

FORAGING FLEXIBILITY OF SEABIRDS (FAMILY ALCIDAE)  
UNDER VARYING PREY BIOMASS

By

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A thesis submitted to the Faculty of Graduate studies of  
The University of Manitoba  
In partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

Department of Biological Sciences

University of Manitoba

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## Abstract

During the breeding season, seabirds may respond to shifts in prey regimes, which can lead to changes in diet, foraging behavior and breeding success. In coastal Newfoundland, seabirds rely on capelin (*Mallotus villosus*), a forage fish that migrates into coastal areas during the summer to spawn, thereby increasing prey availability. However, with increasing variability in ocean climate, capelin biomass as well as the timing of spawning and inshore arrival has become highly variable. In Chapter 1, I measured the association between capelin biomass and three niche metrics for chick-rearing razorbills (*Alca torda*): diet, foraging effort and body condition. For three years, I estimated dietary proportions using blood stable isotope ratios ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ), foraging and dive metrics from GPS and TDR loggers and assessed colony-based measures of body condition with body mass and wing length. During higher capelin biomass years (2017, 2019), foraging effort of razorbills decreased with a higher proportion of capelin in the diet after they arrived inshore to spawn, but not in the year with lower capelin biomass (2020), which was also associated with lower adult and chick body condition. In Chapter 2, I explored how sympatrically breeding razorbills, Atlantic puffins (*Fratercula arctica*) and common murrelets (*Uria aalge*) respond to inter-annual (2017, 2018, 2019) variation in capelin biomass using blood stable isotope ratios ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ) to estimate isotopic niche, as a proxy of dietary niche. At the species-level, niche breadth generally contracted and trophic position shifted toward capelin during the year of higher capelin biomass (2018) relative to years of lower biomass (2017, 2019), indicating a higher reliance on capelin and lower diversity of prey in the diet when more capelin were available. At the assemblage-level, trophic diversity was lower and niche overlap was higher during high capelin availability years (2018) relative to low capelin availability years (2017), suggesting shifts in species interactions with variation in capelin

availability. Overall, these studies examining multi-species responses to variation in prey biomass in a multi-year context provide a better understanding of how species interactions may change and, thus, how species will tolerate future changes in ocean climate.

## Acknowledgements

First and foremost, I would like to thank my advisor, Gail Davoren. Words cannot express how thankful I am to be your student. Your support and encouragement through this entire process both in life and in school has been invaluable. You have been an incredible mentor and inspiration, and I am so glad to have had the chance to learn from you.

Next, I would like to thank my committee members, Kevin Fraser and Jillian Detwiler. Your advice and curiosity for my project have been nothing but encouraging. Even throughout this pandemic and not having the chance to meet in person, I appreciate all the support you have given me.

I would also like to thank the members of the Davoren Lab for your help and support through this process. You have all helped immeasurably and brought something special to this experience. Special thanks to Laura Bliss, Kelsey Johnson, Ed Jenkins, Ashley Tripp, Marissa Berard, Anna Mikhailitchenko, Mikala Epp, Leah Pengelly, Tommy Pontbriand, Megan Athayde, Matt Legard, and Gibson Rieger. To Julia Gulka, thank you for mentoring me in the ways of James Island, without your help none of this would have been possible. It has been incredible to learn from you, from your insight, your encouragement and much more! Amy Irvine, Scott Morrison, Emily Runnells and Mike Schrimpf, I couldn't have made it through this process, this pandemic, or through Canada without you. You all mean the world to me, and I can't wait to watch where life takes you.

To the crew and family of the Lady Easton III, thank you! Not only did you help immensely in the collection of these data, but you showed me a part of this world I would never have had the chance to see. You brought joy and the best love-cooked meals on those long boat rides and helped me to fall in love with Newfoundland more than I thought I ever could.

To all my mentors, supervisors and field friends I've come to know in my career, you've been such a light in this journey of life. Encouraging me to think in different ways and bringing joy and laughter through stressful times. There are far too many people to name but I am so happy and lucky that our paths in life have crossed.

Thank you to my family, especially my 'rents, Karen and Bernard Lescure, and my brothers Mathieu and Etienne, you have always encouraged and supported me and most importantly, inspired me to challenge myself in all my life and adventures. And lastly, to my best friend, my love, my life, Vance Bennett for always being there, for always laughing with me, for encouraging me and making it through some of the hardest parts of our lives so far. You are my light, my world, my ultimate joy.

This project was principally supported by Natural Sciences and Engineering Research Council Discovery Grants (2014-2018, 2019-2024; Davoren) and Ship Time Grants (2017, 2018, 2019, 2020; Davoren) and the University of Manitoba Graduate Fellowship (Lescure). Funding was also provided by University of Manitoba Field Work Support Grants in 2017, 2018, 2019 and 2020 (Davoren). Thank you to all the funding agencies for stipend and conference travel support (Roger Evans Memorial Scholarship, University of Manitoba Faculty of Science).

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## **Thesis Format**

This thesis is presented in manuscript format. Both chapters are independent, with their own introduction, methods, results, discussion, conclusions and references. They are accompanied by an overall general thesis introduction to provide background information, and a synthesis discussion including conclusions and future research. All data analysis and writing were performed by me with guidance from my advisor and committee.

## **Thesis Introduction**

An ecological niche is defined as an n-dimensional set of factors where axes represent different environmental abiotic and biotic factors under which organisms can grow, reproduce and survive (Hutchinson 1978). A species' niche can be influenced through competition with other species when they are competing for limited resources. Although two species cannot coexist if they occupy the same niche (i.e. competitive exclusion principle; Gause 1934), if species-specific niches are distinct enough (e.g., breeding habitat, prey types and size), two sympatric species can coexist (Schoener 1974). Niche partitioning occurs when individuals of different species partition one or more limited resources, whereby species occupy their realized rather than fundamental niche. This ultimately leads to the evolution of traits (e.g., physiological, morphological or behavioral) that further promotes niche partitioning (Schoener 1974, Tilman 1987).

Temporary, super-abundant food resources can lead to temporary release from competition among species as food is no longer in limited supply. Temporary abundance of a certain prey type may result in prey switching to this prey type, but the degree of prey switching may vary among species due to differences in morphological and physiological traits (Lack 1946). Indeed, competitive asymmetry occurs frequently, where species with a competitive advantage, due to these differences, are least affected by competitive interactions (Schoener 1983). Shifts in prey regimes, which may include variation in prey composition or abundance, also may be accompanied by changes in foraging behavior of predators (Randa et al. 2009). In marine systems, where predators rely heavily on forage fish (i.e. small- or medium-sized pelagic fish that are primary prey species for top predators; Alder et al. 2008, Pikitch et al. 2012), understanding how species interactions vary in response to changes in prey regimes in a multi-

year context can help to understand ecosystem-level impacts on marine forage fish which may be due to natural fluctuations, overfishing and climate change (Casaux et al. 2003, 2006, Frederiksen et al. 2007, Einoder 2009).

To examine changing species interactions under varying prey regimes, researchers often use measurements of niche metrics that characterize the variety of prey types in predator diets and the amount of overlap among species (Hutchinson 1978). Studies examining multi-species responses to changes in prey availability have provided insight into potential competitive interactions among marine predators (Chesson & Kuang 2008). For instance, a study examining three predator groups (i.e., gulls, shearwaters, whales) on the northeast Newfoundland coast found that when the availability of a key forage fish, capelin (*Mallotus villosus*), increased inshore, the dietary niche breadth of all groups narrowed, indicating reduced prey diversity in their diets, and dietary niche overlap among predators groups became higher (Gulka et al. 2017). Similarly, two similar murre species (common (*Uria aalge*) and thick-billed (*Uria lomvia*) murre), were found to have high dietary niche overlap during breeding periods when food availability was high but low overlap when food availability was low in Alaska (Barger & Kitaysky 2012). In contrast, Jenkins & Davoren (2020) found that three sympatric breeding seabird species on the northeast Newfoundland coast each experienced niche shifts towards capelin as capelin became more available, but the degree of dietary niche overlap did not vary among species between periods of lower and higher capelin availability. While these few studies have simultaneously examined responses of multiple predator species to varying prey availability, even fewer have investigated how interspecific interactions of seabirds change under varying prey availability in a multi-year context.

Colonial nesting seabirds are central-place foragers during the breeding season, whereby parents return to their nest to incubate eggs and provision chicks (Orians & Pearson 1979). Therefore, seabirds are restricted to forage within a limited range of the colony to adequately provision their offspring. The influence of varying prey availability within foraging ranges on seabird breeding parameters was explored theoretically to determine if these parameters could be used as indicators of marine food supply (Cairns 1987). Cairns (1987) predicted that as food availability became lower, time spent foraging would increase as parental birds spend more time locating and capturing prey at sea. Thus, colony attendance, chick growth, breeding success, adult body mass and ultimately adult survivorship would decrease as a result of this increased foraging effort. Life history theory predicts the optimization of individual survival and reproductive success, yet finite resources often lead to trade-offs where allocation of energy to survival leaves reduced energy available for reproduction (Roff 1992, Stearns 1992, 2000). As seabird species are long-lived, they have evolved the life history strategy where breeding birds will favor their own survival over investment in reproductive effort, abandoning a current year's reproductive effort when food is limited to maximize their lifetime reproductive success (Stearns 1992). Unfortunately, very few studies have tested Cairns' (1987) prediction for seabirds, as these studies often lack independent data on prey availability and limitation.

