

**USING ANIMAL-BORNE CAMERAS TO STUDY THE
FORAGING BEHAVIOUR OF LARGE MARINE
PREDATORS**

by

Susan Gale Heaslip

Submitted in partial fulfillment of the requirements
for the degree of Master of Science

at

Dalhousie University

Halifax, Nova Scotia

July 2014

© Copyright by Susan Gale Heaslip, 2014

*This work is dedicated to my friends and family;
with special gratitude to my parents.*

TABLE OF CONTENTS

TABLE OF CONTENTS.....	iii
LIST OF TABLES.....	vi
LIST OF FIGURES.....	vii
ABSTRACT.....	ix
LIST OF ABBREVIATIONS USED.....	x
ACKNOWLEDGEMENTS.....	xi
Chapter 1. INTRODUCTION.....	1
1.1. FORAGING IS CENTRAL TO ECOLOGY.....	1
1.2. THEORETICAL WORK.....	2
1.2.1. Optimal foraging theory.....	2
1.2.2. Optimal diving theory.....	3
1.3. EMPIRICAL WORK.....	4
1.3.1. Using animal-borne instruments to study the foraging behaviour of marine predators.....	4
1.3.2. Foraging behavior of leatherback turtles and harbour seals.....	5
1.3.3. Tests of theoretical foraging models of optimal diving.....	7
1.4. THESIS OVERVIEW AND OBJECTIVES.....	7
1.5. PUBLISHED MANUSCRIPTS INCLUDED IN THESIS.....	8
1.6. REFERENCES.....	8
Chapter 2. JELLYFISH SUPPORT HIGH ENERGY INTAKE OF LEATHERBACK SEA TURTLES (<i>DERMOCHELYS CORIACEA</i>): VIDEO EVIDENCE FROM ANIMAL-BORNE CAMERAS.....	16
2.1. ABSTRACT.....	16
2.2. INTRODUCTION.....	17
2.3. METHODS.....	20
2.3.1. Ethics statement.....	20

2.3.2.	Study area	21
2.3.3.	Instruments and deployments	21
2.3.4.	Video analysis	23
2.3.5.	Spatial movement	24
2.3.6.	Statistical analyses.....	24
2.3.7.	Energy intake.....	25
2.4.	RESULTS	25
2.4.1.	Foraging behaviour, prey encounters, and spatial movement	26
2.4.2.	Prey size, handling time and energy intake	29
2.5.	DISCUSSION	33
2.6.	ACKNOWLEDGMENTS	37
2.7.	REFERENCES	38
Chapter 3.	TESTING PREDICTIONS OF OPTIMAL DIVING THEORY USING ANIMAL-BORNE VIDEO FROM HARBOUR SEALS (<i>PHOCA VITULINA CONCOLOR</i>)	43
3.1.	ABSTRACT	43
3.2.	INTRODUCTION	44
3.3.	MATERIALS AND METHODS.....	49
3.3.1.	Video analysis	50
3.3.2.	Statistical analysis	51
3.4.	RESULTS	52
3.4.1.	Tests of model predictions	53
3.5.	DISCUSSION	61
3.6.	ACKNOWLEDGEMENTS	70
3.7.	REFERENCES	70
Chapter 4.	DISCUSSION.....	78
4.1.	SUMMARY.....	78
4.2.	FORAGING BEHAVIOUR OF LEATHERBACK TURTLES.....	79

4.3. FORAGING BEHAVIOUR OF MALE HARBOUR SEALS SUPPORTED MOST OF THE TESTED PREDICTIONS OF OPTIMAL DIVING THEORY	80
4.4. LIMITATIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH	82
4.5. USING ANIMAL-BORNE CAMERAS TO ANSWER QUESTIONS IN MARINE ECOLOGY.....	85
4.6. CONCLUSIONS.....	86
4.7. REFERENCES.....	87
REFERENCES.....	89
APPENDIX A COPYRIGHT PERMISSIONS.....	103

LIST OF TABLES

Table 2.1	Instrument deployment details for 19 leatherback turtles (<i>Dermochelys coriacea</i>).....	27
Table 2.2.	Dive and prey encounter data (mean±SD) for 19 leatherback turtles (<i>Dermochelys coriacea</i>) estimated from video, energy intake estimated from prey encounter rate, and speed and distance travelled estimated from GPS locations.....	27
Table 2.3.	Parameter estimates and significance of model terms. This table shows the linear mixed model parameter estimates and significance of model terms for three models: the effect of jellyfish encounters per dive minute on dive duration, the effect of prey size on handling time, and the effect of prey size and prey species on handling time. The results show that jellyfish encounters per dive minute are not correlated with dive duration, that prey size is positively correlated with handling time, and that the relationship between prey size and handling time does not differ among species. The hypothesis that the residuals of these fits follow a normal distribution is not rejected by two-tailed Kolmogorov-Smirnov tests ($P>0.05$).	30
Table 3.1.	Tested predictions of optimal diving theory from harbour seals (<i>Phoca vitulina concolor</i>), including the response variable and covariates used for statistical analysis (for each prediction or model).	45
Table 3.2.	Number of complete dives, prey encounters recorded from video, and proportion of dives with prey encounters per harbour seals (<i>Phoca vitulina concolor</i>).	54
Table 3.3.	Parameter estimates, significance of linear terms, approximate significance of smooth terms, and goodness of fit (adjusted R^2) for the fitted mixed models used to test optimal diving theory predictions for harbour seals (<i>Phoca vitulina concolor</i>).....	55
Table 3.4.	Parameter estimates, significance of linear terms, and goodness of fit (adjusted R^2) for the fitted mixed models used to explore the influence of prey species on foraging behaviour of harbour seals (<i>Phoca vitulina concolor</i>).	64

LIST OF FIGURES

Figure 2.1.	Serrano-V camera and example still images. Camera with suction-cup attachment to the shell of a leatherback turtle (<i>Dermochelys coriacea</i> ; a) and still images extracted from a video file recorded on 3 September 2010 showing a turtle approaching a lion's mane jellyfish (<i>Cyanea capillata</i>) that is surrounded by pilot fish (<i>Naucrates ductor</i> ; b, c) and subsequently consuming this jellyfish (d).....	22
Figure 2.2.	Distance between original camera deployment location and each surfacing location of 19 leatherback turtles (<i>Dermochelys coriacea</i>) as estimated from GPS locations.....	31
Figure 2.3.	Frequency distribution of relative prey size (contracted bell diameter) (a) and handling time (b) of lion's mane jellyfish (<i>Cyanea capillata</i>). Results represent the size distribution of measured lion's mane jellyfish (<i>Cyanea capillata</i> ; $n = 350$) captured by 19 leatherback turtles (<i>Dermochelys coriacea</i>).....	32
Figure 2.4.	Effect of relative prey size (contracted bell diameter) on handling time of lion's mane jellyfish (<i>Cyanea capillata</i>).....	34
Figure 3.1.	Observations and predicted effect of bottom duration of harbour seals (<i>Phoca vitulina concolor</i>) on the number of prey encounters (prediction 1, Tables 3.1 and 3.3). Solid lines represent mean predicted values and broken lines represent \pm SE.	56
Figure 3.2.	Observations and predicted effect of travel duration (a; controlled for dive depth) and dive depth (b; controlled for travel duration) on dive duration (prediction 2, Tables 3.1 and 3.3) of harbour seals (<i>Phoca vitulina concolor</i>). Solid lines represent mean predicted values and broken lines represent \pm SE.	58
Figure 3.3.	Observations and predicted effect of travel duration on (a) bottom duration (prediction 3, Tables 3.1 and 3.3) and (b) on percent bottom duration of a dive, a proxy for the proportion of time spent foraging, (prediction 4, Tables 3.1 and 3.3) of harbour seals (<i>Phoca vitulina concolor</i>). Solid lines represent mean predicted values and broken lines represent \pm SE.	59
Figure 3.4.	Observations and predicted effect of dive depth on descent duration (prediction 5, Tables 3.1 and 3.3) of harbour seals (<i>Phoca vitulina concolor</i>). Solid lines represent mean predicted values and broken lines represent \pm SE.	60

Figure 3.5.	Observations and predicted effect of prey presence (solid circles and black line = present; open circles and grey line = absent) and travel duration (a; controlled for depth) and depth (b; controlled for travel duration) on bottom duration (prediction 7, Tables 3.1 and 3.3) of harbour seals (<i>Phoca vitulina concolor</i>). Solid lines represent mean predicted values and broken lines represent \pm SE.	62
Figure 3.6.	Observations and predicted effect of time to first encounter (a; controlled for descent duration) and descent duration (b; controlled for time to first encounter) on bottom duration of harbour seals (<i>Phoca vitulina concolor</i>) post first encounter (prediction 8, Tables 3.1 and 3.3). Solid lines represent mean predicted values and broken lines represent \pm SE.	63

ABSTRACT

Studying the behaviour of marine animals is challenging; however, the use of animal-borne instruments has great potential to contribute to our understanding of the foraging behaviour of marine predators. Data from animal-borne cameras deployed on leatherback turtles (*Dermochelys coriacea* (Vandelli, 1761)) and harbour seals (*Phoca vitulina concolor* DeKay, 1842) were used to describe foraging behaviour and to provide support for the profitability of the long distance migrations (1000s of km) of turtles. I estimated that turtles consumed a daily energy intake of jellyfish that was 3-7 times their daily metabolic requirements, a result consistent with estimates of mass gain prior to southward migration. Dive data and prey encounter data from harbour seals supported seven of the nine tested predictions of optimal diving models, but these theoretical models did not capture the complexity of the animals' foraging behaviour. This study demonstrates the potential for using animal-borne cameras to describe and quantify foraging behaviour as well as to test theoretical optimality models.

Keywords: foraging behaviour; leatherback sea turtle; *Dermochelys coriacea*; harbour seal; *Phoca vitulina concolor*; animal-borne camera

LIST OF ABBREVIATIONS USED

CC BY	creative commons attribution only
CCL	curved carapace length
CCW	curved carapace width
corAR1	autocorrelation structure of order 1
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
df	degrees of freedom
DMR	diving metabolic rate
FMR	field metabolic rate
GAM	generalized additive model
GAMM	generalized additive mixed model
glmmPQL	generalized linear mixed models fit using penalized quasi-likelihood
GLMM	generalized linear mixed model
GPS	global positioning system
IMASEN	intra-mandibular angle sensors
mgcv	mixed GAM computation vehicle
nlme	linear and nonlinear mixed effects models
no.	Number
NRC	National Research Council
NSERC	Natural Sciences and Engineering Research Council of Canada
OFT	optimal foraging theory
ODT	optimal diving theory
pers. comm.	personal communication
QVGA	quarter video graphics array
SE	standard error
SD	standard deviation
TDR	time-depth recorder
USA	United States of America
VHF	very high frequency
WM	wet mass

ACKNOWLEDGEMENTS

I received a great deal of support, advice, and encouragement from a number of individuals during my time at Dalhousie University and I would like to express my thanks and appreciation to you all. I would like to thank my supervisors Don Bowen and Sara Iverson for welcoming me into their labs, the guidance and encouragement they have provided during my studies, and the amazing opportunity I was given to participate in conducting field research on Sable Island. To my committee members Ian Jonsen and Marty Leonard, thank you for the time you spent talking through my ideas with me and for your comments and suggestions on early manuscript drafts, it is very much appreciated. Thank you also to Véronique Lesage who was the external examiner for my defence and also provided thoughtful comments on my thesis manuscript. A great graduate coordinator and graduate secretary are worth their weight in gold and Hal Whitehead and Carolyn Young are perfect examples of this, thank you for all that you have done to help me complete my program smoothly.

Though not part of my official committee, I would like to thank Joanna Mills Flemming, Andy Horn, Mike James, David Johnston, Chris Taggart, and Boris Worm for their interest and enthusiasm to “talk science” with me. My time spent working with the Dalhousie Association of Graduate students and the Faculty of Graduate Studies was an invaluable experience and I would like to thank Bernie Boudreau, Susan Michel, Dieter Pelzer, and Marsha Scott who provided me with great memories and invaluable skills to supplement my graduate school experience. I would like to express particular gratitude to Sunny Marche whose energy was contagious and fueled my interest in and advocating for professional development opportunities for graduate students. Thank you to the members of the Iverson Lab, particularly Sarah Al-Shaghay, Shelley Lang, and Damian Lidgard for your mentoring in the lab and field; and to colleagues at the Bedford Institute of Oceanography, Shelley Armsworthy, Warren Joyce, Kurtis Trzcynski, Nell den Hyer, Jim McMillan, and Sean Smith, for your pleasant company and assistance in the office and with field work. I would additionally like to thank my colleagues, lab alumni, volunteers, and friends that were also members of our field team over the last few

seasons. Debbie Austin, Ed Beals, Ian Beauprie, Wade Blanchard, Greg Breed, Bob Farmer, Liz Leadon, David McMullin, Rob Ronconi, Christina Scarfe, Heather Smith, Priyanka Varkey, and Sarah Wong, your time, hard work, and pleasant company helped to make our projects a success and my time on Sable even more memorable.

I would like to thank Kyler Abernathy, Birgit Buhleier, Greg Marshall, and the Remote Imaging Team at National Geographic for all of their time, hard work, and dedication to the CRITTERCAM projects on Sable Island. Thank you also to Kathleen Martin and the Canadian Sea Turtle Network for the opportunity to join their team to study leatherback turtles here in our backyard of Nova Scotia, an experience I will never forget.

I would also like to express my heartfelt thanks to my fellow graduate students, colleagues, and friends: Laurie Baker, Maggie Bartkowska, Stephanie Boudreau, Greg Breed, Kate Crosby, Eddie Halfyard, Russell Jones, Anna Maggera, Joey Mingrone, Catherine Muir, Christine Ward-Paige, the Brammanns, Godfreys, Grantmyres, Ritchies, Wilsons, and crews of Hula and Ramillies. Particular thanks go to the Irish-Johnstons, especially for my little cheer leaders Madeline and Rosemary, who provided a supportive and sunny environment for writing. Finally I would like to thank my grandmother, Emilie Martin, and parents, Penny and Doug, for their support, understanding, and unconditional love during my educational pursuits.

CHAPTER 1.

INTRODUCTION

The decisions that animals make while foraging affect their growth, survival, reproduction, and therefore fitness. We expect animals make decisions while foraging that maximize their probability of survival and reproductive success. The allocation of energy intake to growth, reproduction, and survival is governed by the life history strategy of a species (Stearns 1992). Just as there are variations in life history strategies, there are also variations in foraging strategies that individual animals employ in response to constraints, risks, trade-offs, and other sources of variability and uncertainty in their environments. Foraging tactics are expected to have evolved to maximize foraging success. Examining the specific tactics that an individual or group of organisms employs while foraging should allow a better understanding of the foraging strategies, how these strategies may have evolved to contribute to individual fitness, and how flexible these strategies are in unpredictable environments.

1.1. FORAGING IS CENTRAL TO ECOLOGY

Foraging behaviour is a major branch of ecology that aims to explain the movements and decisions of animals in response to their environment. Knowledge of the spatial and temporal characteristics of the foraging habitat, tactics, and diet of a species is necessary to understand the role of foraging in shaping community structure and the functioning of ecosystems, and is necessary to develop conservation measures for endangered species such as the designation of critical habitat. The foraging habitat of a species may vary with the presence of predators and conspecifics as well as with prey availability. Prey characteristics such as patch size and density vary in space and time and in order to understand how such heterogeneous resources are used by animals, the patterns and

magnitude of habitat selection must be understood. Understanding spatial movements over fine (1–10 km), meso (10s–100s of km), and large (>1,000 km) oceanographic scales in conjunction with foraging success is of great importance to understanding the population ecology and dynamics of marine animals (Van Houtan and Halley 2011). The feeding strategies or tactics that an animal employs influence their foraging success and may vary with prey availability, age, sex, presence of conspecifics and predators, and in response to other environmental factors (Moll et al. ; Soto et al. 2006; Beck et al. 2007; Sigler et al. 2009). Foraging tactics may also vary among individuals and with the characteristics of the prey species selected (e.g., density, patch size, net energy gain, and behaviour).

Predators are often categorized as either generalists or specialists, i.e., those with a diverse diet and those with a diet of low prey diversity. However, within a population, the dietary niche breadth of a predator can vary among individuals, with age, sex, by location, and by season (Bowen and Harrison 1996a; Estes et al. 2003; Beck et al. 2005; Beck et al. 2007; Field et al. 2007). Species with narrow dietary niches are presumed to be favoured in stable environments while those with relatively broader dietary niches are thought to be favoured in unstable heterogeneous environments (Kassen 2002). For both generalists and specialists, there is a gradient of realized dietary niches influenced by the temporal variation in prey availability and constrained by plasticity of the foraging tactics of the predator, their morphology, and their physiology. Plasticity in foraging behaviour could be beneficial in uncertain environments and has implications for resilience against climate change and the impact of human activities on prey populations; however, this plasticity may occur at the cost of optimal foraging strategies.

1.2. THEORETICAL WORK

1.2.1. Optimal foraging theory

Foraging tactics are used to finance the growth, survival, and reproduction of a predator. The size, nutritional quality, and behaviour of prey could influence the decisions made by predators, as we expect animals to make decisions that maximize the

potential energetic gain with respect to the energetic cost of pursuing prey. The development of foraging theory was shaped by the ideas of Emlen (1966), MacArthur and Pianka (1966), and Charnov (1976b, a), and resulted in the development of optimal foraging theory (OFT) models about the optimization of energy intake over time. These first models assumed that the predator was all-knowing and did not take into account that suboptimal behaviour may be adopted in the presence of predators or other constraints. Since these early models, individual-based and stochastic dynamic models have been developed which include the consideration of the potential effects of predation risk (e.g., Lima 1988), incomplete information about the available resources (e.g., Iwasa et al. 1981; McNamara 1982), and sensory limitations (e.g., Beauchamp et al. 1999). Although optimal foraging models have not always performed well in predicting the complexities of real life examples (e.g., Kamil et al. 1993), the predictions of these theoretical models provide us with a starting point for understanding the ecological and behavioural factors that determine foraging behaviour and the relationship between foraging and fitness.

1.2.2. Optimal diving theory

Optimal diving theory (ODT) is nested within foraging theory and is applied to breath-hold divers that forage at depth. These divers have the additional constraint that their foraging time is penalized by the surface time required to replenish blood oxygen stores and to recover from the rise in blood lactate concentrations that occurs at depth. Theoretical models of optimal diving predict the optimal allocation of time between foraging at depth and obtaining oxygen at the surface, with the assumption that divers maximize their time spent underwater with dive durations equal to or less than their aerobic dive limit and that prey capture does not result in termination of a dive (Kramer 1988; Houston and Carbone 1992; Carbone and Houston 1994, 1996). The currencies maximized during foraging for optimal diving models could include the proportion of time spent foraging, gross energy gain, and net rate of energetic gain and/or energetic efficiency (Houston and Carbone 1992; Thompson and Fedak 2001). Some models also include predictions of divers making decisions influenced by encountered prey and patch quality (Thompson and Fedak 2001).

1.3. EMPIRICAL WORK

1.3.1. Using animal-borne instruments to study the foraging behaviour of marine predators

Collecting simultaneous information about the prey field of a predator (e.g., prey species and density; Lea and Wilson 2006; Witteveen et al. 2008; Graham et al. 2010) and the movement of a predator is ideal to try to get a better understanding of how animals adjust their behaviour in response to patch quality. However, such sampling is expensive and logistically difficult. Given the difficulties in studying behaviour in the marine environment and given that prey are usually encountered and consumed at depth, the methods used to study foraging behaviour are often inferred from the movement characteristics of a predator. Although diving behaviour (e.g., length of bouts) and animal movements (e.g., distance travelled and path tortuosity) have been shown to vary with prey type and foraging success and have been used to infer patch quality (e.g., Mori and Boyd 2004; Austin et al. 2006; Elliott et al. 2008), one cannot definitively say what the animals are doing solely from two-dimensional patterns of movement.

Instruments used to determine the timing of prey encounters include the use of stomach temperature sensors, jaw sensors, and accelerometers to detect head, neck, and jaw movements (Austin et al. 2006; Kuhn and Costa 2006; Liebsch et al. 2007; Suzuki et al. 2009; Viviant et al. 2010; Doniol-Valcroze et al. 2011). Although these sensors show potential for identifying movements associated with prey encounters, further validation is required to determine capture success and to distinguish between foraging and non-foraging related movements. Foraging data collected using these methods are informative; however, data on the timing of individual prey encounters at the scale of individual dives are necessary to test predictions of ODT. It is also possible to use patterns of movement detected using a combination of speed measurements with changes in depth to identify prey encounters during individual dives. Doniol-Valcroze (2011) successfully used swim speed and values and patterns of acceleration and deceleration to create a detection algorithm that accurately detected lunge feeding events that were validated by visual observations of feeding at the surface and were also identified as

lunge feeding with rolling angles greater than 45°. However, for most species surface validation of feeding behaviours is logistically unfeasible without the assistance of remote imaging tools.

The recent and continuous development of underwater animal-borne video cameras (Marshall 1998; Marshall 2007) provides the opportunity for scientists to directly observe foraging behaviour in conjunction with the predator's two- or three-dimensional movements. Such camera systems have been deployed on a variety of large marine predators, including pinnipeds, whales, sharks, and cheloniid turtles (Heithaus et al. 2001; Bowen et al. 2002; Calambokidis et al. 2007; Hays et al. 2007) and are a powerful tool for studying the foraging behaviour of marine predators.

1.3.2. Foraging behavior of leatherback turtles and harbour seals

Leatherback turtles (*Dermochelys coriacea* (Vandelli, 1761)) are specialist predators that feed almost completely on a diet of gelatinous zooplankton (James and Herman 2001; Houghton et al. 2006), while harbour seals (*Phoca vitulina concolor* DeKay, 1842) are generalist predators that feed on a variety of both benthic and pelagic prey in Atlantic Canadian waters (Bowen and Harrison 1996b). Leatherback turtles undertake long-distance migrations (up to 18,000 km round-trip) between tropical breeding and foraging grounds and northern temperate foraging grounds (James et al. 2005b; Benson et al. 2007; Shillinger et al. 2008). The predictable occurrence of leatherback turtles in high latitude foraging areas during the summer months off the coast of Canada (James et al. 2006b) provides the opportunity to study foraging leatherbacks when they are presumably acquiring the energy required for southward migration and eventually reproduction. During the breeding season, male harbour seals are central-place foragers reliably returning to and hauling out on Sable Island after short foraging trips to sea (Walker and Bowen 1993a; Coltman et al. 1997). The predictable foraging movements of these animals provide an opportunity to fit individual turtles and seals with data-logging instruments and to reliably recover these instruments to download data.

Although there have been opportunistic observations of leatherback turtles consuming jellyfish in their high latitude foraging areas (James and Herman 2001), direct studies of leatherback turtles using animal-borne cameras have previously been limited to short deployments on nesting females and have not documented foraging (Reina et al. 2005). Foraging behaviour of leatherback turtles has previously been inferred from diving behaviour from dive data transmitted via satellite tags deployed over several months and over subsequent years (Hays et al. 2004; James et al. 2005a; James et al. 2005b; Shillinger et al. 2008; Fossette et al. 2010). Surface location data transmitted via satellite tags have also been used to estimate behavioural states of leatherbacks based on parameters such as speed and turning angle (Jonsen et al. 2005; Jonsen et al. 2007; Bailey et al. 2008). Although sensors that can detect mouth opening (Myers and Hays 2006; Fossette et al. 2008) and stomach temperature (Casey et al. 2010) may help estimate the timing of prey capture events, the utility of such indirect measures of foraging are limited since prey consumption is not observed and therefore capture success is unknown. Video data collected from animal-borne cameras deployed on free-ranging leatherback turtles in the shelf waters off Nova Scotia, Canada will be used to describe prey-specific components of foraging behaviour and calculate estimates of daily energy intake in Chapter 2.

Previous studies on the foraging behaviour of harbour seals in Atlantic Canadian waters have included diet estimates from scats, stomach contents, and fatty acids; and foraging behaviour inferred from TDRs, stomach sensors, and observed directly using animal-borne cameras (Bowen and Harrison 1996b; Coltman et al. 1997; Lesage et al. 1999; Bowen et al. 2002; Iverson et al. 2004). The work of Bowen et al. (2002) provided one of the first records of prey-dependent foraging tactics for a marine predator, showing that foraging tactics differed among and within prey types based on prey behaviour. The results of this study suggest that diet selection has important implications for prey profitability as predicted by foraging models (Schoener 1971). Prey encounter and dive data for individual dives of harbour seals, data from the same study as Bowen et al. (2002), will be used to test predictions of theoretical foraging models of optimal diving in Chapter 3.

1.3.3. Tests of theoretical foraging models of optimal diving

Without information on prey encounters or confirmation of foraging behaviour, studies which test ODT are limited to predictions related to time allocation during the dive cycle. Tests of ODT using direct observations of animals at the surface have been limited to testing predictions of the relationships between dive duration and surface duration (Lea et al. 1996; Walton et al. 1998). In order to test predictions related to prey encounter events, direct observations have mostly been limited to experiments conducted with captive animals (Carbone and Houston 1994; Cornick and Horning 2003; Gallon et al. 2007; Sparling et al. 2007). The use of TDRs, speed sensors, and underwater video cameras has permitted the testing of ODT for free-ranging animals (Boyd et al. 1995; Lesage et al. 1999; Mori 2002; Heath et al. 2007). However, the opportunity to validate inferred foraging behaviours from bio-logging devices is rare and a researcher must be present to observe and/or record video footage in a particular location (e.g., Lesage et al. 1999). The development of animal-borne cameras over the last three decades (Moll et al.) provides the potential to validate behaviours inferred from TDRs and to examine foraging tactics with respect to encountered prey species (Bowen et al. 2002) and applicable ODT predictions.

1.4. THESIS OVERVIEW AND OBJECTIVES

In Chapter 2, I describe the prey-specific components of foraging behaviour from video data collected from animal-borne cameras deployed on free-ranging leatherback turtles in the shelf waters off Nova Scotia, Canada. I also provide estimates of daily energy intake in order to better understand the profitability of migratory patterns of leatherback populations to high latitude areas. In Chapter 3, I test predictions of ODT using dive and prey encounter data collected using animal-borne cameras deployed on free-ranging harbour seals in the shelf waters off Sable Island, Nova Scotia, Canada to provide a better understanding of the decisions that harbour seals may be making in order to maximize their foraging profitability. The objectives of this thesis are to demonstrate how video collected using animal-borne cameras can be used to 1) infer energy intake and 2) test predictions of optimality.

1.5. PUBLISHED MANUSCRIPTS INCLUDED IN THESIS

This thesis contains two manuscripts (Chapter 2: Heaslip et al. 2012; Chapter 3: Heaslip et al. 2014) that have previously been published in peer reviewed journals.

Heaslip SG, Iverson SJ, Bowen WD, James MC. 2012. Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): video evidence from animal-borne cameras. PLOS ONE 7(3): e33259.
doi:10.1371/journal.pone.0033259.

Heaslip SG, Bowen WD, Iverson SJ. 2014. Testing predictions of optimal diving theory using animal-borne video from harbour seals (*Phoca vitulina concolor*). Canadian Journal of Zoology 92(4): 309-318. doi:10.1139/cjz-2013-0137.

For Chapter 2: Heaslip et al. 2012, SGH scored the videos, analyzed the video data, conducted the statistical analysis, and wrote the majority of the manuscript with contributions and comments from SJI, WDB, and MCJ. For Chapter 3: Heaslip et al. 2014, SGH analyzed the video data, conducted the statistical analysis, and wrote the majority of the manuscript with contributions and comments from SJI and WDB.

The PLOS ONE manuscript is licensed under a Creative Commons Attribution (CC BY) License; therefore, no permission from PLOS is required for inclusion of the manuscript in this thesis so long as the original authors and sources are cited. Permission to reproduce the Canadian Journal of Zoology manuscript as part of my thesis has been obtained from Canadian Science Publishing (NRC Research Press). Further details of the Creative Commons License and a copy of the NRC Research Press License are included in Appendix A.

1.6. REFERENCES

Austin, D., Bowen, W.D., McMillan, J.I., and Iverson, S.J. 2006. Linking movement, diving, and habitat to foraging success in a large marine predator. Ecology 87(12): 3095-3108. doi:10.1890/0012-9658(2006)87[3095:lmdaht]2.0.co;2.

- Bailey, H., Shillinger, G., Palacios, D., Bograd, S., Spotila, J., Paladino, F., and Block, B. 2008. Identifying and comparing phases of movement by leatherback turtles using state-space models. *Journal of Experimental Marine Biology and Ecology* **356**(1-2): 128-135. doi:10.1016/j.jembe.2007.12.020.
- Beauchamp, D.A., Baldwin, C.M., Vogel, J.L., and Gubala, C.P. 1999. Estimating diel, depth-specific foraging opportunities with a visual encounter rate model for pelagic piscivores. *Canadian Journal of Fisheries and Aquatic Sciences* **56**(Suppl. 1): 128-139.
- Beck, C.A., Iverson, S.J., and Bowen, W.D. 2005. Blubber fatty acids of gray seals reveal sex differences in the diet of a size-dimorphic marine carnivore. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **83**(3): 377-388. doi:10.1139/z05-021.
- Beck, C.A., Iverson, S.J., Bowen, W.D., and Blanchard, W. 2007. Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. *Journal of Animal Ecology* **76**(3): 490-502. doi:10.1111/j.1365-2656.2007.01215.x.
- Benson, S.R., Dutton, P.H., Hitipeuw, C., Samber, B., Bakarbesy, J., and Parker, D. 2007. Post-nesting migrations of leatherback turtles (*Dermochelys coriacea*) from Jamursba-Medi, Bird's Head Peninsula, Indonesia. *Chelonian Conservation and Biology* **6**(1): 150-154.
- Bowen, W.D., and Harrison, G.D. 1996a. Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **74**(1): 125-135. doi:10.1139/z96-017.
- Bowen, W.D., and Harrison, G.D. 1996b. Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. *Canadian Journal of Zoology* **74**(1): 125-135. doi:10.1139/z96-017.
- Bowen, W.D., Tully, D., Boness, D.J., Bulheier, B.M., and Marshall, G.J. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. *Marine Ecology Progress Series* **244**: 235-245.
- Boyd, I.L., Reid, K., and Bevan, R.M. 1995. Swimming speed and allocation of time during the dive cycle in Antarctic fur seals. *Animal Behaviour* **50**: 769-784.
- Calambokidis, J., Schorr, G.S., Steiger, G.H., Francis, J., Bakhtiari, M., Marshal, G., Oleson, E.M., Gendron, D., and Robertson, K. 2007. Insights into the underwater diving, feeding, and calling behavior of blue whales from a suction-cup-attached video-imaging tag (Cittercam). *Marine Technology Society Journal* **41**(4): 19-29.

