1016/j.jmarsys.2008.11.022.
- Brill, R W 1996. "Selective Advantages Conferred by the High Performance Physiology of Tunas, Billfishes, and Dolphin Fish." *Comparative Biochemistry and Physiology A Physiology* 113 (1): 3–15. doi:10.1016/0300-9629(95)02064-0.
- Cairns, D K, A J Gaston, and F Huettmann. 2008. "Endothermy, Ectothermy and the Global Structure of Marine Vertebrate Communities." *Marine Ecology Progress Series* 356 (February 2016): 239–50. doi:10.3354/meps07286.
- Costa, D P, G A Breed, and P W Robinson. 2012. "New Insights into Pelagic Migrations: Implications for Ecology and Conservation." Annual Review of Ecology, Evolution, and Systematics 43: 73–96. doi:10.1146/annurev-ecolsys-102710-145045.
- Dickson, K A, and J B Graham. 2014. "Evolution and Consequences of Endothermy in Fishes." *Physiological and Biochemical Zoology : PBZ* 77 (6): 998–1018. doi:10.1086/423743.
- Fiedler, P C, and H J Bernard. 1987. "Tuna Aggregation and Feeding near Fronts Observed in Satellite Imagery." *Continental Shelf Research* 7 (8): 871–81. doi:10.1016/0278-4343(87)90003-3.
- Floodgate, G D, G E Fogg, D A Jones, K Lochte, and C M Turley. 1981. "Microbiological and Zooplankton Activity at a Front in Liverpool Bay." *Nature* 290: 133–36. doi:10.1017/CBO9781107415324.004.
- Franks, P J S. 1992. "Sink or Swim: Accumulation of Biomass at Fronts." *Marine Ecology Progress Series* 82: 1–12. doi:10.3354/meps082001.

Humphries, N E, N Queiroz, J R M Dyer, N G Pade, M K Musyl, K M Schaefer, D W

Fuller, J M Brunnschweiler, T K Doyle, J D R Houghton, G C Hays, C S Jones, L R Noble, V J Wearmouth, E J Southall, D W Sims. 2010. "Levy and Brownian Environmental Context Explains Le Movement Patterns of Marine Predators." *Nature* 465 (7301). Nature Publishing Group: 1066–69. doi:10.1038/nature09116.

- Hunt, G L, N M Harrison, and J F Piatt. 1993. "Foraging Ecology as Related to the Distribution of Plativorous Auklets in the Bering Sea." In *The Status, Ecology, and Conservation of Marine Birds of the North Pacific*, edited by K Vermeer, K.T. Briggs, K.H. Morgan, and D. Siegel-Causey, 18–26. Can. Wildl. Serv. Spec. Publ.
- JPL MUR MEaSUREs Project. 2010. GHRSST Level 4 MUR Global Foundation Sea Surface Temperature Analysis. Ver. 2. PO.DAAC, CA, USA. Dataset accessed [2016-01-10] at http://dx.doi.org/10.5067/GHGMR-4FJ01.
- Kirby, D 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*, 407–20.
- Kirby, D S, and P J B Hart. 2000. "A Dynamic Optimisation Model for the Behaviour of Tunas at Ocean Fronts," no. August 1999: 328–42.
- Landry, M R, M D Ohman, R Goericke, M R Stukel, K A Barbeau, R Bundy, and M Kahru. 2012. "Pelagic Community Responses to a Deep-Water Front in the California Current Ecosystem: Overview of the A-Front Study." *Journal of Plankton Research* 34 (9): 739–48. doi:10.1093/plankt/fbs025.
- Laurs, R M, and R J Lynn. 1991. "North Pacific Albacore Ecology and Oceanography." In NOAA Technical Report NMFS-105, 69–87.
- Levin, S A. 1992. "The Problem of Pattern and Scale in Ecology." *Ecology* 73 (6): 1943–67.
- Metcalfe, J D, S Wright, C Tudorache, and R P Wilson. 2015. "Recent Advances in Telemetry for Estimating the Energy Metabolism of Wild Fishes." *Journal of Fish Biology*, 284–97. doi:10.1111/jfb.12804.
- Nel, D C, J R E Lutjeharms, E A Pakhomov, I J Ansorge, P G Ryan, and N T W Klages. 2001. "Exploitation of Mesoscale Oceanographic Features\rby Grey-Headed Albatross Thalassarche\rChrysostoma in the Southern Indian Ocean." *Mar Ecol Prog Ser* 217: 15–26.
- Olson, D B, and R H Backus. 1985. "The Concentrating of Organisms at Fronts: A Cold-Water Fish and a Warm-Core Gulf Stream Ring." *Journal of Marine Research* 43 (1): 113–37. doi:10.1357/002224085788437325.
- Olson, D, G Hitchcock, A Mariano, C Ashjian, G Peng, R Nero, and G Podesta. 1994. "Life on the Edge: Marine Life and Fronts." *Oceanography* 7 (2): 52–60. doi:10.5670/oceanog.1994.03.

