FORAGING STRATEGIES OF A PURSUIT-DIVING SEABIRD IN A

DYNAMIC MARINE ENVIRONMENT

by

© Paul Michael Regular

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ABSTRACT

Flexible foraging tactics are critical to survival for predators foraging in dynamic environments. This is especially true for breeding seabirds as they have to fuel their own energy needs and those of their offspring from a fixed breeding site. To succeed parents must employ foraging strategies that maximize overlap with prey through a range of environmental conditions.

Off Newfoundland, breeding common murres *Uria aalge* specialize on capelin *Mallotus villosus*. The spatial and temporal distribution of capelin is, therefore, expected to influence the foraging decisions of murres. Though capelin are predictable in many ways, several physical challenges (travel time, light limitations, etc.) limit the murres' foraging activities. This research focuses on how common murres breeding in Newfoundland deal with their foraging ocean-scape. Integrated analyses of tracking data, colony-based observations, vessel surveys of prey, and physical environmental measurements were used to assess this question.

To deal with environmental change, murres exhibited remarkable behavioural flexibility. Though diel vertical migrations of capelin challenged their diving and visual abilities, murres successfully captured capelin throughout diurnal, crepuscular (twilight), and nocturnal periods. They used moonlight to capture capelin at night and also appeared to rely on non-visual cues to capture capelin under a starlit sky – when virtually no light is available in the water column. Over horizontal scales, murres appear to rely on memory to relocate successful foraging patches and area-restricted search to refine their

foraging efforts. Because capelin tend to occur in predictable patches that are ephemeral at fine scales, this is likely the most efficient strategy. In combination with flexible time budgets, these strategies likely help murres buffer chick-feed rates across a range of prey densities. However, during mismatch between chick-rearing and peak capelin availability, parental murres were unable to fully compensate for limited access to prey and breeding success was consequently reduced. Though murres exhibit remarkable behavioural plasticity, there are limits to their plasticity. Revealing the limits improves our mechanistic understanding of the links between environmental variability and population dynamics.

ACKNOWLEDGEMENTS

"If I have seen further it is only by standing on the shoulders of giants"

- Isaac Newton

While I constantly question if I have seen further, I am certainly thankful for the view provided by several giants. Their knowledge, guidance and encouragement has helped me grow as a research scientist. First, I would like to express my gratitude for the endearing and infectious enthusiasm for research provided by my supervisor Dr. William Montevecchi, you have been a tremendous mentor for me. Thank you for your continuous support and all the thought provoking discussions on seabird ecology, animal behaviour, conservation, oceanography, writing, etc. – the vastness of your knowledge astounds me. I would also like to thank my co-supervisor Dr. Gregory Robertson. You taught me not to fear statistics, code and equations. Though there were several occasions where I was close to quitting on a statistical problem, your advice helped me pull through and figure it out. Thank you for having more faith in my abilities than myself. I owe a special thanks to Dr. April Hedd as well. Though you were not officially a part of my committee, you were like a supervisor to me. I admire your diligent and comprehensive approach to research – I aim to emulate these brilliant qualities. I am also indebted to Fran Mowbray and Dr. Stefan Garthe for serving on my committee and guiding my Ph.D. research with their enlightening fresh perspective. Finally, I consider myself lucky having

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LIST OF ABBREVIATIONS

ARS – Area-restricted search

BMR – Basal metabolic rate

CPF – Central place foraging

DVM – Diel vertical migration

GPS – Global positioning system

LFF – Lévy flight foraging

PAR - Photosynthetically active radiation)

TDR – Temperature-depth recorder

TDLR – Temperature-depth-light recorder

CHAPTER 1 – FORAGING ECOLOGY OF PARENTAL MURRES

Figure 1.1 – Word cloud, generated from thesis text using the 'tm' (Feinerer and Hornik 2013) and 'wordcloud' (Fellows 2013) packages in R, depicting the most prominent terms used throughout.

1.1   Foraging: Constraints and tactics

A central tenet of optimal foraging theory is that natural selection has produced predators that employ behavioural strategies which maximize foraging efficiency (MacArthur and Pianka 1966, Pyke et al. 1977). This assumes that predators have evolved phenotypes that maximize fitness in particular environments. While the degree to which an organism's foraging activities can be adapted to its environment has long been debated (e.g. Pierce and Ollason 1987), the environment faced by an organism is undoubtedly a major selective force. As such, foraging strategies are shaped by a complex interaction between environmental factors (e.g. prey availability) and constraints imposed by phylogenetic history (e.g. sensory limitations).

One phylogenetic constraint experienced by seabirds, birds that spend the majority of their life at sea, is that they must return to land to breed. Breeding seabirds, therefore, have to balance the demands of self- and offspring-provisioning while foraging from a fixed colony (central place foraging [CPF]; Orians and Pearson 1979). Commuting between prey patches and a central place increases energy expenditure and represents a major limitation to time spent foraging. Furthermore, it may be difficult for central place foragers to maintain information about the distribution of their prey since they are separated from prey patches for extended periods. Efficient foraging strategies are, therefore, particularly critical to central place foragers since reproductive success depends on prey delivery rates.

The increased demands of breeding are, in part, why seabirds time breeding to coincide with the seasonal peak in prey availability (Lack 1968, Perrins 1970).

Maximizing temporal overlap between peak energy demand and energy availability should, in theory, ease the burden imposed by rearing offspring from a central place. Indeed, several studies document the reproductive advantages of temporal match with peak prey availability (Hipfner 2008, Reed et al. 2009, Watanuki et al. 2009). Spatial overlap with prey is also important, but seabirds face unique challenges to achieve this goal. First, prey are hidden under the veil of the ocean, which is why seabirds are often considered 'blind' foragers (Sims et al. 2008). Second, prey predictability varies across spatial and temporal scales (Weimerskirch 2007). Both problems make optimal patch choice a moving target. Recent research in optimal foraging theory support the hypothesis that intrinsic Lévy movement patterns help predators maximize overlap with unpredictable and patchy prey (Viswanathan 2011). If prey are somewhat predictable, seabirds may employ more deterministic behaviour, such as area restricted search (ARS) and cognitive maps, to limit search times and increase spatial overlap with resources (Regular et al. 2013). In either case, predators must work within the confines of their psychological and behavioural limitations through efforts to overlap with prey.

Various aspects of seabird physiology, such as sensory and locomotor systems, limit foraging abilities and influence foraging tactics. Sensory systems play a key role in finding prey; vision is particularly important, but olfaction (Nevitt et al. 2008) and perhaps tactile (Grémillet et al. 2005) senses are utilized by some species. The specific capacities of sensory organs are dictated by their adaptive significance and physiological trade-offs. For instance, the amphibious behaviour of seabirds presents major sensory problems to seabirds since optical requirements in air are fundamentally different from

those in water (Lythgoe 1979). This means that the visual systems of seabirds are compromised in both mediums. Analogous trade-offs apply to the locomotory modalities of seabirds. Their amphibious lifestyle means they must trade-off biomechanical efficiency when traveling in air vs. water (Pennycuick 2008). If diving proves evolutionarily advantageous, wings become more efficient for swimming and less efficient for flying (Elliott et al. 2013a). Additionally, eye-sight becomes dark adapted – since light attenuates rapidly in water – making visual foraging more efficient at low light levels and perhaps less efficient at high light levels (Martin 1999). With such trade-offs in mind, foraging strategies and physiological adaptations cannot be optimal across all situations. These examples reiterate that a species' phenotype, and its ecological niche, represents multiple compromises between environmental factors and phylogenetic constraints.

The marine environment is subject to dynamic biophysical variability across both spatial and temporal scales, affecting foraging activities and predator-prey interactions (Domenici et al. 2007). For instance, marine organisms contend with both temporal (i.e. solar cycle) and spatial (i.e. depth) light restrictions. Such restrictions have contributed to the evolution of diel vertical migrations (DVM), whereby prey evade predation by residing in deep and dark waters during the day and move toward the surface at night (Zaret and Suffern 1976). This behaviour directly affects the foraging behaviour of predators at higher trophic levels as predators attempt to track the movements of their prey (Hays 2003). Spatial and temporal variability of oceanographic features – such as fronts, upwelling zones, thermoclines, etc. – also influence the distribution of prey and in

turn influence seabird foraging ecology (Montevecchi and Myers 1997, Ballance et al. 2006). In order to reproduce successfully in variable environments, seabirds must exhibit considerable phenotypic plasticity (Reed et al. 2009). Though mean fitness tends to be buffered by plastic adjustments of behaviour in response to shifting environmental conditions (Walther et al. 2002), there is growing concern that climate change will frequently force conditions that exceed limits to phenotypic plasticity and tolerance (Visser 2008). For this reason, gaining a better understanding of the structure and dynamics of interactions between predators, prey and the environment is critical for appreciating the persistence and stability of specific ecological systems and food web patterns (Dunne et al. 2005).

1.2   Study system

In this thesis, I examine behavioural responses of a pursuit-diving seabird to environmental variability. Specifically, I attempt to gain a better understanding of the foraging patterns of common murres *Uria aalge* in light of constraints imposed by the spatial and temporal distribution of their prey. This research was conducted in the northwest Atlantic marine ecosystem while murres were rearing chicks from a central place. Ultimately, I aim to determine the foraging strategies murres employ to work within their behavioural, physiological and cognitive abilities to effectively deal with the demands of chick-rearing in a dynamic ocean environment.

To successfully reproduce, CPF murres must maintain adequate spatial and temporal overlap with prey. The spatial and temporal distribution of their prey is obviously tied to this goal. In the northwest Atlantic, breeding common murres provision themselves and their chicks primarily on capelin *Mallotus villosus* (Piatt 1987, Wilhelm et al. 2003). Capelin are small, schooling, pelagic fish that lie at the core of the northwest Atlantic food web as they are major consumers of zooplankton and are focal forage fish (Lavigne 1996) in a wasp-waist food web arrangement providing a keystone linkage between lower and upper trophic levels (Buren et al. 2014). Their spatial and temporal distribution could be considered quasi-predictable since patch persistence depends on the spatial and temporal scale considered (Fauchald et al. 2000). One of the most quintessential traits of capelin biology is their seasonal beach spawning behaviour; each year during spring and early summer, capelin migrate from over-wintering areas near the edge of the continental shelf to the coastal waters of Newfoundland to spawn (Nakashima 1992). With the exception of 1991, when a perturbation in the northwest Atlantic delayed capelin spawning by 4 to 6 weeks, the seasonal peak in inshore capelin abundance has been fairly consistent and hence predictable (Nakashima et al. 1997, Regular et al. 2009). Though also interrupted by the 1991 cold water perturbation (Buren et al. 2014), the diel vertical migration (DVM) of capelin represents another predictable behaviour (Mowbray 2002, Davoren et al. 2006). Finally, suitable habitat for staging and spawning along the Newfoundland coast creates persistent aggregations of capelin (Templeman 1948, Davoren et al. 2006). Not all patches are predictable, however; capelin are distributed in hierarchical patches which are generally predictable at large scales but ephemeral at finer

scales (Fauchald et al. 2000, Davoren et al. 2006, Burke and Montevecchi 2009). The abundance and persistence of capelin may be why they are such an important component of the northwest Atlantic food web (Carscadden 1984). Nevertheless, the spatial and temporal dynamics of the distribution of capelin means that murres must face an array of foraging challenges in their pursuit of capelin.

Being a pursuit-diving seabird, common murres use their wings to 'fly' underwater and capture their prey. Murres have taken this adaptation to the extreme and as a consequence have become efficient and agile underwater predators. In fact, of the seabird species that fly and dive, common murres dive the deepest (Piatt and Nettleship 1985, Burger 1991); the only birds that dive deeper than murres are flightless penguins (Elliott et al. 2013a). To maximize foraging opportunities in deeper waters, the eyes of murres – like other deep-diving seabirds – may have become more sensitive to lower light levels (Martin and Young 1984, Martin 1999). Physiological trade-offs, however, mean that these adaptions come at a cost to efficient aerial flight (Thaxter et al. 2010, Elliott et al. 2013a) and perhaps efficient visual foraging at higher light levels (Hall and Ross 2007). Yet, despite compromises to flight and vision, these adaptations allow murres to search volumes of ocean and, perhaps more importantly, exploit subsurface ecological niches which are relatively free from competition from other avian groups (Tuck 1960). Such diving and visual abilities may be crucial for murres to access capelin throughout the diel cycle. The high cost of flight, however, makes the commuting costs associated with CPF particularly pervasive. Associated time and energy costs likely make efficient search strategies critical to murre breeding success. Murres may employ a range of

strategies to minimize flight time and maximize overlap with prey. For instance, innate Lévy movement patterns may optimize searching efforts for patchily distributed capelin (Viswanathan 2011). Alternatively, the hierarchical patch structure of capelin theoretically makes ARS an efficient search strategy (Fauchald et al. 2000). Finally, the persistent nature of some capelin patches facilitates the use of cognitive maps (Davoren et al. 2003a); utilizing knowledge of the distribution of prey patches to optimize foraging patterns has obvious benefits to efficiency (Boyer and Walsh 2010).

Though murres are behaviourally very flexible (Burger and Piatt 1990), costs associated with breeding push murres to the edge of their physiological limits (Elliott et al. 2013b). The economics of chick-rearing likely contribute to the unique 'intermediate' life history strategy of murres (Ydenberg 1989, Houston et al. 1996, Elliott et al. 2013b), whereby chicks fledge at ~20% of adult breeding mass and well before they are able to fly (Sealy 1973). CPF parental murres are unable to sustain the provisioning rates required by larger chicks, regardless of prey availability, forcing early fledging and continued provisioning and development at sea. Likewise, when prey availability drops below a critical level, murres experience difficulty sustaining chick-provisioning (Harding et al. 2007). Because of the murres' K-selected life history strategy (i.e. long-lived heavy investors in individual offspring), such conditions typically translate into reduced chick investment and fledging success (e.g. Uttley et al. 1994). Timing breeding such that chick-rearing, their most energetically demanding phase of breeding, coincides with peak capelin availability is therefore critical to success. This dependence highlights the influences of environmental variability on the timing and predictability of capelin spawning (i.e. peak availability). While behavioural flexibility helps buffer variability in prey availability (Harding et al. 2007),

future climatic warming and variability may increase the severity and frequency of phenological mismatch, potentially overriding buffering capabilities and negatively affecting population persistence and stability (Thackeray et al. 2010). Revealing underlying mechanistic links between foraging ecology and environmental change can therefore aid efforts to model the effects of future environmental change (Grémillet and Boulinier 2009). Through integrative analyses and modeling of murre foraging behaviour and environmental contingencies across multiple spatial and temporal scales, I hope to gain a better understanding of the link between foraging opportunities, environmental change and population ecology.

1.3   General methods

The research in this thesis adds to the growing body of literature utilizing bio-logging devices to study the behaviour of marine organisms and examine responses to environmental conditions (Burger and Shaffer 2008). Specifically, temperature-depth recorders (TDRs), temperature-depth-light recorders (TDLRs) and global positioning system (GPS) devices were used to track fine-scale foraging activities of chick-rearing common murres. Both TDRs and TDLRs record temperature and pressure (depth) every two seconds; TDLRs also record light levels. GPS devices record location every two minutes. Loggers were deployed on murres from two Seabird Ecological Reserves in Newfoundland, Canada: Gull Island (47.26°N, 52.78°W), Witless Bay (~100,000 breeding pairs in the reserve) and Funk Island (49.75°N, 53.19°W; 500,000+ pairs;

Canadian Wildlife Service, unpublished data; Figure 1.2). Sample sizes of deployments

for each study year (2007 – 2011) are shown in Figure 1.3.
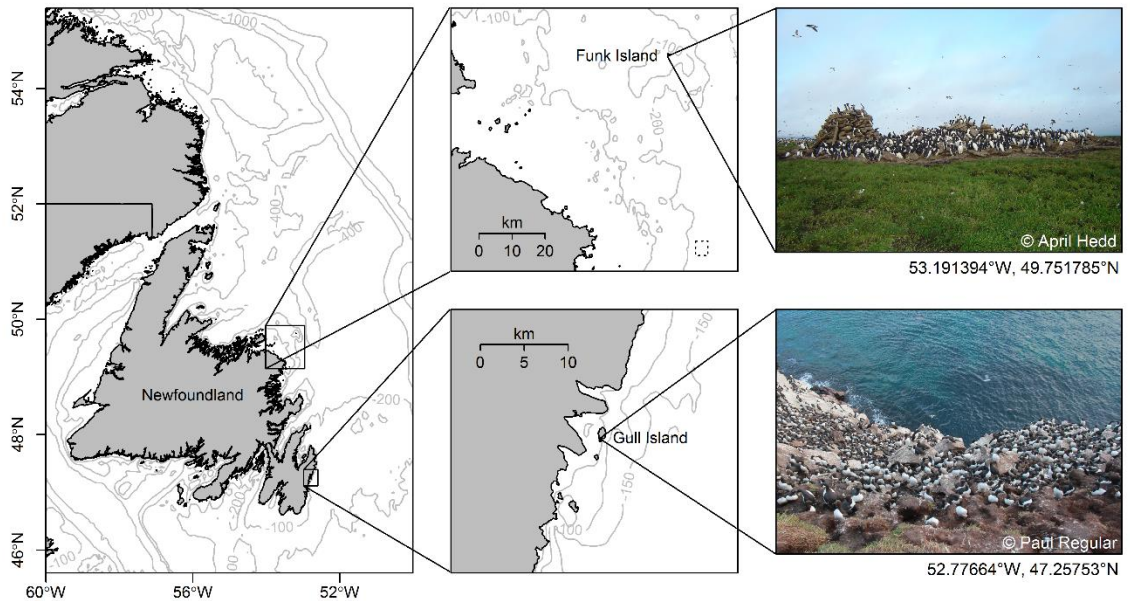
Figure 1.2 – Location of Newfoundland study areas, Funk Island and Gull Island, including pictures of primary study plots on both islands.

Studying foraging behaviour at two colonies using three different types of loggers

allow a range of questions to be asked. TDRs/TDLRs and GPS devices facilitate

assessments of vertical and horizontal movement patterns, respectively. Constraints

experienced by murres are quite different in both dimensions, so both technologies help

reveal how they manage their above- and below-water pursuit of capelin. Biophysical

differences in the ocean-scape faced by murres from Funk Island (large population,

offshore positioning) compared to those from Witless Bay (smaller meta-population,

inshore positioning) have well known consequences to their foraging behaviour and

activity budgets (Davoren et al. 2003a, Davoren and Montevecchi 2003a). Using TDR and TDLR data, I further investigated differences in the activities of murres from Funk and Gull Island, but research direction focused on the general foraging strategies of murres in response to capelin dynamics. Different research programs at both colonies facilitated site-specific questions. For example, fine-scale data collected on the vertical distribution of capelin within the foraging rage of murres from Funk Island allowed comparisons of diel behavioural patterns of murres and capelin (Chapter 2). Additionally, more flexible access to Gull Island allowed more time to collect colony-based observations that could be used in concert with logger data to assess links between foraging ecology and demography (Chapter 5). Though these chapters focused on data collected at specific sites, results are expected to be applicable to both colonies given the ubiquitous nature of the vertical and horizontal (seasonal) migrations of capelin. Likewise, potential device effects were not expected to affect the foraging strategies of parental murres as they likely adjust their activities to compensate for increased locomotory costs (Elliott et al. 2013b). In other words, though they may slightly reduce flight time in response to the attached device, they likely apply the same strategy to maximize overlap with prey.
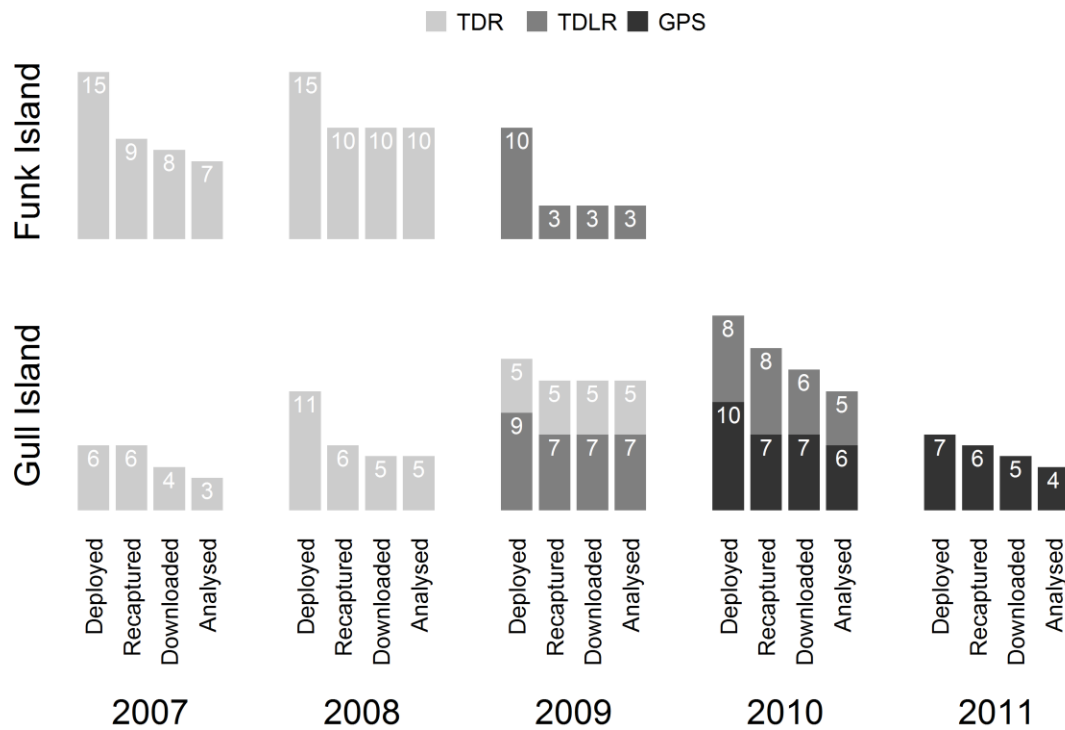
Figure 1.3 – Figure depicting sample sizes of TDR, TDLR and GPS deployments on chick-rearing common murres from Gull and Funk Island.

1.4 Thesis organization

This thesis is organized in manuscript form, wherein Chapters 2 to 4 are based on published works and Chapter 5 is being prepared for submission to a journal. Chapters 2 and 3 focus on the interactive effects of biophysical and physiological constraints to murre foraging. Specifically, Chapter 2 examines the responses of chick-rearing murres to spatial and temporal constraints imposed by DVM capelin. Chapter 3 also examines vertical foraging patterns, except it focuses on the effects of light levels throughout diurnal, crepuscular (twilight) and nocturnal periods. Focus switches to search behaviour

in Chapter 4; this chapter further investigates the strategies parental murres employ –

across both vertical and horizontal dimensions – to efficiently find capelin. Finally,

Chapter 5 attempts to mechanistically link variability in the temporal availability of

capelin to murre foraging activities, energy expenditure, chick-feed rates and

reproductive success. I present a unified discussion of these chapters in Chapter 6.

1.5   Co-authorship statement

Though this dissertation was compiled by myself, the core of my thesis represents a

collaborative effort. This work was initially conceived by my supervisor William A.

Montevecchi and the project was initiated in 2007 with the deployment of TDRs on

murres breeding on Funk and Gull Island. In the first year of the project, WAM and April

Hedd led data collection on Funk Island and I led collection on Gull Island. I initially

started this project as a Masters student with the intention of contrasting the foraging

patterns of murre from Funk and Gull Island. My supervisor, however, had the foresight

to see that the scope of this project could easily constitute a Ph.D, so he advised me to

'roll-over'. In the following years of study, I played a lead role in research planning and

data collection on both Funk and Gull Island with extensive guidance and assistance from

WAM, AH and many others (see Acknowledgements). Subsequent research questions for

the body of my thesis were developed in consultation with AH and my supervisory

committee (WAM, Gregory J. Robertson, Stefan Garthe, Frances K. Mowbray). With the

exception of the capelin data provided by Gail K. Davoren for Chapter 2, I processed all

data. I conducted and interpreted all statistical analyses, with technical advice and direction from GJR, especially for Chapter 5. The text and figures in each manuscript were prepared by myself but AH, WAM, GKD, and GJR provided significant input. Below I provide references for the manuscripts (published and anticipated) that each chapter is based on and I outline specific inputs for each paper:

Chapter 2

Regular, P. M., G. K. Davoren, A. Hedd, and W. A. Montevecchi. 2010. Crepuscular foraging by a pursuit-diving seabird: Tactics of common murres in response to the diel vertical migration of capelin. Marine Ecology Progress Series 415:295–304.

–   *Conceived and designed research:* GKD, PMR, AH, WAM. *Collected data:* PMR, AH, WAM, GKD. *Analyzed the data:* PMR, GKD. *Wrote the paper:* PMR, GKD, AH, WAM.

Chapter 3

Regular, P. M., A. Hedd, and W. A. Montevecchi. 2011. Fishing in the dark: A pursuit-diving seabird modifies foraging behaviour in response to nocturnal light levels. PLOS ONE 6:e26763.

–   *Conceived and designed research:* PMR, AH, WAM. *Collected data:* PMR, AH, WAM. *Analyzed the data:* PMR. *Wrote the paper:* PMR, AH, WAM.

Chapter 4

Regular, P. M., A. Hedd, and W. A. Montevecchi. 2013. Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird. Animal Behaviour 86:545–552.

- – *Conceived and designed research:* PMR, AH, WAM. *Collected data:* PMR, AH, WAM. *Analyzed the data:* PMR. *Wrote the paper:* PMR, AH, WAM.

Chapter 5

Regular, P. M., A. Hedd, W. A. Montevecchi, G. J. Robertson, A. E. Storey, C. J. Walsh. 2014. Why timing is everything: Consequences of resource mismatch for a chick-rearing seabird. Ecosphere *in press*.

- – *Conceived and designed research:* PMR, AH, WAM. *Collected data:* PMR, AH, WAM, AES, CJW. *Analyzed the data:* PMR, GJR, AES, CJW. *Wrote the paper:* PMR, AH, WAM, GJR, AES, CJW.