Studies on seabirds that have supported Cairns' (1987) predictions have found time spent foraging (foraging effort) is the most sensitive to changes in prey availability (Montevecchi et al. 2019, Gulka et al. 2020), while adult body condition and survivorship are the least sensitive (Pons & Migot 1995, Oro et al. 1999, Piatt et al. 2007). The relationship between prey availability and foraging effort, however, may vary between breeding stages and species (Harding et al. 2007). For example, chick-rearing common murrelets were more sensitive to

changes in prey availability than incubating birds due to increased energy demands of provisioning both themselves and their offspring (Harding et al. 2007). In addition, black-legged kittiwake (*Rissa tridactyla*) breeding success was more sensitive to prey variability than common murre potentially because murre are capable of reallocating time spent at the colony to time spent foraging (Piatt et al. 2007). As seabirds can adjust activity budgets during variable food availability to maintain breeding success (Burger & Piatt 1990), breeding success also has low sensitivity to changes in food availability. However, if prey availability drops below a threshold prey biomass breeding success may decline (Cury et al. 2011).

### *Stable Isotope Analysis*

The use of stable isotopes to examine animal diets has become highly popular especially due to the nondestructive sampling process. As seabirds forage in distant locations that are not easy to observe, we can use stable isotope ratios from different tissue types (e.g., plasma, red blood cells, feathers) that reflect the diet over varying temporal scales to reconstruct diet or examine isotopic niche metrics (Hobson & Clark 1992a, Phillips & Eldridge 2006). Indeed, the temporal scale of the diet depends on the isotopic turnover rate of each tissue, therefore, it is key to consider this when interpreting what period the estimated diet represents and when to sample. Delta ( $\delta$ ) notation is used to report the relative difference of isotopic ratios to element-specific international reference materials and expressed as parts per thousand (‰) to facilitate interpretation of  $\delta$  values. Carbon and nitrogen are the elements most often studied because their isotopic ratios of prey are assimilated into the protein of predators in a predictable way. Consumer tissues are enriched in  $^{15}\text{N}$  compared to their prey allowing for inferences of trophic positions of the consumer to be estimated (Vanderklift & Ponsard 2003). Alternately,  $^{13}\text{C}$  values

are not modified to a great degree from prey to predator but are enriched in benthic dwelling organisms, allowing for foraging locations (i.e., inshore or offshore, benthic or pelagic) to be estimated (Hobson et al. 1994). Prior to using  $\delta$  values to reconstruct diet, however, there are a number of important factors to consider during tissue preparation and data analysis for appropriate interpretations of  $\delta$  values.

First, a source of bias in interpreting diet from  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  values includes the lipid content of the tissue sampled, as lipids are depleted in  $^{13}\text{C}$  compared to proteins due to fractionation during lipid synthesis (DeNiro & Epstein 1977). A C:N > 3.5 indicates a tissue with a high lipid content and may cause variation in  $\delta^{13}\text{C}$  values unrelated to diet and, thus, it is recommended to remove lipids through chemical extraction (Post et al. 2007). As lipid extraction may influence  $\delta^{15}\text{N}$  values in some cases, mathematical equations may be preferred for lipid-normalization (Post et al. 2007). Second, when a consumer ingests prey, isotope ratios in prey tissues are altered during the incorporation into consumer tissues. This alteration means that  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  values of prey and consumers cannot be compared directly and a correction factor, also known as a discrimination factor, is required (Inger & Bearhop 2008). The variation in incorporation of isotopes into different tissues (i.e. isotopic routing) are species- and tissue-specific and, thus, discrimination factors are unique to the combination of tissue, consumer and prey (Bond & Jones 2009). During diet reconstruction,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values from consumers and prey are incorporated into mixing models with appropriate discrimination factors to estimate the proportions of each prey type in predator diets (Stock et al. 2018). Discrimination factors can be determined through experiments where study species are kept on a constant diet until the length of time required for complete turnover of the tissue of interest is complete (Hobson & Clark 1992a). Owing to the requirement for captive studies, few discrimination factors exist and, thus,

discrimination factors that are of the same tissue type and similar species are used (Hobson & Clark 1992b, Bearhop et al. 2002, Becker et al. 2009). Third, as prey isotopic ratios may change among seasons and years, it is important to collect prey from the year or season that overlaps with consumer tissue sampling to accurately reconstruct diet (Quay et al. 2003, Bond & Jones 2009).

Metrics are often used to describe the isotopic niches of one or multiple predators. Metrics that have become standard in the literature include isotopic niche breadth, niche overlap, trophic diversity and redundancy, and are typically visualized on biplots of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Layman et al. 2007, Sargeant 2007, Inger & Bearhop 2008, Jenkins & Davoren 2020). Isotopic niche breadth is typically represented by the standard ellipse area (SEA), defined as the standard deviation around the bivariate mean, which is used as a proxy of the diversity of prey types consumed. Isotopic niche overlap measures the amount of overlap in the SEA of two groups, indicating how similar the diversity of prey types consumed is between groups (Sargeant 2007). Trophic diversity and redundancy reflect the relative positions of groups to each other, and the amount of niche space occupied at the assemblage-level (i.e. all groups combined). Trophic diversity is determined through four metrics:  $\delta^{15}\text{N}$  range (NR),  $\delta^{13}\text{C}$  range (CR), total area (TA) and mean distance to centroid (CD; Layman et al. 2007). TA is the polygon encompassing all individuals across two or more groups in the biplot, representing the total amount of niche space occupied by all groups combined. CD is the average distance of the centroid of each group's SEA to the assemblage-level mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values. The extent of trophic redundancy is calculated through two metrics, including the mean nearest neighbor distance (NND) and standard deviation of nearest neighbor distance (SDNND), both of which reflect the relative position of groups to each other. NND is the average distance a group is to its nearest neighbor

and SDNND is the standard deviation of NND which is less influenced by sample size. Due to the natural variability in their values, some metrics, including reconstructed dietary proportions and SEA, are calculated within a Bayesian statistical framework, whereby these metrics are calculated thousands of times to create a posterior distribution of possible estimates from which the most likely value of these metrics, often the mode, is determined (Jackson et al. 2011, Stock et al. 2018).

### *Study System*

In the Northwest Atlantic, capelin are the primary forage fish species consumed by most predator species (Pikitch et al. 2012, Buren et al. 2014). Capelin migrate in high abundance from offshore into coastal regions of Newfoundland to spawn during the summer. The arrival of spawning capelin inshore transforms the coastal prey base into a super-abundant, capelin-dominated prey state from a lower abundance, prey state for marine predators, dominated by other forage fish species (e.g. sandlance, *Ammodytes spp.*; Davoren et al. 2012). In coastal Newfoundland, seabirds are known to shift their diet in relation to availability of capelin. For example, chick-rearing common murre were found to switch from capelin to large mature sandlance during years of low capelin availability and increased time spent foraging to reduce impacts to reproductive success (Burger & Piatt 1990). In addition, breeding Atlantic puffins (*Fratercula arctica*) in Labrador also switched from capelin to post-larval sandlance and other small fish when capelin availability decreased due to a southward distributional shift (Baillie & Jones 2004). In a study of sympatrically breeding razorbills (*Alca torda*) and common murre, Gulka et al. (2019) found dietary shifts in razorbills and common murre from sandlance to primarily capelin after capelin arrived inshore to spawn within foraging ranges.

In Notre Dame Bay (Fig. 1), along the northeast coast of Newfoundland, three species of the Family Alcidae (alcids) breed sympatrically: the common murre, razorbill and Atlantic puffin. Coexistence of similar seabird species is thought to be due, in part, to differences in foraging behavior due to differences in body size allowing species access to different prey (Cody 1973, Croxall & Prince 1980). For instance, common murre are the largest of the species (800-1125 g, Ainley et al. 2002) and dive the deepest (180 m, Piatt & Nettleship 1985), with Atlantic puffins being the smallest (404-538 g, Lowther et al. 2002) and diving the shallowest (60-70 m, Burger & Simpson 1986) and razorbills being relatively intermediate in size (570-880 g, Lavers et al. 2009) and dive depth (120 m, Piatt & Nettleship 1985). The chick-rearing period in coastal Newfoundland of these sympatric species coincides with the inshore movements of spawning capelin (Davoren & Montevecchi 2003). Changes in sea ice dynamics and ocean temperature, however, have resulted in this phenology becoming highly variable (Davoren et al. 2012, Buren et al. 2014, Crook et al. 2017). Variation in the timing of capelin spawning, which coincides with peak capelin biomass in coastal regions, may lead to a phenological mismatch with the seabird chick-rearing period. This is a particularly energetically demanding period of the seabird annual cycle, where breeding adults must provision their offspring and themselves (Gaston 1985, Wood et al. 2000, Benvenuti et al. 2002). The high body mass to wing area ratio (i.e. 'wing loading') of alcids, allows for efficient diving, but much higher energetics costs of flying relative to other bird species (Elliott et al. 2013). Therefore, changes in prey availability that increase time spent flying during chick-rearing can have a major influence on foraging effort and breeding success (Cairns 1987, Chivers et al. 2012). Currently, little is known about how seabirds respond to changes in prey availability through changes in diet and foraging effort in a multi-year and multi-

species context. This information is critical to understand how these marine predators will tolerate future changes in ocean climate.

