

FROM POPULATIONS TO INDIVIDUALS: UNDERSTANDING FORAGING NICHE
DYNAMICS, INDIVIDUAL SPECIALIZATION, AND BEHAVIORAL PLASTICITY IN
THE COMMON MURRE (*URIA AALGE*) AND RAZORBILL (*ALCA TORDA*) IN
NORTHEASTERN NEWFOUNDLAND

By

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Abstract

Understanding variation among individuals, populations, and species under variable environmental conditions can help us to understand each level's sensitivity to change. During the breeding season, the foraging ecology of seabirds is largely influenced by prey availability, reproductive demands, and interactions among conspecifics and heterospecifics. The goal of this thesis was to examine individual specialization, niche partitioning, and phenotypic plasticity in common murre (*Uria aalge*) and razorbills (*Alca torda*) breeding at nearby colonies on the northeastern Newfoundland coast. We used a combination of GPS tracking and stable isotope analysis ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) to examine behavioral and dietary aspects of foraging ecology at the individual and population level in relation to changes in prey availability. For common murre, we found high within-individual variation in foraging trip and dive characteristics, coupled with low spatial overlap of foraging trips both within and between individuals, indicative of flexible foraging behavior, which contrasted a degree of dietary consistency. This behavioral plasticity remained despite inter-annual changes in prey availability. At the population level, murre and razorbills exhibited complete spatial segregation between foraging areas and divergent dive characteristics, which contrasted high dietary overlap, as well as similar habitat preferences and diurnal foraging patterns, suggesting that spatial segregation may be the primary response to competition for the same resources. As prey availability shifted from low to high, individuals of both species foraged closer to the colony and diet proportions shifted similarly, indicative of reduced energy costs and dietary plasticity to take advantage of highly available prey. Together, these findings support flexible foraging strategies for both species and provides insight into how individuals and populations interact and respond to environmental variation, which is critical for conservation.

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Thesis Format

This thesis is presented in manuscript format. Both chapters are independent, with their own introduction, methods, results, discussion, and references. They are accompanied by an overall 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

Foraging theory predicts that an individual will perform an activity until the costs exceed the benefits (Stephens et al. 2007). Indeed, foraging theory predicts that animals that forage in a heterogeneous environment find ways to maximize their net energy gain with the goal of maximizing their fitness (Kowalczyk et al. 2015). While foraging, an animal has a set of choices or options under its control and constraints on those choices, including its ability to find and capture prey, predation risks, physiological needs, and temperament differences (Stephens et al. 2007, Dehnhard et al. 2016). Therefore, a primary underlying assumption of foraging ecology is that the best strategy is based on this core trade-off, maximizing benefits while minimizing costs.

During the breeding season, many species must leave breeding areas to forage but must continuously return to these same areas. As such, they act as central-place foragers, where the central place is the breeding area to which they must return between each foraging trip. The need to return to the central place constrains the total distance from the central location that they can travel, thus limiting their foraging range (Orians and Pearson 1979). In the case of seabirds, breeding birds forage at sea but must return to the breeding island to incubate their egg or feed their chick, which limits their foraging range from the island, impacting resource patch choice. Therefore, a resource patch should only be used until costs outweigh benefits (Olsson and Bolin 2014). Within the limited foraging range of the breeding site, the distribution, abundance, and predictability of food all act as foraging constraints (Paiva et al. 2010). If suitable breeding habitat is aggregated and many conspecifics and heterospecifics forage within a similar limited range, these limitations can lead to increased inter- and intra-specific overlap in resource use, causing the need for resource partitioning if resources are, or become limited (Linnebjerg et al. 2013).

There are different ways to define an ecological niche, but in general, it encompasses the environmental conditions, both abiotic and biotic, required to meet the minimum requirements for survival and reproduction, such that the population is stable (Chase and Leibold 2003). Charles Elton first defined a species' niche as the sum of interactions that link it to other species in an ecosystem (Elton 1927), whereas G.E. Hutchinson defined the ecological niche as the n-dimensional hypervolume with axes that represent environmental variables (Hutchinson 1978). A species' fundamental niche consists of all conditions that allow the population to exist stably, whereas the realized niche represents a subset of that fundamental niche that is actually occupied in the presence of competitors, predators, barriers and other factors (Phillips et al. 2006). There are different ways a niche can be characterized. For instance, niche breadth is an indication of the variety of resources used, whereas niche position indicates the types of resources used, and niche overlap indicates the similarity in resource use among individuals or species (Hammerschlag-Peyer et al. 2011).

Niche Partitioning

Interspecific interactions shape how species interact and communities develop. Niche theory offers important context for the study of resource partitioning, involving different aspects of resource use, interactions among species and individuals, community composition, and evolutionary processes (Polito et al. 2015). The competitive exclusion principle postulates that two species with the same resource requirements cannot coexist if resources are limiting (Gause 1934). Thus, species may use different tactics to reduce niche overlap, with niche partitioning theory positing that if overlap occurs between species in one niche dimension, divergence is predicted in another dimension (Gause 1971). In particular, resource partitioning can result in

differences in prey type, habitat choice, and foraging behavior among sympatric species (e.g., Masello et al. 2010, Beaulieu and Sockman 2012, Linnebjerg et al. 2013, Bonato et al. 2018, Sivy et al. 2018) or among conspecifics (e.g., Lewis et al. 2002, Phillips et al. 2004). The ways in which niche partitioning may occur can be influenced both by species interactions and availability of resources. Species may be disparately affected by heterospecifics, known as asymmetrical competition, whereby one species may be more strongly impacted while the other species is less affected, or competitively dominant (Connell 1983). Asymmetrical competition is common in nature and can relate to physical and behavioral traits (Dupuch et al. 2014). The abundance and distribution of food resources also plays a key role in competitive interactions, as niche overlap may only result in competition when prey is limited, with prey superabundance expected to minimize competition and, thus, the degree of niche partitioning (Giller 1984, Forero et al. 2004).

While aspects of resource partitioning have been examined in many seabird species through the examination of foraging trip and dive characteristics (e.g., Frere et al. 2008, Kokubun et al. 2010, Linnebjerg et al. 2015, Peck-Richardson et al. 2018), habitat use (e.g., Hyrenbach et al. 2002, Nicholls et al. 2002, Gonzalez-Solis et al. 2008, Wakefield et al. 2017), and diet (e.g., Navarro et al. 2009, Young et al. 2010, Mancini and Bugoni 2014, Jiménez et al. 2017), the focus is often on one or a few aspects of niche dynamics between species. The use of multiple techniques simultaneously, particularly the use of tracking devices (e.g., GPS, geolocators, satellite tags) coupled with stable isotope analysis allows for the examination of foraging behavior and diet, providing information on many niche dimensions simultaneously. By using this approach, we can gain greater understanding of niche dynamics between species.

Individual Specialization and Phenotypic Plasticity

Many ecological studies assume individual-level consistency in resource partitioning and ecological niche dynamics within a population. In reality, individuals can exhibit a great deal of variation in resource use (Ceia and Ramos 2015). This individual-level variation may be due to morphological characteristics, sex differences, competition and predation pressures, resource dynamics, or temperament differences. Understanding this variation at the individual level is critical to understanding a species' ecology and a population's resiliency to environmental change (Hückstädt et al. 2012).

Examining foraging behavior and diet of individuals allows further understanding of how individual-level variation contributes to population-, community-, and ecosystem-level patterns (Toscano et al. 2016). Indeed, this fine-scale examination can help characterize intra- and interspecific interactions, including competition, niche partitioning and overlap, competitive exclusion and coexistence (Stephens et al. 2007). Variation among individuals can be characterized by quantifying the degree of individual specialization. On a coarse scale, individual specialization involves the distinction between a specialist and generalist individual or population, with a specialist using a much narrower niche, or set of resources, than that of a generalist (Bolnick et al. 2003). If all individuals in a population use the same narrow niche with little or no variation, a specialist population will result. In contrast, all individuals using different narrow niches will combine to form a wide niche, known as a Type B generalist population. A Type A generalist population, however, consists of generalist individuals that all use an equally wide niche, exploiting a wide variety of resources with large amounts of variation within individuals (Bolnick et al. 2003, Hückstädt et al. 2012, Polito et al. 2015). Individuals may differ in both the types and proportions of resources that they use (Patrick and Weimerskirch 2014a).

An important caveat is that these individual-level differences are not due to sex, age, or distinct morphological characteristics (Bolnick et al. 2003).

Increasingly, ecologists are becoming cognizant of the presence and influence of individual specialization on population dynamics. In particular, specialization has been studied in the foraging behavior of marine predators, including seabirds (Bolnick et al. 2003). Many studies have documented varying levels of specialization in diet and resource use in seabirds, including albatross and petrels (Hedd et al. 2001, Jaeger et al. 2010), penguins (Polito et al. 2015), gannets (Hamer et al. 2007), auks (Woo et al. 2008, Day et al. 2012) and gulls (Masello et al. 2013). As seabirds are apex predators, specialization in resource use is important to quantify for conservation purposes in the face of environmental change. Specialization is a mechanism through which niche differentiation and resource partitioning can occur, but there are ecological trade-offs. Specialists may be more successful in good resource years, but often exhibit higher sensitivity to environmental change in bad years, while generalists with a broad niche tend to be more resilient (Polito et al. 2015). By shifting focus from the population level to the individual level, we can begin to gain a greater understanding of the sources of variation at the population level and how this variation impacts community-level dynamics.

Understanding population vulnerability relies not only on the understanding of individual specialization, but also on phenotypic plasticity. Phenotypic plasticity is defined as the ability of a genotype to modify its outward appearance and/or behavior (i.e. phenotype; Dehnhard et al. 2016). Generally, morphological and physiological traits tend to be less plastic than behavioral traits, and as such, shifting behavioral patterns is the more likely ecological response to immediate environmental change (Linnebjerg et al. 2013). Phenotypic plasticity, or behavioral flexibility, can be studied by looking at individual-level responses to changing environmental

conditions, whereas the population-level response can be a consequence of a multiplicity of individual-level responses (Grémillet and Charmantier 2010). Two scenarios are possible when a population displays an average plastic response: 1) all individuals respond the same or 2) individuals respond in different ways (Reed et al. 2006). Understanding how individuals respond to environmental variation, particularly in the face of current levels of rapid environmental change, is critical for conservation (Reed et al. 2006, Ramírez et al. 2016).

Study Species and Area

This research will focus on two sympatrically nesting seabirds, the common murre (*Uria aalge*) and the razorbill (*Alca torda*), that share a large part of their range during both the breeding and non-breeding season, and even commonly breed in the same colony (Chivers et al. 2012). Sympatric seabirds commonly differ in one or more aspect of their foraging ecology, which may minimize competition through partitioning resources, thereby allowing for species coexistence (Linnebjerg et al. 2015). Murres and razorbills are part of a small group of auks. Auks are wing-propelled, pursuit-diving seabirds that forage underwater for primarily small, schooling fish. Their wing design is a compromise between efficiency of flight in air and diving underwater, resulting in high wing loading (i.e. body mass/wing area), and high energetic costs during aerial flight (Elliott et al. 2013). Murres have 30% higher wing loading in comparison to razorbills, resulting in differences in dive behavior (Thaxter et al. 2010, Shoji et al. 2016). Both exhibit ecological similarities and differences in morphological characteristics and foraging behavior both during the breeding and non-breeding season (see Table 1 for full comparison). Additionally, both species exhibit intermediate juvenile development. Bi-parental care of chicks at the colony lasts for ~21 days, after which flightless chicks fledge and are cared for by the male

at sea for approximately two months, during which time post-breeding molt occurs (Burke et al. 2015).

Previous studies have compared population-level foraging ecology of sympatric common murre and razorbill and have found differences in foraging trip characteristics, with murre having longer trip durations, but razorbill spending a greater proportion of foraging trips in flight (Thaxter et al. 2013). However, there was no difference in total distance traveled and a great deal of overlap in foraging areas (Thaxter et al. 2013). Common murre consistently dive deeper (average range: 20-70 m) than Razorbill (average range: 5-10 m) through all seasons in southwestern Greenland, but isotopic ratios did not differ between species during the breeding season (Linnebjerg et al. 2013, Pratte et al. 2017). These differences may be due to prey preference, physiological differences, or niche partitioning.

Previous dietary studies on both species during the breeding season revealed that murre in the northwest Atlantic tend to specialize on capelin (Davoren and Montevecchi 2003, Davoren et al. 2012), whereas razorbill feed on both capelin and sandlance (Lavers et al. 2009, Pratte et al. 2017), though populations in the northeast Atlantic and Pacific forage on additional forage fish species (Ainley et al. 1996, Buren et al. 2012, Chivers et al. 2012, Lavoie et al. 2012). Multiple studies have described the foraging and dive behavior of murre and razorbill during breeding (Evans et al. 2013, Shoji et al. 2015, 2016). Indeed, both species appear to exhibit some flexibility in foraging behavior in relation to environmental cues or prey availability, suggesting some degree of phenotypic plasticity (Wanless et al. 1990a, Bryant et al. 1999, Harding et al. 2007a, Piatt et al. 2007, Hedd et al. 2009, Barger and Kitaysky 2012, Shoji et al. 2014). Despite this information, population-level comparative studies often focus on one or a few niche dimensions and little is known about the temporal aspects of individual specialization.

The northwest Atlantic low Arctic ecosystem has productive waters, where the intermediate trophic level is dominated by a single small, short-lived forage fish species, capelin (*Mallotus villosus*; Buren et al. 2012, Davoren 2013). Capelin migrate inshore to spawn at beach and deep-water spawning sites (Crook et al. 2017), creating a prey influx partway through the seabird breeding season. Due to this influx of high-quality food, seabirds appear to rely heavily on capelin as an abundant and predictable prey source to provision themselves and their chicks (Davoren et al. 2003, 2007, Davoren 2013), though the timing of spawning in recent years has become highly variable (Davoren et al. 2012, Crook et al. 2017).

Objectives

The goal of this research is to investigate population and individual level foraging ecology of common murre and razorbills during the breeding season to examine foraging niche dynamics, individual specialization, and phenotypic plasticity. Specifically, I begin at a fine-scale, examining the degree of individual specialization in the foraging behavior and diet of breeding common murre during contrasting years of prey availability in northeastern Newfoundland (Chapter 1). I then expand from the individual to the population level and quantify the foraging behavior and diet of both chick-rearing common murre and razorbills to examine niche dynamics between species including foraging trip characteristics, dive characteristics, diurnal foraging patterns, habitat preference, and diet, as well as how these different aspects are impacted by an increase in prey availability (Chapter 2). By examining both individual- and population-level factors and the plasticity of these aspects of the foraging ecology, we provide a greater understanding of the potential impacts of changes in resources to changing ecosystem dynamics and future management implications.

