SEX-SPECIFIC FORAGING BEHAVIOUR BY A LOW-ARCTIC, DIVING SEABIRD OVER THE ANNUAL CYCLE

by

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A dissertation submitted to the School of Graduate Studies

in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Cognitive and Behavioural Ecology Program

Memorial University of Newfoundland

September 2021

St. John's, Newfoundland and Labrador

ABSTRACT

This thesis examines the seasonal foraging ecology of the Common Murre (*Uria aalge*), a circumpolar seabird with physiological adaptations for efficient pursuit-diving and a specialized reproductive strategy (male-biased parental care). The primary research objectives are to assess the behavioural strategies drawn upon by adult murres to survive a seasonally dynamic, Arctic-influenced marine environment, and to investigate how seasonal differences in parental care roles influence sex-specific foraging and survival strategies. To engage this question, I use bird-borne data loggers that collect behavioural observations relating to the distribution, diving and daily activity patterns of individual murres over eight months (July - February) in their annual cycle. Behavioural metrics are integrated with analyses of stable isotope ratios from a variety of tissues that provide corresponding information on seasonal trophic position and dietary niche breadth.

Murres exhibited flexibility in their foraging behaviour over the annual cycle. This was evident in a switch from increased foraging effort with a specialized, high trophic level diet during periods of peak energy demand (summer chick-rearing and late winter) to significantly reduced foraging effort and a generalized, low trophic level diet during the less demanding post-breeding period. Energy savings during moult-induced flightlessness and a flexible moult schedule facilitated by a resident, over-wintering strategy resulted in low energy demands during the post-breeding wing moult. I hypothesise that the post-breeding period represents a buffer event in the annual cycle of adult murres, and may be a key component of survival for a seabird with an otherwise costly pace of life.

Single-parenting males spent twice as much time foraging (self and offspring provisioning) relative to independent females (self provisioning only) and occupied relatively poor quality habitat over the estimated 63 days of paternal care at sea. Despite this, there was no evidence of an energy constraint as single-parenting males consumed the same low trophic-level diet as independent females and allocated equivalent time to self-feeding. Nonetheless, adult males could face time constraints to rear their offspring to independence and complete post-breeding wing moult before the onset of winter if energy limitations during poor-food years are resolved by the extension of either (or both) fitness-related activities.

During late winter, murres experienced a significant increase in estimated daily energy expenditures (DEE), driven in part by high thermoregulatory costs during prolonged exposure to cold water. Murres were able to overcome this energetic challenge by pushing the limits of their diving capabilities but regardless, late winter appears to be an extremely challenging time in their annual cycle.

Overall, this thesis demonstrates remarkable behavioural plasticity by murres over their annual cycle, characterized by highly plastic foraging tactics, dietary strategies and flexibility in the scheduling of wing moult, which may allow them to mediate some of the environmental disruptions predicted to occur with climate change. Yet, persistent declines in the biomass and condition of capelin *Mallotus villosus,* the keystone forage species in the NW Atlantic food web and the primary prey of breeding murres (and their offspring) could challenge this resiliency.

ACKNOWLEDGEMENTS

Funding – This research was funded through support from Natural Sciences and Engineering Research Council (NSERC) Discovery Grants (Dr. W.A. Montevecchi); the Wildlife Habitat Canada and Bird Studies Canada Murre Fund of Newfoundland and Labrador (WAM); Northern Scientific Training Programs (Chantelle M Burke) and an NSERC PGS-D Scholarship (CMB). Personal financial support for CMB was also generously granted through the Canadian Fellowship for University Women Dr. Alice E. Wilson PhD Award, LGL Limited Scholarship in Marine Science, George Weston Graduate Scholarship and the Leslie M. Tuck Avian Ecology Scholarship.

Permits and Logistics - This study was carried out in strict accordance with ethical guidelines outlined by the Canadian Council on Animal Care, and approved by Memorial University of Newfoundland's Institutional Animal Care Committee (Permit Numbers: 10-01-WM, 11-01-WM, 12-01-WM, 13-01-WM). Fieldwork was carried out under Canadian Wildlife Service Migratory Bird Banding permits (WAM-10322 and others). The Newfoundland and Labrador Parks Natural Areas Division permitted access to the Funk Island and Witless Bay Islands Provincial Seabird Ecological Reserves. Logistical support was provided by Environment and Climate Change Canada.

Life Support - The completion of this thesis would not have been possible without the support of many people. Foremost among these is my supervisor, Dr. Bill Montevecchi, whose enthusiasm for this research and confidence in my abilities pushed me to complete this thesis in spite of many challenges. Bill's research is motivated by improving the well-being of Newfoundland's seabirds and it's protected areas, and I feel privileged to have worked so closely with him for so many years and to play a small part in this important work. I am also extremely thankful for the all the amazing field adventures with Bill, most notably the many memorable trips to the Funks. This is where I first experienced the awe-inspiring spectacle of thousands of male murres marching their tiny chicks to sea, typically during a blazing red sunset. This experience inspired me to pursue this research in order to shed light on the lives of murres at sea. For all of this and much more, I am eternally grateful to Bill; a true mentor in research and in life. Yes B'y!

I would also like to acknowledge my supervisory committee members: Dr. Greg Robertson and Dr. Gail Davoren for their guidance during this project, and for providing such stellar examples of leaders and teachers in the field of marine ecology. Throughout this project, I benefitted from the professional and personal relationships that I gained through the Cognitive and Behavioural Ecology Program at Memorial University of Newfoundland; in particular the brilliant group of friends and scholars in the Montevecchi Lab ("the other guys"; Dr. April Hedd, Dr. Paul Regular, Dr. Laura McFarlane Tranquilla, Dave Fifield and Emily Wilson). I value the many hours spent discussing seabirds and research around the table in the Zoo and in the field, and am indebted to you all for your generosity, brilliance and friendship!

I also want to thank Noelle Laite, Abigale Hann, Seth Bennett and Michelle Fitzsimmons for invaluable assistance in the field while working on Gull Island and Funk Island. Special thanks to Environment and Climate Change Canada (Dr. Gregory Robertson, Dave Fifield) and the Canadian Wildlife Service (Dr. Sabina Wilhelm, Pierre Ryan) for all their logistical support and to the crews of the Lady Easton (Easton family) and EcoTours for safe but lively transport to and from Funk Island and Gull Island. I thank Gail Kenny and Nancy Bishop in the Dean of Science Office for assistance throughout my PhD.

It has also been a true pleasure to work with such a great group of professionals in the Salmonids Section at Fisheries and Oceans Canada (N. Kelly, Dr. M. Robertson, S. Duffy, Dr. T van Leuwen, C. Grant, K. Loughlin and many others). I would also like to acknowledge the support of the Federal Government for the educational initiatives that allowed me to complete this thesis while maintaining a full-time position as a Aquatic Biologist.

On a personal level, there are many people to thank. I am grateful for the love and support of my large and loud Burke family. My nine older siblings have always treated me as someone very special and have supported me in every endeavor. I would also like to thank my extended family, the Ploughmans, an equally formidable clan for all their generous love, laughs and moral support.

To my late parents, Jack and Gladys Burke I thank you for your limitless love and support. My father was an inshore fisherman who was greatly respected for his knowledge and skills on the water, but who is remembered for his respect and awe of the ocean. He was keenly aware of the enormous value of the cod and seabirds he harvested, and treated them with due respect. I learned this from him, and am forever grateful. My mother was a force of nature;

strong, capable and wise and my most enthusiastic supporter. She had enormous respect for education, which eluded her as a young woman growing up in pre-Confederation rural Newfoundland. She was beyond proud of my endeavors. My parents took great joy from the simple things in his life: children and grand-children, big fish, gardens, loyal friends and pets. I dedicate this thesis to them.

Finally, I want to thank my husband, Andy Ploughman. He has supported and encouraged me throughout this long journey and in doing so, has become very skilled at the pep talks that never fail to steel my resolve and buoy my spirits. I am very grateful to Andy for all the adventures, meals, lessons (in life and tennis), but mostly for the enduring love and laughs.

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“This planet is above all one of contrasts and contradictions, because of its built in stresses.

Tension is its essential nature. This is its strength. This is its weakness” *Doris Lessing*

CHAPTER 1 – INTRODUCTION AND RESEARCH CONTEXT

1.1. Life History and Foraging Adaptations to Seasonality

An animal's ability to acquire food resources from its environment determines the amount of energy available to support growth, basic metabolism and reproduction. How this energy is allocated is determined by its life history, which is shaped by trade-offs that emerge due to resources being finite (Stearns 1992, Roff 2002). At high latitude and temperate regions, seasonal cycles in abiotic factors (i.e. photoperiod, ambient temperature) cause pronounced and predictable fluctuations in the availability of resources over the annual cycle that exert a strong influence on acquisition and allocation decisions (Varpe 2017).

Long-lived animals with lifespans that exceed the duration of the annual cycle experience seasonality as a repeated, cyclical pattern of environmental variability that exerts strong selective pressures on the scheduling and maintenance of fitness-related activities (e.g. reproduction, migration, moult). The onset of breeding, migration and moult are timed in response to reliable seasonal cues (e.g. photoperiod) that trigger adjustments in some components of behaviour, physiology and morphology (i.e. phenotypic state; Piersma and Drent 2003). These processes are typically organized in a predictable sequence through the annual cycle, with varying degrees of overlap and synchronicity among individuals in a population (Wingfield 2008). Intra-individual, reversible and cyclical adjustments in phenotypic state, which generally correspond with seasonality are defined as 'life-history stages' in the annual cycle, and are a key adaptation to maintaining fitness in a seasonal environment (Jacobs and Wingfield 2000). By example, the breeding life-history stage of most birds involves gonadal development, yolk formation and parental care during spring and summer versus fat storage and migration during the winter stage, with the activities requiring the greatest energetic investment generally coinciding with periods of peak productivity in food availability.

Studies that track mature individuals across life history stages provide critical insights into the behavioural and physiological mechanisms used to balance energy acquisition and allocation processes over the annual cycle (McNamara and Houston 2008). By example, observations during the most challenging periods with the greatest resource limitations and risks to extrinsic survival are critical to identifying potential energy bottlenecks in the annual cycle (Buehler and Piersma 2008, Fort et al. 2009). Moreover, the consequences of an individual's performance in one life history stage can have significant carry-over effects on future performance (Sorensen et al. 2009, Salton et al. 2015, Fayet et al. 2016), and the benefits (or costs) of a given strategy (e.g. fat reserves) may vary according to season (Croll et al. 1991). An annual cycle perspective also provides insight into individual and population-level responses to environmental changes that are predicted to become more frequent and extreme with climate change (Marra et al. 2015, Oliver et al. 2019).

1.2. Plasticity in Foraging Behaviour

Behaviour is governed, in part by rules that determine how an individual should perform as a function of its internal state in a given environment (McNamara and Houston 2008). Accordingly, as seasonal energy demands and resource availability change over time, there is an expected corresponding shift in behaviour (Barta 2016, Gilmour et al. 2018). An animal's foraging strategy is a critical component of its individual fitness (Schoener 1971, Stephens and Krebs 1986) and in long-lived animals selection favors foraging strategies that support current and future energetic demands (Williams 1966, Stearns 1992). Flexible foraging strategies that synchronize effort with the availability of resources needed to support fitness-related activities are therefore a critical survival trait in a seasonal environment (McNamara and Houston 2008). Moreover, in a highly dynamic and quasi-predictable environment, flexible foraging strategies allow animals to surmount unanticipated challenges over shorter temporal scales (Botha and Pistorius 2018).

While flexible foraging strategies allow animals to perform optimally across a range of environmental contingencies; life-history traits related to age, sex, reproductive status and body size (among others) can influence an individual's ability to respond appropriately (Auld et al. 2010, Forsman 2015). Disentangling the interacting effects of extrinsic and intrinsic factors on an animal's behavioural response is challenging but insight can be gained via concurrent behavioural comparisons of individuals of varying ages, sexes or reproductive status over their annual cycle (Daunt et al. 2007, Breed et al. 2009, 2011, Hedd et al. 2014). By example, a comparison of the foraging strategies of adult and young of the year (YOY) grey seals (*Halichoerus grypus*) revealed more complex seasonal patterns by adult seals that had to cope with a combination of reproductive demands and seasonal patterns in food availability (Breed et al. 2011). Long-term behavioural observations of individual animals are increasingly attainable with the widespread availability of miniaturized, sophisticated bio-logging and tracking devices, which combined with seasonal dietary indices from stable isotope ratios can advance our understanding of the foraging strategies of free-ranging animals over their annual cycle (Phillips et al. 2009).

1.3. Seabird Life-history and Environment Interactions

Understanding the behavioural mechanisms used to cope with seasonal environmental variation can also be advanced by studying species that use specialized strategies to survive challenging environments. Seabirds show remarkable variation in their foraging strategies and adaptations (e.g. wing morphology) that reflect their expansive radiation across all environments on the planet, from polar regions to the tropics. Seabirds also exhibit extreme life history characteristics including longevity (i.e. high investment in annual survival), low fecundity and prolonged parental care (i.e. greater investment in fewer offspring), and delayed maturity (Hamer et al. 2001). These collective traits are considered evolved, adaptive responses to a challenging marine lifestyle, characterized by a combination of patchy and ephemeral food resources and elevated activity costs (i.e. flying) and survival risks (i.e. predation) associated with having to rear offspring on land while making a living at sea (Hamer et al. 2001).

At high latitudes where seasonal fluctuations in resources are most pronounced, wing-propelled diving seabirds are among the most dominant avian predators, consisting primarily of auks in the northern hemisphere and penguins in the southern hemisphere (Shealer 2001). These high-latitude divers share the common feature of a small wing-surface area relative to body size that increases the efficiency of wing-propelled diving by reducing resistance during under-water propulsion and facilitates access to prey in larger volumes of water relative to nondiving seabirds. Yet, this morphological design comes at a significant cost. Energetic expenditures during aerial flight increase with body size (via increased wing-loading) with the largest auks (*Uria* spp.) having the highest sustained flight costs of all volant vertebrates and penguins (1-35 kg) having lost the ability to fly (Elliott et al. 2013a).

1.4. The Annual Cycle of Common Murres (*Uria aalge*)

The Common Murre (*Uria aalge*) has a circumpolar distribution and is the largest (1 kg) and deepest diving of the auks (maximum recorded depth of 250 m; Chimienti et al. 2017). Over the course of their annual cycle, adult murres must reproduce, replace their plumage and migrate to a more favorable environment, or alternatively acclimate to unfavorable winter conditions (Fig 1.1). Successful transition through life-history stages involves numerous survival challenges, that with the exception of the well-studied breeding period are poorly understood.

The chick-rearing phase of reproduction is generally considered the most challenging period in the annual cycle of murres. Murres are single-prey loaders and during chick-rearing when they are central-place foragers and must fly frequently to provision their chick, they operate near the maximum sustainable threshold of daily energy expenditure (7 X DEE [daily energy expenditure]; Cairns et al. 1990, Elliott et al. 2013b, Regular et al. 2014). This level of expenditure is unsustainable over time and is considered the most significant driver in the evolution of the intermediate strategy of juvenile development (Gaston 1985, Ydenberg 1989), whereby at roughly one-third of adult size (ca. 21 days post hatch) the flightless chick makes the transition from the nesting site to the accompanied by the male parent (Sealy 1973). The male-chick pair may remain together at sea for an estimated period of months, until the chick attains nutritional independence. Since the male parent is rendered behaviourally flightless by its dependent, it is assumed to undergo synchronous wing moult during this time (Gaston 1985). Upon departure from the colony by the male and chick (hereafter referred to as fledging), the female is released from parental care and relocates to more productive waters away from the colony to recover from breeding and undergo wing moult (Gaston 1985, Harris and Wanless 1990, 2003). A key question in the seasonal ecology of murres is whether male parents that continue to care for their offspring at sea experience different constraints relative to independent females and whether these constraints carry over into subsequent stages in the annual cycle.

Murres undergo sequential wing feather moult during which they are rendered flightless. Wing moult occurs over a reported period of weeks to months (Birkhead and Taylor 1977, Thompson et al. 1998, Bridge 2004, Elliott and Gaston 2014), and is generally assumed to begin immediately after colony departure in late summer. Reduced dispersal abilities during moult-induced flightlessness could influence their ability to track ephemeral prey and also decreases their ability to evade risky encounters with human activities, including exposure to oil (or other pollutants) or being shot during the winter hunt (Burke et al. 2012, McFarlane Tranquilla et al. 2013). This thesis will investigate the timing and duration of wing moult of individual murres to assess how they schedule wing moult in relation to environmental conditions and the timing of other fitness-related activities.

Winter survival is considered a critical life-history trait for long-lived seabirds with increasing evidence that conditions experienced in winter are a major driver of population dynamics (Gaston, 2003, Descamps et al. 2013, Frederiksen et al. 2016). Unlike most auks (including congeneric Thick-billed Murres *Uria lomvia*), murres do not always undergo extensive migrations to more favorable wintering areas (Hedd et al. 2011, Fort et al. 2013, McFarlane Tranquilla 2014). This suggests that seasonal declines in food availability may not be of sufficient magnitude to necessitate costly migration to more productive areas, or alternatively that these highly efficient divers can access sufficient prey by foraging in deeper waters (with relatively low energetic costs). Emerging insights from year-round tracking studies have demonstrated higher than expected energetic demands during winter (e.g. Fort et al. 2009, 2013). Murres experience high thermodynamic costs (Fort et al. 2009) and degraded foraging opportunities during shorter days (with correspondingly longer nights spent fasting) and frequent winter storms that may impede access to prey (Finney et al. 1999). In Newfoundland and Labrador, murres are also hunted in the only legal, non-aboriginal hunt for migratory birds in Canada which occurs from September to March (Montevecchi et al. 2007). Questions relating to the winter survival strategies of murres are addressed in this thesis through assessments of their foraging behavior in combination with an activity-specific estimate of DEE, with the expectation that murres will respond to elevated DEE in winter via adjustment in their foraging effort.

Overall, these unique aspects of the murres' physiology and reproductive strategy, within the context of a challenging high-latitude marine environment provides a suitable model to investigate behavioural responses to seasonally changing energetic demands, which are expected to vary by sex.

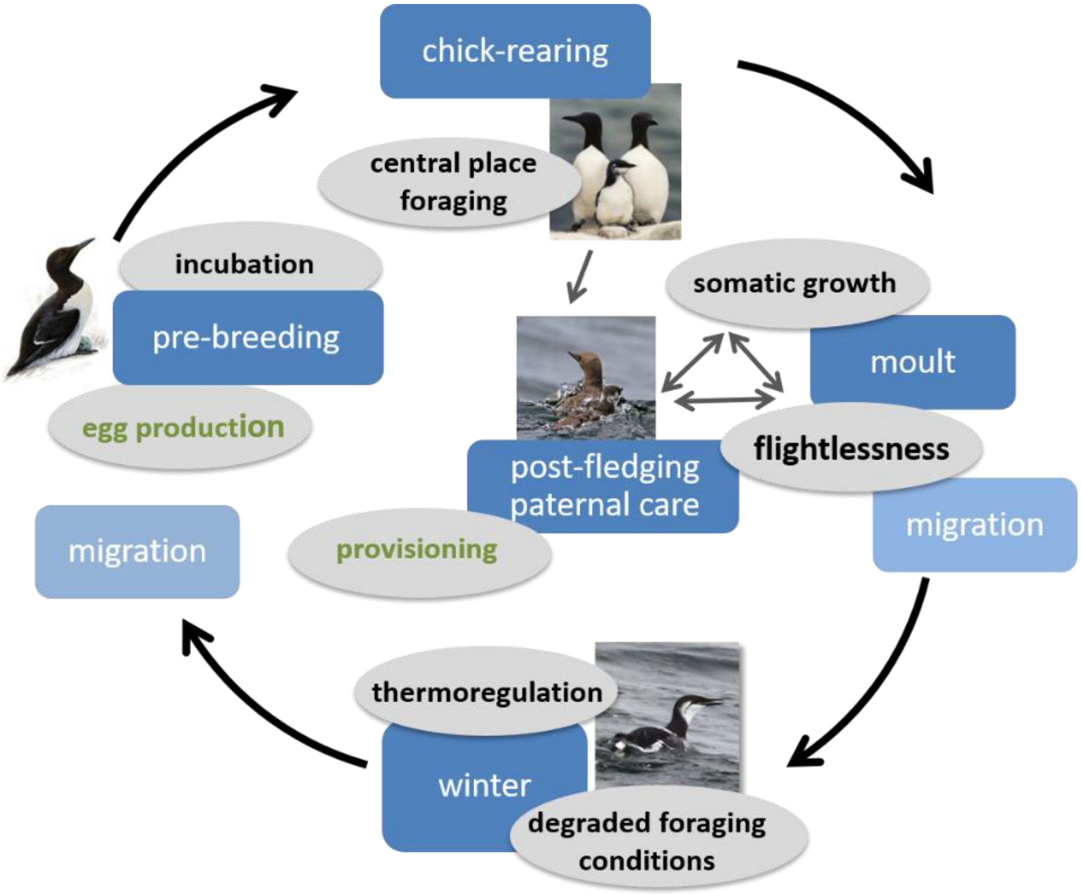

Figure 1. 1. Life-history stages in the annual cycle of murres (blue boxes) showing some of the stage-specific constraints (grey ovals) that emerge in response to the interacting effects of the environment and the murre's internal state, some of which differ according to sex (indicated by green text).

1.5. Study System

This research focuses on murres from two colonies in the Northwest Atlantic: the Funk Island Ecological Reserve (49˚45'N, 53˚11'W) and Gull Island in the Witless Bay Ecological Reserve (47°16’N, 52°46’W), both located off the island of Newfoundland in eastern Canada (Fig. 1.2). Funk Island supports c.a. 470, 000 breeding pairs of murres which represents an estimated 75% of the Northwest Atlantic population (Wilhelm et al. 2015). Gull Island is a relatively smaller colony (c.a. 1632 breeding pairs) that is one of three colonies in the Witless Bay Ecological Reserve, collectively supporting an estimated 77,500 breeding pairs of murres (Robertson et al. 2004).

Murres from these colonies occupy offshore waters on the Newfoundland Shelf (NL Shelf) and Grand Bank throughout the non-breeding period (Hedd et al. 2011, McFarlane Tranquilla 2014). This is a cold and variable marine ecosystem that is strongly influenced by the south-flowing Labrador Current that transports cold Arctic waters across the NL Shelf, extending onto the southern Grand Bank (Fig. 1.2). The convergence of the Labrador Current with the warm, saline Gulf Stream on the Grand Bank creates a highly productive ecosystem that supports globally and regionally significant populations of seabirds (Brown 1986), including resident populations and long-distant migrants from high latitudes in the North (present in winter) and South Atlantic (present in summer; Nettleship and Birkhead 1985, Brown 1986, Montevecchi and Tuck 1987, Hedd et al. 2014). Resident and migratory seabirds in this region feed across a range of trophic levels from small planktivores (*Alle alle*, *Oceanodroma leucorhoa*) to large piscivores (*Morus bassanus*, *Uria* spp.). Breeding murres specialize on capelin (*Mallotus* *villosus*) and parental foraging behaviours and reproductive success are regulated by its timing and abundance (Cairns et al. 1987, Burke and Montevecchi 2008, 2009, Regular et al. 2014, Storey et al. 2020). Capelin is the focal forage species in the Northwest Atlantic marine ecosystem. Following a regime shift in the early 1990s, triggered by Arctic sea ice intrusions and subsequent anomalous cold-water conditions, capelin underwent dramatic changes in their biomass, biology and behaviour (Buren et al. 2014), which involved a decline in somatic condition and a pronounced shift in the timing of their inshore arrival during spawning (c.a. 4-6 weeks later; Carscadden & Nakashima 1997). These changes in capelin biology and behavior were associated with documented declines in the productivity, condition and survival of seabird species in the NW Atlantic (Regehr & Montevecchi 1997, Davoren and Montevecchi 2003a). Sustained declines in the biomass and condition of capelin (Buren et al. 2019, Montevecchi et al. 2019), combined with more recent climate-mediated shifts in the biomass and composition of the zooplankton community on the NL Shelf (Pepin et al. 2017) could have potentially profound consequences for murres (Montevecchi et al. 2019) and other marine apex predators (Sandvik et al. 2005, Sydeman et al. 2015). Accordingly, studies that investigate the behavioural responses and tolerances of apex predators to seasonal and annual changes in their environment are needed to inform conservation initiatives.

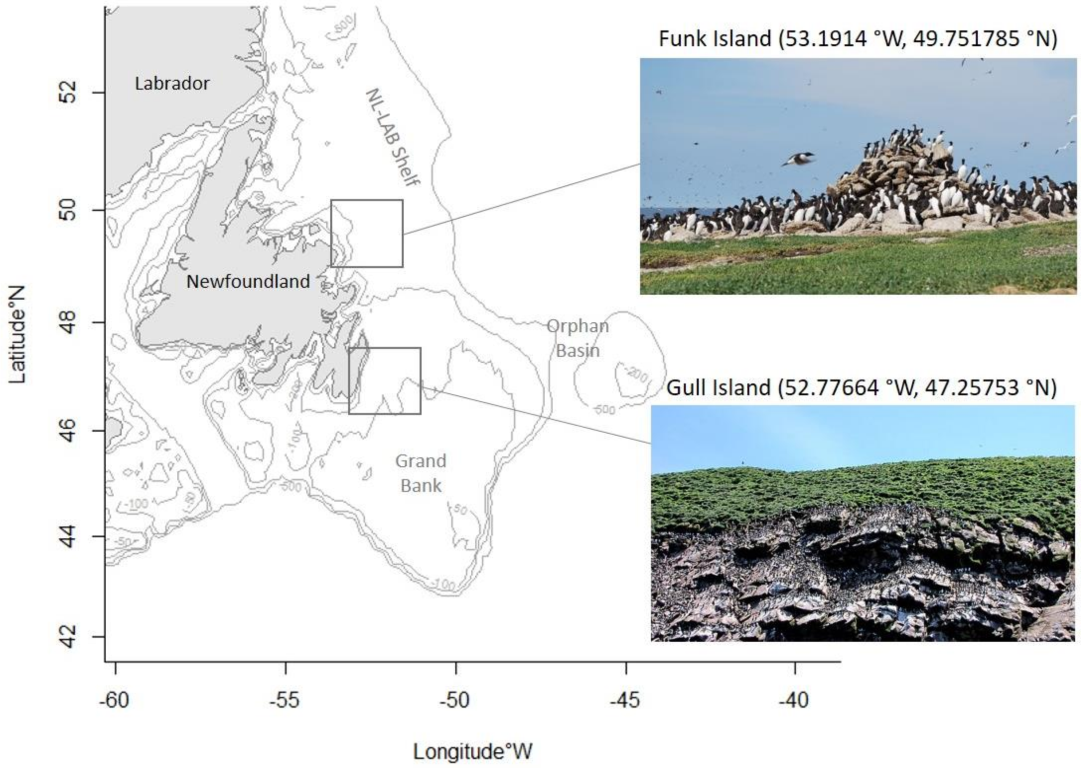

Figure 1. 2. Map of the study area showing the location of the Funk Island Ecological Reserve (top picture) and Gull Island in the Witless Bay Ecological Reserve (bottom picture) in relation to the prominent bathymetric features of the NL Shelf.

1.6. Research Objectives and Approach

This thesis examines the seasonal behavioural ecology of a high latitude seabird, the Common Murre and emphasizes the non-breeding period when the behavioural ecology of murres is relatively less well studied. The primary objective is to investigate the behavioural mechanisms used by murres to cope with seasonal changes in their environment and corresponding life-history stage-specific constraints; specifically related to parental care (summer and autumn), wing moult (autumn) and winter survival.

To do this, I capture fine-scale behavioural information on habitat use, activity budgets, foraging effort and dive tactics of individual murres over 8 months in their annual cycle (July-February) using geolocation-immersion loggers (Lotek LAT 2500 model; 5.9 g with attachment, c.a. 0.7% body mass). The Lotek 2500 model used in this study collects multiple data logs, including light (spatial data), pressure (dive data) and wet/dry activity (time spent flying and time spent on the water), which collectively provide insight into the behavior of individual birds over their annual cycle. Loggers are attached to the leg of breeding murres (Fig. 1.3) during late chick-rearing (adults with chicks > 10-15 days of age). The leg attachment method is considered the preferred option from the perspective of the welfare of the bird and the reliability of the information collected. Unlike other attachment methods (i.e. internal, harness, tail feather mounts), leg-mounts are less likely to influence reproductive success (Carey 2011) or the behavior of diving seabirds (Ropert-Coudert et al. 2009). Regardless, year-long deployments of similarly sized, leg-mounted geolocation devices (British Antarctic Society BAS MK5,7, 13) resulted in increased corticosterone levels and lower body mass of murres (*Uria* spp.*)* relative to control birds (e.g. similar handling but with no device attachment; Elliot et al. 2012). This suggests that long-term deployments of even small devices can negatively influence animal welfare and data reliability.

Over the past three decades, studies investigating the migratory and habitat use patterns of marine birds have relied primarily on light-weight, geolocation devices that produce daily location estimates based on day/night length on a given date (latitude) and the timing of local midday/midnight relative to GMT (longitude). However, the estimated mean positional error generated by light-based geolocation is large, estimated between 180 km ± 114km (Phillips et al. 2004) and 300 ± 413 km (Halpin et al. 2021). As such, the use of these devices for species like the Common Murre that have a relatively limited migratory range (< 500 km; Hedd et al. 2011, McFarlane-Tranquilla, 2014) requires very careful analysis and interpretation. Furthermore, latitudinal estimates around the equinox periods (~8 September – 8 October, and ~6 March – 5 April) are highly uncertain when day length (and night) is nearly equal across all latitudes (Hill 1994), which results in some data gaps during these time periods.

The pressure log generated by Lotek 2500 loggers provides precise information on dive depth and frequency over a fine temporal resolution (here, programmed to record pressure every 8 secs), with a maximum depth range up to 1000 m (Lotek Wireless, St. John's, NL) that far exceeds the dive depth capacity of murres. The precision of Lotek immersion loggers was demonstrated by Elliott and Gaston (2009) via comparisons of depth records from bird-borne loggers (older LAT 1100 model) with those attached to anchors and ropes at known depths, showing precision within ± 2 m. These highly accurate, robust and programmable loggers therefore provide extremely useful measurements of dive behavior, that in this study were collected over a maximum period of eight months. Dive profiles are extracted using MT-Dive 4.0 (Jensen Software) where dive start and end times can be determined for individual dives, in addition to dive duration, maximum depth, dive bottom and surface interval duration. Dive bottom duration is an important parameter as it is generally assumed to represent the foraging time for diving seabirds that can collect multiple prey during individual dives (Mori et al. 2002, Cook and Davoren 2014). Here, bottom time is defined as the time elapsing from the first and last instant when vertical velocity (calculated between successive records) fell below 0.5 ms-1 (e.g., Halsey et al. 2007).

LAT 2500s also provide information on wet/dry state (via a salt water switch) that can be used to differentiate activities whereby a dry state is indicative of time spent at the colony or flight and a wet state is indicative of periods of rest/swimming on the water. This information, collected over an extended period can be used to calculate the activity budgets of individual birds over the annual cycle (Linnebjerg et al. 2013, Dunn et al. 2020). Yet, for species like murres (*Uria* spp.) that occasionally withdraw one leg (or foot) into their plumage while resting on the water (i.e. leg-tucking), differentiation between leg-tucking and flight based on dry events can be challenging and requires very cautious interpretation (Linnebjerg et al. 2014). Here, dry periods at sea that represent flight versus dry periods at sea that represent leg-tucking were differentiated by programming the loggers to record dry state only when ambient temperature was < 28°C. This approach is based on the assumption that heat transfer from the bird (body temperature of 39.6 °C; Gabrielsen et al. 1998) during leg-tucking would result in temperature readings approaching 28°C, which is much greater than the ambient air and water temperatures experienced by North Atlantic murres during the non-breeding period.

Fig. 1. 3. Photo showing a Lotek 2500 (with orange darvic band and cable tie attachment) on the leg of a Thick-billed Murre (Uria lomvia). Photo taken by Dr. Kyle Elliott.

Sex-specific behavioural metrics are integrated with isotopic analysis of different tissues (blood, flight and breast feathers) that are used to characterize seasonal changes in trophic position (types of resources) and dietary niche breadth (variety of resources). Tissue extraction (blood) was also used for sex determination and is based on W-chromosome analysis (Fridolfsson and Ellegren 1999) that was conducted by Dr. Dawn Marshall (Biology Department, Memorial University of Newfoundland). Habitat-specific, oceanographic and environmental variables (water temperature, day length) provide a seasonal environmental context.

Seasonal changes in the behavioural metrics of individual birds are compared across seasons and sex, with a strong focus on foraging behaviour (daily effort, dive tactics). By quantifying behavioural adjustments during the transition through life history stages in the annual cycle using this approach, I attempt to (1) elucidate the influence of parental care, wing moult, and a harsh winter environment on the survival strategies of adult murres, and (2) assess how behavioural adjustments over time mediate survival in a low Arctic seasonal marine environment. I use this approach to assess the expectation that behavioural metrics of murres will vary according to season, both in response to sex-specific life-history constraints and seasonal cycles in the availability of food resources.

1.7. Thesis Organization

This thesis will address the following topics that are broadly organized around the different life-history stages in the annual cycle of murres. Chapter 2 investigates differential parental care as a potential underlying mechanism for sex-specific foraging by size-monomorphic murres. This is approached via behavioural comparisons across three distinct stages that involve different parental care investments by the sexes: bi-parental care (summer breeding), paternal care only (autumn post-breeding) and no parental care (winter). Chapter 3 uses daily activity and diving metrics to quantify the duration and timing of wing moult for murres and to provide some of the first information on their foraging ecology during wing moult. Chapter 4 investigates how murres cope with the energetic challenges of winter in the North Atlantic, and includes an estimate of activity-specific daily energetic expenditures with corresponding information on daily foraging effort and dive tactics. Chapter 5 synthesizes the preceding data chapters (2-4) by linking seasons (according to sex) in an attempt to identify periods of greatest risk and advance our understanding of the selection pressures acting on individuals and populations throughout their annual cycle.

This thesis is presented in a manuscript format with four data chapters (Chapters 2-5), bounded by an introduction (Chapter 1) and overall discussion of the research findings and their implications for the conservation of North Atlantic murres (Chapter 6). Two of the four data chapters (Chapters 2, 4) are published in peer-reviewed journals:

Chapter 2: Burke CM, Montevecchi WA, Regular PM (2015) Seasonal variation in parental investment drives sex-specific foraging by a monomorphic seabird. PLoS ONE 10(11):e0141190. doi.org/10.1371/journal.pone.0141190

Chapter 4: Burke CM, Montevecchi, WA (2018) Taking the bite out of winter: Common Murres (*Uria aalge*) push their dive limits to surmount energy constraints. Frontiers in Marine Science 5:63. doi.org/10.3389/fmars.2018.00063

The manuscript format results in some repetition in the presentation of the methods in this thesis. The two published manuscripts (Chapters 2, 4) provide very detailed descriptions of methods relating to logger deployment/retrieval, data processing and stable isotope sampling and processing. In order to minimize repetition for the reader, descriptions of these methods in Chapters 3 and 5 are not provided in detail, rather previous chapters are cited where appropriate. Formatting of tables and figures are presented consistently throughout, and the literature cited in all chapters are collated into one reference section.

1.8. Co-Authorship Statement

This thesis is the final product of research conducted during my PhD in the Cognitive and Behavioural Ecology Program at Memorial University of Newfoundland under the supervision of Dr. William Montevecchi. The PhD project represents an extension of research conducted in the Montevecchi lab, that involved the first tracking studies of murres (and other seabirds) in the North Atlantic, and described for the first time their year-round distribution and migration routes (e.g. Hedd et al. 2011, Gaston et al. 2011, McFarlane Tranquilla 2014). In collaboration with other lab members, I initiated this research project to extend the scope of our research into year-round investigations of seabird foraging ecology.