- Polovina, J J, D R Kobayashi, D M Parker, M P Seki, and G H Balazs. 2000. "Turtles on the Edge: Movement of Loggerhead Turtles (Caretta Caretta) along Oceanic Fronts, Spanning Longline Fishing Grounds in the Central North Pacific, 1997-1998." *Fisheries Oceanography* 9 (1): 71–82. doi:10.1046/j.1365-2419.2000.00123.x.
- Powell, J R, and M D Ohman. 2015. "Covariability of Zooplankton Gradients with Glider-Detected Density Fronts in the Southern California Current System." *Deep-Sea Research Part II: Topical Studies in Oceanography* 112. Elsevier: 79–90. doi:10.1016/j.dsr2.2014.04.002.
- Queiroz, N, N E Humphries, L R Noble, A M Santos, and D W Sims. 2012. "Spatial Dynamics and Expanded Vertical Niche of Blue Sharks in Oceanographic Fronts Reveal Habitat Targets for Conservation." *PLoS ONE* 7 (2). doi:10.1371/journal.pone.0032374.
- Russell, R W, G L Hunt, K O Coyle, and R T Cooney. 1992. "Foraging in a Fractal Environment: Spatial Patterns in a Marine Predator-Prey System." *Landscape Ecology* 7 (3): 195–209. doi:10.1007/BF00133310.
- Scales, K L, P I Miller, L A Hawkes, S N Ingram, D W Sims, and S C Votier. 2014. "On the Front Line: Frontal Zones as Priority at-Sea Conservation Areas for Mobile Marine Vertebrates." *Journal of Applied Ecology* 51 (6): 1575–83. doi:10.1111/1365-2664.12330.
- Scheffer, A, C A Bost, and P N Trathan. 2012. "Frontal Zones, Temperature Gradient and Depth Characterize the Foraging Habitat of King Penguins at South Georgia." *Marine Ecology Progress Series* 465 (Woehler 1995): 281–97. doi:10.3354/meps09884.
- Siegel, D A, K L Carder, S A Garver, M Kahru, and C McClain. (1998). Ocean color chlorophyll algorithms for SeaWiFS. *Journal Geophysical Research*, 103: 937-953.
- Sims, D W, and V A Quayle. 1998. "Selective Foraging Behaviourof Basking Sharks on Zooplankton in a Small-Scale Front." *Nature* 393: 460–64. doi:10.1038/30959.
- Sund, P N, M Blackburn, and F Williams. 1981. "Tunas and Their Environment in the Pacific Ocean: A Review." Oceanography and Marine Biology Annual Review 19: 443–512.
- Tseng, C T, C L Sun, I M Belkin, S Z Yeh, C L Kuo, and D Chung Liu. 2014. "Sea Surface Temperature Fronts Affect Distribution of Pacific Saury (*Cololabis saira*) in the Northwestern Pacific Ocean." *Deep-Sea Research Part II: Topical Studies* in Oceanography 107. Elsevier: 15–21. doi:10.1016/j.dsr2.2014.06.001.
- Whitlock, R E, A Walli, P Cermeño, L E Rodriguez, C Farwell, and B A Block. 2013. "Quantifying Energy Intake in Pacific Bluefin Tuna (*Thunnus orientalis*) Using

the Heat Increment of Feeding." *The Journal of Experimental Biology* 216 (Pt 21): 4109–23. doi:10.1242/jeb.084335.

- Xu, Y, K Nieto, S L H Teo, S McClatchie, and J Holmes. 2015. "Influence of Fronts on the Spatial Distribution of Albacore Tuna (*Thunnus alalunga*) in the Northeast Pacific over the Past 30 Years (1982-2011)." *Progress in Oceanography*, no. February 2016. doi:10.1016/j.pocean.2015.04.013.
- Zainuddin, M, H Kiyofuji, K Saitoh, and S I Saitoh. 2006. "Using Multi-Sensor Satellite Remote Sensing and Catch Data to Detect Ocean Hot Spots for Albacore (*Thunnus alalunga*) in the Northwestern North Pacific." *Deep-Sea Research Part II: Topical Studies in Oceanography* 53 (3-4): 419–31. doi:10.1016/j.dsr2.2006.01.007.