Seabirds and marine ecosystems face many human-induced threats, including climate change, overfishing, pollutants, habitat destruction, and invasive species (Snell-Rood 2013, Moreno et al. 2016). These threats can compromise energy flow throughout the food web, thus altering the availability of primary and secondary production to consumers (Moreno et al. 2016). Particularly important in the case of seabirds and other marine predators, is understanding plastic responses to changes in prey biomass. Indeed, seabirds are often boasted as environmental indicators due to their conspicuousness and role as apex predators in the marine ecosystem. It is thought that seabirds can be used to indicate the health of marine systems and, thus, can be used to inform management decisions, particularly of fish harvests. If seabirds are to be used as indicators, however, an intimate knowledge of individual- and population-level responses to environmental conditions are needed (Grémillet and Charmantier 2010). By studying niche dynamics at the population and individual level as well as phenotypic plasticity, we can begin to understand whether seabirds can be used as quantitative indicators and how species might or might not adapt to changing resources.

References

- Ainley, D.G., Nettleship, D.N., Carter, H.R., and Storey, A.E. 2002. Common Murre (*Uria aalge*). In *The Birds of North America*. Edited by P.G. Rodewald. Ithaca, New York.
- Ainley, D.G., Reyes, P., Observatory, B., Beach, S., Reyes, P., Observatory, B., Beach, S., and Allen, S.G. 1996. Temporal and spatial patterns in the diet of the common murre in California waters. *Condor* **98**(4): 691–705.
- Barger, C.P., and Kitaysky, a. S. 2012. Isotopic segregation between sympatric seabird species increases with nutritional stress. *Biol. Lett.* **8**(3): 442–445.
- Beaulieu, M., and Sockman, K.W. 2012. One meadow for two sparrows: resource partitioning in a high elevation habitat. *Oecologia* **170**(2): 529–540.
- Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., and Hulsey, C.D. 2003. The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* **161**(1): 1–28.
- Bonato, K.O., Burress, E.D., Fialho, C.B., and Armbruster, J.W. 2018. Resource partitioning among syntopic Characidae corroborated by gut content and stable isotope analyses. *Hydrobiologia* **805**(1): 311–324.
- Bryant, R., Jones, I.L., and Hipfner, J.M. 1999. Responses to changes in prey availability by common murre and thick-billed murre at the Gannet Islands, Labrador. *Can. J. Zool.* **77**(8): 1278–1287.
- Buren, A.D., Koen-Alonso, M., and Montevecchi, W.A. 2012. Linking predator diet and prey availability: common murre and capelin in the Northwest Atlantic. *Mar. Ecol. Prog. Ser.* **445**: 25–35.
- Burke, C.M., Montevecchi, W.A., and Regular, P.M. 2015. Seasonal variation in parental care

- drives sex-specific foraging by a monomorphic seabird. PLoS One **10**(11): e0141190.
- Ceia, F.R., and Ramos, J.A. 2015. Individual specialization in the foraging and feeding strategies of seabirds: a review. Mar. Biol. **162**(10): 1923–1938.
- Chase, J.M., and Leibold, M.A. 2003. Ecological niches: linking classical and contemporary approaches. The University of Chicago, London.
- Chivers, L.S., Lundy, M.G., and Reid, N. 2012. Stable breeding despite variable feeding in two sympatric auk (Alcidae) species. Bird Study **59**(1): 67–73.
- Cleasby, I.R., Wakefield, E.D., Bodey, T.W., Davies, R.D., Patrick, S.C., Newton, J., Votier, S.C., Bearhop, S., and Hamer, K.C. 2015. Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. Mar. Ecol. Prog. Ser. **518**: 1–12.
- Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat. **122**(5): 661–696.
- Crook, K.A., Maxner, E., and Davoren, G.K. 2017. Temperature-based spawning habitat selection by capelin (*Mallotus villosus*) in Newfoundland. ICES J. Mar. Sci. **74**(6): 1622–1629.
- Dall’Antonia, L., Gudmundsson, G.A., and Benvenuti, S. 2001. Time allocation and foraging pattern of chick-rearing razorbills in northwest Iceland. Condor **103**(3): 469–480.
- Davoren, G.K. 2013. Distribution of marine predator hotspots explained by persistent areas of prey. Mar. Biol. **160**(12): 3043–3058.
- Davoren, G.K., May, C., Penton, P., and Reinfort, B. 2007. An ecosystem-based research program for capelin (*Mallotus villosus*) in the Northwest Atlantic : Overview and Results. J. Northwest Atl. Fish. Sci. **39**: 35–48.
- Davoren, G.K., and Montevecchi, W.A. 2003. Signals from seabirds indicate changing biology

- of capelin stocks. *Mar. Ecol. Prog. Ser.* **258**: 253–261.
- Davoren, G.K., Montevecchi, W.A., and Anderson, J.T. 2003. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. *Mar. Ecol. Prog. Ser.* **256**: 229–242.
- Davoren, G.K., Penton, P., Burke, C., and Montevecchi, W.A. 2012. Water temperature and timing of capelin spawning determine seabird diets. *ICES J. Mar. Sci.* **69**(7): 1234–1241.
- Day, R.H., Prichard, A.K., Nigro, D.A., Auk, S.T., and Jul, N. 2012. Ecological specialization and overlap of *Brachyramphus* murrelets in Prince William Sound, Alaska. *Auk* **120**(3): 680–699.
- Dehnhard, N., Eens, M., Sturaro, N., Lepoint, G., Demongin, L., Quillfeldt, P., and Poisbleau, M. 2016. Is individual consistency in body mass and reproductive decisions linked to individual specialization in foraging behavior in a long-lived seabird? *Ecol. Evol.* **6**(13): 4488–4501.
- Dupuch, A., Bertolo, A., Magnan, P., and Dill, L.M. 2014. Indirect effects of asymmetrical competition among top predators determine spatial patterns of predation risk for prey. *Aquat. Sci.* **76**(4): 543–552.
- Elliott, K.H., Ricklefs, R.E., Gaston, A.J., Hatch, S. a., Speakman, J.R., and Davoren, G.K. 2013. High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Proc. Natl. Acad. Sci. U. S. A.* **110**(23): 9380–4.
- Elton, C.S. 1927. *Animal Ecology*. Sidgwick and Jackson, London.
- Evans, T.J., Kadin, M., Olsson, O., and Åkesson, S. 2013. Foraging behaviour of common murrelets in the Baltic Sea, recorded by simultaneous attachment of GPS and time-depth recorder devices. *Mar. Ecol. Prog. Ser.* **475**: 277–289.

- Forero, M.G., Bortolotti, G.R., Hobson, K.A., Donazar, J.A., Bertelotti, M., and Blanco, G. 2004. High trophic overlap within the seabird community of Argentinean Patagonia: A multiscale approach. *J. Anim. Ecol.* **73**(4): 789–801.
- Frere, E., Quintana, F., Gandini, P., and Wilson, R.P. 2008. Foraging behaviour and habitat partitioning of two sympatric cormorants in Patagonia, Argentina. *Ibis* 185(9). **150**(3): 558–564
- Gabrielsen, G.W. 1994. Energy expenditure in Arctic seabirds. University of Tromsø.
- Gause, G.F. 1934. Experimental analysis of Vito Volterra's Mathematical Theory of the struggle for existence. *Science* **79**: 16–17.
- Gause, G.F. 1971. The struggle for existence. Dover Publications, Inc., Meneola, New York.
- Giller, P.S. 1984. Community structure and the niche. Chapman and Hall Ltd, New York.
- González-solís, J., Croxall, J.P., and Afanasyev, V. 2008. Offshore spatial segregation in giant petrels *Macronectes* spp.: differences between species, sexes and seasons. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **17**: S22–S36.
- Grémillet, D., and Charmantier, A. 2010. Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. *Ecol. Appl.* **20**(6): 1498–1503.
- Hamer, K.C., Humphreys, E.M., Garthe, S., Hennenke, J., Peters, G., Grémillet, D., Phillips, R.A., Harris, M.P., and Wanless, S. 2007. Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Mar. Ecol. Prog. Ser.* **338**: 295–305.
- Hammerschlag-Peyer, C.M., Yeager, L.A., Araújo, M.S., and Layman, C.A. 2011. A hypothesis-testing framework for studies investigating ontogenetic niche shifts using stable isotope ratios. *PLoS One* **6**(11): e27104.

- Harding, A.M. a, Piatt, J.F., Schmutz, J. a, Shultz, M.T., Van Pelt, T.I., Pelt, V., Kettle, A.B., and Speckman, S.G. 2007. Prey density and the behavioural flexibility of a marine predator: the common murre (*Uria aalga*). *Ecology* **88**(8): 2024–2033.
- Hedd, A., Gales, R., and Brothers, N. 2001. Foraging strategies of shy albatross *Thalassarche cauta* breeding at Albatross Island, Tasmania, Australia. *Mar. Ecol. Prog. Ser.* **224**: 267–282.
- Hedd, A., Regular, P.M., Montevecchi, W.A., Buren, A.D., Burke, C.M., and Fifield, D.A. 2009. Going deep: common murrens dive into frigid water for aggregated, persistent and slow-moving capelin. *Mar. Biol.* **156**(4): 741–751.
- Hückstädt, L.A., Koch, P.L., McDonald, B.I., Goebel, M.E., Crocker, D.E., and Costa, D.P. 2012. Stable isotope analyses reveal individual variability in the trophic ecology of a top marine predator, the southern elephant seal. *Oecologia* **169**(2): 395–406.
- Hutchinson, G.E. 1978. *An introduction to population biology*. Yale University Press, New Haven, CT.
- Hyrenbach, K.D., Fernández, P., and Anderson, D.J. 2002. Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Mar. Ecol. Prog. Ser.* **233**: 283–301.
- Jaeger, A., Connan, M., Richard, P., and Cherel, Y. 2010. Use of stable isotopes to quantify seasonal changes of trophic niche and levels of population and individual specialisation in seabirds. *Mar. Ecol. Prog. Ser.* **401**: 269–277.
- Jiménez, S., Xavier, J.C., Domingo, A., Brazeiro, A., Defeo, O., Viera, M., Lorenzo, M.I., and Phillips, R.A. 2017. Inter-specific niche partitioning and overlap in albatrosses and petrels: dietary divergence and the role of fishing discards. *Mar. Biol.* **164**(174): 1–21.

- Kokubun, N., Takahashi, A., Mori, Y., Watanabe, S., and Shin, H.C. 2010. Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. *Mar. Biol.* **157**(4): 811–825.
- Kowalczyk, N.D., Reina, R.D., Preston, T.J., and Chiaradia, A. 2015. Environmental variability drives shifts in the foraging behaviour and reproductive success of an inshore seabird. *Oecologia* **178**(4): 967–979.
- Lavers, J., Hipfner, J.M., and Chapdelaine, G. 2009. Razorbill (*Alca torda*). In *The Birds of North America*. Edited by P. Rodewald. Ithaca, New York.
- Lavoie, R. a, Rail, J.F., and Lean, D.R.S. 2012. Diet composition of seabirds from Corossol Island, Canada, using direct dietary and stable isotope analyses. *Waterbirds* **35**(3): 402–419.
- Lewis, S., Benvenuti, S., Dall-Antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S., and Hamer, K.C. 2002. Sex-specific foraging behaviour in a monomorphic seabird. *Proc. R. Soc. B Biol. Sci.* **269**(1501): 1687–1693.
- Linnebjerg, J.F., Fort, J., Guilford, T., Reuleaux, A., Mosbech, A., and Frederiksen, M. 2013. Sympatric breeding auks shift between dietary and spatial resource partitioning across the annual cycle. *PLoS One* **8**(8): e72987.
- Linnebjerg, J.F., Reuleaux, A., Mouritsen, K.N., and Frederiksen, M. 2015. Foraging ecology of three sympatric breeding alcids in a declining colony in southwest Greenland. *Waterbirds* **38**(2): 143–152.
- Mancini, P.L., and Bugoni, L. 2014. Resource partitioning by seabirds and their relationship with other consumers at and around a small tropical archipelago. *ICES J. Mar. Sci.* **71**(9): 2599–2607.

- Masello, J.F., Mundry, R., Poisbleau, M., Demongin, L., Voigt, C.C., Wikelski, M., and Quillfeldt, P. 2010. Diving seabirds share foraging space and time within and among species. *Ecosphere* **1**(6): 1–28.
- Masello, J.F., Wikelski, M., Voigt, C.C., and Quillfeldt, P. 2013. Distribution patterns predict individual specialization in the diet of dolphin gulls. *PLoS One* **8**(7): e67714.
- Moreno, R., Stowasser, G., McGill, R.A.R., Bearhop, S., and Phillips, R.A. 2016. Assessing the structure and temporal dynamics of seabird communities: the challenge of capturing marine ecosystem complexity. *J. Anim. Ecol.* **85**(1): 199–212.
- Navarro, J., Forero, M.G., González-Solís, J., Igual, J.M., Becares, J., and Hobson, K.A. 2009. Foraging segregation between two closely related shearwaters breeding in sympatry. *Biol. Lett.* **5**: 545–548.
- Nicholls, D.G., Robertson, C.J.R., Prince, P.A., Murray, M.D., Walker, K.J., and Elliott, G.P. 2002. Foraging niches of three *Diomedea* albatrosses. *Mar. Ecol. Prog. Ser.* **231**: 269–277.
- Olsson, O., and Bolin, A. 2014. A model for habitat selection and species distribution derived from central place foraging theory. *Oecologia* **175**(2): 537–548.
- Orians, G.H., and Pearson, N.E. 1979. On the theory of central place foraging. In *Analysis of Ecological Systems*. Edited by J. Horn, G.R. Stairs, and R. Mitchell. Ohio State Press. pp. 155–177.
- Paiva, V.H., Geraldés, P., Ramírez, I., Meirinho, A., Garthe, S., and Ramos, J.A. 2010. Foraging plasticity in a pelagic seabird species along a marine productivity gradient. *Mar. Ecol. Prog. Ser.* **398**: 259–274.
- Patrick, S.C., and Weimerskirch, H. 2014. Consistency pays: sex differences and fitness

- consequences of behavioural specialization in a wide-ranging seabird. *Biol. Lett.* **10**: 1–4.
- Peck-Richardson, A.G., Lyons, D.E., Roby, D.D., Cushing, D.A., and Lerczak, J.A. 2018. Three-dimensional foraging habitat use and niche partitioning in two sympatric seabird species, *Phalacrocorax auritus* and *P. penicillatus*. *Mar. Ecol. Prog. Ser.* **586**: 251–264.
- Phillips, R.A., Silk, J.R.D., Phalan, B., Catry, P., and Croxall, J.P. 2004. Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc. R. Soc. B Biol. Sci.* **271**(1545): 1283–1291.
- Phillips, S.B., Aneja, V.P., Kang, D., and Arya, S.P. 2006. Modelling and analysis of the atmospheric nitrogen deposition in North Carolina. *Int. J. Glob. Environ. Issues* **190**: 231–252.
- Piatt, J.F., Sydeman, W.J., and Wiese, F. 2007. Introduction: A modern role for seabirds as indicators. *Mar. Ecol. Prog. Ser.* **352**: 199–204.
- Polito, M.J., Trivelpiece, W.Z., Patterson, W.P., Karnovsky, N.J., Reiss, C.S., and Emslie, S.D. 2015. Contrasting specialist and generalist patterns facilitate foraging niche partitioning in sympatric populations of *Pygoscelis* penguins. *Mar. Ecol. Prog. Ser.* **519**: 221–237.
- Pratte, I., Robertson, G.J., and Mallory, M.L. 2017. Four sympatrically nesting auks show clear resource segregation in their foraging environment. *Mar. Ecol. Prog. Ser.* **572**: 243–254.
- Ramírez, I., Paiva, V.H., Fagundes, I., Menezes, D., Silva, I., Ceia, F.R., Phillips, R.A., Ramos, J.A., and Garthe, S. 2016. Conservation implications of consistent foraging and trophic ecology in a rare petrel species. *Anim. Conserv.* **19**(2): 139–152.
- Reed, T.E., Wanless, S., Harris, M.P., Frederiksen, M., Kruuk, L.E.B., and Cunningham, E.J.A.