Financial support for this research was provided by my supervisor Dr. William Montevecchi (NSERC Discovery Grants, Wildlife Habitat Canada and Bird Studies Canada Murre Fund of Newfoundland and Labrador), NSERC PGS-D Scholarship (CMB) and the Graduate School of Memorial University of Newfoundland. Additional contributions were made as follows:

i) study design and research proposal

CMB played the lead role in study design, research planning and data collection at Funk Island and Gull Island with invaluable input from members of the Montevecchi Lab (Drs. April Hedd, Paul Regular and Laura McFarlane Tranquilla) in very close collaboration with my supervisor.

ii) practical aspects of research

Field data (device deployments and retrievals, blood and tissue samples) at two colonies involved great efforts from a small group of colleagues and field assistants (see

Acknowledgements). CMB processed all behavioural data, with assistance from Dr. Paul Regular who provided invaluable technical advice regarding the processing of raw dive data in MT Dive and Cran R (2003). CMB prepared all tissue samples for stable isotopic analyses (SIA), with assistance from MUN undergraduate students. Processing of SIA samples was out-sourced to the Stable Isotope Facility, University of California, Davis and molecular determination of sex via blood samples were conducted by Dr. Dawn Marshall (Biology Department, Memorial University of Newfoundland). Dr. Gregory Robertson (ECCC) and Dr. Sabina Wilhelm (CWS) generously provided data on the winter masses of murres from the Newfoundland hunt (presented in Chapter 4) and Dr. Laura McFarlane Tranquilla (Bird Studies Canada) provided access to British Antarctic Society (BAS) locational data to run a comparative analysis to assess the precision of latitudinal estimates with Lotek loggers (Appendix 1).

iii) **data analyses:**

CMB performed all statistical analyses, with much appreciated support, advice, and technical expertise from Drs. Regular, Robertson, and McFarlane Tranquilla. Dr. Morten Frederikson provided technical advice and expertise on Lotek geolocation data, in addition to a copy of his R script to run latitudinal adjustments on Lotek positions (Appendix 1).

iv) manuscript preparation:

CMB is the primary author of all chapters in this thesis, which involved analysis and interpretation of data and statistical results, preparation of all tables and figures and final manuscript composition. Thesis chapters were greatly improved by comments and revisions provided by my supervisor, manuscript reviewers and editors from published manuscripts (PLoS, Frontiers in Marine Science).

CHAPTER 2 - SEASONAL VARIATION IN PARENTAL CARE DRIVES SEX-SPECIFIC FORAGING BY A MONOMORPHIC SEABIRD

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*Published as: Burke CM[1], Montevecchi WA[1], Regular PM[2] (2015). Seasonal variation in parental care drives sex-specific foraging in a monomorphic seabird. PLoS ONE 10(11): e0141190

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2.1. Abstract

Evidence of sex-specific foraging in monomorphic seabirds is increasing though the underlying mechanisms remain poorly understood. We investigate differential parental care as a mechanism for sex-specific foraging in monomorphic Common Murres (*Uria aalge*), where the male parent alone provisions the chick after colony departure. Using a combination of geolocation-immersion loggers and stable isotopes, we assess two hypotheses: the reproductive role specialization hypothesis and the energetic constraint hypothesis. We compare the foraging behaviour of females (n = 14) and males (n = 8) during bi-parental at the colony, post-fledging male-only parental care, and winter when parental care is absent. As predicted by the reproductive role specialization hypothesis, we found evidence of sex-specific foraging during post-fledging only, the stage with the greatest divergence in parental care roles. Single-parenting males spent almost twice as much time diving per day and foraged at lower quality prey patches relative to independent females. This implies a potential energetic constraint for males during the estimated 62.8 ± 8.9 (SD) days of offspring dependence at sea. Contrary to the predictions of the energetic constraint hypothesis, we found no evidence of sex-specific foraging during biparental care, suggesting that male parents did not forage for their own benefit before colony departure in anticipation of post-fledging energy constraints. We hypothesize that unpredictable prey conditions at Newfoundland colonies in recent years may limit male parental ability to allocate additional time and energy to self-feeding during biparental care, without compromising chick survival. Our findings support differential parental care as a mechanism for sex-specific foraging in monomorphic murres, and highlight the need to consider ecological context in the interpretation of sex-specific foraging behaviour.

2.2. Introduction

Sex-specific foraging has been documented in a range of taxa (Ruckstuhl and Neuhaus 2005). In seabirds, it is generally considered to arise from competitive exclusion or social dominance of the larger sex, resulting in spatial or temporal segregation of foraging activity and trophic partitioning when the sexes overlap in space and time (Wanless et al. 1995, Weimerskirch et al. 1997, Gonzalez-Solis et al. 2000, Kato et al. 2000, Bearhop et al. 2006, Phillips et al. 2009, Phillips et al. 2011). Yet, sex-specific foraging arises independently of sexual size dimorphism (Fraser et al. 2002, Paredes et al. 2006, 2008, Thaxter et al. 2009, Welcker et al. 2009, Paredes and Insley 2010, Jones et al. 2002, Elliott et al. 2010, Pinet et al. 2012, Hedd et al. 2014) suggesting alternative mechanisms, including how males and females cooperate to allocate resources to parental care, in a manner that optimizes reproductive success (Stearns 1992).

Two main hypotheses are proposed to explain the emergence of sex-specific foraging in monomorphic seabirds in relation to parental care. The Reproductive Role Specialization Hypothesis (RRSH) postulates that sex-specific foraging emerges in response to specialized reproductive roles by the sexes (Fraser et al. 2002, Jones et al. 2002, Paredes et al. 2006, 2008, Paredes and Insley 2010, Hedd et al. 2014). For example, Sooty Shearwaters (*Puffinus griseus*) segregate at sea during egg development when females forage in distant productive waters, while males that guard the nest site during this time forage in close proximity to the colony (Hedd et al. 2014). The Energetic Constraint Hypothesis (ECH) states that divergent energy requirements by the sexes during one reproductive stage are resolved through sex-specific foraging at another stage (Thaxter et al. 2009, Welcker et al. 2009, Elliott et al. 2010, Pinet et al. 2012). For example, females in relatively poor condition after egg-laying (Monaghan et al. 1998) may spend more time foraging for themselves, resulting in male-biased offspring provisioning during early chick-rearing (Welcker et al. 2009).

In the present study, we use a combination of geolocation-immersion loggers and stable isotope analyses to investigate sex-specific foraging in a 1 kg, monomorphic seabird, the Common Murre (*Uria aalge*), where the male parent alone rears the chick to independence at sea following a brief, but demanding period of bi-parental care at the colony. Although murres exhibit slight sex differences in bill size and body mass (Paredes et al. 2006, Cameron-MacMillan et al. 2007), we consider them monomorphic since there is no difference in the first principle component of body size (Stewart 1993). Along with two related members of the tribe Alcini (Thick-billed Murre *Uria lomvia* and Razorbill *Alca torda*), Common Murres (hereafter murres) exhibit an unusual mode of ‘intermediate’ juvenile development (Sealy 1973). This developmental mode involves c.a. 21 days of bi-parental care at the colony (Ainley et al. 2002, Gaston and Jones 1998), followed by c.a. 2 months of male-only care at sea (Varoujean et al. 1979). Murres are single-prey loaders (Gaston and Jones 1998) that experience the highest flight costs of any volant species (Elliott et al. 2013a), and operate near their physiological limit during chick provisioning at the colony (Elliott et al. 2013b, Regular et al. 2014). Consequently, high parental energetic expenditures and limited chick growth potential combine to favor a relatively brief chick-rearing period at the colony (Gaston 1985, Ydenberg 1989). Yet, chicks are unable to fly and weigh only 25% of adult weight when they go to sea (Gaston and Jones 1998), and are totally dependent on the male parent until they attain nutritional dependence, some 2 months later (Varoujean 1979). After colony departure (here, defined as 'fledging'), flightless male-chick pairs swim quickly away from the colony to offshore nursery areas, and male parents moult their flight feathers (Falk et al. 2001, Camphuysen 2002, Davoren et al. 2002). Females continue to attend the colony for c.a. 2 weeks to defend their breeding territory (Harris and Wanless 2003), after which they fly offshore to moult their flight feathers and become temporarily flightless (Birkhead and Taylor 1977, Thompson et al. 1998).

There is support for both RRSH (Jones et al. 2002, Paredes et al. 2008) and ECH (Thaxter et al. 2009, Elliott et al. 2010, Elliott and Gaston 2014) to explain sex-specific foraging by murres but, since most studies are conducted during biparental care there is less support for RRSH. Paredes and Insley (2010) argue that male Thick-billed Murres are more aggressive than females and play a greater role in nest defense; brooding the chick overnight when predation risks are highest (Paredes et al. 2006). As a result, male Thick-billed Murres forage primarily during daylight hours when prey is located deeper in the water column and dive significantly deeper than crepuscular foraging females (Jones et al. 2002, Paredes et al. 2008). However, Elliott et al. (2010) argue that evidence of site-specific variability in the nest attendance patterns of Thick-billed Murres, with males brooding at night at some colonies but not others implies that nest attendance patterns are unrelated to nest defense but rather can be explained by ECH. Specifically, sex differences in nest attendance patterns are driven by diel patterns in the availability of the preferred prey of the sexes, whereby males target risk-averse, shallow-water prey (versus risk-prone benthic prey by females) to maintain body condition in preparation for the post-fledging period (Elliott and Gaston 2014). Additional support for ECH comes from evidence that flightless male-chick pairs (based on one male only) associate with lower quality foraging areas relative to other independent murres, suggesting a potential constraint on energy intake for male parents during the post-fledging period (Elliott and Gaston 2014). Therefore, documented sex differences in the foraging behaviour of chick-rearing murres (Thaxter et al. 2009, Elliott et al. 2010) and female-biased chick-provisioning during chick-rearing at the colony (Wanless and Harris 1986, Thaxter et al. 2009, Elliott et al. 2010, Elliott and Gaston 2014) may be explained by ECH, whereby male parents forage more for their own benefit during bi-parental care in anticipation of energetic constraints after colony departure. Further studies are needed involving larger samples of single-parenting males to draw stronger conclusions bearing on the ECH.

We compare the foraging behaviour and trophic position of male and female murres during three successive stages in the annual cycle, each characterized by a different level of parental care by the sexes. These include: 1) bi-parental care (BPC) during late chick-rearing when both males and females contribute to offspring care, 2) male-only parental care (MOC) during the post-fledging period when males are single-parents and females are independent and 3) no parental care (NPC) during winter when both sexes are released from parental care. The overall goal of the study is to investigate differential parental care as an underlying mechanism for sex-specific foraging by monomorphic murres. Specific objectives are to assess how stage-specific differences in parental care influence the foraging behaviour of the sexes, including: (1) overlap in core foraging areas, (2) diel foraging patterns, (3) daily foraging effort (i.e. time spent diving); (4) foraging tactics (i.e. dive depth, bottom-time, ascent and descent rates, post-dive interval) and (5) trophic position.

If sex differences in the foraging behaviour of murres are driven by specialized reproductive roles (RRSH), we expect to find evidence of sex-specific foraging during MOC, when the parental care roles of the sexes diverge the most, versus no sex differences during BPC when parental care is shared and NPC when parental care is absent. If sex-specific foraging is associated with stage-specific energetic constraints (ECH), we expect male parents to invest proportionally more time in self-feeding prior to colony departure with the chick, resulting in sex-specific foraging during BPC.

2.3. Materials and Methods

2.3.1. Ethics Statement

The study was carried out in strict accordance with ethical guidelines outlined by the Canadian Council on Animal Care, and approved by Memorial University of Newfoundland's Institutional Animal Care Committee (Permit Numbers: 10-01-WM, 11-01-WM, 12-01-WM, 13-01-WM). Fieldwork was carried out under a Canadian Wildlife Service Migratory Bird Banding permit WAM-10322K. Access to the Funk Island and Witless Bay Islands Provincial Seabird Ecological Reserves was permitted through the Newfoundland and Labrador Parks and Natural Areas Division.

2.3.2. Study Sites and Logger Field Work

Fieldwork with murres was carried out at two Northwest Atlantic colonies: Gull Island in the Witless Bay Ecological Reserve (47°16’N, 52°46W) with c.a. 1632 breeding pairs breeding pairs (Robertson et al. 2004) and the Funk Island Ecological Reserve (49°45’N, 53°11’W) with c.a. 470, 000 breeding pairs (Wilhelm et al. 2015). Lotek LAT 2500 geolocation-immersion loggers (5.9 g with attachment, c.a. 0.7% body mass) were attached to plastic leg bands (Pro-Touch Engraving) with cable ties and placed on the left leg of breeding murres during late chick-rearing (adults with chicks > 10-15 days of age). A Canadian Wildlife Service metal band was attached to the right leg. Fifty-one loggers were deployed from 2009-2013: 15 at Funk Island (2009) and 36 at Gull Island (2010-2013). Instrumented birds were recaptured on the nest in the following breeding season. Upon recapture the logger was removed, birds were weighed with a 1 kg Pesola spring balance and 1 ml of blood was collected from the brachial vein for sex determination (Fridolfsson and Ellegren, 1999) and stable isotope analysis (Hobson and Clark 1993, Thompson et al. 1998). Feathers were also collected on recapture, including one secondary covert and 3-6 breast feathers that provide trophic signals for MOC and NPC, respectively (Pyle 2009, Thompson et al. 1998). Throughout deployment and recapture, birds were held in a cloth bag for c.a. 4-6 min with their head covered. Approximately 15 control birds (i.e. no logger attachment) were also captured in each year (n = 61) for comparisons of body mass and trophic position with loggered individuals. This allowed us to assess possible device effects on body condition and foraging behaviour.

2.3.3. Logger Processing

2.3.3.1. Activity Data

Loggers were programmed to record dry state every 60 s when ambient temperature was < 28°C. To conserve memory, wet state was not logged and a temperature criteria was used to distinguish between dry periods at sea that represent flight, versus dry periods at sea that represent leg-tucking (i.e. when the bird draws its leg and foot into its plumage). This approach assumes that heat transfer from the bird’s body (39.6 °C; Gabrielson et al. 1998) during leg-tucking would result in temperature readings approaching 28°C, well above ambient air and water temperatures experienced by North Atlantic murres during the non-breeding period. Patterns in the timing and duration of uninterrupted dry events (> 1 min) were used to determine colony departure (late summer) and arrival (spring) dates, where dry events greater than 360 min (or 6 h) indicated regular colony attendance. In addition, dry periods at night (> 60 min) provided corroborating evidence of colony attendance since murres are known not to fly at night (Robertson et al. 2012). Sex comparisons of the timing of colony departure and arrival were standardized according to mean dates (± SD), and by year when sample sizes allowed. Limited memory capacity and some mid-year device failures resulted in fewer individuals for spring colony arrival estimates.

2.3.3.2. Positional Data

Positional data from Lotek loggers are derived from internal processing algorithms that generate a single daily location, based on measurements of light intensity (Ekstrom 2004). Comparisons of Lotek positions with those generated from British Antarctic Society (BAS) loggers (5.4g, 0.6% adult body mass) deployed on murres at the same colonies (Hedd et al. 2011, McFarlane Tranquilla et al. 2013) revealed a potential bias, with Lotek positions extending further north than expected in autumn, and further south in winter. This bias has been identified by other researchers using Lotek loggers to study the seasonal distribution of North Atlantic murres, and is likely associated with higher light exposure at a given date and latitude than is assumed by the device's on-board algorithm (M. Frederiksen, pers. comm.). Therefore, using an R script validated by M. Frederiksen, all positions were recalculated by: 1) back-calculating times of sunrise and sunset using the built-in sun angle of -3.44°, and 2) re-estimating latitudes assuming a true sun angle between -4.5° - 5.5°. Re-calculations were performed using the R package 'GeoLight' 2.0 (experimental version provided courtesy of S. Lisovski). Inspection of recalculated positions revealed a significant improvement during fall and winter, aligning with seasonal distributional patterns from previous studies on Newfoundland murres (Hedd et al. 2011, McFarlane Tranquilla et al. 2013). A detailed description of this analysis is provided in Appendix 1.

Unfiltered positions were subsequently mapped in ArcMap 10.0 (ESRI, 2010) and inspected visually to remove locations that represented improbable daily movements (i.e. >500 km/day (Phillips et al. 2004), or were outside the expected non-breeding range of murres (Hedd et al.

2011, McFarlane Tranquilla et al. 2013). Erroneous locations around the autumn (c.a. 9 September - 9 October) and vernal equinoxes (c.a. 6 March - 6 April) were excluded since latitudinal data derived from day length are unreliable during equinox when day lengths are similar around the world (Hill 1994). The total number of retained, post-processing positions represented 61% of the original 3452 raw positions.

Fifty percent kernel density contours were used to represent the core foraging areas of males and females during the MOC and NPC (Hamer et al. 2007, Linnebjerg et al. 2013). BPC was excluded since maximum foraging ranges of breeding birds around the colony (max <80 km; Regular et al. 2013a) are less than the 100-200 km mean positional error for geolocation loggers (Phillips et al. 2004). Kernel home ranges were evaluated for unsmoothed positions using a least squared cross validation method with a 50 km grid size, applying the 'kernelUD' function in the 'adehabitatHR' package (Calenge 2006) in Cran R (ver. 3.1.2). Percentage overlap of kernel density contours (50%) of females and males within each stage was calculated using the 'kerneloverlaphr' function (HR method), that calculates the proportional overlap of one sex relative to the other:

$$HR_{(f,m)} = A_{(f,m)} / A_{(f)}$$

where $A_{(f,m)}$ represents the area of intersection between females and males and $A_{(f)}$ is the home range area of females (Calenge 2006). Overlap is presented as the mean 50% core area of females and males.

2.3.3.3. Dive Data

Loggers were programmed to record pressure every 8 s when submerged below 2 m. Individual dives were analyzed using the dive analysis program, MT-Dive 4.0 (Jensen Software). Estimates of dive depth, bottom duration, ascent and descent rate and post dive interval were derived for all dives ($\geq$ 3 m). Dive bouts were identified according to a bout-ending criterion using an empirical maximum likelihood approach (Luque and Guinet 2007) executed in 'diveMove' package in R (Luque 2007). Post-dive intervals greater than the identified bout-ending criteria for each individual dive indicated the onset of a new bout. Bottom duration was defined as the time from the first and last instant when vertical velocity (calculated between successive records) fell below 0.5 ms^{-1} (Halsey et al. 2003). Daily foraging effort of individual murres during each stage was estimated using accumulated dive time per day, or the total dive time per day.

To investigate sex-specific diurnal patterns in diving behaviour, individual dives were assigned to a specific time period (day, twilight, night): day was defined as the period between sunrise and sunset (when the sun angle is above 0°), twilight as the period when the sun is between 0° and -12 (nautical) and night as the period when the sun is below -12°. Sun angle (°) was calculated using astronomical models (Regular et al. 2011), based on the formula by Iqbal (1984) and executed in Cran R (ver 3.1.2) using an R script validated by P. Regular. Chi-square tests were applied to assess sex differences in diurnal diving activity, expressed as mean number of dives per time period on a daily basis, within each stage.

2.3.4. Index of Patch Quality

To investigate sex differences in prey patch quality within stages, we calculated an index of patch quality (IPQ) for all individual dives ($\geq$3 m) using the formula presented by Elliott and Gaston (2014). IPQ is based on theoretical models of optimal dive behaviour for relationships between dive depth, durations and surface pauses (Mori et al. 2002, Elliott and Gaston 2014). IPQ values increase with increasing bottom time for a given dive depth, based on the assumption that bottom time will be increase only when patch quality is high (Mori et al. 2002). To eliminate surface pauses not associated with foraging bouts, we included dives occuring within foraging bouts only, expressed as mean IPQ per dive bout.

2.3.5. Statistical Analysis

Analysis of variance (ANOVA) was used to examine sex-specific differences in δ^{15}N and δ^{13}C values of murres within each stage. Repeated measures ANOVA were applied to examine differences in the δ^{15}N and δ^{13}C values for each sex across stages, using a linear mixed-effects model executed in the R package lme4 (Bates et al. 2015). Post-hoc Tukey's multiple comparison test for unequal sample sizes were applied to statistically significant outcomes. Statistical significance was defined as $p < 0.05$.

The effects of sex, stage, and their interaction on murre foraging effort, diving tactics and IPQ values were examined using generalized linear mixed-effects models (GLMM) with a gamma error distribution. Mixed modeling was used to account for potential pseudo-replication, with individual set as a random effect and an autoregressive variance-covariance matrix (corAR1) to account for the high temporal correlation in the dive data (assessed via autocorrelation function in Cran R). All statistics were run in R (ver 3.1.2) and GLMM models were run using lme4 package (Bates et al. 2015). An outcome was considered significant if the confidence interval of a parameter did not include the value of zero effect (using a confidence level of 95%). Model effects and their significance are presented throughout as mean ± SE [95% confidence intervals].

2.3.6. Trophic Niche

Whole blood that has an isotopic turnover of c.a. 12-15 days (Hobson and Clark 1993) provides an isotopic signal for BPC (n = 65, 36 females, 29 males). Flight feathers (secondary covert), grown over an estimated two-month period (Thompson et al. 1998) provided an isotopic signal for MOC (n = 75, 41 females, 34 males). Breast feathers (n = 78, 43 females, 35 males) that provide a late winter, pre-breeding isotopic signal were used for NPC (Pyle 2009). No appropriate tissue that reflects trophic information during early winter can be sampled from a live murre, therefore late-winter values were assumed to represent an equivalent signal for NPC.

Following Cherel et al. (2007) feathers were cleaned of surface contaminants using a 2:1 ratio solution of chloroform:methanol. Feathers were air-dried under a fume hood and cut into fragments, avoiding the quill and shaft. Blood samples that were preserved in 95% methanol were oven-dried to a constant mass at 60°C. Dried samples were then coarsely ground, and lipids extracted using a 2:1 chloroform:methanol solution. A 1 mg subsample of feather and blood samples were weighed and placed in a tin cup. Instruments were cleaned with acetone between samples to prevent cross-contamination. Isotope values were determined by the Stable Isotope Facility, University of California, Davis. Results are reported in delta notation (δ) in parts per thousand (‰) relative to air ($\delta^{15}N$) and PeeDee Belemnite ($\delta^{13}C$). Replicate measurement of laboratory standards (2 standards for every 12 unknowns) indicated measurement errors of ~0.16 and 0.03 ‰ for nitrogen and carbon, respectively.

Two diet-feather fractionation values were used to convert feather isotopic values to trophic values: 3.7‰ ($\delta^{15}N$) and 1.9‰ ($\delta^{13}C$) for secondary feathers and 3.6‰ ($\delta^{15}N$) and 2.5‰ ($\delta^{13}C$) for breast feathers (Becker et al. 2007). Average diet-blood fractionation of 2.63‰ ($\delta^{15}N$) and 0.37‰ ($\delta^{13}C$) were used for whole blood (Cherel et al. 2005). All fractionation factors were subtracted from raw isotopic values prior to analysis.

2.3.7. Delineation of Stages

Behavioural information derived from data loggers was used to define the three stages in the annual cycle for all individuals, each involving different parental care investments. BPC was defined as the period from logger deployment to colony departure (males) and for females, BPC was defined as the period from logger deployment to one week before colony departure owing to the females tendency to remain at the colony following male and offspring departure (Harris and Wanless 2003). MOC was defined as the period from colony departure to offspring independence for males and females, where offspring independence was estimated based on the daily dive rates of single-parenting males (self and chick-provisioning), that is expected to be higher than for independent females (Elliott and Gaston 2014). The no-parental care stage

(NPC) was defined as 1 November to 31 January. Supplementary Table 2.1 provides detailed information on the range of sampling dates according to each stage for all individuals (for dive data only).

2.4. Results

2.4.1. Device Effects and Data Availability

Following capture and deployment of devices, birds returned consistently to their breeding site either immediately or soon after release (within 30 min), suggesting that attraction to offspring was potent and levels of disturbance due to capture and handling were surmountable. Mass at recapture did not differ between instrumented (982.6 g ± 54.8 SD, n = 29) and control (977.1 g ± 76.3 SD, n = 61) birds ($t_{76} = 0.4$, $p = 0.7$). There was no significant difference ($F_{1,255} = 0.4$, $p = 0.5$) in the mean $\delta^{15}N$ values of loggered and control birds during MOC ($F_{1,75} = 1.9$, $p = 0.2$) or NPC ($F_{1,78} = 1.8$, $p = 0.2$). These results suggest that the body condition and foraging behaviour were not negatively affected by carrying devices over the year.

Of 51 loggers deployed on breeding murres, 29 were retrieved (3 of 15 at Funk I and 26 of 36 at Gull I). Four of these devices failed, resulting in a final sample size of 25 individuals consisting of 15 females, 9 males and one individual of unknown sex that was excluded from analyses (Table 2.1). In addition, the chick of one male parent in 2011 was confirmed lost when both parents were observed on the breeding site after fledging. This unsuccessful male was treated separately from other males during MOC (Supplementary Table 2.1). Inconsistency in logger performance resulted in a variable sample distribution across data types and stages

(Table 2.1). Eighteen of 25 loggers did not successfully record all three data logs, resulting in partial behavioural information for some individuals (Table 2.1). In addition, dive information was unavailable for BPC and MOC for 4 individuals in 2013 (3 F, 1 M), since loggers were programmed to start recording pressure on 1 November (versus at deployment) to capture foraging behaviour through winter and spring.

Table 2.1. Deployments (Out), retrievals (In) and data outcomes by site, year, sex and log type. Numbers refer to individuals. Letter superscripts explain discrepancies in sample size.

Year	**Out**	**In**	**With Data**	**Wet/dry**			**Light**			**Pressure**		
				#	**F**	**M**	**#**	**F**	**M**	**#**	**F**	**M**
2009	15	3^{A}	3^{B}	2 (2^{C})	2 (2^{C})	0	3	2	1	3	2	1
2010	8	7	7	7	4	3 (1^{UM})	7	4	3 (1^{UM})	7	4	3 (1^{UM})
2011	11	7	4^{B}	3	2	1	4	2	2	3	2	1
2012	6	3	2^{B}	2	1	1	1	1	0	2	1	1
2013	11	9	9^{B}	9 (1^{U})	6	2	9 (1^{U})	5	3	8 (1^{U})	5 (3^{W})	2 (1^{W})
Totals	**51**	**29**	**25**	**23 (1^{U})**	**15**	**7**	**24 (1^{U})**	**14**	**9**	**23 (1^{U})**	**14**	**8**

^{A} Arctic fox disturbance (details in Burke et al. 2011), ^{B} partial (i.e. < 3 logs), ^{C} <10 days, ^{UM} unsuccessful male (i.e. not accompanied by chick at sea), ^{U} unknown sex, ^{W} dive data recorded after 1-Nov.

Overall a combined total of 117,052 dives ($\geq$ 3m) were recorded over three stages, with an average of 7580.7 ± 2661.6 dives from 14 females and 8865.3 ± 2939.2 dives from 8 males. We found no significant sex difference in the overall number of dives (independent samples t test: $t_{16} = 0.8$, $p = 0.3$). A total of 2634 bird days were sampled, with a mean sampling period of 121 days for females and 117 days for males ($p = 0.80$). There was no sex difference in the number of bird days sampled within stages, but across stages the sampling distribution was shorter during BPC for both sexes, relative to MOC and NPC (Supplementary Table 2.1).

2.4.2. Timing of Colony Departure and Arrival

Independent females departed the colony later than males in all years, with an average difference of 7 days (Table 2.2). The male of a breeding pair (2012) departed the colony on 25 July, 12 days earlier than the female partner (06 August; Table 2.2). Murres returned consistently to the colony in early-mid May with earlier arrival dates by males in all years by an average difference of 6 days (Table 2.2).

Table 2.2. Summary of colony departure and arrival dates of individually tracked murres (wet-dry log). Values are median dates (± SD days) summarized by sex (and year where sample size allows).

Year	Colony Departure Median Date		Colony Arrival Median Date	
	F (n = 15)	M (n = 7)	F (n = 8)	M (n = 4)
2009	22 Aug ± 0 d (2)	16 Aug (1)	NA	NA
2010	21 Aug ± 4.6 d (4)	17 Aug ± 10 d (2)	20 May ± 4 d (2)	15 May ± 1 d (2)
2011	11 Aug ± 2 d (2)	31 Jul (1)	24 May (1)	06 May (1)
2012[P]	06 Aug (1)	25 Jul (1)	17 May (1)	NA
2013	07 Aug ± 2.5 d (6)	30 Jul ± 8 d (2)	08 May ± 7 d (4)	03 May (1)
Overall	10 Aug ± 7.5 d	3 Aug ± 11.1 d	16 May ± 7.1 d	10 May ± 5.5 d

[P] breeding pair sampled in 2013.

2.4.3. Sex-Specific Overlap in Core Foraging Habitat

There was only partial overlap in the core foraging areas (represented by 50% kernel density contours) of female and male murres during MOC (39.3%), overlapping on the southern Grand Bank of Newfoundland (Fig. 2.1). Independent females utilized a larger area relative to single-parenting males (Table 2.3), extending into nearshore and shelf waters on the Newfoundland-Shelf (Fig. 2.1). During NPC, the core foraging areas of females and males overlapped extensively (85.5%; Table 2.3) on the southern Grand Bank (Fig. 2.1).

Table 2.3. Seasonal kernel home range areas (KHR; km^2) and percentage overlap of core foraging areas (50% kernel distribution) of female and male murres during male-only care (MOC) and no parental care (NPC).

Stage	N		50% KHR (km^2)		Mean Percentage Overlap KHR (50%)
	F	M	F	M	F,M
MOC	14	8	476,664	313,856	39.3%
NPC	12	9	222,747	222,404	85.5%

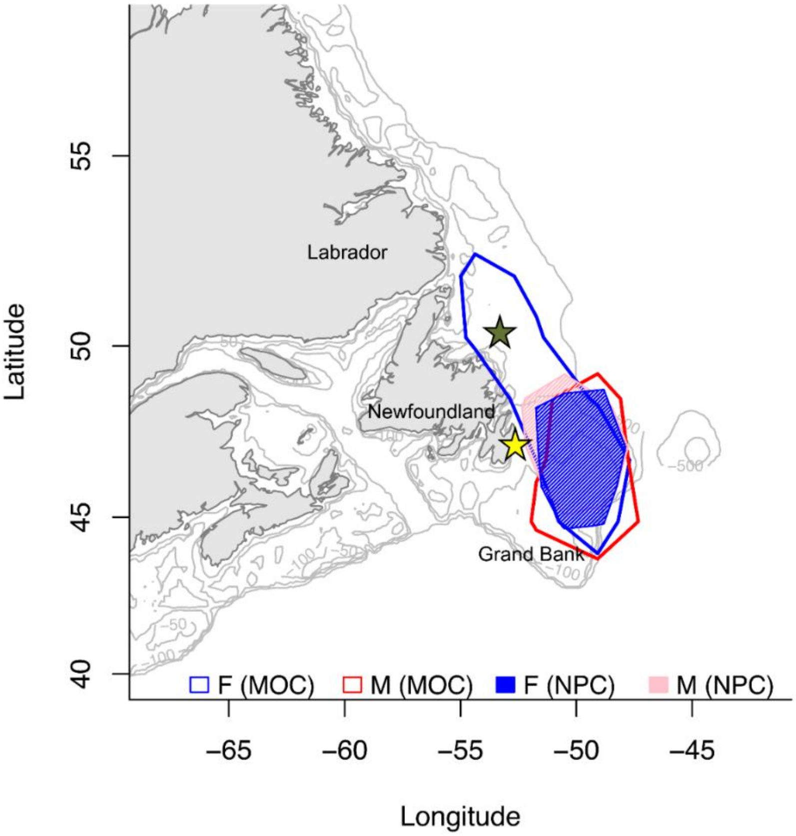

Figure 2.1. Core foraging areas (50% kernel contours) of female (blue) and male (red) murres during MOC (14 F, 8 M) and NPC (12 F, 9 M). Colony locations are indicated by a yellow (Gull I) and green star (Funk I). Depths between isobaths are 100 m. Bathymetry data were obtained online from the GEBCO Digital Atlas (GEBCO one-minute grid, ver. 2, www.gebco.net).

2.4.4. Index of Patch Quality

Sex had a significant effect on IPQ during MOC only (Fig. 2.2), with lower IPQ values for males (0.28 ± 0.03, [95% CI: 0.22 - 0.34]) than females (0.46 ± 0.02, [95% CI: 0.44 - 0.50]). IPQ values of females were higher than males during BPC (0.44 ± 0.02 and 0.37 ± 0.02 for females and males respectively) and NPC (0.52 ± 0.02 and .49 ± 0.02 for females and males respectively), but the differences were not significant (Fig. 2.2).

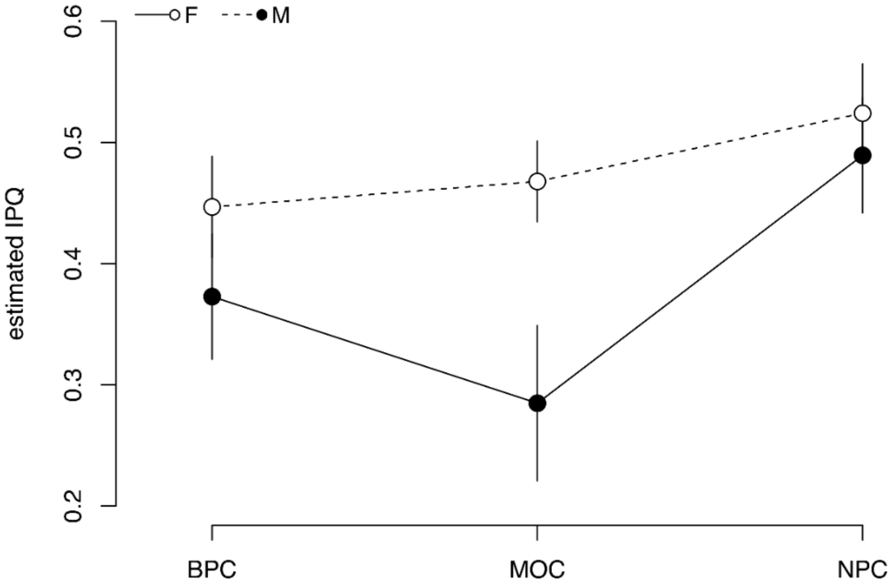

Figure 2.2. Mean (SE) index of patch quality (IPQ) for all within bout dives (>3 m) by female and male murres across successive stages of the annual cycle. Values are GLMM model fits ± confidence intervals. Sample sizes provided in Supplementary Table 2.1.

2.4.5. Sex-Specific Diurnal Foraging

Sex differences in the daily timing of foraging were found during MOC only ($\chi^2 = 6.7$, $p = 0.03$), when males dove more than females during daylight (65.1 ± 2.9% and 54.6 ± 3.8%, females and males respectively) and less than females during twilight (25.0 ± 4.0% and 35.0 ± 4.1%, females and males respectively; Fig. 2.3). Overall, murres dove most frequently during daylight hours (Fig. 2.3), and the frequency of daylight dives increased during NPC, accounting for 79.2 ± 3.3% of dives by females and 76.6 ± 4.6% by males. Night diving occurred during all stages with no significant effect of sex, but was most frequent during BPC for females (13 ± 5.6%) and males (17.9 ± 6.8%; Fig. 2.3).