CHAPTER 6

Conclusions

In **Chapter 2**, I presented methods by which to measure and account for thermal inertia of sensor housings. Sensor housings or protective casings are often applied to temperature sensors in biotelemetry experiments to protect the tag. Researchers have wondered whether these coatings were influencing *in situ* measurements. Through the use of a calibration experiment, *in situ* body temperature measurements, and simulations, I showed that the significance of sensor thermal inertia depends on the thermal inertia of the sensor and that of the organism within the context of environmental temperature fluctuation. Errors associated with thermal inertia were found to increase with increases in the rate of temperature change in the environment and thermal inertia of the sensor, and decreases in the thermal inertia of the organism. With these methods, we now have the tools to assess the question of whether our instruments are providing us with accurate data.

With newfound confidence in the body temperature data, I investigated the impact of thermal environment on the thermoregulation in juvenile albacore tuna in **Chapter 3**. In the current thermal physiology literature, it is becoming apparent that many organisms operate on a continuum between ectotherm and endotherm – rather than strictly adhering to the cold-bodied/warm-bodied dichotomy. This study investigated the influence of the thermal environment on thermoregulatory tactics in a regional endotherm – an organism that is capable of retaining metabolic heat but falls short of homeothermy, albacore tuna. I found that albacore switch between two modes

of behavioral thermoregulation: temperature tracking and shuttling (a behavior in which the fish moves between two temperature extremes in the environment). Regardless of behavior or environment, albacore achieve median water temperatures of approximately $16 \,^{\circ}$ C. This is achieved in part because the albacore switches tactics based on sea surface temperature (SST). As the albacore moves from colder to warmer sea surface temperatures, it spends more time at depth – either through shuttling or tracking in deeper waters.

I found that the albacore can achieve higher body temperatures during tracking than during shuttling. However, tracking incurs higher physiological costs, while shuttling incurred higher costs associated with swimming and lost opportunities. All costs increased as SST increased. It was rare that albacore shuttling behavior could be predicted based on simple critical lower and upper body temperature criteria, suggesting that albacore diving decisions are most likely driven by foraging success or predator avoidance rather than by body temperature cues alone. However, days when albacore behavior could be explained by avoidance of body temperature extremes pointed to a critical lower body temperature, independent of SST. The critical lower body temperature corresponds to the steady-state temperature in waters just below their inhabited SST range.

Chapter 3 led to a mechanistic understanding of how SST limits albacore distribution. My conclusion is that the lower SST limit to albacore distribution is directly related to a limit in their thermoregulatory abilities to maintain a functional body temperature, and that upper SST limit was due to the trade-off of higher metabolic rates, longer transit times, and lower food availability in these waters.

This mechanistic understanding of physiological and energetic limits to albacore distribution led me to investigate juvenile albacore tuna migration patterns with respect to their available thermal habitat in **Chapter 4**. Juvenile albacore are known to undertake basin-wide ontogenetic migrations in the North Pacific Ocean. The Albacore Archival Tagging Program has been tagging albacore off the west coast of the United States since 2003 in two general areas: (1) northern area off the coast of Oregon, and (2) southern area off the coast southern California and off the coast of Baja California, Mexico.

Using their data, I found that the northern albacore traveled much farther, with more precisely timed and directed movements than the fish in the south. This discrepancy can be directly linked to the habitat suitability in the north versus the south. In the north, their nearshore residence areas become too cold for the albacore, whereas the sea surface temperatures at the nearshore residence areas in the south never fall below a habitable range. As an aside, the albacore had a remarkable ability to return to their original locations, regardless of the distance they had traveled.

In **Chapter 5**, I developed a new method to examine predator behavior at fronts. Using the tagging data, I was able to detect days when fish were utilizing fronts, through an examination of temperature gradients within a day in 1 m depth bins. I identified one front where four fish remained for a two-week period. To characterize the front, I pooled their temperature and depth time series data over this time and thus was able to define the temperature depth profiles of the warm and cold sides of the front. By quantifying their movements and distributions during this time relative to the front, I determined that they were utilizing small-scale structures associated with the larger-scale front. I also found that their movement patterns and foraging activity provided evidence that the front served as a dual resource to the tunas, providing both access to higher temperatures and food.