- Carbone, C., and Houston, A.I. 1994. Patterns in the diving behavior of the pochard, *Aythya ferina*: a test of an optimality model. *Animal Behaviour* **48**(2): 457-465. doi:10.1006/anbe.1994.1259.
- Carbone, C., and Houston, A.I. 1996. The optimal allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. *Animal Behaviour* **51**: 1247-1255. doi:10.1006/anbe.1996.0129.
- Casey, J., Garner, J., Garner, S., and Williard, A.S. 2010. Diel foraging behavior of gravid leatherback sea turtles in deep waters of the Caribbean Sea. *Journal of Experimental Biology* **213**(23): 3961-3971. doi:10.1242/jeb.048611.
- Charnov, E.L. 1976a. Optimal foraging: Attack strategy of a mantid. *American Naturalist* **110**(971): 141-151.
- Charnov, E.L. 1976b. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**(2): 129-136.
- Coltman, D.W., Bowen, W.D., Boness, D.J., and Iverson, S.J. 1997. Balancing foraging and reproduction in the male harbour seal, an aquatically mating pinniped. *Animal Behaviour* **54**: 663-678. doi:10.1006/anbe.1997.0470.
- Cornick, L.A., and Horning, M. 2003. A test of hypotheses based on optimal foraging considerations for a diving mammal using a novel experimental approach. *Canadian Journal of Zoology* **81**(11): 1799-1807. doi:10.1139/z03-179.
- Doniol-Valcroze, T., Lesage, V., Giard, J., and Michaud, R. 2011. Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behavioral Ecology* **22**(4): 880-888. doi:10.1093/beheco/arr038.
- Elliott, K.H., Davoren, G.K., and Gaston, A.J. 2008. Time allocation by a deep-diving bird reflects prey type and energy gain. *Animal Behaviour* **75**: 1301-1310. doi:DOI 10.1016/j.anbehav.2007.09.024.
- Emlen, J.M. 1966. Role of time and energy in food preference. *American Naturalist* **100**(916): 611-617.
- Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T., and Lyon, B.E. 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. *Journal of Animal Ecology* **72**(1): 144-155. doi:10.1046/j.1365-2656.2003.00690.x.
- Field, I.C., Bradshaw, C.J.A., van den Hoff, J., Burton, H.R., and Hindell, M.A. 2007. Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche. *Marine Biology* **150**(6): 1441-1452. doi:10.1007/s00227-006-0417-y.

- Fossette, S., Gaspar, P., Handrich, Y., Le Maho, Y., and Georges, J.Y. 2008. Dive and beak movement patterns in leatherback turtles *Dermochelys coriacea* during interesting intervals in French Guiana. *Journal of Animal Ecology* **77**(2): 236-246. doi:10.1111/j.1365-2656.2008.01344.x.
- Fossette, S., Hobson, V.J., Girard, C., Calmettes, B., Gaspar, P., Georges, J.Y., and Hays, G.C. 2010. Spatio-temporal foraging patterns of a giant zooplanktivore, the leatherback turtle. *Journal of Marine Systems* **81**(3): 225-234. doi:10.1016/j.jmarsys.2009.12.002.
- Gallon, S.L., Sparling, C.E., Georges, J.Y., Fedak, M.A., Biuw, M., and Thompson, D. 2007. How fast does a seal swim? Variations in swimming behaviour under differing foraging conditions. *Journal of Experimental Biology* **210**(18): 3285-3294. doi:10.1242/jeb.007542.
- Graham, T.R., Harvey, J.T., Benson, S.R., Renfree, J.S., and Demer, D.A. 2010. The acoustic identification and enumeration of scyphozoan jellyfish, prey for leatherback sea turtles (*Dermochelys coriacea*), off central California. *ICES Journal of Marine Science* **67**(8): 1739-1748. doi:10.1093/icesjms/fsq112.
- Hays, G.C., Houghton, J.D.R., Isaacs, C., King, R.S., Lloyd, C., and Lovell, P. 2004. First records of oceanic dive profiles for leatherback turtles, *Dermochelys coriacea*, indicate behavioural plasticity associated with long-distance migration. *Animal Behaviour* **67**: 733-743.
- Hays, G.C., Marshall, G.J., and Seminoff, J.A. 2007. Flipper beat frequency and amplitude changes in diving green turtles, *Chelonia mydas*. *Marine Biology* **150**(5): 1003-1009. doi:10.1007/s00227-006-0412-3.
- Heaslip, S.G., Bowen, W.D., and Iverson, S.J. 2014. Testing predictions of optimal diving theory using animal-borne video from harbour seals (*Phoca vitulina concolor*). *Canadian Journal of Zoology* **92**(4): 309-318. doi:10.1139/cjz-2013-0137.
- Heaslip, S.G., Iverson, S.J., Bowen, W.D., and James, M.C. 2012. Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): video evidence from animal-borne cameras. *PloS ONE* **7**(3): e33259. doi:10.1371/journal.pone.0033259.
- Heath, J.P., Gilchrist, H.G., and Ydenberg, R.C. 2007. Can dive cycle models predict patterns of foraging behaviour? Diving by common eiders in an Arctic polynya. *Animal Behaviour* **73**: 877-884. doi:10.1016/j.anbehav.2006.10.015.
- Heithaus, M.R., Marshall, G.J., Buhleier, B.M., and Dill, L.M. 2001. Employing Crittercam to study habitat use and behavior of large sharks. *Marine Ecology Progress Series* **209**: 307-310. doi:10.3354/Meps209307.

- Houghton, J.D.R., Doyle, T.K., Wilson, M.W., Davenport, J., and Hays, G.C. 2006. Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. *Ecology* **87**(8): 1967-1972.
- Houston, A.I., and Carbone, C. 1992. The optimal allocation of time during the diving cycle. *Behavioral Ecology* **3**(3): 255-265. doi:10.1093/beheco/3.3.255.
- Iverson, S.J., Field, C., Bowen, W.D., and Blanchard, W. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. *Ecological Monographs* **74**(2): 211-235. doi:10.1890/02-4105.
- Iwasa, Y., Higashi, M., and Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *American Naturalist* **117**(5): 710-723.
- James, M.C., Eckert, S.A., and Myers, R.A. 2005a. Migratory and reproductive movements of male leatherback turtles (*Dermochelys coriacea*). *Marine Biology* **147**(4): 845-853. doi:10.1007/s00227-005-1581-1.
- James, M.C., and Herman, T.B. 2001. Feeding of *Dermochelys coriacea* on medusae in the northwest Atlantic. *Chelonian Conservation Biology* **4**: 202–205.
- James, M.C., Myers, R.A., and Ottensmeyer, C.A. 2005b. Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. *Proceedings of the Royal Society of London Series B: Biological Sciences* **272**(1572): 1547-1555. doi:10.1098/rspb.2005.3110.
- James, M.C., Sherrill-Mix, S.A., Martin, K., and Myers, R.A. 2006b. Canadian waters provide critical foraging habitat for leatherback sea turtles. *Biological Conservation* **133**(3): 347-357. doi:10.1016/j.biocon.2006.06.012.
- Jonsen, I.D., Flemming, J.M., and Myers, R.A. 2005. Robust state-space modeling of animal movement data. *Ecology* **86**(11): 2874-2880.
- Jonsen, I.D., Myers, R.A., and James, M.C. 2007. Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Marine Ecology Progress Series* **337**: 255-264.
- Kamil, A.C., Misthal, R.L., and Stephens, D.W. 1993. Failure of simple optimal foraging models to predict residence time when patch quality is uncertain. *Behavioral Ecology* **4**(4): 350-363. doi:10.1093/beheco/4.4.350.
- Kassen, R. 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of Evolutionary Biology* **15**(2): 173-190. doi:10.1046/j.1420-9101.2002.00377.x.

- Kramer, D.L. 1988. The behavioral ecology of air breathing by aquatic animals. *Canadian Journal of Zoology* **66**(1): 89-94.
- Kuhn, C.E., and Costa, D.P. 2006. Identifying and quantifying prey consumption using stomach temperature change in pinnipeds. *Journal of Experimental Biology* **209**(22): 4524-4532. doi:Doi 10.1242/Jeb.02530.
- Lea, M.A., and Wilson, B. 2006. Techniques for real-time, active tracking of sea lions. *In* *Sea Lions of the World. Edited by A.W. Trites and S.K. Atkinson and D.P. DeMaster and L.W. Fritz and T.S. Gelatt and L.D. Rea and K.M. Wynne. Alaska Sea Grant Coll Program, Fairbanks. pp. 235-253.*
- Lea, S.E.G., Daley, C., Boddington, P.J.C., and Morison, V. 1996. Diving patterns in shags and cormorants (*Phalacrocorax*): tests of an optimal breathing model. *Ibis* **138**(3): 391-398. doi:10.1111/j.1474-919X.1996.tb08056.x.
- Lesage, V., Hammill, M.O., and Kovacs, K.M. 1999. Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Canadian Journal of Zoology* **77**(1): 74-87. doi:10.1139/cjz-77-1-74.
- Liebsch, N., Wilson, R.P., Bornemann, H., Adelung, D., and Plotz, J. 2007. Mouthing off about fish capture: jaw movement in pinnipeds reveals the real secrets of ingestion. *Deep-Sea Research Part II: Topical Studies in Oceanography* **54**(3-4): 256-269. doi:DOI 10.1016/j.dsr2.2006.11.014.
- Lima, S.L. 1988. Vigilance and diet selection: The classical diet model reconsidered. *Journal of Theoretical Biology* **132**(2): 127-143.
- MacArthur, R.H., and Pianka, E.R. 1966. On optimal use of a patchy environment. *American Naturalist* **100**(916): 603-609.
- Marshall, G. 2007. An advanced solid-state animal-borne video and environmental data-logging device ("Crittrecam") for marine research. *Marine Technology Society Journal* **41**(2): 31-38.
- Marshall, G.J. 1998. Crittrecam: an animal-borne imaging and data logging system. *Marine Technology Society Journal* **32**(1): 11-17.
- McNamara, J. 1982. Optimal patch use in a stochastic environment. *Theoretical Population Biology* **21**(2): 269-288.
- Moll, R.J., Millsbaugh, J.J., Beringer, J., Sartwell, J., and He, Z. A new 'view' of ecology and conservation through animal-borne video systems. *Trends in Ecology & Evolution* **22**(12): 660-668. doi:10.1016/j.tree.2007.09.007.

- Mori, Y. 2002. Optimal diving behaviour for foraging in relation to body size. *Journal of Evolutionary Biology* **15**(2): 269-276. doi:10.1046/j.1420-9101.2002.00382.x.
- Mori, Y., and Boyd, I.L. 2004. The behavioral basis for nonlinear functional responses and optimal foraging in antarctic fur seals. *Ecology* **85**(2): 398-410. doi:10.1890/03-4005.
- Myers, A.E., and Hays, G.C. 2006. Do leatherback turtles *Dermochelys coriacea* forage during the breeding season? A combination of data-logging devices provide new insights. *Marine Ecology Progress Series* **322**: 259-267.
- Reina, R.D., Abernathy, K.J., Marshall, G.J., and Spotila, J.R. 2005. Respiratory frequency, dive behaviour and social interactions of leatherback turtles, *Dermochelys coriacea* during the inter-nesting interval. *Journal of Experimental Marine Biology and Ecology* **316**(1): 1-16. doi:10.1016/j.jembe.2004.10.002.
- Schoener, T.W. 1971. Theory of Feeding Strategies. *Annual Review of Ecology and Systematics* **2**(1): 369-404. doi:doi:10.1146/annurev.es.02.110171.002101.
- Shillinger, G.L., Palacios, D.M., Bailey, H., Bograd, S.J., Swithenbank, A.M., Gaspar, P., Wallace, B.P., Spotila, J.R., Paladino, F.V., Piedra, R., Eckert, S.A., and Block, B.A. 2008. Persistent leatherback turtle migrations present opportunities for conservation. *Plos Biology* **6**(7): e171. doi:10.1371/journal.pbio.0060171.
- Sigler, M.F., Tollit, D.J., Vollenweider, J.J., Thedinga, J.F., Csepp, D.J., Womble, J.N., Wong, M.A., Rehberg, M.J., and Trites, A.W. 2009. Steller sea lion foraging response to seasonal changes in prey availability. *Marine Ecology Progress Series* **388**: 243-261. doi:10.3354/meps08144.
- Soto, K.H., Trites, A.W., and Arias-Schreiber, M. 2006. Changes in diet and maternal attendance of South American sea lions indicate changes in the marine environment and prey abundance. *Marine Ecology Progress Series* **312**: 277-290. doi:10.3354/meps312277.
- Sparling, C.E., Georges, J.Y., Gallon, S.L., Fedak, M., and Thompson, D. 2007. How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: a test of a simple model. *Animal Behaviour* **74**: 207-218. doi:10.1016/i.anbehav.2006.06.022.
- Stearns, S.C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.
- Suzuki, I., Naito, Y., Folkow, L.P., Miyazaki, N., and Blix, A.S. 2009. Validation of a device for accurate timing of feeding events in marine animals. *Polar Biology* **32**(4): 667-671. doi:DOI 10.1007/s00300-009-0596-3.

- Thompson, D., and Fedak, M.A. 2001. How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Animal Behaviour* **61**: 287-296. doi:10.1006/anbe.2000.1539.
- Van Houtan, K.S., and Halley, J.M. 2011. Long-term climate forcing in loggerhead sea turtle nesting. *PloS ONE* **6**(4): e19043. doi:10.1371/journal.pone.0019043.
- Viviant, M., Trites, A.W., Rosen, D.A.S., Monestiez, P., and Guinet, C. 2010. Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. *Polar Biology* **33**(5): 713-719. doi:DOI 10.1007/s00300-009-0750-y.
- Walker, B.G., and Bowen, W.D. 1993a. Behavioural differences among adult male harbor seals during the breeding season may provide evidence of reproductive strategies. *Canadian Journal of Zoology* **71**(8): 1585-1591. doi:10.1139/z93-224.
- Walton, P., Ruxton, G.D., and Monaghan, P. 1998. Avian diving, respiratory physiology and the marginal value theorem. *Animal Behaviour* **56**: 165-174. doi:10.1006/anbe.1998.0759.
- Witteveen, B.H., Foy, R.J., Wynne, K.M., and Tremblay, Y. 2008. Investigation of foraging habits and prey selection by humpback whales (*Megaptera novaeangliae*) using acoustic tags and concurrent fish surveys. *Marine Mammal Science* **24**(3): 516-534. doi:10.1111/j.1748-7692.2008.00193.x.

CHAPTER 2.

JELLYFISH SUPPORT HIGH ENERGY INTAKE OF LEATHERBACK SEA TURTLES (*DERMOCHELYS CORIACEA*): VIDEO EVIDENCE FROM ANIMAL-BORNE CAMERAS

2.1. ABSTRACT

The endangered leatherback turtle is a large, highly migratory marine predator that inexplicably relies upon a diet of low-energy gelatinous zooplankton. The location of these prey may be predictable at large oceanographic scales, given that leatherback turtles perform long distance migrations (1000s of km) from nesting beaches to high latitude foraging grounds. However, little is known about the profitability of this migration and foraging strategy. I used GPS location data and video from animal-borne cameras to examine how prey characteristics (i.e., prey size, prey type, prey encounter rate) correlate with the daytime foraging behaviour of leatherbacks ($n = 19$) in shelf waters off Cape Breton Island, Nova Scotia, Canada, during August and September. Video was recorded continuously, averaged 1:53 h per turtle (range 0:08–3:38 h), and documented a total of 601 prey captures. Lion's mane jellyfish (*Cyanea capillata* (L., 1758)) was the dominant prey (83–100%), but moon jellyfish (*Aurelia aurita* (L., 1758)) were also consumed. Turtles approached and attacked most jellyfish within the camera's field of view and appeared to consume prey completely. There was no significant relationship between encounter rate and dive duration ($P = 0.74$, linear mixed-effects models). Handling time increased with prey size regardless of prey species ($P = 0.0001$). Estimates of energy intake averaged 66,018 kJ•d⁻¹ but were as high as 167,797 kJ•d⁻¹ corresponding to turtles consuming an average of 330 kg wet mass•d⁻¹ (up to 840 kg•d⁻¹) or approximately 261 (up to 664) jellyfish•d⁻¹. Assuming our turtles averaged 455 kg body

mass, they consumed an average of 73% of their body mass•d⁻¹ equating to an average energy intake of 3–7 times their daily metabolic requirements, depending on estimates used. This study provides evidence that feeding tactics used by leatherbacks in Atlantic Canadian waters are highly profitable and our results are consistent with estimates of mass gain prior to southward migration.

2.2. INTRODUCTION

Identifying the spatial and temporal characteristics of foraging habitat, search tactics, and diet of predators is fundamental to understanding their role in ecosystems and to developing conservation measures for threatened species, such as the protection of critical habitat. We expect animals to balance the benefits and costs of foraging decisions, since time and energy are spent searching for, capturing, and handling prey (Stephens and Krebs 1986). To begin to understand the foraging decisions of marine predators, it is important to study how prey characteristics (e.g., size of prey and patch density) influence their foraging behaviour and success (e.g., Charnov 1976b; Zollner and Lima 1999; Benoit-Bird and Au 2003). However, prey are usually encountered and consumed at depth by marine animals, therefore, foraging behaviour and diets are typically inferred indirectly, for instance from analyses of dive behaviour and various diet estimate methods. The ability to directly observe and quantify foraging success in conjunction with understanding spatial movements over fine (1–10 km), meso (10s–100s of km), and large oceanographic scales (>1,000 km) is of great importance to better understanding marine animal populations and their variability (Van Houtan and Halley 2011).

The leatherback turtle is the largest living species of marine turtle, and also has the widest global distribution of any reptile. This species is listed as critically endangered globally (Sarti Martinez 2000) and endangered in Canada (COSEWIC 2001). Leatherbacks undertake long-distance migrations (up to 18,000 km round-trip) between tropical breeding and foraging grounds and northern temperate foraging grounds (James et al. 2005b; Benson et al. 2007; Shillinger et al. 2008). Although east-west migrations are typical of some leatherback populations (Benson et al. 2007; Witt et al. 2007) and

return trips to specific foraging areas may span as long as 2–3 years, most sub-adult and adult leatherbacks in the northwest Atlantic perform these migrations annually (James et al. 2005b; James et al. 2007) to feed on gelatinous zooplankton, primarily jellyfish (James and Herman 2001; Houghton et al. 2006), which are often associated with oceanographic features such as areas of upwelling (Benson et al. 2007). For sexually mature adult leatherbacks, such migrations to high latitudes are presumably driven by the need to accumulate resources for reproduction (James et al. 2007). However, during these migrations, leatherback turtles are exposed to a number of threats including fisheries bycatch (e.g., pelagic longline and particularly fixed gear in temperate waters; COSEWIC 2001). In addition to human impacts, climate and oceanographic variability (which also influence prey distributions) no doubt also impact the life history of turtles in the Northwest Atlantic and are expected to influence juvenile recruitment and breeding remigration and contribute to range expansion (e.g., McMahon and Hays 2006; Van Houtan and Halley 2011). Thus, it is of great importance to better understand leatherback foraging strategies to assess their significance to leatherback population energetics and to inform management measures such as the identification of critical habitat.

One of the most intriguing aspects of the foraging strategy of leatherback turtles is the almost complete reliance of such a large-bodied animal (up to 640 kg James et al. 2007) on a diet of gelatinous zooplankton, a low-energy food source (Davenport 1998; Doyle et al. 2007b). It has been estimated that hatchling leatherbacks may consume more than 100% body weight • day⁻¹ (Lutcavage and Lutz 1986) and adults at least 50% body weight • day⁻¹ (Davenport 1998). However, both the remote location of foraging and the sub-surface consumption of prey have precluded verification of such estimates. Found throughout the world's oceans, jellyfish are patchily distributed, but occur predictably at high densities in specific areas and at certain times of year (Purcell et al. 2007). Temperate coastal shelf waters of the North Atlantic are characterized by high concentrations of jellyfish during the summer months (Brodeur et al. 2002; Doyle et al. 2007a). Although dedicated studies of jellyfish distribution and abundance in Atlantic Canadian waters are lacking, spatial distributions of lion's mane jellyfish (*Cyanea capillata* (L., 1758)), the largest extant species of jellyfish and a known prey of the

leatherback turtle (James and Herman 2001), are known to overlap with the occurrence of leatherback turtles (e.g., Witt et al. 2007).

Despite this overlap, the marine environment is dynamic, with prey often distributed heterogeneously within the landscape over space and time. The location of these prey are likely predictable at a large oceanographic scale, given the long-distance migrations of leatherback turtles and inter-annual fidelity to foraging areas (James et al. 2005c). However, locating prey patches of jellyfish at meso-scales may be more difficult, as they vary spatially and temporally with influences from the movement of surface water and associated nutrients caused by wind (Hamner and Schneider 1986) and tidal cycles. Because of this heterogeneity in prey presence with space and time, collecting simultaneous information about a predator's prey field and their movements (Lea and Wilson 2006; Witteveen et al. 2008; Graham et al. 2010) is necessary to try to understand an animal's foraging behaviour. However, such sampling is expensive and logistically difficult.

Tracking data from satellite tags deployed over several months and over subsequent years have been used to explore the migratory movements of leatherback turtles, with foraging behaviour inferred from diving behaviour and dive-shape (Hays et al. 2004; James et al. 2005a; James et al. 2005b; Shillinger et al. 2008; Fossette et al. 2010). Such tracking data have been used to estimate behavioural states of leatherbacks based on changes in movement parameters such as speed and turning angle (Jonsen et al. 2005; Jonsen et al. 2007; Bailey et al. 2008). Movement data, along with concurrently collected dive data, have been used as a proxy for studying leatherback foraging (e.g., James et al. 2006a), and sensors that can detect mouth opening (Myers and Hays 2006; Fossette et al. 2008) and stomach temperature (Casey et al. 2010) may help determine the timing of prey capture events. Despite the utility of such methods, they are indirect measures of foraging since prey consumption is not observed.

The use of underwater animal-borne video cameras, in conjunction with electronic tagging technologies, provides the opportunity to directly observe foraging behaviour. Such camera systems have been deployed on a variety of large marine predators,

including pinnipeds, whales, sharks, and cheloniid turtles (Heithaus et al. 2001; Bowen et al. 2002; Calambokidis et al. 2007; Hays et al. 2007). Given the challenges associated with conducting in-situ studies of leatherback turtles at sea and recovering data loggers from free-swimming turtles, deployments of animal-borne cameras have been limited to nesting females and have not documented foraging (Reina et al. 2005). However, the predictable occurrence of leatherback turtles off the coast of Canada during the summer months (James et al. 2006b) provides the opportunity to study foraging leatherbacks when they are presumably acquiring the energy required for southward migration and, for many, reproduction. We attached an animal-borne video camera with an incorporated global positioning system (GPS) to free-ranging leatherback turtles in shelf waters off Nova Scotia, Canada. Our objectives were to describe prey-specific components of foraging behaviour (e.g., encounter rate, capture success rate, and handling time), and to estimate daily energy intake, with the aim to better understand the profitability of migratory patterns and implications for characterizing critical foraging habitat of leatherback populations.

2.3. METHODS

2.3.1. Ethics statement

This research was conducted in accordance with guidelines of the Canadian Council on Animal Care. The protocol was approved by the University Committee on Laboratory Animals, Dalhousie University's animal ethics committee (protocol numbers 08-077 and 09-069) and Fisheries and Oceans Canada (license and permit numbers 2007-024, MAR-SA-2007-006, 2008-454, MAR-SA-2008-006, 323395, 323398, and 326240).

Instruments were attached to the carapace of free-swimming turtles without capture from a boat to reduce handling effects on the animals. During tracking, a minimum observation distance of ~400 m was maintained to minimize the disturbance of turtles.

2.3.2. Study area

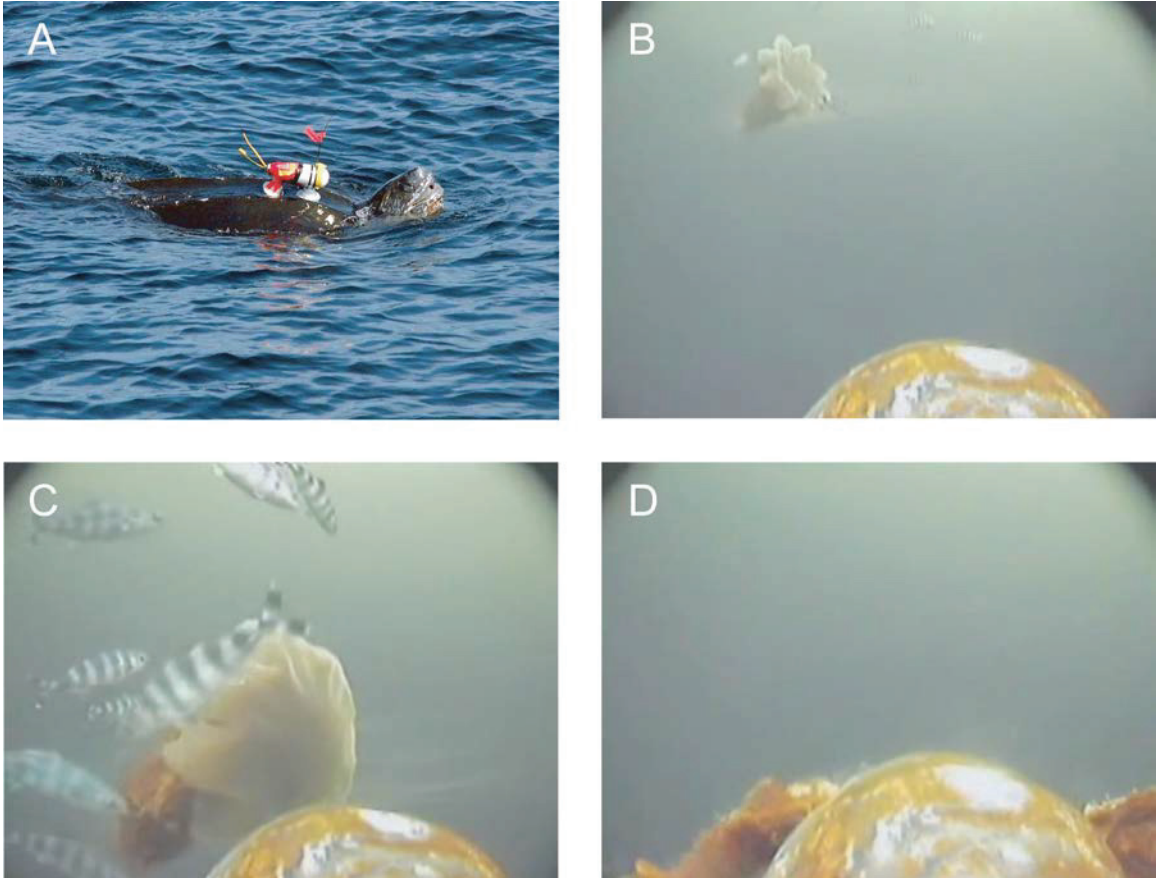
The study was conducted in the temperate shelf waters off Cape Breton Island, Nova Scotia, Canada (approximately 47° N, 60°W). Instruments were deployed at a median distance of 13.1 km off the coast (mean = 15.7 km, range 3.1–35.0 km) during August and September 2007–2010. Previous studies have shown that a relatively large and predictable assemblage of sub-adult and adult leatherbacks feed in this area every year (James et al. 2005b; James et al. 2006b; Jonsen et al. 2007).

2.3.3. Instruments and deployments

The Serrano-V (Fig. 2.1a, Xeos Technologies Inc., Bedford, Nova Scotia, Canada) is a charge-coupled device color, video camera system (235×83 mm, 270 mm with antennae, 1013 g) which operates under low light, without the need for accessory lighting, and records 320×240 QVGA. The unit contains an integrated time-depth recorder unit (TDR; that also measures temperature), GPS receiver, suction cup attachment, remote release, and a 900 MHz spread spectrum two-way radio transceiver to command the unit. The video camera recorded continuously, and was turned on either prior to deployment, or remotely, after the camera was attached to the turtle. The video camera remained on the turtle until it either detached on its own, or was released remotely (≤ 4 hours). All camera deployments occurred during daylight hours to ensure that there was sufficient ambient light to quantify the components of foraging and to recover the instrument.

Leatherbacks basking and/or handling prey at the surface were approached by a 10 m commercial fishing vessel equipped with a 3 m bowsprit. Tags were hand-placed on the carapace just behind the head (Fig. 2.1a) from a rigid platform suspended from the bowsprit, approximately 0.5 m above the water's surface. When possible, turtles were captured after instrument recovery using a breakaway dip-net (for details see James et al. 2005a). Curved carapace length (CCL; ± 1 cm) and width (CCW; ± 1 cm), sex (judged by tail length), and, when feasible, body mass (± 0.5 kg), was recorded. Turtles were equipped with metal flipper tags and a microchip implant (right pectoral muscle) so that recaptured individuals could be identified. The maximum width of the dorsal surface of

Figure 2.1. Serrano-V camera and example still images. Camera with suction-cup attachment to the shell of a leatherback turtle (*Dermochelys coriacea*; a) and still images extracted from a video file recorded on 3 September 2010 showing a turtle approaching a lion's mane jellyfish (*Cyanea capillata*) that is surrounded by pilot fish (*Naucrates ductor*; b, c) and subsequently consuming this jellyfish (d).



the head (which was normally within the camera's field of view, e.g., Fig. 2.1b) was only measured for two of the turtles deployed with video cameras in 2010. We used these values, in addition to those of 21 other separately captured adult turtles in 2010, to represent the mean head width for all video-sampled turtles (mean = 23 cm, range 20.3–25.3, $n = 23$) in order to estimate the size of captured prey (see Video analysis and Energetic intake sections).

