

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

By

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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.

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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 murres 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

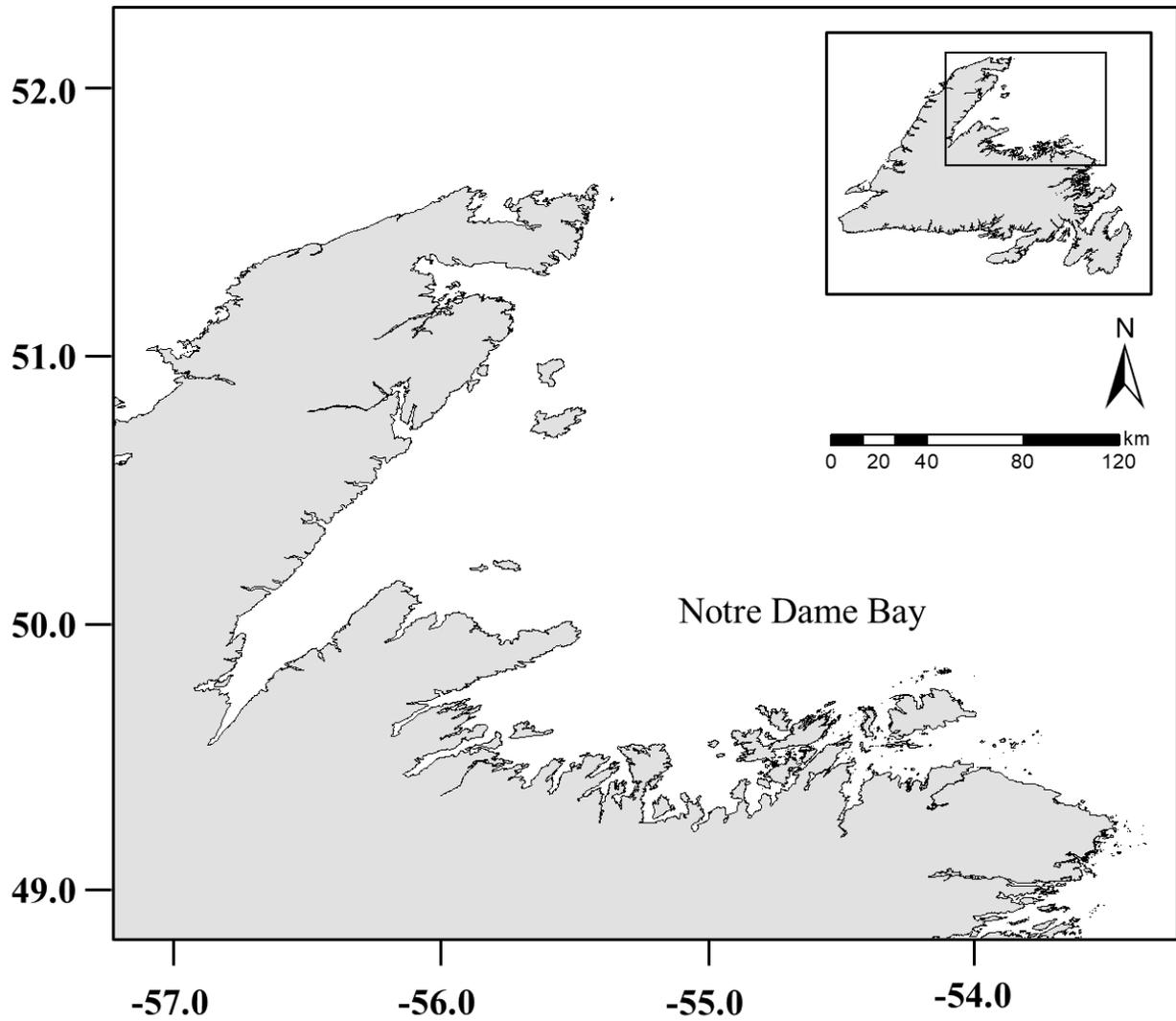


Figure 1. Map of Newfoundland, Canada highlighting the study area in Notre Dame Bay on the northeast coast of Newfoundland.

## **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 murre (*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*® UR1A-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 murrelets and razorbills are closely related, discrimination factors for red blood cells from a captive study on common murrelets (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 murrelets (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 murrelets (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 murrelets 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

Table 3. Mean ( $\pm$  SE)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from red blood cells of razorbills and muscle from capelin and sandlance collected in 2017, 2019 and 2020, where n is the number of samples collected each year. Significant differences ( $p < 0.05$ ) among years within each species are indicated by different letters (e.g., a, b). Values from 2017 are from a previous study conducted by Gulka et al. (2019) and indicated by <sup>1</sup>.

<b>Species</b>	<b>Year</b>	<b>Sampling Date</b>	<b>n</b>	<b><math>\delta^{13}\text{C}</math></b>	<b><math>\delta^{15}\text{N}</math></b>	<b>C:N</b>
<i>Razorbill</i>	2017 <sup>1</sup>	14-August	17	-19.92 $\pm$ 0.06 <sup>a</sup>	14.08 $\pm$ 0.06	3.34 $\pm$ 0.01
	2019	29-July	19	-19.82 $\pm$ 0.03 <sup>a</sup>	14.11 $\pm$ 0.08	3.28 $\pm$ 0.01
	2020	11,16-August	16	-19.43 $\pm$ 0.05 <sup>b</sup>	14.11 $\pm$ 0.08	3.21 $\pm$ 0.01
<i>Capelin</i>	2017 <sup>1</sup>		15	-20.64 $\pm$ 0.07 <sup>a</sup>	12.12 $\pm$ .014 <sup>a</sup>	3.29 $\pm$ 0.02
	2019		12	-20.48 $\pm$ 0.09 <sup>ab</sup>	12.53 $\pm$ 0.07 <sup>b</sup>	3.33 $\pm$ 0.02
	2020		9	-20.35 $\pm$ 0.09 <sup>b</sup>	11.89 $\pm$ 0.09 <sup>a</sup>	3.35 $\pm$ 0.02
<i>Sandlance</i>	2017 <sup>1</sup>		9	-21.19 $\pm$ 0.06	10.11 $\pm$ 0.09 <sup>a</sup>	3.20 $\pm$ 0.01
	2019		10	-21.15 $\pm$ 0.06	10.53 $\pm$ 0.09 <sup>b</sup>	3.20 $\pm$ 0.01
	2020		9	-21.22 $\pm$ 0.08	10.22 $\pm$ 0.09 <sup>b</sup>	3.27 $\pm$ 0.01

Table 4. Summary of mean ( $\pm$ SE) foraging trip and dive characteristics collected from GPS and Time-Depth Recorders deployed on chick-rearing razorbills on James Island in 2017, 2019 and 2020 collected before and after capelin arrival into the study area. Degrees of freedom for foraging trip characteristics and PC1 (year<sub>2,6</sub>, period<sub>1,6</sub>, period\*year<sub>2,6</sub>), diving characteristics, proportion of time spent foraging and PC2 (year<sub>1,6</sub>, period<sub>1,6</sub>, period\*year<sub>1,6</sub>). Differences among prey period and year for each foraging trip and dive characteristic and PCA are indicated by different letters (e.g., a, b).

	2017		2019		2020		Period		Year		Period*Year	
	Before	After	Before	After	Before	After	F	p	F	p	F	p
Individuals	4	1	4	14	12	8						
Male/Female/Unknown	1/3/0	1/0/0	2/1/1	5/7/2	6/4/2	3/3/2						
Total trips	17	22	10	53	19	18						
No. of overnight trips	9	5	2	14	10	12						
Range of foraging trips per individual	1-6	22	2-4	1-11	1-3	1-6						
Number of foraging trips per hour deployed	0.06±0.06	0.09	0.13±0.03	0.22±0.05	0.14±0.04	0.04±0.01	0.43	0.518	0.54	0.589	0.51	0.604
<b>Foraging Trip Characteristics</b>												
<i>Maximum distance (km)</i>	23.7±4.7 <sup>a</sup>	5.7±1.3 <sup>b</sup>	22.7±2.5 <sup>a</sup>	6.1±0.8 <sup>b</sup>	44.9±7.1 <sup>a</sup>	59.4±10.6 <sup>a</sup>	23.4	<0.001	12.0	<0.001	6.4	0.003
<i>Total distance (km)</i>	57.9±13.0 <sup>a</sup>	12.8±2.8 <sup>b</sup>	54.1±6.8 <sup>a</sup>	14.3±1.7 <sup>b</sup>	122.3±20.4 <sup>a</sup>	150.4±25.2 <sup>a</sup>	31.0	<0.001	16.7	<0.001	7.1	0.002
<i>Duration (h)</i>	13.0±3.4 <sup>a</sup>	4.54±1.0 <sup>b</sup>	5.8±1.1 <sup>a</sup>	5.0±0.6 <sup>ab</sup>	12.9±2.3 <sup>a</sup>	21.5±3.8 <sup>a</sup>	11.1	0.001	5.8	0.004	3.2	0.046
<i>50% KD (km<sup>2</sup>)</i>	83.4±32.8 <sup>a</sup>	14.9±6.3 <sup>bc</sup>	72.2±38.1 <sup>ac</sup>	8.3±2.1 <sup>b</sup>	343.8±84.6 <sup>a</sup>	306.7±74.5 <sup>a</sup>	22.0	<0.001	15.5	<0.001	3.8	0.036
<i>95% KD (km<sup>2</sup>)</i>	387.8±144.2 <sup>a</sup>	61.2±25.6 <sup>b</sup>	327.8±108.8 <sup>a</sup>	39.0±9.1 <sup>b</sup>	1727.1±412.2 <sup>a</sup>	2277.9±585.8 <sup>a</sup>	22.5	<0.001	14.1	<0.001	4.7	0.015
<b>Diving Characteristics</b>												
<i>Number of dives*</i>	309.2±70.2 <sup>a</sup>	48.4±11.8 <sup>b</sup>			276.9±56.8 <sup>a</sup>	385.8±67.39 <sup>a</sup>	17.1	<0.001	10.1	0.002	29.6	<0.001
<i>Max dive duration (s)</i>	63.1±3.9	70.8±4.4			73.6±2.6	63.5±1.9	0.2	0.070	0.1	0.825	3.5	0.071
<i>Mean dive duration (s)</i>	33.3±2.5	30.0±1.6			40.7±1.8	34.6±1.6	3.2	0.081	6.8	0.011	0.3	0.061
<i>Number of dive bouts*</i>	22.1±5.7	17.0±3.6			30.6±5.0	41.8±7.7	0.7	0.398	2.8	0.095	0.1	0.747
<i>Dives per bout*</i>	15.2±2.5 <sup>a</sup>	2.7±0.3 <sup>b</sup>			7.9±0.9 <sup>c</sup>	11.2±1.5 <sup>c</sup>	13.4	<0.001	1.1	0.303	28.4	<0.001
<i>Max depth (m)</i>					27.4±1.6 <sup>a</sup>	22.2±1.7 <sup>b</sup>	8.6	0.007				
<i>Mean depth (m)</i>					13.2±1.0	10.4±0.9	3.4	0.092				
<b>PCA</b>												
<i>PC1</i>	0.23±0.56 <sup>ac</sup>	-1.35±0.29 <sup>a</sup>	-0.31±0.23 <sup>abc</sup>	-1.28±0.07 <sup>a</sup>	2.29±0.64 <sup>bd</sup>	2.81±0.91 <sup>cd</sup>	3.4	0.072	14.3	<0.001	0.5	0.608
<i>PC2</i>	-0.91±0.58 <sup>ac</sup>	0.50±0.49 <sup>ac</sup>			1.11±0.48 <sup>a</sup>	-1.01±0.35 <sup>c</sup>	0.2	0.669	0.01	0.935	11.2	0.001