## **Thesis Objectives**

The goal of this thesis was to investigate the responses of multiple alcid species to changes in intra- and inter-annual prey biomass. For Chapter 1, the primary objective was to examine the influence of varying capelin availability within and among years on razorbill diet, foraging effort, and chick and adult body condition. I hypothesized that at the inter-annual scale, diet, foraging effort and chick and adult body condition will be influenced by the timing of spawning and capelin biomass. Across the three years of this study (2017, 2019, 2020), I predicted that during years of low capelin availability, razorbill diet will be comprised of lower percentages of capelin, which will also be associated with higher foraging effort and lower chick and adult body condition. I also hypothesized that at the intra-annual scale, foraging effort of razorbills will be influenced by the inshore arrival of spawning capelin. I predicted that with the arrival of spawning capelin, foraging effort will decrease indicated by decreased distance and duration of foraging trips and time spent diving. While few studies have looked at how prey availability impacts diet and foraging effort in seabirds (e.g., Piatt et al. 2007, Harding et al. 2007, Montevecchi et al. 2019, Gulka et al. 2020), only one has examined how prey biomass affects chick-rearing razorbills during a one year study (Gulka et al. 2019).

For Chapter 2, the primary objective was to examine how isotopic niche metrics of three chick-rearing seabird species (common murre, Atlantic puffin and razorbills) respond to inter-annual changes in capelin biomass across three years (2017-2019). I hypothesized that the isotopic niche metrics of all species would be influenced by inter-annual changes in capelin

availability. At the species-level, I predicted that trophic position would shift toward capelin and isotopic niche breadth would contract in years with higher capelin availability, indicating a dietary convergence on capelin in all species. At the seabird assemblage-level, I predicted that trophic diversity would decrease and niche overlap of all three species would increase in years with higher capelin availability, as all species increase reliance on capelin.

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## Tables and Figures

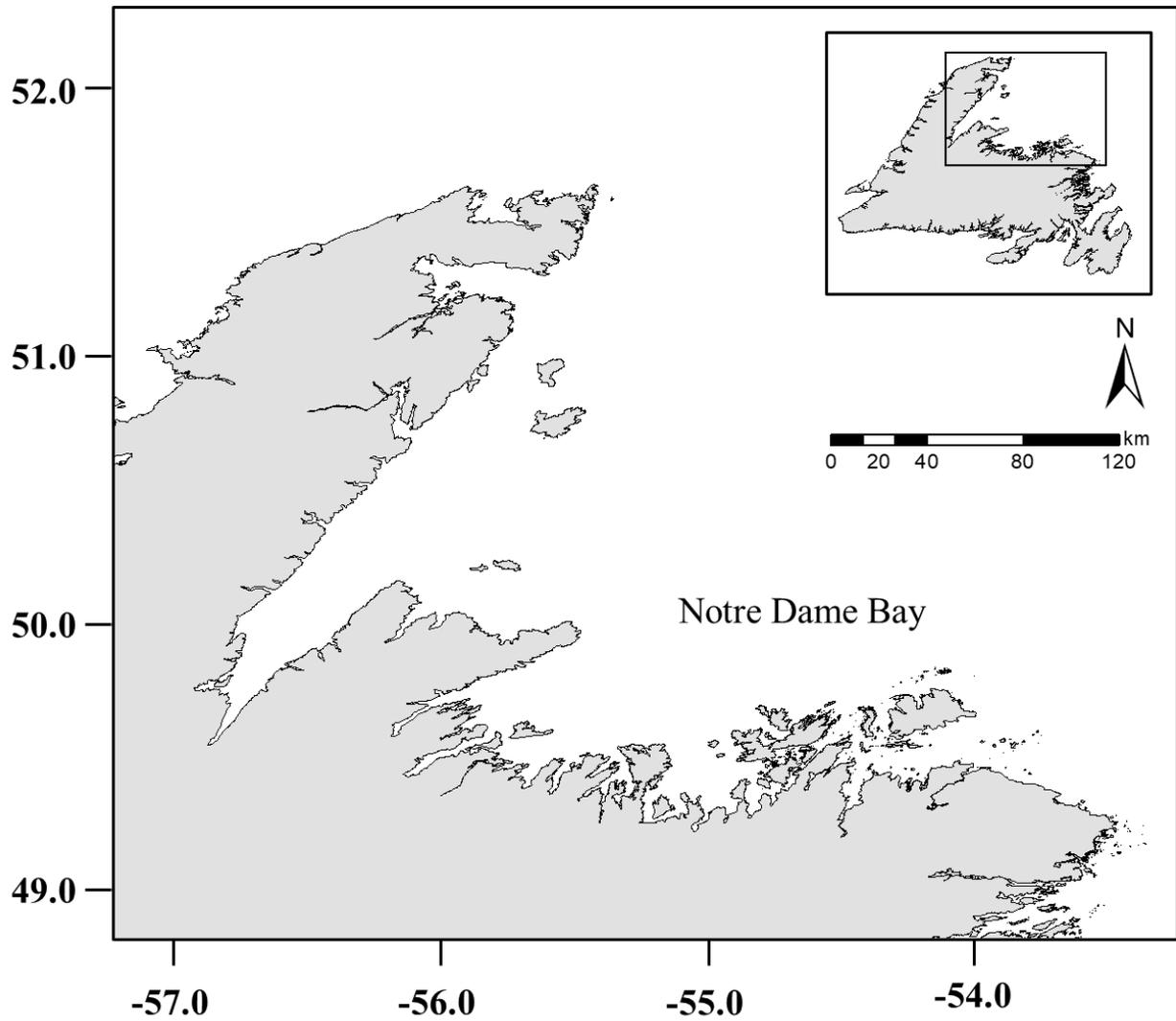


Figure 1. Map of Newfoundland, Canada highlighting the study area in Notre Dame Bay on the northeast coast of Newfoundland.

## **Chapter One. Increased foraging effort of chick-rearing razorbills and decreased chick condition in coastal Newfoundland during reduced prey biomass**

### **Abstract**

Variation in foraging behavior due to changes in prey regimes may lead to changes in diet, foraging behavior and breeding success. We investigated how chick-rearing razorbills (*Alca torda*) respond to inter- and intra-annual variation in capelin (*Mallotus villosus*) biomass in coastal Newfoundland across three years (2017, 2019, 2020). To do this, we combined colony-based measures of body mass and wing length to estimate body condition, blood stable isotope ratios ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ) to estimate dietary proportions, and device-based foraging and dive metrics from GPS and TDR loggers to estimate foraging effort. During 2017 and 2019, when peak capelin biomass (2017: 0.109 g/m<sup>2</sup>; 2019: 0.098 g/m<sup>2</sup>) was near the long-term (2009-2020) average for the study area, foraging effort decreased after capelin arrival and was lower relative to 2020, as indicated by lower foraging trip duration (2017: 4.5 ± 1.0 h; 2019: 5.0 ± 0.6 h) and distance (2017: 12.8 ± 2.8 km; 2019: 14.3 ± 1.7 km) and number of dives (2017: 48.4 ± 11.8). In contrast, during 2020, when peak capelin biomass was the lowest on record (0.002 g/m<sup>2</sup>), foraging trip duration (21.5 ± 3.8 h) and distance (150.4 ± 25.2 km) and number of dives (385.8 ± 67.4) was much higher and did not decrease after capelin spawning. This increased foraging effort during 2020 was also associated with lower chick and adult body condition, which may have been related to birds flying farther to capture capelin. These findings suggest that continued variability in capelin biomass and timing of spawning can lead to increased energy expenditure and reduced adult and chick body condition, which may have long-term population-level consequences for razorbills and other seabirds in this region.

## **Introduction**

Life history theory predicts the optimization of individual survival and reproductive success, yet because resources are finite, these traits can be influenced by ecological challenges from the environment (Roff 1992, Stearns 1992, 2000). Finite resources can lead to trade-offs where allocation of energy to survival leaves reduced energy available for reproduction (Roff 1992, Stearns 1992). Seabirds have evolved the life history strategy whereby breeding birds favor their own survival over investment in reproductive effort in any given year, thereby abandoning a current year's reproductive effort when food is limited to maximize their lifetime reproductive success (Stearns 1992). These long-lived, marine predators nest colonially and are central-place foragers, whereby breeding birds consistently return to the nest to provision and care for their young (Orians & Pearson 1979). Therefore, seabirds are restricted to forage within a limited range of the colony to adequately provision their offspring.

Changes in prey availability within foraging ranges have been used to explore seabird breeding parameters as indicators of marine food supply (Cairns 1987). Under progressively lower food availability within foraging ranges, Cairns (1987) predicted that time spent foraging would increase initially, followed by reductions in colony attendance, chick growth, breeding success, adult body mass and ultimately adult survivorship, aligning with the hypothesis that food limitation controls seabird population dynamics (Lack 1966). Studies have supported these predictions in seabirds, showing increased time spent foraging (Piatt et al. 2007, Montevecchi et al. 2019, Gulka et al. 2020) and lower breeding success (Croxall et al. 1999, Cury et al. 2011) during lower prey availability. However, the relationship between prey availability and foraging effort has been shown to vary among seabird species under the same prey availability (Harding et al. 2007). In particular, species of the family Alcidae have a high body mass to wing area ratio

(i.e. ‘wing loading’), which allows these birds to be efficient divers but increases the cost of flight compared with other seabird species (Elliott et al. 2013). Therefore, lower prey availability nearby the colony that results in increased time spent flying and foraging will likely affect alcids to a greater extent than other seabirds, possibly also having a greater impact on chick growth and breeding success (Cairns 1987, Chivers et al. 2012).