2.3.4. Video analysis

Behaviours were scored using the event-recording software JWatcher (Blumstein and Daniel 2007). The following behaviours were recorded: (1) time at surface (interval between dives); (2) time below surface (dive duration/search time); (3) prey detection (change in head direction); (4) capture/first contact with jellyfish; (5) bites/head movements associated with consuming jellyfish; (6) pursuit – the interval between prey detection and capture; (7) handling time – the interval from the time of capture until the last bite (in view) or contact with a subsequent jellyfish; and (8) capture success. Dives were defined as a time of submersion greater than 30 s. Number of jellyfish attacked and encounter rate per unit time was calculated for each dive. Prey size was estimated by comparing the jellyfish contracted bell diameter relative to the width of the turtle's head. To do this, we froze the video immediately prior to prey capture (e.g., Fig. 2.1c). This relative measure of jellyfish size was then converted to an absolute estimate using an average head width of 23 cm (see Instruments and deployments section). To standardize our estimates, when possible, we measured jellyfish in the contraction stage of movement with the bell draped down, since the demarcation of the bell edge was more defined in the contracted state and was less likely to extend beyond the field of view just prior to capture (e.g. Fig. 2.1d). Additionally, when an estimate of jellyfish size could be made from the video, the bell was most often in a contracted state near the head. Thus, the bell diameters we measured represent a minimum size (i.e., contracted state) in comparison to bell diameters observed during expansion in the video or measured when removed from the water and placed on a flat board (the most frequent method used for measuring jellyfish). We used the contracted-bell measurements to investigate the relative influence of prey size on handling time. Nevertheless, we noted many instances in the video when

the diameter of jellyfish with expanded bells, just prior to capture, exceeded the width of the turtle's head and the entire field of view (e.g., Fig. 2.1d), indicating that turtles were consuming jellyfish >23 cm and of sizes more consistent with previous measurements made for this species (e.g., Doyle et al. 2007b).

2.3.5. Spatial movement

Surface positions of turtles from the Serrano-V's integrated GPS unit were used to determine the spatial extent of turtle movements during foraging. GPS locations were used to calculate the distance travelled from the deployment location. Total distance travelled was not calculated as GPS fixes were not reliably obtained for each surfacing between dives for all turtles; instead, a single displacement value for each turtle was calculated as the maximum distance from the deployment position.

2.3.6. Statistical analyses

Generalised linear mixed models were used to analyze the effect of prey size and prey species on handling time, as well as the effect of dive duration on encounter rate. Separate models were also fitted to explore whether the displacement distance during the period of video sampling was related to the number of prey encounters, i.e., whether the distance between the capture and camera release locations was inversely related to prey encounter rate. The intercept of these models was permitted to vary randomly across animals. A first order autoregressive correlation structure (corAR1) was used to account for serial correlation among repeated measurements. Analyses were performed using the glmmPQL function of the MASS package (Pinheiro and Bates 2000) in R 2.8.1 (R Development Core Team 2008). Residual plots and partial residual plots were examined to assess model fit and the normality of residuals was assessed with a two-tailed Kolmogorov-Smirnov test. All data are expressed as mean \pm standard deviation.

2.3.7. Energy intake

To estimate energy intake during foraging, we assumed that turtles were foraging on lion's mane jellyfish during daylight hours only (at this time of year: ~13.5 hrs), that turtles encountered jellyfish at the mean encounter rate per minute of each turtle, and that the average jellyfish consumed had energy contents comparable to those sampled by Doyle et al. (Doyle et al. 2007b). The assumption of daylight-only feeding is supported by concurrent research using stomach temperature telemetry of leatherbacks in the same study area and during the same time of year which indicates that foraging occurs primarily, if not exclusively, during the daylight hours (J. Casey, unpublished data). This assumption of daylight-only feeding is further supported by archival tags data that demonstrate diving behaviour is largely limited to the photic zone (upper 80-100m), with pronounced diurnal changes in dive depth (K. Hamelin, unpublished data).

Since energy density values for lion's mane jellyfish were not available in our study, we used the average size and energy values determined for lion's mane jellyfish by Doyle et al. (Doyle et al. 2007b) for energy intake calculations: mean bell diameter 30.3 ± 6.6 cm (range 15–47 cm, $n = 27$), wet mass 1263.1 ± 662.3 g, and gross energy density 0.2 ± 0.04 kJ g WM⁻¹. Doyle's measurements were taken from freshly stranded jellyfish specimens (either on the beach or in the water close to shore) collected in the North Atlantic (Layton Beach, County Meath, Ireland; 53.67°N, 6.23°W) between July–October 2004. These size and energy values were also similar to those measured previously for lion's mane jellyfish in the northwest Atlantic (Newfoundland, Canada; Brock 2006). Given that these collections were in similar northern temperate waters and during the same season as our study, and that our observations of expanded bell size of jellies consumed overlap with those sampled by Doyle et al. (2007b), we use Doyle's energy content values as an appropriate proxy for the jellyfish being consumed in our study.

2.4. RESULTS

Video from the Serrano-V camera was recovered from 19 turtles (Table 2.1) during 2008 ($n = 8$), 2009 ($n = 4$), and 2010 ($n = 7$). Video duration averaged 1 hour and 53

minutes per turtle (range 0:08–3:38 h). In 2006–2007, when cameras had been deployed on turtles that were first captured, no foraging behaviour was recorded (MC James, pers. comm.). However, placement of the camera on free-swimming turtles without capture in 2008–2010 resulted in no observed behavioural effects and foraging behaviour was recorded for all camera deployments, suggesting that there was minimal effect of the camera on foraging.

2.4.1. Foraging behaviour, prey encounters, and spatial movement

Eighteen of the 19 turtles foraged mainly on lion's mane jellyfish (range = 83–100% for each turtle), although moon jellyfish (*Aurelia aurita* (L., 1758)) were also consumed. One of the 19 turtles was anomalous in that it was observed scavenging, had a low prey encounter rate, and 2 of the 5 jellyfish consumed were moon jellyfish. Commensal pilot fish (*Naucrates doctor* (L., 1758)) were identified from the video for 4/19 deployments for all years and were observed swimming in the vicinity of the turtle's head and/or near lion's mane jellyfish that were approached and consumed by turtles (e.g., Fig. 2.1b,c).

Jellyfish were consumed at depth in all years, but 2010 was notable in that consumption of dead lion's mane jellyfish floating at the surface was also observed (range = 0–12% for 2010 deployments). The dive durations (3.22 ± 1.77 min; range 0.32–6.84 min) and surface intervals (2.44 ± 1.80 min, range 0.004–11.26 min; Table 2.2) we measured were within the range of values for an additional leatherback turtle equipped with a satellite-linked TDR, but no camera, that used the study area during the months of August and September, 2008 (dive duration 4.64 ± 2.20 min; surface interval 3.32 ± 2.90 min; median dive depth 21.5 m, range 5.5–97.0 m; K. Hamelin, unpublished data). Foraging at depth was restricted to the photic zone, and although the camera routinely switched from color to black and white mode with decreasing light levels at greater depths, there was always sufficient ambient light to identify prey encounters. Prey were encountered in $77 \pm 22\%$ (range 29–100%) of dives (Table 2.2). Jellyfish encounter rates varied among dives and among turtles, with encounters per minute of diving averaging 0.60 ± 0.44 and encounters per minute of video sampling averaging 0.37 ± 0.22 (Table 2.2). There was no significant relationship between encounter rate and dive duration ($P = 0.74$;

Table 2.1 Instrument deployment details for 19 leatherback turtles (*Dermochelys coriacea*).

Turtle ID	Date	Deployment time	Sex	Post-deployment capture	Curved carapace length (cm)	Curved carapace width (cm)	Weight (kg)	Head width (cm)	Video duration (h:m:s)
A	12 August 2008	09:24	♀	Y	153.1	114.5	-	-	1:02:50
B	12 August 2008	15:30	♂	N	-	-	-	-	2:15:49
C	13 August 2008	13:02	-	N	-	-	-	-	1:46:59
D	14 August 2008	09:44	-	N	-	-	-	-	0:07:59
E	14 August 2008	11:27	♀	N	-	-	-	-	3:08:58
F	16 August 2008	09:20	-	N	-	-	-	-	0:09:34
G	18 August 2008	14:02	♀	N	-	-	-	-	1:37:44
H	3 September 2008	10:33	♂	Y	150.7	108.3	460.0	-	1:12:39
I	29 August 2009	14:11	♀	Y	143.5	108.8	450.5	-	1:25:28
J	4 September 2009	11:29	-	N	-	-	-	-	0:44:59
K	8 September 2009	12:04	♂	N	-	-	-	-	1:56:48
L	12 September 2009	10:49	♀	Y	157.5	111.3	-	-	0:56:39
M	11 August 2010	11:51	♂	Y	158.2	120.6	-	25.2	2:38:18
N	14 August 2010	11:47	♀	N	-	-	-	-	2:17:18
O	15 August 2010	17:41	♀	N	-	-	-	-	2:15:46
P	16 August 2010	11:45	-	N	-	-	-	-	3:24:16
Q	24 August 2010	12:29	♂	Y	162.2	112.5	-	24.5	3:36:02
R	29 August 2010	10:12	-	N	-	-	-	-	3:38:52
S	3 September 2010	13:25	♂	N	-	-	-	-	1:43:23

Table 2.2. Dive and prey encounter data (mean \pm SD) for 19 leatherback turtles (*Dermochelys coriacea*) estimated from video, energy intake estimated from prey encounter rate, and speed and distance travelled estimated from GPS locations.

Turtle ID	Number of dives	Proportion of dives that prey were encountered	Dive duration (min)	Surface interval (min)	Jellyfish encounters (attacked (pass/unknown))	Jellyfish encounters per dive minute	Jellyfish encounters per minute	Energy intake ^a (kJ/13.5 hr)
A	16	0.81	2.4 \pm 1.3	1.6 \pm 1.2	29 (4)	0.87 \pm 0.55	0.54	110500 \pm 51215
B	32	0.97	2.3 \pm 1.3	1.8 \pm 1.6	98 (113)	1.57 \pm 0.64	0.82	167797 \pm 77771
C	27	0.93	1.9 \pm 1.0	2.0 \pm 1.5	46 (13) ^b	1.30 \pm 0.69	0.56	103879 \pm 45021
D	3	0.67	3.2 \pm 2.9	0.09 \pm 0.01	4 (2) ^b	0.92 \pm 0.06	0.76	140979 \pm 61100
E	26	0.96	3.6 \pm 1.8	3.5 \pm 2.2	58 (6)	0.73 \pm 0.30	0.34	63070 \pm 27334
F	3	0.33	1.7 \pm 1.9	0.71 \pm 0.66	2	0.17 \pm 0.30	0.22	40810 \pm 17687
G	14	0.93	4.0 \pm 1.3	3.3 \pm 1.5	33 (6) ^b	0.64 \pm 0.32	0.40	74199 \pm 32158
H	9	0.67	4.1 \pm 1.6	4.1 \pm 3.0	25 (2) ^b	0.58 \pm 0.47	0.38	70489 \pm 30550
I	9	0.89	5.9 \pm 0.6	3.9 \pm 1.2	18 (2) ^b	0.37 \pm 0.21	0.24	44520 \pm 19295
J	7	0.29	3.1 \pm 1.0	2.1 \pm 1.4	1 (1) ^b	0.05 \pm 0.13	0.05	9275 \pm 4020
K	14	0.93	5.3 \pm 1.4	2.4 \pm 0.5	30 ^b	0.36 \pm 0.13	0.26	48230 \pm 20903
L	11	0.73	3.9 \pm 0.8	1.9 \pm 0.7	15 ^b	0.34 \pm 0.25	0.27	50085 \pm 21706
M	19	1.00	5.6 \pm 1.5	2.7 \pm 0.7	64 (18) ^b	1.02 \pm 1.19	0.52	96459 \pm 41805
N	10	0.41	6.0 \pm 1.6	2.1 \pm 0.1	5 (5) ^b	0.08 \pm 0.12	0.0017	315 \pm 137
O	15	0.93	6.7 \pm 0.7	2.3 \pm 0.3	35 (6) ^b	0.40 \pm 0.25	0.30	55650 \pm 24118
P	26	0.58	5.4 \pm 3.3	2.5 \pm 2.0	35 (25) ^c	0.24 \pm 0.43	0.29	53795 \pm 23314
Q	16	0.75	7.9 \pm 1.9	4.9 \pm 4.1	33 (3)	0.24 \pm 0.18	0.18	33390 \pm 14471
R	27	0.93	4.9 \pm 1.0	3.3 \pm 2.3	48 (4)	0.35 \pm 0.20	0.25	46375 \pm 20099
S	12	0.92	4.9 \pm 0.8	4.0 \pm 1.3	22 (3)	0.37 \pm 0.20	0.24	44520 \pm 19295

^a Estimated energy intake assuming encounter rate extrapolated over 13.5 hrs daylight and using average size and energy values for lion's mane jellyfish (*Cyanea capillata*) measured in Doyle et al. (2007b).

^b Camera facing to the side or up, head not always in view.

^c Dead jellyfish floating at the surface.

full details of the regressions are provided in Table 2.3). A total of 601 jellyfish captures were recorded and capture success was 100% for all turtles. Turtles attacked an average of $83 \pm 16\%$ jellyfish within the field of view. These predation rates are an underestimate because, for some deployments, the field of view of the camera only included a small part of the head, thus it is possible that additional jellyfish may have been consumed by the turtle outside the field of view of the camera.

The straight-line distance turtles traveled from the position of camera deployment to position of camera release ranged from 0.72–9.02 km and turtles generally traveled away from the deployment position (Fig. 2.2). There was an inverse correlation between prey encounter rate and total distance travelled from the deployment location (i.e., prey encounter rates were relatively lower in turtles traveling further from the deployment location, $p < 0.05$).

2.4.2. Prey size, handling time and energy intake

Six-hundred and ninety lion's mane jellyfish (593 captured) and 24 moon jellyfish (8 captured) were observed in the videos. Of the captured lion's mane jellyfish, 350 were measured to examine the relationship between relative prey size and handling time. Contracted bell diameter of lion's mane jellyfish consumed by turtles averaged 11.2 ± 4.4 cm (range 3.1–22.7 cm; Fig. 2.3a) and moon jellyfish contracted diameter was estimated to be 4.6 ± 2.1 cm (range 2.1–9.3 cm). These values underestimate jellyfish contracted size because it was not always possible to measure the contracted jellyfish right before capture (were measured at a greater distance from the camera), and the relative size of the turtle's head in the field of view differed somewhat among turtles due to the variable placement of the camera on the carapace. Pursuit time for lion's mane jellyfish was estimated to be 22.9 ± 13 s (range 3–79 s) in two turtles for which the head was in view to observe a change in head direction that was assumed to correspond with prey detection. All prey attacked were mostly eaten, with no apparent preference for particular anatomy.

Table 2.3. Parameter estimates and significance of model terms. This table shows the linear mixed model parameter estimates and significance of model terms for three models: the effect of jellyfish encounters per dive minute on dive duration, the effect of prey size on handling time, and the effect of prey size and prey species on handling time. The results show that jellyfish encounters per dive minute are not correlated with dive duration, that prey size is positively correlated with handling time, and that the relationship between prey size and handling time does not differ among species. The hypothesis that the residuals of these fits follow a normal distribution is not rejected by two-tailed Kolmogorov-Smirnov tests ($P>0.05$).

Behaviour	Effect	Estimate	Standard error	<i>T</i>	<i>P</i>
Dive duration	Intercept	0.004	0.0003	12.7	<0.0001
	Jellyfish encounters per dive minute	0.0001	0.0003	0.3	0.74
Handling time	Intercept	0.000014	0.0002	0.07	0.95
	Prey size	0.00006	0.000015	4.04	0.0001
Handling time	Intercept	0.00002	0.0002	0.09	0.93
	Prey size	0.00006	0.000015	3.94	0.0001
	Prey species	-0.00003	0.0003	-0.10	0.92

Figure 2.2. Distance between original camera deployment location and each surfacing location of 19 leatherback turtles (*Dermochelys coriacea*) as estimated from GPS locations.

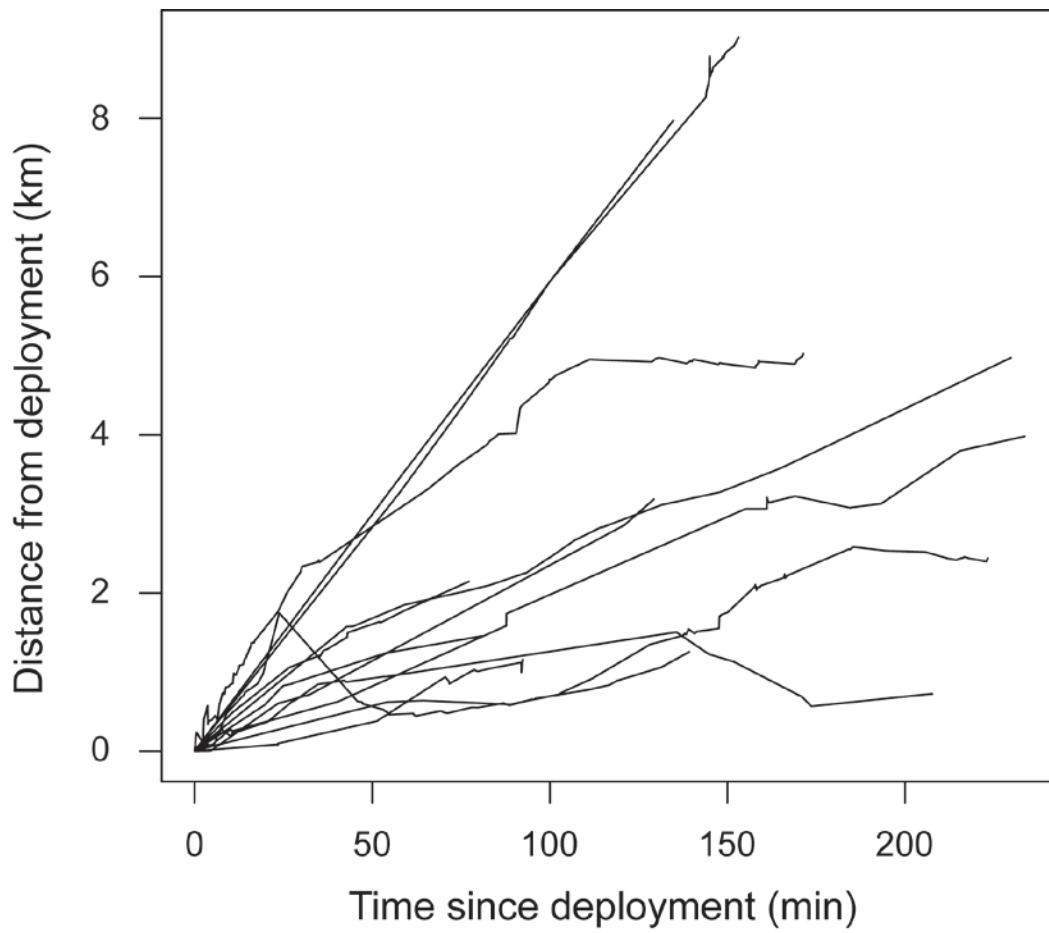
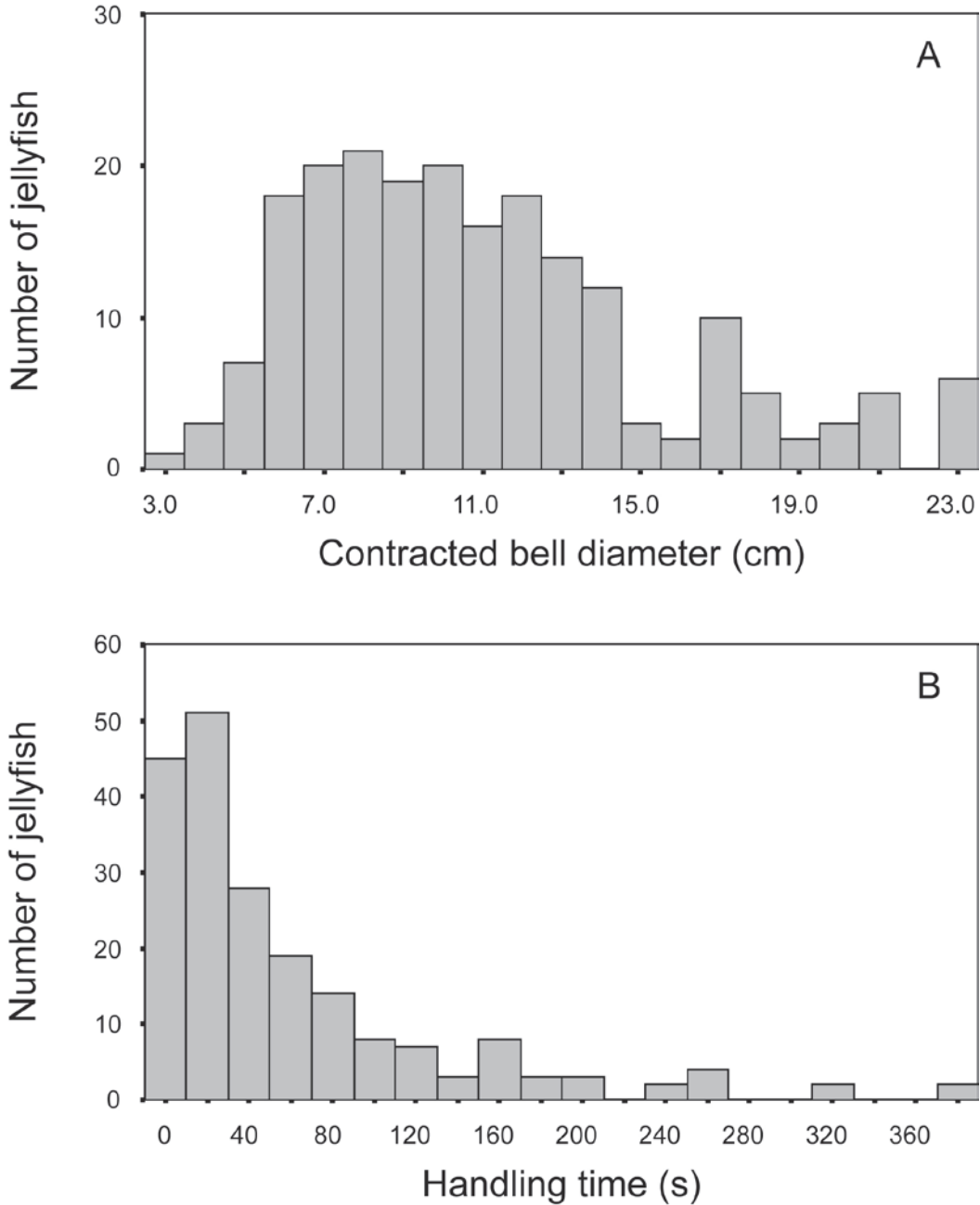


Figure 2.3. Frequency distribution of relative prey size (contracted bell diameter) (a) and handling time (b) of lion's mane jellyfish (*Cyanea capillata*). Results represent the size distribution of measured lion's mane jellyfish (*Cyanea capillata*; $n = 350$) captured by 19 leatherback turtles (*Dermochelys coriacea*).



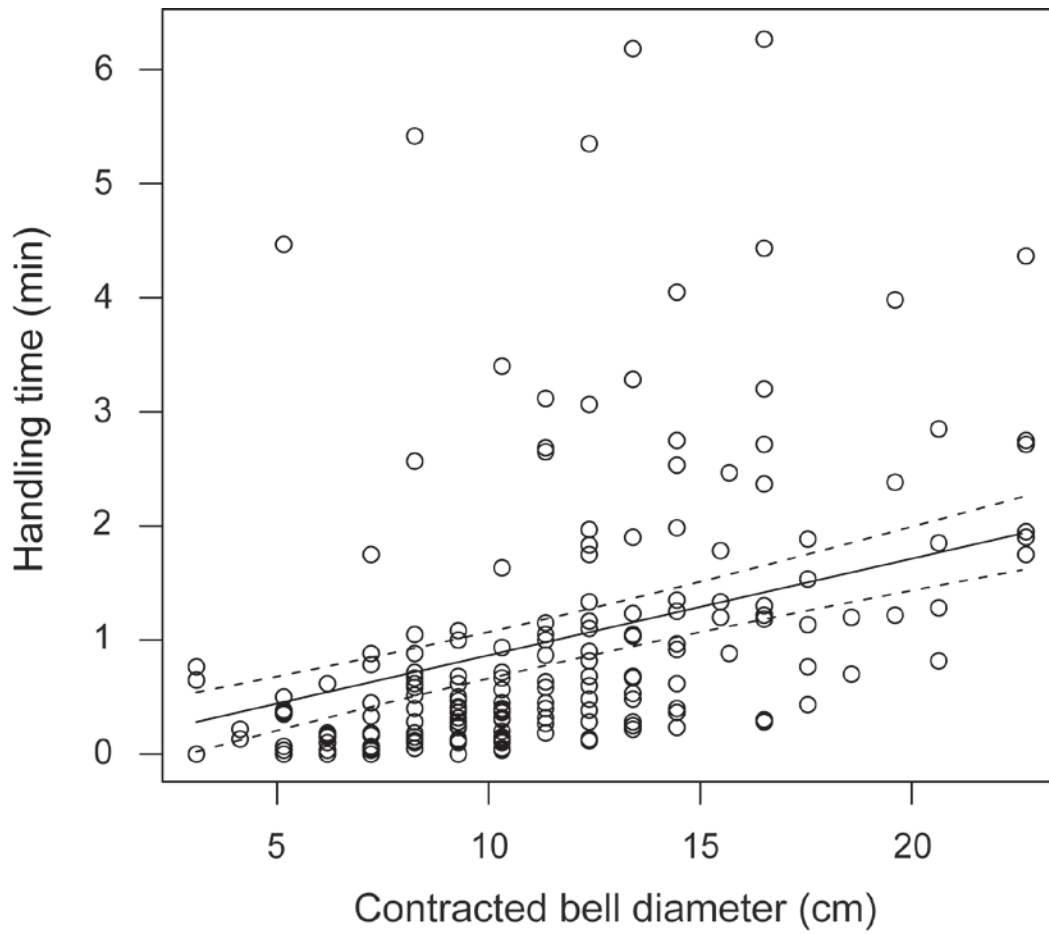
Handling time for lion's mane jellyfish was estimated to average 59.5 ± 72 s overall, but ranged from 0 to 375 s (Fig. 2.3b). This wide range in handling time was explained by differences in prey size. That is, handling time increased significantly with increasing contracted bell diameters of the jellyfish consumed ($P = 0.0001$; Fig. 2.4 and Table 2.3), but there was no difference in the relationship between handling time and prey size between the two prey species ($P = 0.92$; Table 2.3). Following capture of prey at depth, turtles often continued processing jellyfish at the surface, which resulted in a relatively greater handling time for a similar prey size than may have been consumed during a dive. During a dive, handling time of jellyfish was often not complete before the subsequent jellyfish was encountered and attacked. Handling time of the last jellyfish encountered during a dive often had a relatively greater handling time than prey encountered earlier in the dive.

Individual estimates of energy intake averaged $66,018 \pm 42,034$ kJ (range 315–167,797 kJ) per day, assuming a 13.5 hr period of daylight foraging (Table 2.2). These values represent a consumption of 330 ± 210.1 kg (range 2–840 kg) wet mass per day or approximately 261 lion's mane jellyfish (range 1–664) per day.

2.5. DISCUSSION

The temperate waters off eastern Canada support one of the largest seasonal foraging populations of sub-adult and adult leatherback turtles in the Atlantic (James et al. 2006a). The 12,000–18,000 km round-trip migrations of leatherbacks from tropical and subtropical breeding areas to high latitude foraging areas in the western Atlantic is thought to have evolved to permit turtles to capitalize on seasonally-abundant prey in coastal temperate waters. James et al. (2005c) estimated an average ~33% increase in mass of turtles before their initiation of southward migration. Although surface foraging by leatherback turtles has been opportunistically documented in this high latitude foraging area (James and Herman 2001), until now, prey encounter rates, prey size, and handling times at depth had not been quantified nor had daily energy intake been estimated.

Figure 2.4. Effect of relative prey size (contracted bell diameter) on handling time of lion's mane jellyfish (*Cyanea capillata*). Solid line represents mean predicted values with dashed lines indicating \pm SE. Circles represent observed values.



The range of prey encounter rates reported here presumably reflect patchily distributed jellyfish at fine spatial scales (100s of metres) (Hamner and Schneider 1986), even though jellyfish were present in about 75% of dives. The high encounter rates of jellyfish per dive lend support to the identification of this area as a foraging “hotspot” for leatherbacks (e.g., James et al. 2005c; Jonsen et al. 2007). The importance of this foraging area is further supported by our estimate that turtles in this area consume an average of 66,018 kJ and up to 167,797 kJ per day. We were able to measure mass for only two of the turtles equipped with video cameras (mean = 455 kg; Table 2.1). However, mean curved carapace length of six of the turtles was 154 cm, which also roughly corresponds to a body mass of 455 kg (James et al. 2005c; James et al. 2007). Thus, if we assume 455 kg was the average mass of individuals in our study, turtles consumed an average of 73% and up to 184% of their body mass per day in wet mass of jellyfish, equating to an average energy intake of 145 kJ•kg⁻¹ or up to 369 kJ•kg⁻¹ per day. The allometric relationship for the field metabolic rate (FMR, kJ•d⁻¹) of an ectothermic reptile (Nagy et al. 1999) suggests the predicted FMR for a 455 kg reptile would be 46.2 kJ•kg⁻¹. Although it has been proposed that leatherback turtles demonstrate some metabolic endothermy (perhaps regionally), using doubly-labeled water, Bradshaw et al. (2007) estimated the daily diving metabolic rate (DMR) of leatherbacks nesting in the tropics to be 20.7 kJ•kg⁻¹ or less than half that predicted for an ectothermic reptile of similar size (and an order of magnitude lower than a similarly-sized endotherm). These estimates were not dissimilar to earlier measurements of leatherback FMR made by Wallace et al. (2005), supporting the conclusion that leatherbacks appear to be ectothermic and rely on large body size, insulating fat layers, and thermal inertia to regulate body temperatures above ambient (Bradshaw et al. 2007). The turtles in our study consumed an average of 3 (and up to 8) times their daily metabolic requirements as would be estimated by allometry, or 7 (up to 17) times their DMR as measured in nesting leatherbacks.