2006. Responding to environmental change: plastic responses vary little in a synchronous breeder. *Proc. Biol. Sci.* **273**: 2713–2719.
- Shoji, A., Aris-Brosou, S., Owen, E., Bolton, M., Boyle, D., Fayet, A., Dean, B., Kirk, H., Freeman, R., Perrins, C., and Guilford, T. 2016. Foraging flexibility and search patterns are unlinked during breeding in a free-ranging seabird. *Mar. Biol.* **163**(4): 1–10.
- Shoji, A., Elliott, K., Fayet, A., Boyle, D., Perrins, C., and Guilford, T. 2015. Foraging behaviour of sympatric razorbills and puffins. *Mar. Ecol. Prog. Ser.* **520**: 257–267.
- Shoji, A., Owen, E., Bolton, M., Dean, B., Kirk, H., Fayet, A., Boyle, D., Freeman, R., Perrins, C., Aris-Brosou, S., and Guilford, T. 2014. Flexible foraging strategies in a diving seabird with high flight cost. *Mar. Biol.* **161**(9): 2121–2129.
- Sivy, K.J., Pozzanghera, C.B., Colson, K.E., Mumma, M.A., and Prugh, L.R. 2018. Apex predators and the facilitation of resource partitioning among mesopredators. *Oikos* **127**(4): 607–621.
- Snell-Rood, E.C. 2013. An overview of the evolutionary causes and consequences of behavioural plasticity. *Anim. Behav.* **85**(5): 1004–1011.
- Spear, L.B., and Ainley, D.G. 1997. Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis* **139**(2): 221–233.
- Stephens, D.W., Brown, J.S., and Ydenberg, R.C. 2007. *Foraging: behavior and ecology*. University of Chicago Press, London.
- Thaxter, C.B., Daunt, F., Gremillet, D., Harris, M.P., Benvenuti, S., Watanuki, Y., Hamer, K.C., and Wanless, S. 2013. Modelling the effects of prey size and distribution on prey capture rates of two sympatric marine predators. *PLoS One* **8**(11): e79915.
- Thaxter, C.B., Wanless, S., Daunt, F., Harris, M.P., Benvenuti, S., Watanuki, Y., Gremillet, D.,

- and Hamer, K.C. 2010. Influence of wing loading on the trade-off between pursuit-diving and flight in common guillemots and razorbills. *J. Exp. Biol.* **213**: 1018–1025.
- Toscano, B.J., Gownaris, N.J., Heerhartz, S.M., and Monaco, C.J. 2016. Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia* **182**(1): 55–69.
- Wakefield, E.D., Owen, E., Baer, J., Carroll, M.J., Daunt, F., Dodd, S.G., Green, J.A., Guilford, T., Mavor, R.A., Miller, P.I., Newell, M.A., Newton, S.F., Robertson, G.S., Shoji, A., Soanes, L.M., Votier, S.C., Wanless, S., and Bolton, M. 2017. Breeding density, fine-scale tracking, and large-scale modeling reveal the regional distribution of four seabird species. *Ecol. Appl.* **27**(7): 2074–2091.
- Wanless, S., Harris, M.P., and Morris, J.A. 1990. A comparison of feeding areas used by individual common murre (*Uria aalge*), razorbills (*Alca torda*) and an Atlantic puffin (*Fratercula arctica*) during the breeding season. *Colon. Waterbirds* **13**(1): 16–24.
- Weimerskirch, H., Shaffer, S.A., Tremblay, Y., Costa, D.P., Gadenne, H., Kato, A., Ropert-Coudert, Y., Sato, K., and Aurioules, D. 2009. Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. *Mar. Ecol. Prog. Ser.* **391**: 267–278.
- Woo, K.J., Elliott, K.H., Davidson, M., Gaston, A.J., and Davoren, G.K. 2008. Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *J. Anim. Ecol.* **77**(6): 1082–1091.
- Young, H.S., McCauley, D.J., Dirzo, R., Dunbar, R.B., and Shaffer, S.A. 2010. Niche partitioning among and within sympatric tropical seabirds revealed by stable isotope analysis. *Mar. Ecol. Prog. Ser.* **416**: 285–294.

Figures and Tables

Table 1. Comparison of the characteristics of common murres (*Uria aalge*) and razorbills (*Alca torda*) breeding in the northwest Atlantic. Averages are reported as mean \pm SD. Note proportion of time spent in flight and underwater are from foraging trips during breeding and ‘bill load’ refers to how many fish are carried in the bill to the chick at the breeding colony during chick-rearing. Information was gathered from the following sources: Gabrielsen 1994, Spear and Ainley 1997, Dall’Antonia et al. 2001, Ainley et al. 2002, Lavers et al. 2009, Thaxter et al. 2010.

Characteristic	Common Murre	Razorbill
Breeding Range (NW Atlantic)	Labrador, SE Quebec, south to Newfoundland, Bay of Fundy	Labrador, Gulf of St Lawrence, Nunavut south to Maine
Nesting Habitat	Cliffs, slopes, flat surfaces	Rock crevices, burrows
Population Size	1.2 million (Eastern North America)	38,000 (North America)
Clutch Size	1 egg/clutch	1 egg/clutch
Average Body Mass	Male: 958 \pm 87 g Female 928 \pm 11 g	726.4 \pm 48.8 g
Wing-Loading	1.86 g/cm ²	1.32 g/cm ²
Incubation Duration	32-35 days	35-37 days
Chick-rearing Duration	20-22 days	17-23 days
Primary Prey (NW Atlantic)	Capelin	Sandlance and capelin
Proportion of time in flight	10.3 \pm 8.0 %	21.2 \pm 16.6 %
Proportion of time underwater	28.8 \pm 9.5 %	17.5 \pm 10.6 %
Dive Depth	20-70 m, max: 180 m	5-10 m, max: 120 m
Bill Load	Single-prey loader	Multiple prey loader

Chapter One. High individual-level variation in foraging behavior of a marine predator, the common murre

Abstract

Variation in how individuals use resources is an important, yet often ignored aspect of ecology. Many factors can affect resource specialization in both space and time and the foraging ecology of breeding seabirds is largely influenced by prey availability and energy demands related to reproduction. In this study, we used a combination of GPS tracking devices and stable isotope ratios of carbon and nitrogen to examine individual-level behavioral and dietary flexibility in a breeding pursuit-diving seabird, the common murre (*Uria aalge*), over two years (2016, 2017) where the timing of arrival of their primary prey, capelin (*Mallotus villosus*), varied. In both years, we found high within-individual variation in foraging trip and dive characteristics, coupled with low spatial overlap of foraging trips both within and between individuals, indicative of flexible behavior. Alternately, the diet of breeding murre exhibited a higher degree of consistency, evidenced by a correlation between plasma and red blood cell isotope values, though the proportion of different prey items in the diet varied by individual. Although behavioral flexibility remained high in both years, foraging trips were longer and farther from the colony, maximum dive duration decreased, and the proportion of capelin in the diet decreased in 2017 when there was mismatch between breeding and prey arrival. These findings further support flexible foraging strategies, whereby foraging behavior and diet shifted under varying prey availability but with higher energy costs under low availability. Our research suggests an interplay between diet, behavior, and prey availability and provides insight into how individuals respond to environmental variation, which is critical for conservation, particularly in light of current levels of rapid environmental change.

Introduction

Ecological studies exhibit a tendency to generalize, both from individuals to populations or species, and from a single or a few points in time, to longer time scales. However, increasingly, individual-level heterogeneity in both space and time is recognized as an important aspect contributing to resource dynamics (Ceia and Ramos 2015). By examining individual-level variation in foraging behavior and diet, we can begin to understand how variation among individuals influences intra- and interspecific interactions (e.g., niche partitioning and overlap, competitive exclusion and coexistence; Stephens et al. 2007), which ultimately contribute to population-, community-, and ecosystem-level patterns (Toscano et al. 2016). On a coarse scale, individual specialization, or the consistency in foraging behaviour (e.g., search, capture) and resource selection, involves the distinction between a specialist and generalist individual or population, with a specialist using a much narrower niche, or set of resources, than a generalist (Bolnick et al. 2003). A specialist population is characterized by all individuals using the same narrow niche with little or no variation. In contrast, all individuals using narrow niches that are composed of different resources will combine to form a wide niche, known as a Type B generalist population (Polito et al. 2015). A Type A generalist population, however, consists of generalist individuals that all use an equally wide niche, exploiting a wide variety of resources with large amounts of variation within individuals (Bolnick et al. 2003, Hückstädt et al. 2012, Polito et al. 2015). Individual specialization is quantified by attributing variation among and within individuals, where the proportion of total variation due to variation among individuals is known as repeatability, reflecting individual consistency in both behaviour and resource use (Wolak et al. 2012).

Longitudinal studies with repeated measures from the same individuals are required to study temporal consistency and flexibility. To examine within-individual variation in foraging behaviour, long-term deployments of tracking devices on individuals are often employed (e.g. Pettex et al. 2012, Dias et al. 2013, Potier et al. 2015). GPS tracking devices, in particular, provide high temporal and spatial resolution, allowing for the examination of differences in fine-scale movement within and among individuals. To examine repeatability of foraging behaviour for organisms that must return to a central place, movement data are often summarized into foraging trip characteristics (e.g., maximum range, trip duration) as well as activity characteristics (e.g., travel time, colony attendance) and foraging effort (Carneiro et al. 2017). To examine individual-level variation in resource use, diet must be quantified over time (e.g., Woo et al. 2008, Anderson et al. 2009, Scioscia et al. 2014). Increasingly, stable isotope ratios of carbon and nitrogen are used in many types of studies including foraging ecology, feeding habitats, migration, and resource allocation and can provide insight into trophic position, relative prey contributions in consumer diets, niche dynamics, and intraspecific diet variation (Layman et al. 2012, Cherel et al. 2014). As tissues have different isotopic turnover rates, each tissue represents a particular temporal scale of integrated diet and, thus, by examining multiple tissues of the same individuals, variance within and among individuals in isotopic space can be linked qualitatively to variation in diet (e.g. specialist and generalist; Jackson et al. 2011). By examining consistency in diet and behavior simultaneously within individuals, we can begin to understand individual-level plasticity in foraging ecology. Seabirds provide a key opportunity to examine individual specialization when they act as central-place foragers during the breeding season (Camprasse et al. 2017).

The northwest Atlantic low Arctic ecosystem has productive waters, where the intermediate trophic level is dominated by a single small, short-lived forage fish species, capelin (*Mallotus villosus*; Buren et al. 2012, Davoren 2013a). Capelin migrate inshore to spawn at beach and deep-water spawning sites (Crook et al. 2017), creating a prey influx partway through the seabird breeding season. Due to this influx of high-quality food, seabirds appear to rely heavily on capelin as an abundant and predictable prey source to provision themselves and their chicks (Carscadden et al. 2002, Gulka et al. 2017). The common murre (*Uria aalge*, hereafter ‘murre’) is a wing-propelled, pursuit-diving auk that breeds in both the Atlantic and Pacific. Murre wing design is a compromise between flying and diving, resulting in high energetic costs of flight and the highest wing-loading (i.e. body mass/wing area) of all flying birds (Elliott et al. 2013). Due to these high energy demands, murre must eat up to 30% of their body mass per day (Ainley et al. 2002), thus foraging efficiency is of particular importance. In the northwest Atlantic, the northeast Newfoundland coast supports the largest population of breeding murre (Wilhelm et al. 2015). In this area, parental prey deliveries to murre chicks primarily consist of capelin, with 95-100% capelin in chick diets (Davoren and Montevecchi 2003a, Burke 2008, Davoren et al. 2012), and limited data indicate that breeding adults are also reliant on capelin (Davoren 2007). This evidence suggests dietary specialization at the population level. As capelin biomass during chick-rearing varies among years, primarily due to varying timing of spawning in recent years (Davoren et al. 2012, Crook et al. 2017), it is unclear whether and how individuals maintain a capelin-based diet. At the population-level, common murre exhibit flexible time budgets (Burger and Piatt 1990, Monaghan et al. 1994, Wilhelm et al. 2008), whereby breeding murre adjust colony attendance and at-sea foraging time to maintain relatively constant chick feeding rates with interannual changes in prey density both in Newfoundland (Burger and Piatt

1990) and other areas (Zador and Piatt 1999, Harding et al. 2007a). Individual-level specialization in diet and foraging behaviour, however, was illustrated for the closely related thick-billed murre (*Uria lomvia*; Woo et al. 2008). Overall, little is known about the individual-level dietary and behavioural flexibility of common murres and how patterns at the individual-level contribute to population-level behavioral flexibility and dietary specialization in coastal Newfoundland.

The aims of this study were to investigate individual-level temporal consistency in the diet and foraging behavior of chick-rearing murres in coastal Newfoundland. To do this, we examined individual-level variation in foraging trip characteristics, foraging space use, and diet in breeding common murres using long-term deployments of GPS devices to track successive foraging trips of individuals in two years (2016 and 2017) combined with blood stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$). The timing of inshore arrival of capelin varied in relation to the chick-rearing period for murres in both years, allowing us to investigate individual-level variation in foraging ecology under divergent levels of resource availability. We hypothesized that temporal consistency in individual-level foraging behavior is influenced by prey availability during chick-rearing. We predicted that prior to the inshore arrival of capelin within foraging ranges, individuals would exhibit higher within-individual variation in foraging behaviour, as well as generally higher foraging effort, compared to times of high capelin presence in the study area, in order to maintain a capelin-based diet between years. Within years, we predicted that murres would exhibit high within-individual variation in foraging behaviour, to maintain a narrow, primarily capelin-based diet. As energetic demands peak during breeding, understanding variation and dietary and behavioural plasticity of individuals is of particular importance especially under changing prey availability.