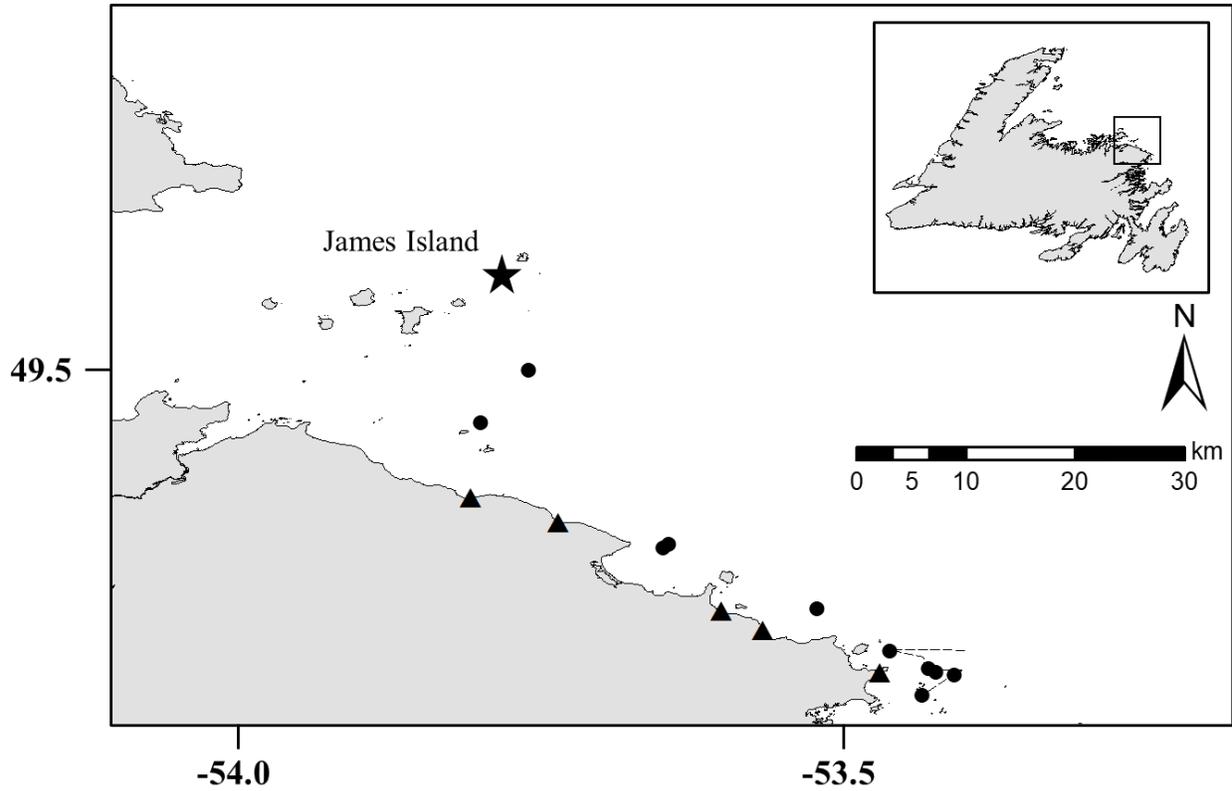


Figure 1. Map of study area showing the northeast coast of Newfoundland. The razorbill breeding colony, James Island, is indicated by a star. The circles indicate the deep-water capelin spawning sites. The triangles indicate capelin beach spawning sites. The dashed line indicates the survey route for hydroacoustic surveys.

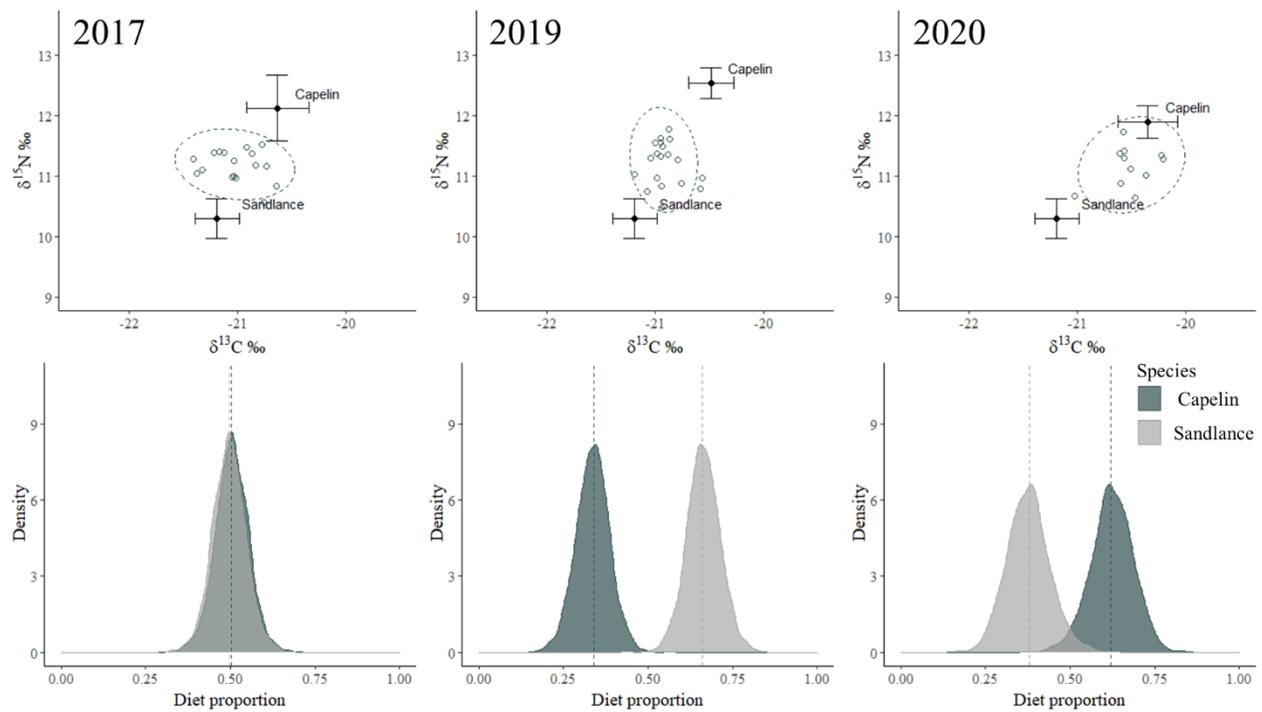


Figure 2. Biplots (top row) of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from red blood cells, with discrimination factors applied, of chick-rearing razorbills breeding on James Island during 2017, 2019 and 2020 where the 95% prediction ellipse is shown. Mean and standard error bars of prey are shown. Dietary proportions (bottom row) reconstructed from red blood cells of razorbills during 2017, 2019 and 2020. Capelin (dark grey) and sandlance (light grey) are shown. Dotted line indicates mode.

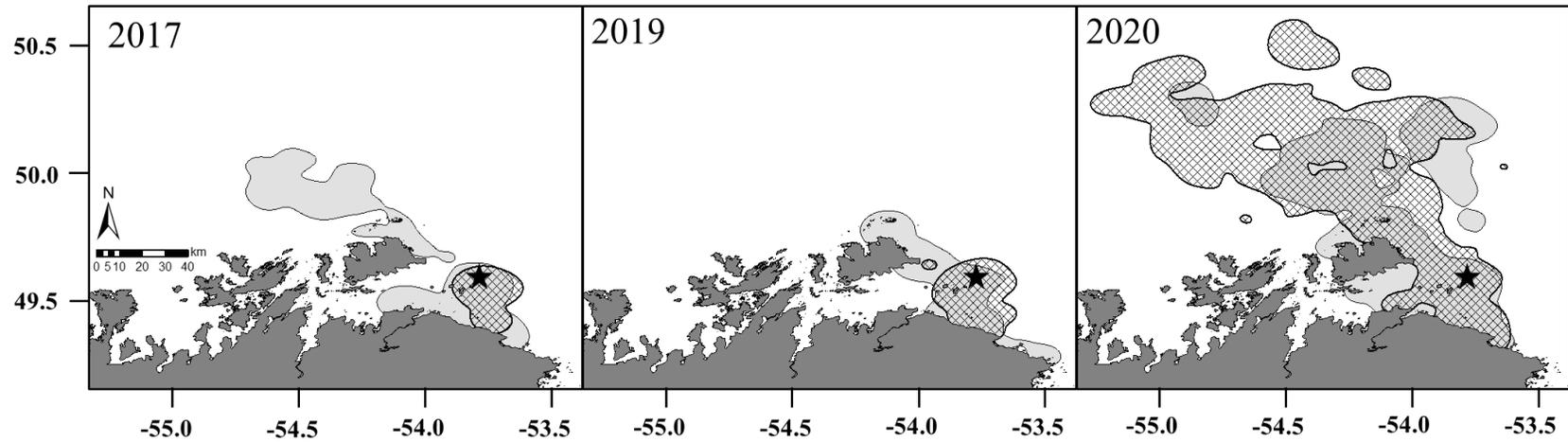


Figure 3. 95% Kernel density estimations from GPS tracks of chick-rearing razorbills nesting on James Island (star) from 2017, 2019 and 2020. Light gray indicating the period prior to capelin arrival while the dark cross-hatch indicates the period after capelin arrival.