CHAPTER 2 – CREPUSCULAR FORAGING BY A PURSUIT-DIVING SEABIRD: TACTICS OF COMMON MURRES IN RESPONSE TO THE DIEL VERTICAL MIGRATION OF CAPELIN

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2.1   Abstract

The spatial and temporal distribution of prey directly influences the foraging and feeding behaviour of predators. To investigate predator–prey interactions through the diel cycle, we examined continuous records of diving activity by a pursuit-diving seabird, the common murre *Uria aalge*, in conjunction with fine-scale data on the vertical distribution of their main prey, capelin *Mallotus villosus*, off the northeast Newfoundland coast, Canada. Diurnal patterns in the diving activities of murres closely reflected changes in the vertical distribution and movements of capelin. During daylight hours, 38% of murre dives were deep ($\geq$50 m), bringing murres into sub-0°C water in the Cold Intermediate Layer (CIL; ~40 to 240 m), where 82% of capelin biomass was located. At night, murres concentrated diving activity at shallower depths (98% of dives were <50 m) when 86% of capelin biomass was in the upper water column. Capelin migrated through the water column during twilight periods, moving up at dusk and down at dawn. In response, murres' diving frequency increased and diving depths were graduated, becoming shallower through dusk and deeper through dawn. Crepuscular habits indicate that capelin are more accessible during twilight periods. In summary, though murres are constrained by commuting costs, they show exceptional behavioural flexibility in their efforts to access capelin throughout their diel vertical migration (DVM). The various trade-offs involved in such predator–prey interactions are discussed, as are the ecological consequences of the DVM pattern across trophic levels.

2.2 Introduction

The phenomenon of diel vertical migration (DVM) by zooplankton has broad-scale ecological consequences, directly influencing the foraging behaviour of predators at higher trophic levels (Hays 2003). In general, the pattern involves the movement of zooplankton from deep, dark water depths during the day to shallow depths at night. Migrating zooplankton may experience reduced predation by using dark waters as a refuge from visually orienting predators (predator evasion hypothesis: Zaret and Suffern 1976). Driven by co-evolution, some predators adapt behaviour to exploit vertically migrating prey (Hays 2003).

Diel behavioural adjustments have been observed in a wide range of taxa, including invertebrates (Tarling et al. 2001), fish (Shepard et al. 2006), seals (Croxall et al. 1985) and seabirds (Wilson et al. 1993). Air breathing marine predators that exploit diel prey are faced with added underwater commuting costs, as they must always return to the surface. This constrains maximum foraging depths and the time they can spend foraging. Furthermore, they risk losing contact with prey between dives. These costs are lower at night when vertically migrating prey are near the surface, but this does not necessarily lead to increased foraging efficiency since darkness likely makes it more difficult to locate, capture or handle prey (Wilson et al. 1993, Bost et al. 2002, Hedd et al. 2009, Regular et al. 2011). Although previous studies document diel behavioural patterns of predators and explain them in relation to general patterns of prey and light availability, we know of no attempt to assess fine-scale associations of the timing of vertical

movements of predators and prey. Likewise, few studies address ecological consequences across multiple trophic levels (Levy 1990, Hays 2003).

Among the seabird species that fly and dive, common murres dive the deepest to pursue and capture their prey (Piatt and Nettleship 1985, Burger 1991). In the northwest Atlantic, breeding common murres provision themselves and their chicks primarily on capelin (Piatt 1987, Davoren and Montevecchi 2003b, Wilhelm et al. 2003). Capelin lie at the core of the northwest Atlantic food web, as they are major consumers of zooplankton and are focal forage fish (Lavigne 1996). They adjust their vertical distribution in a DVM pattern to track that of zooplankton prey and minimize predation by northern cod *Gadus morhua*, their primary predator (Mowbray 2002). Breeding murres are constrained by underwater commuting costs and their physiological capabilities. Their energetic costs are the highest during the land-based chick-rearing period as parental murres have to forage and provision their offspring from a fixed colony location (central place foraging; Orians and Pearson 1979). These extreme conditions often push parental seabirds to their behavioural and physiological limits (Elliott et al. 2013b).

As parents provision both themselves and their chicks with capelin, we hypothesized that their diving activities will track the movements of capelin to the extent that their physiology will allow. In other words, we expected that changes in the vertical distribution of capelin would explain patterns in the diving behaviour of parental murres. Furthermore, because energetic demands are high, we also expected that these pursuit-diving seabirds would exhibit flexible foraging tactics. In particular, we predicted that

murres would minimize costs by concentrating foraging activities during periods when their ability to capture prey is the highest. It is during these times that we also expected the birds to focus chick-provisioning efforts. We assess these diurnal associations by comparing hydroacoustic survey data of capelin and bird-borne device data from common murres collected in the waters surrounding the seabird breeding colony on Funk Island, Newfoundland, in the northwest Atlantic Ocean. The broad-scale vertical movements of capelin (migrate <300 m; Davoren et al. 2007) and diving capabilities of murres (dive <177 m; present study) make these species excellent candidates to evaluate these associations.

2.3   Methods

2.3.1 Study site

DVM patterns of capelin were studied during a 4 d survey (10 to 14 August 2005) on the 60 m Fisheries and Oceans Canada RV 'Wilfred Templeman' (Davoren et al. 2007) off Newfoundland's northeast coast in eastern Canada (49.25°N, 53.03°W; Figure 2.1). The area was within the foraging range of common murres from Funk Island (49.75°N, 53.18°W; Figure 2.1), the site of the species' largest North American colony (500,000+ breeding pairs; Canadian Wildlife Service unpublished data), at a time when most murres were provisioning chicks with capelin. The waters around Funk Island have a gradually sloping bathymetry, whereby water depth increases with increasing distance from the coast (Figure 2.1). Parental murres therefore have access to a range of water depths as

they can forage at distances >80 km from the colony (Burke and Montevecchi 2009). The

water depth (~270 m) in the capelin survey area extends beyond the murre's known

diving capability (<177 m; present study). The spatial and temporal mismatch in data

collection permits, only indirect comparisons between murre foraging behaviour and

capelin distributions; nevertheless, predator–prey comparisons are informative as the

DVM movements of capelin are expected to be conserved. Coarser-scale research

conducted during June 2000 demonstrated that shoals of maturing and spent capelin

across a range of bathymetries exhibited DVM (Davoren et al. 2006). Thus, with the

exception of foraging activity at shallow inshore spawning sites (<50 m; Davoren et al.

2006), the murres studied here were likely foraging on capelin shoals that underwent

DVM.
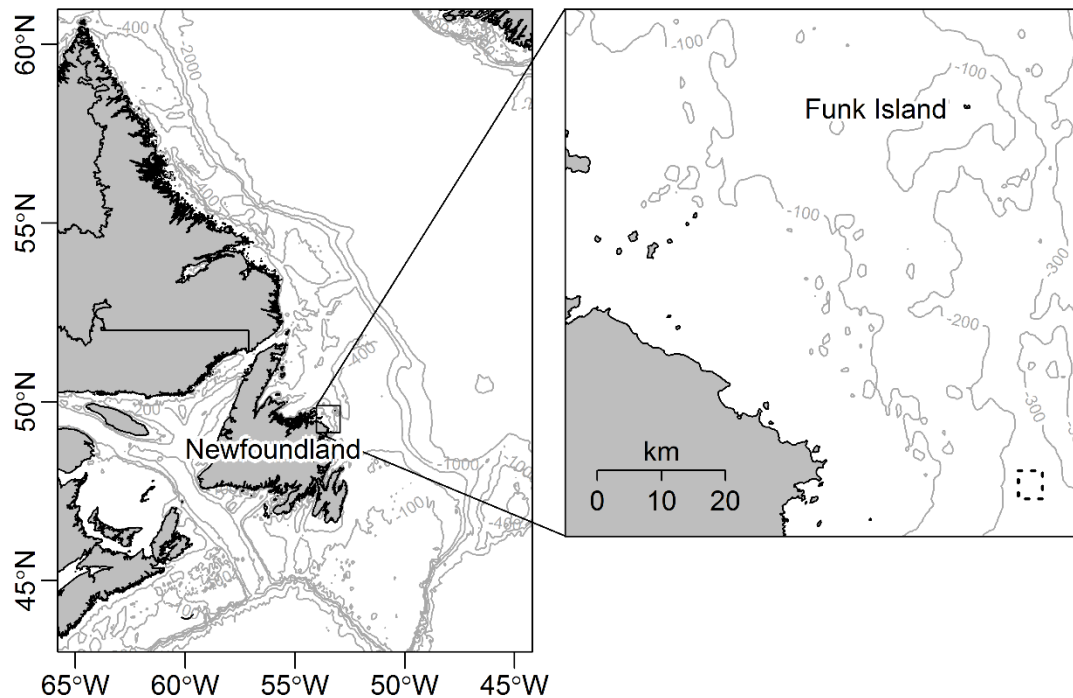
Figure 2.1 – Location of Newfoundland study area, Funk Island and capelin survey area (dotted black square).

2.3.2 Capelin survey design

To quantify the DVM patterns of capelin, we repeatedly collected hydroacoustic data along a star-shaped survey (~30 km) over the main concentration of capelin such that all 1 h time blocks over the 24 h cycle were sampled at least once during the 4 d study. The same survey was repeated ~18 times, resulting in 543 km of acoustic data on the DVM of capelin. Vessel speed (11 to 14 km h^{-1}) was held constant throughout all surveys. A Simrad EK 500 hydro-acoustic system calibrated with a tungsten carbide standard target was used aboard the RV 'Wilfred Templeman'. This system operated through a

hullmounted 38 kHz split-beam transducer. The transducer was at a depth of 4 m and a

beam pattern would not form within a range of 5 m; therefore, acoustic signals were not

reliable until ~10 m. The transducer had a 2-way beam angle of –20.6 dB and the echo

sounder was operated at 1 ping s^{-1} over a depth range of 10 to 300 m, a bandwidth of 3.8

kHz and a pulse duration of 1.0 ms. Raw high-resolution acoustic data (volume

backscattering coefficients, s_v, m^{-1}) were recorded continuously.

2.3.3 Field work on common murres

To study the diving activities of common murres at sea, adults attending chicks were

captured using a telescopic noose pole and were equipped with one of 3 types of

temperature–depth recorders (TDR; <5 g, Lotek LTD 1110, LAT 1500 or 2500). LTD

1110 s (5 g, 11x32 mm; 128 Kb memory) recorded internal device temperature

(resolution ± 0.3°C) and pressure (depth resolution ± 0.49 m when at depths < 125 m and

± 0.98 m when at depths between 125 – 250 m) every 2 s. LAT 1500 and 2500s (3.4 g,

8x35 mm; 512 Kb memory) recorded internal device temperature (resolution >0.05°C)

and wet/dry state every 2 s, and pressure (0.05% resolution) every 2 s when the device

was wet and depth was >1.5 m. TDRs secured to plastic leg bands (Pro-Touch

Engraving) were attached to the left legs of study birds and Canadian Wildlife Service

metal bands were attached to right legs. A total of 40 TDRs were deployed on murres

breeding on Funk Island ($n_{2007} = 15$, $n_{2008} = 15$, $n_{2009} = 10$). Birds were recaptured after ~3

d (range 2 – 7 d), the tag was removed and 0.5 ml of blood was collected from the

brachial vein to determine sex using W-chromosome analysis (Fridolfsson and Ellegren 1999). Birds were handled for ~3 and ~6 min during logger deployment and recapture, respectively. Most birds returned to the chick and resumed parental behaviour within a few minutes of release after deployment and recapture. In total, 22 ($n_{2007} = 9$, $n_{2008} = 10$, $n_{2009} = 3$) of 40 devices were recovered, of which 21 ($n_{2007} = 8$, $n_{2008} = 10$, $n_{2009} = 3$) were successfully downloaded. One record in 2007 was from a parent incubating an egg and was excluded from the analysis. TDRs captured 36-130 h of data; records typically lasted for the duration of the deployment.

2.3.4 Data analysis

All raw hydro-acoustic data files were processed using Echoview 4.0 (Myriax Software). A s_v threshold of −80 dB was applied to the raw data prior to integration, and acoustic signals near the bottom that could not be distinguished as biological or due to the ocean floor (dead-zone, side-lobing; Lawson and Rose 1999) were edited out. The s_v in each file was integrated to determine the average aerial backscattering coefficient (s_a, $m^2\,m^{-2}$) for each 100 m of survey and 10 m depth intervals (MacLennan et al. 2002). The species composition of acoustic signals was regularly sampled throughout the diel cycle using an International Young Gadoid Pelagic Trawl to conduct mid-water trawls (Davoren et al. 2007). Capelin was the dominant fish species sampled (94.7% by mass; G. K. Davoren unpubl. data) and, thus, it was assumed that capelin was the only fish contributing to the acoustic backscatter in the water column. Period by time of day was defined as follows:

day was the period between sunrise and sunset (sun above 0°), dawn and dusk were when

the sun is between 0° and −12° (nautical twilight), and night the point when the sun is

below −12°. The mean proportion of s_a due to capelin over the entire fine-scale survey

was then determined for each 10 m depth interval from 10 to 270 m h^{-1} throughout the

diel cycle. On a finer scale, the mean proportion of capelin by 10 m depth interval was

calculated on a 15 min interval through twilight periods. Data are presented as minutes ±

sunrise and sunset to control for the temporal mismatch with the collection of murre

diving data. Times range from −120 to 30 min from sunrise and −30 to 120 min from

sunset, encompassing the whole of dawn and dusk as well as ~15 min of day and night

for both.

Dive profiles and the timing and maximum depth attained during dives were

extracted using MT-Dive 4.0 (Jensen Software). Further processing and analyses were

conducted using R 3.0.2 (R Core Team 2014). Terminal dives were defined as the last

dive in a foraging trip and were coded manually – it is assumed that chick-feeds are

captured during terminal dives as murres are single prey loaders. As the drift in the zero-

level of the TDRs used exceeded ±1 m in some cases, dives were considered submersions

≥2 m. Dives were categorized into day, dawn, dusk and night, using the definitions

above. To examine patterns in murre diving activity, we plotted frequency distributions

by hour. We tested for a curve-linear trend in dive depths using a generalized additive

mixed model (GAMM), fit with penalized quasi-likelihood, using the 'gamm' function

from the 'mgcv' package (Wood 2006). We used the same function to test linear trends in

diving depths during twilight periods. To control for shifts in sunset and sunrise times

between and within years, minutes ± sunrise (−120 to 30 min) and sunset (−30 to 120

min) were calculated and used in the twilight models. The gamma family (log link) was

used in all models to deal with the zero bounded nature of dive depths and an ARMA

correlation structure (p = 2, q = 0) was applied to account for strong autocorrelation

across dives. Mixed models, with band and date as random factors, were used to account

for individual variation and nested variation across days. Patterns in diving activity and

depths were compared across years and sexes. *F*-tests were used to assess the significance

of effects and model fit was assessed using parameter estimate ±95% upper and lower

confidence intervals. For more details on the general diving behaviour of breeding

common murres see Hedd et al. (2009).

To compare information for capelin and murres, the proportion of capelin present

and the depth of murre dives were separated into shallow (<50 m) and deep (≥50 m)

categories by hour through the diel cycle and by 15 min intervals through twilight

periods. The Labrador Current stratifies Newfoundland waters, creating a Cold

Intermediate Layer (CIL) of sub-0°C water from ~40 to 240 m (Petrie et al. 1988), so this

depth classification acts as a biophysically relevant divide for both capelin (Davoren et al.

2006) and murres (Hedd et al. 2009). This classification facilitates comparisons of broad-

scale patterns while avoiding issues arising from different sampling areas; in other words,

direct comparisons at finer vertical scales are problematic due to the temporal and spatial

mismatch of the data. We also note that murres sometimes forage in shallow inshore

waters (<50 m) on spawning capelin that do not undertake DVM (Davoren et al. 2006).

Shallow diving activity could therefore be inflated overall in the dataset because such

diving activity cannot be excluded from the analysis as the foraging locations of the murres are unknown.

2.4   Results

2.4.1 Vertical distribution of capelin

Over the diel light cycle, capelin exhibited typical vertical migratory pattern, spanning water depths from 10 to 270 m. During dark periods, the highest percentage of s_a due to capelin (86%) was observed in the upper water column (10 to 30 m; Figure 2.2a). In contrast, during daylight periods, the highest percentage of capelin biomass (82%) was found in water >180 m deep, below the CIL (Davoren et al. 2007), and just 18% remained at 10 to 20 m depth (Figure 2.2). During their dawn and dusk migrations, capelin traversed the water column over ~30 min (Figure 2.2b,c). While processing hydro-acoustic files, distinct capelin shoals were observed during the day and through twilight migrations; however, they remained as a scattered layer of individuals at night (see Figure 3 in Davoren et al. 2010).
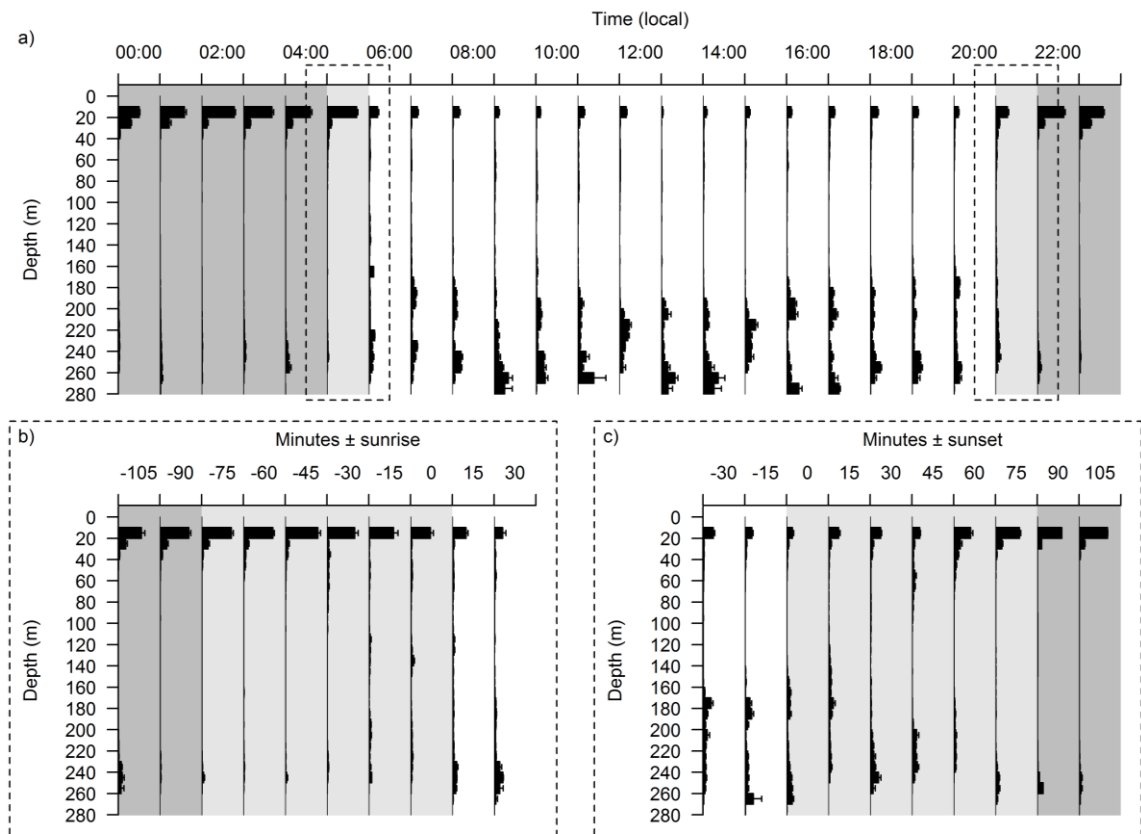
Figure 2.2 – Vertical distribution of percent capelin biomass ± se (scale 0 to 100%) a) by hour, and at 15 min intervals through b) dawn and c) dusk. Shading: twilight (light grey), night time (dark grey), and daytime (unshaded)

2.4.2 Diving by murres
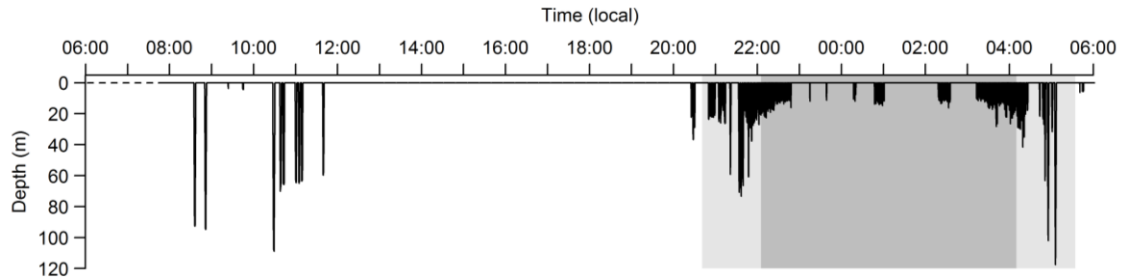
Figure 2.3 – Typical dive profile for a common murre from Funk Island, 25 to 26 July 2007, through day (unshaded), twilight (light grey) and night (dark grey). Dashed lines: periods when the bird was brooding its chick at the colony.

The diving profiles of the murres indicated clear diurnal patterns in the depths attained. Figure 2.3 depicts a typical profile, with the bird diving deeper during the day than at night and displaying graduated patterns in its maximum dive depths during twilight periods. Lumping data for all individuals (n = 20 individuals, 6032 dives), diving activity occurred through the 24 h cycle (Figure 2.4a) with a diel pattern in maximum diving depth, reaching depths up to 177 m during the day and 81 m at night (Figure 2.4b). By constructing a model, including s(time), year, and sex as fixed effects, we found no significant differences across years ($F = 0.977$, p = 0.323) or sexes ($F = 0.938$, p = 0.391). Excluding sex and year from the GAMM, the model indicates that there is a significant curve-linear trend ($F = 15.5$, p < 0.0001) in the diving depths reached by the murres across the 24 h period (Figure 2.4b). For the finer-scale analysis, we found that dive depths increased through dawn [$F = 59.74$, p < 0.0001, $\beta = 0.0095$ (0.0071, 0.012);

Figure 2.4c] and, though at a slower rate, decreased through dusk [$F = 27.02$, p < 0.0001,

β = -0.0054 (-0.0075, -0.0034); Figure 2.4d]. Overall, diving frequency was highest

during dusk and just prior to dawn (Figure 2.4a,b). While diving activity was rapidly

curtailed through dawn (Figure 2.4c), it was at the beginning of dawn and then mid-day

when most terminal (presumed chick-feeding) dives were recorded (Figure 2.4a). There

were no differences in this pattern between sexes.
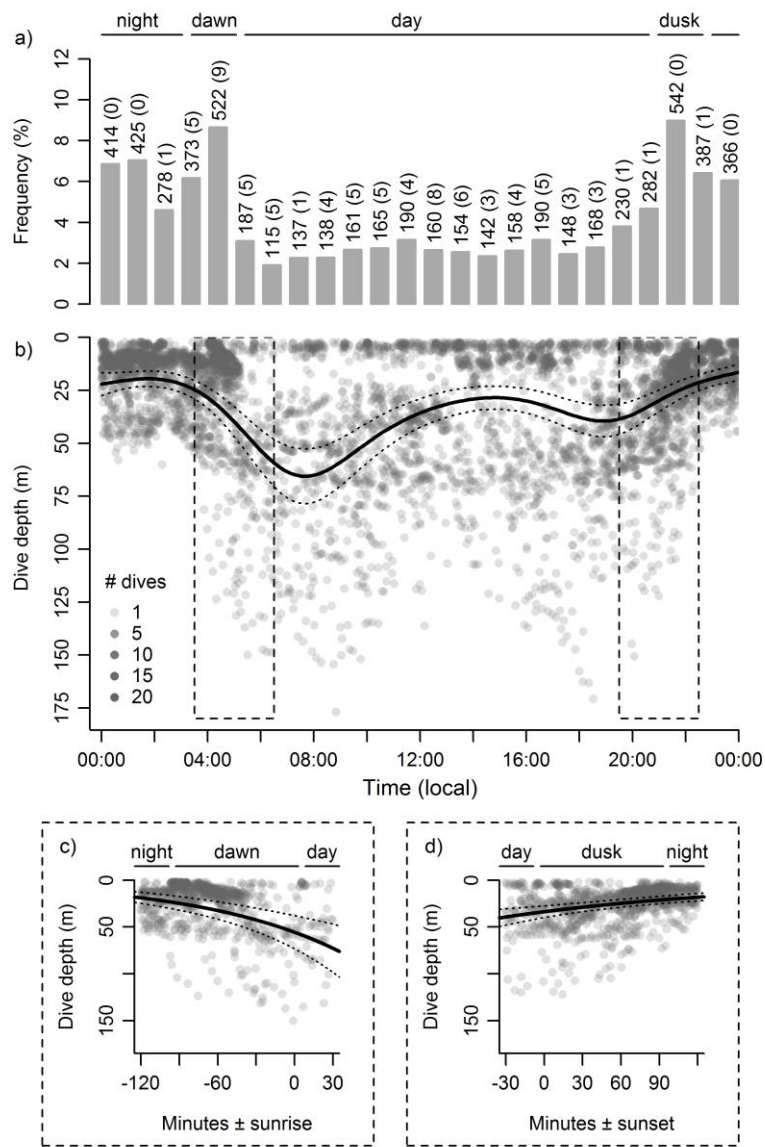
Figure 2.4 – a) Frequency distributions of the timing of dives indicating sample sizes and the number of terminal dives in parentheses, and density scatterplots of dive depth through b) the 24 h cycle, c) dawn and d) dusk for common murres foraging from Funk Island during the chick-rearing periods. Fitted values and confidence intervals indicated by solid and dotted lines, respectively.