Methods

Study Area and Design

Our study was conducted during July and August 2016 and 2017, on South Cabot Island, Newfoundland (N 49.1711°, W 53.3588°; Fig. 1), where approximately 10,000 pairs of common murres breed annually in high densities on flat ground (Wilhelm et al. 2015). Common murres arrive in the study area during April to mate, lay eggs in June, and leave in mid-August when chicks fledge. In mid to late July, spawning capelin arrive in the study area and reach peak abundance during spawning (Davoren et al. 2006), which often corresponds with the chick-rearing period of murres (Davoren and Montevecchi 2003a). As we were interested in individual-level variation in foraging ecology, we targeted long-term deployments of tracking devices starting during peak hatching to allow temporal coverage of the short ~ 3-week chick-rearing period. Following Wolak et al. (2012), increasing the number of repeated measures per individual, rather than increasing the number of individuals tagged, would maximize our ability to quantify individual specialization with high expected within-individual variation. To examine timing of capelin arrival in the study area in relation to the chick-rearing period for murres, we monitored known beach and deep-water (14-40 m) spawning sites of capelin within maximum foraging ranges of breeding common murres (110 km; Linnebjerg et al. 2015) for capelin presence and spawning activity (see methods in Crook et al. 2017). We combined this information with the opening of the capelin fishery in the study area (Bonavista Bay), as the fishery is open for a short period of time (days) corresponding with peak spawning capelin biomass. All research was performed in accordance with the Canadian Council of Animal Care, approved by the University of Manitoba, Fort Garry Campus Animal Care Committee.

Device deployment and diet sampling

Foraging behavior was quantified by deploying GPS tracking devices (Ecotone ® URIA-300) on breeding murrets at peak hatching (2016: n = 6 adults with chicks; 2017: n = 4 adults with eggs, n = 4 adults with chicks). Parents were captured at nests using a telescoping noose pole and loggers were attached using Tesa tape (n = 4 in 2016) or sterilized subdermal sutures (n = 2 in 2016, n = 8 in 2017) for long-term deployment. The total mass of loggers was 14-16 g, corresponding to less than 2% of body weight for the lightest individual (840-1020 g) and handling times during deployments ranged from 11-13 min. GPS tags recorded latitude and longitude every 2 (n=5) or 10 (n=1) minutes during 2016. Foraging trip characteristics did not differ when 2-minute interval data were subsampled to a 10-minute interval and, thus, all tags in 2017 were programmed to record every 10 min to increase battery life. In addition to location data, dive sensors with a salt water switch recorded dive durations whenever tags were submerged in water and, thus, measured dive duration independent of the pre-set GPS interval measurements. Data from all individuals were remotely downloaded via UHF to a base station set up within 10-30 m of nest sites on the colony.

In 2016, blood samples were not taken from tagged individuals, but seven breeding individuals were captured at nest sites with the noose pole on the same date as tag attachment and ~ 1 mL whole blood samples were obtained from the tarsus (25-gauge needle with syringe) for stable isotope analysis. Blood was placed in microcentrifuge tubes on ice (<8 h) and later frozen until analysis. During 2017, all tagged birds except one were blood sampled for sex determination (one drop on FTA cards; Fast Technology for Analysis of nucleic acids; Whatman, General Electric) and stable isotope analysis. To obtain a larger subsample of the population for examining individual-level variation in diet, an additional 21 breeding individuals were captured

at nest sites with the noose pole and blood sampled within a week of tag deployment (July 14, 2017). Blood samples were placed in EDTA tubes, kept on ice (<8 h), and later centrifuged to separate plasma and red blood cells, then frozen until analysis.

To aid in interpreting stable isotope ratios, in 2017, parental prey deliveries to chicks were observed using a camera trap (Reconyx PC800) placed approximately 3-5 m from nest sites, with about 30 nests in the field of view. The motion-sensor was set to trigger daily from 6:00 to 9:00 am local time to capture peak chick-feeding rates (Harris and Wanless 2011), during which one picture was captured when triggered, waiting 2 s between triggers. Additionally, samples of potential prey items were collected for stable isotope analysis throughout the field season using a variety of methods, including seine nets (Bessy's Island), dipnets (Mussel Shells), and sediment grabs (Gull Island; Fig. 1; Table 1). Diet sampling of Atlantic puffin bill loads using mist-nets on a nearby colony (James Island; Fig. 1) was also conducted to obtain additional prey samples, following methods from Lavoie et al. (2012). For larger fish, a 1-2 g sample of dorsal muscle (with skin removed) was collected and frozen. Small fish (<10 cm length) were frozen whole for analysis.

Stable Isotope Analysis

Frozen blood plasma, red blood cells, and prey samples were freeze-dried for ~48 h and homogenized with a mortar and pestle. Lipids were extracted from prey and plasma samples as lipids are depleted in ^{13}C relative to proteins and carbohydrates and, thus, variation in lipid content in these tissues among individuals can bias carbon isotopic ratios (Post et al. 2007). Lipids were extracted by placing samples in a Soxhlet apparatus with petroleum ether solvent for ~8 h, before re-drying and homogenizing (Dobush et al. 1985). As the red blood cell component

of blood and whole blood have low lipid content, as indicated by a C:N ratio of < 3.5 , lipid extraction was deemed unnecessary (Bearhop et al. 2000). Approximately 0.4-0.6 mg of the red blood cell, whole blood, and prey samples and 0.6-0.8 mg of plasma were weighed into tin capsules. Samples were combusted through a continuous-flow isotope-ratio mass spectrometer (University of Windsor Laboratory, Windsor ON). Isotope ratios are expressed using delta (δ) notation as parts per thousand (per mil) relative to atmospheric nitrogen and Vienna Pee Dee Belemnite standards (Becker et al. 2007).

Data Analysis

Foraging Behavior and Repeatability

GPS data were analyzed using R (version 3.3.1, R Development Core Team 2016) and ArcMap (version 10.13, ESRI) with an Azimuthal Equal Area project centered on the study area. As murres have a tendency to “splash down” in the water in close proximity to the colony either before leaving on a foraging trip or upon returning (Burger 1997), locations within 250 m of the colony were categorized as “splashdown area”. Foraging trips were thus defined as trips made beyond the colony and “splashdown area” during which at least one dive ≥ 4 s was made, indicating foraging activity. As tag dive sensors were sensitive, we excluded short dives (< 4 s) from the analysis, as they were likely associated with bathing and other non-foraging activities (Linnebjerg et al. 2013). Foraging trip characteristics examined include total distance (km), maximum distance from nest (km), mean dive duration (s), maximum dive duration (s), and trip duration (h; Hamer et al. 2007, Harris et al. 2014, Patrick et al. 2014, Potier et al. 2015) to provide an indication of the horizontal and vertical (i.e. depth) foraging characteristics as well as effort. With the absence of dive depth, we used dive duration as an indicator of vertical habitat

use (Shoji et al. 2015). As murres perform dive bouts, represented by a sequence of dives separated by short surface intervals, dives were categorized into bouts to examine effort and location of bouts (Evans et al. 2013). A maximum likelihood approach was used to categorize dive bouts by calculating a bout-ending criterion of 149.2 s in the *diveMove* package in R (Luque and Guinet 2007). Therefore, the dive characteristics were examined as the number of dive bouts per trip, the mean number of dives per bout, mean dive efficiency, defined as the ratio of dive duration to dive duration + subsequent time at the surface (Hedd et al. 2009), and active foraging time (h), defined as the sum of time of all dive bouts, including both dives and surface pauses. All response variables were log transformed when necessary to meet assumptions of parametric statistics based on residual analysis and correlation between variables was examined.

As half of the logged birds in 2017 had eggs (late incubation) and the other half had chicks during tag attachment, and hatching date was unknown, we examined the potential impacts of breeding stage prior to analysis. First, we compared the first two trips of adults with eggs to the first two trips of adults with chicks in 2017 using a linear mixed effects model with individual as a random effect and breeding stage as a fixed effect. There were no significant differences between adults with eggs and those with chicks for any foraging trip or dive characteristic ($p > 0.1$) except that birds with eggs had a significantly higher dive efficiency than birds with chicks ($\chi^2_1 = 6.93$, $p = 0.008$). Additionally, we compared the first two trips and subsequent two trips of birds with eggs when tagged and bird with chicks when tagged to determine possible behavior changes, using a linear mixed effects models with individual as a random effect and period (early, late) as a fixed effect. No significant differences were found in foraging trip and dive characteristics, except for significant decreases in mean dives per bout ($\chi^2_1 = 5.65$, $p = 0.02$) and mean dive efficiency ($\chi^2_1 = 5.18$, $p = 0.02$) on later trips. The same patterns

were exhibited for individuals initially tagged with chicks, but were not significant. Owing to these limited differences, breeding stage was not included as a fixed effect in further analyses.

REML-based general linear mixed models were used to characterize variance due to within and among individual variation for each foraging trip characteristic. As sex information was only available for 2017, two models were run for 2017, one with no fixed effects and one with sex as a fixed effect, with individual as the random effect in both (Hückstädt et al. 2012). One model was run for 2016, which included individual as a random effect with no fixed effects. Within these models, we calculated repeatability (for models with fixed effects, adjusted repeatability was calculated), which represents the proportion of total variance accounted for by the among-individual variation while accounting for fixed effects (if any) based on the following equation, where R is repeatability, σ_{α}^2 is between-individual variance and σ_{ϵ}^2 is within-individual variance (Nakagawa and Schielzeth 2010).

$$R = \frac{\sigma_{\alpha}^2}{\sigma_{\epsilon}^2 + \sigma_{\alpha}^2}$$

Repeatability ranges from 0 to 1, with a value of 0 indicating that all variation is explained by within-individual variance, whereas a value of 1 indicates all variation is explained by among-individual variance. The 95% confidence intervals of repeatability were calculated using parametric bootstrapping (1,000 iterations), where the model fit includes random effects and data are generated using the distribution defined by the estimated parameters (Nakagawa and Schielzeth 2010). To examine differences in foraging and dive characteristics between years, we ran additional mixed-effect models including all data with year as a fixed effect. Significance of fixed effects was examined using ANOVA comparisons of models with and without the term of interest (Patrick et al. 2015).

Kernel density analysis was used to examine spatial aspects of foraging behaviour, allowing for a comparison of specialization in spatial overlap among and within individuals, examined separately by year. Kernel density analysis was carried out using the *adehabitatHR* 0.4.14 package in R (Calenge 2006). Only GPS points associated with dives during foraging trips (excluding those in flight and sitting on the water) were used in this analysis. As loggers are unable to record location data while underwater, the previous GPS position was used to estimate the location for dives (Kokubun et al. 2010). Kernel density is sensitive to sample size and, thus, any foraging trips with fewer than 20 dive points were excluded from analysis. We performed non-parametric fixed kernel density analysis to obtain a utilization distribution of each individual over all foraging trips as well as for each foraging trip using the ‘kernelUD’ function in *adehabitatHR*. To allow for comparison among and within individuals, we used a fixed smoothing factor (h) of 750 m and a cell size of 1000 m, based on the amount of estimated error in locations. The smoothing factor was chosen using reference bandwidth calculation methodology (href). Using the ‘getverticeshr’ function, the 50% and 95% utilization distributions (UD) were used to define core foraging area and foraging range, respectively (Hamer et al. 2007). The function ‘kerneloverlap’ was used to calculate Bhattacharyya’s affinity index (Fieberg and Kochanny 2005). The Bhattacharyya’s affinity index (BA) is calculated using the product of the pairwise comparison of two UD_s ($UD_i(x, y)$ and $UD_j(x, y)$).

$$BA = \int_x \int_y \sqrt{UD_i(x, y)} \times \sqrt{UD_j(x, y)}$$

Values for the index range from 0 (no spatial similarity in UD_s) to 1 (complete spatial similarity in UD_s). By comparing the BA index of foraging trips within the same individual to trips among different individuals, we examined the amount of spatial overlap and behavioral consistency within and among individuals for both years. Student’s t-tests were used to examine the

significance of mean spatial overlap between of trips of the same individual and those between different individuals and between years. In addition, to examine whether trips occurring at a similar temporal scale had a larger degree of spatial overlap, we used pairwise comparisons (ANOVAs) to examine whether spatial overlap of trips made by different individuals that started on the same day differed from those one day apart, or two or more days apart. To examine spatial overlap of trips within individuals, we used Student's t-tests to compare the mean spatial overlap of consecutive trips versus non-consecutive trips within individuals.

Diet

To examine individual-level consistency in diet (2017 only), correlation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between plasma and red blood cells were analyzed separately using Pearson's Rank correlation. This analysis included the additional blood-sampled parental murrelets as well as those from the tracked birds to better represent individual-level consistency in diet at the population level. Univariate and multivariate assumptions were checked prior to statistical testing. Instrumental accuracy mean was ≤ 0.22 ‰ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and precision, based on standard deviation of replicate analysis, was ≤ 0.16 ‰ for $\delta^{15}\text{N}$ and ≤ 0.12 ‰ for $\delta^{13}\text{C}$.

For dietary reconstruction of individuals, Bayesian stable isotope mixing models in the package *MixSIAR* (Stock and Semmens 2016) were used to estimate the relative contribution of prey types in the diet of each individual in each year. Probability distributions for proportional contributions of different prey sources were calculated using diet-tissue discrimination values of 1.10‰ for carbon and 2.80‰ for nitrogen from a study of great skuas (Bearhop et al. 2002), mean \pm SD values for prey sources, and murre $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Moore and Semmens 2008) for whole blood (2016) and red blood cells (2017). Whole blood and red blood cells have similar

isotopic values, and thus can be directly compared (Barquete et al. 2013). Potential prey included in the models were restricted to those identified in previous studies or in photographs of parental prey deliveries to chicks and, thus, included large (i.e. > 10 cm) capelin and sandlance (*Ammodytes* sp.), along with small fish (i.e. ≤ 10 cm) including sandlance, Atlantic cod (*Gadus morhua*), and unidentified fish grouped due to similarity in isotopic ratios. All models were run with three Markov chain Monte Carlo chains of 100,000 iterations, 50,000 burn-in, and thinning of 50. The mode of the posterior distribution was used as the most likely proportion of each prey item. Gelman-Rubin and Geweke diagnostic tests were used to examine chain convergence.