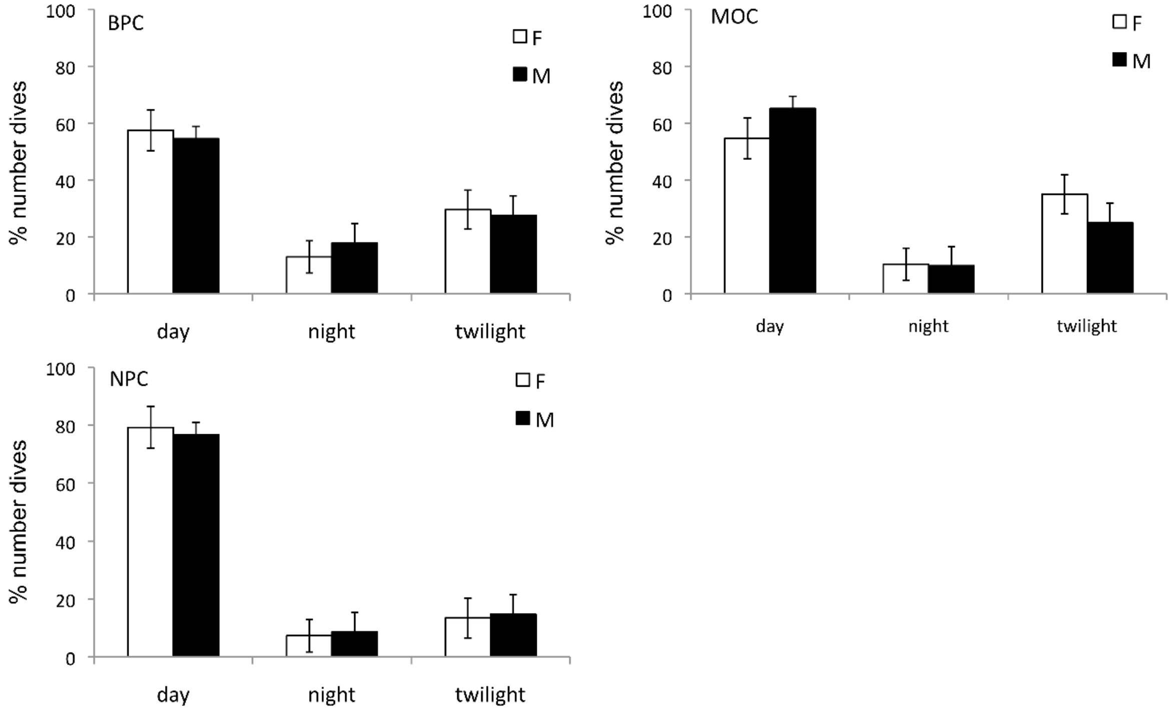

Figure 2.3. Mean percent daily number of dives by female and male murres according to light phase during BPC (top left), MOC (top right) and NPC (bottom left). Values are mean ± SE percent total number of dives day^{-1} across individuals (χ^2 tests: $p < 0005$). Sample sizes provided in Supplementary Table 2.1.

2.4.6. Sex-Specific Foraging Effort

Sex had a significant effect on foraging effort (i.e. accumulated daily dive time) during MOC only (Fig. 2.4), when males spent almost twice as much time diving per day (174.2 ± 9.7 min day^{-1}, [95% CI: 155.2 – 193.2 min day^{-1}]) than independent females (96.1 ± 6.9 min day^{-1}, [95% CI: 82.6 – 109.6 min day^{-1}]). There was no effect of sex on the time spent foraging during BPC or NPC (Fig. 2.4). Daily time spent foraging by females was similar across stages (Fig. 2.4), but males exhibited a significant increase in time spent foraging from BPC (118.6 ± 9.4 min day^{-1}, [95% CI: 100.2 – 137.1 min day^{-1}]) to MOC (174.2 ± 9.7 min day^{-1}), followed by a subsequent decrease during NPC (122.1 ± 9.5 min day^{-1}, [95% CI: 103.4 – 140.8 min day^{-1}]). Daily foraging effort was slightly lower during BPC (113.4 ± 6.9 min day^{-1} and 118.6 ± 9.4 min day^{-1}, females and males respectively) than NPC (125.2 ± 6.8 min day^{-1} and 122.1 ± 9.5 min day^{-1} respectively), despite significantly shorter days in winter (Fig. 2.4).

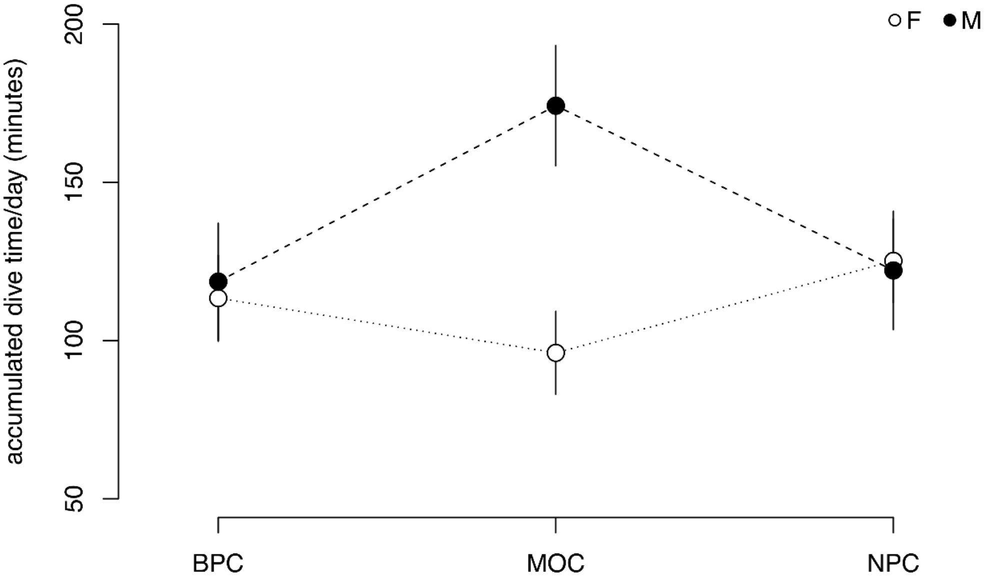

Figure 2.4. Mean accumulated daily dive time of female and male murres across successive stages of the annual cycle. Values are GLMM model fits ± confidence intervals. Sample sizes provided in Supplementary Table 2.1.

2.4.7. Sex-Specific Diving Behaviour

There was a significant effect of sex on dive depth during MOC only, with males (48.6 ± 0.8 m) diving deeper than females (35.5 ± 0.7 m; Table 2.4). During BPC, mean dive depth of males (58.6 ± 5.8 m) was greater than females' (50.0 ± 4.5 m), though the difference was statistically non-significant. Mean dive depths of females (51.6 ± 0.8 m) and males (50.2 ± 1.2 m) were strikingly similar during NPC (Table 2. 4). Mean dive depth of females decreased significantly from BPC (50.0 ± 4.5 m) to MOC (35.5 ± 0.7 m), and increased again in NPC (51.6 ± 0.8 m).

Males dove significantly deeper during BPC (58.6 ± 5.8 m) relative to MOC (48.6 ± 0.8 m) and NPC (50.2 ± 1.2 m). Dive depth and dive duration were highly correlated ($r^2 = 0.92$, $p < 0.0001$), so only information on dive depth is presented here.

Table 2.4. Dive characteristics (using the mean value per bout) of female and male murres during three stages of the annual cycle. Values are GLMM model fits (mean ± SE) and 95% CI (in brackets) by sex according to stage. Bold indicates significant within stage sex differences, with the highest value in bold.

Diving parameters	BPC (n = 18)		MOC (n = 17)		NPC (n = 19)	
	F (11)	**M (7)**	**F (11)**	**M (6)[3]**	**F (12)**	**M (7)**
depth (m)	50.0 ± 4.5 (41.2 – 58.7)	58.6 ± 5.8 (47.3 – 69.9)	35.5 ± 0.5 (33.6 – 37.4)	**48.6 ± 0.8** **(47.1 – 50.1)**	51.6 ± 0.8 (50 .0– 53.1)	50.2 ± 1.2 (47.9 – 52.4)
bottom time[1] (s)	**31.9 ± 0.1** **(31.8– 32.1**)	27.0 ± 0.1 (26.8– 27.3)	**28.8 ± 0.2** **(28.3 – 29.2)**	24.9 ± 0.5 (23.9 – 26.0)	**45.6 ± 0.3** **(45.1 – 46.2)**	43.2 ± 0.4 (42.4 – 44.0)
descent rate (ms^{-1})	1.2 ± 0 (1.2 – 1.3)	1.3 ± 0 (1.3 – 1.4)	1.0 ± 0 (1.0 – 1.1)	**1.2 ± 0** **(1.2 – 1.3)**	1.2 ± 0 (1.1 – 1.2)	1.2 ± 0 (1.1 – 1.3)
ascent rate (ms^{-1})	1.3 ± 0 (1.3 – 1.4)	1.3 ± 0 (1.3 – 1.4)	1.1 ± 0 (1.1 – 1.2)	1.2 ± 0 (1.2 – 1.3)	1.3 ± 0 (1.2 – 1.3)	1.3 ± 0 (1.2 – 1.3)
post-dive interval[2] (s)	151.6 ± 19.8 (112 -191)	160.6 ± 27.4 (106 – 216)	110.2 ± 18.7 (72 -148)	144.8 ± 30.6 (82.3 -206)	174.4 ± 20.7 (133 -216)	191.5 ± 32.2 (126 -257)

[1] excludes bottom time = 0, [2] dives with post dive intervals > 25 min, [3] excludes 1 male whose chick was lost

There was a significant effect of sex on mean bottom duration during all stages, with females spending more time on the bottom phase of dives relative to males (Table 2.4). Mean dive descent rate of males was faster than females during all stages, but the difference was only statistically significant during MOC (Table 2.4). There was no effect of sex on dive ascent rates or post dive interval during any stage (Table 2.4). Despite longer post-dive intervals during

NPC for females (174.4 ± 20.7 sec) and males (191.5 ± 32.2 sec), there was no significant difference across stage for either sex (Table 2.4).

2.4.8. Sex-Specific Trophic Position

There was no effect of sex on mean δ^{15}N isotopic values (fractionation adjusted; mean ± SD) derived from blood (representing BPC; $F_{1,63} = 0.4$, $p = 0.6$), secondary coverts (representing MOC: $F_{1,73} = 0.1$, $p = 0.7$) or breast feathers (representing NPC: $F_{1,75} = 0.4$, $p = 0.6$; Fig. 2.5). Mean δ^{15}N values in secondary coverts of females (+11.8 ± 0.9‰) and males (+11.9 ± 0.7‰) were significantly lower than those of blood (+13.2 ± 0.4‰ and +13.2 ± 0.6‰ and for females and males respectively) and breast feathers (+12.9 ± 0.7‰ for females and males; Fig. 2.5).

Mean (± SD) δ^{13}C isotopic values (fractionation adjusted) in blood and secondary feathers of females and males did not differ (Fig. 2.5), but δ^{13}C in male breast feathers (NPC: -20.5 ± 0.8‰) was significantly higher ($F_{1,75} = 4.3$, $p = 0.04$) than in female breast feathers (-20.9 ± 0.8‰). For females, overlapping δ^{13}C values in flight (-21.0 ± 0.8‰) and breast feathers (-20.9 ± 0.8‰) were significantly lower relative to blood (-19.9 ± 0.8; $F_{2,79} = 41.5$, $p < 0.001$). There was no significant overlap in male blood, flight or breast feathers ($F_{2,60} = 52.5$, $p < 0.001$).

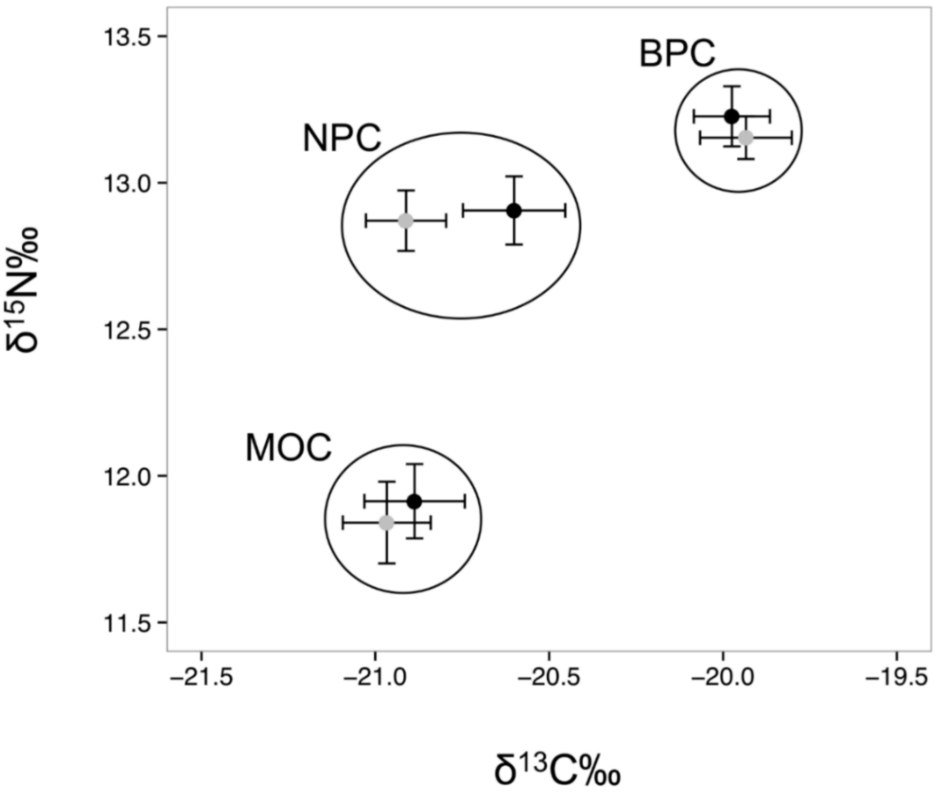

Figure 2.5. Stable isotope values (fractionation adjusted) of murres according to sex and stage. δ^{15}N‰ and δ^{13}C‰ (mean ± SE) values of blood (BPC; n = 65), secondary covert (MOC; n = 75) and breast (NPC; n = 78) feathers of female (grey) and male (black) murres.

2.5. Discussion

We investigated differential parental care as a mechanism for sex-specific foraging in monomorphic Common Murres, evaluating two hypotheses: the reproductive role specialization hypothesis (RRSH) and the energetic constraint hypothesis (ECH). Our results demonstrate sex-specific foraging during the stage with the greatest divergence in parental care roles (MOC) versus a convergence in foraging behaviour during biparental care (BPC) and winter when parental care is absent (NPC). These findings support RRSH as a mechanism for sex-specific foraging in monomorphic murres.

We also demonstrate a potential energetic constraint for single-parenting males, emerging directly from the need to remain with and provision a flightless, growing chick. Yet, contrary to the predictions of ECH; there was no evidence that male parents spent more time foraging for their own benefit before colony departure in anticipation of demanding conditions after fledging. These findings are not in agreement with previous studies that demonstrate male-biased self-feeding (Thaxter et al. 2009, Elliott et al. 2010, Elliott and Gaston 2014), female-biased offspring provisioning (Wanless and Harris 1986, Thaxter et al. 2009, Elliott et al. 2010, Elliott and Gaston 2014) and differential prey specialization by the sexes (Elliott et al. 2010) during the late chick-rearing period (>15 days). We hypothesize that discrepancies in our results reflect context-specific foraging conditions that constrain male parental ability to allocate additional resources for their own benefit during BPC when food is relatively scarce.

Chick-rearing murres at Newfoundland colonies specialize on capelin (*Mallotus villosus)* (Regular et al. 2014, Davoren and Montevecchi 2003a, Davoren and Montevecchi 2003b, Burke and Montevecchi 2008, Hedd et al. 2009, Montevecchi et al. 2016), and the mean δ^{15}N values of male (+13.23‰) and female (+13.15‰) murres during BPC likely correspond to a common diet of capelin (McFarlane Tranquilla 2014). Samples of chick feeds collected concurrently at the colony confirm that capelin were the dominant prey in chick diets during the study (Regular et al. 2014). Capelin is a lipid-rich, schooling fish that forms predictable spawning aggregations during the summer in Newfoundland, typically overlapping with the peak chick-rearing period of murres and other seabirds (Cairns et al. 1987, Carscadden et al. 2002, Regular et al. 2014). It is well established that the parental foraging behaviours and reproductive success of chick-rearing murres throughout the Northwest Atlantic are regulated by the timing and abundance of capelin (Cairns et al. 1987, Burger and Piatt 1990, Doody et al. 2008, Wilhelm et al. 2008, Regular et al. 2014). Murres exhibit resilience to temporary declines in capelin availability, primarily mediated through flexible adjustments in their time budgets and foraging behaviours (Burger and Piatt 1990, Harding et al. 2007). In particular, the co-attendance time of murre parents represents a highly flexible aspect of their daily time budget that allows them to buffer reductions in prey availability by allocating more time to finding food during periods of scarcity (Burger and Piatt 1990, Harding et al. 2007). Therefore, evidence of significant decreases in the co-attendance times of parental murres at Gull Island in recent years (ranging 1.4 hr/day – 4.9 hr/day during 2007-2010; Regular et al. 2014), relative to the 1980s (mean 3.7 hr/day; Burger and Piatt 1990, Wilhelm et al. 2008) suggests that chick-rearing murres may be working harder during peak chick demand than in previous decades.

Observed decadal differences in the co-attendance time of murres could potentially reflect an increase in the frequency of prey mismatch years, whereby the timing of the inshore arrival of spawning capelin does not overlap with the peak hatching dates of murres. In fact, during four of the past eight years (2007-2014), there has been a mismatch in the timing of the inshore arrival of capelin and peak chick-rearing at Gull Island (Regular et al. 2014, Harding et al. 2007, Rector et al. 2012, Storey et al. 2020). Moreover, estimates of the daily energy expenditures (DEE) of murres at Gull Island indicate that even in prey match years the average DEE of parental murres, estimated at 1969.9 KJ/day (Regular et al. 2014), approaches the theoretical upper limit to sustainable energy expenditure (7 X BMR; Cairns et al. 1990, Regular et al. 2014).

Therefore we hypothesize that when food is relatively scarce, male parents may be unable to gather sufficient resources during peak demand to successfully provision their offspring and accumulate reserves for their own benefit. Consequently, male parents could enter the post-fledging stage with an energy deficit during poor food years, and incur potential fitness consequences.

Yet, some limitations in our data could impede our ability to detect differences in the foraging behaviour of the sexes during BPC. For example, while we found no sex difference in the time spent foraging during BPC, it is not known whether males and females allocated their foraging time at sea differently between self-feeding and finding food for their chick. In addition, low spatial resolution during BPC did not allow us to assess whether males and females segregated at sea, or whether males engaged in longer, self-feeding foraging trips as shown previously for murres (Thaxter et al. 2009). However, since murre parents at Newfoundland colonies consume the same prey they fed to their chick, involving an average of c.a. 3 chick feeds per day (Davoren and Montevecchi 2003b, Regular et al. 2014); it is unlikely that the time allocated to finding food for the chick constituted a significant proportion of the total time spent foraging at sea. As well, preliminary information on the foraging ranges of female (n = 4) and male (n = 5) chick-rearing murres at Funk Island (2014), derived from GPS tracking data (PMR and WAM unpubl. data), indicate no sex differences in foraging distributions or maximum foraging ranges, suggesting that males and females do not segregate at sea during BPC.

During MOC, single-parenting males spent almost twice as much time diving per day than independent females. Similar behaviour was found for Thick-billed murres in the Canadian Arctic (Elliott and Gaston 2014), with one single-parenting male performing more than twice as many dives per day than other independent murres. The significant increase in the foraging effort of single-parenting males after colony departure likely reflects the nutritional requirements of their growing chick, and provides a useful indicator of the duration of offspring nutritional dependence. Fig. 2.6 shows that single-parenting males spent significantly more time diving per day compared to females, over an average period of 62.8 ± 8.9 days after colony departure (Supplementary Table 2.1). This was followed by a convergence in the daily time spent foraging by the sexes, which we suggest corresponds to the onset of offspring nutritional independence. In support, one male parent whose chick was lost after fledging did not show an increase in foraging effort following colony departure but rather behaved similarly to independent females (Fig. 2.6). The observed range in the duration of offspring nutritional dependence (range 51-75 days; Supplementary Table 2.1) suggests that the time to offspring independence is variable. Whether this is due to inter-annual variability in environmental conditions or individual quality is difficult to determine here, given the small number of individuals sampled over multiple years. Further research is needed to elucidate the circumstances that influence the duration of chick dependence in alcids with intermediate chick development.

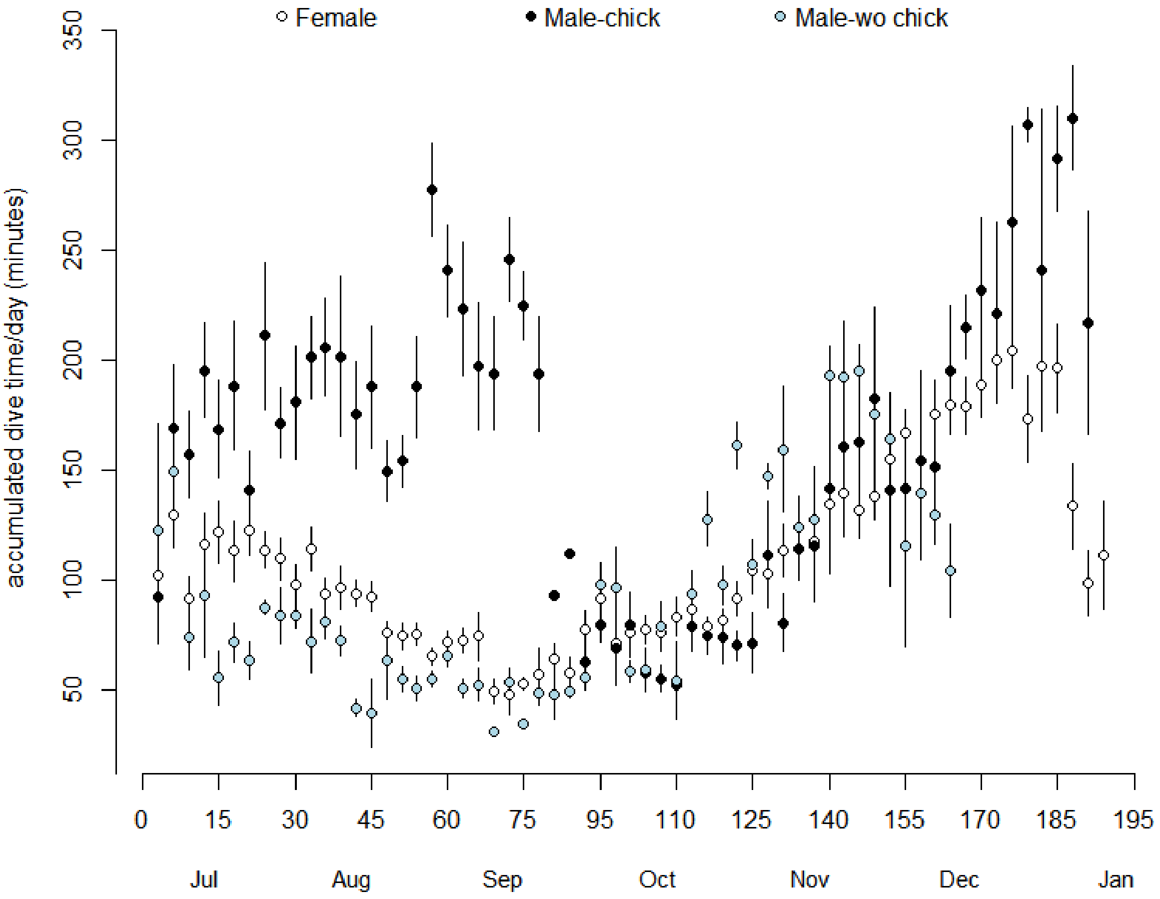

Figure 2.6. Mean time spent foraging (accumulated dive time; mean ± se) of independent females (n = 11; white circle), single-parenting males (n = 6; black circle) and one unsuccessful male (blue circle) from logger deployment to 31 Jan, showing one data point every third day.

The mean $\delta^{15}N$ values of males and females during MOC likely corresponds to a common diet of crustaceans (e.g. shrimp, amphipods, euphausiids) or similar trophic level prey (Davoren et al. 2002). This indicates a decline in the trophic position of adult murres from BPC (capelin) to MOC (crustaceans, juvenile fish), but whether a similar dietary shift occurred for the chicks is unknown. Yet, given the high caloric requirements of a rapidly growing chick (i.e. 13-15 g day^{-1}; Harris et al. 1991) in a cold ocean, and the known limits imposed on chick development and body mass deposition by low-lipid diets (Romano et al. 2006), we expect that growing chicks have nutritional requirements that differ from adults. Furthermore, crustaceans have lower caloric content than fish (Spear 1993) and are therefore likely unsuitable for rapidly growing chicks. A higher frequency of deep dives by single-parenting males compared to females (Fig. 2.7), despite strong overlap in adult diet, suggests that single-parenting males may dive deep to access alternative prey for their chick. Comparative analysis of $\delta^{15}N$ values derived from the primary flight feathers of juveniles grown during the post-fledging period (shot during the winter murre hunt in Newfoundland) with post-breeding adult flight feathers could provide insight into the food requirements of growing chicks, and inform our understanding of this critical stage of juvenile development.

Females also dove deep (i.e. > 50 m) during MOC, but much less frequently than males (Fig. 2.7). Rather, females dove more frequently in shallow waters (<30 m) where they spent comparatively more time on the bottom phase of dives (Fig. 2.7). Since the bottom phase of the dive represents the feeding portion of the dive for murres (Mori et al. 2002), evidence of significantly shorter bottom times by females in relatively shallow water suggests that independent females may have higher dive efficiency and energy intake rates relative to single-parenting males. Males may spend less time on the bottom phase of dives if prey is scarce or patchy. Relatively lower IPQ values for single-parenting males support this, and suggests that the dive efficiency and energy uptake of male parents may be constrained by poor foraging conditions during MOC. Because males are rendered flightless immediately upon departure with their flightless chick, they have limited opportunites to locate high quality foraging areas. Even if they have prior knowledge of ocean nursery areas (using memory; Davoren et al. 2003), they must still initiate long risky swimming migrations to offshore areas (Camphuysen 2002), during which opportunities to locate quality foraging areas may be limited. In contrast, females that spend brief periods at the colony after the male-chick pairs depart (7 days in this study), and can fly during the first days at sea, may use this time to prospect high quality foraging areas for the upcoming period of moult-induced flightlessness. Alternatively, shorter bottom durations by single-parenting males could also reflect parental vigilance, whereby single-parenting males reduce the time spent on the bottom phase of dives to minimize the total time the chick is left unattended at the surface. This behaviour would persumably decrease in importance over time however, as chicks grow larger and become increasingly less vulnerable to avian predators or harassment by other murres. Accordingly, we would expect to observe an increase in bottom duration over time, but this is not supported by our data that shows no change in mean bottom duration over time (CMB unpubl. data).

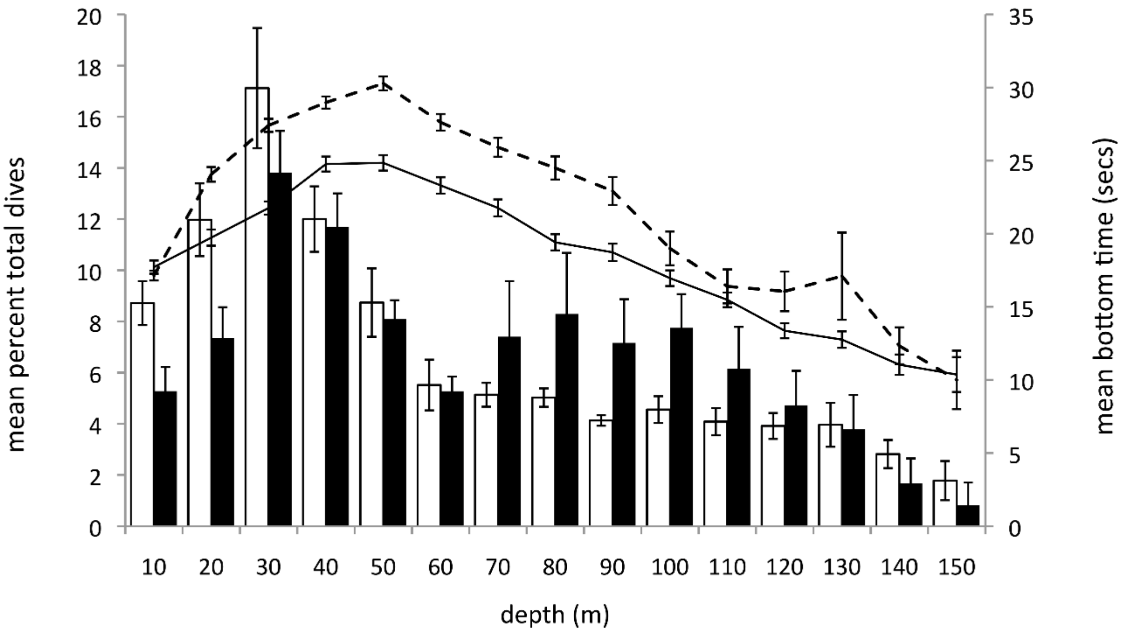

Figure 2.7. Mean percentage daily number of dives (bars) and mean bottom duration (lines) by 10 m intervals for female (white bars, solid line) and male (black bars, dashed line) murres during MOC.

Overall, our results suggest that single-parenting males may experience a significant energetic constraint during MOC. However, the corresponding temporary elimination of flight costs imposed by behavioural flightlessness and prebasic moult may allow males to overcome the constraints associated with offspring provisioning at sea. In support, estimates of the daily energy expenditures of Thick-billed Murres indicate low expenditures during prebasic moult, relative to colony-based chick-rearing and winter (Fort et al. 2009, Elliott and Gaston 2014). Yet, if male parents are unable to allocate additional reserves to self-maintenance before they depart the colony, prolonged energy deficits over the post-fledging period could potentially incur fitness consequences.

During NPC, there was no difference in the foraging behaviour of male and female murres. The convergence in foraging behaviour during a period with no parental care by either sex suggests that sex differences in parental care is a major driver of sex-specific foraging by murres. However, similar foraging behaviour by the sexes during winter could also reflect the minimum level of effort required to survive under conditions of increasingly limited food and light availability during North Atlantic winters. Despite significantly shorter days in winter, there was no difference in the time spent foraging during BPC and NPC. This suggests that murres may be forced to maximize foraging time during short days in winter to achieve their daily energy requirements, which are expected to be high due to thermoregulatory costs (Fort et al. 2009). Therefore, intense foraging during short, cold days may provide murres with the needed energy to overcome periods of fasting during long winter nights, and severe storms that temporarily impede foraging ability (Finney et al. 1999). The winter foraging ecology of murres is poorly known, and further studies investigating behavioural strategies in response to harsh and limiting winter conditions are warranted.

2.6. Conclusions

This study demonstrates sex-specific foraging behaviour by monomorphic Common Murres during a 2-month period of post-fledging, male-only parental care (MOC) when single-parenting males work hard to provision a growing chick under marginal foraging conditions. Despite this, males did not spend more time foraging for themselves before colony departure in anticipation of difficult conditions during the post-fledging period. If chick-rearing murres face unsustainable energy expenditures during prey-mismatch years, as has been shown for Newfoundland murres that rely on capelin (Regular et al. 2014); male parents may be unable to gather sufficient resources during peak demand to successfully provision offspring, and prioritize their own condition. If so, male parents could theoretically enter the post-breeding stage at an energy deficit during poor food years, and incur fitness consequences. Further research is needed to characterize the energy constraints associated with all aspects of parental care in murres to improve understanding of sex-specific responses to seasonally changing parental and environmental constraints.

2.7. Acknowledgements

We thank N. Laite, A. Hann, S. Bennett, L. McFarlane Tranquilla and A. Hedd for invaluable assistance in the field. Key logistical support was provided by Environment Canada (G. Robertson, D. Fifield, S. Wilhelm, P. Ryan). Special thanks to the crews of the Lady Easton (Easton family) and EcoTours for safe transport to and from colonies. We also thank A. Hedd and L. McFarlane Tranquilla for help with experimental design. We especially thank M. Frederikson for providing a copy of his R script to adjust biased Lotek positions and Simeon Lisovski for supplying an experimental version of the 'GeoLight' R package. All procedures were in full compliance with guidelines of the President's Committee on Animal Care at Memorial University of Newfoundland (14-01-WM). Newfoundland and Labrador Parks Division granted access to the Provincial Seabird Ecological Reserves (Funk Island and Witless Bay). H. Nevins and R. Carle provided very helpful comments on an earlier version of the manuscript.

Supplementary Table 2. 1. Summary information for dive data according to individual and sex, showing the start and end dates for each stage. Letter superscripts provide additional information. Values are median (dates) and mean ± SD (days). Bolded bird IDs indicate Funk Island birds.

	Id	BPC			MCO			NPC			Total Days
		Start	**End**	**# days**	**Start**	**End**	**Total days**	**Start**	**End**	**Total days**	
FEMALE (n = 14)	**1604_10**	06-Aug	14-Aug	9	15-Aug	13-Oct	60	01-Nov	30-Jan	91	160
	1613_10	05-Aug	14-Aug	10	15-Aug	13-Oct	60	01-Nov	31-Jan	92	162
	1595_11	03-Aug	09-Aug	7	10-Aug	23-Sep	45	NA	NA	0	52
	1883_11	13-Aug	17-Aug	5	18-Aug	16-Oct	60	01-Nov	27-Jan	88	153
	1885_11	12-Aug	12-Aug	1	13-Aug	12-Oct	60	01-Nov	12-Jan	73	134
	1895_11	12-Aug	17-Aug	6	18-Aug	16-Oct	44	01-Nov	30-Jan	91	141
	2322_12	22-Jul	04-Aug	14	05-Aug	04-Oct	60	01-Nov	31-Jan	92	166
	2475_12	23-Jul	02-Aug	11	03-Aug	01-Oct	60	01-Nov	31-Jan	92	163
	2475_13	17-Jul	25-Jul[C]	9	26-Jul	23-Sep	60	01-Nov	01 Dec	31	100
	2852_14	NA [WS]	NA [WS]	NA [WS]	NA [WS]	NA [WS]	NA [WS]	01-Nov	31-Jan	91	91
	2857_14	NA [WS]	NA [WS]	NA [WS]	NA [WS]	NA [WS]	NA [WS]	02-Nov	25-Jan	85	85
	2861_14	NA [WS]	NA [WS]	NA [WS]	NA [WS]	NA [WS]	NA [WS]	03-Nov	31-Jan	90	90
	2862_14	23-Jul	26-Jul	4	27-Jul	24-Sep	60	01-Nov	07-Jan	68	132
	2889_14	01-Aug	01-Aug	1	31-Jul	29-Sep	60	NA	NA	0	66
Summary		**03-Aug**	**09-Aug**	**7 ± 4.1[1]**	**10-Aug**	**04-Oct**	**57 ± 6.9[1]**	**01-Nov**	**30-Jan**	**82 ± 17.9[1]**	**121.1[1] ± 39.3**
MALE (n = 8)	**1470_10**	08-Aug	15-Aug	8	16-Aug	10-Oct	56	01-Nov	02-Jan	63	127
	1889_11	07-Aug	13-Aug	7	14-Aug	22-Oct	70	01-Nov	16-Dec	46	123
	18**91_11**[UM]	07-Aug	10-Aug	4	11-Aug [UM]	09-Oct [UM]	60 [UM]	01-Nov	31-Jan	92	156
	1894_11	14-Aug	16-Aug	3	17-Aug	15-Oct	60	01-Nov	31-Jan	92	155
	1894_12	28-Jul	30-Jul	3	31-Jul	13-Oct	75	NA	NA	0	78
	2322_13	17-Jul	24-Jul	8	25-Jul	27-Sep	65	01-Nov	29-Dec	59	132
	2854_14	NA [WS]	NA [WS]	NA [WS]	NA [WS]	NA [WS]	NA [WS]	01-Nov	31-Jan	91	91
	2855_14	27- Jul	27-Jul [ACT]	1	28-Jul	16-Sep	51	01-Nov	25-Nov	25	77
Summary		**07-Aug**	**10-Aug**	**4.9 ± 2.8[1]**	**07-Aug**	**10-Oct**	**62.8 ± 8.9[1]**	**01-Nov**	**31-Jan**	**67 ± 26.2[1]**	**117.4[1] ± 31.9**

[C] different from colony departure since partner left with chick on 25 Jul, [UM] unsuccessful male [excluded during MOC], [WS] winter-spring (log starts in November), [ACT] departed colony 2 days earlier, [1] superscripts differ if M ≠ F (t.test).