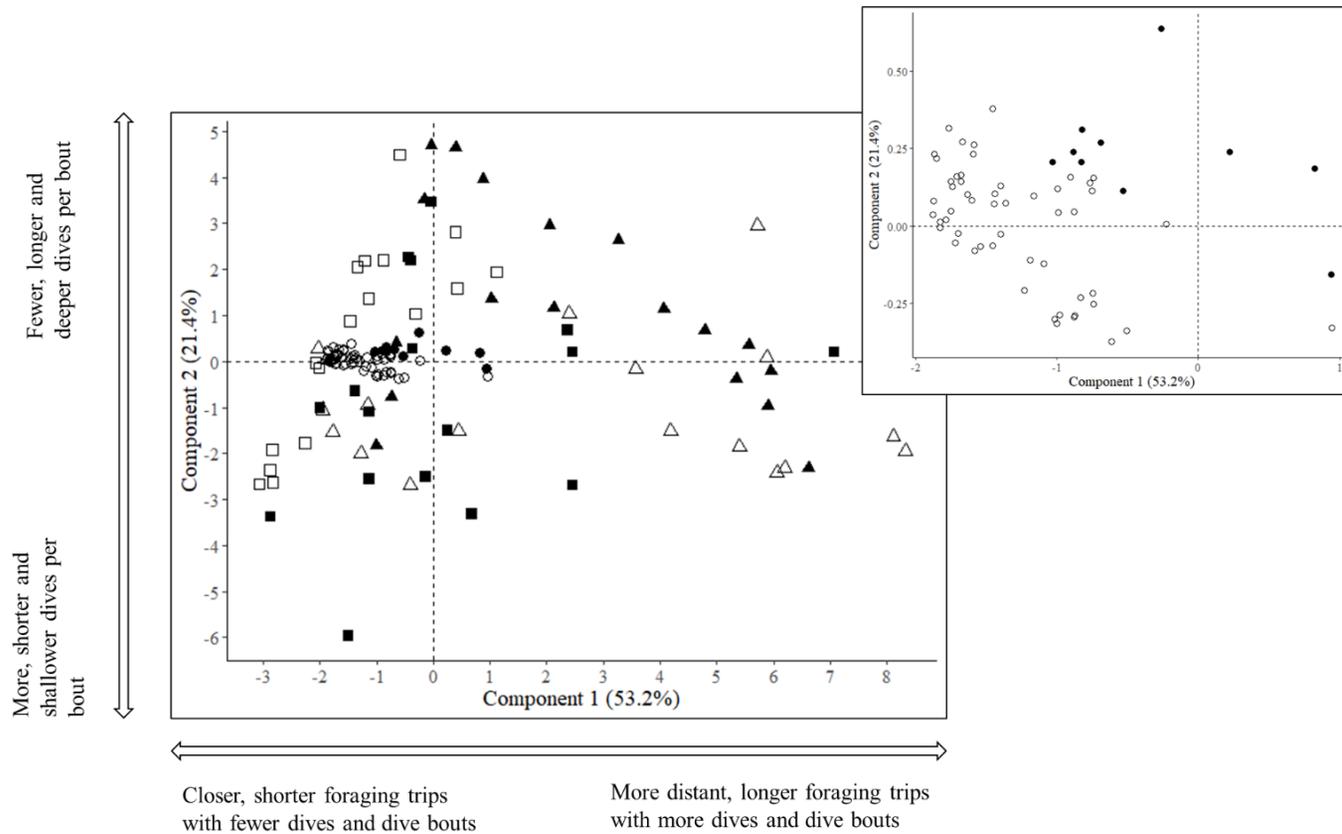


Figure 4. Principal Components 1 and 2 (PC1, PC2), combining all foraging trip and dive variables from chick-rearing razorbills on James Island during 2017 (squares), 2019 (circles) and 2020 (triangles). Solid shapes indicate the period before capelin arrival and open shapes indicate after capelin arrival. Interpretations of positive and negative PC1 and PC2 values are based on component loadings (see Results). Inset shows PC1 and PC2 values for 2019, where PC2 values (y-axis) were estimated due to the lack of dive data in that year and, thus, should be interpreted with caution.

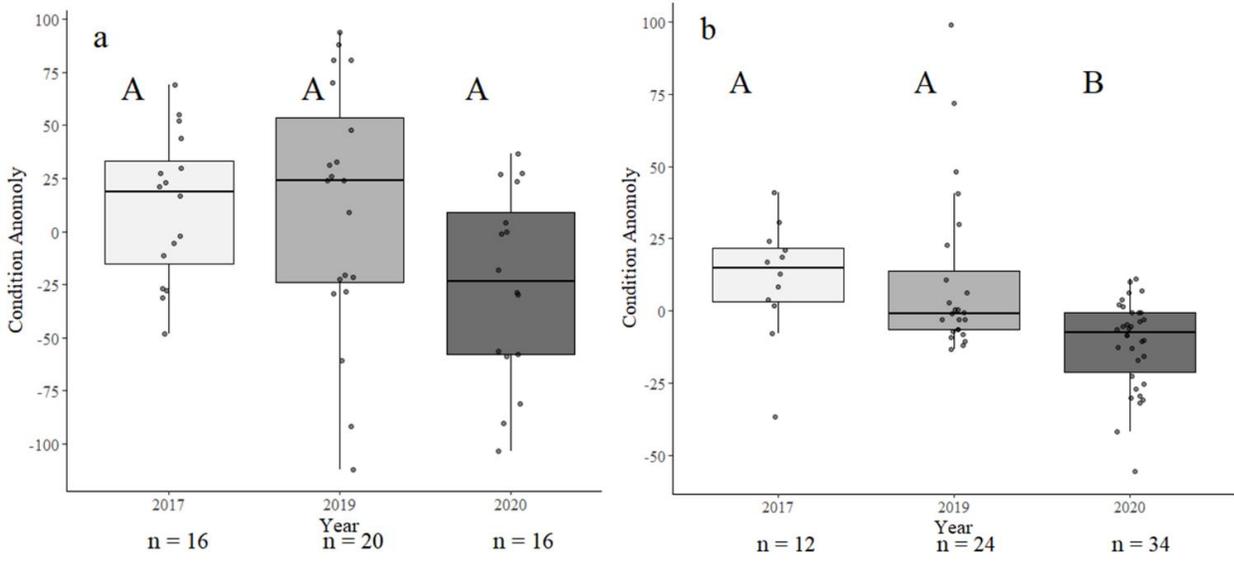


Figure 5. Body condition anomaly (g/mm) from chick-rearing razorbills and chicks on James Island during 2017, 2019 and 2020. Number of individuals measured is indicated by “n”.

Significant differences among years are indicated by different letters (e.g., A, B).

## **Appendix I. Proportion of time spent in different activities**

In an effort to explore time/activity budgets, we examined the proportion of time that birds spent in different activities using a variety of methods due to differences in bird-borne devices used among the years of this study.

### **Methods**

The proportion of time birds spent foraging during each foraging trip of 2017 and 2020 was calculated by summing the total time spent in dive bouts (i.e. dive and surface interval between dives within a dive bout) divided by the total foraging trip duration. In addition, an estimate of the proportion of time spent flying during each foraging trip was calculated from GPS tracks in all years. Within each foraging trip, the speed of travel (i.e. distance traveled between GPS points divided by time between points) was calculated and speeds > 6 km/h were considered flying. Foraging trips where GPS points were recorded every hour, due to low battery life, were removed from analysis ( $n = 4$ ) as speed of travel between points could not be accurately estimated. Proportion of time spent flying was calculated by summing the total time flying divided by the total duration of the foraging trip. We also estimated the proportion of time birds spent at the colony. As deployment periods and number of foraging trips differed among birds, the proportion of time at the colony was calculated for each foraging trip as the amount of time birds spent at the colony after a foraging trip divided by the sum of the duration of the foraging trip and the post-trip period at the colony. The final foraging trip per deployment was not included in the analysis as time spent on the colony would have been shorter due to removal of GPS tag from the bird. Proportion of time spent flying, foraging and on colony were arcsine square root transformed and differences among and within years (e.g. prey periods) were

examined using a general linear mixed model using the package *lme4* in R. Predictor variables were the same as the previous models and significance was estimated using marginal means.

## Results

The mean proportion of time spent foraging per foraging trip differed significantly between years (2017, 2020) and prey periods within years and the interaction between prey period and year was significant (Table A1). *Post-hoc* results showed that the mean proportion of time spent foraging per foraging trip was higher before capelin arrival compared to after during 2017 ( $p < 0.001$ ), but not during 2020 ( $p = 0.764$ ; Fig. A1a). The mean proportion of time spent foraging after capelin arrival was significantly higher during 2020 relative to 2017 ( $p = 0.020$ ; Table A1; Fig. A1a). The mean proportion of time spent flying per foraging trip differed significantly among years (2017, 2019, 2020) and prey periods, but the interaction was not significant (Table A1). *Post-hoc* tests revealed that the mean proportion of time spent flying per foraging trip did not differ significantly before relative to after capelin arrival in all years ( $p$ -values: 0.128-0.991; Table A1; Fig. A1b). The proportion of time spent flying after capelin arrival in 2020 was significantly higher than the same period in 2017 ( $p = 0.024$ ) and 2019 ( $p < 0.001$ ) but did not differ between 2017 and 2019 ( $p = 0.998$ ; Table A1; Fig. A1b). The mean proportion of time birds spent at the colony relative to at sea did not differ significantly among prey periods, years and the interaction between prey period and year was not significant (Table A1; Fig. A1c).

## Tables and Figures

Table A1. Summary of mean ( $\pm$ SE) proportion of time spent foraging, flying and at the colony collected from GPS and Time-Depth Recorders deployed on chick-rearing razorbills on James Island in 2017, 2019 and 2020 collected before and after capelin arrival into the study area. Degrees of freedom for proportion of time spent on colony and proportion of time spent flying (year<sub>2,6</sub>, period<sub>1,6</sub>, period\*year<sub>2,6</sub>), proportion of time spent foraging (year<sub>1,6</sub>, period<sub>1,6</sub>, period\*year<sub>1,6</sub>). Differences among prey periods and years for each proportion are indicated by different letters (e.g., a, b).