Results

Foraging Behavior and repeatability

During 2016, we tracked individuals for 1-7 d, while we tracked individuals for 8-11 d during 2017. Three birds were failed breeders (2016: n = 1; 2017: n = 2) and foraging trips from these individuals were excluded from analysis. Overall, 31 trips in 2016 and 38 trips from 2017 were used to examine individual-level variation in foraging trip characteristics (Table 1). The arrival and timing of capelin spawning varied between 2016 and 2017, resulting in differences in prey availability between years during the tracking periods. During 2016, the murre tracking period (July 17-23) corresponded with the inshore arrival of capelin (July 18-27), indicative of higher capelin availability, while capelin arrived in the study area approximately two weeks later during 2017 (Aug 1-8), resulting in the tracking period (July 21-31) occurring prior to the inshore arrival of capelin, indicative of lower capelin availability relative to 2016.

Of all foraging characteristics examined in 2017, only mean dive duration differed significantly between sexes, with females diving longer (48.0 ± 2.8 s) than males (33.9 ± 2.5 s);

$\chi^2_1 = 4.86$, $p = 0.028$). Active foraging time tended to be higher in males (13.0 ± 3.6 h) than females (6.7 ± 1.4 h) but this was not significant ($\chi^2_1 = 3.51$, $p = 0.061$). Including sex as a fixed factor only affected adjusted repeatability by a small amount (mean \pm SE: 0.00 ± 0.03 range: 0-0.08), except for mean dive duration, where the addition of sex as a fixed factor reduced repeatability by 0.15. Pearson's correlation analysis revealed high correlation between maximum trip distance and total trip distance ($r=0.93$, $p < 0.001$) and between trip duration and active foraging time ($r=0.88$, $p < 0.001$) and, thus, only maximum trip distance and trip duration were used as representative explanatory variables to examine repeatability.

Repeatability (range: 0 to 1) was generally low (<0.5) for all characteristics in both 2016 and 2017 and most did not differ significantly from zero, indicating most variation was explained by within-individual variation rather than among-individual components (Table 2). Repeatability values that differed significantly ($p < 0.05$) from zero included trip duration for 2017, dive efficiency for 2016, and mean dive duration for both years. For most variables, repeatability was similar between years (i.e. varied by <0.1). Exceptions were trip duration and maximum dive duration, which increased by 0.13 and 0.16, respectively, between 2016 and 2017. Other exceptions were mean dive duration and mean dive efficiency, which decreased by 0.17 and 0.29, respectively, between 2016 and 2017. While repeatability varied little between years, foraging and dive characteristics varied by year, whereby foraging trips were significantly longer and farther from the colony in 2017 relative to 2016 (Table 3). In contrast, maximum dive duration decreased from 2016 to 2017 (Table 3).

Spatial analysis revealed that foraging areas were similar at the population level, when all foraging trips per individual were combined. Many individuals used similar core (50% volume contours) and overall (95% volume contours) foraging areas with high spatial overlap of 95%

kernel densities during 2016 (0.68 ± 0.03) and 2017 (0.60 ± 0.04 ; Fig. 2). In contrast, at the individual level within years, there was low spatial overlap (BA <0.5) both of foraging trip locations within individuals and between different individuals. In 2017, within individual spatial overlap was significantly higher than between individuals, however, when all individuals were combined (Table 4), but this pattern was not observed in 2016. However, we found significantly lower spatial overlap both within (Linear Mixed Effect Model: $t_{11.6} = 3.9$, $p < 0.01$) and between (Student's t-test: $t_{825.9} = -3.58$, $p < 0.01$) all individuals during 2016 relative to 2017.

Using pairwise comparisons of the spatial overlap of foraging trips between different individuals on multiple temporal scales, overlap was higher between trips by individuals that occurred on the same day than those that occurred 1 or ≥ 2 days apart (Figure 3A,C) in 2017 (ANOVA: $F_{2,559} = 8.05$, $p < 0.01$) but not in 2016 (ANOVA: $F_{2,327} = 1.43$, $p = 0.26$). Post-hoc tests revealed that spatial overlap during 2017 was higher between trips of different individuals on the same day than those ≥ 2 days apart (Tukey HSD: $p < 0.01$) as well as higher between trips 1 day apart than ≥ 2 days apart (Tukey HSD: $p = 0.05$). When looking at spatial consistency within individuals, the spatial overlap of consecutive trips (0.19 ± 0.02) versus non-consecutive trips (0.21 ± 0.04) did not differ significantly during 2016 (Student's t-test: $t_{136} = -0.28$, $p = 0.78$), whereas consecutive trips had significantly higher spatial overlap (0.50 ± 0.04) than non-consecutive trips (0.25 ± 0.02) during 2017 (Student's t-test: $t_{177} = -4.14$, $p < 0.01$). When examined at the individual level, only some individuals exhibited this pattern (Fig. 3B,D).

Diet

During 2017, stable isotope ratios of carbon and nitrogen of plasma and red blood cells of tracked birds had similar mean values compared to those of the larger sample, thus all

individuals were pooled for analysis. Examining individual-level consistency revealed significant correlations between plasma and red blood cells in $\delta^{13}\text{C}$ ($R=0.65$, $p < 0.001$) and $\delta^{15}\text{N}$ ($R=0.49$, $p < 0.01$). When comparing whole blood values with red blood cells from 2017, $\delta^{13}\text{C}$ values were significantly lower in 2016 ($t_{15.4}=-3.12$, $p=0.007$) while birds had higher $\delta^{15}\text{N}$ values on average ($t_{8.02}=3.48$, $p=0.008$) (Table 5). Mixing model dietary reconstruction estimated that the diet of individuals in 2016 was primarily capelin (mean \pm SE: 0.78 ± 0.03 , range: 0.65-0.90), whereas in 2017, the proportion of capelin in the diet was more varied (mean \pm SE: 0.47 ± 0.03 , range: 0.20-0.69), with the rest of the diet made up of mostly sandlance (Fig. 4). Camera deployments during 2017 corroborated the 2017 reconstructed diet, by revealing that out of the images where parental prey deliveries to chicks during the tracking period could be identified ($n = 123$), 67% were capelin, 26% sandlance, and 7% included other small fish and invertebrates.

Discussion

By examining foraging behavior, space use, and diet of common murres, our findings indicate that individual murres exhibit high within-individual variation in foraging behavior, as predicted. High within-individual variation was evidenced by low repeatability for foraging trip and dive characteristics as well as low spatial overlap in foraging locations within individuals. Contrary to our predictions, low repeatability was maintained in both years regardless of shifts in prey availability during the study periods. Indeed, individuals shifted their foraging behaviour to longer and farther foraging trips during 2017, when the tracking period occurred prior to the inshore arrival of capelin, relative to 2016, when the tracking period occurred after the inshore arrival of capelin. Overall, these findings suggests a high degree of behavioral flexibility although higher energy costs under low prey availability conditions (Bolnick et al. 2003,

Hückstädt et al. 2012, Polito et al. 2015). In contrast with flexible foraging behavior, murres displayed a degree of dietary consistency, as predicted, evidenced by significant correlations between isotopic values in plasma and red blood cell during 2017. Similarly, dietary reconstruction revealed that murres primarily consumed capelin, with lower proportions of sandlance, but proportions varied among years suggesting a degree of dietary flexibility, which was unexpected. Overall, these findings suggest that although murres are considered capelin specialists on the northeast coast of Newfoundland, they may be able to prey switch (parental and chick diet) and adjust foraging behaviour and dietary composition to buffer against temporal changes in the arrival of spawning capelin within foraging ranges during chick-rearing.

Behavioral Flexibility

Common murres appear to exhibit flexible foraging behavior, evidenced by low repeatability and high within-individual variation in foraging trip and dive characteristics, as well as low spatial overlap of foraging trips by individuals. Indeed, repeatability values for most characteristics in both years were below 0.5 and not significantly different from zero, suggesting that the majority of variation was within rather than among individuals (Nakagawa and Schielzeth 2010). Similarly, previous studies of specialization in seabirds considered values above 0.5 to be high repeatability and values below 0.25 to be low or poor repeatability (Potier et al. 2015, Camprasse et al. 2017). Repeatability of most dive characteristics tended to be higher than foraging trip characteristics, suggesting that dive behavior may be less flexible than foraging trip characteristics. Lower flexibility may be due to physiological limitations in dive capacity related to aerobic dive limits (Elliott et al. 2013). High within-individual variation in foraging trip characteristics is supported by previous studies that have found murres to have

flexible time budgets, primarily in colony attendance and foraging trip duration (Burger and Piatt 1990, Harding et al. 2007b, Piatt et al. 2007). Similar flexibility in foraging trip and dive characteristics has also been exhibited in seabirds in other regions, including northern gannets (Pettex et al. 2012) and great cormorants (Potier et al. 2015). Such strategies may be of particular importance for species that feed on pelagic prey, which varies in both space and time (Cairns 1988, Burger and Piatt 1990).

Despite high within individual variation in foraging trip location, there was evidence of population-level consistency. Indeed, when all foraging trips per individual were combined, there was greater spatial overlap among individuals, with all individuals foraging in a few of the same core areas. In contrast, there was low spatial overlap both within and between individuals at the foraging trip level. These differences in overlap exemplify the importance of temporal scale, as similarities among individuals shift from low at the level of the foraging trip (i.e. days) to high at the level of weeks (i.e. all foraging trips per individual combined). The lack of spatial overlap at the foraging trip level may be related to search behaviour by murre. For instance, breeding murre have been shown to exhibit trapline foraging patterns in other regions, where an individual will visit a number of different locations during a foraging trip (Wanless et al. 1990). Additionally, murre in the study area appear to use local enhancement to locate prey patches (Bairos-Novak et al. 2015). Both types of search behaviour for prey patches would result in high variation in space use at the individual level. In contrast, when all trips per individual were combined, spatial overlap was high in both years, suggesting that at the population level, there is a degree of foraging site fidelity to a few core areas along the coast. Such interannual foraging site fidelity has been shown in other seabirds, such as the shy albatross (Hedd et al. 2001), and is often linked to predictability of resources (Phillips et al. 2017). Indeed, spawning capelin follow

a predictable movement pattern within the study area, arriving inshore along a deep-water trench near Greenspond Island and then moving northward in shallow (<50 m) water (Davoren et al. 2006, Davoren 2013b), resulting in predictable areas along the coast where capelin can be located and marine predators aggregate (Davoren 2013a). Predictability of capelin aggregations also may explain the slightly higher spatial overlap in 2016 when capelin had arrived in the study area during the tracking period relative to 2017. Other studies have found differing degrees of individual variation in foraging behavior relating to prey distribution (e.g. Hamer et al. 2001; Horswill et al. 2016). In the case of northern gannets (*Morus bassanus*), consistency of prey related to flexibility in foraging behavior (Hamer et al. 2001). These patterns of population-level consistency with high individual variation suggest generalist strategies in space use that correspond with flexible foraging behavior, which is likely influenced by small-scale patchiness of prey.

Dietary Consistency

In accordance with flexible behavior, we provided evidence for dietary consistency in 2017, but not to the extent we predicted, suggesting an interplay between diet, behavior, and prey availability. Indeed, murre showed individual consistency in diet, represented by a correlation between plasma and red blood cell isotope values, coupled with two primary prey items (capelin and sandlance) in the diet. Overall, this evidence suggests a narrow dietary niche when comparing with seabirds that are considered dietary generalists, such as herring gulls (*Larus argentatus*) and great black-backed gulls (*Larus marinus*) that feed on fish, invertebrates, insects, plants among other items (Lavoie et al. 2012). However, plasma and red blood cells were not highly correlated, as previous studies have found to conclude high dietary specialization (e.g. $r >$

0.8; Rosenblatt et al. 2015, Camprasse et al. 2017), suggesting a degree of within-individual variation. In support, dietary reconstruction showed variation in the amount of capelin and sandlance in the diet of individuals in both years, suggesting that murrelets may be able to utilize alternative prey when capelin is not highly available, supplementing the diet primarily with sandlance, considered to be high-quality prey species for common murrelets in the northeastern Atlantic (Anderson et al. 2014). In contrast, previous studies in Newfoundland found that murrelets continue to bring back primarily capelin to feed chicks under varying capelin availability (Buren et al. 2012). As chick diet observations during our study showed similar proportions of capelin (67%) and sandlance (26%) as estimated in adult diets, an alternative strategy may be to increase the variety of prey in the diet when suitable alternative prey exists, such as sandlance, a strategy that may be possible due to behavioral flexibility.

Interannual Variation

We observed interannual differences in both foraging behavior and diet, corresponding with variation in the arrival of capelin in the study area, further supporting flexibility in the foraging ecology of common murrelets. While repeatability did not vary greatly between years, subtle differences were observed. Based on optimal foraging theory, one would expect a higher degree of individual specialization (i.e. repeatability) with an increase in prey availability (Connan et al. 2017). Our results support this prediction, whereby most dive characteristics (efficiency, mean dive duration, maximum dive duration, and number of dive bouts) tended to have higher repeatability in 2016 when the arrival of capelin spawning corresponded with chick-rearing, compared with 2017. Individual consistency in dive behavior likely relates to higher predictability of locations of prey aggregations, with capelin available along the coast in shallow

waters (Davoren et al. 2006, Davoren 2013b). In contrast, when prey is less abundant and predictable, individuals would need to use more flexible strategies and spend more time searching underwater to obtain food to feed themselves and provision chicks. In contrast, repeatability of foraging trip characteristics either tended to not change (i.e., maximum distance, total distance) or increase slightly (i.e., active foraging time, trip duration) during 2017, possibly as a result of the necessity to spend consistently longer amounts of time searching and actively foraging. However, confidence intervals for all characteristics overlapped, with the larger confidence intervals resulting from small sample sizes, thus subtle differences in repeatability may not be ecologically meaningful.

While repeatability did not vary greatly, many foraging characteristics showed inter-annual differences. During 2017, prior to the inshore arrival of capelin, maximum trip distance, total distance, and trip duration were all significantly higher relative to 2016, illustrating that birds travelled farther and remained away from the central place for longer. Previous studies examining the impact of prey availability on common murres and similar species have found evidence for increased foraging effort under low prey availability conditions. Indeed, when prey availability was low, foraging trip characteristics and effort have increased for many seabird species, such as pigeon guillemots (Litzow and Piatt 2003), black-legged kittiwakes (Suryan et al. 2006), and northern gannets (Garthe et al. 2011, Bertrand et al. 2012). While common murres have been shown to increase foraging trip distance under low prey availability (Burke and Montevecchi 2009), dive characteristics including mean dive duration, surface pause time, and inter-bout period remained unaffected (Monaghan et al. 1994, Uttley et al. 1994). In contrast, however, studies have also found that low prey availability corresponded with increased diving duration or effort in murres (Monaghan et al. 1994, Regular et al. 2014). Interestingly, we found

little evidence of changes in dive characteristics beyond a decrease in maximum dive duration between years. These discrepancies may relate to degrees of variation in prey availability as well as the presence of alternative prey, such as sandlance, and suggest that the relationship between foraging behavior and prey availability may not be straightforward. The additional knowledge of dietary specialization may provide important insight into these complex relationships (Woo et al. 2008).