Although jellyfish are relatively energy-poor (Doyle et al. 2007b), our results demonstrate that leatherback predation on high densities of readily-captured lion's mane jellyfish results in high energy intake at least at this time of year, which is consistent with

the estimated mass gain of leatherback turtles in Canadian waters. Jellyfish graze on copepods, larvaceans, cladocerans, and meroplankton (Båmstedt et al. 1994; Purcell 2003), and leatherbacks in turn graze on patches of these scyphomedusae which tend to ingest the relatively larger size component of available zooplankton prey (Båmstedt et al. 1994; Sullivan et al. 1997). Although jellyfish are patchily distributed in time and space, oceanographic features and processes produce predictable foraging opportunities for leatherbacks such that the benefits of reliance on a diet of jellyfish apparently outweigh the energetic costs of migrating to these northern waters. Leatherbacks were not likely prey-limited in our study, as productivity of jellyfish in temperate coastal areas and particularly here in the strongest outflow of the Gulf of St Lawrence can yield excellent foraging opportunities. Also there seems to be little competition for jellyfish apart from niche overlap with ocean sunfish (*Mola mola* (L., 1758)), a species which is also present in the study area during the same times of year.

Our data further suggest that leatherback turtles are efficient predators since no time was wasted on unsuccessful attacks, a foraging strategy similar to that of grazers. Also jellyfish appeared to be completely consumed. Predation rate on high density prey is likely to be limited by handling time or the animal becoming satiated (Jeschke et al. 2002). We found some evidence for this prediction, as turtles while they were already handling other prey in ~80% of those instances when jellyfish in the field of view of the camera were not targeted. The longer handling times of prey when turtles returned to the surface further suggests that turtles may require further handling for some jellyfish. Given the relatively simple body composition of jellyfish, it is unlikely that digestion time is limiting. Conversely, given the anatomy of lion's mane jellyfish, and particularly those with very large bell diameters and long tentacles, turtles likely face prey handling challenges. Therefore, it is understandable that even with the assistance of the leatherback turtle's specialized esophagus (with papillae pointing towards the stomach), consuming such prey may limit intake. We were unable to distinguish between handling and digesting prey, therefore, it is unclear how digestion may influence the foraging behaviour of turtles.

Our estimates of leatherback turtle foraging behaviour are based on relatively short-term video records compared to a leatherback's typical 3–5 month high-latitude foraging period in the Northwest Atlantic and, therefore, may not be representative of the entire period. Additional information on daily predation rates, sizes of prey consumed, and variability in energy contents of jellyfish in these northwest Atlantic waters during the summer and fall will be useful to refine these estimates. Nevertheless, our results offer evidence that the feeding tactics of leatherbacks in this high latitude coastal foraging area off Atlantic Canada are energetically profitable and are consistent with estimates of mass gain prior to southward migration and preparation for the breeding season. Longer deployments will be needed to confirm our estimates over time periods that have broader ecological implications, and to place the fine- to meso-scale foraging movements of leatherback turtles within the context of the large-scale migratory movements that have been previously described for this population. Further studies of the foraging decisions that turtles make would also benefit from the collection of concurrent conductivity-time-depth recordings, location and three-dimensional movement data, as well as better information on the prey field.

By simultaneously collecting video and high-resolution dive and ocean temperature data, the purpose-built camera we used to study leatherback foraging behaviour during relatively short daytime periods may help confirm inferences of foraging from satellite tracking data that has been collected over much broader spatial and temporal scales. Therefore, this technology offers promise as a tool for determining critical areas of foraging habitat in support of conserving this endangered species.

2.6. ACKNOWLEDGMENTS

We would like to thank D. Inglis, D. Penney and K. Sokolenko for engineering expertise; W. Blanchard for statistical advice; T. Doyle for assistance with jellyfish size and energy estimations; and P. Dutton, R. A. Myers, S. Sherrill-Mix, and C. Upite for support of this project. This manuscript was improved by the helpful reviews of G. Hays, K. Van Houtan, and one anonymous reviewer. We gratefully acknowledge the Canadian

Sea Turtle Network, B. Fricker, H. Fricker, J. Fricker, K. Fricker, K. Martin, P. MacDonald, and M. Nicholson for assistance with fieldwork.

2.7. REFERENCES

- Bailey, H., Shillinger, G., Palacios, D., Bograd, S., Spotila, J., Paladino, F., and Block, B. 2008. Identifying and comparing phases of movement by leatherback turtles using state-space models. *Journal of Experimental Marine Biology and Ecology* **356**(1-2): 128-135. doi:10.1016/j.jembe.2007.12.020.
- Båmstedt, U., Martinussen, M.B., and Matsakis, S. 1994. Trophodynamics of the two scyphozoan jellyfishes, *Aurelia aurita* and *Cyanea capillata*, in western Norway. *ICES Journal of Marine Science* **54**(1): 369-382.
- Benoit-Bird, K.J., and Au, W.W.L. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behavioral Ecology and Sociobiology* **53**(6): 364-373. doi:10.1007/s00265-003-0585-4.
- Benson, S.R., Dutton, P.H., Hitipeuw, C., Samber, B., Bakarbesy, J., and Parker, D. 2007. Post-nesting migrations of leatherback turtles (*Dermochelys coriacea*) from Jamursba-Medi, Bird's Head Peninsula, Indonesia. *Chelonian Conservation and Biology* **6**(1): 150-154.
- Blumstein, D.T., and Daniel, J.C. 2007. *Quantifying Behavior the JWatcher Way*. Sinauer Associates, Inc.
- Bowen, W.D., Tully, D., Boness, D.J., Bulheier, B.M., and Marshall, G.J. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. *Marine Ecology Progress Series* **244**: 235-245.
- Bradshaw, C.J.A., McMahon, C.R., and Hays, G.C. 2007. Behavioral inference of diving metabolic rate in free-ranging leatherback turtles. *Physiological and Biochemical Zoology* **80**(2): 209-219. doi:10.1086/511142.
- Brock, H.M.E. 2006. Leatherback turtles (*Dermochelys coriacea*) in Newfoundland and Labrador: Distribution, diet, threats and the use of education in recovery efforts. *In* School of Graduate Studies, Faculty of Science. Memorial University of Newfoundland, St. John's, N.L. p. 109.
- Brodeur, R.D., Sugisaki, H., and Hunt, G.L. 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Marine Ecology Progress Series* **233**: 89-103.

- Calambokidis, J., Schorr, G.S., Steiger, G.H., Francis, J., Bakhtiari, M., Marshal, G., Oleson, E.M., Gendron, D., and Robertson, K. 2007. Insights into the underwater diving, feeding, and calling behavior of blue whales from a suction-cup-attached video-imaging tag (Critttercam). *Marine Technology Society Journal* **41**(4): 19-29.
- Casey, J., Garner, J., Garner, S., and Williard, A.S. 2010. Diel foraging behavior of gravid leatherback sea turtles in deep waters of the Caribbean Sea. *Journal of Experimental Biology* **213**(23): 3961-3971. doi:10.1242/jeb.048611.
- Charnov, E.L. 1976b. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**(2): 129-136.
- COSEWIC 2001. COSEWIC assessment and update status report on the leatherback turtle *Dermochelys coriacea* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, Ont. p. vii + 25 pp.
- Davenport, J. 1998. Sustaining endothermy on a diet of cold jelly: Energetics of the leatherback turtle *Dermochelys coriacea*. *British Herpetological Society Bulletin* **62**: 4-5.
- Doyle, T.K., Houghton, J.D.R., Buckley, S.M., Hays, G.C., and Davenport, J. 2007a. The broad-scale distribution of five jellyfish species across a temperate coastal environment. *Hydrobiologia* **579**: 29-39. doi:10.1007/s10750-006-0362-2.
- Doyle, T.K., Houghton, J.D.R., McDevitt, R., Davenport, J., and Hays, G.C. 2007b. The energy density of jellyfish: estimates from bomb-calorimetry and proximate-composition. *Journal of Experimental Marine Biology and Ecology* **343**(2): 239-252. doi:10.1016/j.jembe.2006.12.010.
- Fossette, S., Gaspar, P., Handrich, Y., Le Maho, Y., and Georges, J.Y. 2008. Dive and beak movement patterns in leatherback turtles *Dermochelys coriacea* during interesting intervals in French Guiana. *Journal of Animal Ecology* **77**(2): 236-246. doi:10.1111/j.1365-2656.2008.01344.x.
- Fossette, S., Hobson, V.J., Girard, C., Calmettes, B., Gaspar, P., Georges, J.Y., and Hays, G.C. 2010. Spatio-temporal foraging patterns of a giant zooplanktivore, the leatherback turtle. *Journal of Marine Systems* **81**(3): 225-234. doi:10.1016/j.jmarsys.2009.12.002.
- Graham, T.R., Harvey, J.T., Benson, S.R., Renfree, J.S., and Demer, D.A. 2010. The acoustic identification and enumeration of scyphozoan jellyfish, prey for leatherback sea turtles (*Dermochelys coriacea*), off central California. *ICES Journal of Marine Science* **67**(8): 1739-1748. doi:10.1093/icesjms/fsq112.
- Hamner, W.M., and Schneider, D. 1986. Regularly spaced rows of medusae in the Bering Sea: role of Langmuir circulation. *Limnology and Oceanography* **31**(1): 171-177.

- Hays, G.C., Houghton, J.D.R., Isaacs, C., King, R.S., Lloyd, C., and Lovell, P. 2004. First records of oceanic dive profiles for leatherback turtles, *Dermochelys coriacea*, indicate behavioural plasticity associated with long-distance migration. *Animal Behaviour* **67**: 733-743.
- Hays, G.C., Marshall, G.J., and Seminoff, J.A. 2007. Flipper beat frequency and amplitude changes in diving green turtles, *Chelonia mydas*. *Marine Biology* **150**(5): 1003-1009. doi:10.1007/s00227-006-0412-3.
- Heithaus, M.R., Marshall, G.J., Buhleier, B.M., and Dill, L.M. 2001. Employing Crittercam to study habitat use and behavior of large sharks. *Marine Ecology Progress Series* **209**: 307-310. doi:10.3354/Meps209307.
- Houghton, J.D.R., Doyle, T.K., Wilson, M.W., Davenport, J., and Hays, G.C. 2006. Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. *Ecology* **87**(8): 1967-1972.
- James, M.C., Davenport, J., and Hays, G.C. 2006a. Expanded thermal niche for a diving vertebrate: A leatherback turtle diving into near-freezing water. *Journal of Experimental Marine Biology and Ecology* **335**(2): 221-226. doi:10.1016/j.jembe.2006.03.013.
- James, M.C., Eckert, S.A., and Myers, R.A. 2005a. Migratory and reproductive movements of male leatherback turtles (*Dermochelys coriacea*). *Marine Biology* **147**(4): 845-853. doi:10.1007/s00227-005-1581-1.
- James, M.C., and Herman, T.B. 2001. Feeding of *Dermochelys coriacea* on medusae in the northwest Atlantic. *Chelonian Conservation Biology* **4**: 202-205.
- James, M.C., Myers, R.A., and Ottensmeyer, C.A. 2005b. Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. *Proceedings of the Royal Society of London Series B: Biological Sciences* **272**(1572): 1547-1555. doi:10.1098/rspb.2005.3110.
- James, M.C., Ottensmeyer, C.A., and Myers, R.A. 2005c. Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecology Letters* **8**(2): 195-201. doi:10.1111/j.1461-0248.2004.00710.x.
- James, M.C., Sherrill-Mix, S.A., Martin, K., and Myers, R.A. 2006b. Canadian waters provide critical foraging habitat for leatherback sea turtles. *Biological Conservation* **133**(3): 347-357. doi:10.1016/j.biocon.2006.06.012.
- James, M.C., Sherrill-Mix, S.A., and Myers, R.A. 2007. Population characteristics and seasonal migrations of leatherback sea turtles at high latitudes. *Marine Ecology Progress Series* **337**: 245-254.

- Jeschke, J.M., Kopp, M., and Tollrian, R. 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs* **72**(1): 95-112.
- Jonsen, I.D., Flemming, J.M., and Myers, R.A. 2005. Robust state-space modeling of animal movement data. *Ecology* **86**(11): 2874-2880.
- Jonsen, I.D., Myers, R.A., and James, M.C. 2007. Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Marine Ecology Progress Series* **337**: 255-264.
- Lea, M.A., and Wilson, B. 2006. Techniques for real-time, active tracking of sea lions. *In* *Sea Lions of the World. Edited by A.W. Trites and S.K. Atkinson and D.P. DeMaster and L.W. Fritz and T.S. Gelatt and L.D. Rea and K.M. Wynne. Alaska Sea Grant Coll Program, Fairbanks. pp. 235-253.*
- Lutcavage, M., and Lutz, P.L. 1986. Metabolic state and food energy requirements of the leatherback sea turtle, *Dermochelys coriacea*. *Copeia*(3): 796-798.
- McMahon, C.R., and Hays, G.C. 2006. Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Global Change Biology* **12**(7): 1330-1338. doi:10.1111/j.1365-2486.2006.01174.x.
- Myers, A.E., and Hays, G.C. 2006. Do leatherback turtles *Dermochelys coriacea* forage during the breeding season? A combination of data-logging devices provide new insights. *Marine Ecology Progress Series* **322**: 259-267.
- Nagy, K.A., Girard, I.A., and Brown, T.K. 1999. Energetics of free-ranging mammals, reptiles, and birds. *Annual Review of Nutrition* **19**: 247-277. doi:10.1146/annurev.nutr.19.1.247.
- Pinheiro, J., and Bates, D. 2000. *Mixed-Effects Models in S and S-PLUS*. Springer-Verlag, New York.
- Purcell, J.E. 2003. Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*, in Prince William Sound, Alaska. *Marine Ecology Progress Series* **246**: 137-152.
- Purcell, J.E., Uye, S., and Lo, W.T. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series* **350**: 153-174. doi:10.3354/meps07093.
- R Development Core Team. 2008. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Reina, R.D., Abernathy, K.J., Marshall, G.J., and Spotila, J.R. 2005. Respiratory frequency, dive behaviour and social interactions of leatherback turtles, *Dermochelys coriacea* during the inter-nesting interval. *Journal of Experimental Marine Biology and Ecology* **316**(1): 1-16. doi:10.1016/j.jembe.2004.10.002.
- Sarti Martinez, A.L. 2000. *Dermochelys coriacea*. IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4 [online]. Available from www.iucnredlist.org [accessed 20 January 2011].
- Shillinger, G.L., Palacios, D.M., Bailey, H., Bograd, S.J., Swithenbank, A.M., Gaspar, P., Wallace, B.P., Spotila, J.R., Paladino, F.V., Piedra, R., Eckert, S.A., and Block, B.A. 2008. Persistent leatherback turtle migrations present opportunities for conservation. *Plos Biology* **6**(7): e171. doi:10.1371/journal.pbio.0060171.
- Stephens, D.W., and Krebs, J.R. 1986. *Foraging Theory*. Princeton University Press, Princeton, NJ.
- Sullivan, B.K., Suchman, C.L., and Costello, J.H. 1997. Mechanics of prey selection by ephyrae of the scyphomedusa *Aurelia aurita*. *Marine Biology* **130**(2): 213-222.
- Van Houtan, K.S., and Halley, J.M. 2011. Long-term climate forcing in loggerhead sea turtle nesting. *PloS ONE* **6**(4): e19043. doi:10.1371/journal.pone.0019043.
- Wallace, B.P., Williams, C.L., Paladino, F.V., Morreale, S.J., Lindstrom, R.T., and Spotila, J.R. 2005. Bioenergetics and diving activity of internesting leatherback turtles *Dermochelys coriacea* at Parque Nacional Marino las Baulas, Costa Rica. *Journal of Experimental Biology* **208**(20): 3873-3884. doi:10.1242/jeb.01860.
- Witt, M.J., Broderick, A.C., Johns, D.J., Martin, C., Penrose, R., Hoogmoed, M.S., and Godley, B.J. 2007. Prey landscapes help identify potential foraging habitats for leatherback turtles in the NE Atlantic. *Marine Ecology Progress Series* **337**: 231-243. doi:10.3354/Meps337231.
- Witteveen, B.H., Foy, R.J., Wynne, K.M., and Tremblay, Y. 2008. Investigation of foraging habits and prey selection by humpback whales (*Megaptera novaeangliae*) using acoustic tags and concurrent fish surveys. *Marine Mammal Science* **24**(3): 516-534. doi:10.1111/j.1748-7692.2008.00193.x.
- Zollner, P.A., and Lima, S.L. 1999. Search strategies for landscape-level interpatch movements. *Ecology* **80**(3): 1019-1030. doi:10.1890/0012-9658(1999)080[1019:ssfli]2.0.co;2.

CHAPTER 3.

TESTING PREDICTIONS OF OPTIMAL DIVING THEORY USING ANIMAL-BORNE VIDEO FROM HARBOUR SEALS (*PHOCA VITULINA CONCOLOR*)

3.1. ABSTRACT

Optimal diving theory predicts that animals make decisions that maximize their foraging profitability subject to the constraint of oxygen stores. We examined the temporal pattern of prey encounters within a dive from concurrently collected dive data and animal-borne video from a free-ranging pinniped to test predictions of optimal diving theory. CRITTERCAMs were deployed on 32 adult male harbour seals (*Phoca vitulina concolor* De Kay, 1842) at Sable Island, Nova Scotia, Canada, for 3 days each. Deployments resulted in approximately 3 h of video per seal and a total of 2275 capture attempts for 1474 prey encounter events recorded. We found support for seven of the nine selected predictions of optimal diving theory. As predicted, prey encounters increased with bottom duration; dive duration increased with dive depth; and travel duration, bottom duration, and percent bottom duration decreased over a wide range of travel durations. Descent duration did increase with dive depth, and seals terminated dives earlier when no prey were encountered and when prey were encountered later in a dive. Contrary to prediction, bottom duration did not increase and then decrease for short travel durations and dives were not terminated earlier when travel durations were short and prey encounter rate was low.

3.2. INTRODUCTION

Animals are expected to balance the benefits and costs of foraging decisions to maximize their probability of survival and reproductive success. Foraging theory aims to predict how foragers should optimize energy intake over time (predictions 6–9, Table 3.1; Emlen 1966; MacArthur and Pianka 1966; Charnov 1976b), and optimal diving theory (ODT) is nested within foraging theory with the additional constraints that diving imposes on air-breathing predators that forage aquatically at depth. One of the main physiological constraints imposed on diving animals is a rise in blood lactate concentrations once all of the usable oxygen stores have been exhausted during a dive, which is termed an animal's aerobic dive limit (Kooyman 1985). Animals diving beyond their aerobic dive limit pay a penalty of requiring increased time at the surface to clear the accumulated lactic acid. This increased surface duration reduces the time available to forage. Theoretical models of optimal diving predict the optimal allocation of time between foraging at depth and obtaining oxygen at the surface, with the assumption that divers maximize their time spent underwater with dive durations equal to or less than the aerobic dive limit and that prey capture does not result in termination of a dive (Kramer 1988; Houston and Carbone 1992; Carbone and Houston 1994, 1996).

Optimal diving models predict that resource gain should increase linearly with time spent at depth and assume that swimming speed and therefore the rate of oxygen consumption is constant during diving. Therefore energy gain is proportional to the time spent at the bottom of a dive (prediction 1, Table 3.1; Kramer 1988), and depth and /or travel duration (ascent duration plus descent duration) increase with increasing dive duration (prediction 2, Table 3.1; Kramer 1988; Houston and Carbone 1992; Mori et al. 2002). Foraging time is predicted to first increase and then decrease as travel duration increases, and to decrease over a wider range of travel durations (prediction 3, Table 3.1; Houston and Carbone 1992). As travel duration increases, the proportion of time available for foraging decreases (prediction 4, Table 3.1; Houston and Carbone 1992). Depending on the costs of acceleration, swimming speed may also increase with depth (Houston 1986), but when energy intake and efficiency is considered, swimming speed may decrease with depth (prediction 5, Table 3.1; Thompson et al. 1993). In addition to

Table 3.1. Tested predictions of optimal diving theory from harbour seals (*Phoca vitulina concolor*), including the response variable and covariates used for statistical analysis (for each prediction or model).

Prediction	Response variable	Covariate(s)	References
1. Resource gain (no. of prey encountered) increases linearly with search time spent at depth	Prey encountered	Bottom duration	Kramer 1988
2. Dive duration increases with dive depth and/or travel duration	Dive duration	Dive depth and travel duration	Kramer 1988; Houston and Carbone 1992; Mori et al. 2002
3. For relatively short travel durations, foraging time increases and then decreases with travel duration; over a wider range of travel durations, foraging time decreases with travel duration	Bottom duration	Travel duration	Houston and Carbone 1992
4. Proportion of time spent in the foraging area decreases with travel duration	Percent bottom duration (bottom duration/dive duration)	Travel duration	Houston and Carbone 1992
5. Swim speed should remain constant or decrease with dive depth, but should not increase with dive depth; therefore, descent duration should not stay the same or should increase with depth	Descent duration	Dive depth	Thompson et al. 1993
6. Dives are terminated earlier when prey are not encountered before some threshold time	Bottom duration	Prey presence or absence (controlled for descent duration)	Thompson and Fedak 2001

Table 3.1. *continued*

Prediction	Response variable	Covariate(s)	References
7. Dives are terminated earlier for all travel durations regardless of dive depth if no prey are encountered	Bottom duration	Prey presence or absence (controlled for travel duration and depth)	Thompson and Fedak 2001
8. Dives are terminated earlier when prey are not encountered in the early part of the dive	Bottom duration after first prey encounter	Time to first prey encounter (controlled for descent duration)	Thompson and Fedak 2001
9. Dives are terminated earlier when travel duration is short and prey density is low, but not when dives get deeper, no matter the prey density	Bottom duration	Prey encounter rate x percent travel duration + prey encounter rate x depth (controlled for time to first prey encounter)	Thompson and Fedak 2001

terminating dives on the basis of oxygen stores, some models also predict that dives are terminated in relation to prey encounters and success rates.

Optimal diving models require us to choose the currency that is maximized during foraging, such as the proportion of time spent foraging, gross energy gain, and net rate of energetic gain and/or energetic efficiency (Houston and Carbone 1992; Thompson and Fedak 2001). More complicated optimal diving models allow divers to make decisions related to encountered prey and prey-patch quality (e.g., Thompson and Fedak 2001). Models that consider prey include predictions such as seals will terminate dives earlier when prey are not encountered (predictions 6, 7, and 8, Table 3.1; Thompson and Fedak 2001), and that the benefit of terminating a dive when prey density is low varies with depth or travel duration (prediction 9, Table 3.1; Thompson and Fedak 2001).

Prey-patch quality (e.g., prey species and density) is difficult to measure in situ; however, we assume animals adjust their behaviour in response to patch quality. Diving behaviour (e.g., length of bouts) and animal movements (e.g., distance travelled and path tortuosity) have been shown to vary with prey type and foraging success and have been used to infer patch quality (e.g., Mori and Boyd 2004; Austin et al. 2006; Elliott et al. 2008). Patch quality has also been inferred indirectly from daily foraging success using calculations of changes in passive drift rates of seals related to relative lipid content in combination with movement data (Thums et al. 2013). More direct information on the timing of prey encounters can be collected with the use of stomach temperature sensors, jaw sensors that measure the angle of the mouth opening (intra-mandibular angle sensors (IMASEN) and Hall sensors), and accelerometers attached on the head and lower jaw to detect head, neck, and jaw movements (Kuhn and Costa 2006; Liebsch et al. 2007; Suzuki et al. 2009; Viviant et al. 2010). Stomach temperature sensors are unable to distinguish between multiple prey ingestions that are within quick succession of one another and therefore can often only provide data at the resolution of individual meals. Although jaw sensors and head- and jaw-mounted accelerometers show potential for identifying movements associated with individual prey ingestion, further validation is required to distinguish between successful and unsuccessful capture attempts, as well as to distinguish between foraging and non-foraging related movements. Foraging data

collected using these methods are informative; however, data on the timing of individual prey encounters at the scale of individual dives are necessary to test predictions of ODT.

Tests of ODT that include direct observations of individual prey encounter events have mostly been limited to captive experiments (Carbone and Houston 1994; Cornick and Horning 2003; Gallon et al. 2007; Sparling et al. 2007) or to free-ranging animals that are easily observed (Lea et al. 1996). For studies where animals are observed only from the surface (Lea et al. 1996; Walton et al. 1998), tests of ODT have been limited to testing predictions of the relationships between dive duration and surface duration. The development of bio-logging devices such as time–depth recorders (TDRs) and the use of underwater video cameras has permitted further testing of ODT for free-ranging animals (Boyd et al. 1995; Mori et al. 2002; Heath et al. 2007); however, inferred foraging behaviours from bio-logging devices often are not validated and a researcher must be present to record video footage in a particular location. More recently, the use of animal-borne cameras has opened up the possibility to validate behaviours inferred from TDRs and to examine foraging tactics with respect to encountered prey species (Bowen et al. 2002).

The development of underwater animal-borne video cameras (Marshall 1998; Marshall 2007) provides the opportunity to directly collect information on the components of foraging (e.g., encounter rate, capture success, and handling time) concurrently with measures of the diving predator's behaviour (e.g., time, depth, temperature, speed, orientation, and location). Such data have been used to identify foraging habitat, prey species, and feeding success (e.g., Parrish et al. 2000; Hooker et al. 2002; Parrish et al. 2002; Parrish et al. 2005; Heaslip et al. 2012); prey-specific foraging tactics and prey profitability (Bowen et al. 2002); locomotor behaviour and energetic costs of foraging (Williams et al. 2000; Williams et al. 2004); diving physiology (Hooker et al. 2005); and three-dimensional foraging behaviour (Davis et al. 1999; Davis et al. 2001; Davis et al. 2003; Fuiman et al. 2007). When combined with data from TDRs, video-recorded behaviours of predator and prey (e.g., Bowen et al. 2002) can be used to test predictions of optimal diving models (e.g., Cornick and Horning 2003; Heath et al. 2007; Sparling et al. 2007). We used animal-borne cameras to study the foraging

behaviour of adult male harbour seals (*Phoca vitulina concolor* De Kay, 1842) foraging off Sable Island, Nova Scotia, Canada.

Harbour seals are generalist predators that feed on a variety of both benthic and pelagic prey in Atlantic Canadian waters, including sand lance (*Ammodytes dubius* Reinhardt, 1837), Atlantic herring (*Clupea harengus* L., 1758), Atlantic cod (*Gadus morhua* L., 1758), pollock (*Pollachius virens* (L., 1758)), and northern shortfin squid (*Illex illecebrosus* (Lesueur, 1821)) (Bowen and Harrison 1996b). During the breeding season, males are central-place foragers reliably returning to and hauling out on Sable Island after short foraging trips to sea (Walker and Bowen 1993a; Coltman et al. 1997). This behaviour provided an opportunity to fit individual seals with data-logging instruments and to reliably recover these instruments to download data. The objective of Chapter 3 was to test whether dive and prey encounter data support predictions from foraging models of optimal diving (Table 3.1) by analyzing data on the characteristics of individual dives and the number of prey encounters during those dives.

3.3. MATERIALS AND METHODS

Fieldwork was conducted on Sable Island, Nova Scotia, Canada (43°55'N, 60°0'W), a partially vegetated sandbar that is approximately 1.5 km wide and 42 km long. Adult male harbour seals were captured and recaptured after brief foraging trips during the 1995–1997 May–June breeding seasons. Seals were captured with hand-held nets using standard methods (Bowen et al. 1992), weighed (± 0.5 kg, 200 kg, Spring Scale; Salter Industrial Measurement Ltd., West Bromwich, West Midlands, UK), and sedated with approximately 0.2 mg/kg diazepam (Hoffmann-La Roche, Mississauga, Ontario, Canada) to facilitate attachment of the CRITTERCAM and to measure standard dorsal length (McLaren 1993).

The CRITTERCAM (National Geographic, Washington, D.C., USA; Marshall 1998) weighed approximately 2 kg in air with the epoxy mount and averaged about 1.8% of the body mass of the study animals. The aluminium housing was a cylindrical, 25 cm long waterproof tube with a conical floatation section at one end, an outer diameter of

approximately 10 cm, and cross-sectional area that was approximately 4.5% of that of the seals in our study. In addition to video, the camera unit contained a TDR that sampled depth and temperature every 7 s for the entire deployment and a saltwater switch that turned the camera off when the animal was hauled out of the water. The camera was placed on the midline of the back behind the shoulders of the seal and was attached to the pelage using 5 min epoxy, nylon mesh, and stainless steel hose clamps (Bowen et al. 2002). The time elapsed from capture to release was approximately 30 min.

Cameras were programmed to sample video for 10 min every 45 min starting at 0530 or 0600 and ending between 1400 and 1500 local time. This sampling design took into account the limited length of videotape (3 h) and the behaviour patterns of male harbour seals (i.e., hauling out during the afternoon; Walker and Bowen 1993a). Seals wore the camera for about 3 days and a VHF radio transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA) glued to the fur on the seal's head was used to locate seals when they returned to land. The camera and hose clamps were removed upon recapture by cutting the mesh at the base of the camera, leaving only a small amount of mesh that was shed during the annual moult several weeks later. Seals were again weighed and were then released. Because of an ongoing study of male reproductive behaviour, the head-mounted VHF radio transmitter was not removed at this time.

This research was conducted in accordance with guidelines of the Canadian Council on Animal Care. Study protocols were approved by the University Committee on Laboratory Animals (Dalhousie University's animal ethics committee) and by the Animal Care Committee of Fisheries and Oceans Canada.