In the Northwest Atlantic, capelin (*Mallotus villosus*) are the primary forage fish species consumed by most marine predator species (Buren et al. 2019). Capelin migrate in high abundance from offshore into coastal regions of Newfoundland to spawn during the summer. The arrival of spawning capelin inshore more than doubles the coastal prey base and transforms it into an abundant, capelin-dominated state from a lower abundance prey state, dominated by other forage fish species (e.g. sandlance, *Ammodytes* spp.; Davoren et al. 2012). Although chick-rearing in Newfoundland coincides with the inshore movements of spawning capelin (Davoren & Montevecchi 2003b), changes in sea ice dynamics and ocean temperature have resulted in high variability in this phenology since the early 1990s (Davoren et al. 2012, Buren et al. 2014, Crook et al. 2017) and changes in peak capelin biomass within seabird foraging ranges (Carvalho & Davoren 2019, Gulka & Davoren 2019, Berard & Davoren 2020). Variation in the timing of capelin spawning, which typically coincides with peak capelin biomass in coastal regions, may lead to a phenological mismatch with seabird chick-rearing, which in turn may have conservation implications for seabirds in coastal Newfoundland. Seabirds in this region are known to shift their diet in relation to capelin availability (Gulka et al. 2017, 2019, 2020, Carvalho & Davoren 2019, Jenkins & Davoren 2020) and changes in the timing of capelin arrival are known to impact foraging effort and breeding success. For example, when capelin spawned later and were in lower abundance, foraging effort of common murrelets (*Uria aalge*) increased and breeding

success was lower (Burke & Montevecchi 2009, Regular et al. 2014). Foraging effort of chick-rearing common murre and razorbills (*Alca torda*) also was higher under lower relative to higher capelin availability within years (Gulka et al. 2019) and among years for common murre (Gulka & Davoren 2019). In addition, black-legged kittiwakes (*Rissa tridactyla*) experienced lower reproductive success when spawning capelin arrived later into foraging ranges (Regehr & Montevecchi 1997), while *Larus* gulls also experienced reduced reproductive success and switched to seabird eggs, chicks and adults as alternative food sources (Regehr & Montevecchi 1997, Stenhouse & Montevecchi 1999, Massaro et al. 2000). Despite these studies, little is known about the influence of capelin availability on foraging effort of razorbills across years in coastal Newfoundland, and the subsequent impact of higher foraging effort on chick growth and breeding success.

Our goal was to examine the effect of varying capelin availability on razorbill diet, foraging effort (e.g., foraging trip duration and distance) and chick/adult body condition. We hypothesized that diet, foraging effort and chick/adult body condition will be influenced by inter-annual variation in the timing of spawning and capelin biomass. Across the three years of this study (2017, 2019, 2020), we predicted that razorbill diet will be comprised of lower percentages of capelin in years of lower capelin biomass, which will be associated with higher foraging effort and lower chick/adult body condition, but that the degree of these responses will depend on the reduction in capelin biomass from the long-term average (2009-2020). We also hypothesized that foraging effort of razorbills will be influenced by the inshore arrival of spawning capelin within years (intra-annual). We predicted that with the arrival of spawning capelin into the study area, foraging effort will decrease, as indicated by decreased distance and duration of foraging trips and decreased time spent diving.

## Methods

### *Prey Data*

To quantify capelin availability in the area, a ship-based hydroacoustic survey (~15 km; Fig. 1) over a cluster of annually persistent capelin spawning sites in deep water (15-40 m; Davoren et al. 2012) was conducted weekly during July – August, 2017, 2019 and 2020 (Fig. 1). Similar surveys have been conducted in the study area since 2009 providing a 10 year dataset for inter-annual comparisons (Davoren unpubl. data). Capelin biomass was quantified in the water column using a scientific echosounding system (Biosonics DTX 6000; BioSonics Inc., Seattle Washington), whereby a 70 kHz split-beam transducer was towed at a depth of 1 m off the starboard side of a 13.4 m commercial fishing vessel (see detailed methods in Davoren et al. 2006). Hydroacoustic files were edited in Echoview software (Version 4, SonarData, Myriax Software Pty. Ltd., Hobart, Tasmania) to delete the seafloor along with acoustic signals that were indistinguishable from the seafloor. The area backscattering coefficient ( $s_a$ ,  $m^2m^{-2}$ ) was quantified in each 100 m survey segment using a minimum threshold of -80 dB, which was then converted into capelin biomass ( $g m^{-2}$ ) by combining capelin biometrics (i.e., length, mass) from fish collected in or nearby the survey area each year and a target strength-length relationship for capelin (Rose 1998). Due to technical difficulties, surveys conducted in 2020 with increased backscatter not attributed to prey biomass were analyzed with background noise removed based on methods in De Robertis & Higginbottom (2007). Capelin biomass across all 100 m segments in each survey were averaged to quantify the mean capelin biomass per survey. We also regularly monitored known beach (every 2 d) and deep-water (every 3-6 d) capelin spawning sites to determine the first date of capelin spawning (i.e. presence of capelin eggs adhered to sediment; Fig. 1), following methods in Crook et al. (2017). The first date of capelin spawning

within years was used to define two prey periods: before spawning capelin arrival into the study area (i.e. low prey availability) or after spawning capelin arrival (i.e. high prey availability).

### *Foraging Behavior*

To quantify foraging effort, we deployed GPS tracking devices (2017: n = 8, *Ecotone*® URIA-300 with wet/dry sensor; 2019/2020: n = 30/36, *CatLog*® Gen 2) and Time-Depth Recorders (TDRs; 2020: n = 36, *Lotek*® LAT 1800; Table 1) on chick-rearing razorbills on James Island (Fig. 1) before and after the inshore arrival of capelin in all years. Razorbills were captured by hand in rock crevices at night to reduce disturbance within the colony. During 2017, *Ecotone* loggers were attached to the back for long-term deployments (3 weeks) with subdermal sutures (see Gulka et al. 2019 for details), whereas *CatLog* GPS loggers were attached to feathers on the back using Tesa tape during 2019 and 2020 for short-term deployments (1-2 days). All tracking devices were programmed to record latitude and longitude every 10 min. The wet/dry sensor of *Ecotone* tags recorded dive duration when submerged in water. A base station was set up within 30 m of nest sites of tagged birds for remote download of data with UHF equipped tracking devices. During 2019 and 2020, *CatLog* GPS tags were waterproofed prior to deployment by coating connectors with peel-off protective paint and then encapsulated in waterproof shrink wrap. In 2020, TDRs attached to plastic bands using cable ties were deployed on the leg and were programmed to record temperature and depth every 6 s. Prior to deployment, the time on all GPS and TDR devices were synchronized to ensure alignment of tracking and dive data upon retrieval. All devices and device combinations were < 20 g, which is 3.3% of the body weight of the lightest razorbill (range: 600-830 g). Adults were banded using standard metal bands issued by Environment and Climate Change Canada to ensure individuals were only

tagged once during the study (before or after inshore capelin arrival). Upon tag retrieval in 2019/2020 and tag deployment in 2017, a drop of blood was collected from razorbills and applied to an FTA card for genetic sexing (Fast Technology for Analysis of nucleic acids; Fridolfsson & Ellegren 1999).

### *Data Analysis of Tag Data*

GPS data were analyzed in ArcGIS (version: 10.3.1.4959) and R (version 3.6.1 R Core Team 2019). Spatial data (i.e. GPS locations) were projected in the Lambert Azimuthal Equal Area centered around James Island. A foraging trip was defined as a bird departing and returning to the colony, which was determined by creating a 250 m “splashdown” buffer around the island in ArcGIS, as alcids are known to land on the water near the colony after leaving and before returning to nest sites on the island (Burger 1997). For each foraging trip in all three years (2017, 2019, 2020), we calculated maximum distance from nest (km), total trip length (km) and duration (h) using R. In addition, we calculated the number of foraging trips conducted per hour of deployment for each individual. For each prey period within each year, kernel density estimations were used to identify total foraging and core habitat area using 95% and 50% contours, respectively, from both individual foraging trips (used as a response variable) and all individuals together (for mapping) using the package *adehabitatHR* in R (Calenge 2006). For kernel density estimations, all locations were used because dive data were not collected during 2019. The cell size was set to 80 and the smoothing factor (h) *href* was used, which was similar to an h of 3000 m. Using ArcGIS, land area was removed from kernel densities when land and kernel densities overlapped, and total area of 50% and 95% contours was calculated. Foraging

trips with less than five GPS points were excluded from analysis due to issues with calculating kernel densities using 95% or 50% of points to calculate contours.