CHAPTER 3 – FLEXIBLE TIMING AND FLIGHTLESSNESS SUPPORT INTENSIVE WING MOULT IN A DIVING SEABIRD (COMMON MURRE *URIA AALGE*)

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3.1. Abstract

Common Murres (*Uria aalge*) shed all their flight feathers in quick succession during wing moult and are rendered temporarily flightless. Wing moult involves a significant somatic investment but flightless murres may have a limited ability to track patchy, ephemeral prey, resulting in a potential energy bottleneck. I used logger-derived activity data to quantify the duration and timing of wing moult for individual murres and a combination of logger-derived dive metrics and stable isotopes (δ^{15}N and δ^{13}C values in primary and secondary feathers) to investigate the foraging tactics and trophic niche of murres throughout wing moult. Murres were flightless (and assumed to be moulting) over an estimated 53 days (10 September - 1 November), beginning on average 32.2 ± 12.3 days after colony departure. Murres spent 72.8 ± 4.8 minutes per day foraging during wing moult, performing primary shallow dives (< 50 m) with a strong peak in twilight diving activity (40% of dives). Nitrogen values in primary (+12.22 ± 0.5‰) and secondary feathers (+12.20 ± 0.4) were similarly low, with strong overlap in trophic niche space (represented by feather-specific standard ellipse areas). I hypothesize that energy savings during a prolonged flightless state offset the energetic requirements of somatic production resulting in low energy-demands during wing moult. Moreover, the murre's residential, over-wintering strategy may also afford greater flexibility in the timing of wing moult to coincide with seasonal peaks in the availability of prey (zooplankton and juvenile fish) and the occurrence of warm sub-surface waters.

3.2. Introduction

Feathers are non-living structures that deteriorate over time, losing their strength and insulating properties, and must be replaced periodically. This process, referred to as “moult” represents a challenging phase in the annual cycle of birds as evidenced by increased metabolism across a range of species (reviewed by Payne 1972, King 1981; but see Brown and Byrant 1996), and by the temporal separation of moult from other fitness-related activities in the annual cycle (e.g. breeding, migration, winter; Buehler and Peirsma 2008, McNamara and Houston 2008). Energy is required to produce the basic building materials for the biosynthesis of feathers (keratin synthesis) and to maintain a wide spectrum of metabolic adjustments, including whole-body protein turnover (Walsberg 1983, Murphy and King 1992, Murphy 1995). The energy demands associated with feather production do not explain the entirety of increased metabolism during moult, but other contributing factors are poorly understood (Buehler and Piersma 2008). A reduction in the insulating ability of growing plumage and exposure of blood-engorged quills (Payne 1972) also increases heat loss and incurs additional thermoregulation costs that can be significant for diving birds that moult in cold water environments (reviewed by Hedenstrom 2003).

Flight feather moult (hereafter wing moult) involves replacement of the largest feathers, and therefore represents the most extensive production of somatic tissue in the annual cycle (Walsberg 1983). Nutritional requirements to support the growth of many large feathers at one time are likely high and may involve specific nutrient requirements; primarily protein to supply amino acids that are used in feather growth and the development of other epidermal keratins

(Thompson and Drobney 1996). Replacement of flight feathers also impairs flight to varying degrees, which can pose immediate risks to survival if escape responses and feeding abilities are sufficiently compromised. Given these challenges and risks, there is likely strong pressure to complete wing moult as rapidly as possible, and to minimize overlap with other demanding phases in the annual cycle.

Theoretically, birds can minimize wing moult duration by increasing the rate at which individual feathers are grown, or alternatively by increasing moult intensity (i.e. the total number of feathers growing at one time). However, because feather quality is compromised by faster growth rates, with potentially profound consequences on survival and fitness (Dawson et al. 2000), moult intensity is the primary mechanism driving variation in the duration of wing moult (Rohwer and Rohwer 2013) and accounts for 60% of the variation in moult duration for birds that fly during moult, versus 4.4% by feather growth rate (Rohwer and Rohwer 2013). Variation in wing moult intensity across species is generally attributed to differences in body size (and correlated flight feather size), and the extent to which flight determines a bird's ability to feed and escape predators. Passerines and other small birds with short wings that require less time to grow, quickly shed primary feathers in a sequential pattern while retaining the ability to fly. By contrast, larger birds (with larger feathers) that rely on flight for feeding have evolved more complex strategies (e.g. staggered moult) that allow them to schedule moult between other demanding life-history stages while still maintaining flight ability (Pyle 2006).

Birds that do not rely extensively on flight for feeding or predator avoidance shed all their flight feathers simultaneously (synchronous moult) or in quick succession and are rendered flightless throughout the duration of moult. With the exception of gruiformes (that are grazers), synchronous wing moult is primarily restricted to the medium and large diving birds (e.g. alcids, grebes, cormorants, loons, waterfowl, sea ducks). Because these birds are rendered flightless (or at least, severely compromised) by any reduction in wing surface area, synchronous moult provides the only mechanism to shorten the duration of flightlessness. As a result, molting intensity (the proportion of all feathers molting at a time) is higher in these species, with higher expected costs of wing molt per unit of time.

3.2.1. Common Murre Wing Moult

The Common Murre *Uria aalge* (hereafter murre) is the largest diver in the auk family (~1 kg) with a circumpolar distribution in temperate and sub-Arctic waters (Ainley et al 2002). Murres have small wings that function to maximize efficiency during wing-propelled diving but that significantly compromise flight efficiency resulting in the highest absolute sustained flight costs of any vertebrate (Elliott et al. 2013a). Murres moult their wings over an estimated period of weeks to months (Birkhead and Taylor 1977, Thompson et al. 1998, Bridge 2004, Elliott and Gaston 2014), and likely begin shedding worn flight feathers immediately after colony departure in late summer. Adult males attend their still-growing, flightless chick for an estimated two months after colony departure (Burke et al. 2015, Chapter 2), and are assumed to complete wing moult during this time, though information on the precise extent of overlap between wing moult and offspring care at sea is lacking.

3.2.2. Extrinsic Mortality Risks During Moult-induced Flightlessness

Murres consume primarily forage fish during the breeding season and winter (Rowe et al. 2000, Davoren and Montevecchi 2003a) and a combination of macro-zooplankton and juvenile fish during the post-breeding period (Davoren et al. 2002, Burke et al. 2015, Chapter 2). While these forage species are rich in energy (Montevecchi and Piatt 1987), some are highly ephemeral and all experience 'boom and bust' population dynamics (i.e. abundances change rapidly in response to environmental conditions; Lewis et al. 2019). Because flightless murres have a limited ability to track prey (Davoren et al. 2002), they could be more vulnerable to a nutritional bottleneck during wing moult. Moreover, reduced dispersal abilities during moult-induced flightlessness may increase the probability of death during exposure to oil pollution and other contaminants on the surface of the water. In Newfoundland and Labrador, a legal hunt for murres (*Uria* spp.) begins in the fall (1 September in Labrador, 6 October in northeastern Newfoundland) and therefore likely overlaps with some portion of the murre's wing moult (Montevecchi et al. 2007, McFarlane Tranquilla et al. 2013). Moreover, Bridge (2006) demonstrated reduced stroke efficiency by murres during wing moult however the study, which is the only known assessment of dive efficiency during synchronous wing moult was conducted in very shallow water (3 m) aquarium. As such, the influence of a shallow water, artificial environment on dive mechanics and efficiency, including the reduction in dive efficiency due to increased buoyancy near the surface (Elliott et al. 2007) could bias these observations. Unfortunately accurate measurements of dive mechanics are extremely challenging in the wild and are largely outside the scope of this study.

Some of the challenges and risks associated with flightlessness and high energy requirements during wing moult can be partially mediated by the use of offshore nursey or staging areas that provide a relatively safe and productive environment for flightless murres (Camphuysen 2002, Davoren et al. 2002). This strategy is similar to how many waterfowl species relocate to remote environments (free from predators) during intensive wing moult (Salomensen 1968). Vessel-based observations have documented overlap between large concentrations of flightless auks and high-density prey aggregations in offshore waters, in addition to an absence of predatory gulls that can pose a threat to small flightless chicks (Camphuysen 2002, Davoren et al. 2002). Use of nursery areas during wing moult also places flightless murres outside the range of many anthropogenic threats (hunting, fishing) that are typically concentrated around inshore, coastal areas (McFarlane Tranquilla et al. 2013, Frederiksen et al. 2016). Moreover, unlike the chick-rearing period when murres undergo adaptive mass loss to minimize wing-loading and associated flight costs (Croll et al. 1991), lipids could theoretically be accumulated during flightless wing moult which could provide energy reserves in the event of temporary and unpredictable food shortages. This is supported by observations of significantly heavier murres during wing moult (> 1100 g) relative to the breeding (925g), winter (1095g) and pre-breeding (963g) periods (Harris et al. 2000).

In this study, I use logger-derived activity estimates to determine the timing and duration of wing moult for free-ranging murres, and a combination of dive data and stable isotopes to investigate the foraging tactics and trophic niche of murres during wing moult. Previous studies investigating the timing of wing moult and foraging behaviour of murres and other auks have relied on captive birds held in shallow aquaria (e.g. < 3 m) with artificial light (Birkhead and

Taylor 1977, Swennen and Duiven 1991, Bridge 2004). As such, observed patterns in the timing and duration of wing moult, and associated feeding behaviours may not accurately reflect those of deep-diving, wild birds whose behavioural and physiological processes during moult are triggered and maintained by environmental cues and conditions (Buehler and Piersma 2008).

The primary objective of this study is to provide insight into the moult behaviour of murres in the wild and to better understand the adaptive strategies used to meet the challenges of temporary flightlessness and intensive wing moult. Specific objectives are to: 1) describe the timing and duration of wing moult via logger-derived estimates of daily flight activity where a prolonged period of flightlessness is assumed to correspond to wing moult, 2) describe the diving metrics (dive depth and diel timing) and daily foraging effort of individual murres during wing moult, and 3) describe the dietary niche breadth (via isotopic niche) of murres during the sequential growth of primary and secondary wing feathers. Information on the water temperature profile on the NL Shelf (from August to November), taken from hydrographic station 27 (47°31’50’N, 52°35’10’W; Fisheries and Oceans Canada Atlantic Zone Monitoring Program) is also presented, and discussed in relation to wing moult timing and foraging behaviour.

3.3. Methods

Fifty-one murres were captured (using a noose pole) and equipped with a Lotek LAT 2500 geolocation-immersion logger (5.9 g with attachment, c.a. 0.7% body mass) during late chick-rearing (adults with chicks > 10-15 days of age) at two colonies in the Northwest Atlantic during

2009 to 2013: Gull Island in the Witless Bay Ecological Reserve (47°16’N, 52°46W) and the Funk Island Ecological Reserve (49°45’N, 53°11’W; Fig. 3.1). Upon recapture in the following year loggers were retrieved, all birds were weighed with a 1 kg Pesola spring balance and two flight feathers were collected: the tip of one primary (p4) and one secondary covert. One ml of blood was taken from the brachial vein for sex determination and isotope analysis (Fridolfsson and Ellegren, 1999). Throughout deployment and recapture, birds were held in a cloth bag for c.a. 4-6 min with their head covered. Approximately 15 control birds (i.e. no logger attachment) were also captured in each year.

Twenty-nine of 51 loggers were retrieved (3 of 15 at Funk I, 26 of 36 at Gull I), four of which failed resulting in a final sample size of 25 individuals. This included 21 birds with activity data (none at Funk Island) and 20 birds with dive records during the post-breeding period of interest. All males assumed to be attending a chick after colony departure were excluded from the activity (n = 6) and dive data (n = 7). This was necessary since single-parenting males are behaviourally flightless, which precludes the delineation of moult as defined by a flightless state and because they dive deeper and more often while provisioning their growing chick (Chapter 2, Burke et al. 2015, Elliott and Gaston 2014) and exhibit foraging patterns unrelated to moult constraints. This resulted in a final sample of 15 murres with activity data and 13 murres with dive data during the post-breeding moult period. Since not all of these birds have both activity and dive data, the period of wing moult as defined by the activity data and the foraging patterns during wing moult are assumed to be representative of wing moult timing and foraging patterns of all birds.

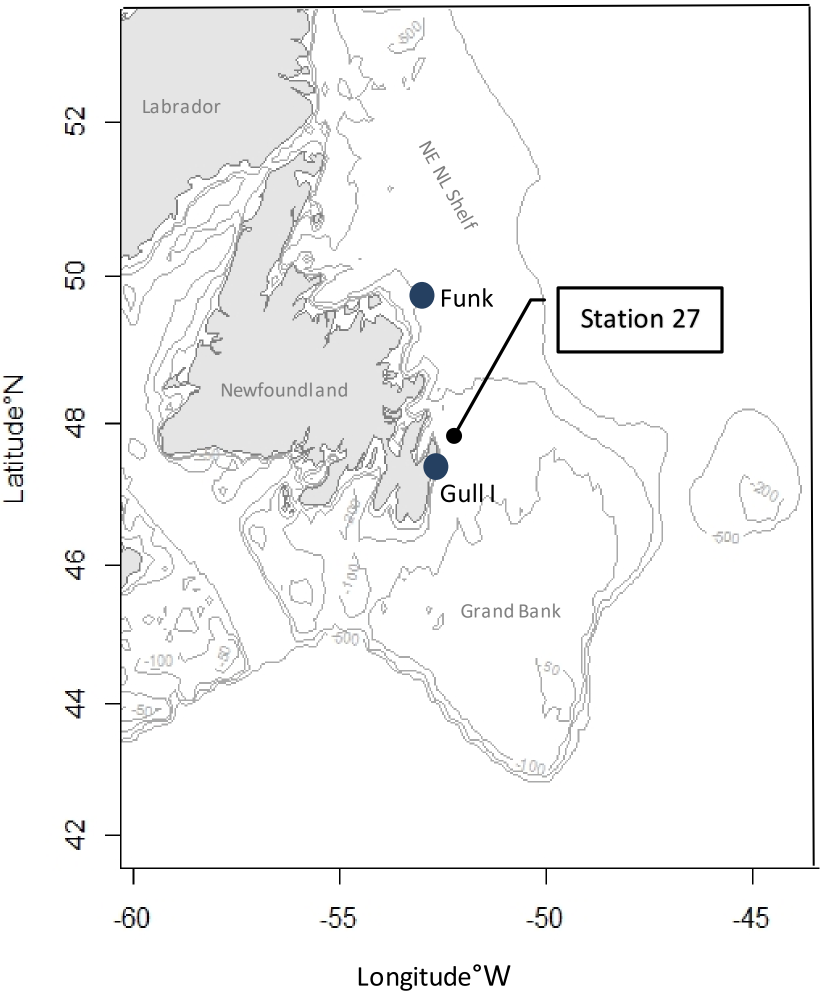

Figure 3.1. Map of the study area indicating the location of Funk Island and Gull Island (large blue circles) and hydrographic Station 27 (black circle).

3.3.1. Delineation of Wing Moult Timing and Duration

Activity (wet-dry) logs from retrieved loggers were used to calculate the total daily time that individual birds spent in flight (dry events) and on the water (wet events). Flight budgets were estimated on a daily basis, whereby all flight events were summed to estimate the total time spent flying per day. The period of time during which there was no flight activity over consecutive days was assumed to represent the flightless period associated with wing moult. This approach is complicated by the tendency of alcids to occasionally withdraw their leg and foot into their plumage when resting on the water (Harris et al. 2010, Linnebjerg et al. 2014), which can result in an over-estimation of the total daily flight time. To distinguish between dry periods at sea that represent flight versus dry periods at sea that represent leg-tucking, we programmed our loggers to record dry state every 60 s but only when ambient temperature was < 28°C. This approach assumes that heat transfer from the bird's body (39.6 °C; Gabrielsen et al. 1998) during leg-tucking would result in temperature readings approaching 28°C, which is well above ambient air and water temperatures experienced by North Atlantic murres during the non-breeding period. A generalized additive mixed model (GAMM) was applied to the activity data to assess temporal trends in daily activity patterns across all birds. The GAMM included total daily flight time as the response variable, date as the explanatory variable and individual as a random factor (negative binomial distribution).

3.3.2. Foraging Behaviour during Wing Moult

Dive metrics (dive depth, duration and diel timing) generated from the pressure logs of retrieved loggers (n = 13) were used to investigate the foraging behaviour of murres during the defined period of moult. Daily foraging effort was calculated as the summed duration of all dives ($\geq$ 3m) over a 24 hour period for each individual. All dives were assigned to a specific time period (day, twilight, night) defined by sun angle (°) which was calculated using astronomical models (Regular et al. 2011) based on the formula by (Iqbal 1984) using an R script validated by P. Regular. Statistical differences in dive depth across defined moult stages were also assessed within each diel cycle (daylight, twilight and night) using a generalized linear mixed-effects models (GLMM) with a gamma error distribution. An outcome was considered significant if the confidence interval of a parameter did not include the value of zero effect (using a confidence level of 95%).

To investigate the influence of wing moult on the foraging behaviour of murres, I defined three stages corresponding to 1) pre-wing moult (i.e. after colony departure and before the onset of wing moult), 2) wing moult, and 3) post wing moult (after the termination of moult). The exact timing of these stages will be defined based on the estimated wing moult period for all birds. Stage-specific differences (pre moult, moult and post moult) in daily foraging effort were assessed using a before and after approach following Guillemette et al. (2007). Cumulative values of total daily time spent diving (i.e. submerged $\geq$ 3 m) for the pre and post moult periods were subtracted from cumulative values during the moult stage. This was repeated for all individuals to obtain a mean difference over all birds, from which 95%

confidence intervals were calculated using a bootstrap method (10,000 re-samplings). When the 95% CIs of mean differences excluded 0, differences were deemed significant (5% level). All statistics were run in R (ver 3.1.2) and GLMM models were run using lme4 package (Bates et al. 2015).

3.3.3. Trophic Niche during Wing Moult

The trophic niche of murres during wing moult is characterized using the δ^{15}N and δ^{13}C values from a sample of primary and secondary flight feathers. As feather keratin is inert after synthesis, the isotopic values of feathers provide information on the diet and location of the consumer during the time they were grown (Hobson and Clark 1993). Isotopic variation among particular feathers regrown at different stages of the moult cycle can also be indicative of temporal shifts in diet and trophic status (Thompson and Furness 1995). Therefore, a selection of appropriate feathers can be used to investigate seasonal variations in diet. Detailed descriptions of the progression of murre wing moult are provided by Thompson et al. (1998) and Bridge (2004). Both of these studies show that primary feathers are dropped first (starting between p4 and p7), followed by secondary feathers that are shed when primary feathers are ~ 25% grown. Therefore, I assume that primary feathers (here p4) represent the earliest stage of wing feather growth, and that secondary feathers represent a later stage when primaries are ~25% grown. Only birds from which a primary and a secondary feather was collected are included (37 individuals). Sampling of multiple flight feathers took place during one year only (2011) at Gull Island (n = 20, including 6 logger birds) and Funk Island (n = 17 control birds). A diet-feather fractionation value was used to convert feather isotopic values to trophic values: 3.7‰ (δ^{15}N) and 1.9‰ (δ^{13}C) for primary and secondary (Becker et al. 2007). All fractionation factors were subtracted from raw isotopic values prior to analysis. A detailed description of tissue sample preparation is provided in Chapter 2 (Burke et al. 2015).

Potential changes in trophic niche over the progression of wing moult was assessed based on the size and extent of overlap in the standard ellipse areas (corrected for sample size SEA_c) and Bayesian standard ellipse areas (SEA_b) of primary and secondary feathers, calculated using the SIBER package in R (Jackson et al. 2011). Statistical comparisons between feathers are based on the proportion of Bayesian iterations (n = 4000) in which the standard ellipse area (SEA_b) of one feather group was larger than the other. The overlap between the 95% prediction ellipses (SEA_c) for each feather group was also calculated using the 'maxLikOverlap' function in SIBER. Repeated measures ANOVAs were also used to examine significant differences in the δ^{15}N‰ and δ^{13}C‰ values between primary and secondary feathers using a linear mixed-effects model executed in package lme4 (Bates et al. 2015). All statistics were computed using Cran R (ver 3.2.1.) and the statistical significance was assumed at $P < 0.05$.

3.3.4. Water Temperature Profile

Water temperature data collected by Fisheries and Oceans Canada at hydrographic Station 27 (47°31'50'N, 52°35'10'W; Fisheries and Oceans Canada Atlantic Zone Monitoring Program; Fig. 3.1) were used to describe the thermal properties of the water column (0 m - 180 m) in relation to the diving profiles of murres during August to November. Station 27 is situated within the Avalon Channel branch of the Labrador Current (Fig. 3.1) and is widely used as an indicator of oceanographic trends across the NL Shelf (e.g. Colbourne et al. 2015). Water temperature was averaged across 10 m intervals by month and included multiple years (2009-2013) to order to increase the number of sampling days per month.

3.4. Results

Information on total daily flight time derived from the activity logs was highly variable across individuals with some birds showing no clear period of flightlessness. This could reflect individual differences in tucking behaviours (if one leg is consistently tucked) or variability in the sensitivity of temperature measurements across loggers. There was also residual noise in the activity data, characterized by intermittent, individual dry events (1 minute each) occurring throughout periods when activity events were primarily wet. As such, the flightless period of individual birds was defined as a continuous period during which the total number of unique dry events was ≤ 5 (i.e. 5 minutes) over 2 consecutive days.

There was a clear decrease in total daily dry time (i.e. time spent flying) after colony departure that persisted over variable periods for 6 females and one male over the post-breeding period (Fig. 3.2). This male was not previously identified as caring for a chick at sea due to the lack of corresponding dive records during the post-breeding period that were used to identify parental care at sea via increased daily foraging effort (Chapter 2, Burke et al. 2015). The activity data of this male shows a brief period of flightlessness immediately after colony departure (~ 5 days), followed by a period of flight (or colony attendance over ~ 5 days), which suggests the chick was lost shortly after colony departure. Another individual (1891_12) is assumed to be a non-breeding male based on post-tagging observations during which this individual did not exhibit normal chick-rearing behaviour (i.e. was not seen with a chick and visited multiple nest sites).

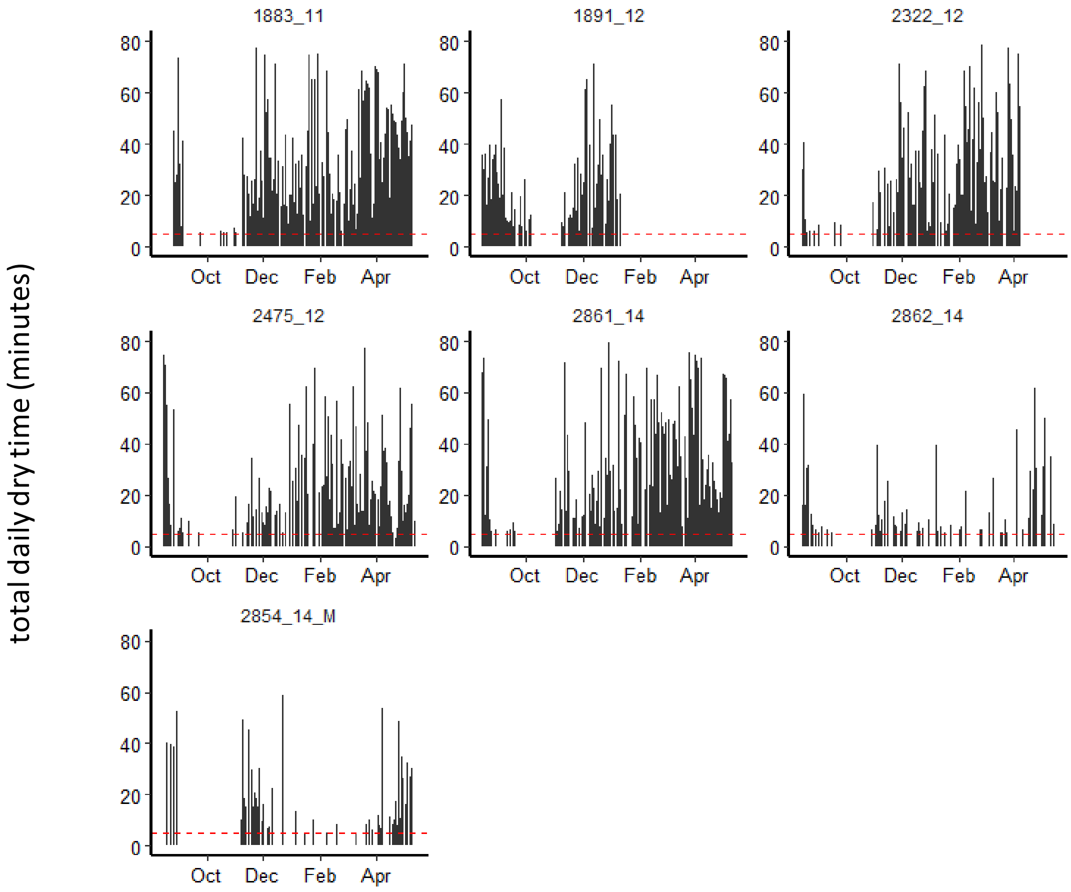

Figure 3.2. Total daily dry time (i.e. time spent flying) for individual murres (6 females and 1 independent male). The dashed red line intersects the daily threshold (5 min) for total dry time (over 2 consecutive days) above which an individual is not considered to be flightless.

3.4.1. Timing and Duration of Wing Moult

The results of the GAMM model indicate a continuous period during which average dry time was ≤ 5 minutes day^{-1} from 10 September to 1 November (53 days; Fig. 3.3), corresponding to the average wing moult period of seven murres from Gull Island, Newfoundland (gamm: edf=8.4, p = 0.001).

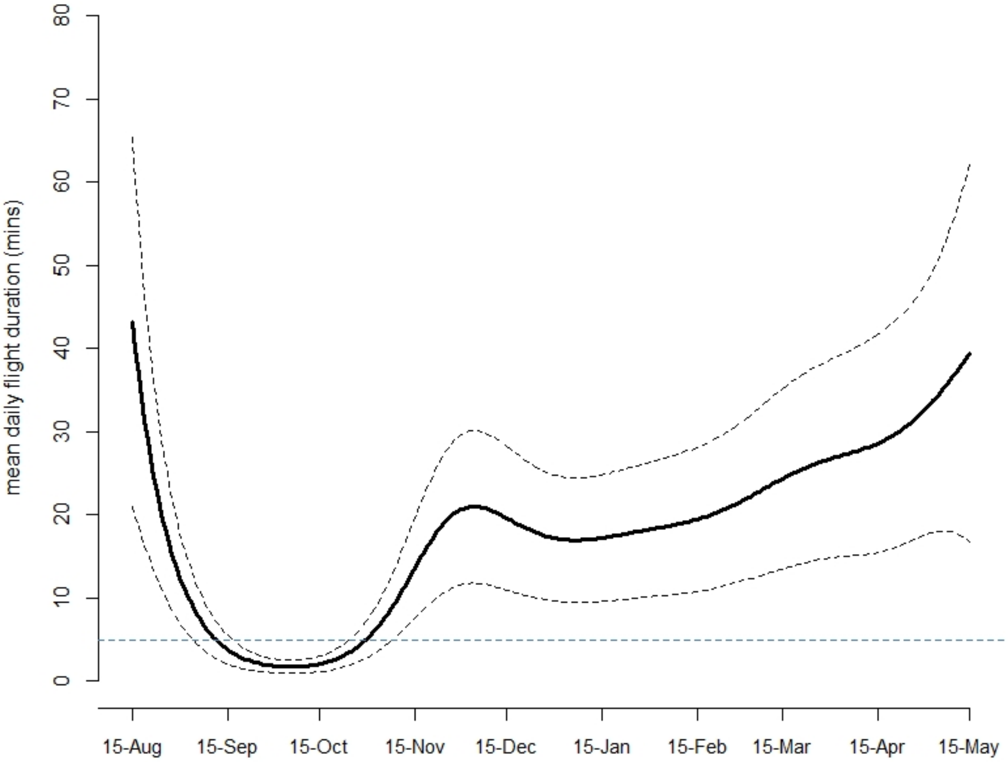

Figure 3.3. Generalized additive mixed model showing the seasonal trend in the mean duration of daily flight time from 15 August to 15 May for independent murres. The area below the blue horizontal line represents the average period of wing moult for seven individual murres.

The estimated timing and duration of the flightless period for each individual is shown in Table 3.1. representing the wing moult period for six females (F) and one male without a chick (M). Wing moult began between 2 September and 2-October (median 6 September), and continued over a range of 39 to 66 days (mean ± SD, 52.4 ± 9.9 days), ending between 29 October and 9 November (median 31 October). Murres did not initiate wing moult immediately after colony departure, rather they delayed moult, on average by 32.2 ± 12.3 days.

Table 3.1. Estimates of timing and duration of the flightless period for seven common murres from Gull Island, Newfoundland including six females (F) and one independent male (M).

Status	Bird Id	Colony Departure	Moult Onset	Moult Termination	Days Before Moult	Moult Duration (days)
F	1883-11	24-Aug	06-Sep	29-Oct	13	54
F	1891-12[1]	11-Aug	02-Oct	09-Nov	52	39
F	2322-12	11-Aug	04-Sep	30-Oct	24	57
F	2475-12	09-Aug	13-Sep	30-Oct	35	48
F	2861-14	11-Aug	20-Sep	31-Oct	40	42
F	2862-14	02-Aug	03-Sep	02-Nov	32	61
M	2854-14[2]	03-Aug	02-Sep	06-Nov	30	66
	MEDIAN DATE				**MEAN ± SD**	
	F,M	11-Aug	06-Sep	31-Oct	32.2 ± 12.3	52.4 ± 9.9

[1] potentially a non-breeder based on post-tagging observations, [2] not identified as an unsuccessful male in Chapter 2 (Burke et al. 2015) as dive records were not available until 1 November

From these results (Table 3.1), the pre-moult, moult and post-moult stages used to assess the effects of wing moult on murre foraging behaviour were defined (Section 3.4.2). The pre-moult stage (26 August to 1 September) covers the period after the last individual departed the colony (25 August) and before the first individual initiated moult (2 September). The moult stage (2 September to 9 November) covers the period after the first individual started moulting

(2 September) and last individual finished moult (9 November), and the post-moult stage (10 to 17 November) begins after the last individual had completed moult and the following eight days, which represents an equivalent duration (8 days) to the pre-moult stage. Given the longer duration of moult (70 days) relative to the other two stages (8 days each), a sub-sample of 8 days was randomly selected from the moult stage to balance sample sizes. To ensure that a random sample of eight days within a 70-day moult stage accurately reflected the foraging behavior of moulting murres, 10 unique randomized 8-day moult periods were generated and their dive metrics (depth, duration) were compared statistically across periods using GLMMs. The results of these statistical tests indicate no significant differences across randomized periods.

3.4.2. Wing Moult and Foraging Behaviour

Overall, murres spent on average 72.8 ± 4.8 (mean ± se) min day^{-1} diving during the wing moult stage, versus 113.8 ± 7.7 min day^{-1} during pre-moult and 71.7 ± 3.7 min day^{-1} during post-moult stages. Mean daily foraging time was significantly greater during the pre-moult stage relative to moult, but there was no significant difference between the moult to post-moult stages (Fig. 3.4).

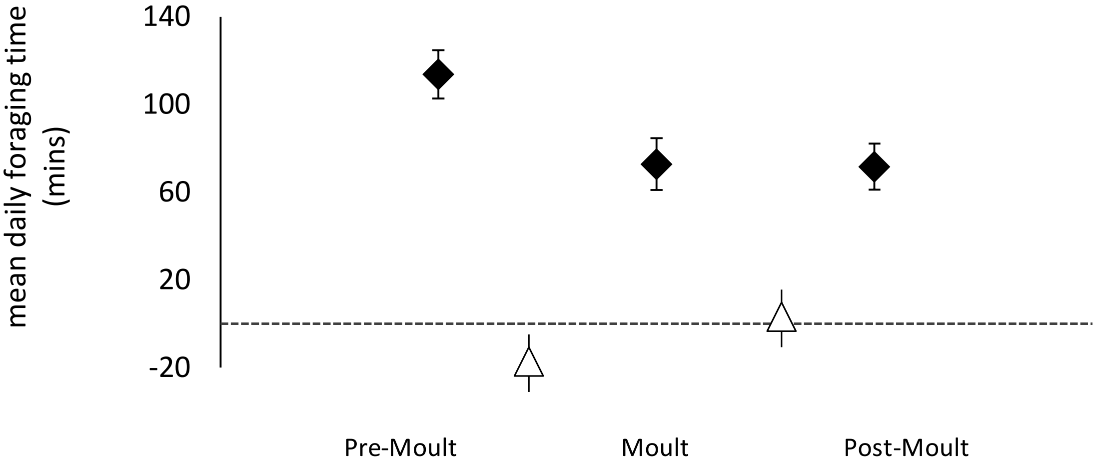

Figure 3.4. Mean (and 95% CI) daily time spent diving for adult murres (n = 13) during pre-moult, moult and post-moult. Open triangles represent the mean difference between two consecutive periods, which are considered significantly different when the 95% CIs exclude zero.

Average (± SE) daylight dive depth was very similar during all stages: pre-moult (44.7 ± 0.5 m [95% CI: 42.2 – 47.2 m]), moult (46.2 ± 0.7 m [95% CI: 43.8 – 48.6 m]) and post-moult (50.1 ± 0.5 m [95% CI: 47.7 – 52.5 m], Fig. 3.5). Average twilight dive depth increased over time, and was significantly deeper during post-moult (38.9 ± 0.7 m [95% CI: 35.9 – 41.9 m]) relative to pre-moult (28.0 ± 0.4 m [95% CI: 25.6 - 35.5 m]), but not to moult (33.1± 0.5 m [95% CI: 30.7 - 35.5 m]). The majority of dives were conducted during daylight hours (60%) in all stages, but the average frequency of twilight dives across all birds was higher during the moult stage (40% ± 4.6% SE) relative to the pre-moult (29.8% ± 3.3%) and post-moult stages (24.3% ± 2.5%; Fig. 3.5).