	2017		2019		2020		Period		Year		Period*Year	
	Before	After	Before	After	Before	After	F	p	F	p	F	p
<b>Proportions</b>												
<i>Time spent foraging</i>	0.38 $\pm$ 0.05 <sup>a</sup>	0.15 $\pm$ 0.02 <sup>b</sup>			0.33 $\pm$ 0.03 <sup>a</sup>	0.28 $\pm$ 0.03 <sup>a</sup>	22.3	<0.001	7.0	0.024	10.1	0.003
<i>Time spent flying</i>	0.25 $\pm$ 0.06 <sup>ab</sup>	0.16 $\pm$ 0.03 <sup>a</sup>	0.32 $\pm$ 0.05 <sup>ab</sup>	0.15 $\pm$ 0.02 <sup>a</sup>	0.37 $\pm$ 0.05 <sup>b</sup>	0.33 $\pm$ 0.07 <sup>b</sup>	6.4	0.016	11.2	0.001	3.3	0.047
<i>Time spent on colony</i>	0.47 $\pm$ 0.07	0.60 $\pm$ 0.07	0.52 $\pm$ 0.05	0.47 $\pm$ 0.03	0.35 $\pm$ 0.07	0.41 $\pm$ 0.08	0.6	0.458	1.8	0.293	0.7	0.489

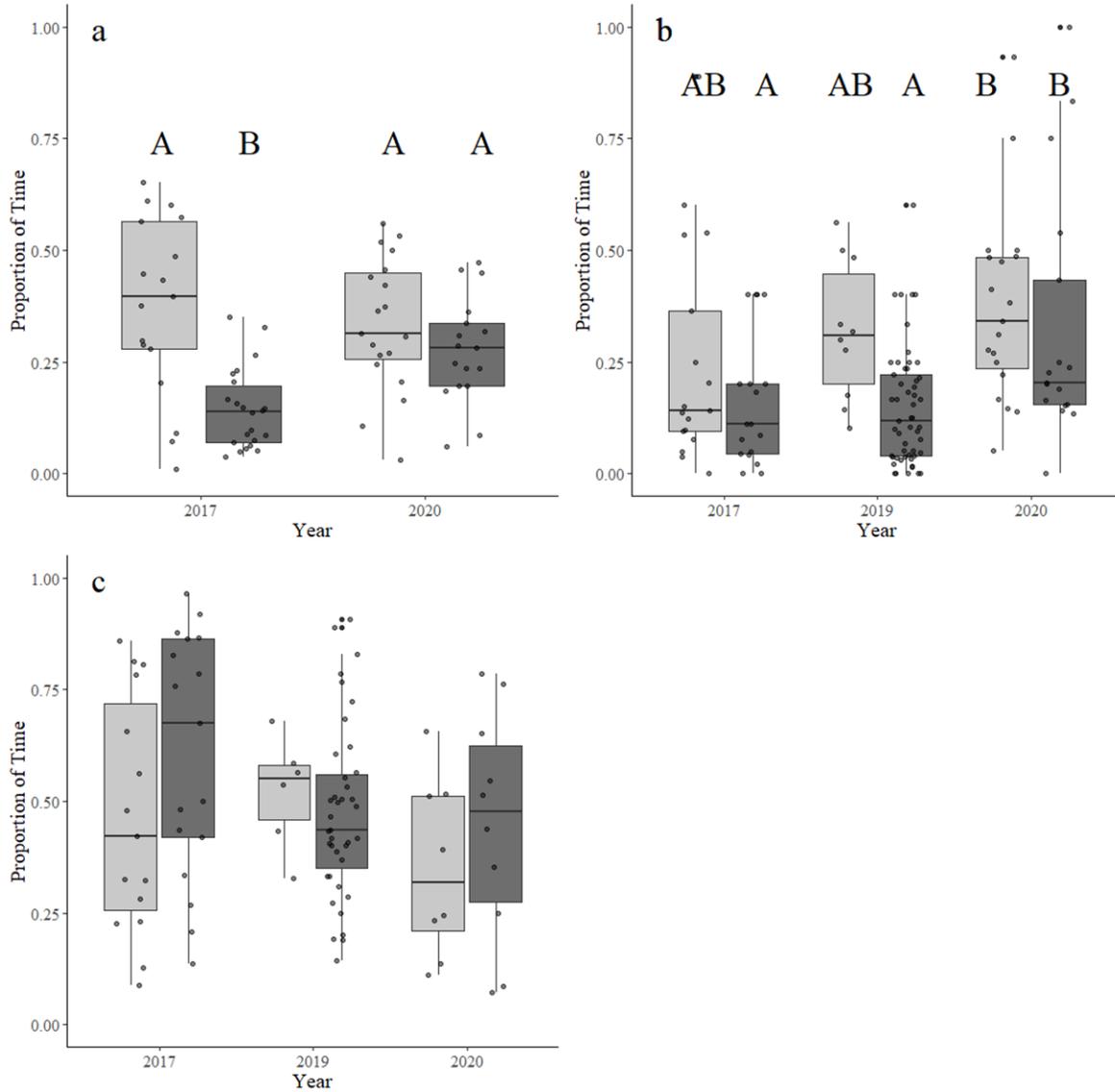


Figure A1. Proportion of time spent foraging (a) collected from diving data loggers (2017, 2020), and proportion of time spent flying (b) and on the colony (c) collected from GPS data loggers (2017, 2019, 2020) on chick-rearing razorbills on James Island in 2017, 2019 and 2020. The lighter gray color indicates the period prior to capelin arrival and the dark gray color indicates the period after capelin arrival. Significant differences between years and prey periods are indicated by different letters (e.g., A, B).

## Chapter 2. Inter-annual isotopic niche shifts of three breeding alcids in coastal Newfoundland under varying capelin biomass

### Abstract

Dietary shifts in seabirds, due to variation in prey availability, can be constrained by interactions with other species that rely on similar prey types. We explored how the isotopic niche of three sympatrically breeding seabirds, razorbills (*Alca torda*), Atlantic puffins (*Fratercula arctica*) and common murrelets (*Uria aalge*), are influenced by inter-annual variation in capelin (*Mallotus villosus*) biomass across three years (2017-2019). We used stable isotopes ratios of carbon and nitrogen ( $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$ ) from blood samples of breeding seabirds as a proxy of dietary niche. During the year of higher capelin biomass (2018), species-level niche breadth contracted and trophic position increased indicating a higher reliance on capelin and a lower diversity of prey in the diet for two of the three species, whereas, common murrelets seemed to consistently incorporate high proportions of capelin in the diet during high and low capelin availability years. At the assemblage-level, niche overlap was generally higher during higher (2018) relative to lower (2017) capelin availability years, suggesting shifts in species interactions among years. Lower trophic diversity during 2019, however, suggested a convergence on fewer alternative prey types under lower prey availability. These findings suggest that increased variability in capelin biomass may lead to higher isotopic niche overlap, which may increase competitive interactions which requires further investigation.

## **Introduction**

Ecological niche is defined as an n-dimensional set of abiotic and biotic factors in space, where axes represent different environmental factors such as habitat, food resources and temperature gradients under which an organism can grow, survive and reproduce (Hutchinson 1978). A species' niche can be restricted through interspecific competition, which occurs when two or more species are competing for a common and limited resource. The competitive exclusion principle states that two species cannot coexist if they occupy the same niche (Gause 1934). If species-specific niches are distinct enough (e.g., different breeding habitat, prey types and sizes), however, the coexistence of two sympatric species is possible (Schoener 1974). Niche differentiation can evolve from interspecific competition and is characterized by individuals of different species partitioning resources (i.e. niche partitioning). Niche partitioning results in species occupying their realized rather than fundamental niche and ultimately leads to the evolution of physiological, morphological or behavioral traits (i.e. character displacement) that further promotes niche partitioning (Schoener 1974, Tilman 1987). Lack (1946) suggested that temporary super-abundance of food resources can lead to a reduction of competition among species because food is no longer in limited supply, but prey switching occurs when this food resource becomes scarce and competition increases, with the degree of prey switching varying among species. Shifts in prey regimes may include variation in prey composition or abundance and may be accompanied by changes in foraging behavior of predators (Randa et al. 2009). Species with a competitive advantage, possibly due to more competitive morphological, physiological and behavioral traits, can lead to competitive asymmetry, whereby the competitively dominant species is least affected relative to other species by competitive interactions (Schoener 1983).

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.,

populations, species), indicating how similar the resource use is between groups (Sargeant 2007). Trophic diversity and redundancy reflect the amount of isotopic niche space occupied and the relative positions of groups to each other at the assemblage-level. Although a few studies using these isotopic niche metrics have provided insight into potential competitive interactions among marine predators in response to changes in prey availability (Chesson & Kuang 2008, Barger & Kitaysky 2012, Gulka et al. 2017, Carvalho & Davoren 2019, Ogloff et al. 2019, Jenkins & Davoren 2020), few have examined changes in niche metrics in a multi-year context.

In the Northwest Atlantic, capelin (*Mallotus villosus*) are the primary forage fish species consumed by most marine predators (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, which also corresponds with the breeding season for many seabirds in the area. The arrival of spawning capelin inshore transforms the coastal prey base 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). In coastal Newfoundland, seabirds are known to shift their diet in relation to the availability of capelin (Burger & Piatt 1990, Davoren et al. 2012, Gulka et al. 2017, 2019, Carvalho & Davoren 2019, Montevecchi et al. 2019, Jenkins & Davoren 2020). For example, during years of low capelin availability, chick-rearing common murre (*Uria aalge*; hereafter referred to as ‘murre’) were found to increase percentages of large mature sandlance in chick diets and increased time spent foraging to reduce impacts to reproductive success (Burger & Piatt 1990). In addition, breeding Atlantic puffins (*Fratercula arctica*; hereafter referred to as ‘puffin’) also switched to post-larval sandlance and other small fish in chick diets in years with decreased capelin availability (Baillie & Jones 2004). In a study of sympatrically breeding razorbills (*Alca torda*) and murre, Gulka et al. (2019) found evidence

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 (murre, puffin, and razorbill) 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.