Beyond foraging trip characteristics, we observed differences in short-term consistency of spatial overlap of foraging trips both within and between individuals. Consistency in foraging location is predicted to increase when prey can be predictably located on short temporal scales (e.g., hours, days; Woo et al. 2008). When capelin was not likely predictably located in 2017, however, consecutive trips by individuals had higher overlap than non-consecutive trips, and trips of different individuals starting on the same date were significantly more similar than trips starting two or more days apart. The short-term consistency in foraging location within and among individuals when prey were likely less predictably located, may indicate that birds are cueing to the presence of other individuals (i.e. local enhancement), thereby foraging in similar areas to one another on the scale of days. In support, a previous study in our area found that murrelets cue to conspecifics at sea, and that this occurs proportionally more when capelin availability is low relative to high (Bairros-Novak et al. 2015). Short-term consistency in foraging location within and among individuals could also indicate that birds are using memory to locate prey patches, with individuals returning to prey patches located on previous trips. Indeed, murrelets appear to be capable of constructing spatial maps for locating resources, and memory appears to be a key foraging strategy (Davoren et al. 2003), whereby revisiting prey patches when prey availability is low may increase foraging efficiency by reducing search time (Camprasse et al.

2017). Lower short-term spatial consistency in 2016 when breeding corresponded with capelin presence in the study area may simply be due to increased encounters with more profitable prey patches than located on previous trips. Overall, local enhancement and memory appear to be important foraging strategies for seabirds (Buckley 1997, Irons 1998, Grünbaum and Veit 2003, Wakefield et al. 2015), but the importance of strategies may vary under changing prey availability.

While we were unable to examine interannual differences in individual-level dietary consistency, comparing individual-level diet between years suggested more variation in diet during 2017, prior to capelin spawning in the study area. Individuals exhibited lower proportions of capelin in the diet, but also greater variation in capelin proportions among individuals, suggesting greater dietary flexibility may be exhibited in years when there is mismatch between breeding and the arrival of capelin. Thus, behavioral flexibility may relate directly to dietary flexibility and may manifest differently over varying time scales. In support, Woo et al. (2008) found a high level of individual specialization of foraging behavior of thick-billed murrelets, but found that the degree was greater over shorter periods (hours and days) than longer periods (years). Other studies also have found both consistency (Masello et al. 2013) and variation (Jaeger et al. 2010, Scioscia et al. 2014) in dietary niche at different temporal scales. It is likely that environmental variation, phenotypic plasticity, and prey availability all play important roles in the manifestation of individual specialization. It is clear, however, that the scale of individual specialization adds complexity and may manifest at different temporal and spatial scales.

Conclusions

Foraging dynamics and the impacts of prey availability on foraging ecology, while not surprising, are complex. Indeed, prey availability and predictability in space and time likely play

a role in determining strategies used by individuals to minimize energy expenditure when locating prey patches. There are ecological trade-offs between specialist and generalist strategies relating to resource availability, as specialists in good resource years may have higher foraging efficiency than generalists, but often exhibit lower foraging efficiency in poor resource years. In contrast, generalists with a broad niche tend to be more stable in their foraging success (Polito et al. 2015). Regardless of strategies used, previous findings suggest that reproductive success (chick feeding rates, chick growth, fledge success, productivity) is often influenced by prey availability (Burger and Piatt 1990, Uttley et al. 1994, Zador and Piatt 1999). Although we did not measure breeding success in this study, individual variation in foraging behaviour and diet coupled with high-quality alternative prey, suggests that murrelets may be able to cope with changes in prey availability.

As the timing and location of capelin spawning has become increasingly unpredictable in recent decades (Crook et al. 2017), and as capelin biomass and timing are influenced by seasonal ice dynamics (Buren et al. 2014), climate change is likely to increase anomalous events, thereby enhancing variability in the timing and abundance of prey in coastal Newfoundland and other regions. Murrelets in our study area appear to be behavioral generalists with a degree of dietary specialization, suggesting behavioral plasticity that may be advantageous in an increasingly unpredictable environment. As murrelets appear to rely heavily on capelin during chick-rearing (Davoren & Montevecchi 2003b, this study) as well as alternative prey including sandlance, monitoring and management of both species is of particular importance. Understanding how individuals respond to environmental variation, particularly in the face of current levels of rapid environmental change, is critical for conservation (Reed et al. 2006, Ramírez et al. 2016).

References

Ainley, D.G., Nettleship, D.N., Carter, H.R., and Storey, A.E. 2002. Common Murre (*Uria aalge*). In The Birds of North America. Edited by P.G. Rodewald. Ithaca, New York.

- Anderson, H.B., Evans, P.G.H., Potts, J.M., Harris, M.P., and Wanless, S. 2014. The diet of common guillemot *Uria aalge* chicks provides evidence of changing prey communities in the North Sea. *Ibis* **156**(1): 23–34.
- Anderson, O.R.J., Phillips, R.A., Shore, R.F., McGill, R.A.R., McDonald, R.A., and Bearhop, S. 2009. Diet, individual specialisation and breeding of brown skuas (*Catharacta antarctica lonnbergi*): an investigation using stable isotopes. *Polar Biol.* **32**(1): 27–33.
- Bairos-Novak, K.R., Crook, K.A., and Davoren, G.K. 2015. Relative importance of local enhancement as a search strategy for breeding seabirds: an experimental approach. *Anim. Behav.* **106**: 71–78.
- Barquete, V., Strauss, V., and Ryan, P.G. 2013. Stable isotope turnover in blood and claws: a case study in captive African penguins. *J. Exp. Mar. Bio. Ecol.* **448**: 121–127.
- Bearhop, S., Teece, M.A., Waldron, S., and Furness, R.W. 2000. Influence of lipid and uric acid on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of avian blood: implications for trophic studies. *Auk* **117**(2): 504–507.
- Bearhop, S., Waldron, S., Votier, S.C., and Furness, R.W. 2002. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiol. Biochem. Zool.* **75**(5): 451–458.
- Becker, B.H., Newman, S.H., Inglis, S., and Beissinger, S.R. 2007. Diet–feather stable isotope ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$) fractionation in common murrelets and other seabirds. *Condor* **109**(2): 451.
- Bertrand, S., Joo, R., Arbulu Smet, C., Tremblay, Y., Barbraud, C., and Weimerskirch, H. 2012. Local depletion by a fishery can affect seabird foraging. *J. Appl. Ecol.* **49**(5): 1168–1177.
- Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., and Hulsey, C.D. 2003. The

- ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* **161**(1): 1–28.
- Buckley, N.J. 1997. Spatial-concentration effects and the importance of local enhancement in the evolution of colonial breeding in seabirds. *Am. Nat.* **149**(6): 1091–1112.
- Buren, A.D., Koen-Alonso, M., and Montevecchi, W.A. 2012. Linking predator diet and prey availability: common murre and capelin in the Northwest Atlantic. *Mar. Ecol. Prog. Ser.* **445**: 25–35.
- Buren, A.D., Koen-Alonso, M., Pepin, P., Mowbray, F., Nakashima, B., Stenson, G., Ollerhead, N., and Montevecchi, W.A. 2014. Bottom-up regulation of capelin, a keystone forage species. *PLoS One* **9**(2): e87589.
- Burger, A.E. 1997. Arrival and departure behavior of common murre at colonies: evidence for an information halo? *Colon. Waterbirds* **20**(1): 55–65.
- Burger, A.E., and Piatt, J.F. 1990. Flexible time budgets in breeding common murre: buffers against variable prey abundance. *Stud. Avian Biol.* **14**: 71–83.
- Burke, C. 2008. Comparative foraging ecology of parental common murre (*Uria aalge*) and Atlantic puffins (*Fratercula Arctica*) in response to the changes in forage fish availability. Memorial University of Newfoundland.
- Burke, C.M., and Montevecchi, W.A. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *J. Zool.* **278**: 354–361.
- Cairns, D.K. 1988. Seabirds as indicators of marine food supplies. *Biol. Oceanogr.* **5**(4): 261–271.
- Calenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Modell.* **197**: 516–519.

- Camprasse, E.C.M., Cherel, Y., Arnould, J.P.Y., Hoskins, A.J., and Bost, C.A. 2017. Combined bio-logging and stable isotopes reveal individual specialisations in a benthic coastal seabird, the Kerguelen shag. *PLoS One* **12**(3): e0172278.
- Carneiro, A., Bonnet-Lebrun, A., Manica, A., Staniland, I., and RA, P. 2017. Methods for detecting and quantifying individual specialisation in movement and foraging strategies of marine predators. *Mar. Ecol. Prog. Ser.* **578**: 151–166.
- Carscadden, J.E., Montevecchi, W.A., Davoren, G.K., and Nakashima, B.S. 2002. Trophic relationships among capelin (*Mallotus villosus*) and seabirds in a changing ecosystem. *ICES J. Mar. Sci.* **59**: 1027–1033.
- Ceia, F.R., and Ramos, J.A. 2015. Individual specialization in the foraging and feeding strategies of seabirds: a review. *Mar. Biol.* **162**(10): 1923–1938.
- Cherel, Y., Jaquemet, S., Maglio, A., and Jaeger, A. 2014. Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between feathers and blood of seabird chicks: Implications for non-invasive isotopic investigations. *Mar. Biol.* **161**(1): 229–237.
- Connan, M., Bonnevie, B.T., Hagen, C., van der Lingen, C.D., and McQuaid, C. 2017. Diet specialization in a colonial seabird studied using three complementary dietary techniques: effects of intrinsic and extrinsic factors. *Mar. Biol.* **164**(8): 1–20.
- Crook, K.A., Maxner, E., and Davoren, G.K. 2017. Temperature-based spawning habitat selection by capelin (*Mallotus villosus*) in Newfoundland. *ICES J. Mar. Sci.* **74**(6): 1622–1629.
- Davoren, G.K. 2007. Effects of gill-net fishing on marine birds in a biological hotspot in the northwest Atlantic. *Conserv. Biol.* **21**(4): 1032–1045
- Davoren, G.K. 2013a. Distribution of marine predator hotspots explained by persistent areas of

- prey. *Mar. Biol.* **160**(12): 3043–3058.
- Davoren, G.K. 2013b. Divergent use of spawning habitat by male capelin (*Mallotus villosus*) in a warm and cold year. *Behav. Ecol.* **24**(1): 152–161.
- Davoren, G.K., Anderson, J.T., and Montevecchi, W.A. 2006. Shoal behaviour and maturity relations of spawning capelin (*Mallotus villosus*) off Newfoundland : demersal spawning and diel vertical movement patterns. *Can. J. Aquat. Sci.* **63**: 268–284.
- Davoren, G.K., and Montevecchi, W.A. 2003a. Signals from seabirds indicate changing biology of capelin stocks. *Mar. Ecol. Prog. Ser.* **258**: 253–261.
- Davoren, G.K., and Montevecchi, W.A. 2003b. Consequences of foraging trip duration on provisioning behaviour and fledging condition of common murre *Uria aalge*. *J. Avian Biol.* **34**: 44–53.
- Davoren, G.K., Montevecchi, W.A., and Anderson, J.T. 2003. Search strategies of a pursuit-diving marine bird and the persistence of prey patches. *Ecol. Monogr.* **73**(3): 463–481.
- Davoren, G.K., Penton, P., Burke, C., and Montevecchi, W.A. 2012. Water temperature and timing of capelin spawning determine seabird diets. *ICES J. Mar. Sci.* **69**(7): 1234–1241.
- Dias, M.P., Granadeiro, J.P., and Catry, P. 2013. Individual variability in the migratory path and stopovers of a long-distance pelagic migrant. *Anim. Behav.* **86**(2): 359–364.
- Dobush, R., Davison, C., and Ankney, C.D. 1985. The effect of apparatus, extraction time , and solvent type on lipid extractions of snow geese. *Can. J. Fish. Aquat. Sci.* **63**: 1917–1920.
- Elliott, K.H., Ricklefs, R.E., Gaston, A.J., Hatch, S. a., Speakman, J.R., and Davoren, G.K. 2013. High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Proc. Natl. Acad. Sci. U. S. A.* **110**(23): 9380–9384.
- Evans, T.J., Kadin, M., Olsson, O., and Åkesson, S. 2013. Foraging behaviour of common

- murre in the Baltic Sea, recorded by simultaneous attachment of GPS and time-depth recorder devices. *Mar. Ecol. Prog. Ser.* **475**: 277–289.
- Fieberg, J., and Kochanny, C.O. 2005. Quantifying home-range overlap: the importance of the utilization distribution. *J. Wildl. Manage.* **69**(4): 1346.
- Garthe, S., Montevecchi, W.A., and Davoren, G.K. 2011. Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator. *Limnol. Oceanogr.* **56**(3): 802–812.
- Grünbaum, D., and Veit, R.R. 2003. Black-browed albatrosses foraging on Antarctic krill: density-dependence through local enhancement? *Ecology* **84**(12): 3265–3275.
- Gulka, J., Carvalho, P.C., Jenkins, E., Johnson, K., Maynard, L., and Davoren, G.K. 2017. Dietary niche shifts of multiple marine predators under varying prey availability on the northeast Newfoundland coast. *Front. Mar. Sci.* **4**: 324.
- Hamer, K.C., Humphreys, E.M., Garthe, S., Hennenke, J., Peters, G., Grémillet, D., Phillips, R.A., Harris, M.P., and Wanless, S. 2007. Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Mar. Ecol. Prog. Ser.* **338**: 295–305.
- Hamer, K.C., Phillips, R.A., Hill, J.K., Wanless, S., and Wood, A.G. 2001. Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies: Foraging trip duration and foraging area fidelity. *Mar. Ecol. Prog. Ser.* **224**: 283–290.
- Harding, A.M. a, Piatt, J.F., Schmutz, J. a, Shultz, M.T., Van Pelt, T.I., Pelt, V., Kettle, A.B., and Speckman, S.G. 2007a. Prey density and the behavioural flexibility of a marine predator: the common murre (*Uria aalga*). *Ecology* **88**(8): 2024–2033.
- Harding, A.M.A., Piatt, J.F., and Schmutz, J.A. 2007b. Seabird behavior as an indicator of food