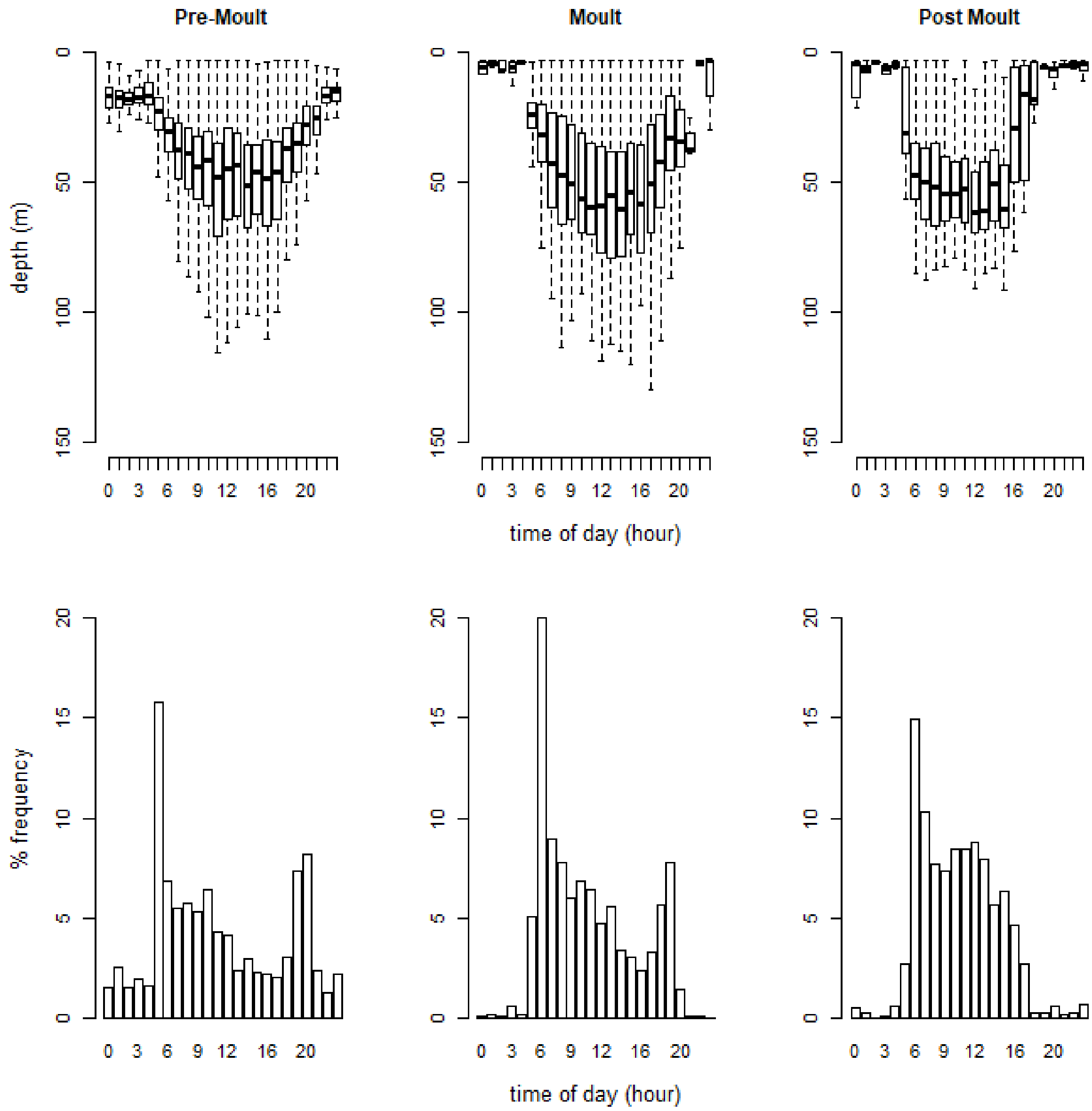

Figure 3.5. Mean dive depth (top panel) and percent frequency of dives (bottom panel) by hour during the pre-moult (n = 7614 dives), moult (n = 4649 dives) and post moult (n = 3068 dives) stages.

3.4.3. Trophic Niche during Primary and Secondary Wing Moult

Mean δ^{15}N isotopic values (fractionation adjusted; mean ± SD) were the same in primary and secondary coverts (+12.22 ± 0.5‰ and 12.20 ± 0.4‰, respectively), and mean δ^{13}C in primary (-21.37 ± 0.39‰) and secondary feathers (-21.42 ± 0.33‰) was similarly depleted. Estimated niche breadth was larger in primary feathers (SEA_b = .58‰^{2}; 95% CR.I. = 0.42 - 0.81‰^{2}) relative to secondary feathers (SEA_b = .43 ‰^{2}; 95% CR.I. = .31 - 0.61‰^{2}) in 90% of the Bayesian iterations (i.e. 4000 pairwise comparisons), with very high overlap in total shared niche space (primary/secondary: 100%; secondary/primary: 75%; Fig. 3.6).

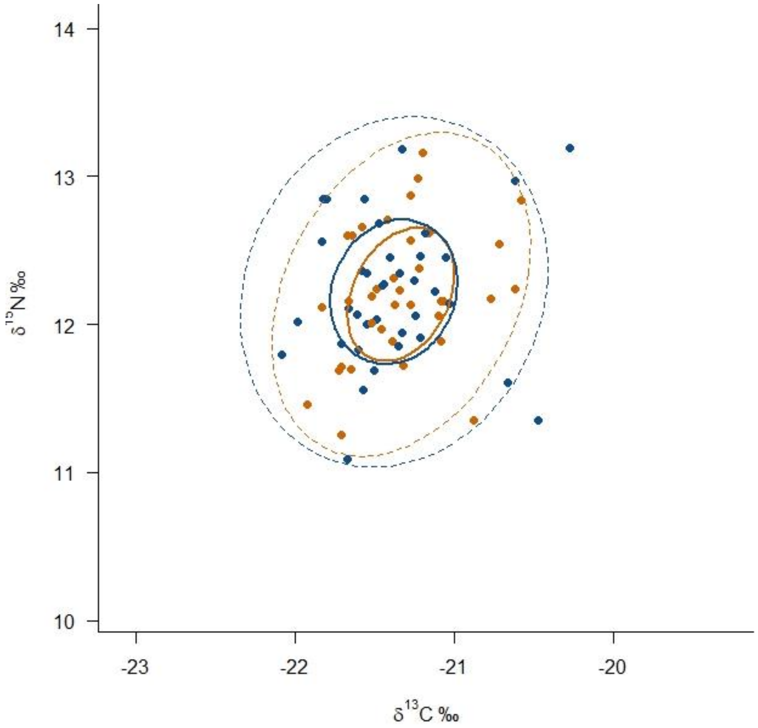

Figure 3.6. Stable isotope ratios (δ^{15}N and δ^{13}C) derived from primary (blue dots and lines) and secondary covert feathers (orange dots and lines) of 37 common murres with their respective standard ellipse areas (SEAc) and 95% ellipse areas (dashed).

3.4.4. Water Temperature Profile

The water column was highly stratified during August with temperatures approaching 0° C just below 40 meters (Fig 3.7). During September and October when murres were moulting, seasonally warmed surface waters extended further into the water column with an average temperature of 6.7 ± 0.1 °C at 50 meters in October, compared to 1.1 ± 0.1°C at 50 m in August and 4.6 ± 0.1 °C in September (Fig. 3.7).

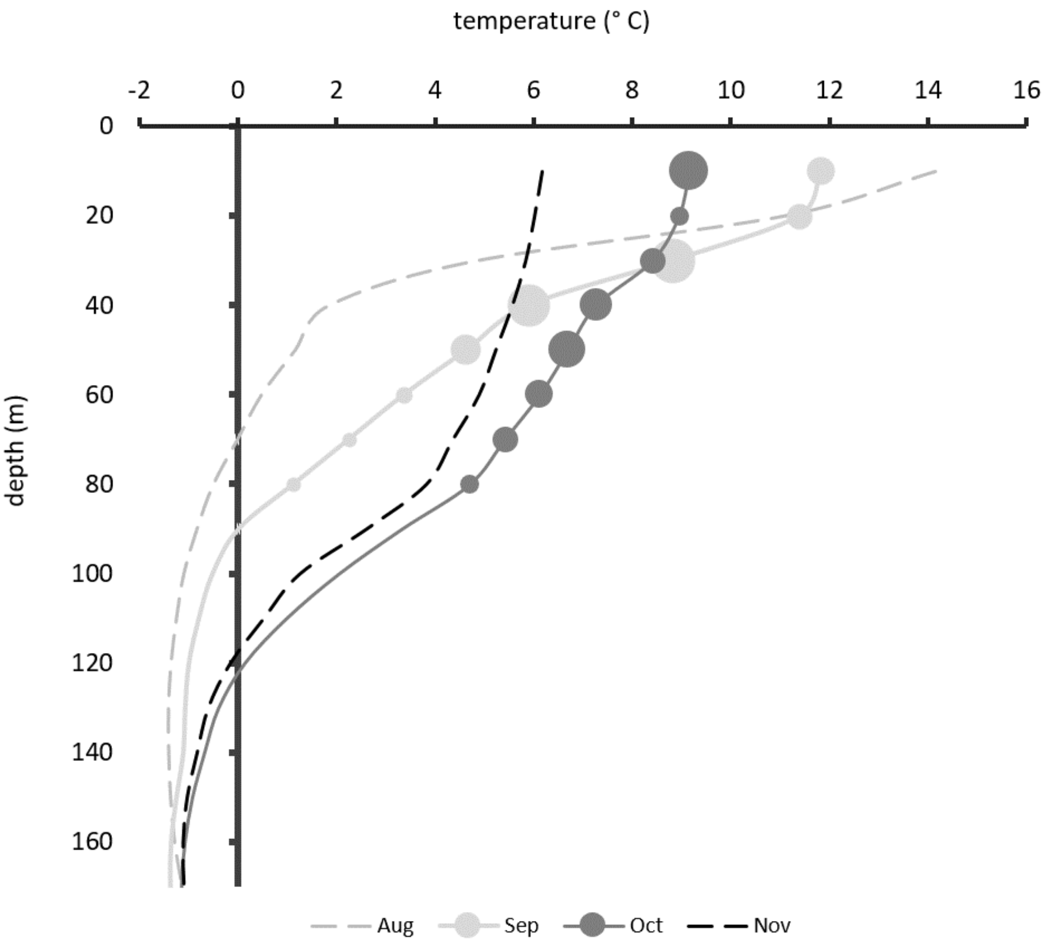

Figure 3.7. Mean water temperature profiles at hydrographic Station 27 during August to November. Expanding symbols during September (light gray) and October (dark grey) when murres are moulting represent the percent frequency of dives at 10 m depth intervals (ranging from 5-20% frequency).

3.5. Discussion

The results of the GAMM model investigating changes in daily time spent flying over the inter-breeding period identifies a period of 53 days (10 September to 1 November) during which daily time spent flying was ≤ 5 minutes (Fig. 3.3), which I suggest represents the average moult period for adult murres (6 females, 1 male without a chick) from Gull Island, Newfoundland. The range in moult duration (39 - 66 days; Table 3.1) is consistent with the degree of variation reported in previous studies (24-81 days; Birkhead and Taylor 1977, Thompson et al. 1998, Ainley et al. 2002 and references therein, Bridge 2004, Elliott and Gaston 2014). Since birds were tracked in different years, this variation could reflect inter-annual variability in environmental conditions during wing moult or individual variation. Thompson et al. (1998) reported a major difference in wing moult duration of murres across two years (25 versus 81 days) that was considered to reflect inter-annual differences in food availability. The non-breeder (1891_12) exhibited a very different moult strategy, starting much later than breeding adults and moulting for a shorter duration. This is in contrast to other studies in which non-breeders were shown to initiate moult earlier than breeding adults (Thompson et al. 1998, Harris and Wanless 1990), but regardless suggests that moult strategies are strongly influenced by annual routines that vary significantly with age in long-lived seabirds.

The consistently low trophic diet of murres throughout the progression of wing moult, in combination with low foraging effort suggests that the energy requirements for flight feather production are easily met, despite the expectation of high nutritional requirements during intensive feather growth (Thompson and Drobney 1996). A number of studies, that collectively cover multiple years and populations also document a low trophic level diet by moulting murres (Davoren et al. 2002, Hedd et al. 2010, Linnebjerg et al. 2013, McFarlane Tranquilla 2014), suggesting it is a consistent feature of their moult ecology. This could reflect specialized nutritional requirements associated with feather synthesis (Thompson and Drobney 1996), but this is a poorly known aspect of seabird moult ecology. Alternatively, a low trophic diet combined with low feeding activity could be explained by lower than expected energy requirements during wing moult if energy saved by the removal of flight can be redirected to support somatic production. The Common Eider *Somateria mollissima,* another diving bird with high flight costs exhibited a 6% savings in daily metabolic rate due to flightlessness during wing moult, that partially offset the estimated 9% increase in daily metabolic rate attributed to the production of feathers (Guillemette at al. 2007). Energy savings in daily metabolic rate are expected to be even higher for murres that have the highest flight costs of any bird (Elliott et al. 2013a). Such an energy trade-off could have significant benefits by ensuring that wing moult is complete before the onset of winter.

All murres in this study delayed the onset of wing moult after colony departure, on average by 32.2 ± 12.3 days with the earliest start date on 2 September and the latest on 2 October (Table 3.1). Unlike other circumpolar auks that undergo extensive seasonal migrations between high Arctic breeding territories and low Arctic wintering areas, murre populations in the North Atlantic exhibit a resident-type over-wintering strategy (Hedd et al. 2011, Fort et al. 2013, Linnebjerg et al. 2013, McFarlane Tranquilla 2014, Burke et al. 2015, Chapter 2). As such, these winter residents have fewer life-history stages in their annual cycle (relative to other auks) and since life-history stages require time to complete, and typically do not overlap, the more stages an individual expresses, the less flexibility there will be in their timing (Wingfield, 2008). By way of comparison, congeneric Thick-billed Murres from Coats Island (Nunavut, Canada), that also overwinter on the Newfoundland Shelf initiated moult immediately after colony departure (4 females, 1 male without a chick), presumably to ensure they completed wing moult before climatic conditions deteriorate on high Arctic breeding-moulting grounds (Elliott and Gaston 2014). Non-migratory murres that are under less severe time constraints may delay the onset of wing moult until environmental conditions are favorable during an extended period of flightlessness. Moult is considered a flexible system in the annual cycle for many passerines, and is scheduled around local environmental conditions (Helm and Gwinner 2006). This contrasts with circumstances during reproduction and migration which can involve greater fitness costs during mismatches in timing (i.e. peak food availability during reproduction, weather systems during migration).

The availability of a spatially predictable food source is a key requirement for the successful completion of wing moult for a flightless bird. The nitrogen ($\delta^{15}N$) values derived from primary and secondary wing feathers indicate that murres consumed a low trophic level diet throughout the progression of wing moult. Concurrent information on the availability of prey consumed by murres during their estimated wing moult is unavailable, however juvenile pelagic fish surveys conducted on the NL Shelf (s. Labrador Shelf to s. Grand Bank; 44°N - 55°N) in the mid-1990s (1994-1995) during late summer (22 August – 22 September) provides some insight into the distribution, composition and biomass of juvenile fish and macro-plankton (Anderson and Dalley 1997) during the murre wing moult period. These surveys also utilized a mid-water trawl designed to target juvenile pelagic fish (10-200 mm) within the upper 60 m of the water column, which corresponds to the dive depth range of moulting murres (Fig. 3.5). These surveys documented strong spatial structure in the biomass and composition of the pelagic community on the NL Shelf during late summer and autumn, with the highest biomass of juvenile fish (dominated by *Mallotus villosus*, *Boreogadus saida*, pelagic squid [species unidentified]; 40-120 mm) and zooplankton (dominated by *Calanus* spp*)* occurring on the NE NL Shelf region (48°N - 55°N) which overlaps with the northern range of the core foraging area of post-breeding female murres (Chapter 2, Burke et al. 2015 (Fig. 2.1)).

While likely not consumed directly by murres, C*alanus* is the primary food source for many pelagic fish (O'Driscoll et al. 2001) with evidence of strong associations between *Calanus*, forage fish (capelin; Buren et al. 2014) and seabirds on an ocean-basin scale (Frederiksen et al. 2013). *Calanus finmarchicus* is the most abundant copepod species on the NL Shelf, accounting for >50% of the total zooplankton biomass, that along with some of the smaller (but energy-rich) copepod species (*Pseudocalanus* spp. and *T. longicornis*) experience a secondary peak in abundance from October to December (Pepin et al. 2015). The peak in twilight foraging activity by murres during wing moult (40% of all dives; Fig 3.5) suggests they may be cueing to the crepuscular feeding patterns of juvenile fish and macro-plankton in response to vertically migrating *Calanus* spp. that move into surface waters at night to feed, and are available to visual predators during vertical dawn and dusk movements (Regular et al. 2010). If so, cueing to an abundant prey source with high temporal predictability could represent an efficient strategy for a flightless bird with a limited ability to track prey over a large horizontal spatial extent (Davoren et al. 2003).

Thermal challenges associated with the loss of plumage insulation and increased blood flow to the skin can increase thermal stress during wing moult if seabirds are exposed to cold water, and therefore may exert strong selection on the timing of moult to coincide with warm water. In support, the estimated timing of wing moult for murres in the NE Atlantic coincided with a seasonal peak in SST (Dunn et al. 2020). Moreover, a literature review of diving sea ducks showing that 84% of species moult when sea surface temperatures (SST) reach a maximum in the annual cycle (Viain 2015). SST on the NL Shelf reaches a maximum during late summer and gradually declines through autumn, remaining between 8 - 10°C into late October (Richaud et al. 2016, Fig. 3.7). Despite relatively warm surface waters into late summer and autumn, the potential for heat loss is still present if murres are diving into the cold-intermediate layer (CIL), which is the vertical band of sub-zero waters (< 0° C) that forms on the NL Shelf in late winter and persists throughout summer and autumn (Colbourne et al. 2005). From June to November, the CIL lies below seasonally warmed surface waters that vary in vertical extent due to seasonal changes in heat flux and wind forced mixing (Colbourne et al. 2005, Enstipp et al. 2006). During the estimated wing moult period of adult murres the vertical extent of warmed surface layers is larger than during any other time in the year (Fig. 3.7). The mean daylight dive depth of murres during moult (46.2 ± 0.7 m; Fig. 3.5) places them well above the CIL within waters ranging between 5 -12 °C, and in warmer waters during shallow twilight diving. This potential thermal refuge could represent a significant energy saving strategy for diving murres via behavioural thermoregulation, and may help explain the observed delay in the timing of wing moult (Table 3.1) since murres would be exposed to sub-zero water temperatures during relatively shallow dives (i.e.< 40 m; Fig 3.7) in August when they are leaving the colony. Moreover, while murres pursuing prey in sub-zero waters may have experience relatively higher capture efficiency due to the reduced burst speeds of mature fish (Hedd et al. 2009), a predominately non-fish diet (excl. juvenile fish) throughout wing moult affords no such advantage.

3.6. Conclusions

Wing moult does not appear to represent an energetic or nutritional bottleneck for murres. This may be explained in part by significant energy savings from the temporary loss of flight that may offset the metabolic costs of somatic production. Moreover, the over-wintering resident strategy of murres arguably facilitates greater flexibility in the scheduling of wing moult to coincide with more favorable prey and environmental conditions, potentially resulting in additional energy savings and a reduced risk of starvation.

CHAPTER 4 - TAKING THE BITE OUT OF WINTER: COMMON MURRES *URIA AALGE* PUSH THEIR DIVE LIMITS TO SURMOUNT ENERGY CONSTRAINTS

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*Published as: Burke CM[1], Montevecchi WA[1] (2018). Taking the bite out of winter: Common Murres (*Uria aalge*) push their dive limits to surmount energy constraints. Frontiers in Marine Science 5:63. doi.org/10.3389/fmars.2018.00063

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4.1 Abstract

Diving seabirds that overwinter at high latitudes experience persistent cold exposure, short days and associated declines in ocean productivity that can challenge their ability to balance daily energy budgets. We used dive-immersion geo-locators to test the hypothesis that pursuit-diving Common Murres (*Uria aalge*) respond to the challenges of winter in the North Atlantic through increased daily energy expenditures (DEE) that will be met by increased foraging effort and adjustments in dive tactics. Largely flightless in winter (< 5% of daylight hours flying), murres spent most of their time on the water (> 85% resting and swimming). Accordingly, when sea surface temperatures (SST) were consistently near freezing in late winter (1.9 ± 0.8 °C), mean DEE (2463.2 ± 109 kJ day^{-1}) exceeded the theoretical limit to sustainable energy expenditure in vertebrates (i.e. 7 X Basal Metabolic Rate or 2450 kJ day^{-1} for murres). Consistently deep (70% > 50m) and long dives in late winter, 38% of which exceeded their calculated aerobic dive limit indicate that targeted prey was distributed in deep (dark) waters. Consequently, foraging was largely diurnal, likely because capture efficiency of deep-water prey is poor in low light. Murres responded to these late winter time and energy constraints with a nearly 2-fold increase in daily time spent diving (95.2 ± 5.6 min and 178.3 ± 6.3 min day^{-1} during early and late winter, respectively), an increase in dive bout frequency and duration, and correspondingly less time resting between bouts. Uniquely adapted for deep-diving, pursuit-diving murres can push their dive limits to maximize daily energy intake when energy demands are high and prey are distributed in deep water. Our study highlights late winter as an extremely challenging phase in the annual cycle of North Atlantic murres and provides critical insights into the behavioural mechanisms underlying their winter survival.

4.2 Introduction

Diving seabirds that over-winter at high latitudes contend with high-energy requirements for thermoregulation and challenging foraging conditions during seasonal lows in ocean productivity and short days. Winter survival is a critical life history trait of long-lived seabirds (Votier et al. 2005, Daunt et al. 2007, Frederiksen et al. 2008, Sorensen et al. 2009) but the challenges of studying seabirds at sea limit our understanding of the behavioural strategies that mediate survival. Advances in bio-logging technology are providing unprecedented insights into the behaviour of diving seabirds at sea but studies that focus on the critical winter period are scarce and are primarily restricted to the larger divers (e.g. *Spheniscidae, Phalacrocoracidae*) that are more amenable to carrying data loggers over the annual cycle (Grémillet et al. 2005a, Green et al. 2005, 2009, Daunt et al. 2006).

Thermoregulation, although partially mediated by morphological adaptations that reduce heat loss (water-proof feathers, lipid stores; Wharton 2002) elevates the daily energy expenditures (DEE) of diving birds that spend most of their time on the water where heat loss is 25 times greater than in air (Croll and McClaren 1993, Enstipp et al. 2006). Moreover, because thermal conductance increases with decreasing body size, thermal costs in cold water are higher for smaller divers (< 1 kg; Croll and McClaren 1993, Richman and Lovvorn 2011). Elevated energy requirements for thermoregulation must be met with an increase in food energy intake during winter but this can be challenged by degraded foraging conditions. By example, many zooplankton (e.g. *Calanus* spp.) and forage fish species over-winter in deep, cold waters (Winters 1983, Longhurst 1995, Planque et al. 1997, Maillet and Colbourne 2007, Olsen et al. 2010) where they are less accessible to diving predators. Unpredictable and extreme weather events (i.e. heat waves, gale-force storms and ice intrusions) can also temporarily impede access to prey (Finney et al. 1999, McFarlane Tranquilla et al. 2010) and ultimately result in starvation over time (Gaston 2004, Grémillet et al. 2005a, Daunt et al. 2007, Piatt et al. 2020). Diving seabirds, that are primarily visual predators (c.f. Regular et al. 2011, Berge et al. 2015) also face additional constraints on foraging time during the shorter days of winter and correspondingly longer periods of nocturnal fasting (Grémillet et al. 2005a, Daunt et al. 2007). This conflict between resource demand and availability in winter raises the critical, but poorly resolved question of how diving seabirds meet the energy demands of survival.

We use dive-immersion geo-locators to study the behavioural strategies of pursuit-diving Common Murres (*Uria aalge*, hereafter murres) during winter in the Northwest Atlantic. Murres are the largest of the pursuit-diving alcids (c.a. 1 kg) and play a key role in the energy flow through circumpolar marine food webs in temperate and sub-Arctic waters (Gaston and Jones 1998, Montevecchi 2000, Brooke 2004). Owing to small wings that reduce underwater drag, they are the deepest diving bird that can fly (250 m; Chimienti et al. 2017) with lower than expected metabolic costs during diving but higher than expected flight costs (Elliott et al. 2013a). Emerging insights into the physiological processes during diving, involving reductions in blood flow to metabolically expensive organs (Niizuma et al. 2007) and reductions in core temperature and heart rate (Wilson et al. 1992, Elliott et al. 2013a) suggest the metabolic costs of diving for murres may be lower than previously predicted, and possibly even decrease with depth which may allow them to extend their aerobic dive limit (Gerlinsky et al. 2013).

Tracking studies of adult murres from Newfoundland and Labrador colonies have established their core wintering area on the NL Shelf, centered on the eastern Grand Bank (Hedd et al. 2011, McFarlane Tranquilla et al. 2013, Chapter 2, Burke et al. 2015). The defining climatic feature of this region is the south-flowing Labrador Current that transports sub-polar waters from the Canadian Arctic across the southern extent of the NL Shelf (Colbourne et al. 2015). A previous study demonstrated that related North Atlantic Thick-billed Murres (*Uria* lomvia) and Dovekies (*Alle alle*) overwintering on the NL Shelf experience a late winter energy bottleneck, driven by harsh climatic conditions (Fort et al. 2009). The NL Shelf supports significant concentrations of fish and invertebrates year-round (Fuller and Myers 2004), including capelin (*Mallotus villosus*) and sandlance (*Ammodytes* spp.) that are the preferred prey of murres during the summer breeding season (Davoren and Montevecchi 2003a, Burke and Montevecchi 2008). Capelin concentrate in large inactive schools in cold, deep water during winter (> 200 m; Winters 1970, Lily 1982) when they attain maximum somatic lipid content (Montevecchi and Piatt 1984), but may be outside the maximum diving range of murres. Sandlance occupy relatively shallow plateau areas of the southeastern Grand Bank (< 80 m maximum) where they partially burrow in the substrate during spawning (November - January; Winslade 1974, Winters 1983) and are well within the foraging range of murres.

Information on the winter diets of murres in the Northwest Atlantic is sparse and comes primarily from birds taken during the inshore “turr” hunt (Gaston et al. 1983, Elliott et al. 1990, Rowe et al. 2000, Moody and Hobson 2007). Diet samples from the hunt are biased to conspecific Thick-billed Murres that generally feed at a relatively lower trophic position (McFarlane Tranquilla 2014) and to juvenile murres (both species) that comprise the highest proportion of murres taken in the hunt but represent 16% of the at sea population in winter (Elliott et al. 1990). While these studies indicate a mixed diet of fish (capelin, sandlance and Arctic cod *Boreogadus saida*) and zooplankton (*Parathemisto* spp., *Thysanoessa* spp.) they may not be entirely representative of the winter diets of adult Common murres in offshore waters.

We test the hypothesis that murres respond to harsh environmental conditions in winter through increased DEE (and nutritional requirements), which will be met through adjustments in daily foraging effort and dive tactics (i.e. how, when and where). Our objective is to gain insights into the behavioural strategies that mediate survival of murres during long, harsh North Atlantic winters.

4.3 Materials and Methods

4.3.1. Ethics Approval Statement

This study was carried out in strict accordance with ethical guidelines outlined by the Canadian Council on Animal Care, and approved by Memorial University of Newfoundland's Institutional Animal Care Committee (Permit Numbers: 10-01-WM, 11-01-WM, 12-01-WM, 13-01-WM). Fieldwork was carried out under a Canadian Wildlife Service Migratory Bird Banding permit WAM-10322K. Access to the Funk Island and Witless Bay Islands Provincial Seabird Ecological Reserves was permitted through the Newfoundland and Labrador Parks and Natural Areas Division.

4.3.2. Study Sites and Species

Fieldwork focused on breeding murres at two Northwest Atlantic colonies in Newfoundland, Canada: Gull Island in the Witless Bay Ecological Reserve (47°16’N, 52°46W) with c.a. 1,632 breeding pairs (Robertson et al. 2004) and the Funk Island Ecological Reserve (49°45’N, 53°11’W) with c.a. 472,259 pairs (Wilhelm et al. 2015). Lotek dive-immersion, geo-locators (Model LAT 2500; 5.9 g with attachment, c.a. 0.7% body mass; 8 X 35 mm, cylindrical in shape) were attached to plastic leg bands (Pro-Touch Engraving) with cable ties, and placed on the left leg of 51 actively breeding murres during late chick-rearing: 15 at Funk Island (2009) and 36 at Gull Island (2010-2013). Twenty-nine devices were retrieved in subsequent years (3 of 15 at Funk Island and 26 of 36 at Gull Island) including 4 with data failures (final sample of 25 individuals). Low logger return rates at Funk Island (3 of 15 retrieved) was due to the presence of an Arctic Fox that caused significant disturbance and breeding failures at this typically mammalian predator free offshore colony (Burke et al. 2011). Of these, the 17 loggers that recorded dive data for more than 30 continuous days were included in our analysis of winter foraging behaviour (Supplementary Table 4.1). Winter is defined as the period from 15 November to 15 February (c.a. 93 days), a delineation that ensures all individuals had completed pre-basic moult (conservatively estimated to end in mid-November; Chapter 3) and that our late winter sample included > 8 individuals. Specific details regarding capture and handling are provided in Chapter 2 (Burke et al. 2015).

4.3.3. Device Effects

The mass of the Lotek 250A geo-locator model used in this study (5 g with attachment) is between 0.6-0.7 % of the average body mass of logger-equipped murres, and is well below the recommended 1-3 % (Phillips et al. 2003, c.f. Vandenabeele et al. 2012). Similarities in body mass between logger-equipped (982.6 ± 6.7 g) and control birds (977.1. ± 11.9 g) suggest negligible device effects, and therefore we assume that behavioural information gathered from our logger-equipped birds reflects normal behaviour of adult murres.

4.3.4. Spatial Data Processing

Comparison of raw Lotek positions with those generated from British Antarctic Society (BAS) geolocators (McFarlane Tranquilla 2014) deployed on Common Murres at the same colonies (Gull Island and Funk Island) revealed a striking difference in latitude. Based on the approach of Frederiksen et al. (2016), we ran latitudinal adjustments on our data, the details of which are explained in Appendix 1. Further processing followed the methods outlined in Chapter 2 (Burke et al. 2015) involving a two position smoothing, and exclusion of data points representing improbable daily movements (i.e. >500 km/day; Hedd et al. 2011, McFarlane Tranquilla et al. 2013). The total number of retained, post-processing winter positions represented 67% (n = 1034 days) of the original 1544 raw positions (n = 17 individuals). Monthly kernel home ranges were evaluated for unsmoothed positions using a least squared cross validation method with a 50 km grid size, applying the 'kernelUD' function in the ‘adehabitatHR’ package (Calenge 2006) in Cran R (ver. 3.1.3), and 50% kernel density contours were used to represent the core winter foraging areas (Linnebjerg et al. 2013).

4.3.5. Environmental Features

Sea surface temperatures (SST) were extracted to the daily locations of individual birds using the Marine Geospatial Ecology Tools (MGET; version 0.8a64) in ESRI ArcGIS (ver 10). SST is an Aqua MODIS product with a daily, 9-km resolution. Habitat variables for missing days (i.e. dates with inaccurate locations) were extracted to a median weekly location for each individual. Estimates of day length were derived for all individuals on a daily basis using the ‘twilight’ function in the R package ‘GeoLight’ (Lisovski and Hahn 2012) that uses latitude and longitude (from geologgers) to calculate time of nautical sunrise and sunset on a given date. Bathymetry data were also extracted from ETOPO2 grids (http://www.ngdc.noaa.gov/mgg/global/etopo2.html) at a 0.2° degree resolution using the xtracto function in the ‘xtractomatic’ R package.

4.3.6. Activity-Specific Daily Energy Expenditures

DEE was calculated by combining time-activity budgets with model-derived estimates of activity-specific energy expenditures from Elliott et al. (2013a), using a modified activity-specific energy expenditure equation from Elliott and Gaston (2014):

$$DEE = 508T_f + 1.01\sum\left[1 - e^{\left(\frac{Duration}{1.23}\right)}\right] + (113 - 2.75T)T_s + (72.2 - 2.75T)T_w$$

where, T_f is hours spent flying per day, Duration is dive time in minutes, T_s and T_w represent hours per day spent active and inactive on the water respectively, and T = SST (Aqua MODIS). The activity-specific metabolic rates for T_w and T_s are reversed from the original equation (cf Elliott and Gaston 2014, pers. comm. K. Elliott 2016) and our equation excludes the colony-specific metabolic value for time spent at the colony ($33T_c$).

Daily time-activity budgets were calculated for individual murres using logger derived estimates of daily time spent diving ≥ 3 m (i.e. total time submerged) and flying (total dry time from wet-dry activity), with the remaining time assumed to represent daily time spent on the water. During winter when birds are exclusively at sea, estimates of the daily time spent flying and resting on the water can be accessed via immersion data (wet-dry) where dry events indicate flight. However, for murres and other alcids delineation of flight behaviour using this approach is confounded by occasional leg-tucking behaviour when birds resting on the water withdraw their leg and foot into their plumage (Harris et al. 2010, Linnebjerg et al. 2014). This behaviour can lead to spurious identification of flights, resulting in over-estimation of the total daily time spent flying. We programmed our loggers to eliminate dry records associated with leg-tucking behaviour (detailed in Chapter 2; Burke et al. 2015), which was successful for 8 individuals (with corresponding dive data in winter). We restrict our activity-budget analysis to these 8 birds for which we are certain that dry periods during the day represent flight time and not some combination of flight and leg-tucking time.

Our modified DEE equation, based on Elliott and Gaston (2014) differentiates time spent on the water into active (i.e. swimming, preening) and inactive (i.e. rest) periods, where time spent with leg(s) tucked is assumed to be equivalent to rest time on the water (Elliott and Gaston 2014). Because our sample (n = 8 individuals) does not include information on time spent resting (tucking), we relied on estimates from Elliott and Gaston (2014) for Thick-billed Murres based on mean time spent with leg(s) tucked according to time of day by month (September-December; from their Figure 2). We calculated the average time spent with leg(s) tucked during the day and night for November and December that we applied across all our winter data (15 Nov-15 Feb). This resulted in approximate estimates of 30.5 ± 1.8% and 5.8 ± 1.9% of time spent with leg(s) tucked during the night and day, respectively.

4.3.7. Foraging Behaviour of Wintering Murres

Explanation of sampling rates, dive and bout processing procedures are provided in detail in Chapter 2 (Burke et al. 2015). Post-dive intervals >1800 sec (30 min) representing 6.7% of all dives by number (n = 83,703) were excluded from analysis of inter-bout rest time since pauses > 30 min were conservatively deemed to be related to inter-foraging activity (i.e. flying or resting on surface). Individual dives were assigned to a specific light phase (i.e. daylight, twilight and night) as defined by sun-angle position (day: sun angle > 0°; twilight: sun angle ≤ 0° and > -12°;

night: sun angle ≤ -12°). This was calculated using astronomical models (Regular et al. 2011) using an R script validated by P. Regular. Dives that exceeded 162 seconds were considered anaerobic dives, based on the calculated aerobic dive limit of breeding Thick-billed Murres (Elliott et al. 2013a).

4.3.8. Data Analysis

Seasonal changes in foraging behaviour and the DEE of murres were examined using linear mixed effects models (LME), fit by restricted maximum likelihood. Mixed modeling was used to account for potential pseudoreplication, with individual set as a random effect, and the inclusion of an autocorrelation term where deemed necessary (evaluated with auto-correlation plots of residuals; Zuur et al. 2009). F-tests were used to assess the significance of effects and model fits were assessed using parameter estimates (± 95% upper and lower confidence intervals). All statistics were run in Cran R software, and unless stated otherwise, values are presented as means ± standard error.

4.3.9. Winter Mass of Hunted Murres (*Uria* spp.)

To investigate murre condition in winter, we calculated mean body mass from a sample of winter birds collected by the Canadian Wildlife Service during the Newfoundland hunt of murres (‘turr hunt’; Montevecchi et al. 2007). Though the sample (n = 145; over 9 years between 1985 and 2015) is weighted to juvenile murres (74%) that dominate the age structure of hunted birds, Gaston et al. (1983) demonstrated very similar winter body mass dynamics for adult and juvenile (for Thick-billed Murres). Therefore, age classes were grouped and mean body mass was assessed according to early (November-December) and late winter (January - February). Differences in body mass between early and late winter were assessed using a one-way ANOVA.

4.4 Results

4.4.1. Core Winter Habitat

Murres over-wintered in offshore waters on the Newfoundland Shelf (NL Shelf: Fig. 4.1). During November and December, murres were highly concentrated over the northeastern Grand Bank (kernel home ranges: 134,390 km^2 and 193,036 km^2, respectively). Kernel home ranges increased in January (316,597 km^2) and February (459,128 km^2) as murres expanded their range to inshore waters (Fig. 4.1). Murres foraged in relatively shallow waters throughout winter, ranging between 50 and 300 meters (96.1 ± 1.5 m) with no significant effect of month on bathymetric depth ($p < 0.3$).