3.3.1. Video analysis

As in Bowen et al. (2002), the Observer version 2.0 (Noldus 1991) software package was used to calculate the duration and frequency of diving, and to describe foraging behaviour (e.g., seals pursuing individual fish, schools of fish, or rooting in the bottom substrate). In contrast with Bowen et al. (2002), this study analyzed foraging behaviour at the level of individual dives rather than the 10 min video-sampling units. Only video

samples where seals were thought to be foraging (having detected prey at some point during a video sample) were used in this analysis. Video samples with seals exhibiting social and mating behaviours were presented elsewhere (Boness et al. 2006a). We measured descent and ascent durations (travel duration), time spent at depth (termed bottom duration, a proxy for time spent foraging), time of the first prey encounter (operationally defined as head orientation towards a prey identified within the camera's field of view), number of prey encounters (i.e., individual fish or schools), number of capture attempts, and prey encounter rate (number of prey encounters/bottom duration) for each prey species from the video. Number of capture attempts was greater than the number of encounters because multiple capture attempts could be made on individuals pursued either singly or from schools. Bottom duration was defined by a change in orientation of the seal associated with an inflexion in dive angle. Surface durations were not included in our analysis since few were complete as a result of the short duration of video-sampling units. Maximum dive depth in metres was determined for each dive from concurrently collected TDR data. Prey were identified to the level of species by freezing playback of the video and/or with the use of digital stills extracted from the video.

3.3.2. Statistical analysis

Generalized additive mixed models (GAMMs) and generalized linear mixed models (GLMMs) were used to model the relationships among the variables: prey encounters, prey encounter rate (no. of prey encounters/bottom duration), time to first prey encounter (time from reaching bottom to first prey encounter), bottom duration and percent bottom duration (bottom duration/dive duration), bottom duration after first prey encounter, travel duration (ascent + descent durations), dive duration, and depth. We also examined the factor variables: prey presence or absence, percent travel duration (travel duration/dive duration, which was split into three categories (<20%, 20%–35%, and \geq 35%) following Thompson and Fedak 2001); the interaction terms included prey encounter rate \times depth and prey encounter rate \times percent travel duration. Models using these variables were fitted for each of the ODT predictions (Table 3.1). For predictions 6–9, the variables descent duration, travel duration, depth, and time to first prey encountered were related to the response variables and were included as control variables

(Table 3.1). For models that included prey encounters or prey presence, we included a prey species term to explore whether foraging behaviour varied with prey species. The intercept of these models was permitted to vary randomly across animals, nested within year, and within-seal residual autocorrelation was modelled using a first-order autoregressive correlation structure to account for repeated measurements on the same animal for sequential dives. Analyses were performed using the gamm function of the mgcv package (Wood 2006) in R version 2.14.1 (R Core Team 2011). The gamm function was used to fit all models, but not all models included smooth terms. In the case where models did not include smooth terms, the model fit is equivalent to a generalised linear mixed effects model. We used the Gaussian distribution (identity link) for continuous data (i.e., dive duration, bottom duration, descent duration, and bottom duration after first prey encounter), Poisson distribution (log link) for count data (i.e., prey encounters), and quasibinomial distribution (logit link) for proportion data (i.e., percent bottom duration). The significance of terms included in the models was examined using P values and approximate P values from the mgcv output. Significance levels were set at $\alpha = 0.05$. Model selection was not conducted for the models fitted for each of the ODT predictions (Table 3.1), as we were interested only in the extent to which the data supported specific theoretical predictions concerning the specified variables. Model fits were assessed using adjusted R^2 , residual plots, and partial residual plots. Values are reported as means \pm SE.

3.4. RESULTS

Video footage of foraging behaviour was recovered from 38 separate deployments of the CRITTERCAM on 32 adult male harbour seals over 3 years (Table 3.2). All instruments were recovered. Two seals had deployments in both 1995 and 1997, and these deployments were treated as independent samples. Six seals sampled during the 1996 season had two deployments, and these two deployments per seal were combined and treated as one sample. Video samples with foraging behaviour contained 20 ± 1.9 complete dives and 46 ± 9.6 prey encounters per seal, and prey were encountered in $60\% \pm 4.9\%$ of these dives (Table 3.2). Dive durations from video samples with foraging

behaviour averaged 3.4 ± 0.04 min (range = 0.8–7.2 min, median = 3.3 min) and maximum dive depth averaged 25 ± 2.0 m (range = 2–65 m, median = 23 m). A total of 2275 capture attempts for 1474 prey encounter events was recorded. The prey species encountered varied among seals: 22 seals encountered cryptic sand lance (i.e., hidden in the sandy bottom), 5 seals encountered flounders (American plaice, *Hippoglossoides platessoides* (Fabricius, 1780), or yellowtail flounder, *Limanda ferruginea* (Storer, 1839)), 28 seals encountered unknown cryptic fish species (probably sand lance), 19 seals encountered schooling sand lance, and 6 seals encountered other fish species. Individual seals each encountered from one to five prey species (3.4 ± 0.16 , median = 3). For some prey encounters, fish were too far from the camera, light level was too low resulting in poor image quality, or prey were seen too briefly to allow identification (Bowen et al. 2002). For further description and quantitative analysis of foraging behaviour see Bowen et al. (2002).

3.4.1. Tests of model predictions

As predicted, the number of prey encounters increased linearly with bottom duration; however, relatively little of the observed variation was explained by the data (prediction 1, Table 3.3; Fig. 3.1). As predicted, dive duration was longer when travel duration was longer (prediction 2, Table 3.3; Fig. 3.2a) and when dives were deeper (prediction 2, Table 3.3; Fig. 3.2b). Over a wide range of travel durations, bottom duration decreased as predicted; however, for short travel durations (i.e., <50 s), bottom duration did not first increase and then decrease as predicted by theory (prediction 3, Table 3.3; Fig. 3.3a). Although bottom duration appeared to decrease at longer travel durations, we had few observations beyond 100 s with which to test this prediction. When expressed as a proportion, time spent foraging decreased with increasing travel duration (prediction 4, Table 3.3; Fig. 3.3b). Descent duration increased with increasing dive depth, suggesting that swim speed did not increase with dive depth as predicted (prediction 5, Table 3.3; Fig. 3.4). However, it is possible that swim speed increased but not proportionally with depth and the angle of descent could have also changed to contribute to the observed relationship.

Table 3.2. Number of complete dives, prey encounters recorded from video, and proportion of dives with prey encounters per harbour seals (*Phoca vitulina concolor*).

Year	Seals (<i>n</i>)	Dives per seal		Prey encounters per seal		Proportion of dives per seal with prey encounters	
		Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
1995	7	18.1 ± 3.5	4 – 31	18.3 ± 4.6	4 – 34	0.53 ± 0.069	0.33 – 0.75
1996	10	30.0 ± 3.9	15 – 46	48.8 ± 24.1	2 – 255	0.37 ± 0.084	0.07 – 0.94
1997	15	14.6 ± 1.2	7 – 23	57.2 ± 12.2	16 – 197	0.79 ± 0.045	0.48 – 1.00
All years	32	20.2 ± 1.9	4 – 46	46.1 ± 9.6	2 – 255	0.60 ± 0.049	0.07 – 1.00

Note: Instruments were deployed on 32 seals over the three years of sampling. Two seals had deployments in both 1995 and 1997, and these deployments were treated as independent samples. Six seals sampled during the 1996 season had two deployments each, and these two deployments per seal were treated as one sample.

Table 3.3. Parameter estimates, significance of linear terms, approximate significance of smooth terms, and goodness of fit (adjusted R^2) for the fitted mixed models used to test optimal diving theory predictions for harbour seals (*Phoca vitulina concolor*).

Follows prediction	Response variable	Covariate	Parametric coefficients			Approximate significance of smooth terms			Adjusted R^2	
			Estimate	SE	t	P	Estimated	df		F
1	Somewhat Prey encounters	Intercept	-0.6046	0.3708	-1.631	0.103				0.05
		Bottom duration	0.0065	0.0009	6.982	<0.0001				
2	Yes Dive duration	Intercept	146.2665	6.4881	22.544	<0.0001				0.37
		Travel duration	0.3141	0.0850	3.694	0.0002				
		Dive depth	1.9600	0.2084	9.403	<0.0001				
3	Somewhat Bottom duration	Intercept	151.5870	4.8610	31.180	<0.0001				0.05
		Travel duration			3.638	10.88	<0.0001			
4	Yes Percent bottom duration (bottom duration/dive duration)	Intercept	2.2027	0.0552	39.94	<0.0001				0.72
		Travel duration	-0.0191	0.0006	-30.78	<0.0001				
5	Yes Descent duration	Intercept	28.5520	1.6870	16.920	<0.0001				0.44
		Dive depth			2.928	72.95	<0.0001			
6	Yes Bottom duration	Intercept	150.4717	7.3856	20.374	<0.0001				0.04
		Descent duration	-0.3986	0.1158	-3.443	0.0006				
		Prey present	23.2387	4.5692	5.086	<0.0001				

Table 3.3. continued

Prediction	Follows	Response variable	Covariate	Parametric coefficients				Approximate significance of smooth terms						
				Estimate	SE	t	P	Estimated df	F	P	Adjusted R ²			
7	Yes	Bottom duration	Intercept	142.6396	6.7753	21.053	<0.0001						0.13	
			Travel duration	-0.6676	0.0848	-7.876	<0.0001							
			Depth	1.7628	0.2195	8.033	<0.0001							
			Prey present	12.0741	4.6639	2.589	0.0099							
8	Yes	Bottom duration after first prey encounter	Intercept	148.4491	9.5353	15.568	<0.0001							0.31
			Time to first prey encounter	-0.6197	0.0514	-	<0.0001							
			Descent duration	-0.2742	0.1537	-1.784	0.0754							
9	No	Bottom duration	Intercept	143.7014	8.9461	16.063	<0.0001							0.50
			Time to first prey encounter	0.26355	0.04515	5.837	<0.0001							
			Prey encounter rate	-575.3411	349.2931	-1.647	0.1006							
			Percent travel duration ≥0.2	-49.0775	7.7214	-6.356	<0.0001							
			Percent travel duration ≥0.35	-82.3735	9.1650	-8.988	<0.0001							
			Dive depth	1.5856	0.2641	6.005	<0.0001							
			Prey encounter rate x percent travel duration ≥0.2	5.6572	192.1192	0.029	0.9765							
			Prey encounter rate x percent travel duration ≥0.35	-833.5062	412.3912	-2.021	0.0442							
			Prey encounter rate x depth	24.2846	12.3479	1.967	0.0502							

Figure 3.1. Observations and predicted effect of bottom duration of harbour seals (*Phoca vitulina concolor*) on the number of prey encounters (prediction 1, Tables 3.1 and 3.3). Solid lines represent mean predicted values and broken lines represent \pm SE.

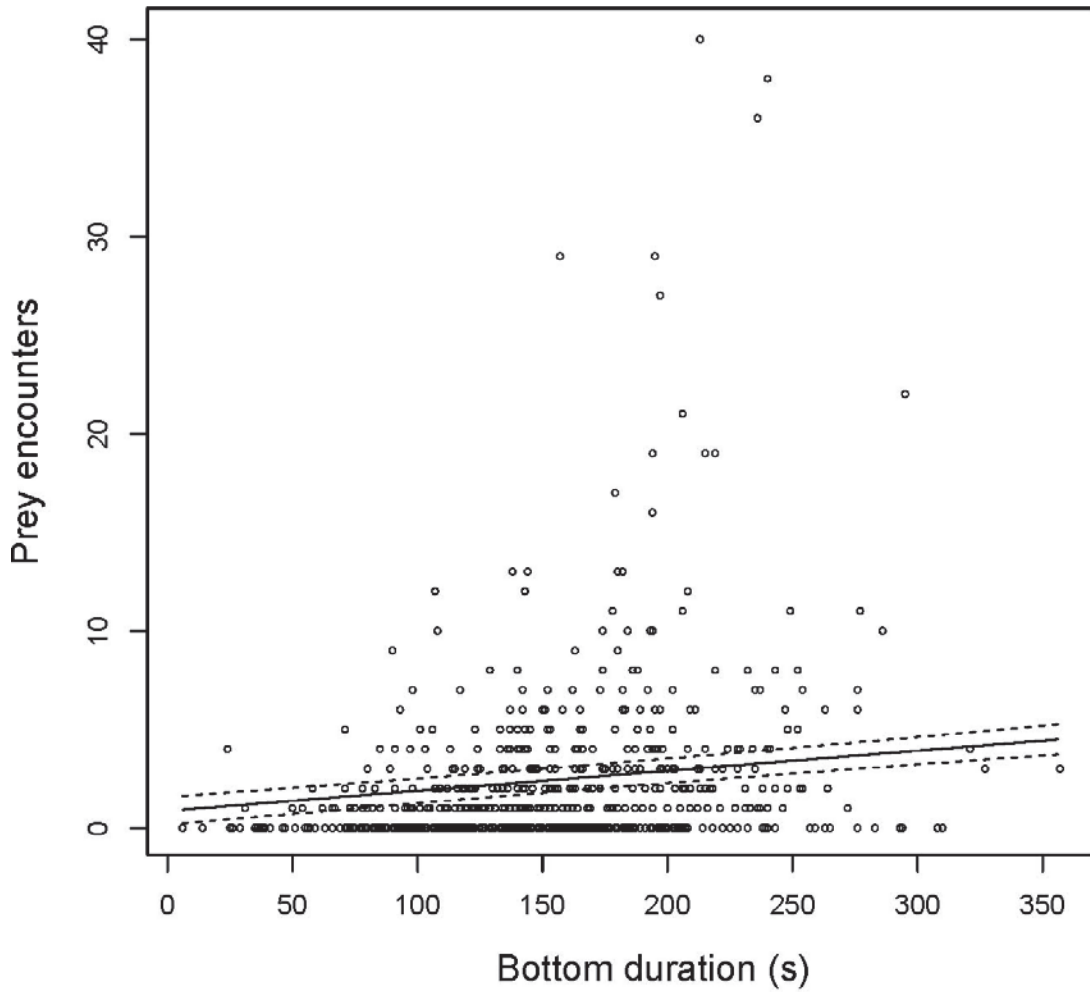


Figure 3.2. Observations and predicted effect of travel duration (a; controlled for dive depth) and dive depth (b; controlled for travel duration) on dive duration (prediction 2, Tables 3.1 and 3.3) of harbour seals (*Phoca vitulina concolor*). Solid lines represent mean predicted values and broken lines represent \pm SE.

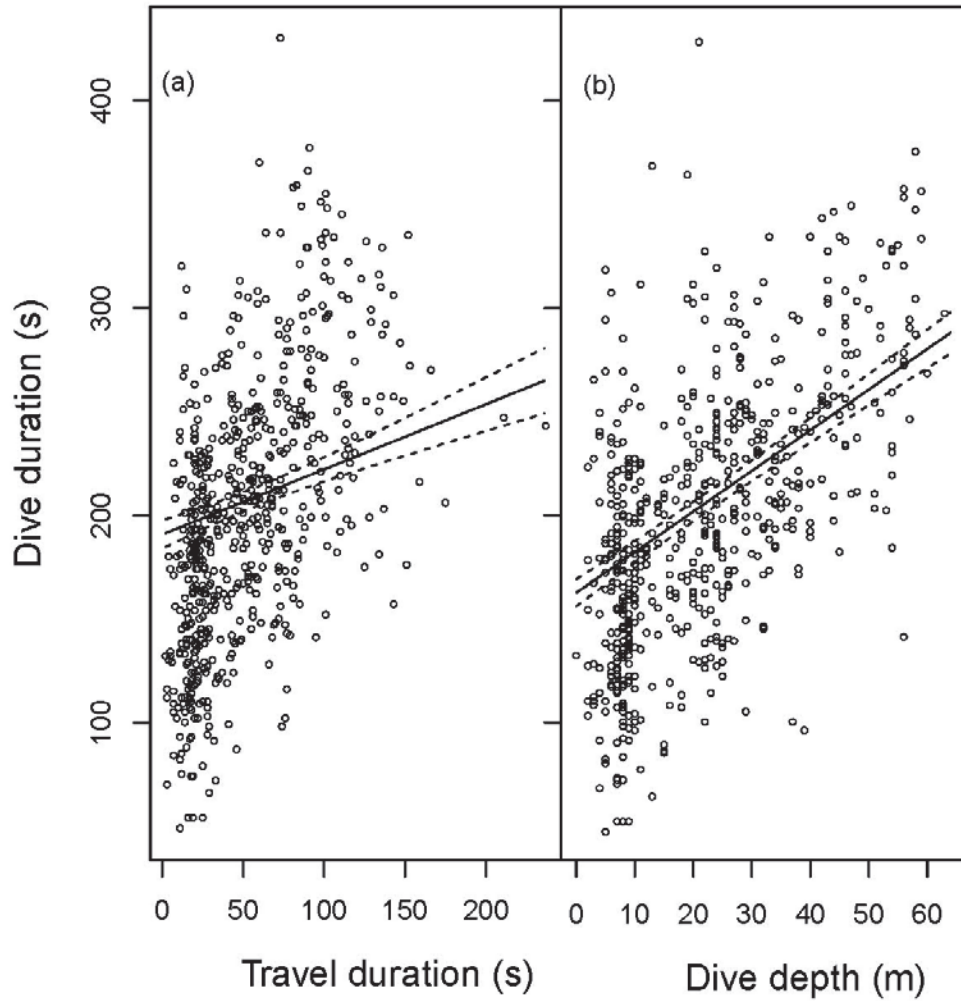


Figure 3.3. Observations and predicted effect of travel duration on (a) bottom duration (prediction 3, Tables 3.1 and 3.3) and (b) on percent bottom duration of a dive, a proxy for the proportion of time spent foraging, (prediction 4, Tables 3.1 and 3.3) of harbour seals (*Phoca vitulina concolor*). Solid lines represent mean predicted values and broken lines represent \pm SE.

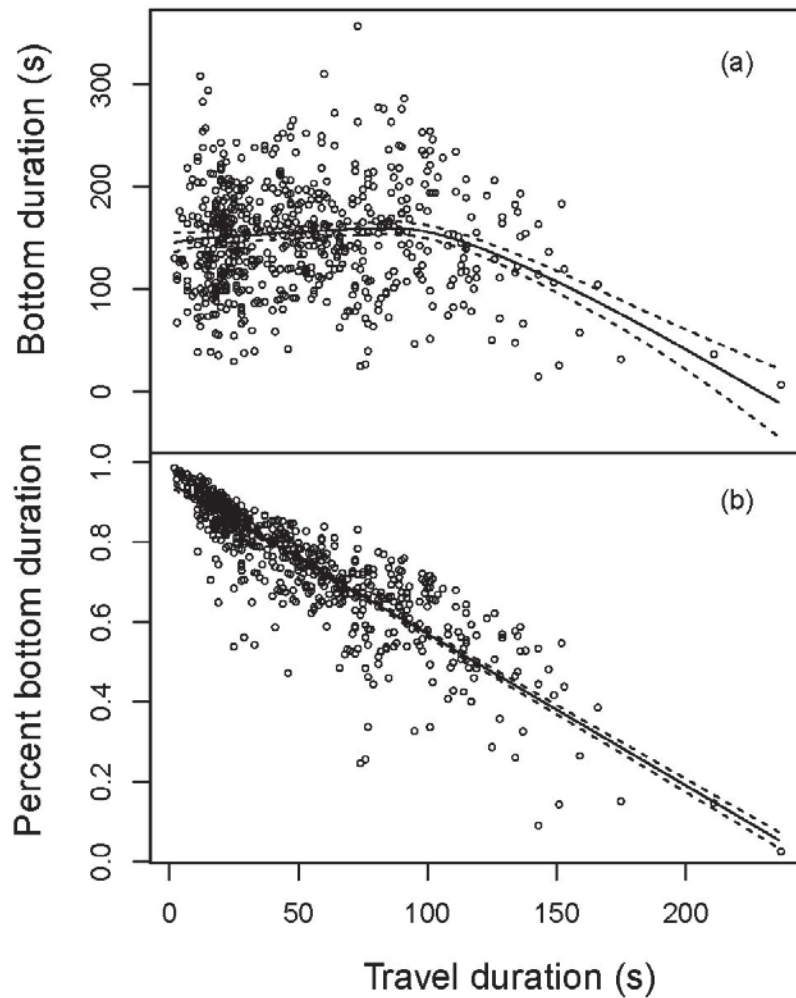
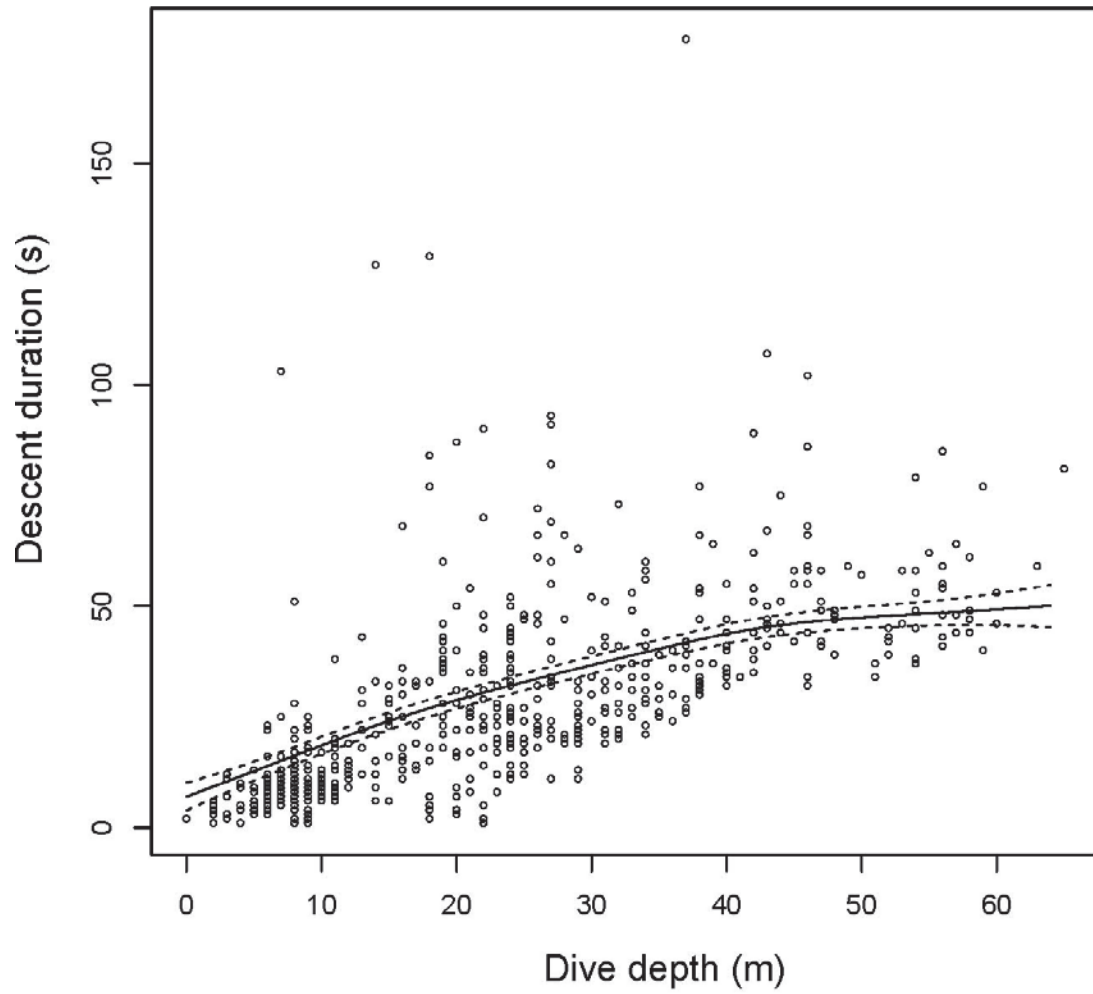


Figure 3.4. Observations and predicted effect of dive depth on descent duration (prediction 5, Tables 3.1 and 3.3) of harbour seals (*Phoca vitulina concolor*). Solid lines represent mean predicted values and broken lines represent \pm SE.



We found evidence for a relationship between prey presence and bottom duration, indicating that seals shortened dives if prey were not encountered (prediction 6, Table 3.3) regardless of travel duration and dive depth (prediction 7, Table 3.3; Fig. 3.5). However, little of the variation in bottom duration was explained by these models. Seals spent less time at the bottom of dives when prey were not encountered in the early part of the dive as predicted (prediction 8, Table 3.3; Fig. 3.6).

Contrary to prediction, we did not find evidence for a relationship between prey encounter rate, our proxy for prey density, and bottom duration. Dives were not terminated earlier when travel duration was short and prey encounter rate was low, and prey encounter rate did not influence the relationship between depth and bottom duration (prediction 9, Table 3.3).

We also examined the relationships between diving behaviour and encounters with sand lance. Cryptic sand lance was observed in 112 dives from 22 seals and schooling sand lance was observed in 111 dives from 19 seals. Seals had fewer separate prey encounters per dive when feeding on schooling sand lance compared with cryptic sand lance (prediction 1, Table 3.4) and spent relatively more time at the bottom of a dive when foraging on cryptic sand lance compared with schooling sand lance (predictions 6 and 7, Table 3.4). There was no significant difference in bottom duration between dives with cryptic and schooling sand lance for predictions 8 and 9.

3.5. DISCUSSION

Although diving behaviour is ultimately constrained by physiological limits, within those limits, air-breathing predators can choose the duration and depth of dives, the speed and angle of travel to and from the bottom of the dive, and foraging tactics while at depth (Thompson et al. 1993). Controlled laboratory experiments provide some support for the predictions of diving models, but few studies have simultaneously measured diving behaviour and direct observations of individual prey encounters to test model predictions in free-ranging marine predators. Video observations of foraging in free-ranging harbour seals, combined with simultaneous measures of the components of diving behaviour,

Figure 3.5. Observations and predicted effect of prey presence (solid circles and black line = present; open circles and grey line = absent) and travel duration (a; controlled for depth) and depth (b; controlled for travel duration) on bottom duration (prediction 7, Tables 3.1 and 3.3) of harbour seals (*Phoca vitulina concolor*). Solid lines represent mean predicted values and broken lines represent \pm SE.

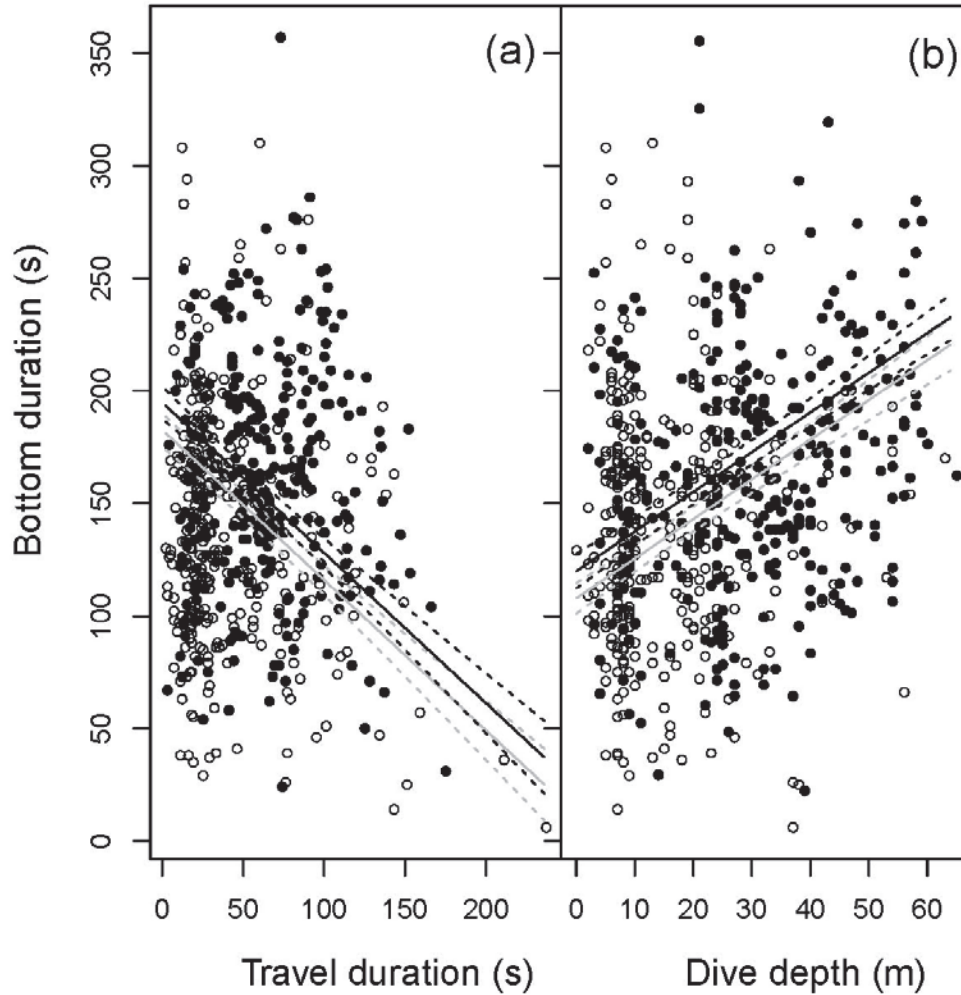


Figure 3.6. Observations and predicted effect of time to first encounter (a; controlled for descent duration) and descent duration (b; controlled for time to first encounter) on bottom duration of harbour seals (*Phoca vitulina concolor*) post first encounter (prediction 8, Tables 3.1 and 3.3). Solid lines represent mean predicted values and broken lines represent \pm SE.