2.4.3 Diel associations between murres and capelin

At an hourly scale, the diving activities of murres generally matched the vertical distribution of capelin (Figure 2.5a). During the day, 38% of murre dives were deep and 62% shallow. Comparing this to capelin, 82% of the biomass was in deep water during the day while just 18% was in shallow water. At night, murre diving activity was primarily concentrated at depths <50 m (98%), where most of the capelin biomass was found (86%). On a finer temporal scale during dawn and dusk periods, murre diving patterns generally matched the vertical movements of capelin. As the sun rises, deep dives of murres gradually increase as capelin move deeper in the water column (Figure 2.5b), whereas dives become shallower as capelin move toward the surface as the sun sets (Figure 2.5c).
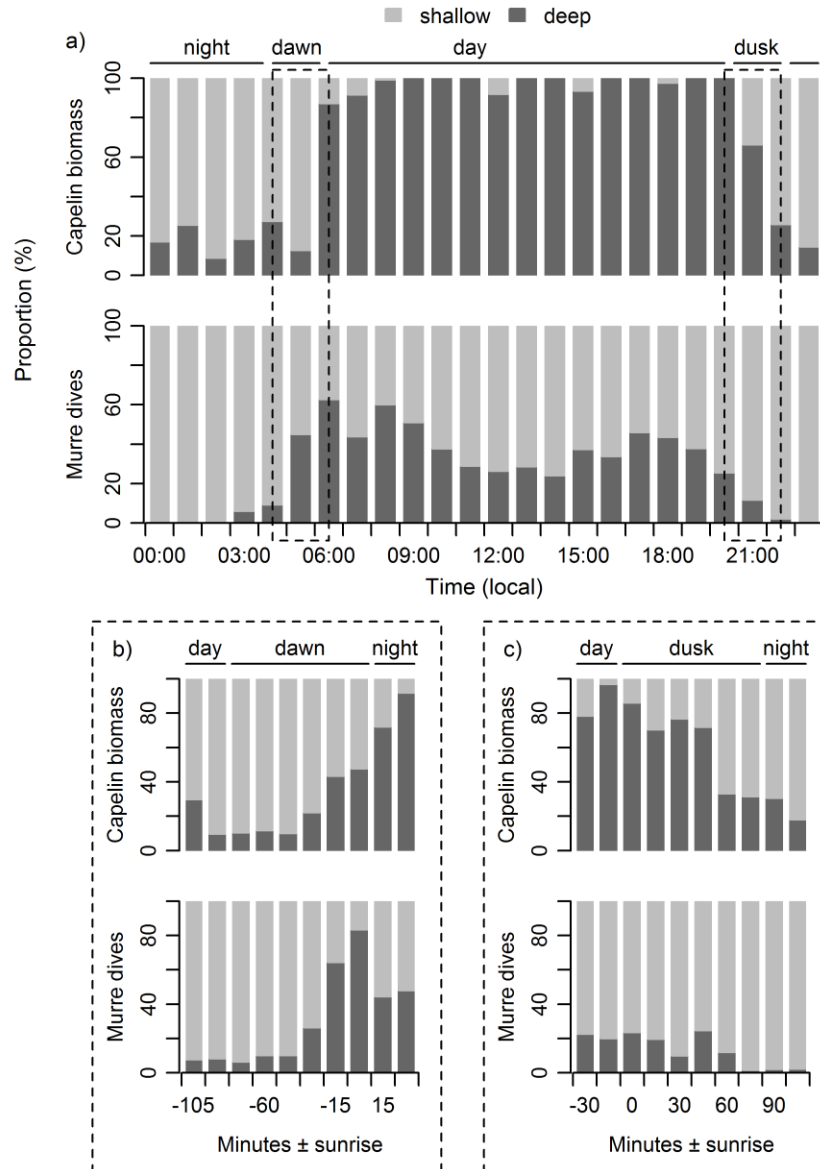
Figure 2.5 – Proportion of shallow (<50 m) and deep (≥50 m) dives by murres in relation to percent biomass of capelin a) by hour and at 15 min intervals through b) dawn and c) dusk.

2.5   Discussion

Predator–prey interactions span trophic levels and occur over multiple spatial and temporal scales (Hunt and Schneider 1987). In the present study, we show that DVM by a forage fish is a pervasive phenomenon, having a cascading effect on the spatial and temporal distribution of an apex seabird predator. The vertical distributions of both capelin and murres are influenced by multiple biophysical factors, each incurring unique limitations. The question is how do both species optimize foraging under such constraints? Furthermore, what are the consequences of such tradeoffs?

Considering limitations imposed by light levels and underwater foraging costs, the murres studied here exhibited an ability to follow the vertical movements of capelin. Owing to the necessity to access capelin to sustain themselves and feed their offspring at the colony (Davoren and Montevecchi 2003b), their diving activities largely reflect the distribution of accessible capelin through the day, night and twilight. During daylight hours, murres frequently made deep dives to pursue capelin in cold water with low light levels. At night, murres dove in the dark, foraging on capelin at shallow depths. Tighter associations were apparent during twilight periods when the birds executed the fine-scale spatial and temporal changes in diving depths required to capture migrating capelin. Such behavioural flexibility is needed to maximize overlap with capelin undertaking broad-scale vertical movements (Davoren et al. 2007).

For diving birds foraging primarily on DVM prey, foraging opportunities may be the best during twilight periods because prey are accessible near the surface when light intensities are high enough to allow efficient prey detection and capture (e.g. great

crested grebes foraging on smelt, Piersma et al. 1988, emperor penguins feeding on Antarctic krill, Zimmer et al. 2008). Murres performed most dives at dusk when capelin were migrating toward the surface. Few terminal dives were observed during dusk; thus, the birds appear to be concentrating on self-feeding efforts at a time when prey are most accessible and detectable. Furthermore, dusk is the last chance in the day to 'easily' capture prey, as low night-time light levels likely compromise foraging success (Wilson et al. 1993, Bost et al. 2002, Zimmer et al. 2008, Hedd et al. 2009, Regular et al. 2011). Moving into dawn, the birds again increase diving activity. As the sun rises, capelin migrate down the water column, increasing underwater commuting costs for murres as they have to pursue the fish toward the bottom. Focusing foraging activity at the start of dawn may therefore be the most effective strategy. The birds studied here did exactly that and, based on the large number of terminal dives, appeared to be taking this opportunity to capture prey for their chicks. Indeed, previous research has shown that chick provisioning rates by murres are highest around dawn (Burger and Piatt 1990). Though the energetic requirements of chicks after a night fasting may necessitate early morning foraging efforts, the behaviour of capelin likely facilitates prey capture and delivery. In short, the presumed higher prey accessibility during dawn and dusk appear to be used as opportunities for chick and self- feeding, respectively. Such crepuscular activity likely helps maximize prey intake and chick provisioning rates.

Though capelin along Newfoundland's northeast coast are located below the CIL during the day (Davoren et al. 2006), parental murres are capable of diving deep to access them (Hedd et al. 2009). They frequently make deep dives through the day, though they

made more shallow dives than would be expected given the distribution of capelin in the water column. Many shallow dives however may represent foraging efforts in shallow coastal water (Figure 2.1). Indeed, murres aggregate and forage at off-beach spawning sites of capelin in shallow coastal water (Davoren 2007). Foraging efficiency is presumed to be higher in these areas due to reduced underwater commuting costs and high light availability, but this benefit comes at the costs of flying ~60 km to the coast – this is no cheap venture as murres experience very high flight costs (Elliott et al. 2013a). Furthermore, time constraints limit the distance to which parental seabirds can forage from the colony (Ichii et al. 2007). If the birds decide to minimize flight time and forage in areas with deep bathymetries near the colony, they may decide to forage on the low proportion of capelin that remain near the surface. Nevertheless, nearly 40% of murre dives take them into deep waters to access shoals of capelin at depth. Regardless of higher underwater commuting costs, it may be profitable for murres to dive deep as capelin are more abundant and are more concentrated in distinct shoals at deeper depths during the day (Davoren et al. 2006). Furthermore, murres may be better able to capture capelin when hunting at depth because the sub-0°C waters of the CIL compromise the burst/escape speeds and recovery times of fishes (Hedd et al. 2009). Murres continue to forage at night when capelin are near the surface. Hedd et al. (2009) showed that common murres experience decreased foraging efficiency at night (indicated by an increase in the number of dives per bout). This is thought to be a consequence of both a reduction in light levels and an increase in the ability of capelin to escape foraging murres in warmer surface waters.

Similar diurnal patterns in diving depths and frequency have been documented for common murres foraging in other low-latitude areas (Monterey Bay, California, 36°N, Nevins 2004, Scotland, 56°N, Thaxter et al. 2009); however, at higher latitudes, such patterns are not observed (Hornøya, Norway, 70°N, Tremblay et al. 2003). This dichotomy has also been found in the diving behaviour of closely related thick-billed murres (c.f. Croll et al. 1992, Falk et al. 2000, Mehlum et al. 2001, Jones et al. 2002). Diel diving rhythms are presumed to be related to diel migrations of local prey. The lack of such rhythms suggests that prey do not undergo DVM during permanent daylight; however, this has yet to be confirmed with congruent studies of prey behaviour.

It is important to consider that capelin too forage on DVM prey (Davoren et al. 2007). This means that the diel patterns observed in murres are ultimately driven by the diel movements of the zooplankton which capelin rely on and follow. Thus, the ecological consequences of DVM act not only over multiple spatial and temporal scales but also across trophic levels. Deviations from the typical diel pattern in capelin and murres may be explained by the various trade-offs involved in pursuing prey, avoiding predators and acting within the tolerances of behavioural and physiological limits. For a seabird that can fly and dive, common murres have exceptional diving capabilities (Piatt and Nettleship 1985, Burger 1991); however, they are ultimately limited by maximum diving depth and visual acuity. The maximum depth recorded for a common murre via TDRs is 177 m (present study). Capelin migrate to depths of 300 m (Davoren et al. 2007) and further in deeper water (Mowbray 2002). Thus, depending on the bathymetry of an area, capelin can be inaccessible to diving murres during the day. The study area near

Funk Island has a gradually sloping and variable bathymetry, decreasing in depth toward the coastline (Figure 2.1). Murres breeding on Funk Island forage on shoaling capelin in persistent patches in a range of bathymetries from the colony to the coast (Davoren et al. 2003a, 2003b, 2006, Davoren 2007), which tend to be <200 m. Foraging murres therefore have to trade-off flight and dive costs when deciding to forage near the colony in deeper waters or to fly to the coast and forage on capelin in shallower water. Commuting costs are much less of an issue for capelin, but unlike murres, capelin have the added factor of predation risk to contend with. Capelin therefore have to adjust their DVM pattern to optimize foraging while minimizing predation risk by northern cod (Mowbray 2002, Davoren et al. 2007). Indeed, deep cold water and warm surface water can act as refugia from predation by cod, their main historical predator, because the inhabited temperatures are outside the range typically occupied by cod (Rose and Leggett 1989, Mowbray 2002). Though capelin can find refuge from cod, the diving capabilities and visual acuity of murres allow them to exploit these fish in deep, dark and cold waters by day and in dark, shallow waters by night.

Until recently it has been difficult to assess associations between the diel vertical movements of predators and prey. This is due primarily to the difficulty in conjointly tracking apex marine predators and their prey. Improvements in technology, however, allow for the investigation of such predator–prey interactions in more detail (Hays 2003). Combining diving data from murres with hydro-acoustic data on capelin allowed for detailed comparisons of DVM patterns. Associations are resolvable even though the murre and capelin data were collected in different years and different, though nearby,

areas. The differences in murre diving and capelin distribution may be in part related to spatial and temporal mismatch, but we suspect they are largely due to the trade-offs faced by foraging murres. Considering the trade-offs, it is clear that murres have adapted their behaviour to exploit vertically migrating capelin. Co-evolution continues. We speculate that predation pressure from marine birds, fish and mammals – major consumers of capelin (Bundy et al. 2000) – may be selective forcers favouring the vertical migration of capelin in the northwest Atlantic. DVM is one of the most widespread and pervasive movements of animals in the world (Hays 2003). Insight regarding its ecological consequences could aid in predicting the influences of potential DVM disruptions forced by ocean climate change (e.g. Mowbray 2002). Murres exhibit great potential to act as indicators of such disruptions owing to their sensitivity to changes in the vertical distribution of capelin.

CHAPTER 3 – FISHING IN THE DARK: A PURSUIT-DIVING SEABIRD MODIFIES FORAGING BEHAVIOUR IN RESPONSE TO NOCTURNAL LIGHT LEVELS

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3.1   Abstract

Visual predators tend not to hunt during periods when efficiency is compromised by low light levels. Yet common murres, a species considered a diurnal visual predator, frequently dive at night. To study foraging of murres under different light conditions, we used a combination of archival tagging methods and astronomical models to assess relationships between diving behaviour and light availability. During diurnal and crepuscular periods, murres used a wide range of the water column (2–177 m), foraging across light intensities that spanned several orders of magnitude (10^3–10^{-10} W m^{-2}). Through daylight and crepuscular periods, light intensity at depth was often equivalent to ambient moonlight (~10^{-4} W m^{-2}) but rarely equivalent to starlight (~10^{-8} W m^{-2}). At night, murres readily foraged during both moonlit and starlit periods, and diving depth and efficiency increased with nocturnal light intensity, suggesting that night diving is at least partially visually guided. Whether visually guided foraging is possible during starlit periods is less clear. Given the dense prey landscape available, random-walk simulations suggest that murres could benefit from random prey encounters. We hypothesise that murres foraging through starlit periods rely either on close-range visual or possibly nonvisual cues to acquire randomly encountered prey. This research highlights the flexibility of breeding common murres and raises questions about the strategies and mechanisms birds use to find prey under very low light conditions.

3.2   Introduction

The foraging abilities and activity patterns of visual predators are strongly influenced by light levels (McMahon and Holanov 1995, Fraser and Metcalfe 1997, White et al. 2007, Zimmer et al. 2008). Because prey detection depends on sufficient lighting, visual predators tend not to forage when efficiency is compromised by low light levels (Wilson et al. 1993, Jetz et al. 2003). In the marine environment, visually orienting predators contend with both temporal and spatial (i.e. depth) light restrictions. Such restrictions have contributed to the evolution of diel vertical migrations (DVM), whereby prey evade predation by residing in deep and dark waters during the day and move toward the surface at night (Zaret and Suffern 1976). Predation pressure has also favored the evolution of lunar cycles in DVM patterns of zooplankton (Gliwicz 1986). Solar and lunar light availability therefore has pervasive effects on the foraging decisions of marine predators since it influences not only their ability to hunt visually, but also the vertical distribution of their prey (Wilson et al. 1993, Horning and Trillmich 1999, Zimmer et al. 2008).

To maximize foraging opportunity, many deep diving marine predators have evolved large, sensitive, dark-adapted eyes (Martin and Young 1984, Levenson and Schusterman 1999, Martin 1999). The caveat is that visual adaptations for foraging at one light level generally compromise efficiency at another (Hall and Ross 2007). Owing to incompatible visual adaptations, species that forage through a wide range of light conditions likely experience the greatest visual constraints. Such species might even use non-visual cues to capture prey when foraging in conditions beyond their visual

capabilities (Grémillet et al. 2005). Indeed, it is not uncommon for marine predators to rely on alternate senses (e.g. tactile) to acquire prey through various conditions (Mouritsen 1994, Janssen 1996, Dehnhardt et al. 2001, Martin et al. 2007). Common murres *Uria aalge*, the deepest-diving flying species, are visually orienting pursuit-diving seabirds that in Newfoundland, Canada forage primarily on capelin *Mallotus villosus*, a DVM forage fish (Piatt 1987, Wilhelm et al. 2003). To maximize overlap with their prey, breeding murres forage through diurnal, crepuscular and nocturnal periods and appear to adjust diving depths according to the DVM of capelin (Hedd et al. 2009, Regular et al. 2010). These foraging patterns expose murres to low light levels through the diel cycle. Such activity may have selected for improved visual sensitivity in murres (Hall and Ross 2007), though visually guided foraging may be ineffective under starlit conditions (Sanford and Harris 1967). In this paper, we report on the use of a combination of archival tagging methods (temperature-depth recorders [TDRs] and temperature-depth-light recorders [TDLRs]) and astronomical models of light availability to investigate how light levels influence the foraging activities of murres.

3.3   Methods

3.3.1 Archival tagging

Archival TDRs and TDLRs were deployed on chick-rearing common murres during July and August, 2007–2010, at two Seabird Ecological Reserves in Newfoundland, Canada:

Gull Island (47.27°N, 52.77°W), Witless Bay (~100,000 breeding pairs in the reserve) and Funk Island (49.75°N, 53.18°W; 500,000+ pairs [Canadian Wildlife Service unpublished data]). Adults were captured using a telescopic noose pole and equipped with an archival tag (Lotek Wireless; either TDR [LTD 1110 or LAT 1500] or TDLR [LAT 2500]). LTD 1110s (5 g, 11x32 mm; 128 Kb memory) recorded internal device temperature (resolution ± 0.3°C) and pressure (depth resolution ± 0.49 m at depths < 125 m, and ± 0.98 m at depths between 125 – 250 m) every 2 s. LAT 1500s (3.4 g, 8x35 mm; 512 Kb memory) recorded internal device temperature (resolution > 0.05°C) and wet/dry state every 2 s, and pressure (0.05% resolution) every 2 s when the device was wet and depth was > 1.5 m. LAT 2500s recorded the same parameters as the LAT 1500s, in addition to light intensity (uncalibrated units) every 2 s when the device was wet and depth was > 1.5 m. TDRs and TDLRs were secured to plastic leg bands (Pro-Touch Engraving) and attached to the left legs of study birds; a Canadian Wildlife Service metal band was attached to the right leg. At Gull Island, 22 TDRs ($n_{2007} = 6$, $n_{2008} = 11$, $n_{2009} = 5$) and 17 TDLRs ($n_{2009} = 9$, $n_{2010} = 8$) were deployed on chick-rearing murres. At Funk Island, 30 TDRs ($n_{2007} = 15$, $n_{2008} = 15$) and 10 TDLRs ($n_{2009} = 10$) were deployed. Birds were typically recaptured after 3 days (range 2 – 7 days); three birds were recaptured the year following deployment. Birds were handled for ~ 3 min and ~ 6 min during logger deployment and recapture, respectively. 53 of 79 devices (67%), were recovered, of which 47 of 53 (87%) were successfully downloaded. Two records were excluded from analyses: one Gull Island bird that lost its chick and one Funk Island bird that was incubating. The analysis therefore included 13 TDR ($n_{2007} = 3$, $n_{2008} = 5$, $n_{2009} = 5$) and 12

TDLR ($n_{2009} = 7$, $n_{2010} = 5$) records from Gull Island, and 17 TDR ($n_{2007} = 7$, $n_{2008} = 10$) and 3 TDLR ($n_{2009} = 3$) records from Funk Island. Device memory lasted 36 h for LTD 1110s and ~150 h for LAT 1500s and 2500s. Records typically lasted for the duration of deployment.

Dives were considered submersions ≥ 2 m since drift in the zero-level of TDRs and TDLRs exceeded ± 1 m in some cases. Using MT-Dive 4.0 (Jensen Software), the start and end time for each dive was determined, as well as the following parameters: maximum depth, bottom time and post-dive pause duration. Bottom time was defined as time elapsed between the first instance when vertical velocity dropped below 0.5 m s^{-1} and the last instance when it rose above 0.5 m s^{-1} (Halsey et al. 2007). Further processing and analyses were conducted using R 3.0.2 (R Core Team 2014). Bouts were defined using maximum likelihood using the 'diveMove' package (Luque and Guinet 2007, Luque 2007), and diving efficiency (bottom time/[dive+pause duration]; Ydenberg and Clark 1989) was calculated for each bout.

Uncalibrated light readings from LAT 2500 TDLRs were calibrated to irradiance in W m^{-2} using a photosynthetically active radiation (PAR; 400 to 700 nm) sensor (Biospherical Instruments). Light level was varied for both devices through 32 synchronous deployments at water depths ranging from 0 to 290 m at sites between Funk Island and the northeast Newfoundland coast. TDLR sensor showed a strong log-linear response to PAR sensor irradiance readings, giving the following regression equation: output = 12.75*ln(irradiance) + 349.04 ($R^2 = 0.97$, $p < 0.0001$). TDLRs were not sensitive enough to detect light when irradiance dropped below 10^{-4} W m^{-2}. This allowed

the capture of complete light profiles for most dives, however light levels for nocturnal dives and the bottom portions of many twilight dives were not recorded. Minimum light intensity was directly calculated for dives with complete light records. For individual twilight dives with missing light data, light levels were predicted using dive specific attenuation values in those instances where sufficient numbers of light records (n > 10) enabled detection of a trend. In other words, available light and depth data allowed the prediction of light levels experienced through the darkest portions of twilight dives. In such cases, predicted minimum light intensities were used. The absence of light records from nocturnal dives meant that minimum light intensities were not detected, nor could they be predicted. For these nocturnal dives, astronomical models were used to estimate light levels experienced.

3.3.2 Astronomical model

For diving activity when in-situ light measurements were unavailable (TDR and night TDLR records), light levels were estimated using astronomical models. Similar to Zimmer et al. (2008), sun angle (°) and absolute solar irradiance (W m^{-2}) for Gull and Funk Island were calculated using the formula in Iqbal (1984). Measures of moon angle, phase and absolute irradiance (W m^{-2}) were based on calculations in Jensen et al. (2001). Twilight light levels were not estimated because of a lack of available models. Global irradiance (light intensity at the water's surface) from the sun and moon was calculated after correcting for extinction of absolute irradiance from the earth's atmosphere and

cloud cover. At St. John's, Newfoundland, Canada, global solar irradiance (measured at Memorial University of Newfoundland:

http://www.physics.mun.ca/chemphysweather.html) was approximately 60%, 50% and 20% absolute solar irradiance during clear, partially cloudy and cloudy periods, respectively (cloud cover data from Environment Canada: http://weather.gc.ca/). Spatially and temporally explicit estimates of light intensity were therefore calculated by applying appropriate percent extinction values, according to local cloud cover (data from nearest Environment Canada weather stations: St. John's for Witless Bay and Gander for Funk Island), to absolute solar and lunar irradiance. PAR (photosynthetically active radiation) at the surface was then approximated by multiplying total global irradiance by 50% (Papaioannou et al. 1993). To calculate underwater light intensity, an attenuation coefficient of -0.11 m^{-1} (mean attenuation experienced by TDLR equipped birds diving in Newfoundland water; sd = 0.06, n = 1687) was applied to the modeled surface light intensity values. Though there were differences in light attenuation experienced by TDLR birds at several levels (year, colony, individual, etc.), for modeling purposes, the mean value was used to estimate underwater light intensity. Overall, considerable natural variation was not incorporated into the model. This should not, however, limit our ability to detect general trends, especially since model results are used in conjunction with in-situ measurements.

3.3.3 Statistics

Period by time of day was defined as follows: day was the period between sunrise and sunset (sun above $0°$), dawn and dusk were when the sun was between $0°$ to $-12°$ (nautical twilight), and night when the sun was below $-12°$. At night, moonlit and starlit periods were defined as occasions when the moon was above and below $0°$, respectively. Lunar phase was defined according to the percentage of the surface visible: new 0–19%, crescent 20–39%, half 40–59%, gibbous 60–79% and full $\geq$80%. We assessed depth and light utilization by examining diving depths and frequencies across periods. To test for light-related effects at night, diving depths were regressed against light intensities. To account for potential pseudoreplication, we used the 'gamm' function from the 'mgcv' package (Wood 2006) to run generalized linear mixed models (GLMMs), fit with penalized quasi-likelihood, with individual set as a random factor. The gamma family (log link) was used to deal with the zero bounded nature of dive depths and an ARMA correlation structure ($p = 2$, $q = 0$) was applied to account for strong autocorrelation across dives. We also tested the effect of the presence of the moon on diving efficiency using a GLMM with individual set as a random factor. The beta family (logit link) was used for this model since the response is a proportion; this model was run using the 'glmmadmb' function from the 'glmmADMB' package (Fournier et al. 2012, Skaug et al. 2013). Confidence intervals ($\pm$ 95%) around parameter estimates were used to assess the significance of effects. Unless stated otherwise, means are presented with standard error values (mean $\pm$ se).