### *Seabird Diet Sampling*

Blood samples were collected from approximately 20 individuals from each species of breeding alcids (murre, puffin, razorbill) during chick-rearing and after capelin spawned in the study area during three consecutive years (2017 – 2019), although timing of sampling was variable due to weather-dependent access to seabird breeding islands (Table 1). Razorbills and puffins were selected haphazardly and captured by hand in their rock crevices and burrows at James Island and murrens were captured by net or noose pole on South Cabot (2017) and Funk Island (2018 & 2019; Fig. 1). Approximately 1.5 mL of blood was collected from the tarsus or brachial 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 for comparison among years, where red blood cells represent the integrated diet over 2-3 weeks (Hobson & Clark 1993, Bearhop et al. 2002).

As prey isotopic ratios may change among seasons and years due to variations in baseline changes, potential prey types in seabird diets were identified and sampled during the same period as seabird tissue sampling for interpretation of seabird stable isotope ratios (Quay et al. 2003, Bond & Jones 2009). Potential prey types and approximate proportions were identified based on chick diet in a variety of ways. Prey were collected from adult murrens returning to the colony using a pole net (2017, 2018; Gulka et al. 2020). In addition, prey were identified as capelin, sandlance, small fish or unknown from parental prey deliveries to chicks of all three species recorded at nearby nest sites using motion sensor camera traps (2017, 2018; Gulka et al. 2019, 2020, Jenkins & Davoren 2020) or observed at nearby nest sites of razorbills and puffins during 2-h observation stints (2019). For use in stable isotope analysis, in all years, capelin samples

were collected on beaches during spawning while other prey types were sampled opportunistically during other research activities, including bottom-grabs (e.g. sandlance; 2017-2019) and opportunistically from fishers (e.g. small fish, where prey were < 10 cm and included sandlance, cod and unidentified fish; 2017; Gulka et al. 2019, 2020, Jenkins & Davoren 2020). In addition, mist nets were set up near puffin burrows on James Island in 2017 for approximately 1-2 h to capture birds as they delivered prey to their chicks (n = 17 bill loads; Gulka et al. 2019, 2020, Jenkins & Davoren 2020). Birds were carefully extracted from the net and released, and prey samples were collected and frozen for use in stable isotope analysis. A skinless muscle sample (1-2 g) was collected from larger fish, while smaller fish were frozen whole.

### *Stable Isotope Analysis*

Red blood cells and prey samples were freeze dried for approximately 48 h, after which they were homogenized. As tissues with high lipid content, indicated by a C:N ratio > 3.5, may cause variation in  $\delta^{13}\text{C}$  values unrelated to diet, fish muscle was lipid-extracted (DeNiro & Epstein 1977, Post et al. 2007). For lipid extraction, samples were processed through a Soxhlet apparatus using petroleum ether for approximately 8 h. Samples were then re-dried for 48 h, re-homogenized, and weighed (red blood cells and muscle: 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). For instrument calibration and ensuring accuracy, five standards (Bovine Liver, USGS 41, Urea 1, Tilapia 1, USGS 40) were analyzed after every 13 samples. Additionally, duplicate and triplicate analyses were run for each 13<sup>th</sup> sample to measure instrument precision. 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:  $\delta X = [(R_{Sample}/R_{Standard}) - 1]$ , where  $X = {}^{13}\text{C}$  or  ${}^{15}\text{N}$ , and  $R = {}^{13}\text{C}/{}^{12}\text{C}$  or  ${}^{15}\text{N}/{}^{14}\text{N}$  (Becker et al. 2009). As isotope ratios of prey are altered when assimilated into consumers tissues, a discrimination factor was applied to the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of the consumer to allow direct comparisons among prey and consumer values (Inger & Bearhop 2008). For puffins, a discrimination factor of  $1.21 \pm 0.22\%$  and  $2.80 \pm 0.28\%$  was applied to  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively, based on values derived from a captive study on puffins using red blood cells (Jenkins et al. 2020). As murre and razorbills are closely related, the discrimination factor for murre red blood cells was applied to both species, with  $1.09 \pm 0.23\%$  and  $2.91 \pm 0.18\%$  applied to  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively (Jenkins et al. 2020).

### *Data Analysis*

We used  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from red blood cells of the three breeding alcid species over three years to examine shifts in isotopic niche metrics. Prior to statistics analyses, assumptions of multivariate normality and homogenous variance were assessed using Q-Q plots, Shapiro-Wilk multivariate normality tests and Levene's tests for homogenous variance. We used a multivariate analysis of variance (MANOVA) to examine differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  among species and years, as carbon and nitrogen isotopes are likely not incorporated into consumer tissues independently of each other. We used a two-factor analysis of variance (ANOVA) to examine differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  separately among species and years. *Post-hoc* tests were used when one or both factors had a significant influence on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  using the Tukey HSD test.

At the species level, we quantified the SEA corrected for small sample size ( $\text{SEA}_c$ ). To provide a more robust measure of SEA, ellipses were quantified within a Bayesian framework ( $\text{SEA}_b$ ), along with niche overlap using the default settings (i.e., 20,000 iterations, 1000 burn in,

10 thinning rate, 2 chains, uninformative prior) in the package *SIBER* in R (Jackson et al. 2011). We present the mode of  $SEA_b$  as the most likely estimate of niche breadth, along with 95% credible intervals. We calculated pairwise measures of niche overlap from  $SEA_c$  between species within years, whereby the percentage of isotopic niche overlap was calculated using the overlapped area divided by the sum of the ellipse areas minus the overlapped area (Gulka et al. 2019). In addition, we quantified the percentage of iterations in which the  $SEA_b$  for one species was narrower than another within years as well as whether the  $SEA_b$  was narrower in one year relative to other years for each species.

We also used  $\delta^{13}C$  and  $\delta^{15}N$  values to describe the trophic diversity and redundancy at the seabird assemblage level. Trophic diversity was estimated using four metrics:  $\delta^{15}N$  range (NR),  $\delta^{13}C$  range (CR), total area (TA) and mean distance to centroid (CD), which represents the amount of niche space occupied by the assemblage (Layman et al. 2007). The extent of trophic redundancy was 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. We quantified trophic diversity and redundancy in a Bayesian framework using methods described by Layman et al. (2007) to qualitatively compare these metrics among years.

## **Results**

### *Capelin Biomass*

Multiple hydroacoustic surveys were conducted throughout July and August during 2017 (14, 21 July; 4, 9, 15 August), 2018 (9, 18, 24, 28 July; 7 August) and 2019 (12, 17, 22, 30 July; 7, 14 August). In 2017, capelin began spawning on August 4 with peak biomass of capelin ( $0.109 \text{ g/m}^2$ ) occurring on August 15. In 2018, capelin spawning began a month earlier on July

10, with a second wave of spawning occurring on July 18. Peak capelin biomass occurred on July 28 (0.259 g/m<sup>2</sup>). In 2019, capelin spawning began July 22 with peak capelin biomass occurring August 7 (0.098 g/m<sup>2</sup>). Overall, capelin biomass was similar during 2017 and 2019, but were two times lower relative to 2018. In addition, prior to arrival in the study area, average capelin biomass ranged from 0.0001 – 0.020 g/m<sup>2</sup>.

### *Seabird diet*

Prior to capelin arrival, prey types identified in parental prey deliveries to razorbill chicks comprised primarily of sandlance, whereas small fish or sandlance made up the majority of prey deliveries to puffin chicks and capelin made up majority of deliveries to murre chicks. After capelin arrival into the study area, capelin comprised the majority of identified prey types in chick diets observed or sampled from all seabird species in all years (Table 2).

Multivariate tests for normality and homogenous variance were met for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Two-factor MANOVA of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  revealed significant differences among species ( $F_{2,174} = 59.36$ ,  $p < 0.001$ ) and among years ( $F_{2,174} = 64.69$ ,  $p < 0.001$ ), with an interaction between species and years ( $F_{4,174} = 15.68$ ,  $p < 0.001$ ). Two-factor ANOVAs of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  separately showed significant differences among species ( $\delta^{13}\text{C}$ :  $F_{2,174} = 31.80$ ,  $p < 0.001$ ;  $\delta^{15}\text{N}$ :  $F_{2,174} = 258.94$ ,  $p < 0.001$ ) and among years ( $\delta^{13}\text{C}$ :  $F_{2,174} = 91.62$ ,  $p < 0.001$ ;  $\delta^{15}\text{N}$ :  $F_{2,174} = 58.31$ ,  $p < 0.001$ ), with an interaction between species and year ( $\delta^{13}\text{C}$ :  $F_{4,174} = 19.74$ ,  $p < 0.001$ ,  $\delta^{15}\text{N}$ :  $F_{4,174} = 12.07$ ,  $p < 0.001$ ). *Post-hoc* tests revealed that mean  $\delta^{13}\text{C}$  did not differ between species pairs in 2018, but did in 2017 and 2019, with the exception of razorbills and puffins in 2019 (Table 1). In addition, there were significant differences in mean  $\delta^{15}\text{N}$  between all species in each year except between murre and razorbills during 2018 and 2019 (Table 1). When comparing among

years within species, mean  $\delta^{13}\text{C}$  differed among all years for puffins, but did not differ among years for murre, and  $\delta^{13}\text{C}$  in razorbills in 2017 and 2019 differed from 2018 (Table 1).

Additionally, there were significant differences in mean  $\delta^{15}\text{N}$  between 2018 and 2019 for all species, while razorbills differed in mean  $\delta^{15}\text{N}$  between 2017 and 2018 and murre and puffins differed between 2017 and 2019 (Table 1).

When examining the percent of iterations that  $\text{SEA}_b$  was narrower for one species relative to another species within years, the niche breadth of razorbills was narrower than puffins and murre during 2017 in > 95% of iterations, while puffins and murre had a similar niche breadth (i.e. puffins < murre in 47.0% of the iterations; Fig. 2a). During 2018, the niche of murre was broader than razorbills and puffins in 77.1-98.6% of the iterations, respectively, while razorbills were broader than puffins in > 93% of the iterations (Fig. 2b). During 2019, murre and razorbills had similar niche breadth with puffins (i.e. puffins < murre and razorbills in 42.1-53.9% of the iterations, respectively), while murre were narrower than razorbills in 62% of iterations (Fig. 2c). Pairwise niche overlap was typically < 20% (0-18.3%) between species within a year, except for murre and razorbills in 2018 (61.5 %) and 2019 (46.1 %; Fig. 2).