- supplies: Sensitivity across the breeding season. *Mar. Ecol. Prog. Ser.* **352**: 269–274.
- Harris, M.P., and Wanless, S. 2011. *The Puffin*. Edited By J. Martin. T & AD Poyser, London.
- Harris, S., Raya Rey, A., Zavalaga, C., and Quintana, F. 2014. Strong temporal consistency in the individual foraging behaviour of Imperial Shags *Phalacrocorax atriceps*. *Ibis* **156**(3): 523–533.
- Hedd, A., Gales, R., and Brothers, N. 2001. Foraging strategies of shy albatross *Thalassarche cauta* breeding at Albatross Island, Tasmania, Australia. *Mar. Ecol. Prog. Ser.* **224**: 267–282.
- Hedd, A., Regular, P.M., Montevecchi, W.A., Buren, A.D., Burke, C.M., and Fifield, D.A. 2009. Going deep: common murrens dive into frigid water for aggregated, persistent and slow-moving capelin. *Mar. Biol.* **156**(4): 741–751.
- Horswill, C., Matthiopoulos, J., Ratcliffe, N., Green, J.A., Trathan, P.N., McGill, R.A.R., Phillips, R.A., and O’Connell, T.C. 2016. Drivers of intrapopulation variation in resource use in a generalist predator, the macaroni penguin. *Mar. Ecol. Prog. Ser.* **548**: 233–247.
- Hückstädt, L.A., Koch, P.L., McDonald, B.I., Goebel, M.E., Crocker, D.E., and Costa, D.P. 2012. Stable isotope analyses reveal individual variability in the trophic ecology of a top marine predator, the southern elephant seal. *Oecologia* **169**(2): 395–406.
- Irons, D.B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* **79**(2): 647–655.
- Jackson, A.L., Inger, R., Parnell, A.C., and Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* **80**(3): 595–602.
- Jaeger, A., Connan, M., Richard, P., and Cherel, Y. 2010. Use of stable isotopes to quantify

- seasonal changes of trophic niche and levels of population and individual specialisation in seabirds. *Mar. Ecol. Prog. Ser.* **401**: 269–277.
- Kokubun, N., Takahashi, A., Mori, Y., Watanabe, S., and Shin, H.C. 2010. Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. *Mar. Biol.* **157**(4): 811–825.
- Lavoie, R. a, Rail, J.F., and Lean, D.R.S. 2012. Diet composition of seabirds from Corossol Island, Canada, using direct dietary and stable isotope analyses. *Waterbirds* **35**(3): 402–419.
- Layman, C.A., Boucek, R., and Hammerschlag-peyer, C.M. 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol. Rev.* **87**: 542–562.
- Linnebjerg, J.F., Fort, J., Guilford, T., Reuleaux, A., Mosbech, A., and Frederiksen, M. 2013. Sympatric breeding auks shift between dietary and spatial resource partitioning across the annual cycle. *PLoS One* **8**(8): e72987.
- Linnebjerg, J.F., Reuleaux, A., Mouritsen, K.N., and Frederiksen, M. 2015. Foraging ecology of three sympatric breeding alcids in a declining colony in southwest Greenland. *Waterbirds* **38**(2): 143–152.
- Litzow, M.A., Piatt, J.F., Prichard, A.K., and Roby, D.D. 2002. Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey. *Oecologia* **132**(2): 286–295.
- Luque, S., and Guinet, C. 2007. A maximum likelihood approach for identifying dive bouts improves accuracy, precision and objectivity. *Behaviour* **144**(11): 1315–1332.
- Masello, J.F., Wikelski, M., Voigt, C.C., and Quillfeldt, P. 2013. Distribution patterns predict individual specialization in the diet of dolphin gulls. *PLoS One* **8**(7): e67714.
- Monaghan, P., Walton, P., Wanless, S., Uttley, J.D., and Burns, M.D. 1994. Effects of prey

- abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge*. *Ibis* **136**: 214–222.
- Moore, J.W., and Semmens, B.X. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. *Ecol. Lett.* **11**(5): 470–480.
- Nakagawa, S., and Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biol. Rev.* **85**(4): 935–956.
- Patrick, S.C., Bearhop, S., Bodey, T.W., Grecian, W.J., Hamer, K.C., Lee, J., and Votier, S.C. 2015. Individual seabirds show consistent foraging strategies in response to predictable fisheries discards. *J. Avian Biol.* **46**(5): 431–440.
- Patrick, S.C., Bearhop, S., Gremillet, D., Lescroel, A., Grecian, W.J., Bodey, T.W., Hamer, K.C., Wakefield, E., Le Nuz, M., and Votier, S.C. 2014. Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* **123**(1): 33–40.
- Pettex, E., Lorentsen, S.H., Grémillet, D., Gimenez, O., Barrett, R.T., Pons, J.B., Le Bohec, C., and Bonadonna, F. 2012. Multi-scale foraging variability in Northern gannet (*Morus bassanus*) fuels potential foraging plasticity. *Mar. Biol.* **159**(12): 2743–2756.
- Phillips, R., Lewis, S., Gonzalez-Solis, J., and Daunt, F. 2017. Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Mar. Ecol. Prog. Ser.* **578**: 117–150.
- Piatt, J.F., Sydeman, W.J., and Wiese, F. 2007. Introduction: A modern role for seabirds as indicators. *Mar. Ecol. Prog. Ser.* **352**: 199–204.
- Polito, M.J., Trivelpiece, W.Z., Patterson, W.P., Karnovsky, N.J., Reiss, C.S., and Emslie, S.D. 2015. Contrasting specialist and generalist patterns facilitate foraging niche partitioning

- in sympatric populations of *Pygoscelis* penguins. *Mar. Ecol. Prog. Ser.* **519**: 221–237.
- Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., and Montaña, C.G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**(1): 179–189.
- Potier, S., Carpentier, A., Grémillet, D., Leroy, B., and Lescroël, A. 2015. Individual repeatability of foraging behaviour in a marine predator, the great cormorant, *Phalacrocorax carbo*. *Anim. Behav.* **103**: 83–90.
- Ramírez, I., Paiva, V.H., Fagundes, I., Menezes, D., Silva, I., Ceia, F.R., Phillips, R.A., Ramos, J.A., and Garthe, S. 2016. Conservation implications of consistent foraging and trophic ecology in a rare petrel species. *Anim. Conserv.* **19**(2): 139–152.
- Reed, T.E., Wanless, S., Harris, M.P., Frederiksen, M., Kruuk, L.E.B., and Cunningham, E.J.A. 2006. Responding to environmental change: plastic responses vary little in a synchronous breeder. *Proc. Biol. Sci.* **273**: 2713–2719.
- Regular, P.M., Hedd, A., Montevecchi, W.A., Robertson, G.J., Storey, A.E., and Walsh, C.J. 2014. Why timing is everything: energetic costs and reproductive consequences of resource mismatch for a chick-rearing seabird. *Ecosphere* **5**(12): 155.
- Rosenblatt, A.E., Nifong, J.C., Heithaus, M.R., Mazzotti, F.J., Cherkiss, M.S., Jeffery, B.M., Elsey, R.M., Decker, R.A., Silliman, B.R., Guillette, L.J., Lowers, R.H., and Larson, J.C. 2015. Factors affecting individual foraging specialization and temporal diet stability across the range of a large “generalist” apex predator. *Oecologia* **178**(1): 5–16.
- Scioscia, G., Raya Rey, A., Saenz Samaniego, R.A., Florentin, O., and Schiavini, A. 2014. Intra- and interannual variation in the diet of the Magellanic penguin (*Spheniscus magellanicus*) at Martillo Island, Beagle Channel. *Polar Biol.* **37**(10): 1421–1433.

- Shoji, A., Elliott, K., Fayet, A., Boyle, D., Perrins, C., and Guilford, T. 2015. Foraging behaviour of sympatric razorbills and puffins. *Mar. Ecol. Prog. Ser.* **520**: 257–267.
- Stephens, D.W., Brown, J.S., and Ydenberg, R.C. 2007. *Foraging: behavior and ecology*. University of Chicago Press, London.
- Stock, B.C., and Semmens, B.X. 2016. Unifying error structures in commonly used biotracer mixing models. *Ecology* **97**(3): 576–582.
- Toscano, B.J., Gownaris, N.J., Heerhartz, S.M., and Monaco, C.J. 2016. Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia* **182**(1): 55–69.
- Uttley, J.D., Walton, P., Monaghan, P., and Austin, G. 1994. The effects of food abundance on breeding performance and adult time budgets of guillemots *Uria aalge*. *Ibis* **136**(2): 205–213.
- Wakefield, E.D., Cleasby, I.R., Bearhop, S., Bodey, T.W., Davies, R.D., Miller, P.I., Newton, J., Votier, S.C., and Hamer, K.C. 2015. Long-term individual foraging site fidelity-why some gannets don't change their spots. *Ecology* **96**(11): 3058–3074.
- Wanless, S., Harris, M.P., and Morris, J.A. 1990. A comparison of feeding areas used by individual common murres (*Uria aalge*), razorbills (*Alca torda*) and an Atlantic puffin (*Fraterecula arctica*) during the breeding season. *Colon. Waterbirds* **13**(1): 16–24.
- Wilhelm, S.I., Mailhiot, J., Arany, J., Chardine, J.W., Robertson, G.J., and Ryan, P.C. 2015. Update and trends of three important seabird populations in the western North Atlantic using a Geographic Information System approach. *Mar. Ornithol.* **43**: 211–222.
- Wilhelm, S.I., Walsh, C.J., and Storey, A.E. 2008. Time budgets of common murres vary in relation to changes in inshore capelin availability. *Condor* **110**(2): 316–324.

- Wolak, M.E., Fairbairn, D.J., and Paulsen, Y.R. 2012. Guidelines for estimating repeatability. *Methods Ecol. Evol.* **3**(1): 129–137.
- Woo, K.J., Elliott, K.H., Davidson, M., Gaston, A.J., and Davoren, G.K. 2008. Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *J. Anim. Ecol.* **77**(6): 1082–1091.
- Zador, S.G., and Piatt, J.F. 1999. Time-budgets of common murres at a declining and increasing colony in Alaska. *Condor* **101**(1): 149–152.

Tables and Figures

Table 1. Summary of individual common murres (*Uria aalge*) tracked during 2016 and 2017 with GPS devices on South Cabot Island, Newfoundland, and data used in analysis including sex of individuals (if known), the number of foraging trips and total number of dives. Foraging trips

include only complete trips. The number in parentheses represents the number of trips excluded from kernel density analysis due to <20 dive locations.

Year	Individual	Sex	Foraging Trips	Dives
2016	URI 15	-	7	775
	URI 16	-	3	628
	URI 18	-	8 (1)	526
	URI19	-	8 (1)	712
	URI 25	-	5	1091
2017	URE03	F	9 (1)	602
	URE06	F	8 (1)	908
	URE07	M	5	889
	URE08	F	5	814
	URE09	M	6	982
	URI11	F	5 (1)	1984

Table 2. Repeatability analysis of foraging trip and dive characteristics and diet of breeding common murres from South Cabot Island, Newfoundland including variance components of between individual variance (ID) and within individual variance (residuals). Repeatability values

include repeatability (R), the 95% confidence interval (CI) from parametric bootstrapping, and significance, indicating whether repeatability is significantly different from zero.

Variable	Variance		Repeatability		
	ID	Residuals	R	CI	p-value
Maximum distance (km)					
2016	0.8	125.9	0.01	0-0.28	1.00
2017	0.0	189.5	0.00	0-0.23	1.00
Trip durations (h)					
2016	10.1	61.9	0.14	0-0.50	0.30
2017	54.9	150.5	0.27	0-0.57	0.03
Maximum dive duration (s)					
2016	0.0	1313.0	0.00	0-0.28	1.00
2017	222.2	1193.1	0.16	0-0.47	0.18
Mean dive duration (s)					
2016	176.0	185.0	0.49	0-0.79	0.01
2017	73.7	155.1	0.32	0-0.64	0.02
Number of Dive Bouts					
2016	0.10	0.60	0.11	0-0.35	0.15
2017	0.03	0.50	0.04	0-0.25	0.30
Dives per bout					
2016	0.0	2.8	0.00	0-0.29	1.0
2017	0.6	4.5	0.11	0-0.41	0.23
Mean Dive Efficiency					
2016	0.002	0.005	0.29	0-0.62	0.05
2017	0.000	0.007	0.00	0-0.24	1.0

Table 3. Summary of foraging trip and dive characteristics of breeding common murrelets from South Cabot Island, Newfoundland in 2016 and 2017. Values for each year include mean \pm standard error.

Variable	2016	2017	χ^2	df	p-value
Maximum distance (km)	17.9 \pm 2.0	27.4 \pm 2.2	9.6	1	0.002

Total distance (km)	48.8 ± 5.6	73.6 ± 6.2	8.6	1	0.003
Trip durations (h)	9.9 ± 1.5	19.6 ± 2.3	5.3	1	0.022
Active foraging time (h)	4.4 ± 0.8	8.5 ± 1.5	3.3	1	0.067
Maximum dive duration (s)	151.1 ± 6.5	125.4 ± 6.0	15.1	1	0.018
Mean dive duration (s)	46.8 ± 3.2	43.9 ± 2.4	0.1	1	0.955
Number of Dive Bouts	28.4 ± 4.0	32.2 ± 3.6	0.2	1	0.684
Dives per bout	3.8 ± 0.3	4.4 ± 0.4	1.1	1	0.292
Mean Dive Efficiency	0.5 ± 0.02	0.4 ± 0.01	3.5	1	0.062

Table 4. Spatial overlap (mean Bhattacharya's Affinity (BA) ± SE) of foraging trips of breeding common murrelets on the northeast Newfoundland coast in 2016 and 2017, including overlap of foraging trips of the same individual (within) and overlap of foraging trips of different individuals (between) and whether within and between individual BA differed significantly.

Year	ID	BA Within	BA Between	t	df	p-value
2016	URI 15	0.16 ± 0.05	0.22 ± 0.02	1.13	24.1	0.27
	URI 16	0.26 ± 0.22	0.29 ± 0.03	0.14	2.1	0.90
	URI 18	0.21 ± 0.05	0.23 ± 0.03	0.42	34.2	0.68
	URI19	0.25 ± 0.05	0.24 ± 0.02	-0.33	26.7	0.75
	URI 25	0.16 ± 0.05	0.17 ± 0.02	1.01	11.1	0.33
ALL INDIVIDUALS		0.23 ± 0.03	0.20 ± 0.01	1.10	107.6	0.27
2017	URE03	0.44 ± 0.05	0.32 ± 0.02	-2.39	43.2	0.02
	URE06	0.19 ± 0.05	0.26 ± 0.02	1.24	32.7	0.22
	URE07	0.36 ± 0.06	0.35 ± 0.02	-0.19	10.8	0.85
	URE08	0.31 ± 0.05	0.30 ± 0.02	-0.21	52.1	0.83
	URE09	0.41 ± 0.05	0.30 ± 0.02	-2.05	78.5	0.04
	URI11	0.15 ± 0.04	0.18 ± 0.02	0.62	11.7	0.55
ALL INDIVIDUALS		0.34 ± 0.02	0.29 ± 0.01	-2.06	258.0	0.04

Table 5. Mean (\pm SE) stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in whole blood (WB; 2016), blood plasma and red blood cells (RBC; 2017) of breeding common murre on South Cabot Island, Newfoundland and potential prey including capelin, sandlance, and small fish, including juvenile Atlantic cod (*Gadus morhua*), sandlance (*Ammodytes* sp.), and an unidentified species, grouped due to similarity in isotopic values. Prey sample size in 2016/2017.