Appendix

Supplementary Information for Chapter 3

In our paper, we take a different approach to the estimation of thermal rates than previously published literature. We were concerned that our choice of windowing could bias the estimates of thermal rates derived from the data. Our reasoning was as follows: (1) By necessity, rates must be estimated using several time steps of body temperature data, and are thus assumed constant over the time period of estimation; (2) There is ample evidence that organisms – ranging from tunas to mice – can alter their rates of heating and cooling by an order of magnitude on timescales of minutes. (3) The time periods over which the rates remain constant are unknown at the outset of the analysis. (4) Thus, the time periods chosen could potentially bias or smooth away actual fluctuations in thermal rates. Therefore, we searched for an approach that would allow the data to reveal the appropriate window size over which to calculate thermal rates.

THE MODEL

Our thermal rate model follows Brill and colleagues (1984), and has widespread usage in the tuna literature:

$$\frac{dT_b}{dt} = k_b(T_a - T_b) + \dot{T_m} \tag{1}$$

This model can be used to derive the specific rate of temperature loss or gain (k_b , min⁻¹) due to the temperature difference between the ambient and body temperatures at time t, and the rate of temperature gain due to metabolic processes ($\vec{T_m}$, °C min⁻¹) by using

As biotelemetry data are collected at discrete time intervals, we use the Euler method to solve this equation:

$$T_b(t) = k_b \Delta t \left(T_a(t) - T_b(t - \Delta t) \right) + \dot{T_m} \Delta t + T_b(t - \Delta t)$$
(2)

where Δt is the sampling interval (min). This solution is rearranged into a matrix:

$$C * \begin{bmatrix} k_b \\ T_m \end{bmatrix} = D \tag{3}$$

where C and D are vectors of the time series:

$$C = [(T_a(t_i) - T_b(t_i - \Delta t))\Delta t \quad \Delta t]$$
(4)

$$D = [T_b(t_i) - T_b(t_i - \Delta t)]$$
⁽⁵⁾

and $i = \{2, 3, ..., N\}$ and N= length of the window of data. A matrix inversion of Eqn 3 provides one estimate of k_b and T_m for a given time interval.

ADAPTIVE WINDOWING

Our method differs from traditional methods in that we use a range of windows rather than an arbitrarily defined a fixed window length (i.e., N in Eqn 4-5). The adaptive window approach calculates rates iteratively using window lengths W_i based on multiples of a base time period during which the rates are unlikely to change (the base timescale, t_{base} , min):

$$W_i = n_i * \frac{t_{base}}{\Delta t} \tag{6}$$

where *n* is the multiple of the base timescale, i = [1...N] where N is the number of windows, and Δt is the sampling interval. In our study we used a base timescale of 5 minutes where:

$$n = \left\{1, 3, 6, 9, \dots, \frac{2880}{t_{base}}\right\}$$
(7)

Each window of length W_i was used to provide one estimate of the thermal rates corresponding to that time period of data, and then was moved a distance $\frac{t_{base}}{\Delta t}$ along the time series, and the thermal rates were calculated again using the same window length but with an updated start time. Note that successive windows overlap the previous windows thus giving multiple estimates of the thermal rates at each time *t* (Fig. A1b). This was repeated until the entire time series had been analyzed. The window size was then increased, and the procedure repeated from the beginning of the time series.

The rate estimates k_b and T_m for each window were used alongside the ambient temperature time series T_a to calculate a modeled body temperature, $T_{b-model}$ for that window:

$$T_{b-model}(t) = k_b \Delta t (T_a(t) - T_{b-model}(t - \Delta t)) + T_{b-model}(t - \Delta t)$$

$$+ T_m^{i} \Delta t$$

$$T_{b-model}(0) = T_b(0)$$
(8)

The root-mean square error between $T_{b-model}$ and T_b was calculated for each combination of window length (W_i) and window center:

$$RMSE_{TR} = \sqrt{\frac{\sum_{t=1}^{N} (T_{b-model}(t) - T_{b}(t))^{2}}{W_{i}}}$$
(9)
The thermal rate estimates that corresponded to the minimum $RMSE_{TR}$ value for each time point were accepted as the best estimates (Fig. A2c).

To accurately estimate k_b and T_m , both the ambient temperature (T_a) and the body temperature (T_b) must change such that a unique solution can be found for a particular window of data. As can be seen in Eqn 2, if either the thermal excess ($T_a - T_b$) or the change in body temperature is constant, then the solution is simply a balancing between the two parameters and thus not unique. Therefore, this study only estimated rates for windows of data during which both the ambient temperature and the body temperature changed by at least 1 °C. Additionally, physically or physiologically impossible rate estimates (i.e., negative values) were discarded. This ensured that the rate estimates were appropriate approximations of the processes governing the body temperature response to environmental temperatures.