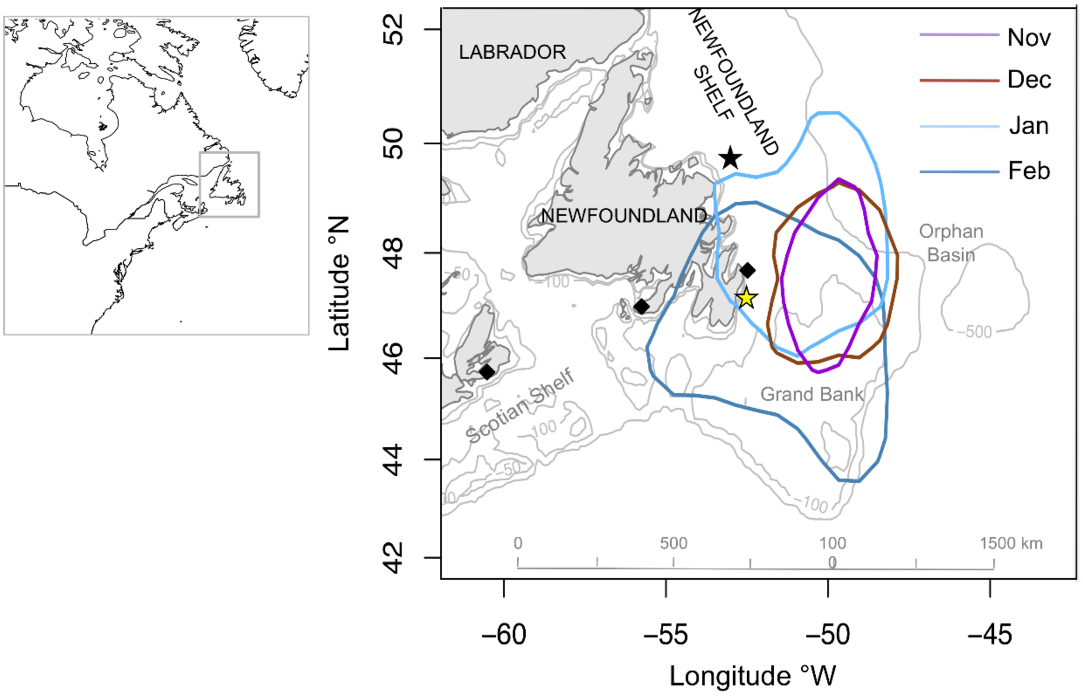

Figure 4.1. Core foraging areas (50% KHR) of Common Murres (n = 17) according to month. Colored stars indicate Funk Island (black) and Gull Island (yellow). Bathymetric contours (by 100 m) obtained from GEBCO Digital Atlas (GEBCO one-minute grid, ver. 2, www.gebco.net) and mapped in Cran R (ver. 3.1.3).

4.4.2. Activity Specific Daily Energy Expenditures (DEE)

Murres spent on average less than 2% (1.6 ± 0.1%) of their time flying in winter (4.1 ± 0.1% of daylight hours) and 9.6 ± 0.2% of their time diving, with the remaining time spent on the water (17.3 ± 0.03% resting and 71.5 ± 0.2% active). Mean DEE increased significantly over winter ($F_{1,643} = 319.2$, $p < 0.0001$) and exceeded 7 X BMR (>2450 kJ day^{-1}) throughout most of January and February (2463.2 ± 109 kJ day^{-1}; Fig. 4.2). The maximum time spent resting scenario

(12% day, 37% night**)** resulting in lower DEE values (Fig. 4.2), with an average difference of 138 kJ day^{-1} (93 – 168 kJ day^{-1}) between the maximum and minimum scenarios.

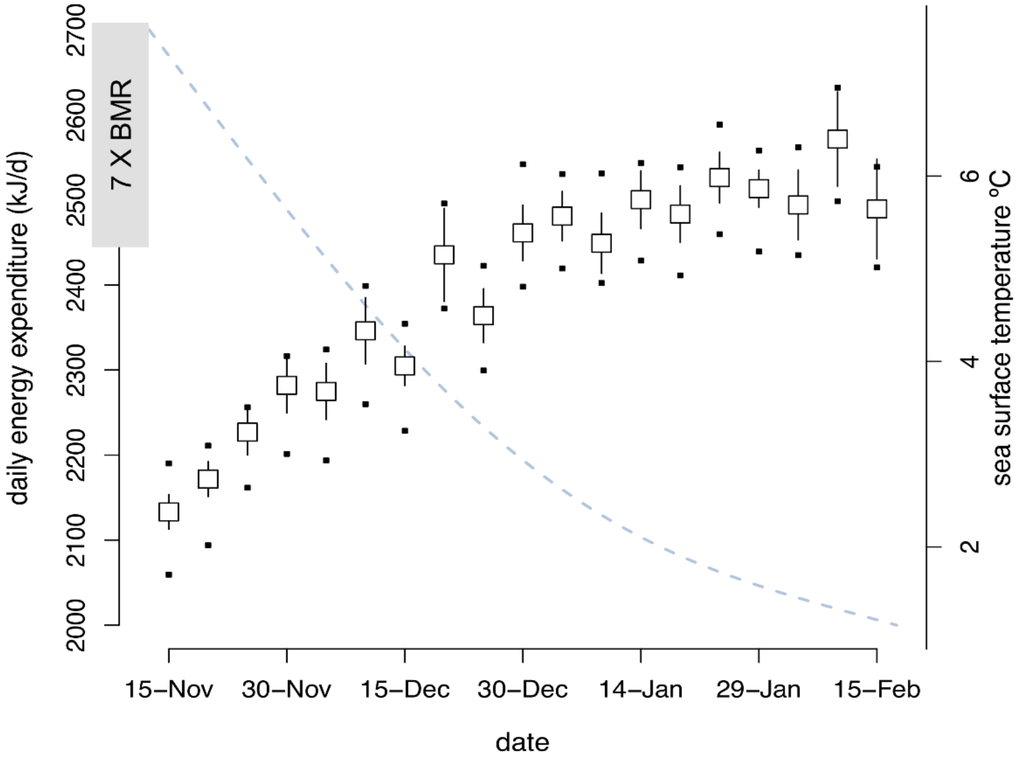

Figure 4.2. Mean (± SE) daily energy expenditure (DEE) of murres (n = 8) over winter (15 November to 15 February) averaged over 5-day intervals. The dotted blue line shows associated daily sea surface temperature from generalized additive mixed model output (GAMM). Black symbols indicate estimated DEE using minimum and maximum time spent resting (on the water) scenarios.

4.4.3. Daily Time Spent Diving

All murres dove every day in winter with total daily dive time ranging from 10 to 468 minutes. Mean daily time spent diving (i.e. time spent submerged > 3m) increased significantly over winter ($F_{1,1273} = 260.2$, $p < 0.0001$), with no significant effect of year ($p = 0.6$), colony ($p > 0.09$) or sex ($p > 0.84$). Murres increased daily dive time at an average rate of c.a. 4 min day^{-1} before reaching a plateau around winter solstice (Fig. 4.3). This trend highlights two potentially distinct phases of winter during which murres may experience different foraging conditions and (or) nutritional demands. Consequently, we consider differences in behaviour between these two unique phases of winter in all further analyses; defined hereafter as early winter (EW: 15 November – 21 December) and late winter (LW: 22 December – 15 February) according to the timing of winter solstice (c.a. 21 December) after which day length begins to gradually increase.

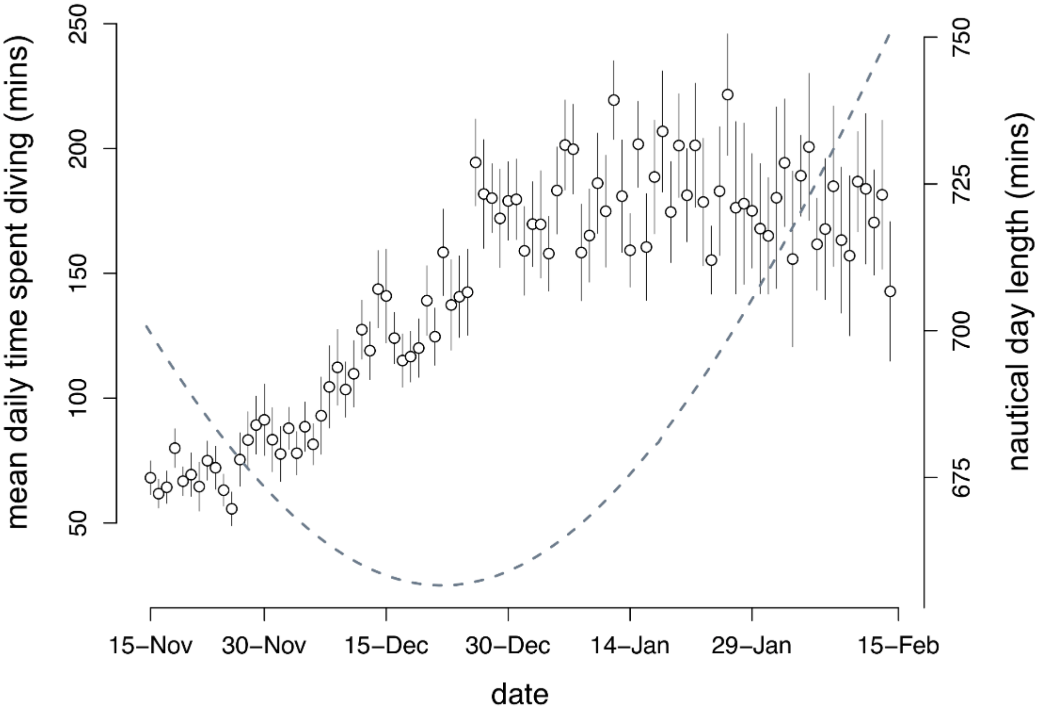

Figure 4.3. Mean (SE) daily dive effort (minutes) by murres (n = 17) in winter (15 November to 15 February). Continuous line (dashed gray) shows day length (minutes) at 47.6°N from nautical sunrise to nautical sunset. Linear mixed model output for differences in mean daily dive effort during EW (95.2 ± 5.6 minutes; 95% CI: 84.2 - 106.3 minutes) and LW (178.3 ± 6.3 minutes; 95% CI: 165.9 - 191.0 minutes).

4.4.4. Individual Dive Characteristics

Eighty three thousand seven hundred and three dives (83,703) were recorded over winter. As predicted, murres dove deep in winter with 65.2% of all dives ≥ 50 m. The mean percent frequency of dives peaked at intermediate depths (50 - 80 m) during both winter phases (Fig. 4.4), with intermediate dives accounting for 54.7 ± 2.7% and 56.5 ± 4.7% of all dives in EW and

LW, respectively. The percent frequency of shallow dives (< 50 m) decreased over winter (40.5 ± 3.2% and 29.8 ± 5.2% in EW and LW, respectively) while the frequency of deep dives (> 80 m) increased (4.9 ± 1.6% and 13.7 ± 4.1% in EW and LW, respectively). Overall there was a significant increase in mean dive depth (daily average) over winter ($F_{1,1273} = 167.1$, $p < 0.0001$) and dives were significantly deeper in LW (59.8 ± 1.2 m; 95% CI: 56.0 – 63.8 m) relative to EW (49.9 ± 1.9 m; 95% CI: 46.0 – 53.7 m).

Figure 4.5 presents information on individual dive characteristics as a function of dive depth during EW and LW (categorized by shallow, intermediate and deep dives). Mean dive duration increased with depth and was significantly higher for intermediate dives in LW (155.8 ± 6.0 sec; Fig 4.5A) relative to EW (143.8 ± 4.1 sec; Fig 4.5A). Percentage of dives exceeding the calculated aerobic dive limit for murres (162 sec) accounted for 16.7 ± 3.0% of dives in EW versus 37.4 ± 5.4% in LW, with high variability between individuals (Supplementary Table 4.1). Mean bottom duration of dives peaked at intermediate depths during EW and LW (Fig. 4.5B). Bottom duration was significantly higher in LW for intermediate (45.5 ± 1.6 s and 56.1 ± 1.3 s for EW and LW, respectively) and deep dives (40.3 ± 1.5 s and 49 ± 1.9 s for EW and LW, respectively; Fig 4.5B). Mean descent rate decreased significantly with depth (Fig. 4.5C) with significantly higher values during LW for intermediate (122.8 ± 1.6 cm/s and 128.7 ± 0.8 cm/s for EW and LW) and deep dives (132.3 ± 1.0 and cm/s 139.6 ± 1.2 cm/s for EW and LW, respectively). Mean bottom velocity followed a reverse trend to bottom duration. During EW, bottom velocity of intermediate dives was significantly lower (10.5 ± 0.4 cm/s, Fig. 4.5D) than shallow (17.8 ± 0.6 cm/s) and deep dives (14.9 ± 0.9 cm/s). During LW, mean bottom velocity of shallow dives was significantly higher (15.8 ± 0.5 cm/s; Fig. 4.5D) relative to intermediate (11.0 ± 0.6 cm/s) and deep dives (11.8 ± 1.0 cm/s) that were not different. There was no significant phase effect on mean bottom velocity for shallow or intermediate dives, but mean bottom velocity of deep dives was significantly higher in EW (14.9 ± 0.9 cm/s) than LW (11.8 ± 1.0 cm/s; Fig 4.5D). Mean ascent rate increased significantly with depth (in both phases), with overlapping ascent rates between EW and LW at all depths (Fig. 4.5E).

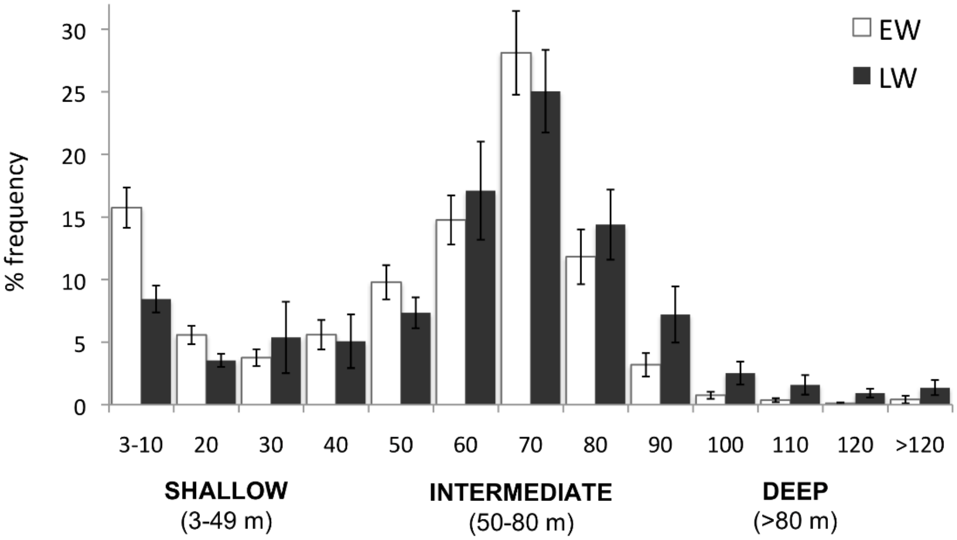

Figure 4. 4. Percentage dive depth frequency according to 10-m depth bins. Values are mean percent (+ SE) frequency of dives averaged across individuals in early winter (EW; white bars) and late winter (LW; black bars).

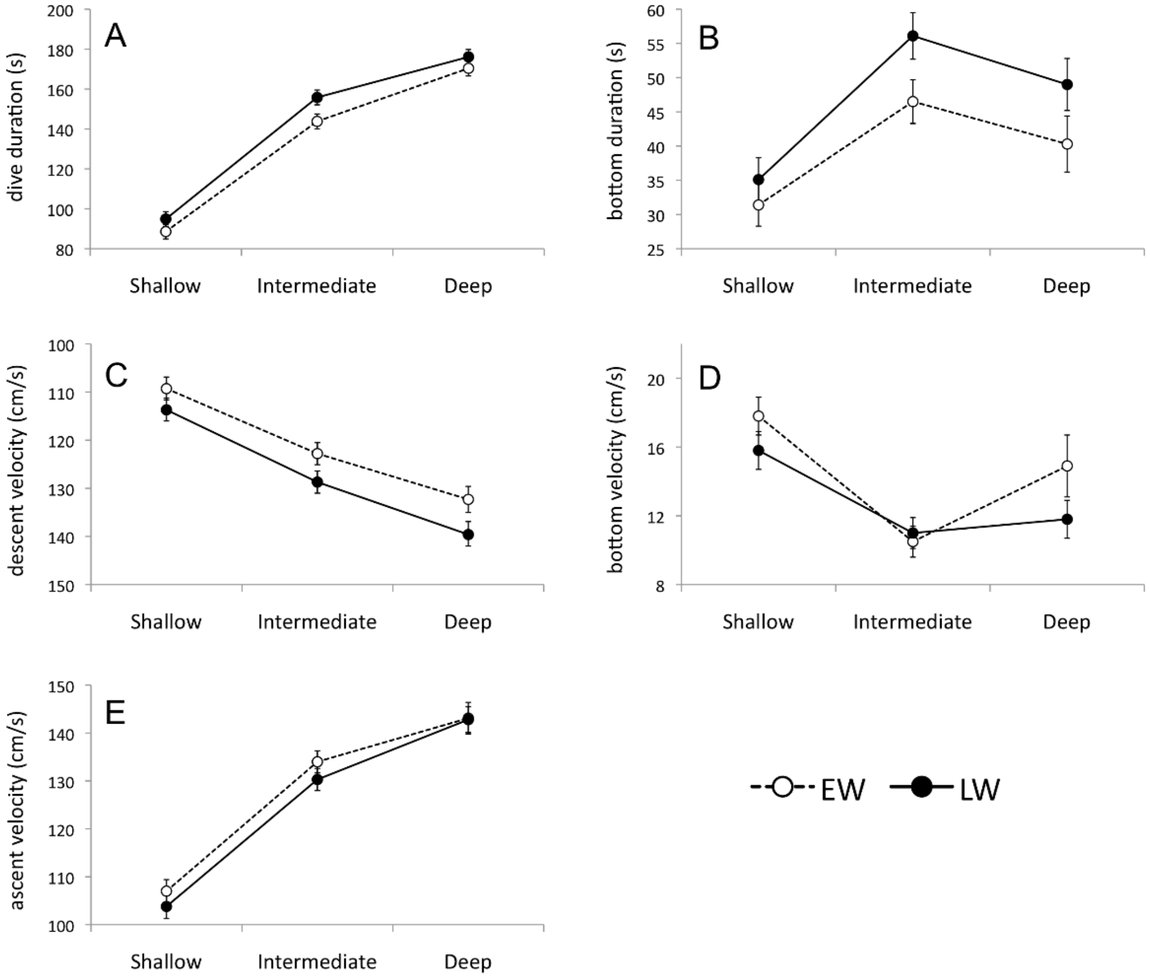

Figure 4.5. Individual dive characteristics according to shallow (≥ 3 - 49 m), intermediate (50 – 80 m) and deep (> 80 m) depth intervals during early winter (EW) and late winter (LW). Parameters include: (A) dive duration (n = 73946; dives ≥10 and ≤150 m), (B) bottom duration (n = 72108 dives; dives ≥10 and ≤150 m, excludes V dives), (C) descent velocity (n = 66370 dives; dives ≥30 and ≤150 m), (D) bottom velocity (n = 70586 dives; dives ≥10 and ≤150 m, excludes V dives) and (E) ascent velocity (n = 66352 dives; dives ≥30 and ≤150 m) and (F) inter-bout pause duration (n = 39925 bouts, pauses ≤ 1800 s). Values are linear mixed model and generalized linear mixed model (where appropriate) model fits ± 95% confidence intervals where non-

overlapping confidence intervals indicate significant differences. Note*:* due to high variability in the parameter estimates for shallow dives, dive data were truncated by depth to overcome problems with heterogeneity (≥10 m, except ≥30 m for ascent and descent velocities).

4.4.5. Diel Dive Behaviour

The majority of dives occurred during daylight hours throughout winter (Fig. 4.6; 76.0 ± 1.9% and 85.7 ± 1.6% of all dives in EW and LW, respectively), however the proportional frequency of daylight dives increased over time as twilight and night dives decreased (Fig. 4.6A). Twilight dives accounted for 14.5 ± 0.9% in EW and 10.9 ± 0.7% in LW and night dives accounted for 9.6 ± 1.7% in EW and 3.3 ± 1.3% in LW. During EW, daylight dives were significantly deeper (54.7 ± 2.1 m; 95% CI: 50.7 – 58.8 m) than twilight (46.1 ± 2.1 m; 95% CI: 42.1 – 50.2 m) and night dives (28.5 ± 2.1 m; 95% CI: 24.4 – 32.6 m; Fig. 4.6B). Mean depth of daylight (63.4 ± 4.4 m; 95% CI: 54.9 – 72.0 m) and twilight dives (57.1 ± 4.4 m; 95% CI: 48.5 – 65.6 m) was not significantly different in LW (Fig. 4.6C), and both were significantly deeper than night dives (34.6 ± 4.5 m; 95% CI: 25.8 – 43.4 m).

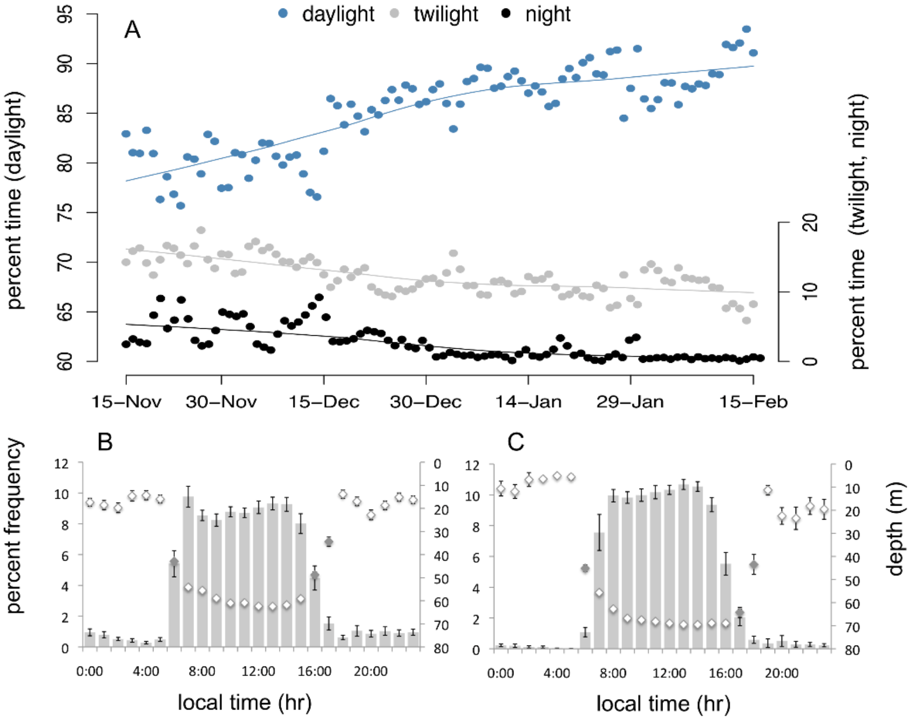

Figure 4.6. (A) Proportion of total daily dive activity occurring during daylight (blue), twilight (gray) and night (black) over time in winter (with a loess smoothing function for each light period). Mean percentage number of dives (bars) and mean dive depth (diamonds; inverted y-axis) according to time of day (local time) during early winter (B) and late winter (C). Grey diamonds (B, C) indicate approximate transitional hours during twilight (i.e. sun angle ≥ - 12 and ≤ 0).

4.4.6. Organization of Foraging Bouts

Forty-five thousand five hundred and forty three (45,543) foraging bouts were recorded over winter, the majority of which consisted of a single dive: 74.3% in EW and 80.5% in LW. There were significantly more dive bouts per day in LW (41.7 ± 2.0; 95% CI: 37.7 – 45.7) relative to EW (28.0 ± 2.0, 95% CI: 24.0 – 32.0; Table 4.1). Mean duration of dive bouts containing multiple dives (excluding post-pause time of terminal dives) was significantly higher in LW (831.2 ± 2.4 s; 95% CI: 826.6 – 835.9 s) relative to EW (595.7 ± 1.8 s; 95% CI: 592.1 – 599.2 s; Table 4.1). Similarly, mean bout duration of single dive bouts was significantly higher in LW (154.7 ± 0.6 s; 95% CI: 153.6 – 155.9 s) relative to EW (130.1 ± 0.5 s; 95% CI: 129.3 – 130.9 s). The time spent resting on the water between dive bouts (for single and multiple dive bouts) was also lower in late winter (309.5 ± 15.2 s) relative to EW (364.0 ± 15.3 s), but the difference was not significant (Table 4.1).

Table 4. 1. Dive bout characteristics for individual Common Murres (n=17) during EW and LW. Values are LME model outputs (mean ± standard error; 95% CI). Different letter superscripts between early winter (EW) and late winter (LW) indicate significant differences.

Dive Bout Parameters	**EW**	**LW**
Number Bouts Day^1	28.0 ± 2.0 [24.0 – 32.0]^A	41.7 ± 2.0 [37.7 – 45.7]^B
Bout Duration (sec)^2	595.7 ± 1.8 [592.1 – 599.2]^A	831.2 ± 2.4 [826.6 – 835.9]^B
Inter-Bout Pause Duration (sec)^3	364.0 ± 15.3 [334 .1– 394.0]^A	309.5 ± 15.2 [279.7 – 339.3]^A

Poisson distribution^1, excludes single dive bouts^2, excludes inter-bout pauses ≥ 1800 sec^3

4.4.7. Winter Mass of Hunted Murres

Murres collected during the Newfoundland 'turr' hunt were significantly heavier ($F_{1,143}$ = 4.6, p = 0.03) in late winter (January and February: 1043.8 ± 7.1 g), relative to early winter (November and December: 988.8 ± 23.6 g).

4.5 Discussion

Seabirds over-wintering at high latitudes face the double jeopardy of high DEE and degraded foraging conditions. Winter survival strategies while poorly known are vital aspects of the annual cycle of marine birds (Frederiksen et al. 2008). Using fine-scale behavioural information gathered from pursuit-diving murres equipped with dive-immersion geo-locators, we demonstrate overlapping trends in mean DEE (Fig. 4.2) and mean daily time spent diving (Fig. 4.3) over winter, both showing a steep increase through EW followed by a LW asymptote. These results support our prediction that an increase in DEE (and nutritional requirements) would be met by a corresponding increase in foraging effort, and balanced energy budgets. Patterns in the diving profiles of murres also indicate a distributional shift in prey over winter (from shallow to deep waters), likely driven by seasonal declines in water temperature. We show that murres meet their daily energy requirements in the face of these challenges by pushing the limits of their diving capabilities. Murres are the largest of the pursuit-diving alcids, and due to small wings (that reduce underwater drag) and physiological adaptations that minimize metabolic costs during diving, they can dive deeper, longer and more efficiently than any bird capable of flight (Elliott et al. 2013a). These traits afford murres the flexibility to routinely access prey in deep water and explain, in part how they survive the challenges of winter on the NL Shelf.

4.5.1. Daily Energy Expenditures of North Atlantic Murres in Winter

Mean DEE of murres during LW exceeds the sustainable level of 7 X BMR for vertebrates (Weiner 1992, Speakman and Król 2011). This finding supports previous studies showing higher than expected energy and nutritional requirements for diving seabirds in winter (Grémillet et al. 2005a, Daunt et al. 2007, Fort et al. 2009) and more specifically for North Atlantic alcids (Fort et al. 2009, 2013, Elliott and Gaston 2014). Diving birds have significant energy requirements for thermoregulation in winter owing to high heat loss during exposure to cold water (Croll and McClaren 1993, Enstipp et al. 2006). Murres in our study were largely flightless throughout winter (< 5% time spent flying) and spent most of their time on the water (> 85% of the day in LW). Accordingly, as SST decreased through winter murres experienced a corresponding increase in thermodynamic costs with high DEE estimates throughout LW when SST was consistently near freezing (1.9 ± 0.8 °C). Murres also spent more time diving in LW, however diving expenditures contributed relatively little to overall DEE (12 ± 0.3%), presumably due to low metabolic activity during deep-diving (Wilson et al. 1992, Niizuma et al. 2007, Elliott et al. 2013a).

While we took great care in our approach and used the most current information available, we consider specific limitations and assumptions that may bear, in particular on the magnitude of our DEE estimates that are significantly higher than those reported by Fort et al. (2009) for Thick-billed Murres during North Atlantic winters. The applied DEE equation (Eqn 1; adapted from Elliott and Gaston 2014) incorporates thermodynamic costs during rest and activity periods on the water (based on SST data extracted from Aqua MODIS using the daily locations of logger-equipped murres). Activity-specific metabolic rates are derived from studies of captive murres held in 16°C water (Croll and McClaren 1993), and could therefore overestimate the thermoregulatory costs of wild birds acclimated to cold water (e.g. 0-12°C seasonal range for Northwest Atlantic Common Murres; McFarlane Tranquilla 2014). We also acknowledge that activity-specific metabolic rates, derived from breeding birds may not be representative of the winter period when seasonal variations in body mass and composition (lean mass versus lipid loading) could influence diving and flight costs (Elliott et al. 2008). Indeed, the effects of seasonal physiological adjustments on the metabolic machinery of murres are largely unaccounted for in our study. For example, it is possible that if seasonal increases in DEE are sufficiently predictable; adjustments in the size of digestive organs (occurring over sufficient time) would allow murres to increase their energy assimilation rates (Wu et al. 2014) and to function at a higher level of energy expenditure. In addition, assumptions regarding the estimated time spent resting versus time spent active on the water could also influence our DEE results. Our activity data did not provide reliable estimates of time spent resting since we programmed our loggers to eliminate tucking behaviour (assumed to represent rest time; Elliott and Gaston 2014). Therefore, we relied on estimates of time spent with leg(s) tucked from Elliott and Gaston (2014) for Thick-billed Murres, with average values of 5% (day) and 30% (night) respectively. To assess how variability around these assumptions influenced our DEE estimates, we calculated minimum and maximum time spent resting scenarios (also based on Elliott and Gaston 2014) using 25% (minimum) and 75% (maximum) inter-quartile ranges of mean percent time spent with legs tucked during the day (0.1% and 11.7% for minimum and maximum, respectively) and night (23.9% and 37.0%, for minimum and maximum, respectively), averaged over the entire winter period. The maximum resting scenario resulted in lower DEE since correspondingly less time is spent active on the water (which involves higher energy costs), and the average difference between the maximum and minimum time spent resting scenarios was 138 kJ day^{-1} (93 – 168 kJ day^{-1}). The reality of these scenarios for murres in the Northwest Atlantic is largely unknown, however Robertson et al. (2012) estimated "many hours" of dry records at night (assumed to represent tucking) for murres equipped with time-depth recorders. Therefore, it is likely that the mean (30% or 3.5 hours tucking) or maximum (37% or 4.5 hours) time spent resting scenarios are the most realistic. Given these assumptions, we acknowledge that our DEE results are largely 'theoretical' and should be considered as best current estimates. Nonetheless we emphasize the striking overlap in seasonal DEE trends with Fort et al. (2009) and the similarly high values reported by Elliott and Gaston (2014) for Thick-billed Murres during December; all of which support the notion of late winter as an extremely challenging phase in the annual cycle of North Atlantic murres.

4.5.2. Optimal Foraging Strategies in a Marginal Environment

Prey behaviour influences the foraging strategies of diving predators. In particular, the vertical distribution of prey in the water column determines dive depth and to a large extent, the duration of time spent feeding at depth. Water masses on the NL Shelf undergo pronounced seasonal modifications in their properties due to heat flux, wind-forced mixing and shifting ice extent (Colbourne et al. 2015, Richauld et al. 2016). Over the progression of winter, the vertical extent of warm water in the upper water column diminishes, and by late December cold water persists throughout the water column (Petrie et al. 1988, Richauld et al. 2016). When surface waters are cold, prey that otherwise migrate from deep waters during the day into warm surface waters at night (i.e. diel vertical migration) remain at depth. This could explain the observed decrease in the frequency of shallow dives in LW (Fig. 4.4) and the corresponding increase in daylight dives (with fewer crepuscular and nocturnal dives). Consequently, murres facing high-energy demands in LW spend more time foraging in deeper waters where capture efficiency of prey is limited by light availability (Hedd et al. 2009, Regular et al. 2010), resulting in a shorter foraging day (Fig 4.6B).

We suggest that murres operating under severe time (short days) and energy (high DEE, deep diving) constraints in LW push the limits of their diving capabilities to maximize their total net daily energy gain (i.e. rate maximizing behaviour, Houston 1987, Ydenberg et al. 1994). Specifically, they spend more time feeding in productive areas and dive intensively where and when foraging efficiency is maximized. Murres dove most frequently to intermediate depths (50 – 80 m) throughout winter (Fig. 4.4), which suggests that prey was most abundant or of the highest quality within this foraging zone. Though we have no corresponding information on winter diets, intermediate diving would potentially place murres within range of sandlance (and possibly cod, sculpin *Cottidae* spp.; Winters 1970, 1983, Lily 1982, Montevecchi and Piatt 1984) that occur over large portions of the Grand Bank (< 100 m; Fig. 4.1). Congeneric Thick-billed Murres on the NL Shelf were estimated to consume approximately half their body weight (c.a. 550 g) in wet food every day (Fort et al. 2009) during LW, which we assume is a realistic estimate for our murres. Forage fish are energy-dense and would be highly suitable prey for murres facing such demanding nutritional requirements. They are also rich in lipids, which make them profitable from an energy assimilation perspective since lipid-rich prey have relatively higher assimilation efficiencies (Brekke and Gabrielsen 1994). For murres that are primarily restricted to daylight diving in winter (see below), the ability to quickly process prey may be critically important to attaining sufficient energy reserves within a relatively limited foraging window.

Although murres performed fewer shallow and more deep dives in late winter (Fig. 4.4), there was no change in the frequency of intermediate dives (55 ± 2.7 and 57 ± 4.7% in EW and LW, respectively). They did however spend significantly more time on the bottom phase of intermediate dives in LW (Fig 4.5B), 43% of which exceeded their aerobic dive limit (ADL). Frequent anaerobic diving results in acidotic blood and eventual fatigue (Butler, 2001) and is considered unsustainable, yet murres and many diving species regularly exceed ADL during deep diving (e.g. 40% for King Penguin *Aptenodytes patagonicus*; Butler 2001). Theoretical explanations as to why (rather than how) divers frequently exceed their ADL involve energy trade-offs whereby individuals extend the duration of dives when the quality or density of prey is sufficiently high to ensure higher capture success and energy intake (Ydenberg and Clarke 1989, Kooyman and Ponganis 1998). Accordingly, we suggest that the high frequency of ADL dives at intermediate depths in LW reflects such a trade-off whereby murres facing high nutritional requirements extend feeding times at high quality prey patches (i.e. 50 – 80 m or intermediate depths) where energy intake per unit of time is maximized. Murres also exceeded their ADL during 85% of deep dives (n = 6497) in LW, however time spent on the bottom of deep dives was significantly lower relative to intermediate dives (Fig. 4.5B) and suggests travel time (versus feeding time) explains the high frequency of ADL dives in deep water. To our knowledge, the high frequency of ADL dives by murres in LW (36% over all dives) exceeds previous records (21% during chick-rearing; Elliott at al. 2008), most of which come from the breeding season. Consequently, an increase in the frequency of ADL dives could represent an important behavioural adjustment for winter survival (possibly facilitated by physiological adjustments; Gerlinsky et al. 2013).

We also show that visually-oriented murres respond to an increasingly deep-water prey field in LW by greater diving intensity during daylight hours (Fig. 4.6). During LW, murres exhibited significant increases in mean dive (and dive bout) frequency and duration (relative to EW) and a corresponding decrease in inter-bout rest time (Table 4.1). While the difference in inter-bout rest times between EW and LW was not significant (Table 4.1), it is striking that murres that are diving more (and frequently exceeding ADL) are spending less time resting at the surface between dive bouts in LW. Presumably, murres are expending maximum effort when foraging efficiency is highest (i.e. during daylight hours) which allows them to satisfy their significant food energy requirements when visually hunting for prey in deep water.