3.4 Results

The diving behaviour described here is based on 9446 dives from 45 individuals across 114 recording days. Approximately half (4977) of these dives are from murres with TDLRs. By comparing model estimates of light intensities with in-situ measurements from TDLRs, it is apparent that modeled values are a good analog of actual light intensities experienced (Figure 3.1). These data confirmed that light levels experienced by murres during foraging were highest during the day, rapidly declined through twilight and remained low at night (Figure 3.1). Murres dive to extreme depths (max 177 m) only during daylight hours (Figure 3.1). During the bottom phase of daytime dives birds frequently encountered light conditions equivalent to ambient twilight and moonlight levels (Figure 3.1 and Figure 3.2). It was very rare for murres to forage under light intensities equivalent to starlight during the day; light intensities remained $>10^{-8}$ W m^{-2} for $100 \pm 0.02\%$ (range: $99 - 100\%$) of diurnal dives (Figure 3.2). Diving depths and the light intensities experienced rapidly increased through dawn and decreased at dusk (Figure 3.1). During twilight some foraging by TDLR birds occurred with lighting equivalent to starlight (Figure 3.1), but almost all twilight dives ($93 \pm 2.9\%$, range: $61 - 100\%$), were performed with light intensities $>10^{-8}$ W m^{-2} (Figure 3.2). Diving depths were restricted to <50 m at night (Figure 3.1), when murres often foraged with $<10^{-8}$ W m^{-2} of available light; $56 \pm 8.3\%$ (range: $0 - 100\%$) of nocturnal dives occurred in waters with lighting brighter than ambient starlight (Figure 3.1, Figure 3.2). Therefore, while murres rarely forage under extremely dim conditions during diurnal and twilight periods, they readily forage under such conditions at night.
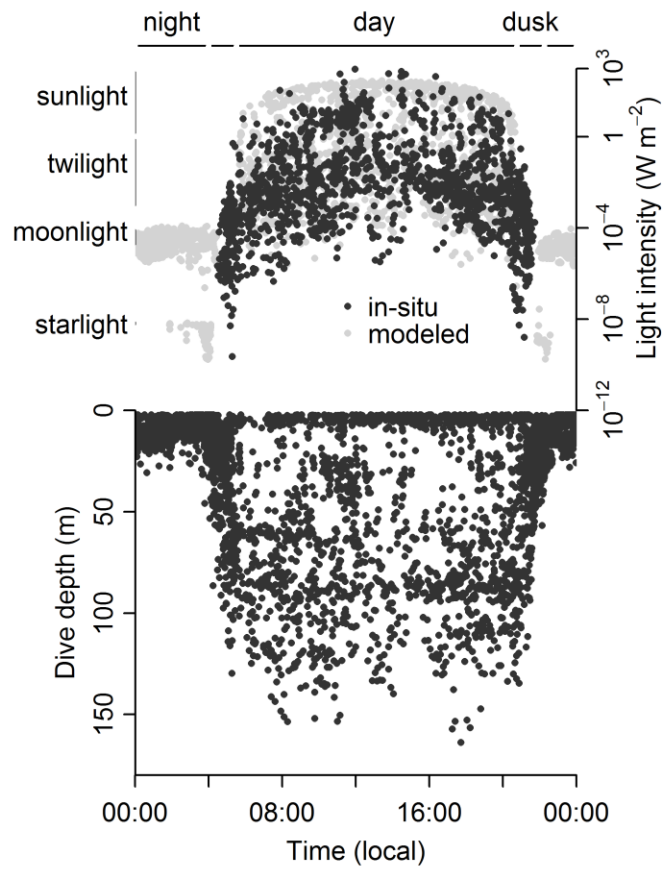
Figure 3.1 – In-situ and modeled minimum light levels and associated maximum dive depths for 15 TDLR equipped murres across the 24 h period. Period duration and range of ambient light levels experienced from the sun, moon and stars are indicated.
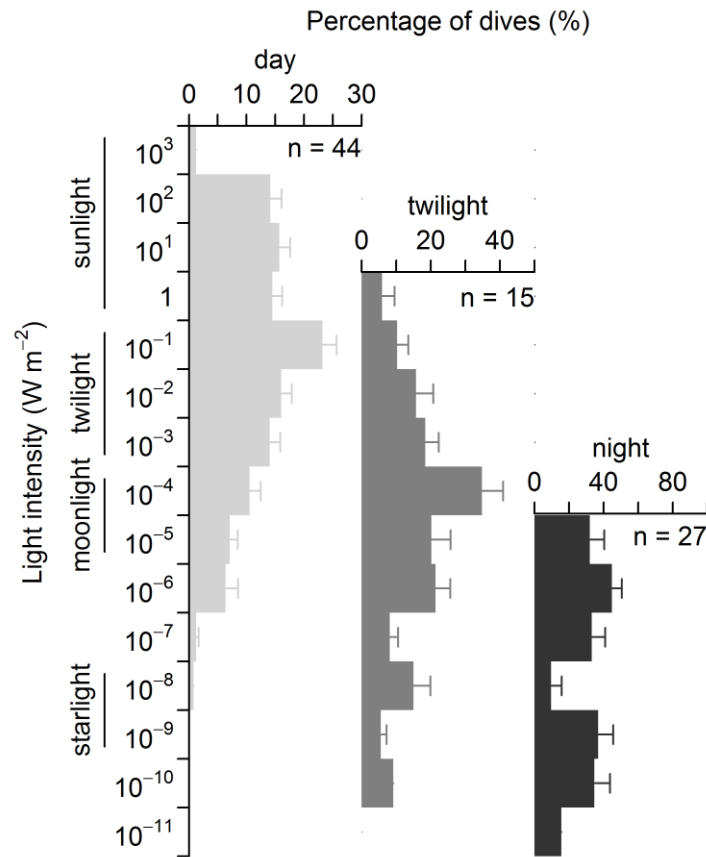
Figure 3.2 – Histograms of light utilization during diving separated by period. Mean ± se values across all individuals (n indicated). Daytime values are based on both in-situ and modeled light intensity whereas the twilight histogram is based solely on in-situ values and the night histogram was generated from modeled values (see methods). Lines left of plot give equivalent range of ambient light levels from the sun, moon and stars.

Murres exhibit considerable variation in nocturnal foraging behaviour. Some birds limited diving activity to periods when moonlight was available (Figure 3.3a) while others dived regardless of the availability of moonlight (Figure 3.3b). Moreover, some individuals made different decisions on different nights. Such variation could be driven

by a number of factors, such as colony specific constraints, individual differences, and/or location specific prey availability. But regardless of this variation, moonlight had a striking and consistent effect on murre diving behaviour (Figure 3.4). Murres increased diving depth with increased lunar irradiance (β = 3469 [LCI = 2407, UCI = 4532]; Figure 3.4a). Though bottom efficiency tends to decrease with increased depth (Hedd et al. 2009), efficiency was significantly improved under a moonlit relative to a starlit sky (odds ratio = -0.77 [LCI = -1.20, UCI = -0.35]; Figure 3.4b). There were no annual or colony differences in these trends.
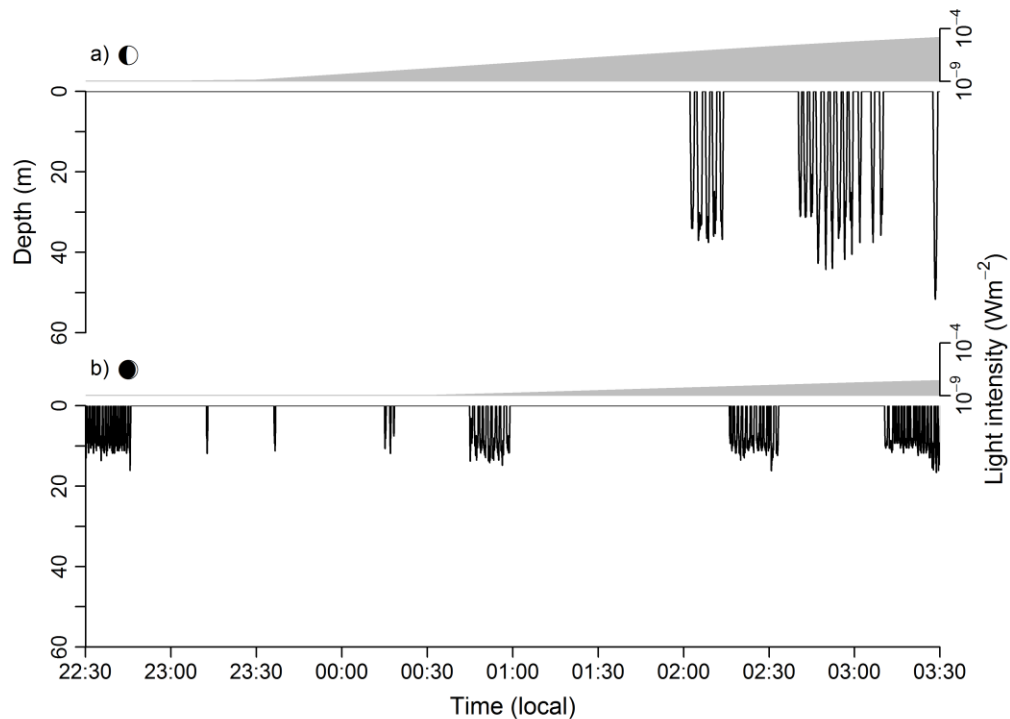
Figure 3.3 – Changes in nocturnal diving behaviour, shown via dive profiles (black lines), in relation to modeled surface light intensity (grey area) from a) one murre diving during a half moon and b) another during a crescent moon.
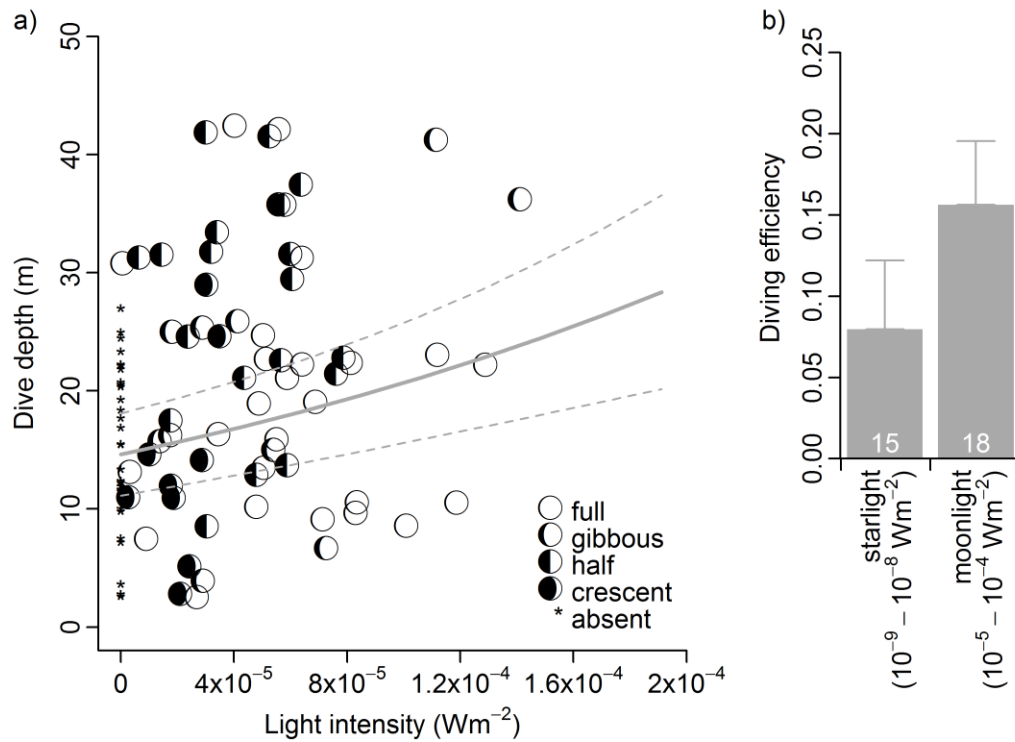
Figure 3.4 – a) Diving depth as a function of light intensity (lines are GLMM fitted values ± 95% confidence intervals; hourly mean values by individual presented for presentation purposes) and b) diving efficiency + 95% confidence interval under a moonlit versus a starlit sky (n indicated).

3.5   Discussion

Murres dived through a broad range of light levels – from sunlit to starlit – as they foraged throughout the day and night. This is perplexing since it seems unlikely that their eyes could be adapted for visually guided foraging across all conditions (Land and Nilsson 2002, Hall and Ross 2007). Previous research suggests that murres are adapted for diurnal and crepuscular hunting (Tuck 1960, Ainley et al. 1990, Regular et al. 2010), implying that they are foraging at the limits of their visual abilities at night. It is

important to consider, however, that deep diurnal and crepuscular diving frequently exposes murres to conditions that match the light available from the moon. Though low light levels can constrain visual abilities and reduce foraging success (Wilson et al. 1993, Bost et al. 2002, White et al. 2007), the propensity of murres to forage under such conditions suggests they are better suited for nocturnal diving than previously thought. Their diurnal and crepuscular foraging activities likely necessitate eyes optimized for visual sensitivity (Martin 1999, Hall and Ross 2007). Such visual adaptations would improve their ability to forage at night, especially when moonlight is available. The eye structure of murres may therefore share features of nocturnal birds. For example, king penguins *Aptenodytes patagonicus* – a pursuit-diving seabird which also forages throughout the diel cycle and experience similar light levels (10^3–10^{-4} lux $\approx$ 1–10^{-7} W m^{-2}; Bost et al. 2002) share similarities in axial length, corneal diameter and maximum pupil diameter with those of nocturnally active tawny owls *Strix aluco* (Martin 1999).

Patterns in murre diving behaviour suggest that moonlight aids visual hunting at night. Light availability during moonlit periods matched conditions experienced during crepuscular and deep diurnal dives. Further, diving depths increase with increased nocturnal light levels. We therefore suspect that foraging is visually guided under moonlit skies. But what of foraging activity during starlit periods when light intensities drop below 10^{-8} W m^{-2}? Murres rarely encounter such dark conditions during diurnal and crepuscular periods yet, contrary to expectations, they readily forage under these conditions at night. Reduced diving efficiency implies that there are behavioural consequences for foraging under starlit conditions. It is unknown whether murres have

the spatial resolution necessary for visual foraging under starlight. Martin (1999) suspects that king penguins lack the visual abilities to detect the outline of individual prey during starlit periods and considers the possibility that their nocturnal foraging activities are guided by the detection of light from the photophores of their prey (Wilson et al. 1993, Martin 1999, cf Bost et al. 2002). Though prey with photophores, such as euphausiids and myctophids, have not been recorded in the diet of murres during the breeding season (Piatt 1987, Wilhelm et al. 2003), it is possible that murres switch to taking such prey under low light conditions. It seems more plausible, however, that breeding murres forage on capelin through the diel cycle since they feed almost exclusively on capelin (Piatt 1987, Wilhelm et al. 2003) and their diving patterns match capelin DVM (Regular et al. 2010). Capelin do not have photophores thus murres are left to rely on ambient light for their detection. Though the murres' visual capacities are unknown, their ability to hunt visually is likely reduced under starlit conditions. If visual detection of prey occurs, it would seem possible only at close range (White et al. 2007), a constraint that would presumably greatly reduce foraging efficiency. Nevertheless, the fact that birds persistently dive during starlit periods suggests that their ability to capture prey is not completely compromised. How then is this possible?

In theory, murres foraging through starlit periods should be able to capture prey they encounter randomly at close range. We explored the viability of this foraging strategy using correlated random walk simulations (Appendix 1) and found that hunting through random encounters could be viable if prey were available in sufficiently high densities. Assuming they are able to detect and capture prey within 15 cm, simulations

suggested that birds would have to forage in capelin aggregations in excess of 0.15 fish m^{-3} in order to gain energy (Figure 3.5). Capelin are not always this dense in Newfoundland waters; density depends on time and place (O'Driscoll et al. 2002). However, capelin occur in coastal aggregations in densities exceeding 0.15 fish m^{-3} during their spawning period (Brian Nakashima, Fisheries and Oceans Canada, personal communications); and such densities have been recorded at night in shallow waters near Funk Island (Gail K. Davoren, University of Manitoba, unpublished data). In general, murres in the present study were rearing chicks during the capelin spawning period, but capelin are patchily distributed (Burke and Montevecchi 2009) and thus prey encounters would at least partially depend on being in the right location. Murres could decide whether to forage during starlight based on knowledge of patch quality gained earlier in the evening, as they tend not to fly/search at night (PMR unpublished observations). Such dynamics likely contributed to the variable nocturnal foraging patterns observed in this study.
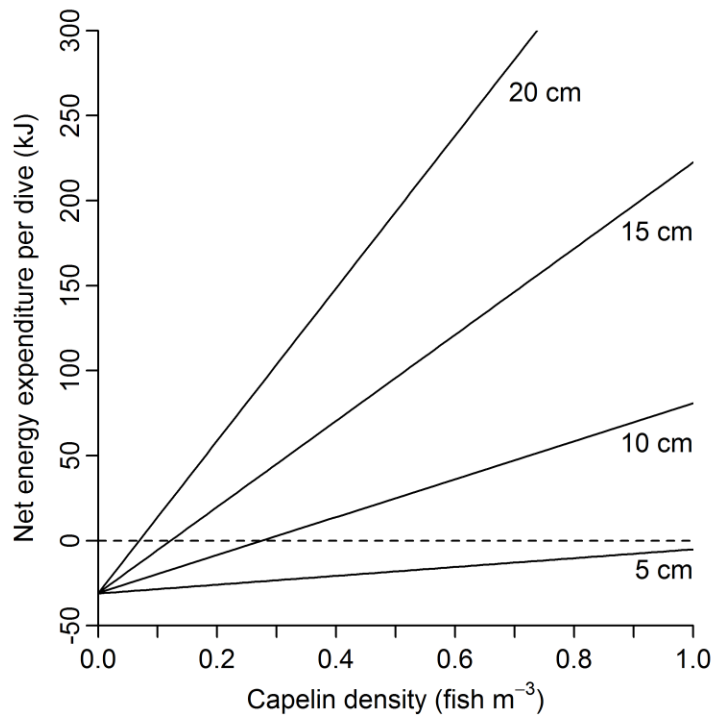
Figure 3.5 – Modeled relationship between capelin density, detection distance and net energy expenditure per dive (black line). Results are based on 200,000 three-dimensional correlated random walk simulations.

The murres' nocturnal diving behaviour might also provide information about capelin vertical distribution. Increases in murre diving depths with heightened nocturnal light levels might indicate that capelin limit their vertical migration under these conditions. Galápagos fur seals *Arctocephalus galapagoensis* exhibit a similar response to lunar light, and this change was attributed to vertical shifts in prey distribution (Horning and Trillmich 1999). Murres track the diel vertical movements of capelin (Regular et al. 2010) and it is common for diel vertical migrants to adjust their vertical distribution at night according to lunar cycles (Horning and Trillmich 1999). Thus,

perhaps murres dive deeper during moonlit periods to access prey located deeper in the water column.

In conclusion, we interpret our data to indicate that murres use moonlight to hunt visually at night but that they may switch foraging tactics when diving during starlit periods. If murres are able to visually detect prey under starlight, then the distance at which this is possible is likely to be greatly reduced relative to forging during moonlight. We hypothesise that murres foraging through starlit periods rely on close-range visual and/or non-visual cues to capture prey that are encountered randomly. Our research revealed aspects of a species' behavioural ecology which caused us to rethink their foraging abilities. Like several other deep diving marine predators (Martin and Young 1984, Levenson and Schusterman 1999, Martin 1999), murres may indeed possess exceptionally sensitive eyes. By the same token, they may rely on alternate sensory cues when vision is constrained (cf Mouritsen 1994, Janssen 1996, Dehnhardt et al. 2001, Martin et al. 2007). Though the physiological mechanisms behind the murres' ability to hunt through wide-ranging light conditions have yet to be understood, their ability to function through such conditions is a testament to their adaptability.

CHAPTER 4 – MUST MARINE PREDATORS ALWAYS FOLLOW SCALING LAWS? MEMORY GUIDES THE FORAGING DECISIONS OF A PURSUIT-DIVING SEABIRD

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4.1 Abstract

Foraging animals are expected to adapt their movement patterns to their environment in a way that maximizes efficiency. Identifying the search strategies they rely on to achieve this is an enduring question in ecology. Scale-free Lévy and Brownian search strategies have received particular attention as both strategies are considered effective when prey are abundant and Lévy search is thought to optimize success when prey are patchy. Environmental context has been shown to explain Lévy and Brownian movement patterns for various marine predators, but potential effects of habitat structure and cognitive skills are often overlooked. We used bird-borne global positioning sensors (GPS) and temperature depth recorders (TDR) to assess flight paths and dive profiles of foraging parental common murres, *Uria aalge*. Movement patterns while flying and diving were best approximated by Brownian motion even though their primary prey, capelin, *Mallotus villosus*, are patchily distributed. Contrary to expectations, there was virtually no support for Lévy flights. Further analyses revealed that murre foraging activities are not random, but are rather more deterministic. Murres repeatedly returned to previously visited sites (within ~2 km), indicating a role of memory, and they focused foraging activities using small-scale area restricted search (ARS; < 2 km radius). Such behaviour appears to induce movement patterns that reflect the distribution of capelin. These findings highlight the efficacy of assessing deterministic search behaviour when interpreting the movement patterns of animals that may be informed about their environment.

4.2 Introduction

Successful and efficient foraging by predators depends largely on the spatial and temporal distribution of prey and the search strategies used to find them (Bell 1991). Because finding food is crucial to survival, strategies that maximize net energy gain are expected to emerge through natural selection (MacArthur and Pianka 1966). The strategies predators should use to maximize encounter rates with prey are a central, but largely unresolved, issue in ecology (Stephens and Krebs 1986). To help resolve the issue, recent work in optimal foraging theory has drawn extensively from concepts and methods used in statistical physics to quantify diffusion processes, such as Lévy and Brownian flights (Viswanathan 2011). The concept of Lévy flights has received particular attention because it describes scale-free fractal movement patterns that theoretically optimize encounters with unpredictable prey that are patchily or uniformly distributed (Viswanathan et al. 1999). Brownian motion describes more localized searching behaviour, which may be equally efficient when prey are uniformly distributed (Bartumeus et al. 2002). Lévy and Brownian search patterns have been demonstrated in a wide range of taxa, from bacteria to great white sharks (Korobkova et al. 2004, Humphries et al. 2010, 2012, Sims et al. 2011, Hays et al. 2012). The general assumption under the Lévy flight foraging (LFF) hypothesis is that movement patterns represent innate random searching behaviour that maximizes foraging efficiency under specific prey landscapes (Viswanathan 2011). Recent research supports the possibility that such a search strategy could have evolved in response to unpredictable resources (Humphries et al. 2012). In some cases, however, Lévy and Brownian search patterns may be

outperformed and can emerge from processes such as composite Brownian walks (Benhamou 2007), olfactory search behaviour (Reynolds 2012a) or memory-based foraging (Boyer et al. 2006). Nevertheless, most studies accept observed patterns as optimal and scale-free without ruling out other processes.

In nature, resources are rarely uniformly distributed; rather, prey are typically clustered hierarchically with fine-scale high-density patches nested within broad-scale low-density patches. Most predators therefore have to respond to complex heterogeneity at multiple scales in order to maximize overlap with prey (Russell et al. 1992). As such, widespread observations of scale-dependant shifts in movement patterns, commonly termed area restricted search (ARS), have often been interpreted as adaptive behavioural responses to local prey abundance (Tinbergen et al. 1967, Fauchald and Tveraa 2003, Thums et al. 2011). Under this strategy, the forager is expected to travel rapidly across large-scale, low-density prey patches and increase searching effort when it enters finer-scale, higher-density patches (Fauchald 1999). ARS shares similarities with Lévy or composite Brownian random walk models since clustered movements are typically separated by longer steps (Grünbaum 1998). A Lévy distribution may therefore emerge from ARS behaviour, or vice versa (Avgar et al. 2011). The question then remains whether the organism acts autonomously by adjusting foraging decisions based on recent experience or whether behaviour can be explained by statistically optimal movement patterns.

Beyond random or ARS, it is well known that some animals rely on cognitive maps to navigate their environment (Gould 1986, Garber 1989, Laughlin and Mendl

2000). These maps contain information, outside the individual's perceptual range, on the location and perhaps quality of various targets and their geometric relationships (Burt de Perera 2004). Cognitive maps allow predators to make optimal foraging decisions that minimize search time while maximizing overlap with prey. Such deterministic foraging behaviour generates individual space use features like site fidelity (Gautestad and Mysterud 2010, Gautestad 2011) and has obvious benefits for foraging success (Boyer and Walsh 2010). Individuals under the statistical diffusion paradigm are assumed to lack the capacity for spatial memory. The danger with this assumption is that scale-free movement patterns may emerge from spatially aware foraging animals that are interacting with a particular distribution of resources (Boyer et al. 2006). A memory-based strategy, however, is contingent upon the cognitive capacity of individuals and the predictability of their prey (Kamil and Roitblat 1985). In the real world, information is rarely perfect. Resources are often ephemeral and quasi-predictable, and as such a forager capable of applying such cognitive skills may have to rely on a combination of strategies to efficiently acquire prey (Boyer and Walsh 2010).

Efficient search strategies are particularly important to central place foragers raising offspring in a location that is physically separated from their foraging environment (Orians and Pearson 1979). In contrast to free-ranging predators, central place foragers must balance self and offspring provisioning while travelling to and from prey patches. Time spent travelling and searching for prey are critical constraints to reproductive performance since both factors limit provisioning rates (Clode 1993). Central place foragers are therefore expected to employ tactics that minimize time spent

searching for prey. Here we attempt to reveal the foraging strategies employed by parental common murres, *Uria aalge*, using global positioning sensors (GPS) and temperature depth recorders (TDR). During the breeding season in Newfoundland, murres feed themselves and their chicks primarily on capelin, *Mallotus villosus* (Piatt 1987, Davoren and Montevecchi 2003b, Wilhelm et al. 2003). Capelin is a small, schooling, pelagic fish that aggregates in large staging and spawning sites along the Newfoundland coast during summer (Templeman 1948). Capelin are distributed in hierarchical patches, which can be ephemeral but can also be persistent (Davoren et al. 2006, Burke and Montevecchi 2009). Such a system allows for testing scale-free, scale-dependent and memory-based foraging strategies. Since capelin patches are sparse and often unpredictable, our null hypothesis is that murre foraging patterns are governed by innate scaling laws approximated by Lévy flight. Alternatively, murres may utilize deterministic foraging strategies to maximize overlap with prey. Given the hierarchical and quasi-predictable nature of capelin patches, previous research suggests that murre foraging efficiency could be improved by applying ARS (Fauchald et al. 2000) or cognitive maps (Davoren et al. 2003a). These strategies, however, require higher-order sensory abilities not required for Lévy search; it is unclear whether murres have such capabilities. Scale-free search is therefore an important limiting model to test. We realize that these strategies may not be mutually exclusive; depending on navigational and learning abilities, it is plausible that murres rely on a combination of strategies to efficiently acquire capelin. By considering a variety of possibilities, we hope to elucidate the most parsimonious explanation.