MODEL PERFORMANCE

To compare our method with those currently in the literature, we estimated thermal rates using fixed, sliding (i.e., the fixed window was moved a distance $\frac{t_{base}}{\Delta t}$ forward, overlapping the previous window) window lengths of 30 min, 1 hour, 12 hours, and 24 hours. The fixed window method differed from our adaptive windowing approach solely in that the fixed window method utilized only one window length whereas our adaptive windowing method utilized estimates generated using a variety of window lengths. The extent to which an individual model's thermal rate estimates explain the variation seen in T_b was quantified by (i) the difference between T_b and T_b . *model*, and (ii) the percent of time estimates of thermal rates met the quality control criteria described above.

Thermal rates were estimated for 99.1% of the year-long time series (521,103 out of 526,000 body temperature measurements) using the adaptive windowing method. The modeled body temperature ($T_{b-model}$, Eqn. 8), accurately reproduced the albacore's measured body temperature (T_b) in response to changes in ambient temperature (Fig. A3a-b), with differences between the time series averaging 0.16 ± 0.6 °C over the year. 98.1% of these differences were less than the standard deviation of T_b of the year-long time series (Fig. A3c).

The choice of window length greatly influenced the estimated thermal rates. Shorter fixed windows had more instances of windows lacking the information needed to calculate thermal rates, resulting in greater time periods with unknown thermal rates; while, longer fixed windows generated thermal rate estimates that were less accurate in reproducing the body temperature $T_{b-model}$ (Table A1). Flexibility in the window length allows the variable window method to achieve an accuracy comparable to the fixed short window lengths, but for a much greater percent of the time series.

In addition to improving the model-data fit and ability to estimate rates, a flexible window length provides information on the time scales over which thermal rates change. For the albacore we found that the majority of the thermal rate estimates resulted from window lengths between 3 and 6 h, the 25th and 75th percentiles respectively (Fig. A3a). The accuracy of the model in reproducing the body temperature decreased for window lengths greater than about one day, suggesting that for this juvenile albacore, thermal rates varied on time scales less a day (Fig. A3a). We also

130

characteristic of a step function, suggesting that thermal rates can vary at the same scale as diving (Fig A3b).



Figure A1 Thermal rate calculation **a** An example of a day of environmental (black line) and body (red line) temperature data from free-swimming albacore tuna and schematic of the model used to generate a thermal rates time series. **b** For a single time point of interest, t_i , multiple window lengths (Eqn 3) were slid along the time series to provide multiple estimates of thermal rates **c** The combination of window length and window center time that resulted in the minimum $RMSE_{TR}$ (Eqn 9) was chosen. In this example, the 30-sample window (W₂) centered at 7 minutes before the point of interest gave the best fit.



Figure A2 *Thunnus alalunga.* **a.** Example of measured (red line) and modeled body temperature (black line) for 10 hours of daytime diving behavior between warm and cold ambient temperatures (blue line). **b.** Differences between the modeled and the measured body temperature (solid lines), and standard deviation in body temperature (dashed lines) during this time. **c.** Histogram of the differences between the modeled and the measured body temperature over the entire year of minute-to-minute observations with the yearly standard deviation of body temperature (dashed lines), and the 10th and 90th percentiles of the differences (solid lines).

		, ,								
	Percent of	R	<i>MSE_{TR}</i> valı	Je	k_b	(x10 ⁻² min ⁻	(1)	T_m^{i}	, (x10 ⁻² min	1 ⁻¹)
Window Length	year with									
	estimates	Q1	Median	Q3	Q1	Median	Q3	Q1	Median	Q3
Variable	66	0.06	0.10	0.17	0.5	1.0	1.6	1.0	2.5	5.3
30 min	ω	0.06	0.12	0.20	1.0	1.5	2.2	2.8	4.8	6.6
1 h	11	0.06	0.09	0.16	0.8	0.79	1.9	3.1	4.7	6.7
12 h	87	0.17	0.25	0.36	0.4	1.1	1.3	0.8	2.5	5.8
24 h	93	0.53	0.71	0.98	0.1	0.2	0.6	0.2	0.6	1.4

Table A1. The effect of window length on the ability to estimate thermal rates.



Figure A3 Time scales of thermal rate fluctuations. (a) Histogram of window lengths chosen through the adaptive windowing method with their corresponding RMSE values, with the solid line as the median and the dotted line as the interquartile range. (b) Spectrum of k_b and T_m showing the dominant frequencies in the thermal rates time series.