When examining the percentage of iterations that  $\text{SEA}_b$  was narrower for one year relative to another year within a species, the niche breadth of razorbills in 2019 was broader than in 2017 and 2018 in > 90% of iterations, while 2017 and 2018 had a similar niche breadth (i.e. 2017 > 2018 in 42.5% of the iterations; Fig. 2). For puffins, niche breadth in 2018 was narrower than in 2017 and 2019 in > 99% of iterations, while 2019 was narrower than 2017 in 72% of iterations (Fig. 2). Murre niche breadth in 2017 was broader than in 2019 and 2018 in 76.6-84.2% of iterations, respectively, while the niche breadth in 2018 was narrower than 2019 in 60.6% of iterations (Fig. 2).

In 2017, the seabird assemblage occupied a larger isotopic niche space than subsequent years as indicated by the greater carbon and nitrogen range as well as total area, distance to centroid and average distance to nearest neighbor with similar distances noted by the lower SDNND (Table 3; Fig. 2). In the following years, the total area occupied decreased during 2018 and decreased even further in 2019 with the exception of carbon range.

## **Discussion**

Overall, we found support for the hypothesis that isotopic niche metrics of razorbills, puffins and murre are influenced by capelin availability. As predicted, niche breadth contracted and trophic position shifted towards capelin during higher (2018) relative to lower capelin availability years (2017, 2019) for two of the three species, as evidenced by contraction of  $SEA_c$  and higher mean  $\delta^{15}N$ ; suggesting lower dietary diversity and a higher reliance on capelin when capelin availability increased. Trophic diversity also decreased as predicted during a higher (2018) relative to a lower capelin availability year (2017), as indicated by decreased total area and  $\delta^{15}N$  and  $\delta^{13}C$  range, suggesting that the seabird assemblage fed on a narrower variety of prey when capelin availability was higher. Alternately, trophic diversity was lower during a lower (2019) relative to higher capelin availability year (2018).

Differences in the timing of blood sampling relative to capelin spawning among years may have influenced our interpretations of shifts in isotopic niches and trophic diversity among years. Indeed, during 2017, seabird blood sampling occurred 7-10 days after capelin began spawning, similar to 2018 (6-10 days after spawning), while blood sampling during 2019 occurred either 1-2 days before (puffins, murre) or 7 days after (razorbills) capelin spawning. As stable isotope ratios of red blood cells represent the averaged diet across 2-3 weeks (Hobson & Clark 1993, Bearhop et al. 2002), stable isotope ratios from puffins and murre in 2019

primarily represent the period of lower capelin availability before spawning in the study area, while 2017 and 2018 primarily represent the period of higher capelin availability after spawning. As observations of parental prey deliveries to chicks during 2019 indicate a dietary switch to capelin after capelin arrived in the study area (Table 2), blood sampling puffins and murres later in the season, to allow for increased incorporation of capelin into the averaged diet, likely would have resulted in higher trophic position and niche breadth contraction during 2019. This variation of blood sampling in relation to capelin reiterates the need to carefully consider sampling dates and tissue turnover rates when planning diet studies using stable isotopes (Inger & Bearhop 2008, Bond & Jones 2009).

#### *Species-level differences*

With higher relative to lower capelin availability, puffins and razorbills increased trophic position and isotopic niche breadth contracted, as has been observed in previous studies examining intra-annual changes in diet after capelin arrival inshore, including non-breeding shearwaters and whales (Carvalho & Davoren 2019; Gulka et al. 2017) and alcids (Jenkins & Davoren 2020). These isotopic niche shifts likely indicate reduced prey diversity in the diet and a higher reliance on capelin, which were supported by parental prey deliveries to chicks. In contrast to these findings, however, murre trophic position and dietary niche breadth changed less between lower and higher capelin availability years, suggesting that murre isotopic niche metrics are less influenced by varying capelin availability and may search for capelin regardless of availability. In support, murres in the study area are known to specialize on capelin, shown by consistently high proportions of capelin in parental prey deliveries to chicks (Davoren & Montevecchi 2003, Montevecchi et al. 2019) but may incorporate more alternate prey types (e.g.,

sandlance) into the parental diet when they are more abundant (Gulka & Davoren 2019, Gulka et al. 2020). As murrelets are single-prey loaders, delivering one prey item to their chicks at a time, whereas razorbills and puffins are multiple-prey loaders, it would be advantageous to deliver higher quality prey, like capelin, to their chicks. In support, single-prey loading seabirds, including murrelets, have been shown to be more affected by the quality of available prey compared to multi-prey loaders (Wanless et al. 2005, Frederiksen et al. 2006). Indeed, energy densities of gravid female capelin appear to be higher (Montevecchi & Piatt 1984) relative to adult (Lawson et al. 1998) and juvenile sandlance (Van Pelt et al. 1997), although energy densities of forage fish have not been assessed during the breeding season in coastal Newfoundland. In addition, capelin form persistent, high density spawning aggregations (Davoren et al. 2006) where predators can locate highly abundant prey (Davoren et al. 2003) while sandlance exhibit highly patchy distributions (Staudinger et al. 2020). Although dietary flexibility has been observed in common murrelets in the Atlantic (Bryant et al. 1999, Montevecchi et al. 2019), Pacific (Oedekoven et al. 2001) and thick-billed murrelets (*Uria lomvia*) in the Arctic (Gaston & Elliott 2014), another study showed that murrelets continued to feed on higher trophic level prey when prey was limited during the breeding season in Alaska (Barger & Kitaysky 2012), similar to our findings. Razorbills and puffins, on the other hand, seem to be more flexible and are known to feed and provision their chicks with both fish and crustaceans throughout their ranges (Harris & Wanless 1986, 2011, Thompson et al. 1999, Barrett 2015) and studies in the northwest Atlantic have shown altered dietary proportions when capelin availability is low (Baillie & Jones 2004, Lavers & Jones 2007, Gulka et al. 2019). Overall, these findings suggest that razorbills and puffins are more flexible under varying capelin availability during the

breeding season and, thus, decreased biomass of high-quality capelin may have a greater impact on murre than these other alcid species.

#### *Assemblage-level differences*

Higher trophic diversity during lower (2017) relative to higher (2018) capelin availability years suggested that the seabird assemblage fed on a narrower variety of prey types under higher capelin availability conditions. These findings are consistent with generally higher isotopic niche overlap between species during higher (2018) relative to lower (2017) capelin availability years, as found in other studies on marine predator isotopic niches in coastal Newfoundland under varying capelin availability both within years (Gulka et al. 2017, Jenkins & Davoren 2020) and across years (Carvalho & Davoren 2019). Higher isotopic overlap during high capelin availability was especially evident for razorbills and murre and appeared to result from razorbills feeding at a higher trophic level. Similarly, previous studies have found high niche overlap and similar dietary proportions of razorbills and murre (Pratte et al. 2017, Gulka et al. 2019) but overlap decreased during lower capelin availability periods (i.e. pre-spawning) within years (Gulka et al. 2019, Jenkins & Davoren 2020). Alternately, the relatively high isotopic niche overlap of murre and razorbills during lower capelin availability in 2019, which appeared to result from murre feeding at a lower trophic level, could be explained by the later sampling date of razorbills (post-capelin spawning) and the earlier sampling date of murre (pre-capelin spawning).

In contrast to our predictions, trophic diversity and other niche metrics at the assemblage level, with the exception of  $\delta^{13}\text{C}$  range, were lower during 2019, when isotope niches of murre and puffins primarily represented the low capelin availability period prior to spawning. This finding suggests that seabird diets also may converge on fewer, alternative prey types under

lower capelin availability conditions. In support, puffin niche overlapped more with the niches of razorbills and to a degree with murrelets during lower (2017, 2019) relative to higher (2018) capelin availability years. As puffins are known to feed on lower trophic level prey (Barrett 2002, 2015, Pratte et al. 2017), supported by the consistently lower  $\delta^{15}\text{N}$  of puffins relative to the other two species in this study, all three species may converge on these lower trophic level prey when capelin availability is low. This is supported by chick diet observations (Table 2), where all species tended to capture sandlance and other small fish prior to capelin spawning in the study area.

Despite high isotopic niche overlap during years of this study, we cannot preclude that these species partition their niches along alternate axes under low prey availability. Indeed, coexistence of these similar seabird species is thought to result in part from differences in foraging behavior (Cody 1973, Croxall & Prince 1980). As maximum dive depths vary among murrelets (180 m, Piatt & Nettleship 1985), razorbills (120 m, Piatt & Nettleship 1985) and puffins (60-70 m, Burger & Simpson 1986), due to body size differences, these species have access to different prey types. For instance, studies showing similar dietary proportions of murrelets and razorbills during the breeding season also found that these species differ in either dive depth (Linnebjerg et al. 2013, 2015) or foraging locations (Gulka et al. 2019), suggesting that they vertically and horizontally partition their foraging environment. Similarly, sympatrically breeding murrelets, razorbills and puffins have been found foraging in different locations (Wanless et al. 1990, Pratte et al. 2017) while incorporating different proportions of the same prey types into their diet (Pratte et al. 2017). As capelin have become highly variable in the timing of arrival and spawning (Davoren et al. 2012, Crook et al. 2017), however, this may lead to increased periods of low capelin availability and higher isotopic niche overlap during the breeding season,

which could alter species interactions among seabirds and possibly their ability to coexist during breeding in coastal Newfoundland.

## **Conclusion**

Overall, understanding a species' niche, where niche axes represent a wide variety of environmental factors (e.g. habitat and food availability), can provide insight into ecological processes, including resource selection and predator-prey interactions, as well dynamics in species interactions and ultimately food webs if studied in a multi-species context. This is particularly important during energetically demanding periods of the annual cycle, such as the breeding season, when adults must provision both their offspring and themselves (Gaston 1985, Wood et al. 2000, Benvenuti et al. 2002). Increasing variability in capelin biomass and timing of availability related to dynamic oceanographic conditions (Davoren et al. 2012, Crook et al. 2017, Buren et al. 2019) may lead to increased reliance on other forage fish, sandlance in particular, for which there is little known in the northwest Atlantic (Staudinger et al. 2020). Despite the high reliance of breeding seabirds on capelin in coastal Newfoundland, few studies directly link varying capelin biomass and breeding success (Burke & Montevecchi 2009, Regular et al. 2014). Future studies, focused on investigating how changes in dietary proportions of adult and chick diet affect foraging behavior and reproductive success at the seabird assemblage level in a multi-year context will provide further understanding of how the coastal Newfoundland food web will shift under future changes in ocean climate.