4.3   Methods

4.3.1 Study sites and field methods

Research was conducted at two Seabird Ecological Reserves in Newfoundland, Canada: Gull Island (47.26°N, 52.78°W), Witless Bay (~100,000 breeding pairs in the reserve) and Funk Island (49.75°N, 53.19°W; 500,000+ pairs; Canadian Wildlife Service, unpublished data). Archival temperature depth recorders (TDR; < 5 g, Lotek LTD 1110, LAT 1500 or 2500) were deployed on murres from both colonies during 2007 – 2010, and global positioning systems (GPS; ~ 17 g, earth & OCEANS mGPS, Kiel, Germany) were deployed on Gull Island murres in 2010 and 2011. Chick-rearing adults were captured in July and August using a telescopic noose pole and were equipped with an archival tag. TDRs were set to record temperature (accuracy < 0.2°C) and depth (accuracy < 1 m) every 2 s for each dive. TDRs were secured to plastic leg bands (Pro-Touch Engraving, Saskatoon, SK, Canada) and attached to the left legs of study birds. GPS devices recorded locations (accuracy < 20 m) at 2 min intervals and were attached to the back feathers of study birds using Tesa tape. All loggered birds were banded with a Canadian Wildlife Service metal band on the right leg. A total of 79 TDR (39 on Gull Island: $n_{2007} = 6$, $n_{2008} = 11$, $n_{2009} = 14$, $n_{2010} = 8$; 40 on Funk Island: $n_{2007} = 15$, $n_{2008} = 15$, $n_{2009} = 10$) and 17 GPS deployments were made (all on Gull Island: $n_{2010} = 10$, $n_{2011} = 7$). Birds were typically recaptured after 3 days (range 2 – 7 days). TDR birds were handled for about 5 min and GPS birds for about 10 min during logger deployment and recapture. Forty-seven of 53 recovered TDRs and 11 of 13 recovered GPS devices were

successfully downloaded; 45 TDR and 10 GPS records, respectively, were used in the analysis following the exclusion of records that did not capture chick-rearing foraging activity. TDRs captured 36 – 130 h of data (memory limited) and GPS devices captured 28 – 48 h of data (battery limited). These data were processed and analysed using R 3.0.2 (R Core Team 2014).

4.3.2 Data analysis

Lévy and Brownian models were fitted to both flying and diving movement patterns. Flights and dives were identified using temperature and pressure data from TDRs (for methods, see Tremblay et al. 2003). For presentation purposes, the distance (m) of each flight was estimated by multiplying flight duration by 19.1 m/s (estimate of mean flight speed of common murres; Pennycuick 1987) and dive depth (m) was characterized by the maximum depth reached during each dive. GPS data confirmed that flight distance is an appropriate measure of horizontal steps since there were few significant turns within flights (see 4.4 Results). This measure is analogous to the step values used in Humphries et al. (2012) as it represents the distance between landed sites. Nevertheless, for comparison against the TDR-derived distributions, we fitted Lévy and Brownian models to step distances derived from flights from GPS-equipped murres (course alterations $>90°$ were considered significant turns; Reynolds et al. 2007). Similarly, maximum dive depths were used to represent the vertical step length as 99% of dives were U- or V-shaped and unlike W-shaped dives, U- and V- shaped dives lack significant within-dive turns (i.e.

analogous to step values used in Humphries et al. 2010). Unless murres are capable of limiting their foraging efforts to areas where prey encounters are high, neither measure should be confounded by resource detection patterns (sensu Miramontes et al. 2012) because water turbidity likely limits large-scale patch-to-patch visibility of capelin. There were no apparent spatiotemporal shifts in flying behaviour, but clear diurnal patterns in diving behaviour were apparent (Hedd et al. 2009, Regular et al. 2010). Split-moving window analysis (30 min window size; for methods, see Humphries et al. 2010) corroborated these results; thus, diurnal, crepuscular (twilight) and nocturnal dives were analysed separately. Since GPS-tracked murres showed commuting behaviour (see 4.4 Results; Weimerskirch 2007), TDR-derived flight distances were analysed with and without inclusion of inbound and outbound flights. Using methods outlined in Edwards et al. (2007) and Edwards (2011), maximum likelihood estimation (MLE; numerical optimization of likelihood functions performed using R function 'nlm') was used to fit exponential (Exp), bounded exponential (ExpB), power law (Lévy; PL) and bounded power law (Pareto-Lévy; PLB) models to step distributions for all birds combined and on an individual basis (sensu Petrovskii et al. 2011). Values of parameter a were set to 100 m and 5 m for flights and dives, respectively, and b values were set as the maximum observed step length. Exponential (λ) and power law (μ) parameter and log-likelihood estimates were calculated for each model and Akaike Information Criteria (AIC) values computed. Models were ranked by Akaike weights and evidence ratios were computed; best-fit models were considered those with evidence ratios < 2.7 (Burnham and Anderson 2002). Lévy or Brownian type walks were further teased apart by applying the power

spectra and first significant digit methods outlined in Reynolds (2012b). These methods ensure that composite Brownian random walks (mixture of two Brownian walks) are not misidentified as Lévy walks (Reynolds 2012b). The start and end of each flight and dive characterized the time series of significant steps for the spectral analysis (pauses on the surface and at the colony were excluded). Spectral density was calculated using function 'spec.pgram'. Flight distances ≥ 100 m and dive depths ≥ 10 m were used in first significant digit analyses.

To identify zones of ARS, we applied first-passage time (FPT) analysis to GPS data, following Fauchald and Tveraa (2003), using the R function 'fpt' ('adehabitat' package; Calenge 2006). Locations along the whole track were interpolated at a uniform distance interval of 100 m, ensuring that all points along foraging tracks are equally represented (Pinaud 2008). FPT was then calculated every 100 m for a radius r from 1 m to 100 km. Plots representing variance in log(FPT) as a function of r allow the identification of ARS scales by peaks in the variance. ARS could not be tested for murre dives since the devices used in this study could not record underwater horizontal movements.

To assess the potential use of memory, we examined indicators of homing behaviour and site fidelity in murre foraging behaviour. Using GPS data, straightness index (straight line distance/path length; a value of 1 represents the most efficient flight; Benhamou 2004) was calculated for each flight to assess the degree of active orientation between locations. As a coarse indicator of site fidelity, departure bearings were compared to the return bearing from the previous trip (Weimerskirch et al. 2010). Finer-

scale site fidelity was assessed by calculating the distance of each presumed foraging location (sites where birds were sitting on the water) from all locations visited in the previous 48 h; if individuals are site faithful, they are expected to utilize known locations and forage near those sites. Persistent use of areas at-depth were assessed by comparing maximum diving depths of TDR-loggered individuals that performed more than 40 diurnal, crepuscular or nocturnal dives at separate locations (i.e. areas separated by flights). Period and location subsets accounted for spatial and temporal shifts in depth utilization. Pearson correlation was used to test for fidelity in locations (longitude and latitude) and circular correlation tested for fidelity in bearings (package 'circular'; Agostinelli and Lund 2013). Autocorrelation values were calculated for dive depths by location and period. Unless stated otherwise, means are presented with standard errors.

4.4 Results

4.4.1 Scale-free search

Through TDR tagging efforts, 1073 flights (23.8 ± 1.8 flights/individual, range $2 - 57$) and 9446 dives (209.9 ± 43.0 dives/individual, range $5 - 1873$) were recorded from murres foraging from Gull and Funk Islands. Distributions of flight durations and daytime dive depths showed rapid decay and were approximated by Brownian (Exp or ExpB) models (flights: $\lambda \approx 0.0001$/m, dives: $\lambda \approx 0.02$/m; Figure 4.1a). PL and PLB models were not competitive. Ensemble-averaged power spectra (Figure 4.1b) provided further support for Brownian type walks ($\beta \approx 0$) over Lévy walks ($\beta \approx 0.7$). Finally, first

digit distributions (Figure 4.1c) significantly deviated from values expected from Lévy walks (flights: $\chi_8^2 = 643$, p < 0.001; dives: $\chi_8^2 = 6341$, p < 0.001). Results were similar across individuals (see Appendix 2, Figures A2.1-5), for twilight and nocturnal dives, and for flight distances with inbound and outbound flights excluded. The same analyses were performed on flight distance distributions derived from GPS tracks and they yielded similar results.
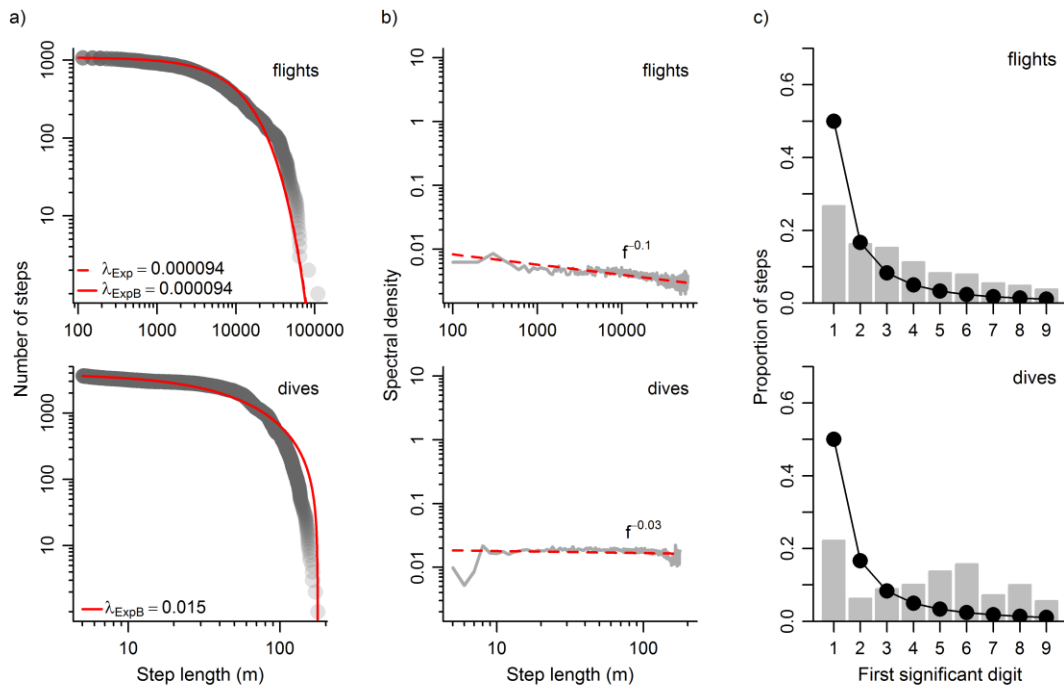
Figure 4.1 – a) Rank-frequency distribution showing model fits and parameter estimates of μ and/or λ for best-fit exponential (Exp), bounded exponential (ExpB), power law (Lévy; PL) and bounded power law (Pareto-Lévy; PLB) models. b) Ensemble-averaged power spectrum of the time series of 'turning points' ($f^{-\beta}$ presented). c) First significant digit distribution (bars); analytic prediction of a Lévy walk with $\mu = 2.0$ is shown for comparison (line) of flight distances and daytime dive depths of all murres fitted with temperature depth recorders.

4.4.2 Area restricted search

From GPS data, we obtained 26 tracks (2.6 ± 0.6 tracks/individual, range $1 - 4$; for a map displaying all tracks, see Appendix 2, Figure A2.6) from murres foraging from Gull Island. While visual inspection suggested little evidence of ARS behaviour, FPT analyses revealed fine-scale peaks in the variance of log(FPT); ARS zones were primarily centred on presumed foraging locations (sites where birds were sitting on the water or diving; Figure 4.2a). Peaks in FPT occurred at a median scale of 1.3 km (range $0.2 - 6.9$ km); 32% of zones were less than 500 m and 68% were less than 2 km (Figure 4.3a). Overall, these results show that murres rarely perform coarse-scale area restricted searches while flying; rather they primarily perform finer-scale searches while they are sitting on the water.
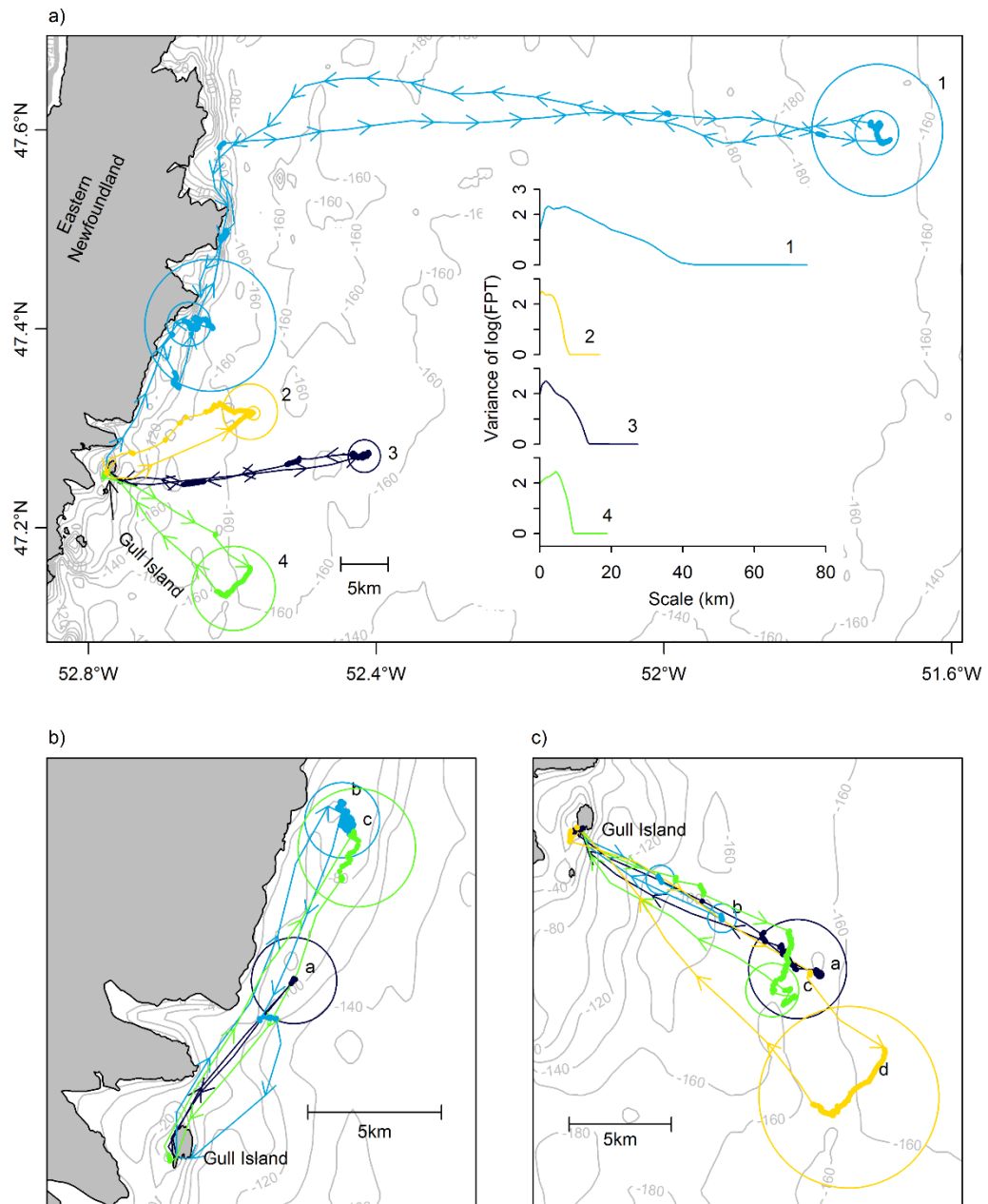
Figure 4.2 – Individual GPS tracks from four loggered murres with a) corresponding plots of variance in log(first-passage time, FPT) and b, c) sequential foraging tracks from two loggered murres. Lines with arrows represent flights, dots indicate fixes where birds were sitting on the water or diving and circles are area restricted search (ARS) zones.

4.4.3 Memory-based search

Taking a sequential look at GPS tracks, the directed nature of murre foraging paths becomes apparent. Foraging tracks of murres from Gull Island revealed several generalities; flights were straight, path headings matched those of return headings from previous trips and locations visited were close to previously visited sites (Figure 4.2b,c). Analyses confirmed that flights were primarily straight; 88% of flights showed a straightness index > 0.8 (Figure 4.3b). This finding supports our contention that flights are directed and involve little active search. Murres also showed a tendency to depart from the colony on the same heading that they used to return to the colony during the previous foraging trip (50% of departure headings were within 20° of return headings of previous trip; Figure 4.3c), although headings were not significantly correlated (circular correlation: $r_{14} = 0.36$, $p = 0.18$). Finally, murres visited sites within close range of sites with which they had previous experience (30% of locations were with 2 km of a previous location; Figure 4.3d); the latitude and longitude of these nearest neighbours were correlated (Pearson correlation: latitude: $r_{41} = 0.80$, $p < 0.001$; longitude: $r_{41} = 0.35$, $p = 0.02$). Autocorrelation values also showed that murres' dive depths were positively correlated, repeatedly taking them to the same general depth (~ 4 dives; Figure 4.3e). Such behaviour is not expected for a randomly foraging predator. These results suggest that horizontal and vertical site fidelity are driven by memory.
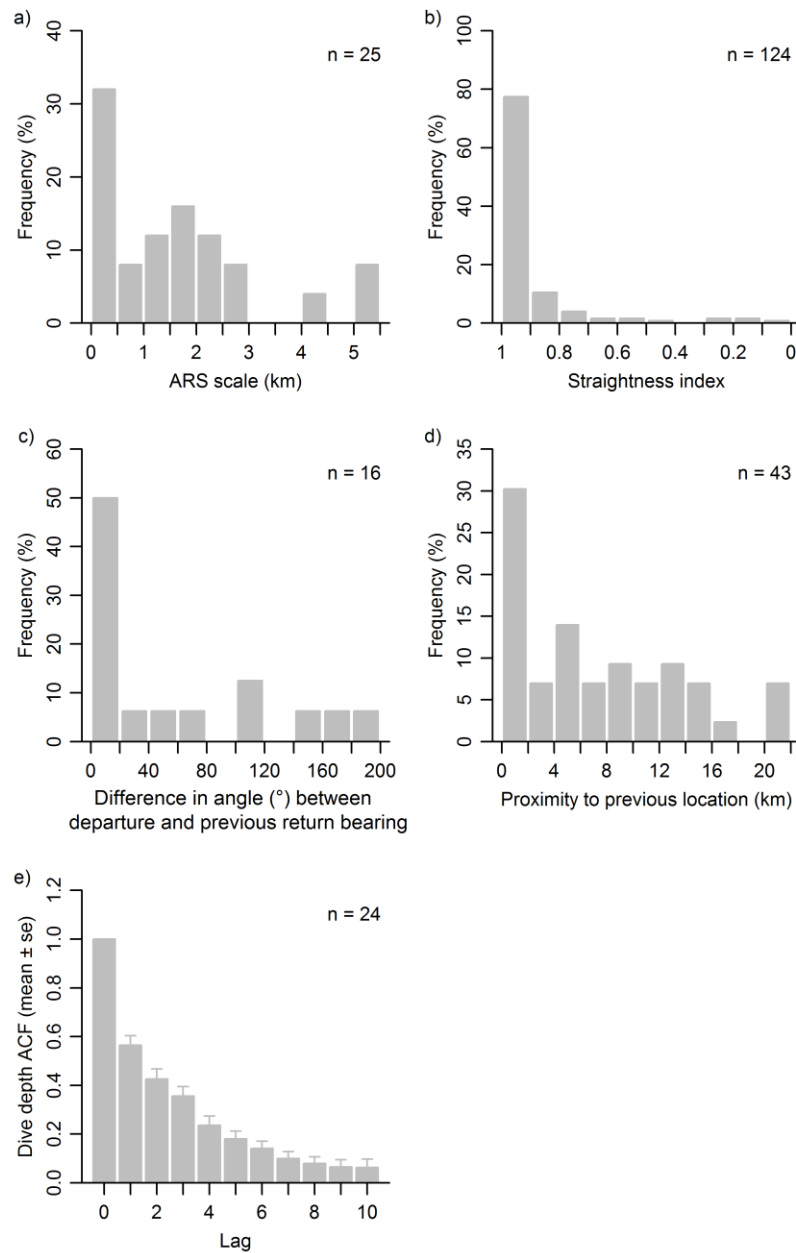
Figure 4.3 – Distributions of the a) scale of area restricted search (ARS) zones, b) straightness index of flights (straight line distance/path length), c) difference in angle between return and departure bearing during the next foraging trip, d) proximity of locations to previously visited locations for murres tracked using GPS devices and e) autocorrelation of murre dive depths from murres fitted with temperature depth recorders.

4.5   Discussion

Despite increasing support for scale-free Lévy search behaviour across a range of species (reviewed in Viswanathan 2011), our analysis provided little support for Lévy flights in murre movement patterns (see also Elliott et al. 2009a, Miramontes et al. 2012). Instead, movement patterns were best approximated by Brownian motion. Under the LFF hypothesis, predators displaying Brownian movement patterns are thought to be searching for abundant and uniformly distributed prey (Humphries et al. 2010). Capelin, however, are distributed in discrete horizontal and vertical patches (Davoren et al. 2006); thus, Brownian motion would be an inefficient strategy to use to maximize overlap with prey (Bartumeus et al. 2002). It therefore seems likely that murres are employing more deterministic strategies to find capelin.

Given the hierarchical distribution of capelin patches, murres are expected to display ARS behaviour (Fauchald et al. 2000). Here we confirm the presence of ARS in murres and show that murres primarily exhibit this behaviour at small scales (< 2 km) when sitting on the water. At this scale, Fauchald et al. (2000) found no overlap between the at-sea distribution of capelin and murres because capelin patches are much more unpredictable at this scale. The murres studied here may have used ARS to find small-scale stochastic prey patches. There was little indication of larger-scale (>2 km) ARS behaviour because of the directed nature of murre flights. Straight flights suggest that murres navigate to and from known locations. This supposition is supported by the finding that murres tended to visit the same general area (~ 2 km) they visited previously. In a landscape where their degree of freedom is hundreds of kilometres, it is impressive

that foraging murres return to the same general area with such consistency. In all, murre search patterns were characterized by relatively long travel times interspersed with small-scale ARS. This strategy is likely reinforced by the spatiotemporal dynamics of capelin patches. As in the Barents Sea, medium-scale capelin patches likely persist for days, and hence are more predictable, than smaller-scale patches (Fauchald et al. 2000). Overall, this indicates that murres may rely on memory to relocate medium-scale patches and use ARS to hone in on the best small-scale patches. This foraging strategy is expected to minimize costly search activity.

Using memory to return repeatedly to previously visited sites might be an efficient foraging strategy given the temporal persistence (both inter- and intra-annually) of some capelin hotspots (Davoren et al. 2003a). In Newfoundland, capelin shoals are often predictable in both horizontal and vertical dimensions. As diel vertical migrants, capelin aggregate near the bottom during the day and migrate to shallower depths at night (Davoren et al. 2006). Previous studies have shown that murres adjust the depth at which they focus foraging activity according to the diel, and perhaps lunar, vertical migration of capelin (Regular et al. 2010, 2011). Although vertical movement patterns within diurnal, crepuscular and nocturnal periods were approximated by Brownian motion, positive autocorrelation of diving depths across multiple dives showed that murre diving activity is directed. This suggests that murres are often aware of the vertical location of capelin and they repeatedly visit the same patch at-depth.

These findings draw attention to the efficacy of assessing both random and deterministic search behaviour when interpreting movement patterns. Sole reliance on the

LFF hypothesis could have led us to assume that murres were foraging for uniformly distributed capelin using a Brownian search strategy. Careful consideration of prey landscape characteristics and navigational abilities, however, suggest that murres utilize information gained on capelin distribution in the short term to guide foraging decisions. Species that utilize cognitive maps can show diffuse properties (e.g. Lévy), but these patterns can simply emerge from the distribution of prey patches (e.g. Boyer et al. 2006). Such appears to be the case for murres; when we plotted the horizontal and vertical distribution of capelin shoals (Figure 4.4; digitized data from Figure 3a in Davoren et al. 2006), patterns and model exponents roughly matched those observed in the flying and diving movements of murres (cf. Figure 4.1a and Figure 4.4).
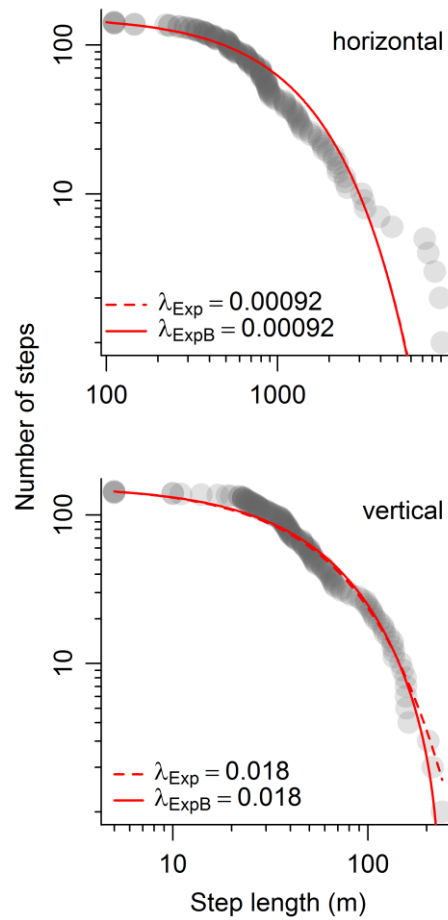
Figure 4.4 – Rank-frequency distribution plots of the a) horizontal and b) vertical distribution of capelin. Model fits and parameter estimates of μ and/or λ are presented for best-fit exponential (Exp), bounded exponential (ExpB), power law (Lévy; PL) and bounded power law (Pareto-Lévy; PLB) models. Data derived from digitized Figure 3a in Davoren et al. (2006). Capelin were assumed to be benthic during the day.

Repeated returns to known capelin patches would be reinforced through repeated success but would extinguish after a few visits of limited success (win-stay/lose-switch rule; Kamil 1983). The searching component of this strategy occurs when predators have

to switch locations. The presence of small-scale ARS behaviour suggests that murres would utilize this strategy when searching at larger scales. Although longer-term tracking efforts may reveal periods when birds utilize Lévy search, it seems likely that murres would use short-term information in combination with that gained through lifetime foraging efforts. Learning how and where to forage is considered a protracted process for seabirds (Lack 1968). Young and naïve seabirds are less proficient foragers than more experienced adults (Daunt et al. 2007). Murres show delayed maturity and spend several years visiting the colony before recruiting into the population (~ 6 years; Halley et al. 1995). This period may be an important life-history stage to gather information on the local environment before attempting to breed, ultimately improving foraging efficiency and future reproductive success. Tracks from naïve juvenile murres could provide insights into the presence of innate Lévy search behaviour; Lévy search should optimize the foraging success of juvenile murres since they lack knowledge of spatiotemporal dynamics of capelin patches.