Intensive diurnal foraging (possibly consuming lipid rich prey) could also allow murres to gather surplus energy reserves to sustain them during nocturnal fasting (McNamara and Houston 2008). This behaviour could explain our finding of significantly heavier birds in LW (> 1000 g) that is supported by frequent reports of relatively heavy seabirds in winter (e.g. murres and kittiwakes; Falk and Durinck 1993, Erikstad 1990, Harris et al. 2000) including an observation of murres collected during the Newfoundland “turr” hunt carrying heavy subcutaneous fat (Gaston et al. 1983). Accumulation of lipid reserves would also improve insulation and significantly reduce heat loss to the water (Richman and Lovvorn 2011) resulting in potentially lower thermodynamic costs (and DEE). Whether murres carry enough reserves to sustain them through more prolonged periods of fasting is uncertain, however the occurrence of large numbers of dead and starving alcids coming ashore following extreme weather events (winter wrecks; McFarlane et al. 2010) suggests that the amount of reserves that these relatively small birds can carry is insufficient to sustain them over extended periods, particularly in late winter when energy demands are high.

4.6 Conclusions

Our results contribute to our understanding of the tolerances of murres in response to a prolonged and demanding LW period in a low Arctic ecosystem, and demonstrate that murres are capable of coping with predictable, seasonal environmental extremes over an extended period. During the LW period when energy demands are high and foraging conditions are relatively poor, murres push the physiological limits of their diving capabilities to balance their energy budgets. Evidence from studies on foot-propelled cormorants indicate that although birds can sustain high rates of feeding activity when energy demands are high in winter, they deplete reserves over time and come close to, or succumb to starvation by early spring (Daunt et al. 2007). The physiological consequences associated with intensive foraging during a prolonged period of peak energy demand are unclear but if murres are working at maximum capacity, predicted extremes in environmental conditions associated with future climate change (Reid and Valdés 2011) could have potentially catastrophic consequences for winter survival, particularly if prey conditions are negatively affected. Future research investigating the physiological mechanisms that drive such extreme behavioural responses are needed to better understand and predict the tolerances of murres to environmental extremes and variability.

High DEE during late winter for related alcids (Fort et al. 2009, 2013, Elliott and Gaston 2014) suggests the existence of a potential energy bottleneck for these pursuit divers, driven by climatic factors during long, harsh North Atlantic winter. Our results indicate that murres can, and indeed need to forage intensively on a consistent schedule to avoid an energy bottleneck in LW. Whether other alcids can rely to such an extent on intensive feeding to sustain them during periods of extreme energy demand is unclear, and requires further study.

4.7 Acknowledgements

We thank N. Laite, A. Hann, and S. Bennett for assistance in the field. Key logistical support was provided by Environment Canada (G. Robertson, D. Fifield, S. Wilhelm, P. Ryan). Special thanks to the crews of the Lady Easton (Easton family) and EcoTours for safe transport to and from colonies. We thank P. Regular for the valuable input and insight throughout the progression of the manuscript. We thank M. Frederikson for providing a copy of his R script and L. McFarlane Tranquilla for access to BAS data to run adjustments on Lotek positions. G. Robertson (Env. Can.) and S. Wilhelm (CWS) also generously provided data on the winter masses of murres from the Newfoundland “turr” hunt. Research support was provided by an NSERC Post-graduate Fellowship to CMB, the Graduate School of Memorial University of Newfoundland, and NSERC Discovery Grants to WAM.

Supplementary Table 4. 1. Summary statistics (mean ± SE) for diving activity of individual Common murres in winter. * indicates a decrease in the proportion of anerobic dives (ADL) from EW to LW.

Year	Bird Id	Dive Log Duration (starting 15 November)		Dive Effort	Dive Characteristics			
		End Date	Number days	Number dives/day	Depth (m)	Duration (s)	Bottom Time (s)	% ADL Dives LW (% Change)
2009	1470_10	02-Jan	48	96.6 ± 11.1	39.9 ± 0.3	103.6 ± 0.5	43.8 ± 0.3	0.1% (99%)*
	1604_10	30-Jan	76	84.8 ± 4.6	43.6 ± 0.3	112.7 ± 0.5	41.6 ± 0.3	21.6% (96%)
	1613_10	06-Feb	84	77.0 ± 3.8	48.1 ± 0.4	111.0 ± 0.6	36.1 ± 0.3	21.7% (39%)
2010	1883_11	27-Jan	74	50.3 ± 2.3	74.2 ± 0.4	156.5 ± 0.7	52.9 ± 0.4	82.3% (45%)
	1885_11	12-Jan	58	73.7 ± 4.1	57.0 ± 0.4	127.5 ± 0.6	41.3 ± 0.3	14.6% (57%)*
	1891_11	09-Feb	87	54.6 ± 2.6	55.5 ± 0.4	133.2 ± 0.7	49.7 ± 0.4	51.6% (73%)
	1894_11	14-Fen	93	53.5 ± 2.0	50.9 ± 0.3	134.9 ± 0.7	60.0 ± 0.4	48.8% (12%)
	1895_11	30-Jan	77	51.7 ± 2.8	57.4 ± 0.4	129.2 ± 0.7	44.9 ± 0.4	40.4% (56%)
2011	1891_12	11-Jan	58	61.3 ± 3.6	49.1 ± 0.4	112.8 ± 0.7	41.6 ± 0.4	8.4% (57%)*
	2322_12	15-Feb	93	59.5 ± 3.5	47.5 ± 0.4	110.5 ± 0.7	36.3 ± 0.3	26.4% (84%)
	2475_12	15-Feb	93	46.6 ± 2.3	67.1 ± 0.5	141.1 ± 0.7	45.3 ± 0.4	57.6% (65%)
2012	2322_13	29-Dec	45	39.1 ± 3.2	52.8 ± 0.5	132.9 ± 1.1	51.0 ± 0.3	47.0% (45%)
2013	2852_14	15-Feb	93	88.4 ± 5.5	51.6 ± 0.3	120.0 ± 0.5	43.7 ± 0.2	21.0% (29%)
	2854_14	15-Feb	93	73.9 ± 3.4	69.2 ± 0.3	148.4 ± 0.5	50.9 ± 0.3	62.9% (79%)
	2857_14	25-Jan	72	53.6 ± 2.9	46.0 ± 0.3	134.3 ± 0.9	60.5 ± 0.6	56.3% (87%)
	2861_14	15-Feb	93	70.5 ± 4.7	51.1± 0.3	122.4 ± 0.5	45.3 ± 0.3	23.4% (85%)
	2862_14	07-Jan	54	69.9 ± 3.5	51.3 ± 0.5	119.8 ± 0.8	40.3 ± 0.4	52.0% (81%)

CHAPTER 5 – BEHAVIOURAL TRANSITIONS IN THE ANNUAL ROUTINE OF COMMON MURRES

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5.1. Abstract

Seasonality influences the scheduling and maintenance of annual routines (e.g. reproduction, moult, migration) and their energy involvements. Delineating how events are linked in the annual cycle is essential to understanding individual and population level responses to environmental variation. I use a combination of logger-derived foraging metrics (daily effort and dive tactics) and dietary niche indices (via stable isotope ratios) is to assess how a low Arctic, deep-diving seabird (Common Murre *Uria aalge*) adjusts its foraging behaviour in response to fluctuating energy requirements and environmental conditions over their annual cycle in a cold and variable environment. Non-linear patterns in the daily foraging effort (DFE) of murres involved peaks in summer and winter, with consistently low feeding activity throughout the intervening post-breeding (autumn) period. This corresponded with seasonal shifts in dive tactics and dietary niche (trophic position and breadth) involving a higher frequency of shallow, brief dives and a lower trophic level diet during the post-breeding autumn period. I hypothesize that the post-breeding period represents a buffer event in the murres' annual cycle during which costly activities (e.g. flight, anaerobic diving, thermoregulation) are minimized. Competing energetic demands for males (paternal care and wing moult) are managed, though they could incur time and energy deficits during years when food availability is reduced, with potential consequences on winter survival.

5.2. Introduction

Seasonality represents the predictable component of environmental variation in the annual cycle (Varpe 2017). At high latitudes seasonality involves pronounced fluctuations in the bio-physical environment (photoperiod, temperature) that strongly influences the scheduling of fitness-related activities (e.g. reproduction, migration, moult) in the annual cycle (i.e. life-history stages; McNamara and Houston 2008). Fitness-related activities that involve significant energetic investments (reproduction and periodic growth) are supported during productive seasons (spring, summer) versus energy-minimizing activities (diapause and hibernation) during less productive seasons (winter). Although predictable fluctuations in the environment determine the scheduling of life-history stages, sex differences in reproductive roles can lead to divergence in the timing of activities with expected differences in nutritional demands, foraging strategies and habitat choices by the sexes (Breed et al. 2009, Elliott et al. 2010, Hedd et al. 2014). Understanding these processes is critical in light of phenological changes in the timing of recurring events and associated temporal trophic mismatches that are an anticipated response to ocean climate change (Cushing 1990, Edwards and Richardson 2004, Oliver 2019), and that are predicted to be more pronounced in high latitude pelagic ecosystems (Durant et al. 2019).

Information regarding the behavioural responses and resilience of seabirds to environmental variation is derived primarily from studies conducted during the relatively short breeding period, and primarily in the context of inter-annual changes in food resources needed to support reproduction and its associated high activity costs (Garthe et al. 2011; Osbourne et al. 2020). Our understanding of the strategies used by seabirds to cope with fluctuations in energy requirements and prey availability during the remainder of the year is by comparison relatively limited.

The Common Murre (*Uria aalge*, hereafter murre) is a pursuit-diving seabird with a circumpolar distribution (Gaston and Jones, 1998). Their capacity to cope with environmental constraints via behavioural flexibility during the breeding season is well documented (Burger and Piatt 1990, Harding et al. 2007, Regular et al. 2014). Murres are long-lived seabirds (25 + years) with high adult annual survival rates (87-97%; Ainley et al. 2002, Robertson et al. 2006), yet they exhibit higher than expected field metabolic rates (FMRs) during bi-parental chick-rearing when activity costs are high (Cairns et al. 1990, Elliott et al. 2013a, Regular et al. 2014) and during winter when thermodynamic costs and nutritional requirements are high (Fort et al. 2009, Chapter 4; Burke and Montevecchi, 2018). How these demanding energy phases are managed through their annual cycle is largely unknown, however the fact that murres undergo seasonal energy bottlenecks repeatedly over a long life and maintain high annual survival suggests the existence of compensatory mechanisms that buffer them from accumulated stress (carryover effects) over their annual cycle (Senner et al. 2014, Briedis et al. 2018). The strategies that support this apparent resilience are poorly understood, but can be investigated using behavioural assessments of individuals through the annual cycle.

In previous chapters I have shown that the foraging behaviour of murres reflects energy expenditures associated with fitness-related activities (chick-rearing, moult) and the interacting effects of their local environment (forage fish availability, winter acclimation), with important differences by the sexes related to parental care roles. Here, I attempt to link these events by quantifying the timing and magnitude of behavioural transitions associated with fitness related activities over the annual cycle. To do this, I apply a non-linear modelling approach to detect seasonal and sex-specific fluctuations in the daily foraging effort (DFE) of adult murres over eight months in their annual cycle (mid-July to mid-February), in combination with information on seasonal dive tactics (depth, bottom duration) and dietary niche (via isotopic values) to assess seasonal adjustments in foraging behaviour.

This annual-cycle perspective is intended to shed light on the annual survival strategies of adult murres, and to assess potential sex differences in seasonal energy constraints associated with male-biased parental care. This is important for understanding individual and population level responses to natural environmental variability, which can inform our understanding of the capacity of murres to cope with climate-mediated environmental contingencies (Grémillet and Boulinier, 2009).

5.3. Materials and Methods

5.3.1. Seasonal Analysis of Behavioural Transitions

This research was carried out on Common Murres at two seabird colonies on the island of Newfoundland in eastern Canada from 2009-2013: Gull Island (47°16’N, 52°46W) in the Witless Bay Ecological Reserve (47°16’N, 52°46W) with c.a. 1632 breeding pairs breeding pairs (Robertson et al. 2004) and the Funk Island Ecological Reserve (49°45’N, 53°11’W) with c.a. 470, 000 breeding pairs (Wilhelm et al. 2015). Seasonal information on foraging metrics were collected over 8 months of the year (July - February) using Lotek LAT 2500 geolocation-immersion loggers (5.9 g with attachment, c.a. 0.7% body mass) that were attached to the leg of breeding murres during late chick-rearing (adults with chicks > 10-15 days of age). Detailed descriptions of the methods relating to logger deployments and data processing are provided in Chapters 2 and 4.

To assess seasonal patterns in DFE, I applied a generalized additive mixed-effects model (GAMM) using the 'gamm' function in the R-package 'mgcv' (Wood 2012). Penalised regression splines for day of year and a Gamma distribution (log link) were applied, optimised by the restricted maximum likelihood (REML) method. Individual was included as a random effect to account for pseudoreplication due to multiple data points from individual murres and a correlation term (corARMA) was included to account for dependence in daily measurements. Sex, year and colony were included as fixed effects, however, since year and colony did not significantly influence outcomes, they were excluded from the final model.

To identify periods of significant change in the estimated seasonal trend of DFE, I calculated first derivatives of fitted trend splines for each sex separately, with estimated confidence intervals. Derivatives were calculated using the 'Deriv' function in the R-package 'gratia' (Simpson 2019). Seasonal changes in the dive tactics of murres are also presented according to the average dive depth and bottom duration (summarized by hour on individual days) for all dives from 15 July to 15 February. Females in this analysis also include one independent male whose chick was confirmed lost after colony departure.

Owing to limitations on the temporal range of the loggers used in this study, behavioural activity in the pre-breeding spring season is lacking. There is however some relevant information on daily maximum dive depth (from the light log) and activity data over the full year. These data were used to assess colony arrival dates where total daily dry time exceeded

360 min (or 6 h) indicated regular colony attendance, and dive behavior during the pre-breeding period. While this amount of detail is insufficient to understand spring ecology, it does provide some insights that are worth consideration in the context of the full annual cycle.

5.3.2. Seasonal Dietary Niche

Isotopic values ($\delta^{15}N$ and $\delta^{13}C$) were derived from a variety of tissues that were sampled over the annual cycle: whole blood has an isotopic turnover of c.a. 12–15 days (Hobson and Clark, 1993) and provided an isotopic signal for the summer breeding period, flight feathers (primary and secondary coverts) are grown over an estimated two-month moult period and provide a fall signal (September - October; Chapter 3) and alternative breast feathers provide a late winter/spring (pre-breeding) isotopic signal (Pyle, 2009). Detailed descriptions of methods relating to stable isotope processing are provided in Chapter 2 (Burke et al. 2015).

To assess potential shifts in trophic niche across life-history stages in the annual cycle, $\delta^{15}N$ and $\delta^{13}C$ values were used to estimate the stage-specific standard ellipse areas, corrected for small sample size (SEA_c) and the Bayesian standard ellipse area (SEA_b), both calculated in the SIBER package in R (Jackson et al. 2011). The SEA_c was set to contain 40% of the data and SEA_b estimates were derived from 4000 posterior iterations, reported as the mode with 95% credible intervals (Jackson et al. 2011). Significant differences in SEA_b were assessed by calculating the probability that the ellipse of one group was larger than another, which for this study was assessed across three groups corresponding to life-history stages in the annual cycle. In addition, percentage overlap between standard ellipse areas was calculated using the ‘maxLikOverlap’ function in SIBER. Layman metrics were also estimated, which provide complementary information on the spread and extent of isotopic values, including δ^{15}N range (NR) which provides a measure of trophic length (i.e. the distance between minimum δ^{15}N‰ - maximum δ^{15}N‰) and δ^{13}C range (CR) which represents the difference between the most enriched and depleted δ^{13}C signatures and provides an index of trophic diversity (Layman et al. 2007). Significant differences in the δ^{15}N‰ and δ^{13}C values between tissues were assessed via repeated measures ANOVAs using a linear mixed-effects model executed in package lme4 (Bates et al. 2015). All statistics were computed using Cran R (ver 3.2.1.) and the statistical significance was assumed at $p < 0.05$.

5.4. Results

5.4.1. Seasonal Patterns in Daily Foraging Effort (DFE)

Mean DFE of adult murres varied nonlinearly over time (adjusted $R^2 = 0.38$; Fig. 5.1) with significantly greater effort by males ($t = 3.5$, $p < 0.001$). Mean DFE was highest during late winter, followed by summer chick-rearing with the lowest values during the intervening autumn season (Fig. 5.1). The model fit was relatively poor for male murres in late winter due to a small sample of only 2 individuals.

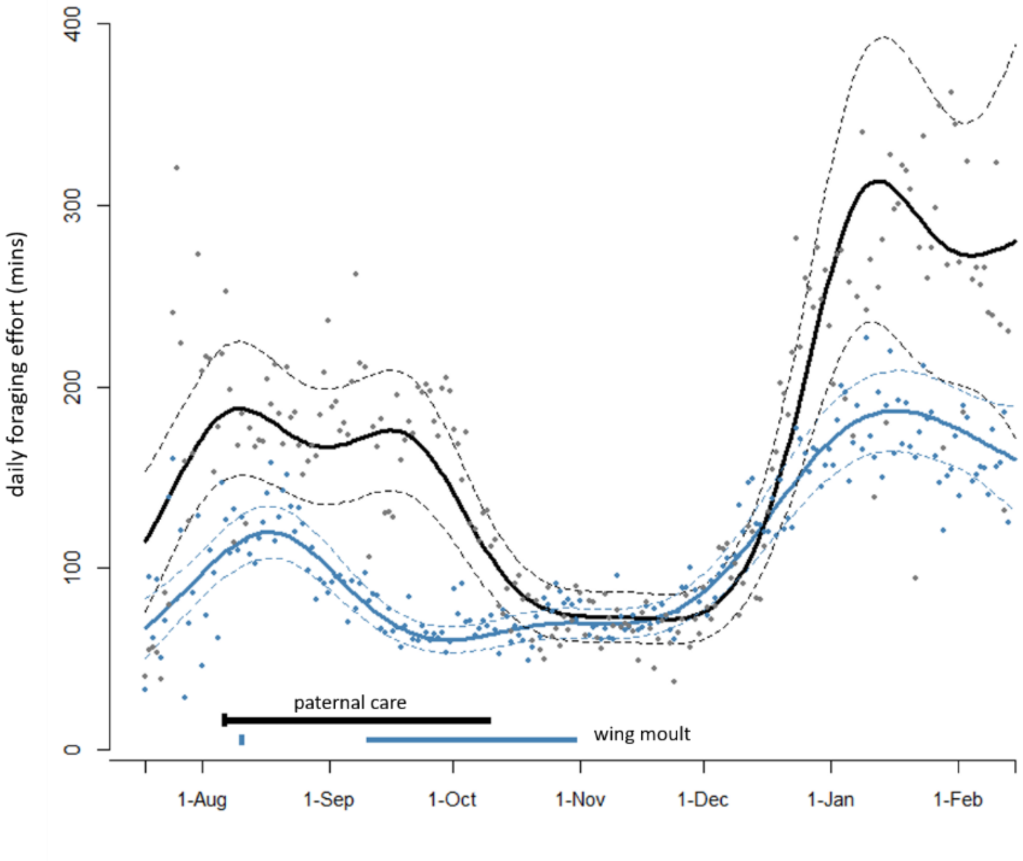

Figure 5.1. Results of generalized additive model (GAMM) showing the trend in mean DFE (with 95% CI) of 15 female (blue line) and 7 male murres (black line) from 15 July to 15 February. Continuous lines indicate the model predictions with ± 95% confidence intervals (dashed lines). Points correspond to average DFE values according to sex. Solid horizontal lines along the *x*-axis indicate the estimated average timing of male only parental care at sea (black line: 7 August to 10 October; Chapter 2; Burke et al. 2015) and wing moult for females (blue line: 10 September to 1 November; Chapter 3). Small vertical lines (along x-axis) indicate the median date of colony departure for females (10 August) and males (3 August; Chapter 2; Burke et al. 2015).

Estimates of the first derivatives of the fitted trend splines for female and male murres indicate two periods of statistically significant change in DFE over time (Fig. 5.2): one decreasing trend (solid heavy lines) after the chick-rearing period, that was later for males, and one increasing trend (dashed heavy lines) before the late winter peak with very similar timing by the sexes (Fig 5.2). The intervening period during which there was no significant change in DFE over time, involves an estimated 53 days for females (25 September to 17 November; Fig. 5.2, top panel) and 29 days for males (late 28 October to 23 November; Fig. 5.2, bottom panel) corresponding to the lowest DFE values in the time series.

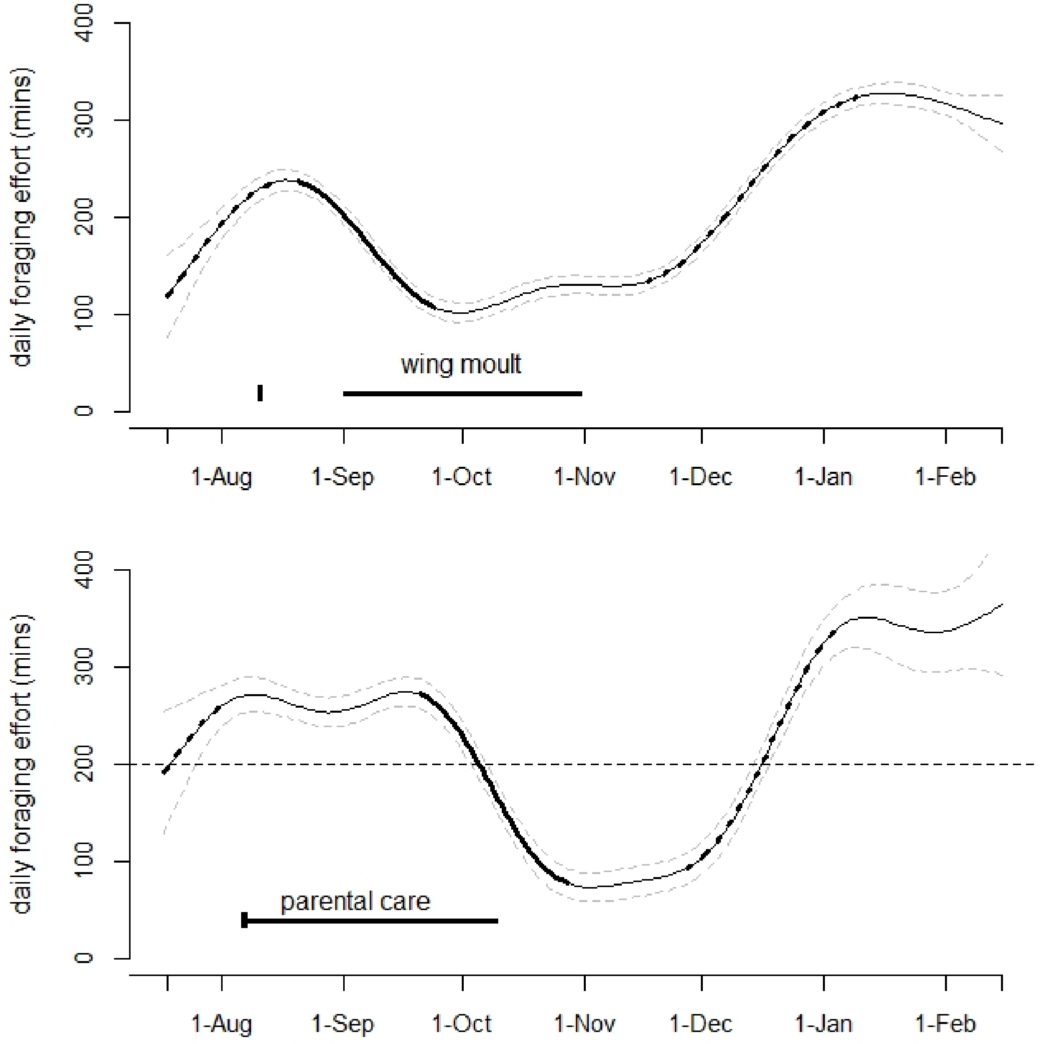

Figure 5.2. Periods of significant change over time as identified by first derivatives of fitted trend splines (darker, thicker lines; dashed = increasing, solid = decreasing), super-imposed on the fitted trend in mean DFE (with 95% CI) of 15 female (top) and 7 male murres (bottom) from 15 July to 15 February (lighter, thin lines). Horizontal lines show the estimated timing of wing moult (females) and paternal care at sea, with short vertical lines corresponding to colony departure dates.

5.4.2. Seasonal Transitions in Dive Tactics

Figure 5.3 illustrates the fine-scale dive tactics of female and male murres from 15 July to 15 February, showing dive depth and bottom time (averaged by hour on individual days), which is assumed to be an increasing function of energy intake for breath-hold divers like murres that can consume multiple prey at depth (Mori et al. 2002, Elliot et al. 2008). Females show a gradual increasing trend in dive depth and bottom duration over time with the longest, deepest dives in late winter. Males show a similar increasing trend in bottom duration, however the seasonal pattern in dive depth differs as males continue to perform deep dives (> 60 m) with short bottom durations throughout the chick-rearing period at sea (Fig. 5.3). Both sexes show a clear termination of deep diving after chick-rearing, corresponding to the estimated date of colony departure for females (10 August; Chapter 2; Burke et al. 2015) and the estimated date of offspring independence for males (10 October; Chapter 2; Burke et al. 2015).

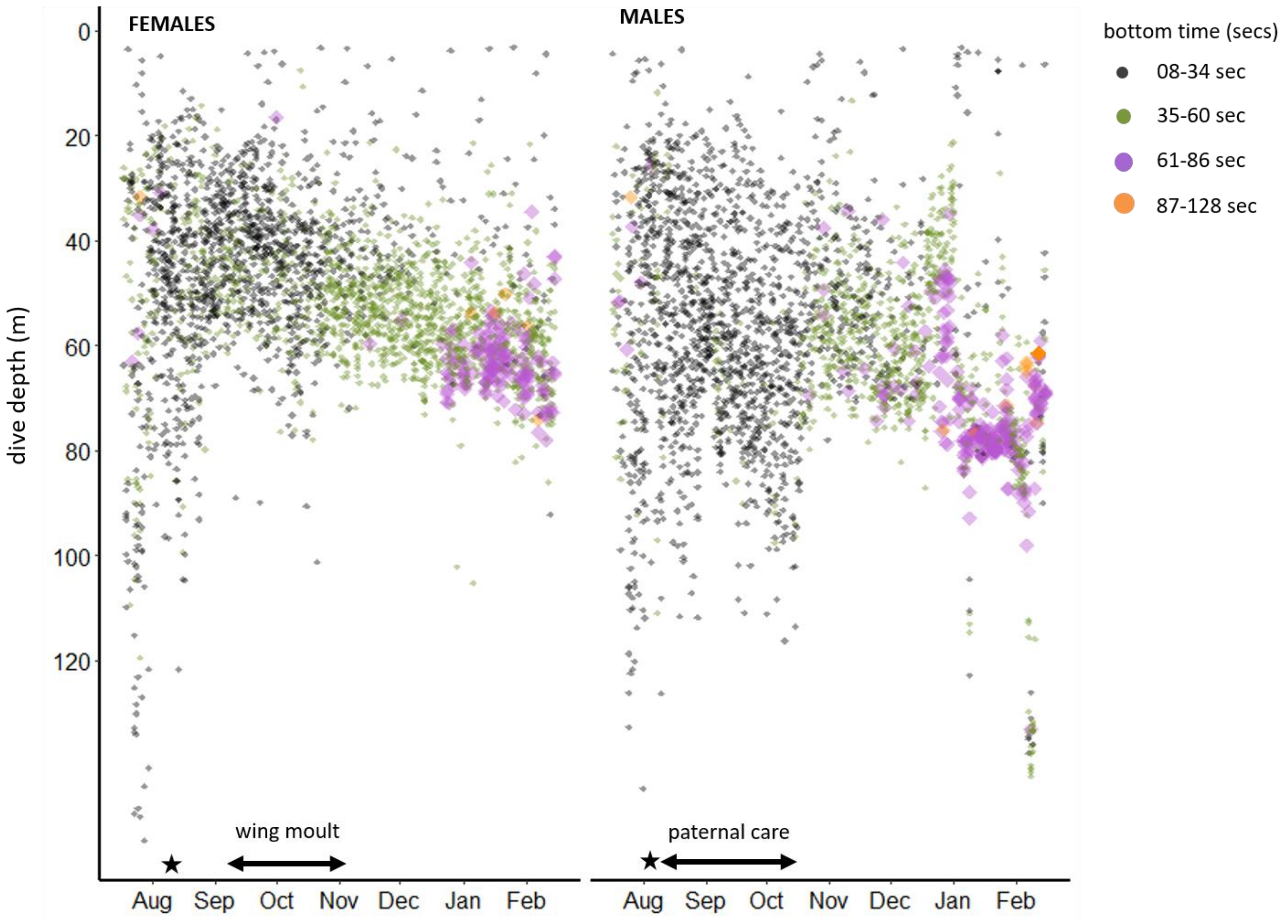

Figure 5.3. Bubble chart showing mean dive depth and bottom duration (both averaged by hour and date) for female (n = 2941 hours; add number of individuals) and male (n= 2885 hours) murres from 15 July to 15 February. Colors correspond to mean bottom duration (binned by 26 second intervals). Values exclude night dives (8% of all dives) that are shallow with short bottom times regardless of season and V-shaped dives (10% of dives) where bottom time is 0. The timing of colony departure (black stars), wing moult and paternal care at sea (black arrows) are indicated along the x-axis .

Sex-specific seasonal trends in maximum dive depth over the full year are illustrated in Figure 5.4, showing a divergence by the sexes in spring when females are diving significantly deeper than males. The median timing of colony arrival by male and female murres in the spring is indicated on the x-axis, showing an earlier return date by males (16 May ± 7.1 days) relative to females (10 May ± 5.5 days).

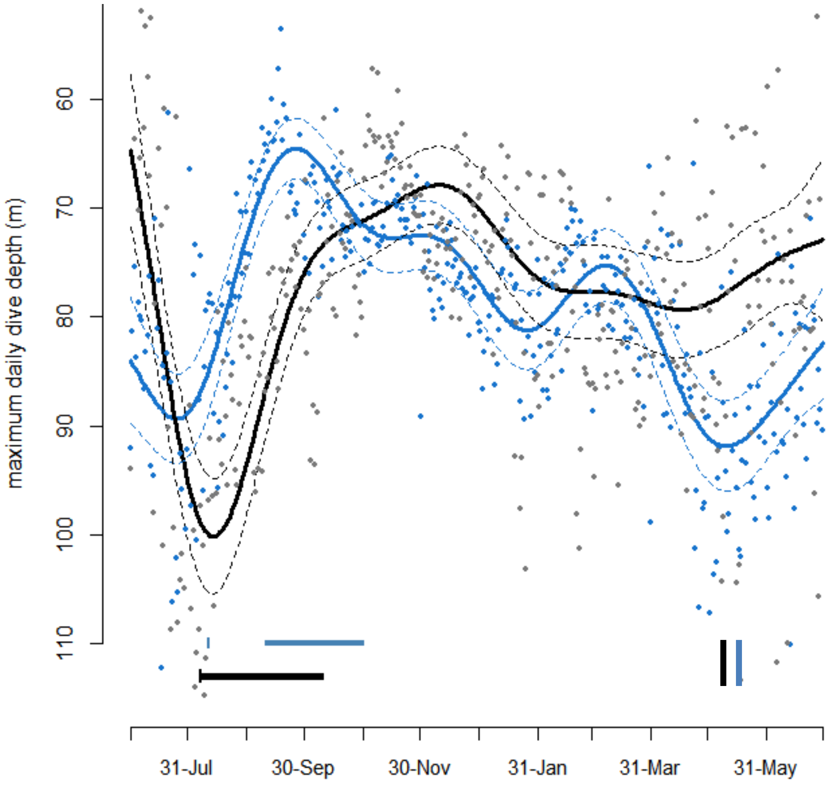

Figure 5.4. Results of generalized additive model of maximum daily dive depth (with 95% CI) for adult female (blue) and male (black) murres over the full annual cycle (15-July to 15-June). Points show average daily values according to sex. Horizontal bars along the *x*-axis indicate the estimated dates of wing moult for females (blue) and male parental care at sea (black).

5.4.3. Seasonal Trophic Niche

Estimated niche breadth (SEA_b) during the autumn (SEA_b = .74 ‰^{2}) and late winter (SEA_b = .73 ‰^{2}) were very similar (Fig. 5.5, Table 5.1), and were larger than during summer (SEA_b = .39 ‰^{2}) in 100% of the Bayesian iterations (for both comparisons). There was no overlap in the standard ellipse area for summer with either the autumn or late winter ellipses, however there was 40% overlap in the shared niche space for autumn and late winter (Fig. 5.5, Table 5.1). NR was larger in autumn (4.1 NR; Table 5.1) relative to summer (2.3 NR) and late winter (3.4 NR), and CR was smallest during summer (1.3 CR) and largest in late winter (2.0 CR). Tissue-specific δ^{15}N‰ values were significantly lower in the fall (flight feathers = 11.9 ± 0.8‰) relative to summer (blood = 13.1 ± 0.5‰) and late winter (breast feathers =12.9 ± 0.8‰) which were not different (Table 5.1).

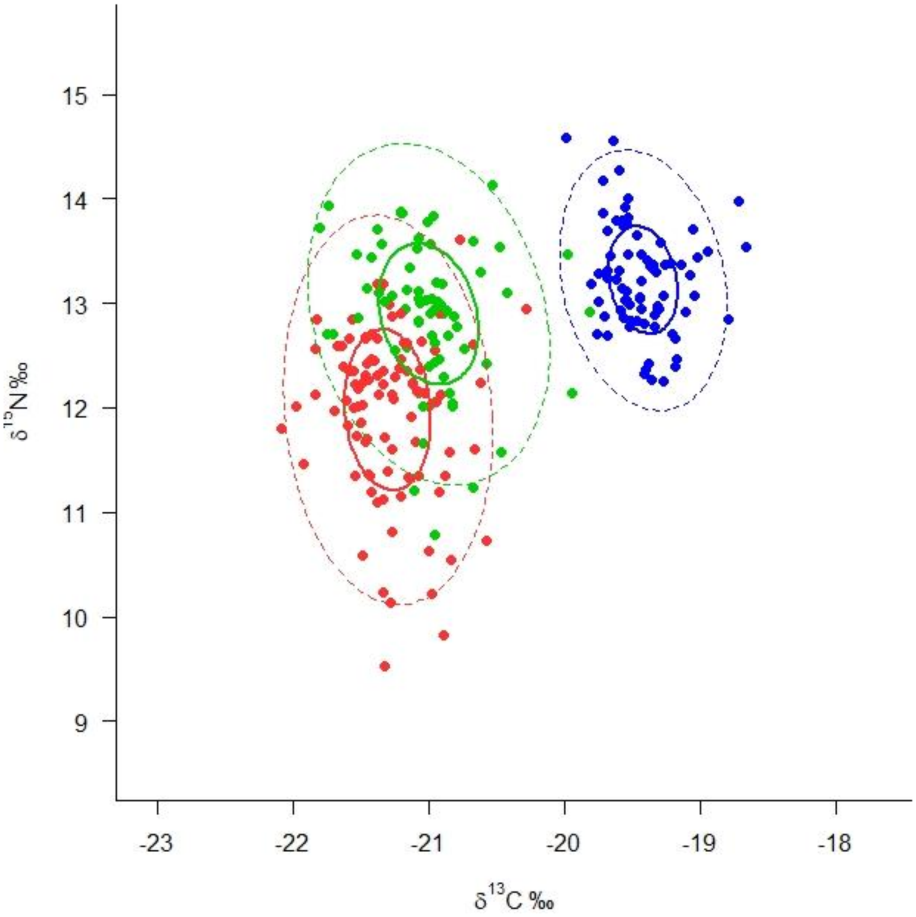

Figure 5.5. Stable isotope ratios of δ^{15}N‰ and δ^{13}C‰ derived from blood (blue = summer), flight (red = fall moult) and breast feathers (green = late winter) of murres showing standard ellipse area (SEA$_c$; solid line) and 95% ellipse area (dashed line).