Within each foraging trip in 2017 and 2020, dive characteristics were quantified, including the number of dives, number of dive bouts, maximum and mean dive depth (m; in 2020 only) and mean dive duration (s). Dive characteristics were quantified using *diveMove* in R (Luque 2007) from the TDR data in 2020, while similar characteristics were quantified using R from the wet/dry sensor data in 2017. In 2020, dives < 1.5 m were not included in analysis and dives  $\leq 6$  s were excluded in both years as they are not typically associated with foraging activities (Linnebjerg et al. 2013). A dive bout was defined as a series of dives, followed by a longer surface pause, which was quantified using a maximum likelihood approach (Luque & Guinet 2007). Bout ending criteria (BEC: 70.3 s) was calculated across both 2017 and 2020 using *diveMove* in R to define dive bouts (Luque 2007, Luque & Guinet 2007).

We used general linear mixed models to examine differences in response variables (i.e., dive and foraging trip characteristics) for all except count data (i.e., number of dives, number of dive bouts and dives per bout), which we used a generalized linear mixed model with a poisson distribution and log link to examine the differences between prey periods (i.e. before/after capelin arrival) within years and after inshore capelin arrival among years (2017, 2019, 2020) using the *lme4* package in R (Bates et al. 2015). Assumptions of linear models were tested with Shapiro-Wilk's normality test, Q-Q Plots and Levene's test for homogenous variance and all foraging trip characteristics and dive characteristics were log transformed to meet assumptions. Fixed predictor variables included sex (male/female), prey period (before/after capelin arrival), year, and interactions between prey period and year. Individual ID was included as a random effect as there were often multiple foraging trips per tracked individual (i.e. repeated measures

on an individual). Additionally, a time-of-day category (i.e., daylight, daylight-dark) was included as a random effect to account for variation in foraging trip duration, as overnight trips included long periods when foraging activity was low due to low-light conditions (Gulka et al. 2019). Significance of variables across years were examined using estimated marginal means with the *emmeans* package in R (Lenth et al. 2021).

Finally, as foraging trip and dive characteristics were highly correlated and therefore not independent of each other, we input all foraging trip and dive characteristics into a Principal Components Analysis (PCA) using JMP Pro (Version 15.2, SAS Institute Inc.). This allowed us to derive fewer variables that represented foraging effort but still retained the majority of the variation in the dataset. Eigenvectors were orthogonally rotated (varimax) to increase correlations of response variables with principal components (i.e. newly derived variables) to aid interpretation (Quinn & Keough 2002). As 2019 did not have diving data and 2017 did not have depth data, these values were estimated using multivariate normal estimation. The newly derived variables (principal components) were then used as response variables, while the predictor variables were the same as the previous models and significance was estimated using marginal means.

### *Body Condition*

For adult body condition, non-tagged, chick-rearing razorbills (2017 n = 16; 2019 n = 20; 2020 n = 16) were captured to record body mass (g) and wing chord length (mm), and blood samples were collected for stable isotope analysis (see below). For chick body condition, body mass (g) and wing chord length (mm) was recorded from chicks during adult sampling in 2017 (n = 12) and from chicks of tracked individuals prior to tag deployment in 2019 (n = 24) and

2020 (n = 34). To examine inter-annual trends in body condition of adults and chicks, we calculated the residuals of body mass regressed against wing chord of all individuals from the three years following Ronconi et al. (2010) using only one morphometric; negative values indicate lower condition and positive values higher condition. Assumptions of a linear model were tested and met with Shapiro-Wilk's normality test, Q-Q plots and Levene's test for homogenous variance. The residuals were compared across years using an ANOVA and significance of variables was examined using Tukey HSD.

### *Stable Isotope Analysis*

Each year, razorbill adults captured to measure body condition (2017 n = 16; 2019 n = 20; 2020 n = 16) were also blood sampled for stable isotope analysis. Approximately 1.5 mL of blood was collected from the tarsus vein using a 25-gauge needle and syringe and stored in EDTA tubes to prevent coagulation. Whole blood samples were placed on ice for < 8 h and later centrifuged to separate into plasma and red blood cells and stored at -20°C. In this study, stable isotope analysis was conducted on red blood cells only for comparison among years, which represents the averaged diet over 2-3 weeks based on tissue turnover rates (Hobson & Clark 1993, Bearhop et al. 2002).

For accurate dietary reconstruction using stable isotope ratios, potential prey types in razorbill diets were identified and sampled in multiple ways across years. During 2017, approximate proportions of prey types were identified using motion-triggered camera traps set up near nest sites on James Island to capture images of parental prey deliveries to razorbill chicks (see details in Gulka et al. 2019). During 2019 and 2020, 2-hour observational stints to record parental prey deliveries were conducted near razorbill nest sites on James Island by two

observers in different locations both before (2019: n=2 stints; 2020: n=4 stints) and after (2019: n=4 stints; 2020: n=2 stints) capelin arrival into the study area. Potential prey were identified as capelin, sandlance and other fish which included larval sandlance, juvenile Atlantic cod (*Gadus morhua*) and an unidentified fish. In all years, capelin were collected during spawning at beaches and from commercial fishers, while sandlance was sampled using sediment grabs during other research. Other fish were only collected during 2017 (Gulka et al. 2019). All prey samples were frozen, and a skinless muscle sample (1-2 g) was later collected from the dorsal surface of the fish once thawed.

For stable isotope analysis, red blood cell and fish muscles samples were freeze dried for approximately 48 h, after which they were homogenized. Due to high lipid content (C:N ratios > 3.5), fish muscle was lipid extracted (Post et al. 2007) using a Soxhlet apparatus with petroleum ether for approximately 8 h (Elliott et al. 2017). Samples were then re-dried for 48 h and re-homogenized. Red blood cells and fish muscle samples were weighed (0.4-0.6 mg) into tin capsules. Stable isotope ratios of carbon and nitrogen were quantified using a continuous-flow isotope ratio mass-spectrometer (University of Windsor, Ontario, Canada). Duplicate and triplicate samples were run on every 13<sup>th</sup> sample along with five in-house standards to estimate data precision and accuracy, respectively. Isotopic ratios are expressed in ( $\delta$ ) notation as parts per thousand (‰) relative to the standards of Vienna Pee Dee Belemnite ( $\delta^{13}\text{C}$ ) or atmospheric nitrogen ( $\delta^{15}\text{N}$ ) according to the equation:  $\delta\text{X} = [(R_{\text{Sample}}/R_{\text{Standard}}) - 1]$ , where  $\text{X} = {}^{13}\text{C}$  or  ${}^{15}\text{N}$ , and  $R_{\text{Sample}} = {}^{13}\text{C}/{}^{12}\text{C}$  or  ${}^{15}\text{N}/{}^{14}\text{N}$  (Becker et al. 2009). As common murre and razorbills are closely related, discrimination factors for red blood cells from a captive study on common murre (Jenkins & Davoren 2020) were applied to  $\delta^{15}\text{N}$  ( $2.91 \pm 0.18\text{‰}$ ) and  $\delta^{13}\text{C}$  values ( $1.09 \pm 0.23\text{‰}$ ) to account for variation in the assimilation of prey into consumer tissues.

Prior to statistical analyses, assumptions of multivariate normality and homogenous variance were tested and met for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values with Q-Q plots, Shapiro-wilk multivariate normality tests and Levene's test for homogenous variance. To examine differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  among years for razorbills, capelin and sandlance, we used a multivariate analysis of variance (MANOVA). In addition, we used an ANOVA to examine differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  separately among years for each species. Significant differences were assessed using Tukey HSD tests.

We reconstructed dietary proportions by year from  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values using the package *MixSIAR* in R to further examine population-level changes in the diet of razorbills across years (Stock & Semmens 2016). Potential prey used in mixing models were determined through diet observations and photographs from camera traps and included capelin and sandlance (Table 2). Bayesian mixing-models were run using three Monte Carlo Markov chains with 100,000 iterations, 50,000 burn-ins and a thinning rate of 50. From posterior distributions, the mode was used as the most likely proportion of each prey species consumed. Models were run using uninformed and informed priors (using proportions from diet observations, Table 2) and diagnostic tests (Gelman-Rubin, Geweke) were run to examine chain convergence as a metric of model performance. The results from uninformed models are presented as diagnostic tests suggested informed model chains did not converge.

## **Results**

### *Capelin Biomass*

Hydroacoustic surveys were conducted throughout July and August during 2017 (14, 21 July; 4, 9, 15 August), 2019 (12, 17, 22, 30 July; 7, 14 August) and 2020 (16, 21, 31 July, 5, 12, 17 August). During 2017, capelin spawned on August 4 with peak biomass occurring on August

15 (0.109 g/m<sup>2</sup>). Similar peak capelin biomass was observed during 2019 (0.098 g/m<sup>2</sup>) but was earlier (August 7) as was capelin spawning (July 22). In 2020, capelin spawned on July 29, with peak biomass occurring on July 22 (0.002 g/m<sup>2</sup>). Overall, peak capelin biomass was lower and peaked earlier in 2020 relative to 2017 and 2019, with the date of capelin spawning (i.e. high prey period) occurring earlier in 2019 and 2020 relative to 2017.

Peak capelin biomass was lower in all three study years than the long-term average (2009-2020: 0.137 ± 0.03 g/m<sup>2</sup>) in the study area (Davoren unpubl. data). Although 2017 and 2019 were closer to this long-term average, peak biomass in 2020 was the lowest in the time series. In 2017 and 2019, the date of peak biomass was later than the long-term average (July 23) and occurred earlier during chick-rearing in 2020.