Foraging decisions may, in some cases, be influenced by local enhancement, a process by which individuals cue in on the foraging activities of conspecifics within their visual range (Wittenberger and Hunt 1985). Game theory predicts that individuals will balance searching effort and competition by actively switching between 'producing' and 'scrounging'. Scrounging is expected to increase when prey patches are difficult to locate but decrease when competition is high (Beauchamp 2008). Thus, depending on circumstances, scrounging may be more efficient than searching or sampling mental maps, and vice versa. Because capelin shoals can be both persistent and ephemeral, a

mixed strategy of memory and local enhancement could be essential (Davoren et al. 2003a). The scale and circumstances under which murres rely on each strategy depends on the resolution of cognitive maps and perceptual range (above and below water), as well as the spatial and temporal distribution of capelin and conspecifics. Working out such detail requires further research

4.5.1 Conclusions

A central assumption of the LFF hypothesis is that predators are foraging for unpredictable resources (Viswanathan 2011). This strategy has been shown to be very efficient for predators searching for stochastic prey (Humphries et al. 2012). Violations of this assumption, however, are easily overlooked given the general assumption that marine predators are foraging for unpredictable resources. This is not always the case (*sensu* Weimerskirch 2007); prey predictability is not uncommon; thus, the ability to retain information regarding the spatial and temporal distribution of prey patches should greatly improve foraging efficiency (Boyer and Walsh 2010). Moreover, many animals are capable of utilizing information gathered while foraging to strategically adjust foraging patterns (e.g. ARS; Fauchald 2009). Although little is known of the cognitive abilities of murres, they are capable of returning to previously visited sites. Of course, their knowledge of prey locations is not perfect; they appear to rely on ARS when information is sparse. This creates horizontal and vertical diffusion patterns similar to the distribution

of their primary prey, capelin. It is therefore important to consider both prey

predictability and cognitive skills when interpreting movement patterns.

CHAPTER 5 – WHY TIMING IS EVERYTHING: ENERGETIC COSTS AND REPRODUCTIVE CONSEQUENCES OF RESOURCE MISMATCH FOR A CHICK-REARING SEABIRD

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5.1 Abstract

Timing reproduction to overlap with peak prey availability is vital to success for many species. This may be especially true for species that rely on one or a few prey species that exhibit strong seasonal peaks in abundance. Any mismatch must be mediated by parents that provision offspring through flexible behavioral changes within the bounds of their physiological tolerances. In Newfoundland, common murre *Uria aalge* breeding coincides with the inshore movement of capelin *Mallotus villosus* – their primary prey – such that peak prey availability overlaps with chick-rearing, the most energy demanding phase of breeding. We use colony-based observations and temperature-depth recorders to track the behavioral responses of murres to temporal match and mismatch with capelin availability. Activity budgets, daily energy expenditure (DEE) and chick-provisioning rates were constant across years when chick and capelin timing matched. However, when capelin were late, despite increasing diving effort and DEE, parents delivered fewer fish to chicks per day and reduced breeding success was observed. While parents partially buffered the effects of variable capelin abundance by reducing co-attendance time (time spent at the colony with mates) and increasing foraging time, physiological constraints on energy output likely limited their ability to maintain chick-provisioning rates in a mismatch year. Such responses could have demographic consequences if ocean climate changes decouple the timing of chick-rearing and prey availability.

5.2   Introduction

Birds that rely on seasonally abundant prey have a limited window to reproduce and, as such, time breeding to coincide with seasonal peaks in food availability (Lack 1954, Perrins 1970). Climate changes, however, are disrupting trophic interactions by altering prey phenology and generating mismatch between peak food supply and energetic demand for predators that fail to adjust their phenology accordingly (Visser et al. 1998, 2011). Mismatches between food supply and energy demand must be mitigated by parents, affecting foraging costs and individual fitness (Thomas et al. 2001). The match-mismatch hypothesis predicts that reproductive success will be high when the adult's most energetically demanding phase of breeding matches peak prey availability (Cushing 1990, Durant et al. 2005). This hypothesis is of great interest today as there is growing concern that climate change is increasing the severity and frequency of phenological mismatch, thereby disrupting trophic interactions and population dynamics (Thackeray et al. 2010).

Predicting how any one system will be affected by climate driven asynchrony is difficult because responses vary by species, population and habitat. While increasing mismatch has reduced fitness and caused population declines for some species (Both et al. 2006, 2010, Saino et al. 2011, Reed et al. 2013), there are no apparent fitness consequences for others (Drever and Clark 2007, Dunn et al. 2011, Vatka et al. 2011). Selective forces ultimately dictate specific responses; reproductive timing will be under direct natural selection if mismatch limits a species' ability to successfully raise their young. Conversely, mismatch may be adaptive if selection is acting on another life-

history trait (e.g. egg production; Visser et al. 2011). In either case, sufficient resources have to be available to sustain reproductive costs, whether they be for egg production or chick provisioning. The economics of parental foraging is therefore a key selective force shaping the evolution of seasonal breeding in birds (Thomas et al. 2001).

Species that rely heavily on one or a few prey species while breeding, such as many seabirds, may be particularly vulnerable to strong temporal mismatch since the availability of key prey species is vital to successful reproduction (Regehr and Montevecchi 1997, Durant et al. 2003, Hipfner 2008, Gaston et al. 2009, Watanuki et al. 2009). Indeed, population consequences have been documented in such systems (Both et al. 2006). Parental common murres *Uria aalge* breeding at Newfoundland colonies primarily rely on capelin *Mallotus villosus* for self-sustenance and chick provisioning (Piatt 1987, Wilhelm et al. 2003, Burke and Montevecchi 2008). Owing to this dependence, hatching generally coincides with the inshore movements of maturing schools of capelin such that peak prey availability overlaps with the chick-rearing period, the murres' most energetically demanding phase of breeding (Cairns et al. 1987, Carscadden et al. 2002). Chick-provisioning rates, fledging weights and success therefore depend on the timing and abundance of capelin (Burger and Piatt 1990, Davoren and Montevecchi 2003b). Though flexible time budgeting allows common murres to maintain chick feeding rates across a wide range of prey densities (Harding et al. 2007), there are limits to their flexibility and mismatch with capelin can override their buffering capabilities (Wilhelm et al. 2008). Harding et al. (2007) showed that when prey density was low murres reduced co-attendance time (time mates spent together at the colony) and

increased foraging time by more than 2 hr/day. In the northeast Atlantic, murres spent

this extra time diving in an attempt to compensate for low prey abundance (Monaghan et

al. 1994). Mistiming breeding in the northwest Atlantic would equate to low prey

abundance inshore, however, the migratory behavior of capelin could mean that prey are

in fact abundant further from the colony (Nakashima 1992). In Newfoundland, breeding

murres could increase flying time to compensate for mismatch with peak inshore capelin

availability. This strategy, however, may be difficult to sustain as murres experience the

highest flight costs of any volant species and operate near physiological limits (Elliott et

al. 2013b).

Though the mechanism remains unclear, sustainable energy budgets of vertebrates

are generally limited to ≤ 7 times basal metabolic rate (BMR; Weiner 1992, Hammond

and Diamond 1997, Speakman and Król 2011). Metabolic rates in excess of $7 \times$ BMR

can of course be achieved in the short-term, but such expenditures must be fuelled by

lipid reserves and not concurrent energy intake (Hammond and Diamond 1997). Chick-

rearing thick-billed murres *Uria lomvia* are thought to be operating near maximum

intensity, leaving a small buffer between performance and capacity (Elliott et al. 2013b).

Thus, continued investment in chick-rearing comes at a cost to lipid reserves if poor

conditions force expenditures beyond sustainable limits. Handicap studies have shown

that thick-billed murres either reduce investment in their offspring to maintain energetic

capability *or* they reduce investment in themselves by running energetic deficits (meta-

analysis in Elliott et al. 2013b). The natural handicap generated by resource mismatch

could impose a similar effect. The question then remains whether common murres will

reduce investment in offspring or themselves when capelin timing and chick-rearing are decoupled? Moreover, how do behavioral responses and physical limitations interactively influence this decision? Here we present an analysis of parental murre behavior at the colony and at sea in response to mismatch with prey and we attempt to uncover the mechanistic links between behavior and prey availability.

5.3   Methods

5.3.1 Study site and field methods

Archival temperature-depth recorders (TDRs; <5 g, Lotek LTD 1110, LAT 1500 or 2500 from Lotek Wireless, Canada) were deployed on chick-rearing common murres during July and August, 2007-2010 at Gull Island (47.26ºN, 52.78ºW), Witless Bay Ecological Reserve, Newfoundland, Canada (~100,000 breeding pairs in the reserve; Canadian Wildlife Service unpublished data). Adults were captured using a telescopic noose pole and were equipped with an archival tag secured to a plastic leg band (Pro-Touch Engraving, Canada) and attached to the left leg; a Canadian Wildlife Service metal band was attached to the right leg. TDRs were set to record temperature (accuracy < 0.2 ºC) and depth (accuracy < 1 m) every 2 s for each dive. A total of 39 TDRs were deployed of which 32 were retrieved (~ 3 days later [range 2-7 days]), 27 were successfully downloaded, and 25 captured chick-rearing foraging activity ($N_{2007} = 3$, $N_{2008} = 5$, $N_{2009} = 12$, $N_{2010} = 5$),. Birds were weighed during each interaction using a Pesola scale.

Handling time was ~3 min and ~6 min during logger deployment and recapture, respectively.

At the same site, ~50 focal breeding sites were observed each year from a bird blind situated < 10 m from a large colony on the island (site 1; Mahoney 1979). Feeding and productivity watches were conducted to calculate prey delivery rates and fledging success, respectively. Feeding watches were conducted during daylight hours (~05:00 to 21:00; most spanned this period) and focused on a subset of breeding sites (~10) that were continuously observed. Pairs in which individuals could be distinguished (e.g. bridled/un-bridled, banded/un-banded pairs) were observed preferentially; the time of arrival, change-over and departure were recorded. It was also noted whether a bird arrived with prey, and if so, the species was recorded. For productivity watches, the breeding status of each focal pair (unknown, empty, egg, chick) were noted nearly every day between the late egg laying and late fledging periods. Murre chicks were considered fledged if they disappeared from their nest site at ≥16 days of age – the minimum fledging age for murre chicks at Gull Island (Mahoney 1979). Hatching and/or fledging success was undetermined for many pairs that were difficult to observe from the blind. Productivity data at site 1 was supplemented with data from another site on the southeastern corner of Gull Island. At both sites, hatching and breeding success may be slightly biased as observations typically began in late-June, following the laying of most eggs; as such, losses of earlier eggs may have been missed.

5.3.2 Capelin timing and abundance

Though quantitative data on the timing and abundance of capelin in the Witless Bay area are not available, data collected by Fisheries and Oceans Canada (DFO) on capelin spawning times and spring abundance were used as a rough index. The timing of capelin spawning has been monitored by DFO in Trinity Bay at Bellevue Beach, approximately 80 km from Gull Island, since the 1990s (DFO 2013). It is likely that capelin timing is relatively consistent between the sites as spawning has been shown to be synchronous at such a scale (Frank and Leggett 1981, Leggett et al. 1984). We therefore assume that the start and end of spawning activity at Bellevue Beach approximates the period during which capelin were available inshore to murres rearing chicks at Gull Island. Our proxy for capelin abundance involved the assumption that local abundance varied in accordance with abundance estimated from spring surveys conducted by DFO on the Grand Bank (see Mowbray 2013 for methods).

5.3.3 Data analysis

The data collected in this study were processed using R (R Core Team 2014) and analyzed using OpenBUGS (Lunn and Spiegelhalter 2009) via the R2OpenBUGS function in R (Sturtz et al. 2005); model building was largely guided by Kéry (2010). Credible intervals (95%) for all estimates were derived from the 2.5% and 97.5% quantiles of the MCMC results generated in OpenBUGS. Five chains were run concurrently with 15,000 repetitions, a burn in period of 5,000 and a thinning of 10. Each

estimated variable had a $\widehat{R}$ value of 1.0 (where 1 is equivalent to convergence). Vague

priors were used for all parameters. Here we consider a trend or difference "significant"

if the credible interval of a parameter or contrast does not bound zero.

Activity budgets (proportion of time spent at the colony, sitting on water, diving

and flying) were calculated for each loggered individual on a daily basis using methods

similar to Tremblay et al. (2003). To ensure typical activity budgeting was captured, the

analysis was limited to days in which individuals were tracked for > 12 h. Compositional

data, such as activity budgets, are peculiar because the components sum to 1; attempts to

apply statistical methods designed for unconstrained data may therefore lead to

inappropriate inference. To account for this numerical constraint, we use a Dirichlet

mixed model (log link) with activity budget set as the response, date and year set as

explanatory variables and individual set as a random effect. As the multivariate

generalization of the beta distribution, the Dirichlet distribution is quite useful for

analyzing compositional data (Hijazi and Jernigan 2009). Applying this distribution

allows for the simultaneous assessment of the effects of covariates on the relative

contribution of multiple activities (Gueorguieva et al. 2008). So for year i, bird j, activity

k and day x_{ij} we fit the following model for the observed vector of proportions $p_{ijk} = p_{ij1}, \cdots, p_{ij4}$:

Distribution: $\qquad\qquad\qquad p_{ijk} \sim \text{Dirichlet}(\alpha_{ijk})$

Linear predictor: $\qquad\qquad \log(\alpha_{ijk}) = \beta_{1,ijk} + \beta_{2,ijk} \cdot x_{ij}$

Random effects: $\qquad\qquad \beta_{1,ijk} \sim \text{Normal}(\mu_{\beta_1(ik)}, \sigma^2_{\beta_1(ik)})$

$$\beta_{2,ijk} \sim \text{Normal}(\mu_{\beta_2(ik)}, \sigma^2_{\beta_2(ik)})$$

Random intercepts and slopes (hyperparameters) were applied to account for repeated measures across the same individuals (Schielzeth and Forstmeier 2009). This model was simplified using the following logic: 1) if there was a lack of covariance in slopes, the contrasting factor(s) were analyzed separately; 2) if there were no clear temporal trends in the global model or sub-models, day was removed as a covariate; and 3) if there were no annual differences, year was removed as a covariate.

The same covariates and model simplification rules were used to model trends in daily energy expenditure (DEE), diving frequency (dives/day), co-attendance time (hr/day), prey delivery rate (feeds/day) and prey composition (percent capelin). To estimate DEE, we first calculate total energy expenditure from the activity budgets of each bird for each day using the highest ranked activity specific energy expenditure model presented in Table 1 of Elliott et al. (2013a) for thick-billed murres. These values were scaled to DEE by dividing total energy expenditure by the proportion of the day captured by the TDR. Likewise, co-attendance time was scaled to hr/day by dividing the observed duration by the proportion of the day observed through feeding watches (feeding watches < 8 hr in duration were excluded). Both DEE and co-attendance time were analyzed using linear mixed models. Diving frequency and the number of prey delivered were analyzed using generalized linear mixed models with a Poisson error structure (log link); proportion of the day observed was used as an offset (feeding watches < 8 h in duration were excluded) to scale the response to dives/day and feeds/day. Our prey composition analysis was limited to identified prey items from all feeding watches across all individuals; since capelin and sandlance, *Ammodytes* spp.,

constitute 99.7% of observed prey items (379/380; only one unidentified flatfish was delivered in 2010), these data were analyzed using a generalized linear model (binomial error, logit link) with proportion of capelin set as the response. Finally, hatching, fledging (proportion of chicks fledged), and breeding success (proportion of eggs resulting in fledged chicks) were analyzed using generalized linear models (binomial error, logit link) with year as the only explanatory variable.

5.4   Results

Based on spawning times at Bellevue Beach, capelin were presumed to be inshore and therefore available to murres throughout the chick-rearing period at Gull Island in all years, except 2009 (Figure 5.1). During 2009, chicks hatched before the onset of capelin spawning; capelin availability probably increased mid-way through the chick-rearing period (Figure 5.1). Estimates of capelin spring abundance on the Grand Bank were similar from 2007-2009 (262,200 – 300,500 t), but dropped 10-fold in 2010 (23,200 t); we therefore assume that this translates into a large, perhaps 10-fold, decrease in inshore capelin abundance (Figure 5.1).
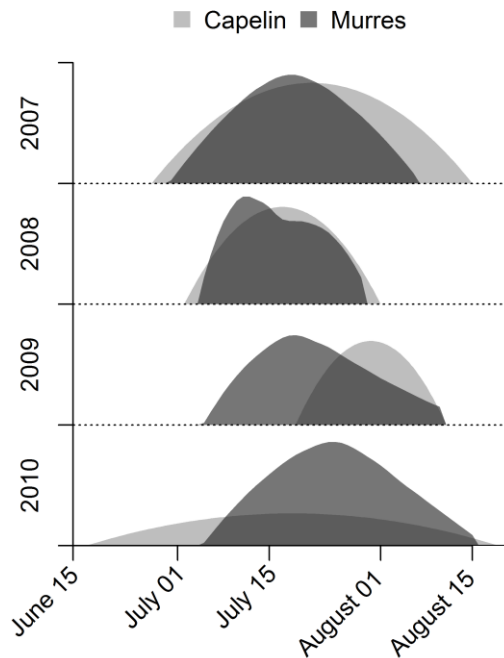
Figure 5.1 – Diagram of the timing and relative abundance of capelin and common murre chicks across years. Capelin curves were generated from best available proxies for local timing and abundance (see Methods), and murre chick curves were derived from direct observations conducted on Gull Island, Witless Bay Ecological Reserve, Newfoundland.

Activity budgets, dive rates and DEE were obtained from 24 birds ($N_{2007} = 2$, $N_{2008} = 5$, $N_{2009} = 12$, $N_{2010} = 5$) across 25 unique dates ($N_{2007} = 4$, $N_{2008} = 4$, $N_{2009} = 10$, $N_{2010} = 7$), and co-attendance time and prey delivery rates were obtained from 66 sites ($N_{2007} = 19$, $N_{2008} = 20$, $N_{2009} = 14$, $N_{2010} = 13$) across 20 unique dates ($N_{2007} = 7$, $N_{2008} = 4$, $N_{2009} = 6$, $N_{2010} = 3$). Global models revealed that 2009 was the only year exhibiting significant within-season change in the proportion of time spent diving, diving rates, DEE and chick feeding rates; prey composition and co-attendance time were apparently

constant through time in all years. Activity budgets, diving rates, DEE and feed rates were similar during 2007, 2008 and 2010 (Figure 5.2a). From 2007-2010, chick-rearing common murres spent 51% (credible interval 36 to 65%) of their time at the colony, 39% (credible interval 26 to 53%) of their time sitting on the water, and just 6% (credible interval 5 to 9%) and 5% (credible interval 4 to 8%) of their time diving and flying, respectively. Each day, birds performed 52 dives (credible interval 39 to 68 dives/day) and provided chicks with 2.8 prey (credible interval 2.4 to 3.2 prey/day). Their activities resulted in an average DEE of 1969.9 KJ/day (credible interval 1761.0 to 2184.0 KJ/day); this value is not far from the their theoretical upper limit to sustainable energy expenditure of $7 \times$ BMR ($7 \times 350 = 2450$ KJ/day; Cairns et al. 1990). Annual co-attendance time ranged from a high of 4.9 hr/day (credible interval 4.0 to 5.8 hr/day) during 2008 to just 1.4 hr/day (credible interval 0.9 to 1.8 hr/day) during 2009. Co-attendance time increased by 2.3 hr/day (credible interval 1.0 to 3.6 hr/day) between 2007 and 2008, it decreased by 3.5 hr/day (credible interval 2.5 to 4.5 hr/day) from 2008 to 2009, and it was similar from 2009 to 2010 (-0.1 hr/day [credible interval -0.9 to 0.7 hr/day]). The proportion of capelin fed to chicks was 99% (141/142), 99% (90/91), 97% (118/121) and 90% (47/52) for 2007, 2008, 2009, and 2010, respectively (Figure 5.3). Contrasts revealed that percent capelin was significantly different only between 2007 and 2010, when it was reduced by 9% (credible interval -2 to -18%).
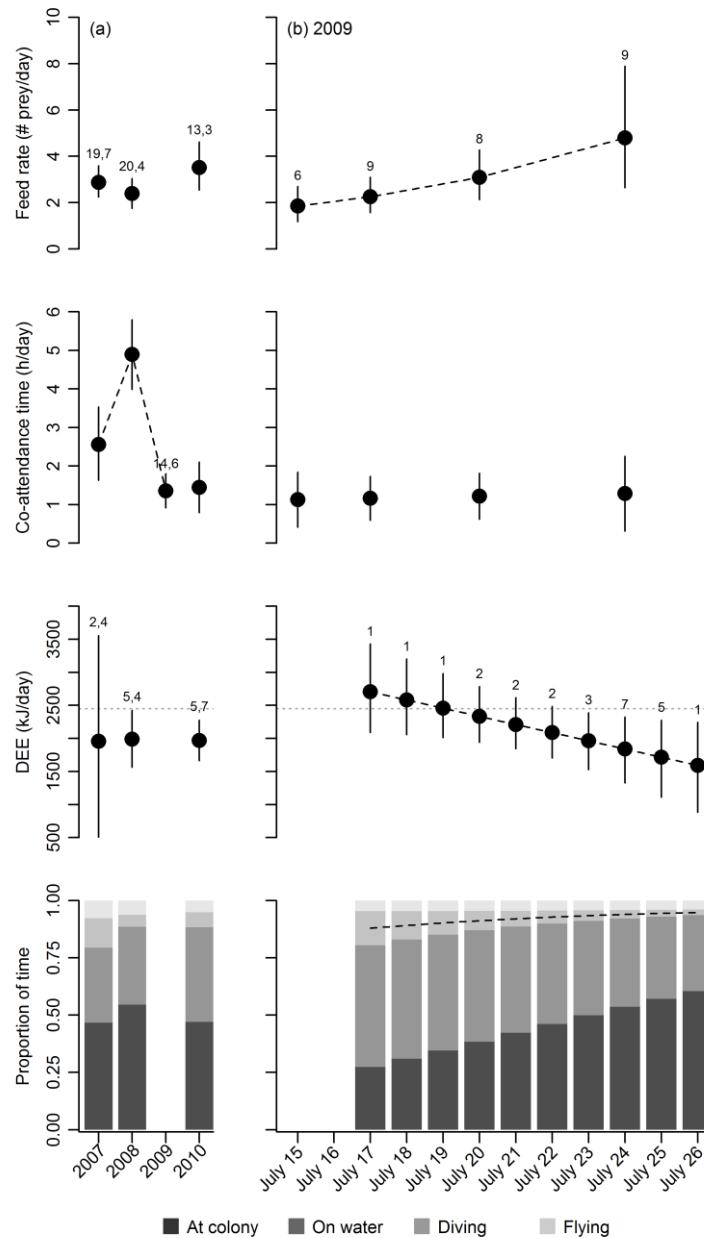
Figure 5.2 – Estimates of feed rates, co-attendance time, daily energy expenditure (DEE) and proportion of time spent at the colony, sitting on the water, diving and flying by chick-rearing common murres a) across all years and b) during 2009. Values indicate sample size (birds/sites, days) and dashed lines indicate significant trends. Grey dotted line indicates theoretical upper limit to sustainable energy expenditure (7 × BMR of 350 KJ/day; Cairns *et al.* 1990).
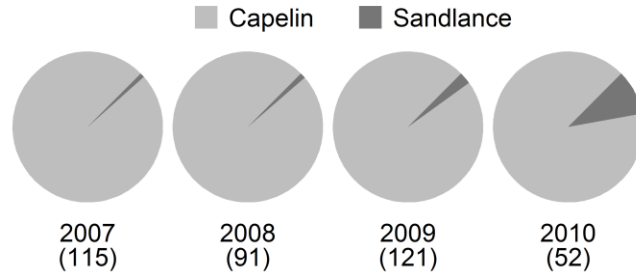
Figure 5.3 – Proportion of capelin and sandlance in chick diets at Gull Island from 2007-2010. Sample size indicated in brackets**.**

During 2009, chick-rearing murres initially spent ~15% of their time diving, but gradually decreased diving effort to ~2% later in the season (-0.4 /day [credible interval -0.6 to -0.2 /day]; Figure 5.2b). Diving frequency was concurrently reduced from ~100 to ~20 dives/day (-28 %/day [credible interval -41 to -17 %/day]). The change in diving effort corresponded with a reduction in DEE from ~2500 to ~1600 KJ/day (-123.7 KJ/day^2 [credible interval -254.6 to -8.0 KJ/day]) and an increase in chick feed rates from ~2 to ~4 fish/day (10 %/day [credible interval 3 to 18 %/day]; Figure 5.2b). The proportion of time spent flying and co-attendance time was constant through the season (Figure 5.2b). Coincidentally, reduced hatching, fledging and breeding success was observed in 2009 (Figure 5.4), declining from 72 to 55 % (-17% [credible interval -3 to -30 %]), 88% to 55% (-33% [credible interval -17 to -49 %]) and 62% to 29% (-33% [credible interval -19 to -47 %]) from 2008 to 2009, respectively.
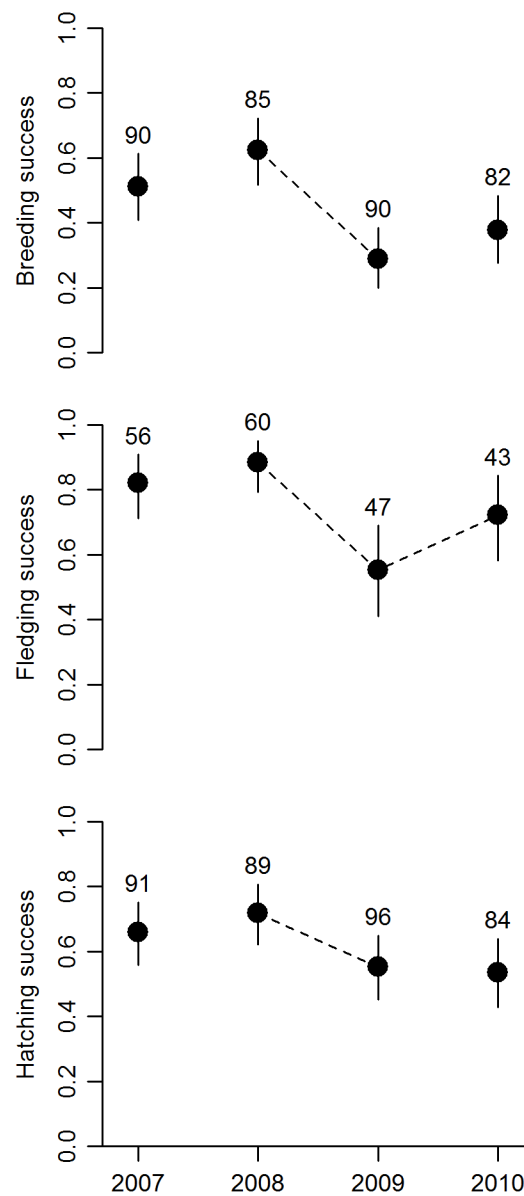
Figure 5.4 – Estimates of hatching, fledging and breeding success of common murres from 2007-2010.