Table 5. 1. Isotopic values (δ^{15}N‰ and δ^{13}C‰) for summer (blood), autumn (flight feathers) and late winter (breast feathers) for murres, including bayesian standard ellipse areas (SEA$_b$; mode with 95% credible intervals), ellipse area overlap (%) and Layman metrics (NR, CR).

Season (Tissue)	n	δ^{15}N‰ (± SD)	δ^{13}C‰ (± SD)	Bayesian SEA$_b$ (‰^{2})		% Overlap			Layman's Metrics	
				MODE	95% CI	B	FF	BF	NR	CR
Summer (Blood)	75	13.1 ± 0.5^{A}	-20.0 ± 0.7^{A}	0.39	0.31 - 0.49	-	0%	0%	2.3	1.3
Fall (Flight Feathers)[1]	77	11.9 ± 0.8^{B}	-20.9 ± 0.8^{B}	0.74	0.61 - 0.90	0%	-	40%	4.1	1.8
Late Winter (Breast Feather)	78	12.9 ± 0.7^{A}	-20.8 ± 0.8^{B}	0.73	0.59 - 0.93	0%	40%	-	3.4	2.0

[1] includes both primary and secondary that have overlapping isotopic values (Chapter 3)

5.5. Discussion

An animal's ability to modify its foraging behaviour in response to changing state-dependent constraints and environmental conditions is a critical determinant of survival in a seasonal environment (McNamara and Houston 2008, Marra et al. 2015). Here, I show evidence of behavioural plasticity by a pursuit-diving seabird in a low-Arctic, marine environment over 8 months (mid-July to mid-February) in their annual cycle. Plasticity is characterized by seasonal adjustments in DFE, dive tactics, and trophic niche (trophic position and niche breadth). I also highlight a post-breeding (autumn) period of significantly reduced activity that I hypothesize represents an important buffer event in the annual cycle of a seabird with an otherwise costly lifestyle.

Pronounced seasonal patterns in mean DFE of adult murres were evident, with some important mean behavioural differences by the sexes. The overall pattern shows high DFE during chick-rearing and late winter, and an intervening lull during the post-breeding period (Fig. 5.1). The fine scale dive tactics of murres over time provide indirect information on seasonal changes in the vertical distribution of prey available to these divers, and dietary information from stable isotopes inform seasonal patterns in dietary niche breadth that are interpreted in the context of shifting energetic constraints.

The interpretation of mean DFE by male murres as being indicative of seasonal nutritional requirements is biased by the fact that DFE during paternal care at sea also reflects the nutritional requirements of their growing chick (Chapter 2; Burke et al. 2015). Yet, unique characteristics associated with dives during chick-rearing periods can be used to refine estimates of the time allocated to self versus offspring provisioning. Specifically, there are striking changes in the dive profiles of chick-rearing adult murres (females and males; Fig. 5.3), whereby dives exceeding c.a. 60 m largely disappear after colony departure (the end of chick-rearing for females) and after chick independence at sea (the end of chick-rearing for males). These observations support previous studies showing that chick-provisioning dives are deeper than self-provisioning dives (Jones et al. 2002; Elliott et al. 2008), presumably in response to the specialized nutritional requirements of a growing chick. As such, when all dives > 60 m are excluded from DFE estimates of males during the period of chick rearing at sea, sex differences in mean DFE disappear ($p = 0.5$; Fig 5.6).

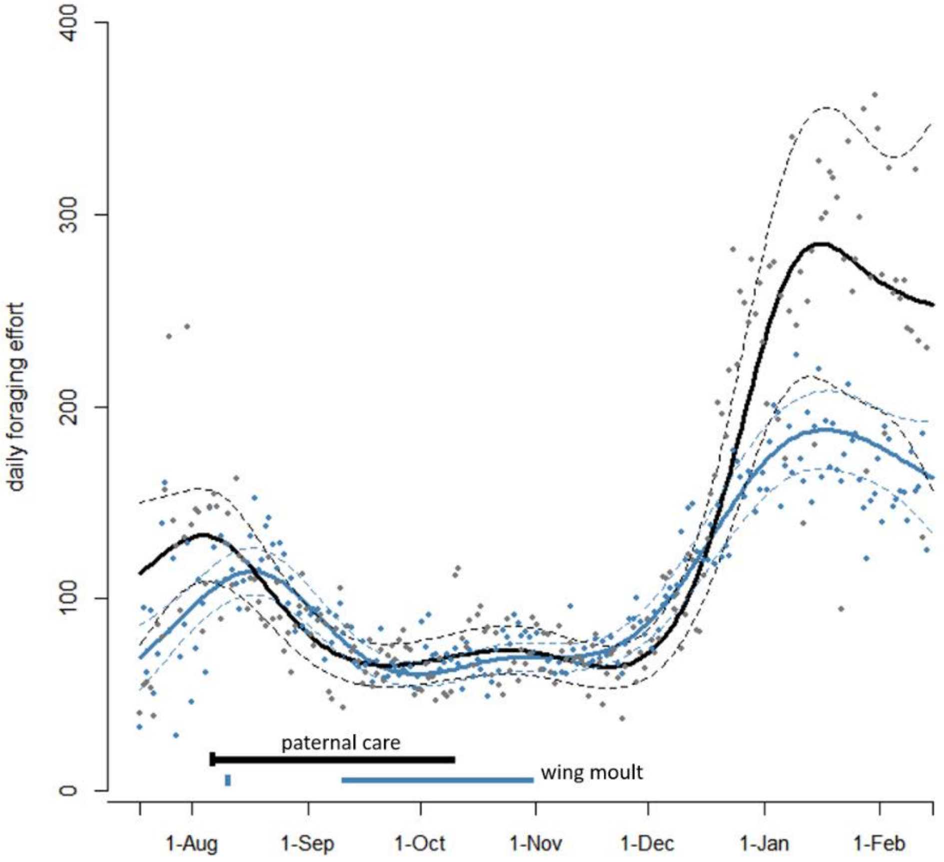

Figure 5.6. Revised generalized additive model (GAMM) showing the trend in mean daily foraging effort (with 95% CI) of 15 female (blue line) and 7 male murres (black line) from 15 July to 15 February ($R^2 = .4$). Excludes all dives > 60 m for males during the chick-rearing period at sea.

5.5.1. Post-Breeding Buffer Event

A striking and unexpected feature in the seasonal DFE pattern of murres is the sustained period of low activity in the intervening post-breeding period between summer chick-rearing and late winter (Fig. 5.1). During this time murres spent on average < 1 hour day^{-1} diving, which according to the first derivatives analysis (Fig. 5.2) involved an estimated two months during which there is no significant change in DFE over time for females (25 September to 17 November; Fig. 5.2) versus c.a. 1 month for males (28 October to 23 November). This arguably reflects a seasonal decline in the nutritional (energetic) requirements of adult murres, or alternatively that the time required to gather sufficient food energy is relatively low (or a combination of the two). Regardless, it suggests that adult murres may transition to a slower pace of life during a less demanding post-breeding period.

A portion of the proposed buffer period overlaps with the estimated timing of wing moult (Fig. 5.1) for females (10 September to 1 November; Chapter 3) and the timing of paternal care at sea for males (7 August to 10 October). In Chapter 3, I speculated that energy savings during moult-induced flightlessness may offset some of the energetic requirements of synchronous feather production. Similarly, paternal males may also benefit from energy savings during behavioural flightlessness (i.e. caring for a flightless chick), that could potentially offset some of the costs associated with caring for a chick at sea.

The dive profiles of murres throughout this time indicate that murres are foraging at intermediate depths in the water column (excluding chick-provisioning dives), and are spending very little time on the bottom phase of dives. Accordingly, only 7.0 ± 2.8% of dives exceed the aerobic dive limit (ADL) during post-breeding period, versus 8.5 ± 7.8% during summer and 26.5 ± 2.8% in winter. While information on prey availability is unavailable, these patterns suggest that prey is accessible (Fig. 5.3) during relatively shallow, short dives. Moreover, the switch to a lower trophic diet suggests a possible relaxation in nutritional (energetic) requirements during this time. The dietary niche breadth of murres during both non-breeding periods was larger than during summer chick-rearing when murres are specializing on capelin and are restricted in their foraging range by the constraints of central place foraging. Although the niche breadth of murres is very similar during both non-breeding periods (Fig. 5.5), the autumn post-moult period is characterized by a wider trophic range (NR=4.1) relative to late winter (NR = 3.4) and a smaller carbon range (CR=1.8 during autumn and 2.0 during late winter), indicative of a more generalized feeding strategy (Layman et al. 2007). Selective foraging for high-lipid prey (capelin or sandlance) is considered a key strategy to maximize energy per unit of prey (during self and offspring provisioning) and/or to improve digestive efficiency and energy assimilation (Brekke and Gabrielsen 1994), and is likely only critical when murres are facing an energy bottleneck.

As discussed in Chapter 3, the winter resident strategy of murres may provide greater flexibility in the timing of wing moult to coincide with favorable environmental conditions, and may therefore contribute to a less demanding lifestyle during the post-breeding period. A final consideration is that because murres are spending very little time engaged in costly activities including sustained flight, anaerobic diving, thermoregulation and the assimilation of large volumes of prey, they could theoretically minimize the size of metabolically costly organs (e.g. heart, lungs, gut). While there is no evidence of this for murres, many animals (including Rhinoceros auklets *Cerorhinca monocerata*; Niizuma et al. 2002) have been shown to exhibit plasticity in organ size; typically involving enlargements during metabolically active periods and reversal in size when maintenance costs outweigh the benefits during less active periods (Piersma 1988, Piersma and Lindstrom 1997, Wu et al. 2014).

I hypothesise that the period of relaxed foraging and flight activity during the post-breeding (autumn) period represents a critical buffer event in the annual cycle of murres during which they can theoretically overcome deficits incurred during a very demanding chick-rearing period and undergo maintenance activities (i.e. moult) in preparation for winter. This is supported by Dunn et al. (2020) who demonstrate a seasonal low in the estimated daily energy expenditures of Common Murres in the Northeast Atlantic (via estimated activity-specific costs and daily activity budgets) that coincides with the estimated timing of post-breeding wing moult (September to October) and a seasonal peak in sea surface temperature (SST; > 14 °C). Buffer events have been documented in the annual cycle of long-distance migrants (e.g. Hudsonian godwits *Limosa haemastica*) and are considered a key mechanism to minimize seasonal carryover effects (Senner et al. 2014, Briedis et al. 2018). Specifically, an abundance of resources at post-breeding, stopover sites allow individual godwits to regain condition and to minimize delays accumulated during previous migratory movements, resulting in realignment of the timing of subsequent movements with the population mean (Senner et al. 2014, Briedis et al. 2018). Murres experience seasonal energy bottlenecks (Fort et al. 2009, Elliott et al. 2013a, Regular et al. 2014, Burke and Montevecchi 2018; Chapter 4) repeatedly over a long life (+25 years), and the existence of a buffer event could have significant fitness consequences, including enhanced winter survival if a buffer period supports recovery (from breeding) and conditioning (for winter survival).

5.5.2. Sex Differences in Seasonal Constraints

Revised DFE estimates that exclude provisioning dives (Fig. 5.6) in combination with sex-specific overlap in δ^{15}N values of flight feathers suggest that single-parenting males experience similar energetic requirements to independent females. This is unexpected given the additional foraging time required to rear a chick to independence and the fact that paternal males occupy relatively poor quality habitat (Chapter 2; Burke et al. 2015), which is a consistent feature of at sea paternal care for murres across multiple regions and years (Elliott et al. 2017). This is also supported by independent information on the potential prey field available to post-breeding murres (Anderson and Dalley 1997) characterized by a significantly lower pelagic biomass (i.e. juvenile pelagic fish and macro-zooplankton) on the Grand Bank (core foraging area of males; Chapter 2, Burke et al. 2015) relative to the NE NL Shelf (core foraging area of females; Chapter 2, Burke et al. 2015), with one and two year old capelin dominating the nekton community. These results imply that male murres are somehow better adapted to survive a prolonged period of parental care at sea, however explanations as to why this may be the case are difficult to reconcile. The prolonged deep-diving activity of paternal males throughout late summer and autumn suggests that despite the lack of sex-specific structural differences, males may be more specialized or efficient in their diving capacity during this time. This could be explained by differential physiological adjustments that influence aerobic capacity, if for example, males maintain larger organs (heart and lungs) to support frequent deep-diving, versus females that may benefit from a reduction in the size of metabolically costly organs once they are finished provisioning their offspring (Piersma 1988, Piersma and Lindstrom 1997). Deeper, longer diving activity by males could also be supported by increased haematocrit levels (indicator of blood oxygen capacity), which play a key role in maximum oxygen consumption and has been shown to improve dive performance in Macaroni Penguins *Eudyptes chrysolophus* (Crossin et al. 2015) and to vary over the course of the annual cycle, involving reductions during post-nuptial moult in birds (Williams 2012). Furthermore, evidence of inter-annual adjustments in haematocrit levels by chick-rearing murres during years of varying food availability suggest that murres can undergo such physiological adjustments in response to changing energetic constraints (Storey et al. 2017).

Although single-parenting males do not appear to experience an energy constraint, competing fitness-related demands during the post-breeding period could potentially result in less flexibility in the scheduling of wing moult to coincide with optimal environmental conditions. Furthermore, similar timing in the transition to the late winter peak by female and male murres (Fig. 5.3) suggests that deteriorating environmental conditions place rigid time constraints on the completion of these activities. Since males depart the colony much earlier than females (Fig. 5.1), there is theoretically sufficient time for them to complete both fitness-related activities before the onset of winter, either separately or with some overlap. Yet if energy is limited during this time there is an increased risk that male murres could experience time constraints and enter into winter in relatively poor condition. Elliott et al. (2017) compared the duration of male-only paternal care at sea between conspecific murres across multiple colonies and years (including murres in this study) and demonstrated a longer duration of paternal care by Common Murres (by 19 days). This was explained as a potential advantage for murres breeding in the Arctic due to longer foraging days during summer that facilitate faster chick-growth rates. This comparison is informative as it suggests that the duration of parental care at sea is regulated by prey availability. If so, there is potential for increased overlap between wing moult and paternal care in poor food years, or the extension of wing moult into early winter. Alternatively, energy limitations could result in males abandoning their chick, however abandoning an offspring that is nearing independence would presumably be costly from a fitness perspective (Trivers 1974).

Recent disruptive trends in the NW Atlantic ecosystem (Buren et al. 2014) warrant a closer examination of the potential challenges faced by parental males. In particular, declines in the zooplankton biomass on the NL Shelf, involving a decline in the larger *Calanaus finmarchicus* and increase in the abundance of the smaller *Pseudocalanus* (Pepin et al. 2017) is predicted to have a detrimental effect on the fall condition of capelin (Lewis et al. 2019). Capelin is the primary prey of murre chicks (Regular et al. 2014, Davoren and Montevecchi 2003a, 2003b, Burke and Montevecchi 2008, Hedd et al. 2009) and declines in fall condition could force parental males to prolong the duration of offspring care at sea (via slower growth rates), resulting in greater time constraints to complete moult and rear their chick before the onset of winter.

Dunn et al. (2020) demonstrated an increase in DEE for Northeast Atlantic murres during the pre-breeding period, which they argue is driven by an increase in flight activity costs when birds begin returning to the colony after winter. While their study did not report sex effects, it is possible that males and females experience different constraints during this time, consistent with sex-specific reproductive roles (e.g. yolk production by females versus territory defence by males), each of which involve unique time and energetic investments. Males murres in this study returned to the colony earlier than females (median ± SD days: 10 May ± 5.5 days and 16 May ± 7.1 days for males and females respectively), and the seasonal trend in maximum dive depth shows a divergence by the sexes in spring with females diving significantly deeper than males (Fig. 5.4). This divergence in foraging behaviour coincides with the timing of colony return and persists over a period of weeks (up to early June). Female murres produce a large egg (11% body weight; Ainley et al. 2002) during the pre-breeding period and since murres are income breeders (Bond and Diamond 2010) that rely on locally derived nutrients, females may need to adjust their diving behaviour to locate suitable, energy-rich food. Alternatively, the observed divergence in dive depth by the sexes could reflect differences in foraging location if males are staying closer to the colony when they are defending their nest site, and are more restricted in the range of prey options available within a smaller foraging range.

5.6. Conclusions

This research sheds light on the seasonal transitions of a low Arctic seabird (Common Murre) and highlights the existence of a potential buffer event in their annual cycle that could represent an important component of the annual survival strategy of a long-lived seabird with an otherwise costly pace of life. This annual cycle perspective illustrates the importance of studying animals across life history stages to better understand how they manage carryover effects, and to identify periods of vulnerability and resilience that can inform conservation and research initiatives.

CHAPTER 6 – GENERAL DISCUSSION

Animals that inhabit northern latitudes experience seasonal fluctuations in the bio-physical environment (light, temperature, food availability) that determine the timing and magnitude of energy demands over the annual cycle. Survival, growth and reproductive success are determined by an individual's ability to acquire, assimilate and distribute (to offspring) food energy at the least possible cost (Pyke et al. 1977) and individuals that can maximize efficiency across a range of environments will incur a selective advantage.

The main goal of this thesis was to assess the behavioural mechanisms used by a high-latitude, pursuit-diving seabird (Common Murre *Uria aalge*) with a unique male-biased parental strategy to cope with shifting ecological constraints over their annual cycle. To do this, fine-scale behavioural observations were collected (via bird-borne data loggers) on individual murres during 8 months in their annual cycle (July - February). Behavioural observations were integrated with stable isotope analysis of different tissues (blood, flight and breast feathers) that captured dietary information over an equivalent time period. Overall, the results demonstrate resilience to natural fluctuations in seasonal energetic requirements, primarily mediated by highly flexible foraging behaviours. This resiliency may bear on the ability of murres to adapt to novel and extreme disruptions in their environment predicted to occur with climate change.

6.1. Significant Findings

I show that sex differences in the foraging behavior and habitat use of monomorphic murres emerge only when parental care roles diverge. To rear their chick, single-parenting males spent almost twice as much time diving per day (174 ± 10 min day^{-1}) relative to independent females (96.1 ± 6.9 min day^{-1}) and exhibited a high frequency of deep provisioning dives, persumably to select capelin for their growing chick. The duration of time over which murres exhibited sex differences in their foraging behavior was a very reliable indicator of the duration of paternal care at sea (c.a. 63 days). Single-parenting males occupied relatively poor quality habitat (centered on the Grand Bank) but regardless exhibited a similar trophic position to females and allocated equivant time to self provisioning.

These results suggest that males do not experience a significant energetic constraint associated with male-biased parental care, and further that males may somehow be more specialized or efficient in their diving behavior during this time. Yet, Robertson et al. (2014) reported lower annual survival rates for male murres (4%) relative to females from our main study site at Gull Island, Newfoundland. A lack of supporting evidence for sex-biased annual survival by adult murres has not however been demonstrated in other regions or populations (Sydeman 1993, Ainley et al. 2010 and references therein), and suggests that other factors may be contributing to differential survival by the sexes at these sites. Murres in the Northwest Atlantic specialize on capelin during chick-rearing, both at the colony (for self and offspring provisioning) and at sea (offspring provisioning only). Persistent declines in the biomass and condition of capelin (Buren et al. 2014, 2019) and mismatches in the timing of the inshore arrival of capelin during peak chick-rearing (Regular et al. 2014, Harding et al. 2007, Rector et al. 2012, Storey et al. 2020) may be limiting the ability of male parents to accumulate reserves for their own benefit. If so, male parents could potentially enter the post-fledging stage in an energy deficit during poor capelin years that could impact survival if they are unable to recover before the onset of winter. Predicted declines in the fall condition of capelin on the NL Shelf (Lewis et al. 2019) could exacerbate this deficit if energy-limitations are resolved by the extension of offspring care at sea resulting in less time to complete wing moult and regain condition before the onset of winter.

I defined the timing and duration of wing moult for female murres based on estimates of the duration of flightlessness via logger-derived activity data. While limited by a small sample size, the results were nonetheless informative for a poorly known life-history stage in the annual cycle of murres. My results indicate that murre wing moult occurs over an estimated 53 days with an unexpected delay in onset after colony departure by c.a. 32 days, that I suggest represents a flexible strategy whereby winter resident murres delay the onset of moult until a predictable food source is located (or becomes available) and/or sub-surface water temperatures within their dive range reach a seasonal maximum. Overall, the post-breeding period emerged as a time of relaxed energy demand that I argue is supported by a combination of favorable environmental conditions and a reduction in costly metabolic activities (flight, anaerobic diving, assimilation of large volumes of food). While not previously considered, such a buffer event could allow these long-lived animals to mediate deficits incurred during other demanding life history stages in their annual cycle. Studies investigating the daily energy expenditures of adult murres (and other seabirds) over the annual cycle, involving comparisons across different regions, populations and sexes are needed to support the existence of a post-breeding buffer and to elucidate the factors that may support (or constrain) such an event.

Murres in this study over-wintered on the Grand Bank and during the coldest months of late winter (January - February) estimated daily energy expenditures exceeded the theoretical limit to sustainable energy expenditure in vertebrates (i.e., 7 X Basal Metabolic Rate or 2450 kJ day^{-1} for murres). This suggests that murres experience a late winter energy bottleneck driven by thermodynamic costs during persistent cold exposure in North Atlantic winters. Yet, murres appear to overcome this bottleneck by pushing their dive limits (37% of dives exceeded their aerobic dive limit). Murres also had higher body mass in late winter relative to early winter and summer chick-rearing that likely represents a risk adverse strategy to avoid starvation during temporary food shortages. Nonetheless if murres are working at maximum capacity, predicted extremes in environmental conditions (Reid and Valdés 2011) could negatively influence winter survival, particularly if prey conditions deteriorate.

6.2. Research Limitations

Overall, these results contribute significantly to our understanding of the seasonal behavioral ecology of murres, and importantly demonstrate behavioral plasticity by murres that may allow them to buffer potential climatic disruptions associated with climate change. Yet, some limitations bear on the interpretation of results and necessitate cautious interpretation. Foremost, the research is limited by a relatively small number of birds that were sampled across multiple years and colonies. This is compounded by inconsistent information on behavioural metrics across individuals, with some birds having behavioural data in winter versus others in summer only. These limitations had a significant bearing on my ability to interpret the mechanisms driving the observed variability in behavioural metrics, specifically whether behaviour was driven by inter-annual differences in environmental conditions or individual strategies. This is significant given the emerging importance of understanding how individual variation underlies population level responses to environmental variation.

In addition, large geographical error (associated with light-derived geolocation) in the seasonal distributions of a bird with a fairly limited range of movement limited my ability to link behavioural metrics to environmental conditions. This includes how murres respond to (and cope with) extreme, localized weather events, including north-easterly gales and anomalous sea ice conditions that in some cases are known to result in winter wrecks (McFarlane Tranquilla et al. 2010). Future studies using more spatially precise GPS technology or a combination of temperature and dive loggers could provide a better context to assess environmental drivers of behaviour over the annual cycle.

6.3. Future Directions

This work sheds light on the seasonal ecology of a high-latitude diving seabird, yet a number of lines of future research are needed to truly understand how environment and phylogenetic history influence behavioural responses, and the ability of murres to survive in a potentially increasingly variable environment. Throughout this project, I reflected on the possible influence of physiological plasticity on the seasonal survival strategies of murres. Information on the role of seasonal adjustments in physiological state variables (i.e. energy reserves, feather quality, organ and gut size, hormone regulation) and energetic expenditures would be extremely valuable in understanding how murres regulate and manage seasonal changes in their metabolic state. This type of information is largely out of reach for non-breeding seabirds that are not accessible for sampling during most of the year. Regardless, opportunistic sampling from the winter hunt could be informative to provide information on winter condition (e.g. mass, lipid reserves, feather quality) and the use of using heart-rate monitors (e.g. Guillemette et al. 2007) or accelerometers (Wilson et al. 2006) could also significantly advance our understanding of the internal mechanisms controlling the annual routines of wild animals.

6.4. Conservation Implications

Murre populations in the NW Atlantic are largely stable, with some having recently experienced moderate growth due to declines in anthropogenic threats, including the large-scale removal of gillnets after a ground-fish moratorium in 1992 and reductions in chronic oil pollution (Regular et al. 2013b, Wilhelm et al. 2015). By contrast, murre populations in the NE Atlantic are experiencing troubling declines (Svalbard, Norway, Greenland and Iceland ; Frederiksen et al. 2016 and references therein). While a combination of factors are driving these population declines, including hunting pressure, fisheries interactions and other anthropogenic pressures (Erikstad et al. 2013); the role of winter survival on population dynamics is becoming increasingly realized (Gaston 2003, Fredericksen et al. 2016). This is due in part to the proliferation of tracking studies, some of which have demonstrated correlations between wintering areas and breeding population status (Fredericksen et al. 2016). The winter energy expenditures and dive performance information presented here support the notion of winter as a potential bottleneck in the annual cycle of murres, but it also suggests that murres can tolerate 'normal' winter conditions. Yet, if murres are operating close to a threshold, this may not be sustainable in the face of novel or extreme environmental changes in winter (Irons et al. 2008). As such, studies that integrate winter habitat use with foraging metrics (e.g. Dunn et al. 2020) with comparisons across years, regions, age classes and sex are needed to provide some insight into the behavioral tolerances of murres in the face of varying ecological constraints.

This thesis also presents a hypothesis of a post-breeding buffer event in the annual cycle of murres, which is supported by evidence of a seasonal low in the daily energy expenditures of NE Atlantic murres during September and October (Dunn et al. 2020). Recent declines in the biomass of zooplankton on the NL Shelf, as well as projections for associated declines in the fall condition of capelin could disrupt this buffer event and bear on the post-fledging survival of chicks and the fitness of single-parenting males and moulting murres. Beaugrand and Reid (2003) documented associations between large scale changes in the distribution of calanoid copepod crustaceans in the northeast Atlantic (northward by 10 degrees) and increases in sea surface temperature. Predicted warming trends in on the NL Shelf (1.4 °C increase in SST from 2011-2069; Han et al. 2019) could have catastrophic consequences if prey conditions become less predictable and further challenge a seabird that lives close to the edge of survival during a significant portion of their annual cycle.

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Appendix 1. 1. Lotek Positional Corrections

Unlike British Antarctic Society (BAS) geolocators that store raw light data and derive positions based on a user-defined light threshold and sun angle, the Lotek geolocator model used in this study (LAT 2500) estimates positions using onboard algorithms that apply fixed threshold and sun angle values. Comparison of raw positions from Lotek (this study) and BAS geolocators (McFarlane Tranquilla 2014) of Common Murres revealed striking differences in latitude, which changed over the annual cycle (Fig. A1). Specifically, Lotek positions were further north after colony departure in late summer and further south after the equinox in mid-October relative to BAS positions (Fig. A1). The magnitude of the observed shift in latitude over a period of ~ 25 days during the autumnal equinox is an unrealistic range of movement for murres that are known to be flightless during this time due to flight feather moult and paternal care of flightless offspring (Burke et al. 2015, Chapter 2, Elliott et al. 2017). In winter, Lotek positions were consistently farther south relative to BAS (Fig. A1) with the majority of positions located in deep off-shelf waters, well outside the expected winter range of murres (McFarlane Tranquilla et al. 2013, Hedd et al. 2011). The positional difference in BAS and Lotek positions decreased over winter and disappeared after the spring equinox (Fig. A1).

Strikingly similar differences in BAS and Lotek positions were reported for Thick-billed Murres at Greenland colonies with the same northward bias in autumn and a southward bias in winter (Frederiksen et al. 2016). To investigate the hypothesis that the fixed sun angle used in the Lotek algorithm (-3.44°) is inappropriate for murres, Frederiksen et al (2016) used the R package 'GeoLight' 2.0 to back-calculate times of sunrise and sunset from the estimated positions, and to estimate new positions using a user-defined, appropriate sun angle (-5°). Comparison of adjusted Lotek and BAS positions for murres from the same colonies (but different years) showed a significant improvement with greater overlap between BAS and Lotek positions (Frederiksen et al. 2016).

Following the approach of Frederiksen et al. (2016) we used the 'GeoLight' package to adjust the sun angle for Lotek positions and compare the outcome with positions derived from BAS loggers deployed on murres at the same Newfoundland colonies (but different years). We applied the same sun angle used for BAS loggers (-5.5°) as McFarlane Tranquilla (2014). The adjustment performed very well for positions from August to December (Figs. A2, A3), however during January and February when raw Lotek positions are closer to BAS positions (Fig A1), the adjusted positions were further north than BAS positions. Consequently, we applied a sun angle of -5° for January and -4.5° for February which resulted in better overlap between BAS and Lotek positions (Figs. A1, A2, A3). Similar to Frederiksen et al (2016) there was strong overlap between the raw Lotek and BAS positions after the spring equinox, and therefore we retained the original Lotek positions (from -3.44 sun angle) for this period (Figs. A2, A3).

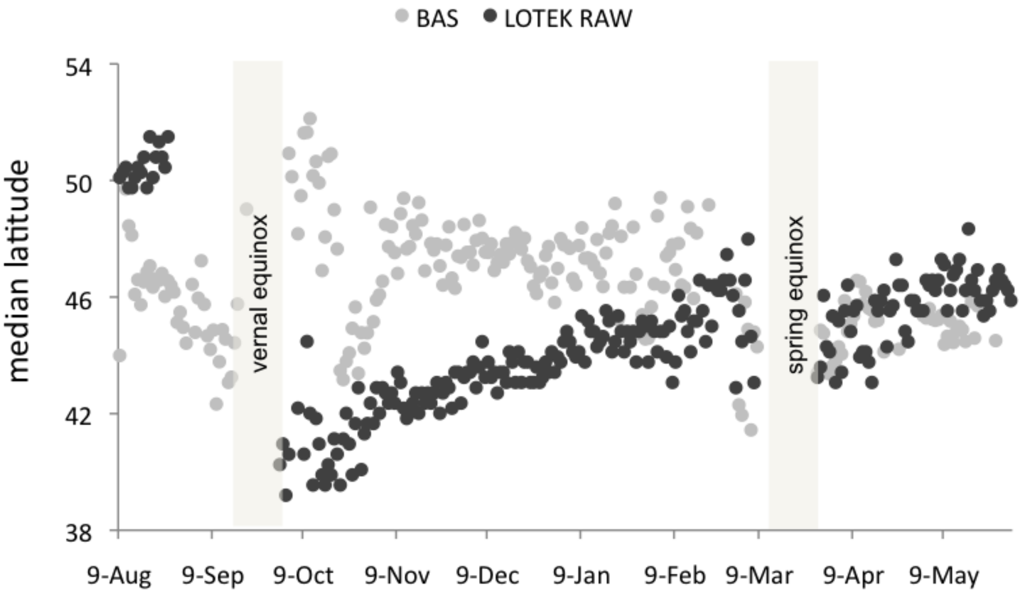

Figure A1. Median daily latitude from BAS (n = 31) and Lotek (n = 20) geolocators for Common Murres during the inter-breeding period. BAS and Lotek positions are grouped by colony and year. Gray vertical panels indicate the approximate timing of the vernal and spring equinox.

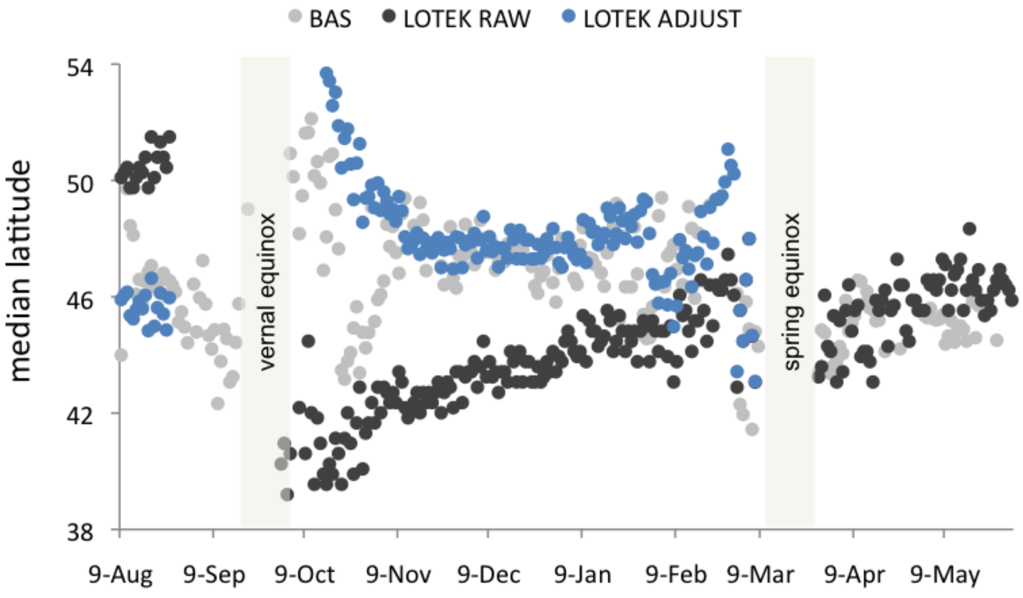

Figure A2. Median daily latitude from BAS (n = 31) and Lotek (n = 20) geolocators with adjusted Lotek positions for Common Mmurres during the inter-breeding period. The gray vertical panels indicate the approximate timing of the vernal and spring equinox.

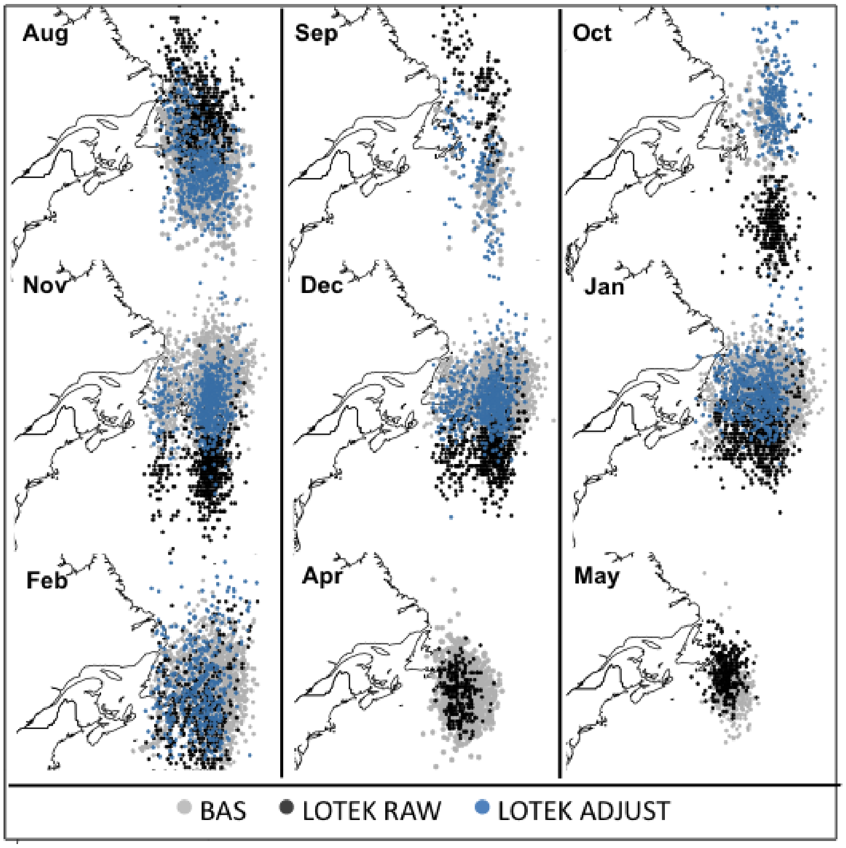

Figure A3. Maps showing the positions of raw (black) and adjusted (blue) Lotek positions (with the best performing sun angle) relative to BAS positions (gray) according to month during the inter-breeding period on the Newfoundland Shelf. Applied sun angles: -5.5 (Aug – Dec), -5 (Jan), -4.5 (Feb), -3.44 (Apr-May). Note: Lotek and BAS positions involve birds from the same colonies.