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## Tables and Figures

Table 1. Mean ( $\pm$  SE) carbon ( $\delta^{13}\text{C}$ ), nitrogen ( $\delta^{15}\text{N}$ ) values and carbon to nitrogen (C:N) ratios of red blood cells from breeding razorbills (RAZO), Atlantic puffins (ATPU) and common murrelets (COMU) across three years (2017 – 2019) from different breeding islands ('location') on the northeast Newfoundland coast. Date of blood sampling is indicated for each year, along with the number of days sampling occurred before ('pre') or after ('post') capelin began spawning in the study area. The number of blood samples collected is indicated by "n". Statistically significant differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values among species and years are indicated by different letters (e.g., a, b). Modal Bayesian standard ellipse area ( $\text{SEA}_b$ ) and 95% confidence intervals (in parentheses) are provided. Data sources for mean ( $\pm$  SE) carbon ( $\delta^{13}\text{C}$ ), nitrogen ( $\delta^{15}\text{N}$ ) values for prey (capelin, sandlance, and small fish) are <sup>1</sup>Gulka et al. 2019, <sup>2</sup>Gulka et al. 2020.

Species	Year	Sampling Date	Pre/Post Spawn	Location	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C:N	SEAb
RAZO	2017	14-August	10 post	James	17	-19.92±0.06 <sup>c</sup>	14.08±0.06 <sup>b</sup>	3.34±0.01	0.099 (0.059, 0.163)
	2018	20-July	10 post	James	20	-19.56±0.03 <sup>a</sup>	14.82±0.06 <sup>a</sup>	3.20±0.01	0.108 (0.069, 0.162)
	2019	29-July	7 post	James	19	-19.82±0.03 <sup>bc</sup>	14.11±0.08 <sup>b</sup>	3.28±0.01	0.154 (0.106, 0.251)
ATPU	2017	14-August	10 post	James	15	-20.22±0.06 <sup>d</sup>	13.22±0.07 <sup>c</sup>	3.27±0.01	0.185 (0.107, 0.316)
	2018	20-July	10 post	James	20	-19.46±0.03 <sup>a</sup>	13.33±0.04 <sup>c</sup>	3.15±0.01	0.066 (0.047, 0.103)
	2019	20-July	2 pre	James	18	-19.82±0.05 <sup>c</sup>	12.83±0.06 <sup>d</sup>	3.36±0.01	0.155 (0.010, 0.245)
COMU	2017	11-August	7 post	Cabot	20	-19.72±0.03 <sup>ab</sup>	14.78±0.09 <sup>a</sup>	3.29±0.00	0.181 (0.111, 0.287)
	2018	16-July	6 post	Funk	20	-19.60±0.03 <sup>a</sup>	14.62±0.09 <sup>a</sup>	3.25±0.00	0.131 (0.085, 0.211)
	2019	21-July	1 pre	Funk	20	-19.65±0.03 <sup>a</sup>	13.95±0.09 <sup>b</sup>	3.22±0.01	0.144 (0.094, 0.225)
Capelin	2017 <sup>1</sup>	1, 5 August			15	-20.64±0.07	12.12±0.14		
	2018 <sup>2</sup>	7, 26, 27 July			10	-20.27±0.05	12.18±0.07		
	2019	24, 28 July; 3-August			12	-20.48±0.09	12.53±0.07		
Sandlance	2017 <sup>1</sup>	14-July; 4-August			9	-21.19±0.06	10.11±0.09		
	2018 <sup>2</sup>	6-June; 3-July; 7, 9, 18 August			12	-21.01±0.06	10.55±0.14		
	2019	22-July; 7, 14, 18 August			10	-21.15±0.06	10.53±0.09		
Small Fish	2017 <sup>1</sup>	14-August			23	-22.58±0.03	9.26±0.09		

Table 2. The percentage of known prey types in parental prey deliveries to chick by chick-rearing razorbills (RAZO), Atlantic puffins (ATPU) and common murrelets (COMU) collected from camera traps, observations and pole nets of adults during 2017-2019 divided into two periods of capelin availability: before capelin arrival in the study area (low) and after capelin arrival (high). Percent (%) identified is the percentage of prey items that were identified out of all the bill loads observed. The number of prey deliveries observed (camera, observations) or captured (pole nets) is indicated ('n'). Data from Gulka et al. (2020) are reported as percentage of capelin only, as the percentage of sandlance, small fish and prey items identified were not provided.

Species	Year	Prey period	Sampling date range	Location	n	Prey percentages (%)				Method	Source
						Capelin	Sandlance	Small Fish	% Identified		
RAZO	2017	Low	July 31 – August 2	James	8	28.6	71.4	0	87.5	Camera	Gulka et al. 2019; Jenkins & Davoren 2020
		High	August 4 – August 10	James	3	100	0	0	66.7	Camera	
	2019	Low	July 19	James	10	0	100	0	100	Observation	This study
		High	July 28; August 6	James	35	88.6	11.4	0	100	Observation	This study
ATPU	2017	Low	July 28 – August 3	James	26	8.3	91.7	0	46.2	Camera	Jenkins & Davoren 2020
		High	August 9 – August 10	James	3	100	0	0	100	Camera	Jenkins & Davoren 2020
	2019	Low	July 19	James	18	5.6	5.6	88.9	100	Observation	This study
		High	July 28; August 6	James	120	60.8	9.2	30	100	Observation	This study
COMU	2017	Low	July 22 – August 1	Cabot	315	77.9	22.1	0	47.3	Camera	Gulka et al. 2019; Jenkins & Davoren 2020
		High	August 2 – August 11	Cabot	427	99.6	0.4	0	60.2	Camera	
		High	August 5 – August 11	Funk	234	89	-	-	-	Pole net	Gulka et al. 2020
	2018	High	July 15 – August 2	Cabot	276	99.2	0.9	0	42.8	Camera	Gulka et al. 2020
	2018	High	August 12 – August 14	Funk	51	98	-	-	-	Pole net	Gulka et al. 2020

Table 3. Mode and 95% credible intervals for Bayesian Layman’s metrics for seabird assemblage consisting of razorbills, Atlantic puffins and common murrens from 2017 – 2020.

	<b>2017</b>	<b>2018</b>	<b>2019</b>
<i>Trophic diversity</i>			
<b>δ<sup>15</sup>N range</b>	1.48 (0.75, 2.19)	1.39 (0.85, 1.99)	1.21 (0.58, 1.77)
<b>δ<sup>13</sup>C range</b>	0.42 (0.05, 1.02)	0.31 (0.01, 0.75)	0.38 (0.02, 0.87)
<b>Total area</b>	0.06 (0.00, 0.51)	0.03 (0.00, 0.40)	0.03 (0.00, 0.43)
<i>Trophic redundancy</i>			
<b>Distance to centroid</b>	0.61 (0.35, 0.89)	0.60 (0.37, 0.83)	0.54 (0.30, 0.80)
<b>Nearest neighbor distance</b>	0.75 (0.41, 1.11)	0.64 (0.37, 0.98)	0.58 (0.31, 0.98)
<b>Standard deviation of nearest neighbor</b>	0.24 (0.00, 0.71)	0.45 (0.01, 0.82)	0.37 (0.00, 0.71)

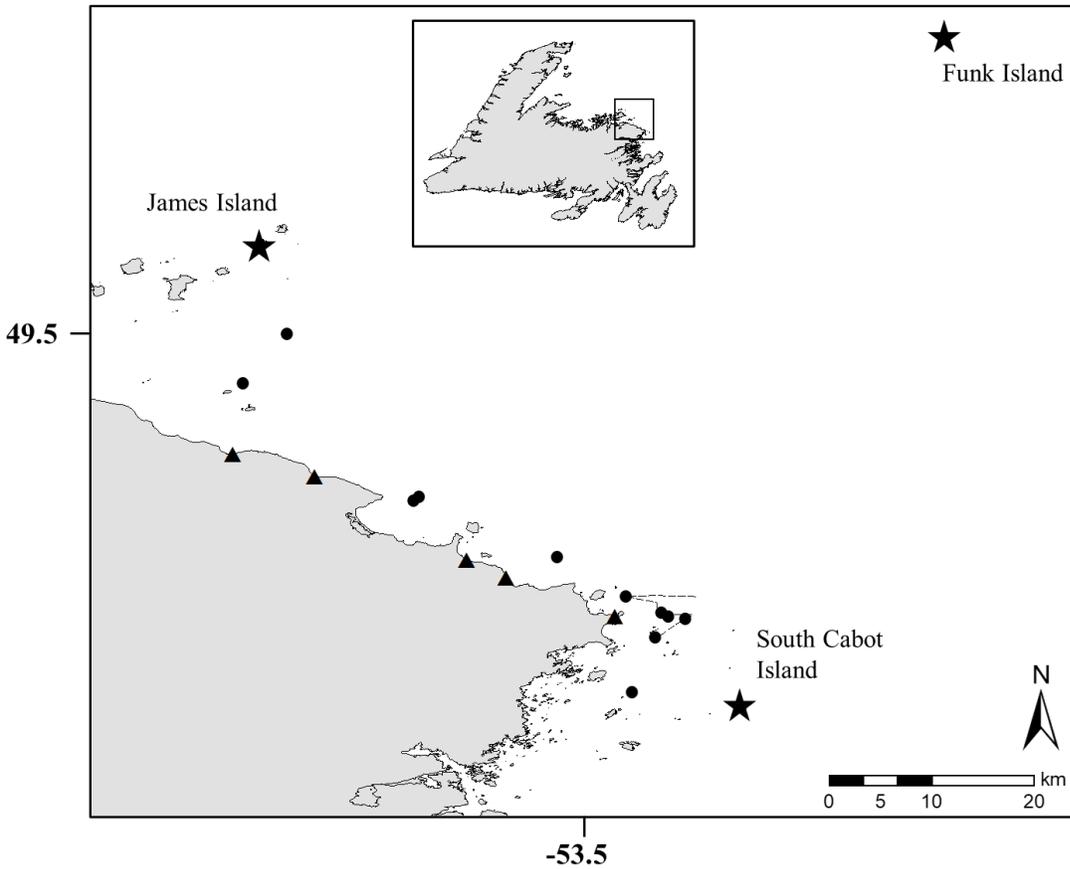


Figure 1. Map of study area showing the northeast Newfoundland coast. Dashed line indicates survey route for hydroacoustic surveys. Deep-water capelin spawning sites (circles) and beach spawning sites (triangles) are indicated. Stars indicate seabird breeding colonies where seabird blood sampling and prey observations and sampling were conducted.