Values indicate sample size and dotted lines indicate significant trends.

5.5   Discussion

While this research adds to the growing body of literature showing that flexible time budgets allow common murres to maintain chick feed rates across a wide range of local prey densities (Burger and Piatt 1990, Monaghan et al. 1994, Uttley et al. 1994, Harding et al. 2007, Wilhelm et al. 2008), it also highlights a staggering stability in foraging effort and daily energy expenditure of parental murres across wide ranging conditions. It was only during severe mismatch with peak prey availability that limits to behavioral flexibility were apparent. When capelin arrived late in 2009, murres rearing chicks could not buffer chick provisioning rates despite increasing diving effort (cf. Monaghan et al. 1994). Contrary to expectation, they did not increase time spent flying, even though capelin were presumably more abundant offshore. High flight costs coupled with low dive costs (Elliott et al. 2013a) likely contribute to their apparent inability to increase flight time. Time and energy budget models postulate that foraging range has a strong influence on the ability of thick-billed murres to sustain the demands of chick-rearing (Houston et al. 1996). If the same applies to chick-rearing common murres, this could imply that their flying time is highly constrained during chick-rearing. Increasing underwater search time must be the more beneficial and economical foraging strategy.

Much of the murres' ability to buffer the effects of variable prey abundance is derived from flexible leisure time at the colony (minimum ≈ 45 min/day, maximum ≈ 3 hr/day) such that chick-rearing murres can increase foraging time by up to 2 hr/day when prey abundance is low (Harding et al. 2007). If they spend this extra time flying, they would expend 1065 KJ, whereas 2 hr worth of diving would cost only 194 KJ

(expenditures calculated using activity-specific rates [148 and 27 watts for flying and diving, respectively] from model 8, Table 1 in Elliott et al. 2013b). Though increased flight time may improve access to capelin, the associated costs could quickly outweigh the benefits. These extra costs would result in a DEE of 3035 KJ equating to nearly 8.5 × the BMR of common murres (350 KJ/day; Cairns et al. 1990). A recently developed bio-energetics model for common murres echoes the dramatic energetic consequences of increased flight time in response to dispersed prey (Thaxter et al. 2013).

Generally, vertebrates are unable to sustain energy budgets exceeding 7 × BMR, as very few species are capable of assimilating this amount of energy in a day. The only way to afford such energy expenditure, if at all, would be to resort to running short-term energy deficits by utilizing lipid reserves (Weiner 1992, Hammond and Diamond 1997). Such a strategy would be unsustainable in the long-term, providing no fitness benefit to either the parent or chick. Increasing underwater search effort for sparse inshore capelin, or alternate prey, may be the only viable option.

Chick-rearing murres have to consume substantial quantities of food each day to meet their energy demands (Cairns et al. 1990). Because foraging trips are short and flight costs are high, natural selection has favored rapid digestion – at the expense of digestive efficiency – to minimize mass retained and maximize energy turnover (Hilton et al. 2000a, 2000b). The reduction in digestive efficiency likely limits the murres' capacity to metabolize energy on a daily scale, thereby imposing an energy ceiling (~2000 KJ/day; Elliott et al. 2013b). In other words, the digestive tract's capacity to assimilate food into energy constrains energy input which in turn imposes a ceiling on sustainable energy

output (Weiner 1992). Murres may be able to maximize energy intake, and subsequent output, by acquiring prey that are assimilated more efficiently. This may be a viable tactic since assimilation improves as fat content increases (Brekke and Gabrielsen 1994). Perhaps this is why common murres select larger prey and/or supplement their diet with alternate prey during poorer conditions (Burger and Piatt 1990, Uttley et al. 1994, Burke and Montevecchi 2009, Buren et al. 2012). We were unable to measure the size of capelin delivered to chicks, yet we did observe an increase in the proportion of sandlance delivered during 2009 and 2010. The selection of larger capelin or alternate prey such as sandlance could, in theory, increase daily energy assimilation because fat content in capelin increases with size (Montevecchi and Piatt 1984) or because sandlance has a higher relative lipid content than capelin (Montevecchi et al. 1984). To exemplify this point, let us assume for a moment that murres typically catch one capelin per dive; since they dive ~50 times each day, we assume they catch ~50 capelin/day. If these are gravid and spent female capelin measuring ~158 mm long and weighing ~24 g, as described in Montevecchi & Piatt (1984), then their assimilation efficiency will be ~72% given their fat content is ~3.4 %; in contrast, the assimilation efficiency of smaller capelin (~141 mm and ~15.9 g; Eaton et al. 1975) would be 70% given their fat content is 1.9 % (assimilation efficiencies were estimated using equations in Brekke & Gabrielsen 1994). Given large capelin (158 mm, 24 g) have an energy density of ~4.2 KJ/g and small capelin (141 mm, 15.9 g) ~3.7 KJ/g, potential metabolized energy from small capelin would be ~2100 KJ/day whereas larger capelin would provide ~3600 KJ/day. This example indicates that mean catch per unit effort must be high (~0.55 to 0.95

capelin/dive) to sustain a DEE of 1969.9 KJ/day. Assuming assimilation is the primary

physiological bottleneck limiting energy output, this example also illustrates that a small

shift in prey selection may make a big difference in the economics of murre foraging. It

may be the case that the murres studied here were able to increase energy output during

the mismatch year by using this tactic rather than relying on energy reserves. Jacobs et al.

(2011) suggest that trade-offs between flight costs and fasting endurance limit the

murres' lipid stores, thereby constraining their energy buffer. Prey selection or switching

may therefore serve as an alternate buffer to variable prey accessibility.

Murres substantially increased diving effort early during the 2009 chick-rearing

period, presumably in response to limited access to capelin. Catch per unit effort must

also have been significantly lower at this time. Assuming they were targeting large

female capelin and they achieved energy balance, we estimate that catch per unit effort

was ~0.4 capelin/dive. Capelin likely became more accessible when spawning began,

which is probably why diving effort decreased as the season progressed. Estimated catch

per unit effort increased to ~1 capelin/dive later in the season. Though prey availability

apparently improved, parents did not increase co-attendance time, rather they continued

to devote effort to foraging. Unfortunately, the ensuing increase in parental effort and

chick investment was not enough to buffer fledging success.

Elliott et al. (2013b) demonstrated that older handicapped parents were more

likely to run energy deficits because their prospects for future reproduction are relatively

limited. Given older murres are much more likely to persist and successfully hatch chicks

(Hedgren 1980, de Forest and Gaston 1996, Elliott et al. 2013b), it seems likely that low

hatching success during 2009 was primarily caused by younger individuals abandoning their breeding attempt in response to poor prey accessibility. Though our study area was colonized relatively recently (expanded in the early 2000s; GJR personal observations), our sample was probably biased towards the oldest individuals at the site (i.e. experienced breeders [>10 years]), which may explain why we observed continued investment in chick-provisioning. Perhaps only the 'best birds' could sustain the extra investment while others abandoned their breeding attempt. More experienced breeders are more proficient foragers than young and naïve seabirds (Daunt et al. 2007); perhaps their knowledge of the prey base and distribution minimized required efforts (Regular et al. 2013). Higher BMRs may have also allowed these birds to exert the extra effort.

5.5.1 Comparisons with previous studies

Comparing the parameters observed in this study to those from other relevant studies, there are a mix of striking similarities and disconcerting differences. First, mean activity budget and DEE values of chick-rearing murres in Witless Bay during 1984 and 1985 (Cairns et al. 1987, 1990) all lie within the credible intervals reported here, and activity budgets in particular were similar with point estimates differing by less than 1%. Feed rates were also similar to those recorded in Witless Bay from the 1980s and late-1990s/early-2000s, differing by less than 1 fish/day (Burger and Piatt 1990, Davoren and Montevecchi 2003a, Wilhelm et al. 2008). Co-attendance times, however, were more divergent; with the exception of 2008, durations recorded by Burger & Piatt (1990)

during the 1980s were up to 4 h greater than the values reported here (i.e. murres are currently working harder). These differences lend further support to the argument that an abrupt state change in capelin timing and abundance following a regime shift in the early 1990s (Buren et al. 2014) caused breeding murres to be more constrained than they were in the 1980s (Wilhelm et al. 2008). Capelin biomass and timing are influenced by seasonal sea ice dynamics which are key determinants of the pelagic spring bloom and subsequent emergence of *Calanus finmarchicus*, capelin's primary prey, from diapause (Buren et al. 2014).

It is unclear how ocean climate change will influence sea ice dynamics and how these physical changes will influence biological match-mismatch dynamics in the system. Nevertheless, extreme ice conditions can create profound bottom-up food web effects (Buren et al. 2014). In fact, there were peaks in ice area (predictor for capelin timing) when murres and Atlantic puffins *Fratercula arctica* indicated late arrival of capelin during 2000 and 2009 (Doody et al. 2008, Wilhelm et al. 2008, Rector et al. 2012; this study), and slumps in the timing of ice retreat (predictor of capelin abundance) when murres indicated low capelin abundance during 1984 and 2010 (Burger and Piatt 1990).

5.5.2 Conclusions

Our study sheds light on the underlying mechanisms forcing previously reported behavioral thresholds and expands our understanding of the murres' buffering capabilities during difficult conditions. First, there appears to be an upper limit on the time murres

can spend with their partner at the colony (~3 hr/day; Harding et al. 2007). The energetic

demands of chick-rearing appear to force parental murres to operate near maximum

intensity ($7 \times$ BMR), even during the best years, thus the above mentioned threshold may

be imposed by the minimum amount of foraging time required to meet their chicks' and

their own energetic requirements (time minimising tactic; Schoener 1971). Second, when

parents spend less than 45 min/day with their partner at the colony, chick-provisioning is

reduced (Harding et al. 2007). As suggested by Harding et al. (2007), the extra foraging

time gained by reducing discretionary time at the colony helps murres buffer variation in

prey availability. Though this extra time often allows parents to maintain chick feeding

rates, murres have to strategically adjust their time and energy budget since they lack a

large safety margin between performance and capacity. In other words, chick-rearing

murres have a limited energy buffer because they operate at or near their energy ceiling

(Elliott et al. 2013b) and they have a limited capacity to store lipids (Jacobs et al. 2011).

To improve their energy buffer, we hypothesize that murres employ foraging tactics that

maximize energy turnover during prey shortages. More specifically, we suspect

improvements to assimilation explain why murres select larger prey during poor food

years (Burke and Montevecchi 2009, Buren et al. 2012). If prey selection or switching is

not a viable option or is insufficient, then murres, particularly older individuals, may rely

on energy reserves to maintain chick investment (Elliott et al. 2013b). The final threshold

response of chick abandonment is likely mediated by lipid stores, whereby murres decide

to abandon in favor of replenishing their reserves when lipid stores are pushed below a

minimum threshold (Gaston and Hipfner 2006, Jacobs et al. 2011). Put simply, when

poor prey accessibility causes parental murres to run out of time and energy, they abandon their chicks. The circumstances that cause such responses are rare because of multifaceted buffering capabilities, but our results suggest that mismatch with prey could be drastic enough to reduce breeding success.

If ocean climate changes increase the incidences of anomalous ice events, then the potential increase in variability in capelin timing and abundance could have negative population consequences for murres. Gaining a better understanding of threshold responses, and the environmental conditions that invoke them, is key to predicting the consequences of climate driven mismatch on energy flow and population dynamics of different species in different systems.

CHAPTER 6 – UNDERSTANDING THE FORAGING ACTIVITIES OF A MARINE PREDATOR
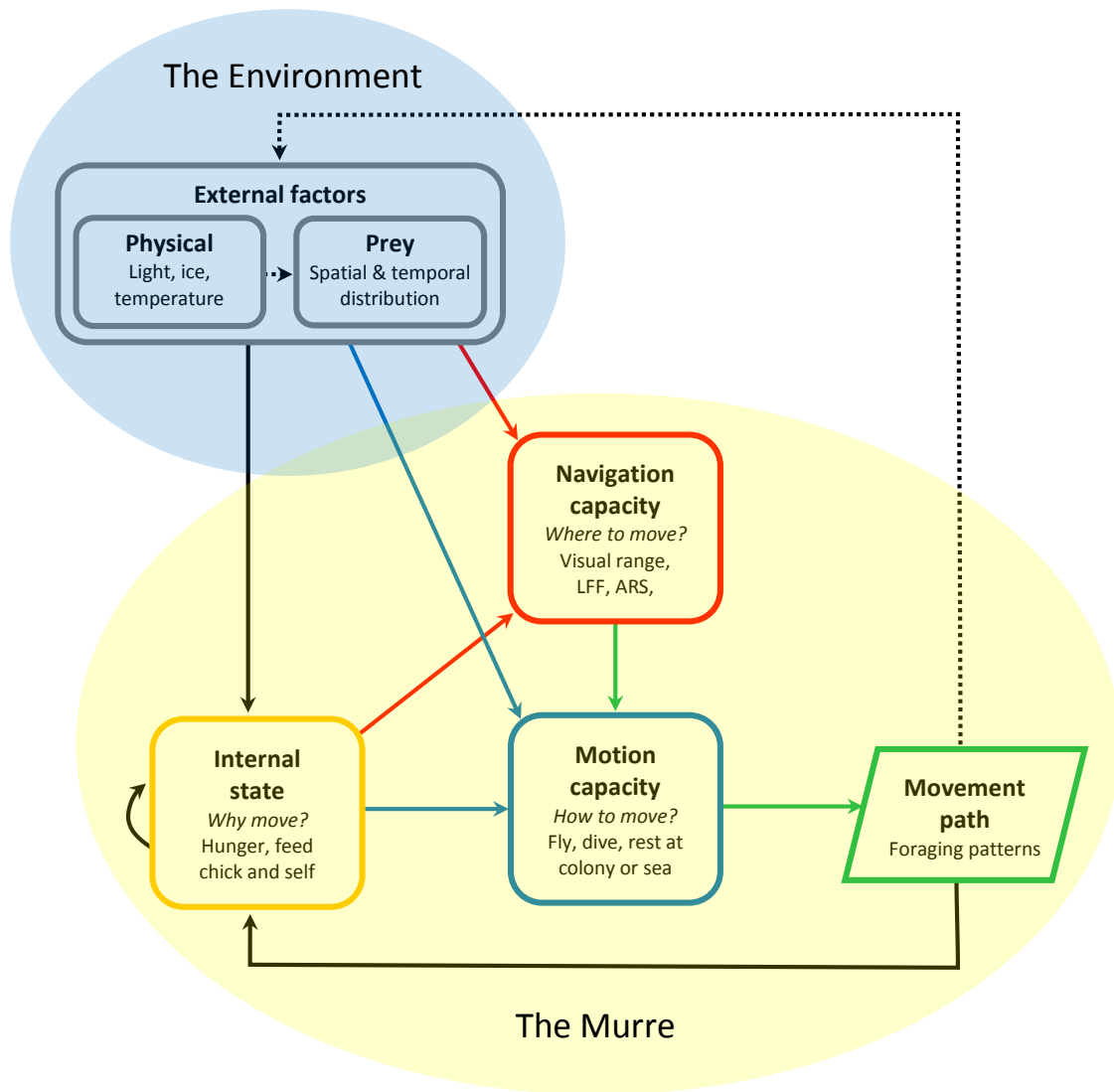
Figure 6.1 – Selected thesis concepts fit into the conceptual framework for movement ecology developed by Nathan et al. (2008). This framework outlines the processes through which the environment affects the internal state, navigation capacity, motion capacity and ultimately the movement path of a foraging murre.

6.1   Linking foraging concepts

Though the concepts covered in this thesis are admittedly fragmented, the framework for movement ecology developed by Nathan et al. (2008) provides a holistic means of integrating these ideas (Figure 6.1). Using this framework, I summarize the findings of this thesis and further explore the mechanistic links between environmental conditions and the foraging activities of chick-rearing common murres. This exercise is valuable because it forces comprehensive evaluations of movement patterns and broadens the scope of movement research (Nathan et al. 2008). Such assessments improve our ability to predict the fate of individuals and their offspring under a range of conditions (Morales et al. 2010).

Multiple biotic and abiotic environmental factors affect the foraging activities of murres. Likewise, their primary prey, capelin, are influenced by multiple biotic and abiotic factors. In response to predation pressure, it is hypothesised that capelin undergo diel vertical migrations (DVM) – residing in deep, dark waters during the day and rising to shallow, dark waters at night – to avoid visual detection by air-breathing predators such as murres and whales (Davoren et al. 2006). This behaviour is mediated by light levels and generates a cyclical vertical pattern in their spatial and temporal distribution. On a horizontal scale, capelin distribute in hierarchical patches on or near inshore spawning grounds (Davoren et al. 2006, Burke and Montevecchi 2009). While patches are generally predictable at larger scales but ephemeral at smaller scales (Fauchald et al. 2000), some fine-scale aggregations persist across years as biophysical features (e.g. temperature, seabed sediment composition and size) create suitable habitat for spawning

and staging (Davoren et al. 2003b). Finally, the annual abundance and peak spawning period of capelin are influenced by seasonal sea ice dynamics as it affects the timing and abundance of their primary prey, *Calanus finmarchicus* (Buren et al. 2014). Given the murres' dependence on capelin for successful reproduction (Burger and Piatt 1990, Davoren and Montevecchi 2003b), spatial and temporal dynamics of capelin and the physical environment is expected to have a direct effect on the internal state, motion capacity, navigation and ultimately the movement path of chick-rearing murres (Figure 6.1).

The internal state of an organism accounts for the physiological and neurological factors driving the animal's ability and motivation to fulfil one or more goals, hence the question why move? (Nathan et al. 2008). Chick-rearing murres are not lacking in factors affecting their motivation to move. With respect to foraging, hunger motivates self-sustenance and an individual's chick and partner motivate chick-provisioning (Takahashi 2013, Rector et al. 2014). Individuals must capture enough prey to maintain pair-bonds (Moody et al. 2005), chick-condition (Davoren et al. 2006) and energy balance (Weiner 1992). As such, their ability to acquire prey has a strong effect on lifetime reproductive success. Parental murres appear so motivated by these demands that they work at maximum capacity (Elliott et al. 2013b). While they are able to work harder via metabolizing lipid reserves, this is only a short-term solution as trade-offs with flight limit their ability to store energy – murres lack the fasting endurance of lipid loading species such as the northern fulmar *Fulmarus glacialis* (Jacobs et al. 2011). Lipid levels likely affect a parent's motivation to move; if levels drop below a critical level the parent

may decide to abandon the current brood (Jacobs et al. 2011). This is where interactions between internal state, movement path and environmental conditions interact to influence population parameters. Yet, despite all this ultimate and proximate motivation to move, murres spend a significant amount of time sitting on the water (Chapter 5; Cairns et al. 1987). This behaviour may appear lazy, however it represents a feedback loop in their internal state as they need this time for oxygen reloading and digestion. To clarify, each dive must be matched with time on the surface to recover oxygen stores used during the dive (Halsey and Butler 2006). More time on the surface is required if the rate of prey intake exceeds their gut's maximum rate of digestion; the ensuing bottleneck forces them to sit on the water and digest the food in their stomach before they can acquire more food (Hilton et al. 2000b). Because energy acquisition is, in theory, a function of prey availability (Buren et al. 2012), an individual's decision to move is affected by prey availability at their current location. Presumably a foraging murre will be motivated to move if they are not gaining enough energy at a particular location. If this is the case, they have to figure out how and where to move?

With the ability to fly and dive, natural selection has provided murres the motion capacity to search volumes of ocean for prey. Physiological trade-offs, however, mean these birds are constrained using both modes of motion (Thaxter et al. 2010, Elliott et al. 2013a). Flight costs are particularly high, thus murres may prioritize underwater vs. above-water search for prey. Murres are incredibly proficient underwater predators and are capable of diving deeper than any other bird that can fly (Piatt and Nettleship 1985, Burger 1991). While their horizontal foraging range is restricted compared to other

species, the murres' diving capabilities gain them access to subsurface prey patches which are relatively free from competition from other avian groups (Tuck 1960, Cody 1973). How deep they have to dive and how far they have to fly to access prey is defined by the spatial and temporal distribution of their prey. Prey are inaccessible if they lie outside their three-dimensional foraging range (~ 100 km wide $\times$ 100 m deep). This is why it is critical for murres to time breeding to coincide with peak inshore capelin availability since it is difficult for them to increase their foraging range to access capelin (Chapter 5).

The navigation capacity of a species also affects their access to prey. It is impossible for an individual to possess perfect knowledge of the spatial and temporal distribution of their prey, thus they have to obtain, process and use external information to inform their foraging decisions. Being visual predators, murres depend on their sight to find and capture prey. As a general rule, murres are expected to forage in locations with ample light levels for efficient prey capture. Like other deep diving marine predators (Martin and Young 1984, Levenson and Schusterman 1999, Martin 1999), murres likely evolved sensitive, dark adapted eyes in response to reduced light levels experienced at depth. Such adaptations presumably allow murres to capture capelin through the diel cycle (Chapter 2 and 3). But before visual detection and pursuit occurs, murres contend with a larger scale problem of finding prey patches in the first instance. A popular null hypothesis is that marine predators innately employ Lévy walks to maximize overlap with patchy prey (Viswanathan 2011). However, the cognitive abilities of murres may override this behaviour since they appear to use their knowledge of patch locations and

dynamics to optimize search (Chapter 4). To paraphrase an English idiom, it seems *a fish in the beak is worth two in the water column*. The predictability of some capelin patches along with their general hierarchical structure makes the combined strategy of memory-based foraging and fine-scale area-restricted search an efficient tactic.

Applying this framework to population processes is inherently difficult, nevertheless, a more detailed mechanistic understanding of movement can help explain higher-level population dynamics (Revilla and Wiegand 2008). Moreover, such holistic assessments can improve our ability to predict responses to environmental change. A species' tolerance to environmental variability has been shaped by its evolutionary history. The contemporary environment, however, is changing and there is growing concern that current levels of phenotypic plasticity are no longer sufficient (Visser 2008). Though clear effects of human driven climate change have yet to be demonstrated for capelin or murres in the northwest Atlantic, physical forcers can have pervasive bottom-up effects on the local marine ecosystem (Buren et al. 2014). A perturbation in the early 1990s forced a dramatic shift in capelin timing and quality which, in turn, negatively affected murre chick condition (Davoren and Montevecchi 2003b). More recent variability in sea ice extent (predictor of capelin timing; Buren et al. 2014) likely contributed to phenological mismatch between the murres' chick-rearing period and peak capelin availability during the 2009 breeding season (Chapter 5). Though parental murres increased diving efforts, they failed to buffer breeding success (Chapter 5). Reduced access to inshore capelin likely exceeded the foraging capacities of many parental murres causing them to abandon their current brood and focus on self-provisioning.

Understanding the limits to their plasticity is key to predicting the population consequences of future ocean climate variability.

6.2   Future directions

Biologging techniques have opened the floodgates to an array of research on the foraging ecology of chick-rearing murres (Cairns et al. 1987, Monaghan et al. 1994, Benvenuti et al. 2002, Tremblay et al. 2003, Elliott et al. 2008, 2009b, 2009a, 2010, 2013a, 2013b, Paredes et al. 2008, Woo et al. 2008, Hedd et al. 2009, Thaxter et al. 2009, 2010, 2013, Regular et al. 2010, 2011, 2013, Linnebjerg et al. 2013, 2014, Evans et al. 2013). Not only have these devices allowed researchers to describe the at-sea foraging behaviour of parental murres (Cairns et al. 1987, Tremblay et al. 2003, Evans et al. 2013), they have revealed sex (Paredes et al. 2008, Thaxter et al. 2009, Elliott et al. 2010) and stage (Benvenuti et al. 2002) specific behaviour, individual specialization (Woo et al. 2008), energetic limitations (Elliott et al. 2013b), and helped test predictions of classic and modern foraging theory (Elliott et al. 2009b, 2009a, Regular et al. 2013). I have only scratched the surface here. The diversity of this research certainly indicates that the data used in this thesis holds much more potential. For instance, my interrogations of colony and sex specific differences in foraging behaviour has been limited at best.

Though much has been learned about the foraging ecology of murres, it seems they have many more secrets to reveal and theory to inform. Tracking devices are constantly improving. Continued miniaturization of TDRs and GPS devices allow the

simultaneous tracking of the horizontal and vertical movements of breeding murres

(Evans et al. 2013); geologgers are also becoming smaller and more advanced with the

integration of depth and activity sensors that facilitate year-round 'observations' of the

foraging behaviour of murres (Linnebjerg et al. 2013). Synthetic analyses of such data in

conjunction with information on environmental conditions (prey abundance, bathymetry,

temperature, etc.) and anthropogenic activities (fishing, oil production, etc.) would help

define marine protected areas and inform conservation schemes (Burger and Shaffer

2008, Grémillet and Boulinier 2009).