### *Diet*

Two-factor MANOVA of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  revealed significant differences among years for razorbills ( $F_{2,49} = 9.25$ ,  $p < 0.001$ ), capelin ( $F_{2,31} = 5.09$ ,  $p = 0.001$ ) and sandlance ( $F_{2,25} = 3.24$ ,  $p = 0.019$ ). ANOVAs on  $\delta^{13}\text{C}$  showed significant differences in mean  $\delta^{13}\text{C}$  among years for razorbills ( $F_{2,49} = 29.49$ ,  $p < 0.001$ ) and capelin ( $F_{2,31} = 3.61$ ,  $p = 0.039$ ), but not sandlance ( $F_{2,25} = 0.21$ ,  $p = 0.809$ ). *Post-hoc* tests revealed that mean  $\delta^{13}\text{C}$  of razorbills in 2020 was significantly lower than 2017 and 2019 but did not differ between 2017 and 2019 (Table 3; Fig. 2). Mean  $\delta^{13}\text{C}$  of capelin was significantly higher in 2017 relative to 2020, but 2019 did not differ from 2017 and 2020 (Table 3; Fig. 2). Mean  $\delta^{15}\text{N}$  was significantly different among years for capelin ( $F_{2,31} = 6.82$ ,  $p = 0.004$ ) and sandlance ( $F_{2,25} = 5.74$ ,  $p = 0.009$ ), but not razorbills ( $F_{2,49} = 0.05$ ,  $p = 0.954$ ). *Post hoc* tests revealed that mean  $\delta^{15}\text{N}$  of capelin in 2019 was significantly higher than in 2017 and 2020, but 2017 and 2020 did not differ (Table 3; Fig. 2). Mean  $\delta^{15}\text{N}$  of sandlance in

2017 was significantly lower than 2019 and 2020, but 2019 and 2020 did not differ (Table 3; Fig. 2).

In 2017 and 2019, capelin was the primary prey type observed in parental prey deliveries to chicks after capelin arrived in the study area, while sandlance dominated prior to inshore capelin arrival (Table 2). In contrast, sandlance was the primary prey type in parental prey deliveries both before and after capelin arrival during 2020 (Table 2). Uninformed MixSIAR models in each year revealed that capelin comprised the majority of adult diet in 2017 (mode: 50.8%, range: 40.6-60.9%) and 2020 (mode: 63.9%, range: 51.3-76.2%), but not in 2019 (mode: 33.9%, range: 24.0-43.6%; Fig. 2).

#### *Foraging Trip and Dive Characteristics*

During 2017, we tracked 4 individuals across a total of 39 foraging trips (44% before capelin arrival; 56% after capelin arrival; Tables 1, 4), with only one individual tracked after capelin arrival, indicating a need for cautious consideration of comparisons of foraging effort among years after capelin arrival. During 2019 and 2020, we tracked 15 and 19 individuals respectively, across a total of 63 foraging trips in 2019 (16% before; 84% after) and 37 foraging trips in 2020 (51% before; 49% after; Tables 1, 4). One individual was tracked both in 2019 and 2020. For all foraging trip and dive characteristics, there were no significant differences between sexes ( $p$ -values: 0.064-0.984; Table 4), but sex was included in all models to account for sex-based variation. Due to unbalanced design (i.e. no females tagged after capelin arrival during 2017), all *post-hoc* tests were run without sex.

Maximum distance traveled (km), total distance traveled (km), foraging trip duration (h) and both the 50% and 95% KD (km<sup>2</sup>) differed significantly among years and between prey

periods within years (Table 4; Fig. 3). All foraging trip characteristics, except for foraging trip duration, had a significant interaction between prey period and year (Table 4). *Post-hoc* results showed that all foraging trip characteristics (except foraging trip duration) were significantly lower after capelin arrival relative to before in 2017 (p-values: <0.001-0.016) and 2019 (p-values: 0.003-0.011), but not in 2020 (p-values: 0.994-0.999; Table 4). In addition, after capelin arrival, all foraging trip characteristics in 2020 were significantly higher relative to the same period during 2017 (p-values: <0.001-0.004) and 2019 (p-values: <0.001; Table 4) but did not differ between 2017 and 2019 (p-values: 0.831-0.999; Table 4). Foraging trip duration followed similar trends, being significantly lower after capelin arrival relative to before in 2017 (p = 0.014) but not in 2019 (p = 0.241) or 2020 (p = 0.999; Table 4). After capelin arrival, foraging trip duration was significantly lower in 2017 relative to 2020 (p = 0.002), but did not differ between 2019 and 2017 (p = 0.273) or between 2019 and 2020 (p = 0.137; Table 4). The mean number of foraging trips conducted per hour of deployment did not differ significantly between prey periods, years and the interaction between prey period and year was not significant (Table 4).

The average number of dive bouts and maximum dive duration (s) did not differ significantly between years (2017, 2020) or prey periods within years and the interaction between prey period and year was not significant (Table 4). Mean dive duration was significantly higher in 2020 relative to 2017, but there was no significant difference between prey periods within years and the interaction was not significant (Table 4). The number of dives and dives per bout differed significantly between prey periods within years and the interactions between prey periods and year were significant, while only the number of dives differed significantly between years (Table 4). *Post-hoc* results showed that the number of dives and dives per bout were

significantly lower after capelin arrival relative to before during 2017 (p-values: <0.001) but not during 2020 (p-values: 0.222-0.550; Table 4). In addition, the number of dives and dives per bout during the period after capelin arrival was significantly lower in 2017 relative to the same time period in 2020 (p-values: <0.001; Table 4). Dive depth data were only compared between prey periods within 2020 (no dive data for 2019, no depth data in 2017). Mean dive depth (m) did not differ significantly between prey periods in 2020 (Table 4), but maximum depth (m) was significantly deeper before relative to after capelin arrival (Table 4).

The PCA revealed that the first three axes had eigenvalues greater than 1 (PC1: 6.4, PC2: 2.6, PC3: 1.2) and accounted for 84% of the variance (PC1: 53.2%, PC2: 21.4%, PC3: 9.8%; Fig. 4). PC3 was not examined further because correlations of response variables with PC3 were generally low (component loadings: -0.40-0.45). The response variables most positively correlated with the first axis (PC1) were all foraging trip characteristics (loadings: 0.85-0.96), number of dives (loading: 0.85) and number of dive bouts (loading: 0.89). Therefore, higher PC1 values represent more distant and longer foraging trips with increased numbers of dives and dive bouts ('higher foraging effort'), while lower PC1 values represent closer, shorter foraging trips covering less area with fewer dives ('lower foraging effort'; Fig. 4). Response variables most positively correlated with the second axis (PC2) were the remaining dive characteristics (loadings: 0.67-0.78) except for the number of dives per bout which was negatively correlated with PC2 (loading: -0.51). Therefore, higher PC2 values represent fewer, longer and deeper dives per bout, while lower PC2 values represent more, shorter and shallower dives per bout (Fig. 4). The PC1 values did not differ significantly between prey periods and the interaction between prey period and year was not significant but did differ significantly among years (Table 4; Fig. 4). *Post-hoc* tests revealed that after capelin arrival, foraging effort was higher in 2020

than the same period in 2017 ( $p = 0.034$ ) and 2019 ( $p < 0.001$ ), but 2017 and 2019 did not differ ( $p = 0.999$ ; Fig. 4). The mean PC2 values did not differ significantly between prey period or year but the interaction between prey period and year was significant (Table 4; Fig. 4). *Post-hoc* tests revealed that prior to capelin arrival, PC2 values were higher in 2020 ( $p = 0.034$ ), indicating that birds performed fewer, longer and deeper dives per bout, compared to the period after capelin arrival, but this was not the case in 2017 ( $p = 0.250$ ; Fig. 4).

### *Body Condition*

Body condition of adult razorbills differed significantly across years (ANOVA:  $F_{2,49} = 3.20$ ,  $p = 0.049$ ) and, although *post-hoc* tests did not reveal significant differences in pairwise comparisons between years, adult body condition tended to be much lower during 2020 relative to the other years (Fig. 5a). Chick body condition also differed among years (ANOVA:  $F_{2,67} = 9.20$ ,  $p < 0.001$ ; Fig. 5b), with *post-hoc* tests indicating significantly lower condition in 2020 compared to 2017 ( $p = 0.007$ ) and 2019 ( $p = 0.001$ ) but 2017 and 2019 did not differ ( $p = 0.994$ ; Fig. 5b). Although breeding success was not systematically measured, we anecdotally noted a higher presence of dead razorbill chicks at nests and lower recapture rates of tagged razorbills during 2020 relative to 2019, which appeared to be due to the increased disappearance of young chicks from nests. In addition, there was a lower availability of razorbill chicks during early tag deployment in 2017 (July 28 – August 13) relative to 2019 (July 18 – August 9) and 2020 (July 13 – August 15; Table 1), suggesting that razorbills may have delayed nesting during 2017.