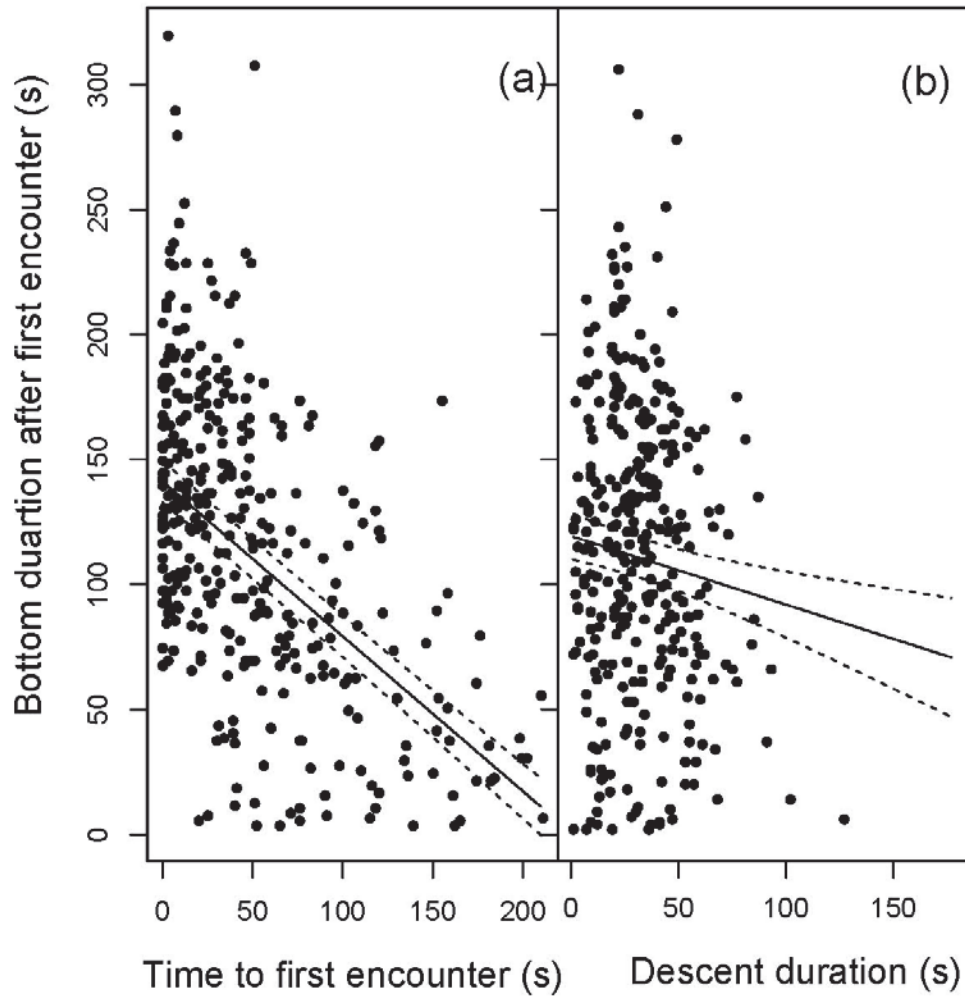


Table 3.4. Parameter estimates, significance of linear terms, and goodness of fit (adjusted R^2) for the fitted mixed models used to explore the influence of prey species on foraging behaviour of harbour seals (*Phoca vitulina concolor*).

Prediction	Response variable	Covariate	Estimate	SE	t	P	Adjusted R^2
1	Prey encounters	Intercept	0.8946	0.2489	3.595	0.0004	0.17
		Bottom duration	0.0044	0.0012	3.678	0.0003	
		Sand lance (schooling)	-0.7380	0.1213	-6.082	<0.0001	
6	Bottom duration	Intercept	151.9133	7.7493	19.604	<0.0001	0.07
		Descent duration	-0.4320	0.1325	-3.261	0.0012	
		Sand lance (cryptic)	26.2111	6.8683	3.816	0.0002	
		Sand lance (schooling)	20.4513	6.2378	3.279	0.0011	
7	Bottom duration	Intercept	144.1043	6.8863	20.926	<0.0001	0.16
		Travel duration	-0.6661	0.0988	-6.743	<0.0001	
		Depth	1.6570	0.2829	5.858	<0.0001	
		Sand lance (cryptic)	19.5990	7.0570	2.777	0.0057	
		Sand lance (schooling)	6.9633	6.6387	1.049	0.2948	

Note: Covariate prey species is the sand lance (*Ammodytes dubius*).

enabled us to test a number of predictions of both dive-cycle and prey-encounter models of optimal diving. We found qualitative support for most model predictions. However, there was little support for two of the nine predictions that we tested (predictions 3 and 9, Table 3.1). We found that bottom duration did not first increase and then decrease for shorter travel durations (predictions 3 and 9, Table 3.1; Fig. 3.3a) and that bottom duration was not shorter for dives with short travel durations and low prey encounter rates (prediction 9, Table 3.1). Nonetheless, we note that we may not have had entirely appropriate data with which to test these predictions, as we assumed that the rate of prey encounters was a good measure of prey density and this may not be true.

The effects of instrument attachment on the behaviour of pinnipeds has been reported for a number of species (e.g., Kooyman et al. 1986; Walker and Boveng 1995; Boyd et al. 1997), including effects related to the attachment of animal-borne cameras (Bowen et al. 2002; Littnan et al. 2004; Heaslip and Hooker 2008). For this study, Bowen et al. (2002) found that dive durations for male seals carrying cameras (4.0 ± 0.12 min, $n = 37$) were similar to males fitted with smaller TDR and VHF transmitters only (3.8 ± 0.13 , $n = 31$; Coltman et al. 1997), and that the rate of mass loss for the camera animals was significantly less (-0.4 ± 0.16 kg/day, $t_{[34]} = 3.1$, $P = 0.004$) than for males without cameras during the breeding season (-0.9 kg/day; Walker and Bowen 1993b, their Fig. 2). However, comparable trip duration data over short periods of time for seals without cameras were not available to assess whether seals with cameras spent more time at sea. Although the attachment of a relatively large animal-borne instrument (1.8% mean body mass) may have affected the behaviour of seals, we expect that any such effects were minor over the short duration of deployments.

The most common assumption of optimal diving models is that resource acquisition increases linearly with time spent foraging (Kramer 1988). Although we found some support for this assumption (prediction 1, Table 3.3; Fig. 3.1), relatively little of the variation in bottom duration (i.e., time spent foraging) was explained by the number of prey encounters, indicating that other factors also influenced prey encounter rate. Variability in prey encounter rate could be the result of differences in prey behaviour (e.g., schooling vs. individual fish), variation in prey density, or a reduction in patch

quality during a dive or sequence of dives as prey are disturbed and consumed. For dives where seals were foraging on sand lance, we did find that prey encounters varied with prey behaviour, with fewer prey encounters for schooling vs. cryptic sand lance (prediction 1, Table 3.4).

Thompson and Fedak (2001) predicted that seals should adjust their dive duration in response to perceived changes in prey density. Sparling et al. (2007) tested this prediction for grey seals (*Halichoerus grypus* (Fabricius, 1791)) by experimentally varying prey density and distance to surface in a large experimental pool and seals responded by leaving low-quality patches earlier. Similarly, captive Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) also increased dive duration and foraging time with prey encounter rate (Cornick and Horning 2003). We did not find a relationship between prey encounter rate, our assumed proxy for prey density, and bottom duration; we also did not find any suggestion that there was a benefit to terminating dives when prey encounters and travel times were relatively low. However, we had a narrow range of prey encounter rates with which to test these predictions and the number of prey encountered per dive may not be a reasonable proxy for prey density. Unfortunately, the relatively narrow field of view of the video camera precluded the estimation of prey density from the video.

The timing of when prey are encountered occur during a dive may also influence the amount of time spent foraging. We did find that the decision to terminate a dive was influenced by prey presence regardless of travel durations, dive depth, and the time to first prey encounter. The early termination of dives when prey were encountered relatively later in a dive supports a giving-up rule whereby seals terminate dives irrespective of the numbers or rate of encountered prey, for example, when prey are encountered later in a dive (Thompson and Fedak 2001). Additional variation in the relationship between bottom duration and prey encounters could also be introduced by variation in swimming speed among dives associated with pursuing fast or slow moving prey (e.g., Bowen et al. 2002).

Swimming speed was not measured for individual dives, but the positive relationship between descent duration and dive depth suggests that swim speed did not change with

dive depth to depths of about 40 m (prediction 5, Table 3.3; Fig. 3.4). However, for dives >40 m, there was an indication that descent duration levelled off with increasing dive depth, suggesting that seals either increased their swim speed and/or descended at a steeper dive angle. Without information on swim speed and dive angle, we are not able to test this prediction thoroughly. Captive grey seals reduced their swim speed significantly as travel duration increased (Gallon et al. 2007), supporting the prediction that swim speed should decrease for deeper dives or that seals should swim at the minimum cost of transport (Thompson et al. 1993). Contrary to prediction, free-swimming species including Antarctic fur seals (*Arctocephalus gazella* (Peters, 1875)), New Zealand sea lions (*Phocarctos hookeri* (Gray, 1844)), and northern (*Mirounga angustirostris* (Gill, 1866)) and southern (*Mirounga leonina* (L., 1758)) elephant seals have been shown to increase swim speed with dive depth (Boyd et al. 1995; Hindell and Lea 1998; Crocker et al. 2001; Hassrick et al. 2007). It is possible that such increases in speed may not in fact be costly if they are a result of negative buoyancy at greater depths and a change in swim method with longer passive glide phases.

The models of Thompson et al. (1993) also predict that both the net rate of energy gain at low prey density and foraging efficiency will be maximized if seals remain stationary when hunting active prey. Male harbour seals in our study did not behave this way; in fact, they swam continuously while hunting schooling sand lance and flatfish (Bowen et al. 2002). Harbour seals foraging in Froan, Norway, swam continuously at close to the maximum cost of transport as predicted in both the efficiency and the net-rate maximizing models (Thompson et al. 1993).

For short travel durations, Houston and Carbone's (1992) model predicts that divers benefit from making short dives and maintaining low oxygen stores with higher rates of oxygen intake at the surface; as travel durations increase, divers increase oxygen stores to allow for increased foraging time, which enables them to reduce the number of trips between the foraging patch and the surface; and that maximum dive duration is reached as travel durations increase, further forcing the diver to decrease foraging time to compensate for longer travel durations. Not unexpectedly, seals dove longer when travel durations were longer (prediction 2, Table 3.3; Fig. 3.2a) and when dives were deeper

(prediction 2, Table 3.3; Fig. 3.2b). Sparling et al. (2007) also found that the dive durations of grey seals increased with dive distance, as well as with an increase in prey encounter rate. Over a wide range of travel durations, bottom duration decreased as predicted for the few dives that we had with travel durations >100 s; however, for short travel durations, bottom duration did not first increase and then decrease (prediction 3, Table 3.3; Fig. 3.3a). Comparable results have been found for diving Common Eiders (*Somateria mollissima sedentaria* Snyder, 1941) (Heath et al. 2007). We may not have had sufficient data for dives with short travel durations to detect an increase in bottom duration for shallow dives. Estimates of oxygen intake at the surface and oxygen consumption at depth would be needed to rigorously test this prediction. A greater amount of the variation in bottom duration was explained when bottom duration was expressed as a proportion of dive duration (percent bottom duration), and percent bottom duration also decreased with increasing travel duration in agreement with predictions from theory (prediction 4, Table 3.3; Fig. 3.3b).

Our data provided qualitative support for many of the model predictions, but in some cases, relatively little of the observed variation in behaviour was explained by these models (Table 3.3). There are undoubtedly several reasons for this. First, our results were obtained during the breeding season over relatively short sampling periods and therefore may not reflect the range of foraging behaviours used by this species. The short deployment durations restricted the number of consecutive dives for which we have data and may have also reduced variability in the numbers and types of prey encountered. Diving data from complete dive bouts may be needed to provide the contrast in behaviour required to provide stronger tests of some predictions. Sampling over a longer period would permit us to test predictions related to the number of dives per bout (Mori 1998b) and those that are an extension of basic dive models such as allowing for nonlinearity in intake rate and heterogeneity in patch quality, abundance, and profitability (e.g., Thompson and Fedak 2001; Mori et al. 2002; Heithaus and Frid 2003; Houston et al. 2003). Sampling over a longer period would also permit testing of predictions at additional temporal scales (over seasons and foraging trips) so that we could examine how foraging decisions and the currencies being optimized may vary with respect to the

seasonal life-history events of an individual (e.g., breeding and moult). Second, as noted in other studies, current models are too simplistic to predict the behaviour of diving animals (e.g., Halsey and Butler 2006). These deterministic models aim to explain how foragers make decisions that optimize energy intake over time under the constraint of oxygen stores in a stochastic environment and without perfect knowledge. Not included in these models is how animals may make trade-offs between foraging and other behaviours. Other factors that could influence time allocation during foraging dives are competition (Halsey et al. 2006); behaviours related to mating, especially for pinnipeds that mate aquatically such as harbour seals (Boness et al. 2006b); and risk of predation (Wirsing et al. 2008). Including body mass as a covariate in models testing predictions of ODT (Mori 1998a, 2002) might also improve the amount of explained variation, as mass can be a significant predictor of dive behaviour as a result of differences in oxygen stores and metabolic rate (Costa 1993; Boyd and Croxall 1996; Schreer et al. 2001). Modifications in dive behaviour in the presence of predators may also depend on foraging mode and/or prey species (e.g., schooling prey vs. cryptic prey) when the foraging mode affects vigilance (Wirsing et al. 2011). Foraging decisions of male harbour seals may vary with the risk of predation, as sharks are a known predator of harbour seals (Lucas and Stobo 2000; Bowen et al. 2003).

Despite physiological limitations, air-breathing divers are able to vary their foraging behaviour in response to prey cues. Our study is one of the few studies to simultaneously measure diving behaviour and direct observations of individual prey encounters, allowing us to test predictions of optimal diving models for free-ranging pinnipeds. We found that prey encounters increased with bottom time, dive duration increased with travel duration, bottom duration decreased with travel duration, and that seals maximized bottom duration when prey were present and when prey were encountered relatively earlier in a dive, but we did not find any relationship between bottom duration and prey encounter rate. From our modelling results, it was clear that there are other factors which influence how male harbour seals made foraging decisions. An examination of complete dive bouts in addition to prey field data, rather than only the prey encountered, could give us better

insight into the decisions that these animals make to maximize their energy intake and ultimately fitness.

3.6. ACKNOWLEDGEMENTS

We thank C. Beck, D. Boness, J. McMillan, and D. Tully for their assistance with the fieldwork; B. Bulheier, G. Marshall, and the National Geographic Remote Imaging Department for their collaboration with the harbour seal CRITTERCAM project on Sable Island; P. O’Laughlin and A. Legere for their work scoring the video footage; and L. Baker, I. Jonsen, S. Lang, M. Leonard, D. Lidgard, R. Ronconi, and C. Scarfe for helpful comments on various drafts of the manuscript. We are grateful for the helpful comments and criticisms provided by two anonymous reviewers. Funding for this research was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), the National Geographic Society, the Smithsonian Abbott and Nelson Restricted Endowment Funds, the Friends of the National Zoo, and Fisheries and Oceans Canada. S.G.H. was supported by a NSERC Postgraduate Scholarship.

3.7. REFERENCES

- Austin, D., Bowen, W.D., McMillan, J.I., and Iverson, S.J. 2006. Linking movement, diving, and habitat to foraging success in a large marine predator. *Ecology* **87**(12): 3095-3108. doi:10.1890/0012-9658(2006)87[3095:lmdaht]2.0.co;2.
- Boness, D.J., Bowen, D.W., Bulheier, B.M., and Marshall, G.J. 2006a. Mating tactics and mating system of an aquatic-mating pinniped: The harbor seal, *Phoca vitulina*. *Behavioral Ecology and Sociobiology* **61**: 119-130.
- Boness, D.J., Bowen, W.D., Bulheier, B.M., and Marshall, G.J. 2006b. Mating tactics and mating system of an aquatic-mating pinniped: the harbor seal, *Phoca vitulina*. *Behavioral Ecology and Sociobiology* **61**: 119-130.
- Bowen, W.D., Ellis, S.L., Iverson, S.J., and Boness, D.J. 2003. Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. *Journal of Zoology (London)* **261**: 155-163. doi:10.1017/s0952836903004047.

- Bowen, W.D., and Harrison, G.D. 1996b. Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. *Canadian Journal of Zoology* **74**(1): 125-135. doi:10.1139/z96-017.
- Bowen, W.D., Oftedal, O.T., and Boness, D.J. 1992. Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). *Physiological Zoology* **65**: 844-866.
- Bowen, W.D., Tully, D., Boness, D.J., Bulheier, B.M., and Marshall, G.J. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. *Marine Ecology Progress Series* **244**: 235-245.
- Boyd, I.L., and Croxall, J.P. 1996. Dive durations in pinnipeds and seabirds. *Canadian Journal of Zoology* **74**(9): 1696-1705.
- Boyd, I.L., McCafferty, D.J., and Walker, T.R. 1997. Variation in foraging effort by lactating Antarctic fur seals: response to simulated increased foraging costs. *Behavioral Ecology and Sociobiology* **40**(3): 135-144. doi:DOI 10.1007/s002650050326.
- Boyd, I.L., Reid, K., and Bevan, R.M. 1995. Swimming speed and allocation of time during the dive cycle in Antarctic fur seals. *Animal Behaviour* **50**: 769-784.
- Carbone, C., and Houston, A.I. 1994. Patterns in the diving behavior of the pochard, *Aythya ferina*: a test of an optimality model. *Animal Behaviour* **48**(2): 457-465. doi:10.1006/anbe.1994.1259.
- Carbone, C., and Houston, A.I. 1996. The optimal allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. *Animal Behaviour* **51**: 1247-1255. doi:10.1006/anbe.1996.0129.
- Charnov, E.L. 1976b. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**(2): 129-136.
- Coltman, D.W., Bowen, W.D., Boness, D.J., and Iverson, S.J. 1997. Balancing foraging and reproduction in the male harbour seal, an aquatically mating pinniped. *Animal Behaviour* **54**: 663-678. doi:10.1006/anbe.1997.0470.
- Cornick, L.A., and Horning, M. 2003. A test of hypotheses based on optimal foraging considerations for a diving mammal using a novel experimental approach. *Canadian Journal of Zoology* **81**(11): 1799-1807. doi:10.1139/z03-179.
- Costa, D.P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. *Symposium of the Zoological Society of London* **66**: 293-314.

- Crocker, D.E., Gales, N.J., and Costa, D.P. 2001. Swimming speed and foraging strategies of New Zealand sea lions (*Phocarctos hookeri*). *Journal of Zoology* (London) **254**: 267-277. doi:Doi 10.1017/S0952836901000784.
- Davis, R.W., Fuiman, L.A., Williams, T.M., Collier, S.O., Hagey, W.P., Kanatous, S.B., Kohin, S., and Horning, M. 1999. Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* **283**(5404): 993-996.
- Davis, R.W., Fuiman, L.A., Williams, T.M., Horning, M., and Hagey, W. 2003. Classification of Weddell seal dives based on 3-dimensional movements and video-recorded observations. *Marine Ecology Progress Series* **264**: 109-122.
- Davis, R.W., Fuiman, L.A., Williams, T.M., and Le Boeuf, B.J. 2001. Three-dimensional movements and swimming activity of a northern elephant seal. *Comparative Biochemistry and Physiology, Part A: Molecular & Integrative Physiology* **129**(4): 759-770.
- Elliott, K.H., Davoren, G.K., and Gaston, A.J. 2008. Time allocation by a deep-diving bird reflects prey type and energy gain. *Animal Behaviour* **75**: 1301-1310. doi:DOI 10.1016/j.anbehav.2007.09.024.
- Emlen, J.M. 1966. Role of time and energy in food preference. *American Naturalist* **100**(916): 611-617.
- Fuiman, L.A., Madden, K.M., Williams, T.M., and Davis, R.W. 2007. Structure of foraging dives by Weddell seals at an offshore isolated hole in the Antarctic fast-ice environment. *Deep-Sea Research Part II: Topical Studies in Oceanography* **54**(3-4): 270-289.
- Gallon, S.L., Sparling, C.E., Georges, J.Y., Fedak, M.A., Biuw, M., and Thompson, D. 2007. How fast does a seal swim? Variations in swimming behaviour under differing foraging conditions. *Journal of Experimental Biology* **210**(18): 3285-3294. doi:10.1242/jeb.007542.
- Halsey, L.G., Brand, O.J., Woakes, A.J., and Butler, P.J. 2006. Experiments on single diving birds in the laboratory often measure dives of decreased effort. *Ibis* **148**(1): 164-166. doi:10.1111/j.1474-919X.2006.00476.x.
- Halsey, L.G., and Butler, P.J. 2006. Optimal diving behaviour and respiratory gas exchange in birds. *Respiratory Physiology & Neurobiology* **154**(1-2): 268-283. doi:10.1016/j.resp.2006.01.012.
- Hassrick, J.L., Crocker, D.E., Zeno, R.L., Blackwell, S.B., Costa, D.P., and Le Boeuf, B.J. 2007. Swimming speed and foraging strategies of northern elephant seals. *Deep-Sea Research Part II-Topical Studies in Oceanography* **54**(3-4): 369-383. doi:DOI 10.1016/j.dsr2.2006.12.001.

- Heaslip, S.G., and Hooker, S.K. 2008. Effect of animal-borne camera and flash on the diving behaviour of the female Antarctic fur seal (*Arctocephalus gazella*). *Deep-Sea Research Part I: Oceanographic Research Papers* **55**(9): 1179-1192. doi:DOI 10.1016/j.dsr.2008.05.006.
- Heaslip, S.G., Iverson, S.J., Bowen, W.D., and James, M.C. 2012. Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): video evidence from animal-borne cameras. *PloS ONE* **7**(3): e33259. doi:10.1371/journal.pone.0033259.
- Heath, J.P., Gilchrist, H.G., and Ydenberg, R.C. 2007. Can dive cycle models predict patterns of foraging behaviour? Diving by common eiders in an Arctic polynya. *Animal Behaviour* **73**: 877-884. doi:10.1016/j.anbehav.2006.10.015.
- Heithaus, M.R., and Frid, A. 2003. Optimal diving under the risk of predation. *Journal of Theoretical Biology* **223**(1): 79-92. doi:10.1016/s0022-5193(03)00073-0.
- Hindell, M.A., and Lea, M.A. 1998. Heart rate, swimming speed, and estimated oxygen consumption of a free-ranging southern elephant seal. *Physiological Zoology* **71**(1): 74-84.
- Hooker, S.K., Boyd, I.L., Jessopp, M., Cox, O., Blackwell, J., Boveng, P.L., and Bengtson, J.L. 2002. Monitoring the prey-field of marine predators: combining digital imaging with datalogging tags. *Marine Mammal Science* **18**(3): 680-697. doi:10.1111/j.1748-7692.2002.tb01066.x.
- Hooker, S.K., Miller, P.J.O., Johnson, M.P., Cox, O.P., and Boyd, I.L. 2005. Ascent exhalations of Antarctic fur seals: a behavioural adaptation for breath-hold diving? *Proceedings of the Royal Society of London Series B: Biological Sciences* **272**(1561): 355-363. doi:10.1098/rspb.2004.2964.
- Houston, A.I. 1986. The optimal flight velocity for a bird exploiting patches of food. *Journal of Theoretical Biology* **119**(3): 345-362. doi:10.1016/s0022-5193(86)80146-1.
- Houston, A.I., and Carbone, C. 1992. The optimal allocation of time during the diving cycle. *Behavioral Ecology* **3**(3): 255-265. doi:10.1093/beheco/3.3.255.
- Houston, A.I., McNamara, J.M., Heron, J.E., and Barta, Z. 2003. The effect of foraging parameters on the probability that a dive is successful. *Proceedings of the Royal Society of London Series B: Biological Sciences* **270**(1532): 2451-2455. doi:10.1098/rspb.2003.2540.
- Kooyman, G.L. 1985. Physiology without restraint in diving mammals. *Marine Mammal Science* **1**(2): 166-178. doi:10.1111/j.1748-7692.1985.tb00004.x.

- Kooyman, G.L., Davis, R.W., and Croxall, J.P. 1986. Diving behavior of Antarctic fur seals. *In* Fur seals: maternal strategies on land and at sea. *Edited by* R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 115-125.
- Kramer, D.L. 1988. The behavioral ecology of air breathing by aquatic animals. *Canadian Journal of Zoology* **66**(1): 89-94.
- Kuhn, C.E., and Costa, D.P. 2006. Identifying and quantifying prey consumption using stomach temperature change in pinnipeds. *Journal of Experimental Biology* **209**(22): 4524-4532. doi:Doi 10.1242/Jeb.02530.
- Lea, S.E.G., Daley, C., Boddington, P.J.C., and Morison, V. 1996. Diving patterns in shags and cormorants (*Phalacrocorax*): tests of an optimal breathing model. *Ibis* **138**(3): 391-398. doi:10.1111/j.1474-919X.1996.tb08056.x.
- Liebsch, N., Wilson, R.P., Bornemann, H., Adelung, D., and Plotz, J. 2007. Mouthing off about fish capture: jaw movement in pinnipeds reveals the real secrets of ingestion. *Deep-Sea Research Part II: Topical Studies in Oceanography* **54**(3-4): 256-269. doi:DOI 10.1016/j.dsr2.2006.11.014.
- Littnan, C.L., Baker, J.D., Parrish, F.A., and Marshall, G.J. 2004. Effects of video camera attachment on the foraging behavior of immature Hawaiian monk seals. *Marine Mammal Science* **20**(2): 345-352. doi:DOI 10.1111/j.1748-7692.2004.tb01164.x.
- Lucas, Z., and Stobo, W.T. 2000. Shark-inflicted mortality on a population of harbour seals (*Phoca vitulina*) at Sable Island, Nova Scotia. *Journal of Zoology (London)* **252**: 405-414. doi:10.1111/j.1469-7998.2000.tb00636.x.
- MacArthur, R.H., and Pianka, E.R. 1966. On optimal use of a patchy environment. *American Naturalist* **100**(916): 603-609.
- Marshall, G. 2007. An advanced solid-state animal-borne video and environmental data-logging device ("Cittercam") for marine research. *Marine Technology Society Journal* **41**(2): 31-38.
- Marshall, G.J. 1998. Cittercam: an animal-borne imaging and data logging system. *Marine Technology Society Journal* **32**(1): 11-17.
- McLaren, I.A. 1993. Growth in pinnipeds. *Biological Reviews of the Cambridge Philosophical Society* **68**: 1-79.
- Mori, Y. 1998a. Optimal choice of foraging depth in divers. *Journal of Zoology (London)* **245**: 279-283. doi:10.1111/j.1469-7998.1998.tb00102.x.

- Mori, Y. 1998b. The optimal patch use in divers: optimal time budget and the number of dive cycles during bout. *Journal of Theoretical Biology* **190**(2): 187-199. doi:10.1006/jtbi.1997.0550.
- Mori, Y. 2002. Optimal diving behaviour for foraging in relation to body size. *Journal of Evolutionary Biology* **15**(2): 269-276. doi:10.1046/j.1420-9101.2002.00382.x.
- Mori, Y., and Boyd, I.L. 2004. The behavioral basis for nonlinear functional responses and optimal foraging in antarctic fur seals. *Ecology* **85**(2): 398-410. doi:10.1890/03-4005.
- Mori, Y., Takahashi, A., Mehlum, F., and Watanuki, Y. 2002. An application of optimal diving models to diving behaviour of Brunnich's guillemots. *Animal Behaviour* **64**: 739-745. doi:10.1006/anbe.2002.3093.
- Noldus, L.P.J.J. 1991. The Observer: a software system for collection and analysis of observational data. *Behavior Research Methods, Instruments, & Computers* **23**(3): 415-429.
- Parrish, F.A., Abernathy, K., Marshall, G.J., and Buhleier, B.M. 2002. Hawaiian monk seals (*Monachus schauinslandi*) foraging in deep-water coral beds. *Marine Mammal Science* **18**(1): 244-258.
- Parrish, F.A., Craig, M.P., Ragen, T.J., Marshall, G.J., and Buhleier, B.M. 2000. Identifying diurnal foraging habitat of endangered Hawaiian monk seals using a seal-mounted video camera. *Marine Mammal Science* **16**(2): 392-412.
- Parrish, F.A., Marshall, G.J., Littnan, C.L., Heithaus, M., Canja, S., Becker, B., Braun, R., and Antonelis, G.A. 2005. Foraging of juvenile monk seals at French Frigate Shoals, Hawaii. *Marine Mammal Science* **21**(1): 93-107.
- R Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Schreer, J.F., Kovacs, K.M., and O'Hara Hines, R.J. 2001. Comparative diving patterns of pinnipeds and seabirds. *Ecological Monographs* **71**: 137-162.
- Sparling, C.E., Georges, J.Y., Gallon, S.L., Fedak, M., and Thompson, D. 2007. How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: a test of a simple model. *Animal Behaviour* **74**: 207-218. doi:10.1016/i.anbehav.2006.06.022.
- Suzuki, I., Naito, Y., Folkow, L.P., Miyazaki, N., and Blix, A.S. 2009. Validation of a device for accurate timing of feeding events in marine animals. *Polar Biology* **32**(4): 667-671. doi:DOI 10.1007/s00300-009-0596-3.