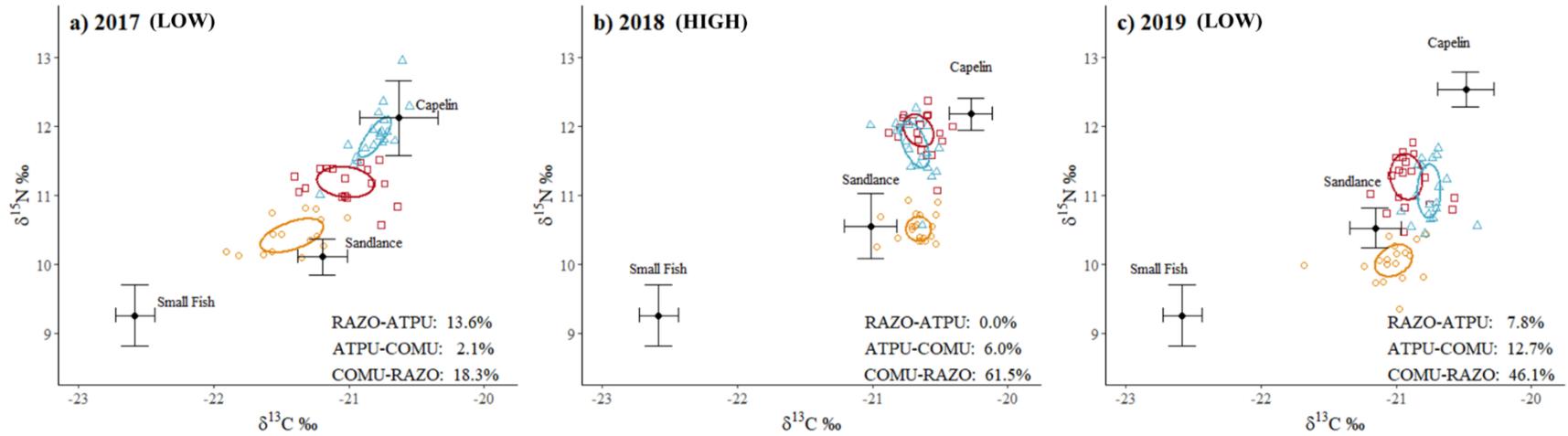


Figure 2. Biplots of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values and  $\text{SEA}_c$  from red blood cells of razorbills (RAZO; red square), Atlantic puffins (ATPU; orange circle), and common murrelets (COMU; blue triangles) during lower (LOW) and higher (HIGH) capelin availability years from a) 2017, b) 2018 and c) 2019 in coastal Newfoundland. Mean and standard error bars of prey are shown. Text indicates the percent overlap in  $\text{SEA}_c$  between each pair of species.

## General Conclusion

Understanding how prey biomass influences the responses of multiple predator species in an inter-annual context provided insight into predator-prey interactions and dynamics in species interactions. In this thesis, I found evidence that decreased capelin (*Mallotus villosus*) biomass resulted in increased foraging effort, decreased adult and chick body condition and dietary reliance on alternative prey types by chick-rearing razorbills (*Alca torda*) in coastal Newfoundland. During the year when peak capelin biomass was the lowest on record in a decadal time series (2020), foraging effort was higher as indicated by increased foraging trip duration and distance and number of dives, relative to years with higher capelin biomass (2017, 2019). Additionally, foraging effort did not decrease after the arrival of spawning capelin in 2020, as was seen in other years. Increased foraging effort during 2020 was also associated with lower chick and adult body condition, which may have been related to birds traveling farther to capture capelin. Findings from razorbills suggest that continued variability in capelin biomass and timing of spawning can lead to increased energy expenditure and reduced adult and chick body condition, although long-term effects of varying prey availability on adult and chick survival are unclear. Due to the short chick-rearing period of razorbills (~ three weeks) along with logistical difficulties of landing on James Island (i.e., weather) and the need to minimize human-induced disturbance (i.e., short stays on the island), we were unable to collect high-quality reproductive success data. In the future, directly measuring reproductive success, in combination with foraging effort and prey availability, will provide a better understanding of how varying prey regimes will affect seabird population dynamics. Additionally, long-term studies examining how variation in body condition of chicks at fledging and of post-breeding adults influence return rates of seabirds to breeding colonies (i.e. recruitment and annual survival

rates) will also be important to understand how these populations may be affected by changing prey biomass.

While I was able to combine data from multiple years to examine the influence of prey biomass on foraging effort, consistent use of similar GPS-TDR bird-borne devices would have allowed comparable measurements of time/activity budgets within and across years.

Time/activity budgets are critical to understand individual-level allocation decisions of time and energy to different activities under environmental challenges to test life history predictions.

Unfortunately, I was unable to directly quantify the proportion of time spent in different activities (i.e., foraging, flying, resting at sea, chick brooding) due to the use of variable device types and, thus, I recommend future studies consistently use the same combined GPS-TDR loggers across years.

Although it is unknown whether other sympatric breeding seabirds in the study area experienced similar challenges during these low capelin biomass years, previous studies have shown that common murre (*Uria aalge*) foraging effort is higher and adult body mass is lower in lower capelin biomass years in my study area (Montevecchi et al. 2019, Gulka et al. 2019).

Unfortunately, little is known about the responses of Atlantic puffins (*Fratercula arctica*) to these changes in prey availability in coastal Newfoundland. With continued decreases in the size of bird-borne loggers, tracking these and other smaller species in the area (i.e. storm-petrels) will provide further knowledge on the impacts of prey availability on seabirds. Insight on the lower trophic level prey that puffins feed on may also help to understand what other alternate prey types are available for other seabird species. Overall, studies simultaneously examining multiple seabird species will provide insight on how sympatrically breeding seabirds are impacted by

variable prey regimes along with the potential long-term population-level consequences for seabirds in coastal Newfoundland as well as other regions.

Understanding shifts in dietary niche metrics of sympatric breeding seabirds under varying prey availability can provide insight into species interactions. At the species-level, I found that razorbill and Atlantic puffin niche breadth contracted and trophic position increased during higher capelin availability years, indicating a higher reliance on capelin and a lower diversity of prey in the diet, although Atlantic puffins continued to feed at a lower trophic level relative to razorbills and common murre. Alternatively, common murre seemed to consistently incorporate higher proportions of capelin in the diet under varying capelin availability. At the assemblage-level, trophic diversity was lower during higher (2018) relative to lower (2017) capelin availability years, as indicated by the total space occupied by the assemblage and increased overlap among species. Indeed, increased isotopic niche overlap of razorbills, Atlantic puffins and common murre, resulted in a convergence on capelin, although increased overlap was also observed during a lower capelin biomass year. This convergence on alternate prey types during lower prey periods/years may have an impact on species interactions as species may compete for lower density, less predictable alternative prey. Indeed, while 2017 and 2019 were considered lower biomass years in Chapter 2, these years are considered average across the 10-year capelin biomass dataset (Davoren unpubl. data). The convergence on alternate prey during 2019 suggests that there may be a higher probability of competition among seabird species in this year and possibly other average capelin availability years. As timing of sampling impacted interpretation of isotopic niche metrics, careful consideration of timing of tissue sampling for stable isotope analysis is key to understanding how these species interactions vary among years in relation to prey availability. Ultimately, I showed that variability in capelin biomass among

years may lead to changing interactions among predator species. Therefore, future studies that examine how multiple predator species respond to changes in prey availability in a multi-year context will continue to provide insight into how predator interactions may be affected by changes in prey availability.

Overall, my thesis revealed that seabird species in coastal Newfoundland may experience high foraging effort, decreased adult and chick body condition and potentially increased competition for less available, lower quality prey types when capelin availability during the summer breeding season is lower. Throughout my thesis, I was able to assess seabird responses to one of the highest capelin biomass years (2018) and the lowest capelin biomass years (2020) on record along with two average capelin biomass years (2017, 2019) over a decadal-scale dataset (Davoren unpubl. data). Independently collecting prey biomass concurrently with colony-based measures of seabird foraging behavior, within a long-term context, provided an important framework to assess responses of seabirds to varying prey availability, which few studies have done (e.g., Piatt et al. 2007, Carvalho & Davoren 2019, Montevecchi et al. 2019, Gulka et al. 2020). As prey conditions may continue to increase in variability due to natural and human-induced changes, these changes in predator foraging effort and species interactions may become more drastic and impact the coexistence of these species.

### *Future research*

Quantifying the quality of various forage fish species is key to understanding the impact of varying dietary proportions of marine predators. A typical metric of fish quality is energy densities (kJ/g). Energy densities of forage fish may vary seasonally, due to changing energy reserves in different periods of their life cycle combined with habitat use (e.g., inshore, offshore),

and among years, due to inter-annual changes in oceanography and productivity (Lawson et al. 1998). Energy densities of the primary forage fish species in coastal Newfoundland have not been assessed in over 20 years and have not been consistently assessed in coastal regions during the summer seabird breeding season (Montevecchi & Piatt 1987, Lawson et al. 1998). Future research focusing on quantifying energy densities of forage fish species during the summer in coastal Newfoundland will be important to provide a better understanding of prey quality and the impact of dietary variation during the seabird breeding season.

With increasing variability in capelin availability, other forage fish species, especially sandlance (*Ammodytes spp.*), may become more important in seabird diets. Indeed, sandlance species are the primary food source for seabirds in other regions (Harris & Wanless 1986, Barrett & Furness 1990), Unfortunately, little is known about the environmental drivers of sandlance population dynamics (Staudinger et al. 2020) and, thus, how increasing climate variability will impact sandlance availability in coastal Newfoundland. Additionally, it is unknown whether environmental drivers of population dynamics are similar across forage fish species and, thus, whether abundance will vary inter-annually in unison or not. Future research, focusing on environmental drivers of the population dynamics of multiple forage fish species will provide insight into the tolerance of top predators, like seabirds, to future climate change.

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