## **Discussion**

### *Inter-annual Foraging Effort*

Inter-annual variation in capelin biomass was associated with differences in foraging effort and chick body condition. During 2017 and 2019, when peak prey biomass in the study area was near the long-term average (2009-2020), foraging trip duration (2017:  $8.2 \pm 1.7$  h; 2019:  $5.1 \pm 0.5$  h) and maximum distance from the nest (2017:  $13.5 \pm 2.6$  km; 2019:  $8.7 \pm 1.1$  km) across both prey periods were within ranges reported in other studies on razorbill trip duration (Linnebjerg et al. 2015:  $5.5 \pm 4.4$  h; Delord et al. 2020:  $6.0 \pm 4.8$  h) and maximum foraging range (Delord et al. 2020:  $11.1 \pm 10.2$  km; Linnebjerg et al. 2015:  $12.4 \pm 10.5$  km). Interestingly, foraging effort did not differ between sexes as found previously for razorbills (Gulka et al. 2019; cf Paredes et al. 2008) and common murre (Burke et al. 2015), possibly due to low and variable sample sizes of males and females. In contrast, when peak prey biomass was the lowest on record during 2020, foraging trips were higher than published maximum foraging trip durations ( $17.0 \pm 2.3$  h) and ranges ( $51.8 \pm 6.3$  km). These longer, farther trips during 2020 were associated with a higher proportion of time spent foraging and flying per foraging trip relative to the other years of this study (Appendix I) as well as higher number of dives, number of dives per bout and overall higher foraging effort. Such increased foraging effort during poor prey conditions has been found for other seabirds, such as common murre (Monaghan et al. 1994, Gulka et al. 2020), black-legged kittiwakes (Suryan et al. 2006) and cape gannets (*Morus capensis*; Cohen et al. 2014). Overall, as predicted by Cairns (1987), foraging effort increased under lower prey availability conditions.

Although peak prey biomass occurred later in the season during 2017 relative to 2019, chick body condition was similar in both years. In contrast, the higher foraging effort during 2020 was associated with significantly lower chick body condition. It is unclear, however, whether lower chick body condition in razorbills results in lower breeding success due to the

short chick-rearing period on the colony that is unique to murres and razorbills, after which males continue chick-provisioning at sea for several weeks. For instance, increased trip durations of common murres may lead to lower feeding rates and reduced chick condition (Davoren & Montevecchi 2003a), but adults may increase chick growth rates post-fledging (Birkhead 1977, Varoujean et al. 1979) by leading their chicks to productive foraging areas at sea. Lower breeding success during 2020, however, was suggested by lower recapture of tagged razorbills due to the increased disappearance of chicks from nests along with the higher presence of dead chicks at nests in 2020 relative to 2019. Decreased reproductive success during years of lower prey availability have also been found in other seabird species such as herring gulls (*Larus argentatus*; Pons & Migot 1995), Audouin's gulls (*Larus audouinii*; Oro et al. 1999), black-legged kittiwakes (Oro & Furness 2002, Piatt et al. 2007, Kitaysky et al. 2010) and common murres (Kitaysky et al. 2007). Peak capelin biomass in 2020 was 1% of the maximum peak biomass on record (2018: 0.259 g/m<sup>2</sup>) for this study area, whereas 2017 and 2019 were 38-42% of maximum. Interestingly, when peak capelin biomass was 10% of maximum during 2016, breeding common murres in the study area showed increased foraging effort and chick body condition was lower (Montevecchi et al. 2019, Gulka et al. 2020). These findings suggest that the prey biomass threshold needed to maintain chick condition, and possibly breeding success, is between 10% and 38% for these two species of seabird and, thus, might be similar to the 33% of maximum prey biomass that was suggested by Cury et al (2011). It is also possible, however, that the prey biomass threshold is lower than 33%, as lower breeding success in northern gannets (*Morus bassanus*) was observed at 8% of maximum prey biomass (Guillemette et al. 2018).

Life history theory predicts that adult survival would not be compromised in a long-lived species, like many seabirds, until prey conditions are extremely low (Stearns 1992). Razorbill

adult body condition, however, was lower during 2020 relative to the other years, likely due to increased foraging effort to feed both themselves and their chicks under these extremely low prey availability conditions. Although we did not measure adult survival, previous studies showed that lower adult body mass at the end of the breeding season may be linked to adult mortality or desertion of the following breeding season (Kitaysky et al. 2010, Harding et al. 2011). Therefore, the lower body condition found in razorbills in this study and common murre previously in the study area (2016; Montevecchi et al. 2019) may influence adult survival or future reproductive success. In contrast, other studies have found no relationship between low food availability and adult body condition in other seabird species (Pons & Migot 1995, Oro et al. 1999, Piatt et al. 2007); however, these studies examined prey data across shorter periods (< 5 years) and longer time series ( $\geq 11$  years) may be needed to inform high versus low prey availability years (Cury et al. 2011). Overall, our findings suggest that breeding razorbills in 2020 had reached the prey biomass threshold where adult body condition would reflect food availability, as predicted by Cairns (1987), and suggests that these parents may experience increased survival challenges due to poor overall energy reserves during the non-breeding season (Oro & Furness 2002, Harding et al. 2011).

### *Inter-annual Diet*

Higher foraging effort (i.e., longer, more distant foraging trips with a higher number of dives) throughout 2020 and prior to capelin arrival in all years studied may be associated with foraging for alternative prey types. Indeed, prior to capelin arrival during 2017 and 2019, chick-rearing birds traveled farther from the colony to provision their chicks with alternative prey (e.g. sandlance) as evidenced by diet observations. Unexpectedly, dietary reconstruction from stable

isotope analysis in 2019 revealed a lower proportion of capelin in the diet relative to other years despite an increased proportion of capelin in chick diet observations and higher capelin biomass early in the season. Lower proportions of capelin from dietary reconstruction, however, may have resulted from sampling blood only 7 days after capelin spawning began (i.e. arrived inshore) compared to 2017 and 2020 sampling which occurred 10 and 13-18 days after capelin spawning, respectively. As red blood cells have a turnover rate of 2-3 weeks (Hobson & Clark 1993, Bearhop et al. 2002), stable isotope ratios used to reconstruct diet may have only partially incorporated this switch in assimilated diet during 2019. Increased trip distances during 2020 were associated with birds collecting alternate prey types both before and after capelin arrival, but due to limited chick dietary observations during 2020 we cannot preclude that birds traveled farther to capture capelin outside of normal foraging ranges, as suggested by dietary reconstruction. In support, central place foraging theory predicts that birds traveling farther from the colony would capture a larger and/or more energy-dense prey item for their chicks, as shown in previous studies on common (Burke & Montevecchi 2009) and thick-billed murre (*Uria lomvia*; Brisson-Curadeau & Elliott 2019). Although the energy density of various forage fish in coastal Newfoundland has not been assessed during the seabird breeding season, gravid female capelin appear to have higher energy densities (Montevecchi & Piatt 1984) relative to adult sandlance (Lawson et al. 1998) and juvenile sandlance (Van Pelt et al. 1997). Spawning capelin also form high-density and spatially persistent spawning aggregations (Davoren et al. 2006), indicating predators can predictably locate highly abundant prey (Davoren et al. 2003). If razorbills were traveling farther to capture capelin, however, one might predict that the number of dives would have decreased due to their higher quality and higher density aggregations.

Regardless of whether higher foraging effort resulted from capturing capelin or alternative prey types, these circumstances resulted in lower adult and chick body condition.

### *Intra-annual Foraging Effort*

Arrival of capelin into the study area was associated with decreased foraging effort (i.e., shorter, closer foraging trips and lower number of dives) within all years, except 2020, indicating behavioral flexibility and suggesting that the temporal match of spawning capelin arrival with the onset of chick-rearing is key to mitigate the high energy demands of this breeding stage. Despite the later arrival of capelin in 2017 relative to 2019, however, chick-rearing razorbills appeared to be able to compensate for this temporal mismatch, as shown by similar adult and chick body condition in both years. This finding may be explained by delayed breeding during 2017 relative to 2019, suggested by anecdotal evidence, which may have resulted in capelin arriving inshore at similar timing relative to the onset of chick-rearing. The temporal match between capelin inshore arrival and chick-rearing is supported by a number of studies. For instance, a study on common murre found reduced breeding success when the timing of capelin spawning and chick-rearing did not match (Regular et al. 2014). Indeed, since delayed capelin spawning began in the early 1990s, associated with the capelin population collapse (Buren et al. 2019), studies have shown that seabirds breed later (e.g. Davoren & Montevecchi 2003b) and have altered dietary proportions and foraging strategies (Carscadden et al. 2002). For instance, large gulls, that previously provisioned their chicks with capelin, increased predation on seabird adults (e.g. storm-petrels; Stenhouse & Montevecchi 1999) and eggs (Regehr & Montevecchi 1997, Massaro et al. 2000), although this shift was also associated with concurrent fisheries closures. The importance of this temporal match may not be only related to the increase in

coastal prey biomass, but also to capelin behavior during spawning. Indeed, razorbills were able to decrease the time spent foraging and to an extent time spent flying when predictably located, high-density spawning capelin aggregations were available within foraging ranges during chick-rearing (Davoren et al. 2006, Davoren 2013), similar to breeding common murrelets in the study area (Gulka & Davoren 2019, Montevecchi et al. 2019, Gulka et al. 2019, 2020). When these aggregations did not form within typical foraging ranges in 2020, however, the time spent foraging remained high throughout chick-rearing, suggesting that the predictability of these high-density capelin aggregations may be important to minimize foraging effort (Gende & Sigler 2006, Davoren 2013). Overall, these findings suggest that razorbills are behaviorally flexible and can adjust their behavior to successfully raise their chick but will reach the limit of this flexibility at a certain prey biomass threshold, as previously suggested (Cairns 1987, Cury et al. 2011).