- Thompson, D., and Fedak, M.A. 2001. How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Animal Behaviour* **61**: 287-296. doi:10.1006/anbe.2000.1539.
- Thompson, D., Hiby, A.R., and Fedak, M.A. 1993. How fast should I swim? Behavioural implications of diving physiology. Symposium of the Zoological Society of London **66**: 349-368.
- Thums, M., Bradshaw, C.J.A., Sumner, M.D., Horsburgh, J.M., and Hindell, M.A. 2013. Depletion of deep marine food patches forces divers to give up early. *Journal of Animal Ecology* **82**(1): 72-83. doi:10.1111/j.1365-2656.2012.02021.x.
- Viviant, M., Trites, A.W., Rosen, D.A.S., Monestiez, P., and Guinet, C. 2010. Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. *Polar Biology* **33**(5): 713-719. doi:DOI 10.1007/s00300-009-0750-y.
- Walker, B.G., and Boveng, P.L. 1995. Effects of time-depth recorders on maternal foraging and attendance behavior of antarctic fur seals (*Arctocephalus gazella*). *Canadian Journal of Zoology* **73**(8): 1538-1544. doi:Doi 10.1139/Z95-182.
- Walker, B.G., and Bowen, W.D. 1993a. Behavioural differences among adult male harbor seals during the breeding season may provide evidence of reproductive strategies. *Canadian Journal of Zoology* **71**(8): 1585-1591. doi:10.1139/z93-224.
- Walker, B.G., and Bowen, W.D. 1993b. Changes in body mass and feeding behaviour in male harbour seals, *Phoca vitulina*, in relation to female reproductive status. *Journal of Zoology (London)* **231**: 423-436.
- Walton, P., Ruxton, G.D., and Monaghan, P. 1998. Avian diving, respiratory physiology and the marginal value theorem. *Animal Behaviour* **56**: 165-174. doi:10.1006/anbe.1998.0759.
- Williams, T.M., Davis, R.W., Fuiman, L.A., Francis, J., Le Boeuf, B.L., Horning, M., Calambokidis, J., and Croll, D.A. 2000. Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* **288**(5463): 133-136. doi:10.1126/science.288.5463.133.
- Williams, T.M., Fuiman, L.A., Horning, M., and Davis, R.W. 2004. The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke. *Journal of Experimental Biology* **207**(6): 973-982.
- Wirsing, A.J., Heithaus, M.R., and Dill, L.M. 2011. Predator-induced modifications to diving behavior vary with foraging mode. *Oikos* **120**(7): 1005-1012. doi:10.1111/j.1600-0706.2010.18844.x.

Wirsing, A.J., Heithaus, M.R., Frid, A., and Dill, L.M. 2008. Seascapes of fear: evaluating sublethal predator effects experienced and generated by marine mammals. *Marine Mammal Science* **24**(1): 1-15. doi:10.1111/j.1748-7692.2007.00167.x.

Wood, S.N. 2006. *Generalized Additive Models: An Introduction with R*. Chapman & Hall/CRC, Boca Raton, FL.

CHAPTER 4.

DISCUSSION

4.1. SUMMARY

Although observations of surface foraging by leatherback turtles has been documented opportunistically (James and Herman 2001), Chapter 2 provides the first estimates of prey encounter rates, prey size, handling times at depth, and daily energy intake of leatherback turtles in the high latitude foraging area of the temperate waters off eastern Canada using video observations of foraging and simultaneous measures of dive behaviour. Estimates of energy intake that are on average 3-7 times their daily metabolic requirement support James et al.'s (2005c) estimate of an average ~33% increase in mass of turtles before their initiation of southward migration. It is clear that although leatherback turtles are a specialist species feeding on relatively low energy gelatinous zooplankton (Davenport 1998; Doyle et al. 2007b), the 12,000–18,000 km round-trip migrations of leatherbacks have evolved to permit turtles to capitalize on seasonally-abundant prey in coastal temperate waters of the western Atlantic. In contrast with specialist predators like leatherback turtles, generalist predators such as harbour seals feed upon a variety of prey species and have been shown to exhibit prey-specific foraging tactics (Bowen et al. 2002). Building upon the work of Bowen et al. (2002), Chapter 3 provides support for predictions of optimal diving models using video observations of foraging in free-ranging harbour seals, combined with simultaneous measures of diving behaviour. The work presented in Chapter 3 is one of few studies to simultaneously measure diving behaviour along with direct observations of individual prey encounters to test model predictions in free-ranging marine predators; most studies have previously been limited to captive experiments. Though there was qualitative support for most model predictions, dives with short travel durations and low prey encounter rates were

not shorter (prediction 9, Table 3.1). However, the rate of prey encounters may not be a good measure of prey density since the field of view of the camera was relatively narrow; therefore, to test these predictions appropriately it is ideal to have concurrent measures of the prey field of the predator.

4.2. FORAGING BEHAVIOUR OF LEATHERBACK TURTLES

Results from animal-borne video support the view that leatherback turtles are specialist predators of relatively low-energy gelatinous zooplankton. The identification of the shelf waters off Cape Breton Island, NS, Canada as a foraging “hotspot” for leatherbacks (e.g., James et al. 2005c; Jonsen et al. 2007) is supported by the high encounter rates of jellyfish recorded in the video and by my estimate that turtles in this area consume an average of 66,018 kJ and up to 167,797 kJ per day. These consumption estimates equate to turtles consuming an average of 3 (and up to 8) times their daily metabolic requirements (estimated by allometry), or 7 (up to 17) times their DMR (as measured in nesting leatherbacks) and were based on an average mass estimate of 455 kg (Table 2.1), since only two of the turtles equipped with video cameras were measured.

Although the prey species of leatherback turtles are relatively energy-poor (Doyle et al. 2007b), leatherback predation on relatively high densities of lion's mane jellyfish appears to result in high energy intake, consistent with the estimated mass gain of leatherback turtles in Canadian waters (James et al. 2005c). Although zooplankton are patchily distributed in time and space, oceanographic features and processes produce predictable foraging opportunities for leatherbacks such that the reliance on a narrow dietary niche of jellyfish is a beneficial feeding strategy despite the energetic costs of migrating to northern waters. The only species known to potentially compete with leatherback turtles in this study area is the ocean sunfish that also feeds on jellyfish during the same time of year.

Leatherback turtles appear to be efficient predators since no time was wasted on unsuccessful attacks, similar to grazing animals, and jellyfish also appeared to be completely consumed. I found some evidence for leatherbacks being limited by handling

time in areas of high prey density, as turtles were already handling other prey in ~80% of the instances when jellyfish in the field of view of the camera were not pursued. Turtles also returned to the surface to consume jellyfish, suggesting that turtles may require long handling times for some prey. Given the anatomy of lion's mane jellyfish, and particularly those with very large bell diameters and long tentacles, prey intake by leatherback turtles are likely limited by handling time even with the assistance of the leatherback turtle's specialized esophagus. Although handling prey at the surface minimizes the time available to forage at depth, turtles seem to make decisions to capture large jellyfish despite the relatively longer handling time suggesting that this is a profitable strategy. Further research using the prey encounter and dive data of leatherback turtles could be used to explore the profitability of remaining at depth to consume a number of relatively smaller jellyfish versus consuming a relatively larger jellyfish that requires increased handling time at the surface as well as to test prediction from theoretical foraging models of optimal diving.

4.3. FORAGING BEHAVIOUR OF MALE HARBOUR SEALS SUPPORTED MOST OF THE TESTED PREDICTIONS OF OPTIMAL DIVING THEORY

I found support for the most common assumption of optimal diving models, that resource acquisition increases linearly with time spent foraging (prediction 1, Table 3.3; Fig. 3.1; Kramer 1988), however, little of the variation in bottom duration (i.e., time spent foraging) was explained by the number of prey encounters, indicating that other factors also influenced prey encounter rate. For dives where seals were foraging on sand lance, I found that prey encounters varied with prey behaviour, with fewer prey encounters for schooling vs. cryptic sand lance (prediction 1, Table 3.4). Contrary to Thompson and Fedak's (2001) prediction that seals should adjust their dive duration in response to perceived changes in prey density there was no relationship between prey encounter rate, an assumed proxy for prey density, and bottom duration. There was also no suggestion that there was a benefit to terminating dives when prey encounters and travel times were relatively low. In contrast, captive studies have shown that grey seals leave low-quality patches earlier (Sparling et al. 2007) and that Steller sea lions also

increased dive duration and foraging time with prey encounter rate (Cornick and Horning 2003). However, prey encountered per dive may not be a reasonable proxy for prey density and there was a narrow range of prey encounter rates with which to test these predictions. A video camera with a relatively wider field of view or employing another method to determine the available prey field would allow for the estimation of prey density in order to test predications which include decisions related to patch quality.

The decision to terminate a dive by harbour seals was influenced by prey presence regardless of travel durations, dive depth, and the time to first prey encounter. Thompson and Fedak (2001) suggest a giving-up rule whereby seals terminate dives irrespective of the numbers or rate of encountered prey, for example, when prey are encountered later in a dive. The harbour seal data supported the idea of this giving-up rule, with seals terminating dives earlier when prey were encountered relatively later in a dive.

Although captive studies have shown that grey seals reduced their swim speed significantly as travel duration increased (Gallon et al. 2007), contrary to predictions of optimal diving models, free-swimming seal and sea lion species have been shown to increase swim speed with dive depth (Boyd et al. 1995; Hindell and Lea 1998; Crocker et al. 2001; Hassrick et al. 2007). Such increases in speed with dive depth may not in fact be costly if they are a result of negative buoyancy at greater depths and/or a change in swim method that includes longer passive glide phases. Even though swimming speed was not measured, the positive relationship between descent duration and dive depth for harbour seals suggests that swim speed did not change with dive depth to depths of about 40 m. For dives >40 m, however, there was an indication that descent duration levelled off with increasing dive depth, suggesting that seals either increased their swim speed and/or descended at a steeper dive angle. Without information on swim speed and dive angle, it is unclear whether swim speed remained constant or decreased with deeper dives (prediction 5, Table 3.3; Fig. 3.4).

Houston and Carbone's (1992) model predicts that for short travel durations, divers benefit from making short dives and maintaining low oxygen stores with higher rates of oxygen intake at the surface; and that as travel durations increase, divers increase oxygen

stores to allow for increased foraging time, enabling them to reduce the number of trips between the foraging patch and the surface. It follows that once maximum dive duration is reached as travel durations increase, the diver is forced to decrease foraging time to compensate for longer travel durations. Captive studies by Sparling et al. (2007) found that the dive durations of grey seals did increase with dive distance, as well as with an increase in prey encounter rate following Houston and Carbone's (1992) predictions. Not unexpectedly, harbour seals also dove longer when travel durations were longer (prediction 2, Table 3.3; Fig. 3.2a) and when dives were deeper (prediction 2, Table 3.3; Fig. 3.2b). Over a wide range of travel durations, bottom duration decreased as predicted for the few dives with travel durations >100 s; however, for short travel durations, bottom duration did not first increase and then decrease (prediction 3, Table 3.3; Fig. 3.3a) for harbour seals. Comparable results have been found for diving Common Eiders (Heath et al. 2007). Without measures of swim speed and surface duration I was unable to explore optimal diving model predictions related to allocation of time over the dive cycle. Estimates of oxygen intake at the surface and oxygen consumption at depth would be needed to rigorously test predictions of optimal diving time allocation models. A greater amount of the variation in bottom duration was explained when bottom duration was expressed as a proportion of dive duration (percent bottom duration), and percent bottom duration also decreased with increasing travel duration in agreement with predictions from theory (prediction 4, Table 3.3; Fig. 3.3b).

4.4. LIMITATIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

Estimates of both leatherback turtle and harbour seal foraging behaviour were based on relatively short-term video records. Deployment durations of animal-borne instruments were limited by data capacity and battery life and for leatherback turtles, deployment lengths were restricted as a result of having to follow the animal in real-time in order to recover the instrument. Memory capacity should be less of a concern for future studies, however the development of camera and battery technologies, including features that allow for reliable timed remote release of the instruments, are necessary to allow for longer deployment durations that are ecologically meaningful in length.

Unfortunately, it is unlikely that there will be developments in technology in the short term that will allow sufficient bandwidth and battery power to transmit video, therefore scientists will continue to be challenged with the requirement to recover instruments in order to receive the recorded data.

Longer deployments of animal-borne cameras are necessary to confirm prey consumption estimates over time periods that are more ecologically relevant. Leatherback turtles typically remain in the Northwest Atlantic for a 3-5 month foraging period and the observations of this study may not be representative of the entire period. Longer deployments are required to place the fine- to meso-scale foraging movements of leatherback turtles within the context of the large-scale migratory movements that have been previously described for this population. Further studies of the foraging decisions that turtles make would also benefit from the concurrent collection of video and movement data, as well as independent information on the prey field of the predator. Similar to leatherback turtles, the foraging behaviour for male harbour seals is known to vary throughout the year (e.g., males must balance foraging behaviour with reproduction during the breeding season; Coltman et al. 1997). As is required to better understand leatherback turtle foraging, longer instrument deployments, information on sizes of prey consumed, energy content of prey, and independent measures of the prey field for these predators are necessary to better understand the decisions that these animals are making in response to their environment.

For some predictions, relatively little of the observed variation in the diving behaviour of harbour seals was explained by the models (Table 3.3). We expect generalist predators such as harbour seals to exhibit a range of behaviours and the relatively short sampling durations of the video are unlikely to have recorded the range of foraging and other behaviours used by this species over such short deployments. The short deployment durations also restricted the number of consecutive dives for which I have data and the variability in the numbers and types of prey encountered would be likely to increase with deployment duration. Testing of predictions at additional temporal scales (over bouts, seasons, and foraging trips) would allow an examination of how foraging decisions and the currencies being optimized may vary with respect to the seasonal life-history events

of an individual (e.g., breeding and moult). Given that deployments on harbour seals were made during the breeding season, harbour seals reduce foraging effort between the pre-mating and mating periods (Boness et al. 2006b), and only dives with foraging behaviour were analyzed, further analysis could include an examination of the dive data to see determine how foraging behaviour may have been interrupted by mating behaviours. Additional considerations on how animals may make trade-offs between foraging and other behaviours such as mating and vigilance are important to understand how predators are prioritizing foraging decisions in order to increase their probability of survival and reproductive success in response to their environment.

Plasticity in foraging behaviour has implications for resilience against climate change and the impact of human activities on prey populations. Generalist predators such as harbour seals would likely be able to respond to temporal and spatial changes in prey availability (e.g., changes in species presence, abundance, distribution, and timing of prey availability) relatively better than specialist predators such as leatherback turtles since they employ a variety of prey-dependent foraging tactics (Bowen et al. 2002). As specialist predators, leatherback turtles have morphological adaptations (e.g., beak and esophageal spines) that allow them to successfully exploit a diet of gelatinous zooplankton that are easily captured. Even though the occurrence of jellyfish varies in space and time, the relative predictability and abundance of this patchy food source warrants the migration of leatherback turtles from tropical to temperate Atlantic Canadian waters in the summer months. However, the reliance on a specialized prey resource such as jellyfish puts this species at risk if there are changes in the timing, distribution, and abundance of prey as a result of climate change since they may not be able to adapt their foraging tactics to alternate prey and may be limited by their morphology. As generalist predators, harbour seals feed on a wide variety of fish species that require different foraging tactics. The variety of prey-specific foraging tactics exhibited by harbour seals would make them relatively more resilient to changes in prey characteristics as a result of climate change since they would likely be able to exploit alternate prey species if necessary. Although plasticity in the foraging behaviour of predators may make them more resilient to changes in prey availability, resiliency in foraging strategies is likely at

the cost of optimality. A lack of information on the prey available to predators, for example how prey patch size and density varies in space and time, limits our further understanding of how heterogeneous resources are used by predators and how they may be impacted by factors such as climate change.

4.5. USING ANIMAL-BORNE CAMERAS TO ANSWER QUESTIONS IN MARINE ECOLOGY

To explain the movements and decisions that animals make in response to their environment, we must collect information about the environment. Animal-borne cameras allow us to collect information about an animal's environment along with concurrently collected prey and movement data and these data could help us to better understand how foraging habitat, tactics, and diet of a species vary spatially and temporally. The spatial and temporal aspects of foraging behaviour are particularly necessary for the designation of critical habitat of endangered species. Movement data collected using satellite location tags has been used to infer foraging habitat quality and propose areas of critical habitat for leatherback turtles, and the estimates of energy intake data collected using animal-borne cameras presented in Chapter 2 providing support for the importance of these foraging areas in the absence of prey abundance estimates from prey surveys (DFO 2011). Although animal-borne cameras can provide information on prey encounters, the relatively narrow field of view and shallow depth of field of most cameras does not permit collection of prey field data. Even with these limitations, it is possible for encounters with conspecifics and predators to be recorded with the use of animal-borne cameras though these encounters may be rare and not captured during relatively short instrument deployments. Deployment lengths of animal-borne video are limited not only by battery life, but also as a result of the logistics of camera recovery. Despite the promise of animal-borne cameras as a tool for answering questions in marine ecology, short deployment lengths and the requirement of a light source for recording at night and deeper depths remain as two of the main challenges limiting the utility of this tool over ecologically meaningful durations.

4.6. CONCLUSIONS

This thesis is one of the few studies to simultaneously collect direct observations of individual prey encounter and dive data from marine predators. The deployments of an animal-borne camera on leatherback turtles provide evidence that the feeding tactics of leatherbacks in the high latitude foraging area off Atlantic Canada are energetically profitable. Even though camera deployments were made during relatively short daytime periods, these data could provide support to measures of inferred foraging behaviour from movement data collected over broader spatial and temporal scales and could be used as a tool for determining critical areas of foraging habitat for this endangered species. Concurrently collected dive data from the camera deployments on leatherbacks could also be utilized further to explore predictions of optimal diving theory similar to the harbour seal study. The deployments of animal-borne cameras on male harbour seals provides support for optimal diving predictions of prey encounters increasing with bottom time, dive duration increasing with travel duration, bottom duration decreasing with travel duration, and seals maximizing bottom duration when prey were present and when prey were encountered relatively earlier in a dive. However, I did not find any relationship between bottom duration and prey encounter rate. It was clear that male harbour seals made decisions related to prey encounters, but unsurprisingly it was also clear that there are other factors which influence how male harbour seals made foraging decisions. For both the leatherback turtle and harbour seal studies, contrasting foraging tactics among individuals, in the presence and absence of predators and conspecifics, and with prey field data would give us a better understanding of the decisions that these animals are making to increase their probability of survival and fitness in response to their environment. In this thesis I provide support for the utility of using video from animal-borne cameras to explore the foraging decisions of marine predators in order to infer energy intake in Chapter 2 and test predictions of optimality in Chapter 3; thus demonstrating potential for the use of animal-borne cameras in answering questions related to the ecology of marine predators and the testing and validation of theoretical models.

4.7. REFERENCES

- Boness, D.J., Bowen, W.D., Bulheier, B.M., and Marshall, G.J. 2006b. Mating tactics and mating system of an aquatic-mating pinniped: the harbor seal, *Phoca vitulina*. *Behavioral Ecology and Sociobiology* **61**: 119-130.
- Bowen, W.D., Tully, D., Boness, D.J., Bulheier, B.M., and Marshall, G.J. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. *Marine Ecology Progress Series* **244**: 235-245.
- Boyd, I.L., Reid, K., and Bevan, R.M. 1995. Swimming speed and allocation of time during the dive cycle in Antarctic fur seals. *Animal Behaviour* **50**: 769-784.
- Coltman, D.W., Bowen, W.D., Boness, D.J., and Iverson, S.J. 1997. Balancing foraging and reproduction in the male harbour seal, an aquatically mating pinniped. *Animal Behaviour* **54**: 663-678. doi:10.1006/anbe.1997.0470.
- Cornick, L.A., and Horning, M. 2003. A test of hypotheses based on optimal foraging considerations for a diving mammal using a novel experimental approach. *Canadian Journal of Zoology* **81**(11): 1799-1807. doi:10.1139/z03-179.
- Crocker, D.E., Gales, N.J., and Costa, D.P. 2001. Swimming speed and foraging strategies of New Zealand sea lions (*Phocarctos hookeri*). *Journal of Zoology (London)* **254**: 267-277. doi:Doi 10.1017/S0952836901000784.
- Davenport, J. 1998. Sustaining endothermy on a diet of cold jelly: Energetics of the leatherback turtle *Dermochelys coriacea*. *British Herpetological Society Bulletin* **62**: 4-5.
- DFO. 2011. Using satellite tracking data to define important habitat for leatherback turtles in Atlantic Canada. *DFO Can. Sci. Advis. Sec. Sci. Advis. Rep.* **2012/036**.
- Doyle, T.K., Houghton, J.D.R., McDevitt, R., Davenport, J., and Hays, G.C. 2007b. The energy density of jellyfish: estimates from bomb-calorimetry and proximate-composition. *Journal of Experimental Marine Biology and Ecology* **343**(2): 239-252. doi:10.1016/j.jembe.2006.12.010.
- Gallon, S.L., Sparling, C.E., Georges, J.Y., Fedak, M.A., Biuw, M., and Thompson, D. 2007. How fast does a seal swim? Variations in swimming behaviour under differing foraging conditions. *Journal of Experimental Biology* **210**(18): 3285-3294. doi:10.1242/jeb.007542.

- Hassrick, J.L., Crocker, D.E., Zeno, R.L., Blackwell, S.B., Costa, D.P., and Le Boeuf, B.J. 2007. Swimming speed and foraging strategies of northern elephant seals. *Deep-Sea Research Part II-Topical Studies in Oceanography* **54**(3-4): 369-383. doi:DOI 10.1016/j.dsr2.2006.12.001.
- Heath, J.P., Gilchrist, H.G., and Ydenberg, R.C. 2007. Can dive cycle models predict patterns of foraging behaviour? Diving by common eiders in an Arctic polynya. *Animal Behaviour* **73**: 877-884. doi:10.1016/j.anbehav.2006.10.015.
- Hindell, M.A., and Lea, M.A. 1998. Heart rate, swimming speed, and estimated oxygen consumption of a free-ranging southern elephant seal. *Physiological Zoology* **71**(1): 74-84.
- Houston, A.I., and Carbone, C. 1992. The optimal allocation of time during the diving cycle. *Behavioral Ecology* **3**(3): 255-265. doi:10.1093/beheco/3.3.255.
- James, M.C., and Herman, T.B. 2001. Feeding of *Dermochelys coriacea* on medusae in the northwest Atlantic. *Chelonian Conservation Biology* **4**: 202-205.
- James, M.C., Ottensmeyer, C.A., and Myers, R.A. 2005c. Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecology Letters* **8**(2): 195-201. doi:10.1111/j.1461-0248.2004.00710.x.
- Jonsen, I.D., Myers, R.A., and James, M.C. 2007. Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Marine Ecology Progress Series* **337**: 255-264.
- Kramer, D.L. 1988. The behavioral ecology of air breathing by aquatic animals. *Canadian Journal of Zoology* **66**(1): 89-94.
- Sparling, C.E., Georges, J.Y., Gallon, S.L., Fedak, M., and Thompson, D. 2007. How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: a test of a simple model. *Animal Behaviour* **74**: 207-218. doi:10.1016/i.anbehav.2006.06.022.
- Thompson, D., and Fedak, M.A. 2001. How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Animal Behaviour* **61**: 287-296. doi:10.1006/anbe.2000.1539.

REFERENCES

- Austin, D., Bowen, W.D., McMillan, J.I., and Iverson, S.J. 2006. Linking movement, diving, and habitat to foraging success in a large marine predator. *Ecology* **87**(12): 3095-3108. doi:10.1890/0012-9658(2006)87[3095:lmdaht]2.0.co;2.
- Bailey, H., Shillinger, G., Palacios, D., Bograd, S., Spotila, J., Paladino, F., and Block, B. 2008. Identifying and comparing phases of movement by leatherback turtles using state-space models. *Journal of Experimental Marine Biology and Ecology* **356**(1-2): 128-135. doi:10.1016/j.jembe.2007.12.020.
- Båmstedt, U., Martinussen, M.B., and Matsakis, S. 1994. Trophodynamics of the two scyphozoan jellyfishes, *Aurelia aurita* and *Cyanea capillata*, in western Norway. *ICES Journal of Marine Science* **54**(1): 369-382.
- Beauchamp, D.A., Baldwin, C.M., Vogel, J.L., and Gubala, C.P. 1999. Estimating diel, depth-specific foraging opportunities with a visual encounter rate model for pelagic piscivores. *Canadian Journal of Fisheries and Aquatic Sciences* **56**(Suppl. 1): 128-139.
- Beck, C.A., Iverson, S.J., and Bowen, W.D. 2005. Blubber fatty acids of gray seals reveal sex differences in the diet of a size-dimorphic marine carnivore. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **83**(3): 377-388. doi:10.1139/z05-021.
- Beck, C.A., Iverson, S.J., Bowen, W.D., and Blanchard, W. 2007. Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. *Journal of Animal Ecology* **76**(3): 490-502. doi:10.1111/j.1365-2656.2007.01215.x.
- Benoit-Bird, K.J., and Au, W.W.L. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behavioral Ecology and Sociobiology* **53**(6): 364-373. doi:10.1007/s00265-003-0585-4.
- Benson, S.R., Dutton, P.H., Hitipeuw, C., Samber, B., Bakarbessy, J., and Parker, D. 2007. Post-nesting migrations of leatherback turtles (*Dermochelys coriacea*) from Jamursba-Medi, Bird's Head Peninsula, Indonesia. *Chelonian Conservation and Biology* **6**(1): 150-154.
- Blumstein, D.T., and Daniel, J.C. 2007. *Quantifying Behavior the JWatcher Way*. Sinauer Associates, Inc.
- Boness, D.J., Bowen, D.W., Bulheier, B.M., and Marshall, G.J. 2006a. Mating tactics and mating system of an aquatic-mating pinniped: The harbor seal, *Phoca vitulina*. *Behavioral Ecology and Sociobiology* **61**: 119-130.

- Boness, D.J., Bowen, W.D., Bulheier, B.M., and Marshall, G.J. 2006b. Mating tactics and mating system of an aquatic-mating pinniped: the harbor seal, *Phoca vitulina*. *Behavioral Ecology and Sociobiology* **61**: 119-130.
- Bowen, W.D., Ellis, S.L., Iverson, S.J., and Boness, D.J. 2003. Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. *Journal of Zoology (London)* **261**: 155-163. doi:10.1017/s0952836903004047.
- Bowen, W.D., and Harrison, G.D. 1996a. Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **74**(1): 125-135. doi:10.1139/z96-017.
- Bowen, W.D., and Harrison, G.D. 1996b. Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. *Canadian Journal of Zoology* **74**(1): 125-135. doi:10.1139/z96-017.
- Bowen, W.D., Oftedal, O.T., and Boness, D.J. 1992. Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). *Physiological Zoology* **65**: 844-866.
- Bowen, W.D., Tully, D., Boness, D.J., Bulheier, B.M., and Marshall, G.J. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. *Marine Ecology Progress Series* **244**: 235-245.
- Boyd, I.L., and Croxall, J.P. 1996. Dive durations in pinnipeds and seabirds. *Canadian Journal of Zoology* **74**(9): 1696-1705.
- Boyd, I.L., McCafferty, D.J., and Walker, T.R. 1997. Variation in foraging effort by lactating Antarctic fur seals: response to simulated increased foraging costs. *Behavioral Ecology and Sociobiology* **40**(3): 135-144. doi:DOI 10.1007/s002650050326.
- Boyd, I.L., Reid, K., and Bevan, R.M. 1995. Swimming speed and allocation of time during the dive cycle in Antarctic fur seals. *Animal Behaviour* **50**: 769-784.
- Bradshaw, C.J.A., McMahon, C.R., and Hays, G.C. 2007. Behavioral inference of diving metabolic rate in free-ranging leatherback turtles. *Physiological and Biochemical Zoology* **80**(2): 209-219. doi:10.1086/511142.
- Brock, H.M.E. 2006. Leatherback turtles (*Dermochelys coriacea*) in Newfoundland and Labrador: Distribution, diet, threats and the use of education in recovery efforts. *In* School of Graduate Studies, Faculty of Science. Memorial University of Newfoundland, St. John's, N.L. p. 109.

- Brodeur, R.D., Sugisaki, H., and Hunt, G.L. 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Marine Ecology Progress Series* **233**: 89-103.
- Calambokidis, J., Schorr, G.S., Steiger, G.H., Francis, J., Bakhtiari, M., Marshal, G., Oleson, E.M., Gendron, D., and Robertson, K. 2007. Insights into the underwater diving, feeding, and calling behavior of blue whales from a suction-cup-attached video-imaging tag (Cittercam). *Marine Technology Society Journal* **41**(4): 19-29.
- Carbone, C., and Houston, A.I. 1994. Patterns in the diving behavior of the pochard, *Aythya ferina*: a test of an optimality model. *Animal Behaviour* **48**(2): 457-465. doi:10.1006/anbe.1994.1259.
- Carbone, C., and Houston, A.I. 1996. The optimal allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. *Animal Behaviour* **51**: 1247-1255. doi:10.1006/anbe.1996.0129.
- Casey, J., Garner, J., Garner, S., and Williard, A.S. 2010. Diel foraging behavior of gravid leatherback sea turtles in deep waters of the Caribbean Sea. *Journal of Experimental Biology* **213**(23): 3961-3971. doi:10.1242/jeb.048611.
- Charnov, E.L. 1976a. Optimal foraging: Attack strategy of a mantid. *American Naturalist* **110**(971): 141-151.
- Charnov, E.L. 1976b. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**(2): 129-136.
- Coltman, D.W., Bowen, W.D., Boness, D.J., and Iverson, S.J. 1997. Balancing foraging and reproduction in the male harbour seal, an aquatically mating pinniped. *Animal Behaviour* **54**: 663-678. doi:10.1006/anbe.1997.0470.
- Cornick, L.A., and Horning, M. 2003. A test of hypotheses based on optimal foraging considerations for a diving mammal using a novel experimental approach. *Canadian Journal of Zoology* **81**(11): 1799-1807. doi:10.1139/z03-179.
- COSEWIC 2001. COSEWIC assessment and update status report on the leatherback turtle *Dermochelys coriacea* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, Ont. p. vii + 25 pp.
- Costa, D.P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. *Symposium of the Zoological Society of London* **66**: 293-314.
- Crocker, D.E., Gales, N.J., and Costa, D.P. 2001. Swimming speed and foraging strategies of New Zealand sea lions (*Phocarctos hookeri*). *Journal of Zoology (London)* **254**: 267-277. doi:Doi 10.1017/S0952836901000784.