6.3   Concluding remarks

When I started this work I remember my supervisor, Dr. William A. Montevecchi,

referring to seabirds as Olympic athletes. It is not until now that I have a true appreciation

for the comparison. Chick-rearing is an extreme endurance event for murres; their efforts

are analogous to Tour de France cyclists (Peterson et al. 1990). They spend

approximately three weeks working near maximum capacity in an effort to raise their

young to ~20% adult breeding mass (Houston et al. 1996, Elliott et al. 2013b). To

effectively deal with the challenge, it is essential for murres to be versatile and apply

foraging tactics that maximize overlap with prey. I believe this thesis is a testament to the

remarkable versatility of chick-rearing common murres. Their abilities gain them access

to prey nearly 100 km from the colony, at depths >100 m and across light levels spanning

approximately 10 orders of magnitude. Moreover, behavioural flexibility allows them to

maintain chick provisioning rates across a 10-fold change in prey densities. To borrow another sentiment of my supervisor, "these birds are not just common, they are extraordinary."

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APPENDICES

Appendix 1 - Methods used for the correlated random walk model simulations

To test the viability of searching randomly for prey (i.e., foraging in the dark), we used a correlated random walk model to determine prey densities whereby the cost of encountering prey by chance would be offset by success. Capelin are the primary prey in this model because available evidence suggests that adult murres feed primarily on capelin during chick-rearing (stomach contents >80% capelin; Piatt 1987, Wilhelm et al. 2003). Dives were simulated in three-dimensions using Gaussian distributed step-lengths and Wrapped-Cauchy distribution (WCD) turning angles (Bartumeus et al. 2005). Step-lengths were based on the mean±sd horizontal velocity of foraging common murres, 2.18m s^{-1} ± 0.43 (Swennen et al. 1991). The WCD turning angle parameter was set at 0.7, which resulted in dive profiles with 'wiggles' analogous to those observed in murres diving under starlight. Birds are presumed to be foraging during the bottom portion of dives (Halsey et al. 2007), thus simulations were based on the average bottom depth and duration of murre dives during starlit periods. Capelin were randomly distributed in space since they form a scattered layer of individuals at night (Davoren et al. 2010). Encounters were considered instances where murres occupied the same space (± 5, 10, 15, 20 cm) as one capelin. Catch per dive was calculated under capelin densities between 0.00001 and 1

fish m^{-3} (range in Newfoundland water (O'Driscoll et al. 2002)). 200,000 simulations

were run (10,000 simulations at 20 capelin densities). To approximate net energy

expenditure, energy obtained from a gravid female capelin (121 kJ; Montevecchi and

Piatt 1984) was multiplied by obtained estimates of catch per dive and subtracted from

diving cost (31 kJ; 28 W for resting and 27 W for diving metabolic rate (Elliott et al.

2013) were used to approximate diving costs, including post surface pause, for an

average starlight dive [34 s dive with 1076 s pause]).
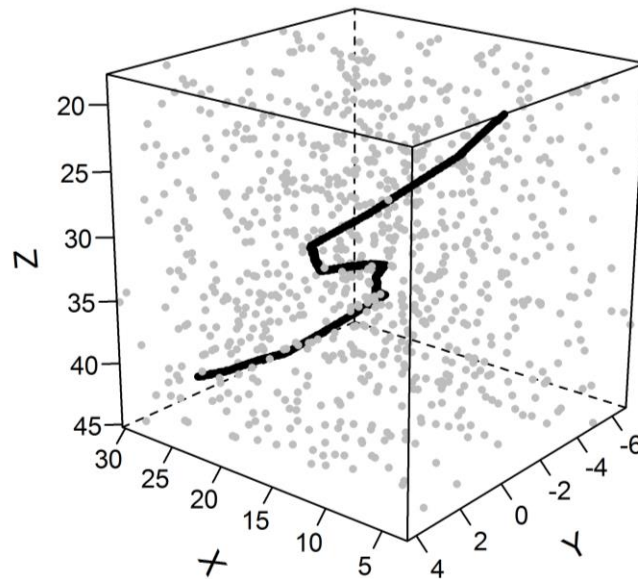
Figure A1.1 – Three-dimensional correlated random walk simulation of a murre dive (black line) with

capelin (grey points) occurring at a density of 0.1 fish m^{-3}.

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Appendix 2 - Supplementary figures for Chapter 4 – Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird
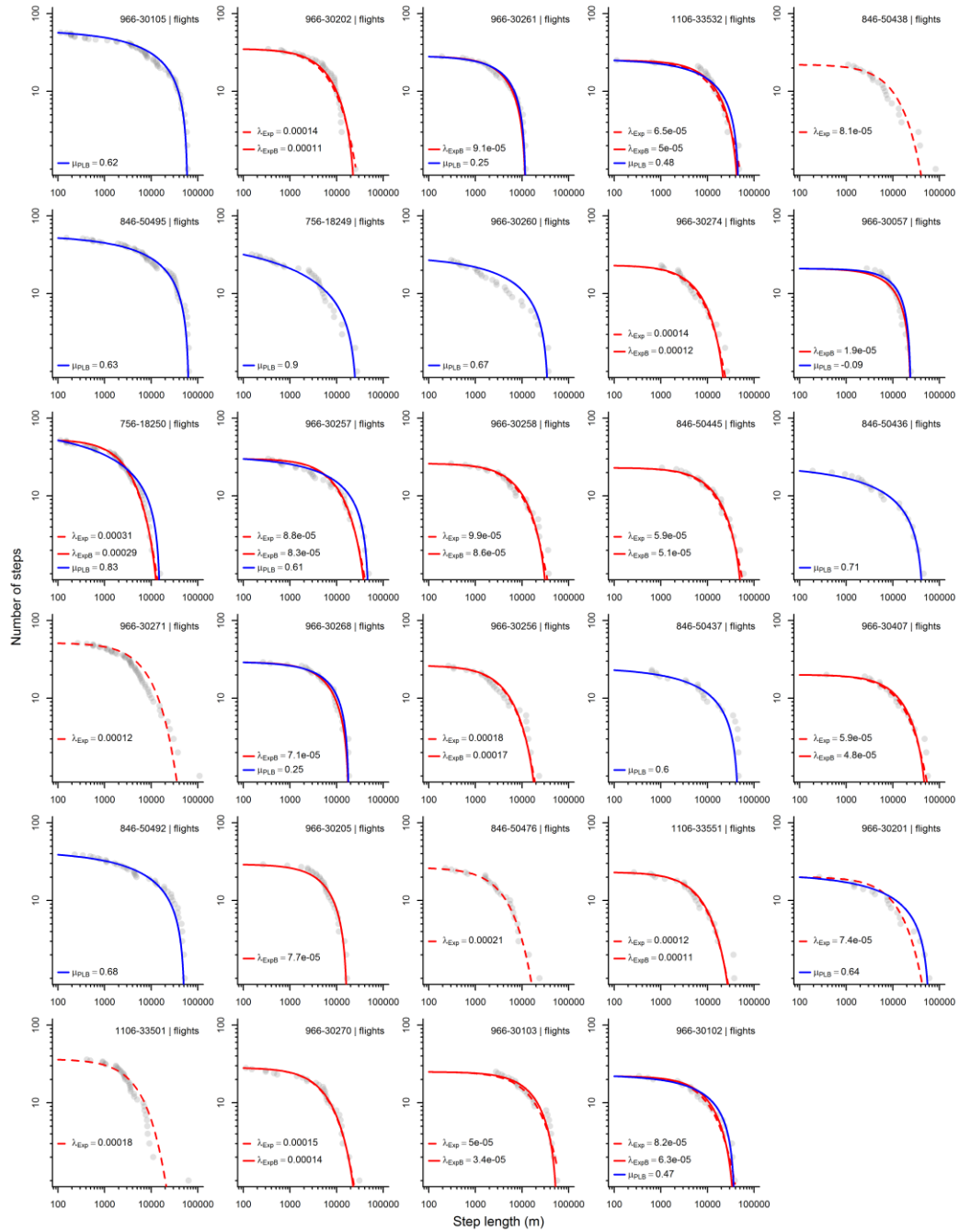
Figure A2.1 – Rank–frequency distributions of flight distances on logarithmic axes for 29 murres fitted with temperature depth recorders. Model fits and parameter estimates of μ and/or λ are presented for best-fit exponential (Exp), bounded exponential (ExpB), power law (Lévy; PL) and bounded power law (Pareto-Lévy; PLB) models (evidence ratio < 2.7). Data sets with < 20 steps were excluded.
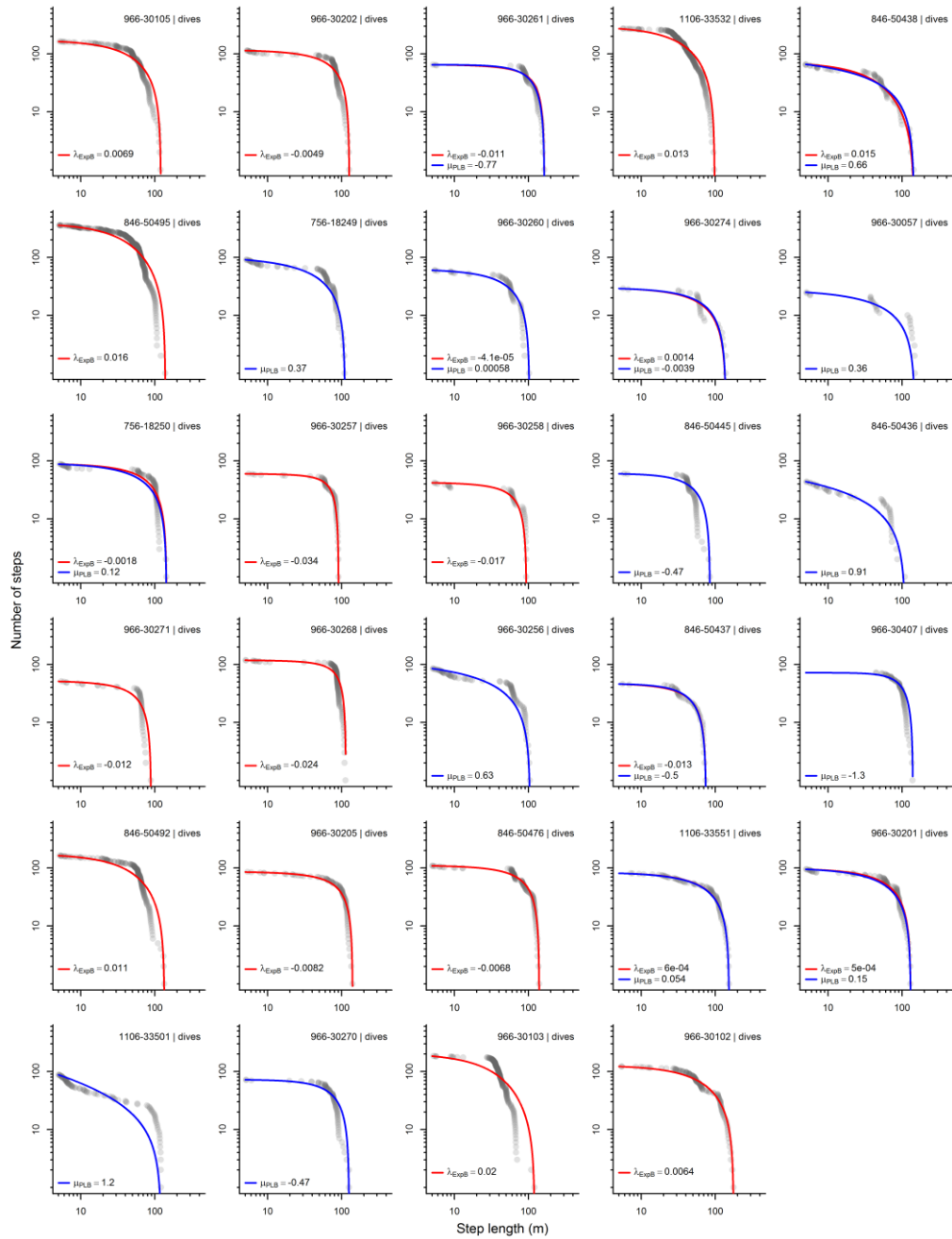
Figure A2.2 – Rank–frequency distributions of daytime dive depths on logarithmic axes for 29 murres fitted with temperature depth recorders. Model fits and parameter estimates of μ and/or λ are presented for best-fit exponential (Exp), bounded exponential (ExpB), power law (Lévy; PL) and bounded power law (Pareto-Lévy; PLB) models (evidence ratio < 2.7). Data sets with < 20 steps were excluded.
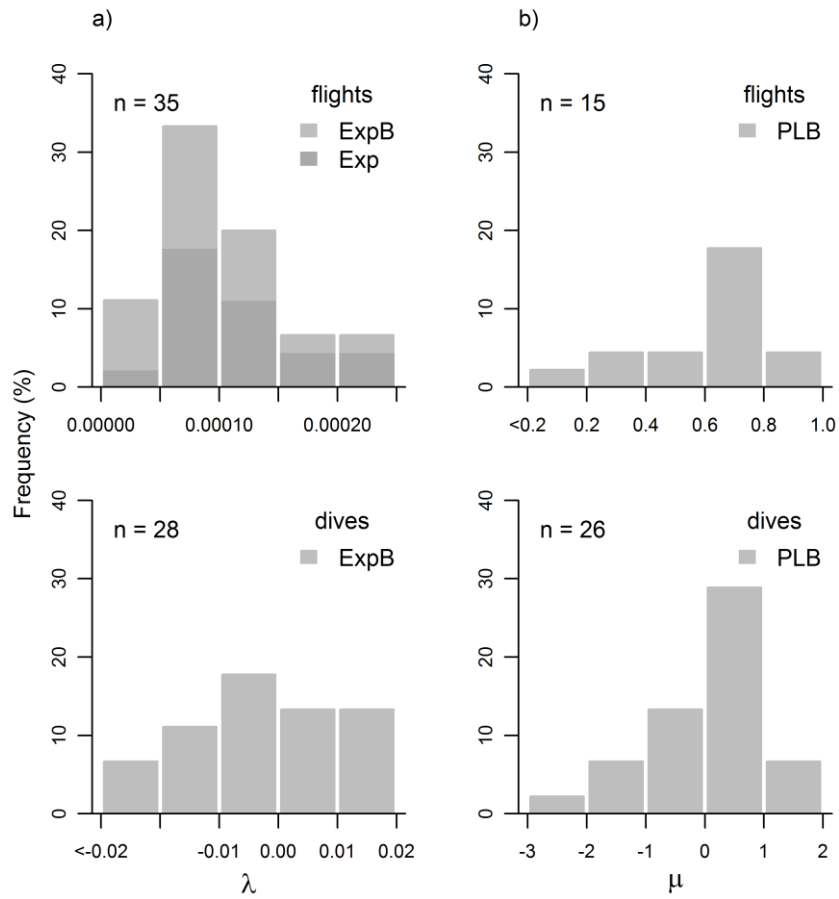
**Figure A2.3** – Distribution of maximum likelihood estimation parameter values of λ (a) and μ (b) for flights and daytime dives of murres from best-fit exponential (Exp), bounded exponential (ExpB), power law (Lévy; PL) and bounded power law (Pareto-Lévy; PLB) models.
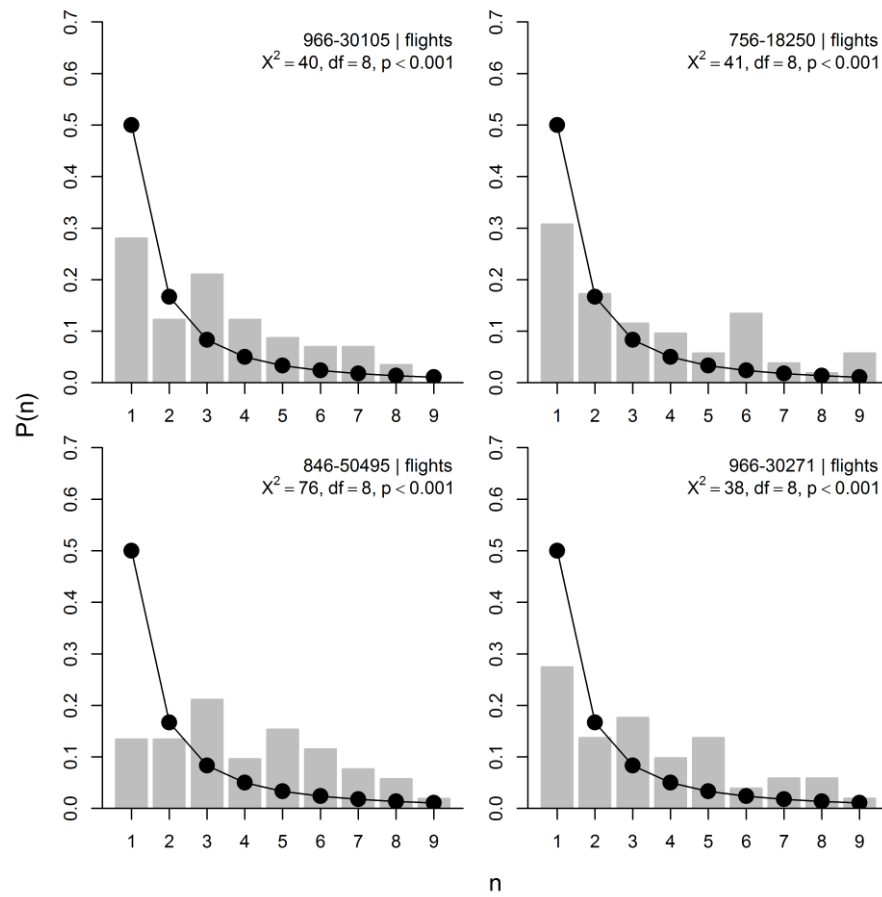
Figure A2.4 – First significant digit distributions of flight distances from four murres fitted with temperature depth recorders that preformed ≥50 steps of ≥100 m (bars). The analytic prediction of a Lévy walk with μ = 2.0 is shown for comparison (line). Chi-square test results are also presented.
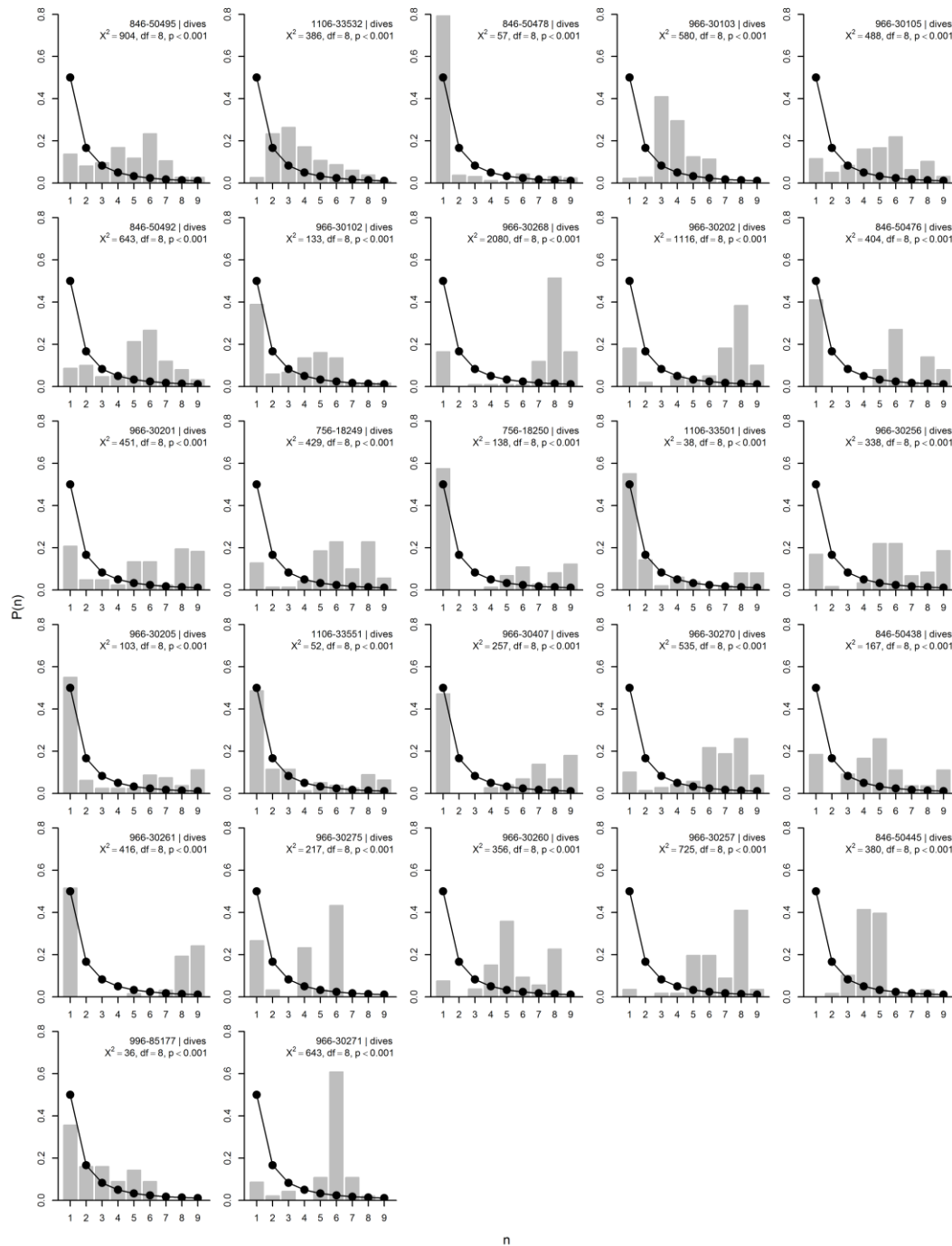
Figure A2.5 – First significant digit distributions of daytime dive depths from 27 murres fitted with temperature depth recorders that preformed ≥50 steps of ≥10 m (bars). The analytic prediction of a Lévy walk with μ = 2.0 is shown for comparison (line). Chi-square test results are also presented.
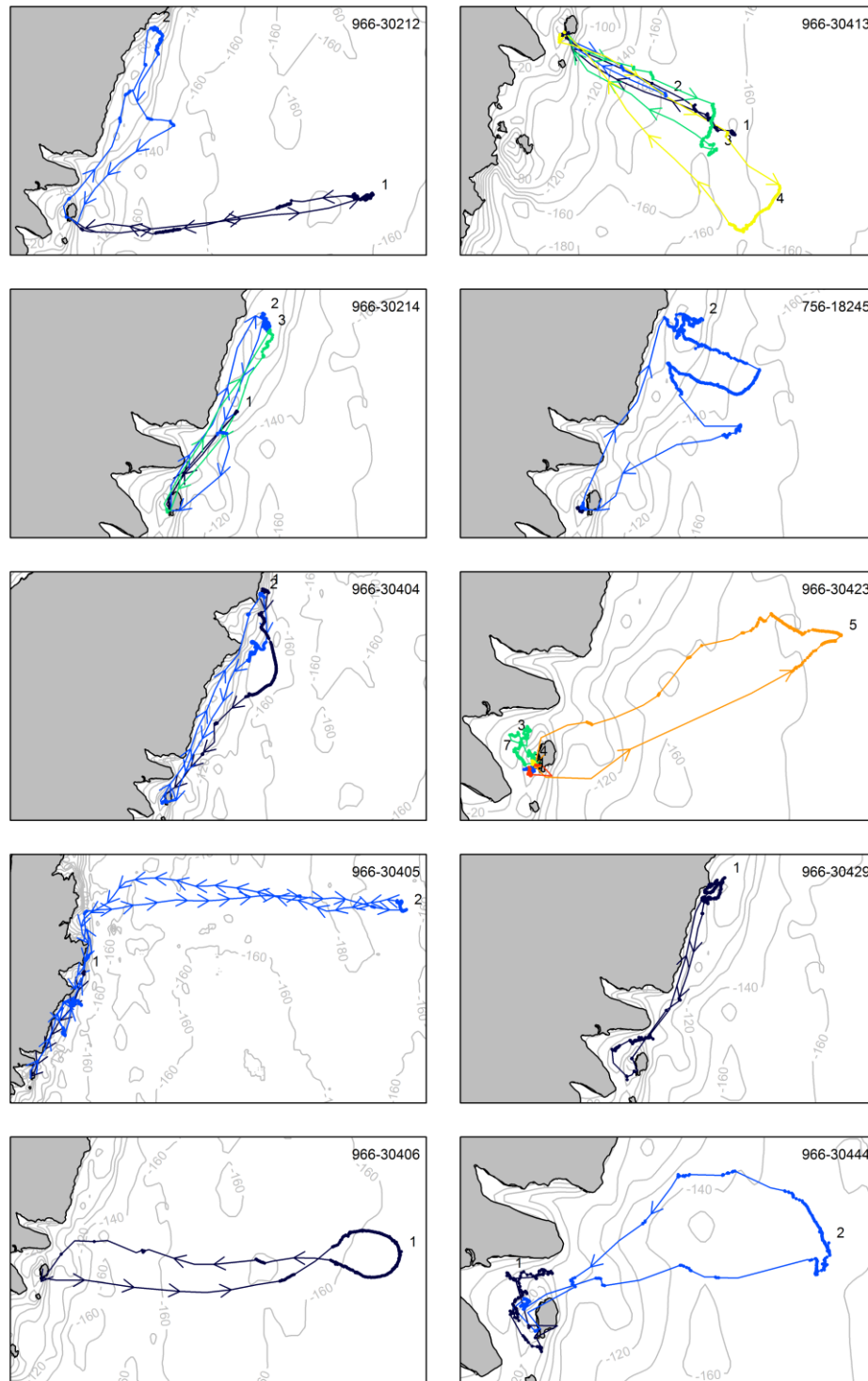
Figure A2.6 – Foraging tracks from 10 GPS-loggered murres (lines represent flights and dots represent landings) from Gull Island.