## **Conclusion**

While some studies have linked changes in seabird foraging effort to different prey types in the diet, few have been able to directly link foraging effort to variation in prey biomass (Regular et al. 2014, Gulka & Davoren 2019, Gulka et al. 2019). Indeed, our independent prey biomass data provides insight into the lower critical prey biomass threshold for breeding razorbills and potentially other seabirds in coastal Newfoundland. Razorbills were able to maintain chick condition and adult body mass at slightly less than half of maximum prey biomass (38-42%), but chick body condition (and potentially breeding success) along with adult condition (and potentially survival) will decline somewhere between 10-38% of maximum prey biomass. This prey threshold may be more similar to the 33% of maximum prey biomass (Cury et al. 2011), but may be lower (e.g. 8%; Guillemette et al. 2018), possibly due to the importance of predictably located, high-density spawning aggregations of capelin (Davoren 2013, Gulka et

al. 2020), whose presence is associated with reduced foraging effort (Gulka & Davoren 2019, Gulka et al. 2019, this study). Chronically low spawning capelin biomass on the Newfoundland coast due to the collapsed state of the population (Buren et al. 2019), along with increased variability in the timing of capelin arrival and spawning associated with climate change (Davoren et al. 2012, Buren et al. 2014, Crook et al. 2017), may lead to increased temporal mismatches with the seabird breeding season and ultimately to long-term population-level consequences for these razorbills and other seabird species. Therefore, continued monitoring of the impact of capelin biomass and timing of spawning on seabird productivity will inform how these changes will affect long-term population dynamics. Additionally, as sandlance, a non-commercial forage fish, are understudied, a further understanding of sandlance population dynamics and the importance of this and other alternative forage fish species in adult seabird diets will become important as variability in capelin availability increases.

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## Tables and Figures

Table 1. Summary of tags deployed on chick-rearing razorbills on James Island during July-August 2017, 2019 and 2020. GPS (all years) recorded data at 10 min intervals; the wet/dry sensor (2017) recorded dive information at 1 s intervals once submerged; the temperature/depth sensor (2020) recorded data at 6 s intervals.

	<b>2017</b>	<b>2019</b>	<b>2020</b>
Tags retrieved	4	18	20
Tag model	Ecotone UR1A-300	CatLog Gen 2	CatLog Gen 2 + Lotek LAT 1800
Tag weight	16 g	13 g	13 g + 6 g
Tag sensors	GPS + wet/dry sensor	GPS	GPS + temperature/depth
Data collection intervals	10 min + 1 s	10 min	10 min + 6 s
Attachment method	Subdermal suture	Tesa tape to feathers	Tesa tape to feathers (GPS) + leg band (TDR)
Range of days tracked	1-29	1-6	1-5
Start and end dates of tag deployments	July 28 – August 13	July 18 – August 9	July 13 – August 15

Table 2. The percentage of prey types in parental prey deliveries by chick-rearing razorbills collected from photographs from camera traps and observations on James Island, Newfoundland during July-August 2017, 2019-2020 and divided into periods before and after capelin arrival into the study area. The number of prey deliveries observed is indicated (n).

<b>Year</b>	<b>Prey Period</b>	<b>Prey Percentages (%)</b>			<b>n</b>	<b>Method</b>	<b>Source</b>
		<b>Capelin</b>	<b>Sandlance</b>	<b>Other</b>			
2017	Before	20	50	30	10	Camera trap	Gulka et al. 2019
	After	67	0	33	3	Camera trap	Gulka et al. 2019
2019	Before	0	100	0	10	Observation	This study
	After	89	11	0	35	Observation	This study
2020	Before	8	92	0	12	Observation	This study
	After	33	67	0	3	Observation	This study





























In marine systems, predators rely heavily on forage fish species, small- or medium-sized pelagic fish that funnel energy from lower to higher trophic levels (Alder et al. 2008, Pikitch et al. 2012). Therefore, understanding how species interactions among predators vary in response to changing prey regimes can indicate the ecosystem-level impacts of variations in marine forage fish resulting from natural fluctuations, overfishing and/or climate change (Casaux et al. 2003, 2006, Frederiksen et al. 2007, Einoder 2009). To examine changing species interactions under varying prey regimes, dietary niche metrics that characterize the variety of prey types in predator diets and the amount of overlap among species represent valuable tools (Hutchinson 1978). As seabirds forage at sea and underwater prey consumption is difficult to observe, stable isotope analysis provides a method to examine diet using a nondestructive sampling process for different tissue types (e.g., plasma, red blood cells, feathers) that reflect diet over varying time periods based on tissue turnover rates (Hobson & Clark 1992, Phillips & Eldridge 2006). Consumer tissues are enriched in  $^{15}\text{N}$  compared to their prey, allowing  $^{15}\text{N}/^{14}\text{N}$  ratios (expressed as  $\delta^{15}\text{N}$ ) to be used as estimates of trophic position of the consumer (Vanderklift & Ponsard 2003). Alternately,  $^{13}\text{C}/^{12}\text{C}$  ratios (expressed as  $\delta^{13}\text{C}$ ) stay relatively similar from prey to predator but are much higher in benthic dwelling organisms, often allowing for foraging locations to be estimated as either inshore or offshore and as pelagic or benthic (Hobson et al. 1994). Isotopic niche metrics that have become standard in the literature include isotopic niche breadth, niche overlap, trophic diversity and redundancy, which are typically visualized on biplots of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Layman et al. 2007, Sargeant 2007, Inger & Bearhop 2008, Jenkins & Davoren 2020). Isotopic niche breadth, typically represented by the standard ellipse area (SEA), or the standard deviation around the bivariate mean, is a proxy of the diversity or variety of prey types consumed. Niche overlap measures the amount that the SEA overlaps between two groups (e.g.,



of dietary shifts from sandlance to incorporate primarily capelin after the inshore arrival of spawning capelin within foraging ranges. A study conducted by Jenkins & Davoren (2020) found that sympatrically breeding alcids' isotopic niche position and niche breadth shifted within a summer coinciding with the inshore arrival of spawning capelin (i.e. higher capelin availability). Interestingly, each species' niche shifted differently with higher capelin availability, suggesting variable reliance on capelin.

Although seabird chick-rearing in Newfoundland often coincides with the inshore movements of spawning capelin (Carscadden et al. 2002), changes in sea ice dynamics and ocean temperature have resulted in this phenology becoming highly variable (Davoren et al. 2012, Buren et al. 2014, Crook et al. 2017). Variation in the timing of capelin spawning, which coincides with peak capelin biomass in coastal regions, may lead to a phenological mismatch with the seabird chick-rearing period, resulting in conservation concerns for seabirds and other marine predators in coastal Newfoundland. Using dietary niche dynamics, we can begin to understand the potential conservation implications of this mismatch. Therefore, we examined how the isotopic niche dynamics of three chick-rearing (July-August) seabird species of the family Alcidae (murrelets, puffins, and razorbills) respond to inter-annual changes in capelin biomass across three years (2017-2019) in coastal Newfoundland. We hypothesized that isotopic niche metrics of all species would be influenced by inter-annual changes in capelin availability. At the species-level, we predicted that isotopic niche breadth would contract and trophic position would shift towards capelin in years with higher capelin availability, suggesting a capelin-dominated diet. At the seabird assemblage-level, we predicted that niche overlap of all three species would increase and trophic diversity would decrease in years with higher capelin availability.

## Methods

### *Capelin Biomass*

To quantify capelin availability in the study area, a ship-based hydroacoustic survey (~15 km) over a cluster of annually persistent capelin deep water spawning sites (15-40 m; Penton & Davoren 2012) was conducted approximately weekly during July – August, 2017 – 2019 (Fig. 1). Capelin biomass was measured, following methods from Davoren et al. (2006), using a Biosonics DTX 6000 (BioSonics Inc., Seattle Washington) echosounding system with a 70 kHz transducer towed 1 m below the surface of the water. At the end of the field season, we used Echoview software (Version 4, SonarData, Myriax Software Pty. Ltd., Hobart, Tasmania) to separate and omit acoustic signals that could not be distinguished from the seafloor and quantified acoustic biomass ( $s_a$ , area backscattering coefficient,  $m^2m^{-2}$ ) in each 100 m survey segment using a minimum threshold of -80 dB. We then converted  $s_a$  into capelin biomass ( $g/m^2$ ) by combining capelin biometrics (i.e., length, mass) from fish collected in the area and a target strength-length relationship for capelin (Rose 1998) for each 100 m segment of each survey. The average capelin biomass was then calculated across all 100 m segments for each survey to identify mean capelin biomass per survey. To determine timing of capelin spawning, persistent deep-water and beach spawning sites were monitored for capelin spawning (i.e. presence of capelin eggs adhered to sediment) weekly or every second day, respectively, following methods in Crook et al. (2017). Peak capelin biomass within each year along with the timing of peak capelin biomass and the start of capelin spawning were integrated to allow inter-annual comparisons of capelin availability.



































