- Davenport, J. 1998. Sustaining endothermy on a diet of cold jelly: Energetics of the leatherback turtle *Dermochelys coriacea*. *British Herpetological Society Bulletin* **62**: 4-5.
- Davis, R.W., Fuiman, L.A., Williams, T.M., Collier, S.O., Hagey, W.P., Kanatous, S.B., Kohin, S., and Horning, M. 1999. Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* **283**(5404): 993-996.
- Davis, R.W., Fuiman, L.A., Williams, T.M., Horning, M., and Hagey, W. 2003. Classification of Weddell seal dives based on 3-dimensional movements and video-recorded observations. *Marine Ecology Progress Series* **264**: 109-122.
- Davis, R.W., Fuiman, L.A., Williams, T.M., and Le Boeuf, B.J. 2001. Three-dimensional movements and swimming activity of a northern elephant seal. *Comparative Biochemistry and Physiology, Part A: Molecular & Integrative Physiology* **129**(4): 759-770.
- DFO. 2011. Using satellite tracking data to define important habitat for leatherback turtles in Atlantic Canada. *DFO Can. Sci. Advis. Sec. Sci. Advis. Rep.* **2012/036**.
- Doniol-Valcroze, T., Lesage, V., Giard, J., and Michaud, R. 2011. Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behavioral Ecology* **22**(4): 880-888. doi:10.1093/beheco/arr038.
- Doyle, T.K., Houghton, J.D.R., Buckley, S.M., Hays, G.C., and Davenport, J. 2007a. The broad-scale distribution of five jellyfish species across a temperate coastal environment. *Hydrobiologia* **579**: 29-39. doi:10.1007/s10750-006-0362-2.
- Doyle, T.K., Houghton, J.D.R., McDevitt, R., Davenport, J., and Hays, G.C. 2007b. The energy density of jellyfish: estimates from bomb-calorimetry and proximate-composition. *Journal of Experimental Marine Biology and Ecology* **343**(2): 239-252. doi:10.1016/j.jembe.2006.12.010.
- Elliott, K.H., Davoren, G.K., and Gaston, A.J. 2008. Time allocation by a deep-diving bird reflects prey type and energy gain. *Animal Behaviour* **75**: 1301-1310. doi:DOI 10.1016/j.anbehav.2007.09.024.
- Emlen, J.M. 1966. Role of time and energy in food preference. *American Naturalist* **100**(916): 611-617.
- Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T., and Lyon, B.E. 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. *Journal of Animal Ecology* **72**(1): 144-155. doi:10.1046/j.1365-2656.2003.00690.x.

- Field, I.C., Bradshaw, C.J.A., van den Hoff, J., Burton, H.R., and Hindell, M.A. 2007. Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche. *Marine Biology* **150**(6): 1441-1452. doi:10.1007/s00227-006-0417-y.
- Fossette, S., Gaspar, P., Handrich, Y., Le Maho, Y., and Georges, J.Y. 2008. Dive and beak movement patterns in leatherback turtles *Dermochelys coriacea* during interesting intervals in French Guiana. *Journal of Animal Ecology* **77**(2): 236-246. doi:10.1111/j.1365-2656.2008.01344.x.
- Fossette, S., Hobson, V.J., Girard, C., Calmettes, B., Gaspar, P., Georges, J.Y., and Hays, G.C. 2010. Spatio-temporal foraging patterns of a giant zooplanktivore, the leatherback turtle. *Journal of Marine Systems* **81**(3): 225-234. doi:10.1016/j.jmarsys.2009.12.002.
- Fuiman, L.A., Madden, K.M., Williams, T.M., and Davis, R.W. 2007. Structure of foraging dives by Weddell seals at an offshore isolated hole in the Antarctic fast-ice environment. *Deep-Sea Research Part II: Topical Studies in Oceanography* **54**(3-4): 270-289.
- Gallon, S.L., Sparling, C.E., Georges, J.Y., Fedak, M.A., Biuw, M., and Thompson, D. 2007. How fast does a seal swim? Variations in swimming behaviour under differing foraging conditions. *Journal of Experimental Biology* **210**(18): 3285-3294. doi:10.1242/jeb.007542.
- Graham, T.R., Harvey, J.T., Benson, S.R., Renfree, J.S., and Demer, D.A. 2010. The acoustic identification and enumeration of scyphozoan jellyfish, prey for leatherback sea turtles (*Dermochelys coriacea*), off central California. *ICES Journal of Marine Science* **67**(8): 1739-1748. doi:10.1093/icesjms/fsq112.
- Halsey, L.G., Brand, O.J., Woakes, A.J., and Butler, P.J. 2006. Experiments on single diving birds in the laboratory often measure dives of decreased effort. *Ibis* **148**(1): 164-166. doi:10.1111/j.1474-919X.2006.00476.x.
- Halsey, L.G., and Butler, P.J. 2006. Optimal diving behaviour and respiratory gas exchange in birds. *Respiratory Physiology & Neurobiology* **154**(1-2): 268-283. doi:10.1016/j.resp.2006.01.012.
- Hamner, W.M., and Schneider, D. 1986. Regularly spaced rows of medusae in the Bering Sea: role of Langmuir circulation. *Limnology and Oceanography* **31**(1): 171-177.
- Hassrick, J.L., Crocker, D.E., Zeno, R.L., Blackwell, S.B., Costa, D.P., and Le Boeuf, B.J. 2007. Swimming speed and foraging strategies of northern elephant seals. *Deep-Sea Research Part II-Topical Studies in Oceanography* **54**(3-4): 369-383. doi:DOI 10.1016/j.dsr2.2006.12.001.

- Hays, G.C., Houghton, J.D.R., Isaacs, C., King, R.S., Lloyd, C., and Lovell, P. 2004. First records of oceanic dive profiles for leatherback turtles, *Dermochelys coriacea*, indicate behavioural plasticity associated with long-distance migration. *Animal Behaviour* **67**: 733-743.
- Hays, G.C., Marshall, G.J., and Seminoff, J.A. 2007. Flipper beat frequency and amplitude changes in diving green turtles, *Chelonia mydas*. *Marine Biology* **150**(5): 1003-1009. doi:10.1007/s00227-006-0412-3.
- Heaslip, S.G., Bowen, W.D., and Iverson, S.J. 2014. Testing predictions of optimal diving theory using animal-borne video from harbour seals (*Phoca vitulina concolor*). *Canadian Journal of Zoology* **92**(4): 309-318. doi:10.1139/cjz-2013-0137.
- Heaslip, S.G., and Hooker, S.K. 2008. Effect of animal-borne camera and flash on the diving behaviour of the female Antarctic fur seal (*Arctocephalus gazella*). *Deep-Sea Research Part I: Oceanographic Research Papers* **55**(9): 1179-1192. doi:DOI 10.1016/j.dsr.2008.05.006.
- Heaslip, S.G., Iverson, S.J., Bowen, W.D., and James, M.C. 2012. Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): video evidence from animal-borne cameras. *PloS ONE* **7**(3): e33259. doi:10.1371/journal.pone.0033259.
- Heath, J.P., Gilchrist, H.G., and Ydenberg, R.C. 2007. Can dive cycle models predict patterns of foraging behaviour? Diving by common eiders in an Arctic polynya. *Animal Behaviour* **73**: 877-884. doi:10.1016/j.anbehav.2006.10.015.
- Heithaus, M.R., and Frid, A. 2003. Optimal diving under the risk of predation. *Journal of Theoretical Biology* **223**(1): 79-92. doi:10.1016/s0022-5193(03)00073-0.
- Heithaus, M.R., Marshall, G.J., Buhleier, B.M., and Dill, L.M. 2001. Employing Crittercam to study habitat use and behavior of large sharks. *Marine Ecology Progress Series* **209**: 307-310. doi:10.3354/Meps209307.
- Hindell, M.A., and Lea, M.A. 1998. Heart rate, swimming speed, and estimated oxygen consumption of a free-ranging southern elephant seal. *Physiological Zoology* **71**(1): 74-84.
- Hooker, S.K., Boyd, I.L., Jessopp, M., Cox, O., Blackwell, J., Boveng, P.L., and Bengtson, J.L. 2002. Monitoring the prey-field of marine predators: combining digital imaging with datalogging tags. *Marine Mammal Science* **18**(3): 680-697. doi:10.1111/j.1748-7692.2002.tb01066.x.

- Hooker, S.K., Miller, P.J.O., Johnson, M.P., Cox, O.P., and Boyd, I.L. 2005. Ascent exhalations of Antarctic fur seals: a behavioural adaptation for breath-hold diving? *Proceedings of the Royal Society of London Series B: Biological Sciences* **272**(1561): 355-363. doi:10.1098/rspb.2004.2964.
- Houghton, J.D.R., Doyle, T.K., Wilson, M.W., Davenport, J., and Hays, G.C. 2006. Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. *Ecology* **87**(8): 1967-1972.
- Houston, A.I. 1986. The optimal flight velocity for a bird exploiting patches of food. *Journal of Theoretical Biology* **119**(3): 345-362. doi:10.1016/s0022-5193(86)80146-1.
- Houston, A.I., and Carbone, C. 1992. The optimal allocation of time during the diving cycle. *Behavioral Ecology* **3**(3): 255-265. doi:10.1093/beheco/3.3.255.
- Houston, A.I., McNamara, J.M., Heron, J.E., and Barta, Z. 2003. The effect of foraging parameters on the probability that a dive is successful. *Proceedings of the Royal Society of London Series B: Biological Sciences* **270**(1532): 2451-2455. doi:10.1098/rspb.2003.2540.
- Iverson, S.J., Field, C., Bowen, W.D., and Blanchard, W. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. *Ecological Monographs* **74**(2): 211-235. doi:10.1890/02-4105.
- Iwasa, Y., Higashi, M., and Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *American Naturalist* **117**(5): 710-723.
- James, M.C., Davenport, J., and Hays, G.C. 2006a. Expanded thermal niche for a diving vertebrate: A leatherback turtle diving into near-freezing water. *Journal of Experimental Marine Biology and Ecology* **335**(2): 221-226. doi:10.1016/j.jembe.2006.03.013.
- James, M.C., Eckert, S.A., and Myers, R.A. 2005a. Migratory and reproductive movements of male leatherback turtles (*Dermochelys coriacea*). *Marine Biology* **147**(4): 845-853. doi:10.1007/s00227-005-1581-1.
- James, M.C., and Herman, T.B. 2001. Feeding of *Dermochelys coriacea* on medusae in the northwest Atlantic. *Chelonian Conservation Biology* **4**: 202-205.
- James, M.C., Myers, R.A., and Ottensmeyer, C.A. 2005b. Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. *Proceedings of the Royal Society of London Series B: Biological Sciences* **272**(1572): 1547-1555. doi:10.1098/rspb.2005.3110.

- James, M.C., Ottensmeyer, C.A., and Myers, R.A. 2005c. Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecology Letters* **8**(2): 195-201. doi:10.1111/j.1461-0248.2004.00710.x.
- James, M.C., Sherrill-Mix, S.A., Martin, K., and Myers, R.A. 2006b. Canadian waters provide critical foraging habitat for leatherback sea turtles. *Biological Conservation* **133**(3): 347-357. doi:10.1016/j.biocon.2006.06.012.
- James, M.C., Sherrill-Mix, S.A., and Myers, R.A. 2007. Population characteristics and seasonal migrations of leatherback sea turtles at high latitudes. *Marine Ecology Progress Series* **337**: 245-254.
- Jeschke, J.M., Kopp, M., and Tollrian, R. 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs* **72**(1): 95-112.
- Jonsen, I.D., Flemming, J.M., and Myers, R.A. 2005. Robust state-space modeling of animal movement data. *Ecology* **86**(11): 2874-2880.
- Jonsen, I.D., Myers, R.A., and James, M.C. 2007. Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Marine Ecology Progress Series* **337**: 255-264.
- Kamil, A.C., Misthal, R.L., and Stephens, D.W. 1993. Failure of simple optimal foraging models to predict residence time when patch quality is uncertain. *Behavioral Ecology* **4**(4): 350-363. doi:10.1093/beheco/4.4.350.
- Kassen, R. 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of Evolutionary Biology* **15**(2): 173-190. doi:10.1046/j.1420-9101.2002.00377.x.
- Kooyman, G.L. 1985. Physiology without restraint in diving mammals. *Marine Mammal Science* **1**(2): 166-178. doi:10.1111/j.1748-7692.1985.tb00004.x.
- Kooyman, G.L., Davis, R.W., and Croxall, J.P. 1986. Diving behavior of Antarctic fur seals. *In* *Fur seals: maternal strategies on land and at sea*. Edited by R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 115-125.
- Kramer, D.L. 1988. The behavioral ecology of air breathing by aquatic animals. *Canadian Journal of Zoology* **66**(1): 89-94.
- Kuhn, C.E., and Costa, D.P. 2006. Identifying and quantifying prey consumption using stomach temperature change in pinnipeds. *Journal of Experimental Biology* **209**(22): 4524-4532. doi:Doi 10.1242/Jeb.02530.

- Lea, M.A., and Wilson, B. 2006. Techniques for real-time, active tracking of sea lions. *In* Sea Lions of the World. *Edited by* A.W. Trites and S.K. Atkinson and D.P. DeMaster and L.W. Fritz and T.S. Gelatt and L.D. Rea and K.M. Wynne. Alaska Sea Grant Coll Program, Fairbanks. pp. 235-253.
- Lea, S.E.G., Daley, C., Boddington, P.J.C., and Morison, V. 1996. Diving patterns in shags and cormorants (*Phalacrocorax*): tests of an optimal breathing model. *Ibis* **138**(3): 391-398. doi:10.1111/j.1474-919X.1996.tb08056.x.
- Lesage, V., Hammill, M.O., and Kovacs, K.M. 1999. Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Canadian Journal of Zoology* **77**(1): 74-87. doi:10.1139/cjz-77-1-74.
- Liebsch, N., Wilson, R.P., Bornemann, H., Adelung, D., and Plotz, J. 2007. Mouthing off about fish capture: jaw movement in pinnipeds reveals the real secrets of ingestion. *Deep-Sea Research Part II: Topical Studies in Oceanography* **54**(3-4): 256-269. doi:DOI 10.1016/j.dsr2.2006.11.014.
- Lima, S.L. 1988. Vigilance and diet selection: The classical diet model reconsidered. *Journal of Theoretical Biology* **132**(2): 127-143.
- Littnan, C.L., Baker, J.D., Parrish, F.A., and Marshall, G.J. 2004. Effects of video camera attachment on the foraging behavior of immature Hawaiian monk seals. *Marine Mammal Science* **20**(2): 345-352. doi:DOI 10.1111/j.1748-7692.2004.tb01164.x.
- Lucas, Z., and Stobo, W.T. 2000. Shark-inflicted mortality on a population of harbour seals (*Phoca vitulina*) at Sable Island, Nova Scotia. *Journal of Zoology (London)* **252**: 405-414. doi:10.1111/j.1469-7998.2000.tb00636.x.
- Lutcavage, M., and Lutz, P.L. 1986. Metabolic state and food energy requirements of the leatherback sea turtle, *Dermochelys coriacea*. *Copeia*(3): 796-798.
- MacArthur, R.H., and Pianka, E.R. 1966. On optimal use of a patchy environment. *American Naturalist* **100**(916): 603-609.
- Marshall, G. 2007. An advanced solid-state animal-borne video and environmental data-logging device ("Critttercam") for marine research. *Marine Technology Society Journal* **41**(2): 31-38.
- Marshall, G.J. 1998. Critttercam: an animal-borne imaging and data logging system. *Marine Technology Society Journal* **32**(1): 11-17.
- McLaren, I.A. 1993. Growth in pinnipeds. *Biological Reviews of the Cambridge Philosophical Society* **68**: 1-79.

- McMahon, C.R., and Hays, G.C. 2006. Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Global Change Biology* **12**(7): 1330-1338. doi:10.1111/j.1365-2486.2006.01174.x.
- McNamara, J. 1982. Optimal patch use in a stochastic environment. *Theoretical Population Biology* **21**(2): 269-288.
- Moll, R.J., Millsaugh, J.J., Beringer, J., Sartwell, J., and He, Z. A new 'view' of ecology and conservation through animal-borne video systems. *Trends in Ecology & Evolution* **22**(12): 660-668. doi:10.1016/j.tree.2007.09.007.
- Mori, Y. 1998a. Optimal choice of foraging depth in divers. *Journal of Zoology (London)* **245**: 279-283. doi:10.1111/j.1469-7998.1998.tb00102.x.
- Mori, Y. 1998b. The optimal patch use in divers: optimal time budget and the number of dive cycles during bout. *Journal of Theoretical Biology* **190**(2): 187-199. doi:10.1006/jtbi.1997.0550.
- Mori, Y. 2002. Optimal diving behaviour for foraging in relation to body size. *Journal of Evolutionary Biology* **15**(2): 269-276. doi:10.1046/j.1420-9101.2002.00382.x.
- Mori, Y., and Boyd, I.L. 2004. The behavioral basis for nonlinear functional responses and optimal foraging in antarctic fur seals. *Ecology* **85**(2): 398-410. doi:10.1890/03-4005.
- Mori, Y., Takahashi, A., Mehlum, F., and Watanuki, Y. 2002. An application of optimal diving models to diving behaviour of Brunnich's guillemots. *Animal Behaviour* **64**: 739-745. doi:10.1006/anbe.2002.3093.
- Myers, A.E., and Hays, G.C. 2006. Do leatherback turtles *Dermochelys coriacea* forage during the breeding season? A combination of data-logging devices provide new insights. *Marine Ecology Progress Series* **322**: 259-267.
- Nagy, K.A., Girard, I.A., and Brown, T.K. 1999. Energetics of free-ranging mammals, reptiles, and birds. *Annual Review of Nutrition* **19**: 247-277. doi:10.1146/annurev.nutr.19.1.247.
- Noldus, L.P.J.J. 1991. The Observer: a software system for collection and analysis of observational data. *Behavior Research Methods, Instruments, & Computers* **23**(3): 415-429.
- Parrish, F.A., Abernathy, K., Marshall, G.J., and Buhleier, B.M. 2002. Hawaiian monk seals (*Monachus schauinslandi*) foraging in deep-water coral beds. *Marine Mammal Science* **18**(1): 244-258.

- Parrish, F.A., Craig, M.P., Ragen, T.J., Marshall, G.J., and Buhleier, B.M. 2000. Identifying diurnal foraging habitat of endangered Hawaiian monk seals using a seal-mounted video camera. *Marine Mammal Science* **16**(2): 392-412.
- Parrish, F.A., Marshall, G.J., Littnan, C.L., Heithaus, M., Canja, S., Becker, B., Braun, R., and Antonelis, G.A. 2005. Foraging of juvenile monk seals at French Frigate Shoals, Hawaii. *Marine Mammal Science* **21**(1): 93-107.
- Pinheiro, J., and Bates, D. 2000. *Mixed-Effects Models in S and S-PLUS*. Springer-Verlag, New York.
- Purcell, J.E. 2003. Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*, in Prince William Sound, Alaska. *Marine Ecology Progress Series* **246**: 137-152.
- Purcell, J.E., Uye, S., and Lo, W.T. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series* **350**: 153-174. doi:10.3354/meps07093.
- R Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reina, R.D., Abernathy, K.J., Marshall, G.J., and Spotila, J.R. 2005. Respiratory frequency, dive behaviour and social interactions of leatherback turtles, *Dermochelys coriacea* during the inter-nesting interval. *Journal of Experimental Marine Biology and Ecology* **316**(1): 1-16. doi:10.1016/j.jembe.2004.10.002.
- Sarti Martinez, A.L. 2000. *Dermochelys coriacea*. IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4 [online]. Available from www.iucnredlist.org [accessed 20 January 2011].
- Schoener, T.W. 1971. Theory of Feeding Strategies. *Annual Review of Ecology and Systematics* **2**(1): 369-404. doi:doi:10.1146/annurev.es.02.110171.002101.
- Schreer, J.F., Kovacs, K.M., and O'Hara Hines, R.J. 2001. Comparative diving patterns of pinnipeds and seabirds. *Ecological Monographs* **71**: 137-162.
- Shillinger, G.L., Palacios, D.M., Bailey, H., Bograd, S.J., Swithenbank, A.M., Gaspar, P., Wallace, B.P., Spotila, J.R., Paladino, F.V., Piedra, R., Eckert, S.A., and Block, B.A. 2008. Persistent leatherback turtle migrations present opportunities for conservation. *Plos Biology* **6**(7): e171. doi:10.1371/journal.pbio.0060171.

- Sigler, M.F., Tollit, D.J., Vollenweider, J.J., Thedinga, J.F., Csepp, D.J., Womble, J.N., Wong, M.A., Rehberg, M.J., and Trites, A.W. 2009. Steller sea lion foraging response to seasonal changes in prey availability. *Marine Ecology Progress Series* **388**: 243-261. doi:10.3354/meps08144.
- Soto, K.H., Trites, A.W., and Arias-Schreiber, M. 2006. Changes in diet and maternal attendance of South American sea lions indicate changes in the marine environment and prey abundance. *Marine Ecology Progress Series* **312**: 277-290. doi:10.3354/meps312277.
- Sparling, C.E., Georges, J.Y., Gallon, S.L., Fedak, M., and Thompson, D. 2007. How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: a test of a simple model. *Animal Behaviour* **74**: 207-218. doi:10.1016/i.anbehav.2006.06.022.
- Stearns, S.C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.
- Stephens, D.W., and Krebs, J.R. 1986. *Foraging Theory*. Princeton University Press, Princeton, NJ.
- Sullivan, B.K., Suchman, C.L., and Costello, J.H. 1997. Mechanics of prey selection by ephyrae of the scyphomedusa *Aurelia aurita*. *Marine Biology* **130**(2): 213-222.
- Suzuki, I., Naito, Y., Folkow, L.P., Miyazaki, N., and Blix, A.S. 2009. Validation of a device for accurate timing of feeding events in marine animals. *Polar Biology* **32**(4): 667-671. doi:DOI 10.1007/s00300-009-0596-3.
- Thompson, D., and Fedak, M.A. 2001. How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Animal Behaviour* **61**: 287-296. doi:10.1006/anbe.2000.1539.
- Thompson, D., Hiby, A.R., and Fedak, M.A. 1993. How fast should I swim? Behavioural implications of diving physiology. *Symposium of the Zoological Society of London* **66**: 349-368.
- Thums, M., Bradshaw, C.J.A., Sumner, M.D., Horsburgh, J.M., and Hindell, M.A. 2013. Depletion of deep marine food patches forces divers to give up early. *Journal of Animal Ecology* **82**(1): 72-83. doi:10.1111/j.1365-2656.2012.02021.x.
- Van Houtan, K.S., and Halley, J.M. 2011. Long-term climate forcing in loggerhead sea turtle nesting. *PloS ONE* **6**(4): e19043. doi:10.1371/journal.pone.0019043.
- Viviant, M., Trites, A.W., Rosen, D.A.S., Monestiez, P., and Guinet, C. 2010. Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. *Polar Biology* **33**(5): 713-719. doi:DOI 10.1007/s00300-009-0750-y.

- Walker, B.G., and Boveng, P.L. 1995. Effects of time-depth recorders on maternal foraging and attendance behavior of antarctic fur seals (*Arctocephalus gazella*). *Canadian Journal of Zoology* **73**(8): 1538-1544. doi:Doi 10.1139/Z95-182.
- Walker, B.G., and Bowen, W.D. 1993a. Behavioural differences among adult male harbor seals during the breeding season may provide evidence of reproductive strategies. *Canadian Journal of Zoology* **71**(8): 1585-1591. doi:10.1139/z93-224.
- Walker, B.G., and Bowen, W.D. 1993b. Changes in body mass and feeding behaviour in male harbour seals, *Phoca vitulina*, in relation to female reproductive status. *Journal of Zoology (London)* **231**: 423-436.
- Wallace, B.P., Williams, C.L., Paladino, F.V., Morreale, S.J., Lindstrom, R.T., and Spotila, J.R. 2005. Bioenergetics and diving activity of internesting leatherback turtles *Dermochelys coriacea* at Parque Nacional Marino las Baulas, Costa Rica. *Journal of Experimental Biology* **208**(20): 3873-3884. doi:10.1242/jeb.01860.
- Walton, P., Ruxton, G.D., and Monaghan, P. 1998. Avian diving, respiratory physiology and the marginal value theorem. *Animal Behaviour* **56**: 165-174. doi:10.1006/anbe.1998.0759.
- Williams, T.M., Davis, R.W., Fuiman, L.A., Francis, J., Le Boeuf, B.L., Horning, M., Calambokidis, J., and Croll, D.A. 2000. Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* **288**(5463): 133-136. doi:10.1126/science.288.5463.133.
- Williams, T.M., Fuiman, L.A., Horning, M., and Davis, R.W. 2004. The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke. *Journal of Experimental Biology* **207**(6): 973-982.
- Wirsing, A.J., Heithaus, M.R., and Dill, L.M. 2011. Predator-induced modifications to diving behavior vary with foraging mode. *Oikos* **120**(7): 1005-1012. doi:10.1111/j.1600-0706.2010.18844.x.
- Wirsing, A.J., Heithaus, M.R., Frid, A., and Dill, L.M. 2008. Seascapes of fear: evaluating sublethal predator effects experienced and generated by marine mammals. *Marine Mammal Science* **24**(1): 1-15. doi:10.1111/j.1748-7692.2007.00167.x.
- Witt, M.J., Broderick, A.C., Johns, D.J., Martin, C., Penrose, R., Hoogmoed, M.S., and Godley, B.J. 2007. Prey landscapes help identify potential foraging habitats for leatherback turtles in the NE Atlantic. *Marine Ecology Progress Series* **337**: 231-243. doi:10.3354/Meps337231.

- Witteveen, B.H., Foy, R.J., Wynne, K.M., and Tremblay, Y. 2008. Investigation of foraging habits and prey selection by humpback whales (*Megaptera novaeangliae*) using acoustic tags and concurrent fish surveys. *Marine Mammal Science* **24**(3): 516-534. doi:10.1111/j.1748-7692.2008.00193.x.
- Wood, S.N. 2006. *Generalized Additive Models: An Introduction with R*. Chapman & Hall/CRC, Boca Raton, FL.
- Zollner, P.A., and Lima, S.L. 1999. Search strategies for landscape-level interpatch movements. *Ecology* **80**(3): 1019-1030. doi:10.1890/0012-9658(1999)080[1019:ssfli]2.0.co;2.

APPENDIX A

COPYRIGHT PERMISSIONS

Chapter 2 was published in the PLOS journal PLOS One and is reproduced here with permission under the license Creative Commons Attribution 3.0 Unported. “PLOS applies the Creative Commons Attribution (CC BY) license to all works [they] publish... Under the CC BY license, authors retain ownership of the copyright for their article, but authors allow anyone to download, reuse, reprint, modify, distribute, and/or copy articles in PLOS journals, so long as the original authors and source are cited. No permission is required from the authors or the publishers.” See <http://www.plosone.org/static/license> and <http://creativecommons.org/licenses/by/3.0> for license details.

Heaslip, S.G., Iverson, S.J., Bowen, W.D., and James, M.C. 2012. Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): video evidence from animal-borne cameras. PLOS ONE 7(3): e33259. doi:10.1371/journal.pone.0033259.

Chapter 3 was published in the NRC journal Canadian Journal of Zoology and is reproduced here with permission under an NRC Research Press License that is included on the following pages.

Heaslip, S.G., Bowen, W.D., and Sara, J.I. 2014. Testing predictions of optimal diving theory using animal-borne video from harbour seals (*Phoca vitulina concolor*). Canadian Journal of Zoology 92(4): 309-318. doi:10.1139/cjz-2013-0137.

**NRC RESEARCH PRESS LICENSE
TERMS AND CONDITIONS**

Jul 13, 2014

This is a License Agreement between Susan G Heaslip ("You") and NRC Research Press ("NRC Research Press") provided by Copyright Clearance Center ("CCC"). The license consists of your order details, the terms and conditions provided by NRC Research Press, and the payment terms and conditions.

All payments must be made in full to CCC. For payment instructions, please see information listed at the bottom of this form.

License Number	3427380608161
License date	Jul 13, 2014
Licensed content publisher	NRC Research Press
Licensed content publication	Canadian Journal of Zoology
Licensed content title	Testing predictions of optimal diving theory using animal-borne video from harbour seals (<i>Phoca vitulina concolor</i>)
Licensed content author	Susan G. Heaslip, W. Don Bowen, Sara J. Iverson
Licensed content date	Apr 1, 2014
Volume number	92
Issue number	4
Type of Use	Thesis/Dissertation
Requestor type	Author (original work)
Format	Print and electronic
Portion	Full article
Order reference number	None
Title of your thesis / dissertation	Using animal-borne cameras to study the foraging behaviour of large marine predators
Expected completion date	Jul 2014
Estimated size(pages)	125
Total	0.00 CAD

Terms and Conditions

General Terms & Conditions

Permission is granted upon the requester's compliance with the following terms and conditions:

1. A credit line will be prominently placed in your product(s) and include: for books the author, book title, editor, copyright holder, year of publication; for journals the author, title of article, title of journal, volume number, issue number, and the inclusive pages. The credit line must include the following wording: "© 2008 Canadian Science Publishing or its licensors. Reproduced with permission," except when an author of an original article published in 2009 or later is reproducing his/her own work.
2. The requester warrants that the material shall not be used in any manner that may be derogatory to the title, content, or authors of the material or to Canadian Science Publishing, including but not limited to an association with conduct that is fraudulent or otherwise illegal.
3. Permission is granted for the term (for Books/CDs-Shelf Life; for Internet/Intranet-In perpetuity; for all other forms of print-the life of the title) and purpose specified in your request. Once term has expired, permission to renew must be made in writing.
4. Permission granted is nonexclusive, and is valid throughout the world in English and the languages specified in your original request. A new permission must be requested for revisions of the publication under current consideration.
5. Canadian Science Publishing cannot supply the requester with the original artwork or a "clean copy."
6. If the Canadian Science Publishing material is to be translated, the following lines must be included: The authors, editors, and Canadian Science Publishing are not responsible for errors or omissions in translations.

v1.4

If you would like to pay for this license now, please remit this license along with your payment made payable to "COPYRIGHT CLEARANCE CENTER" otherwise you will be invoiced within 48 hours of the license date. Payment should be in the form of a check or money order referencing your account number and this invoice number 501350327. Once you receive your invoice for this order, you may pay your invoice by credit card. Please follow instructions provided at that time.

**Make Payment To:
Copyright Clearance Center
Dept 001
P.O. Box 843006
Boston, MA 02284-3006**

For suggestions or comments regarding this order, contact RightsLink Customer Support: customercare@copyright.com or +1-877-622-5543 (toll free in the US) or +1-978-646-2777.

Gratis licenses (referencing \$0 in the Total field) are free. Please retain this printable license for your reference. No payment is required.