Species	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Common murre (<i>Uria aalga</i>)			
Plasma	26	-22.1 ± 0.2	12.6 ± 0.2
RBC	26	-19.8 ± 0.0	14.0 ± 0.1
WB	7	-19.9 ± 0.0	14.7 ± 0.2
Capelin (<i>Mallotus villosus</i>)	40/17	-20.4 ± 0.4	12.2 ± 0.4
Sandlance (<i>Ammodytes</i> sp.)	2/9	-22.6 ± 0.1	10.2 ± 0.4
Small fish	0/26	-22.6 ± 0.1	9.3 ± 0.4

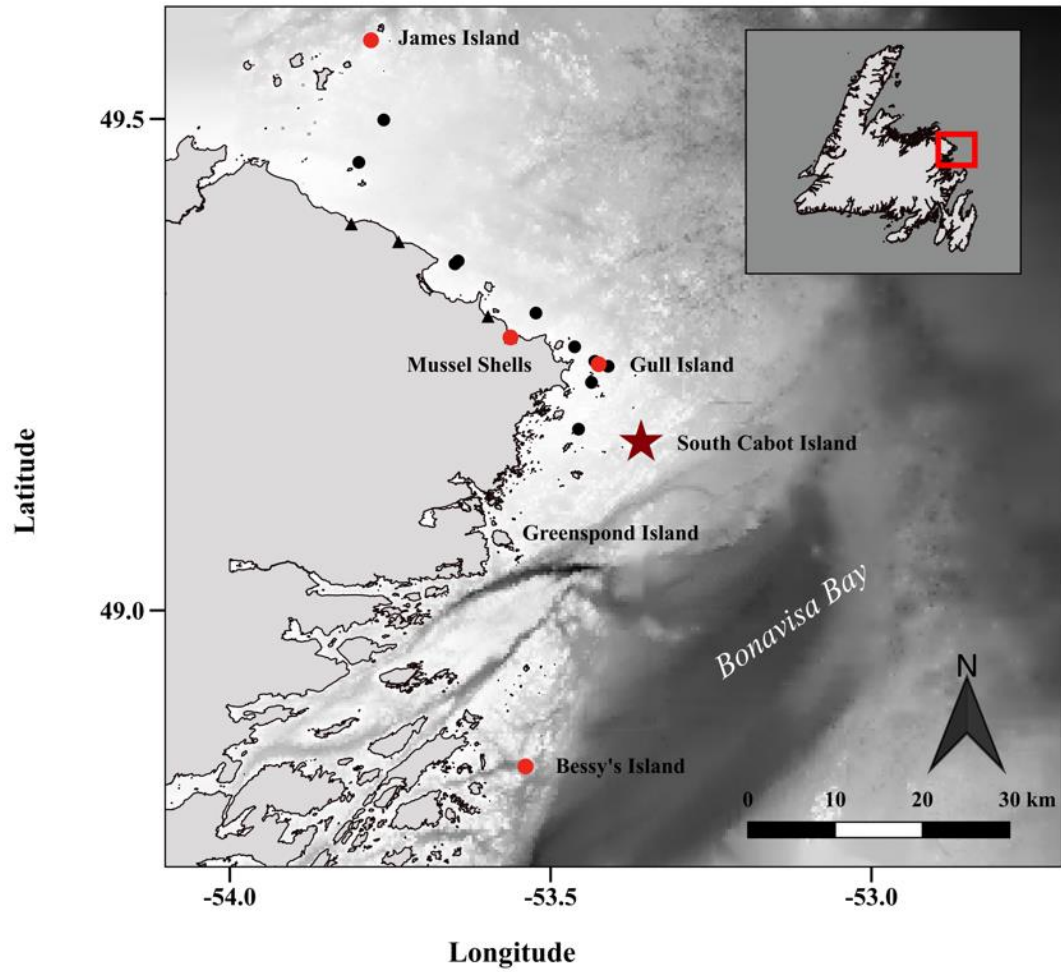


Figure 1. Study area on the northeastern Newfoundland coast, including the breeding colony of common murrens on South Cabot Island (star), fish sampling sites (red circles), along with beach (triangles) and deep-water (black circles) capelin spawning sites.

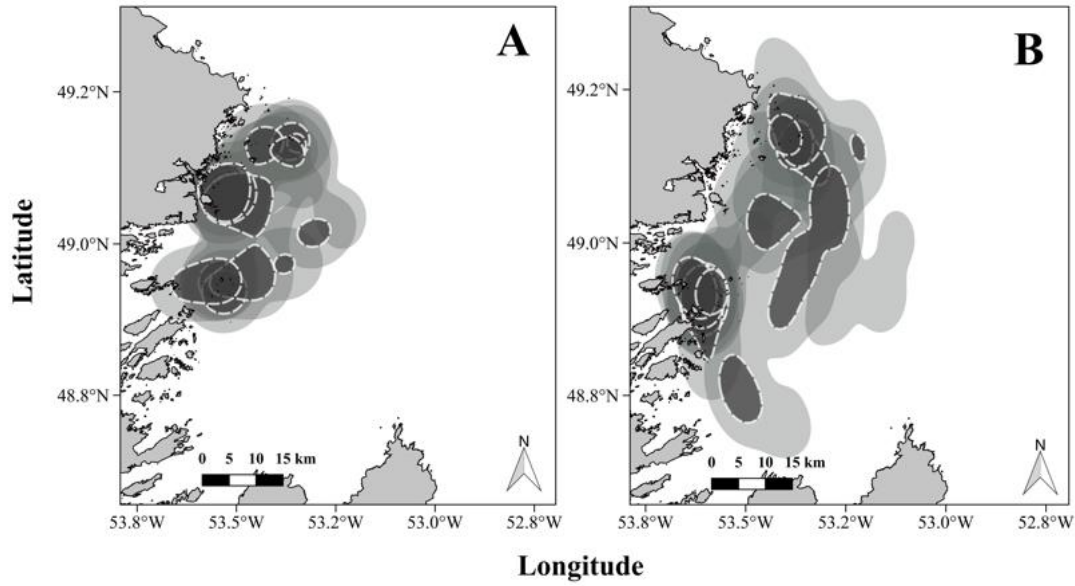


Figure 2. Foraging areas of individual common murrelets depicted with 50% (dark grey, dashed) and 95% (light grey, solid) volume contours, based on kernel density analysis of all dive locations from all foraging trips per individual during A) 2016 (n=5 birds) and B) 2017 (n=6 birds).

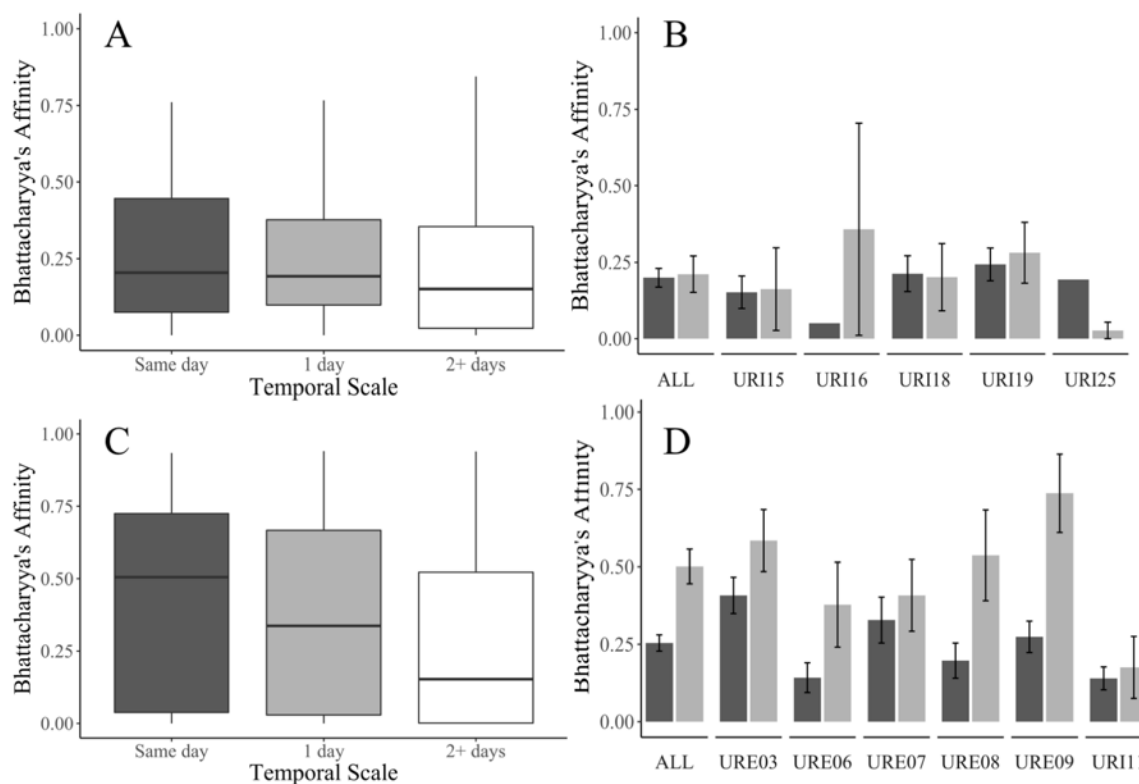


Figure 3. Spatial overlap (Bhattacharya's Affinity, BA) of foraging trips of common murres on the northeast Newfoundland coast. Left panel: overlap of foraging trips of different individuals beginning either on the same date (n= 73, 54 combinations), 1 day apart (n=112, 92 combinations), or 2 or greater days apart (n=145, 412 combinations) in 2016 (A) and 2017 (C) respectively. Line represents median, box includes 25 and 75 percentiles, whiskers are largest value no greater than 1.5*IQR. Right panel: mean (\pm SE) spatial overlap (Bhattacharya's Affinity, BA) of consecutive (light grey) and non-consecutive (dark grey) trips of the same individuals in 2016 (B) and 2017 (D).

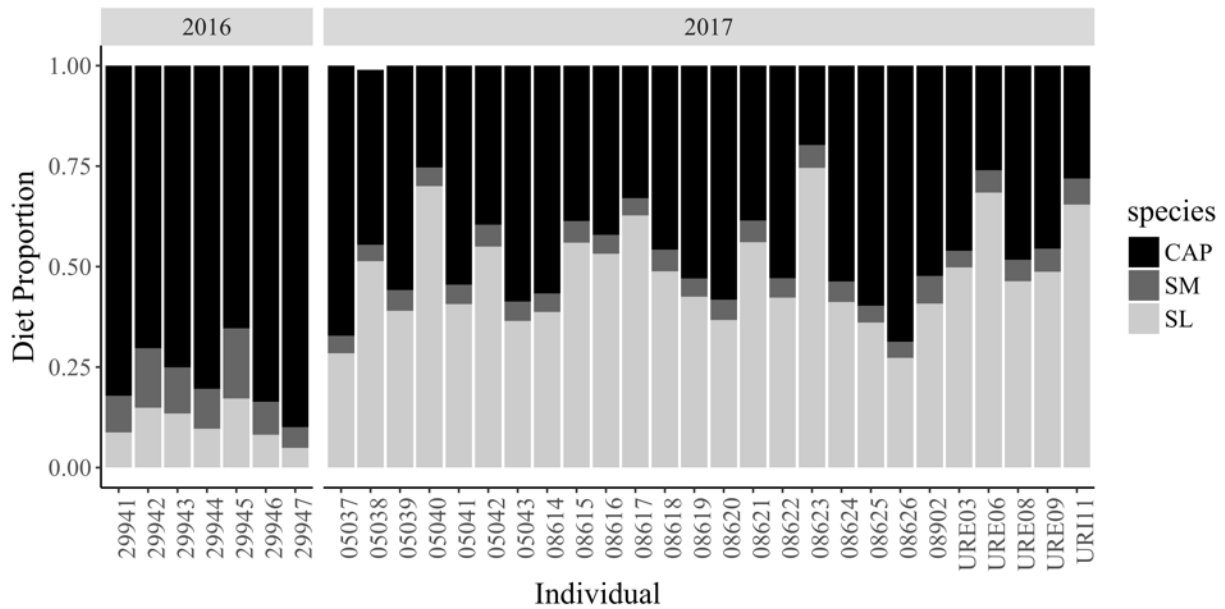


Figure 4. Estimated diet proportions of individual breeding common murrelets using stable isotope mixing models of carbon and nitrogen during 2016 (whole blood, n=7) and 2017 (red blood cells, n=26) on the northeastern Newfoundland coast. Prey species include capelin (CAP), small fish (SM) and sandlance (SL).

Chapter Two. Spatial segregation contrasting dietary overlap: niche partitioning of two sympatric alcids during shifting resource availability

Abstract

Interspecific interactions help to shape individual- and population-level dynamics. As such, similar species breeding sympatrically are expected to have a high potential for competition and, thus, have developed strategies to reduce niche overlap to allow for coexistence. We combined GPS tracking and stable isotope analysis ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) to simultaneously compare multiple behavioral and dietary niche dimensions of common murre (*Uria aalge*) and razorbills (*Alco torda*) breeding at nearby colonies on the northeastern Newfoundland coast under varying prey availability. Complete spatial segregation between foraging areas of the two species was observed, along with divergent dive characteristics, as would be predicted based on body size and dive capacity. These differences contrasted a high degree of overlap in diet, habitat preference, and diurnal foraging patterns, suggesting that spatial segregation may be the primary response to competition for the same resources. As prey availability shifted from low to high, murre and razorbills foraged closer to the colony and diet proportions changed, indicative of reduced energy costs and dietary plasticity to take advantage of highly available prey; however, foraging areas continued to be segregated. Understanding variation in space, time, and habitat selection allowed for a more comprehensive view of the possible ways these species may partition their niche and how resource availability impacts these interspecific relationships.

Introduction

Interspecific interactions shape how species interact and communities develop. Niche theory offers important context for the study of resource partitioning, involving different aspects of resource use, interactions among species and individuals, community composition, and evolutionary processes (Polito et al. 2015). There are different ways to define an ecological niche, but it generally encompasses the environmental conditions, both abiotic and biotic, required to meet the minimum requirements for survival, and can be thought of as an n-dimensional hypervolume (Hutchinson 1978, Chase and Leibold 2003). A niche can be characterized in a number of ways, and the dietary niche represents the food resources used by an organism. For instance, dietary niche breadth is an indication of the variety of food resources used, whereas niche position indicates the types of resources used, and niche overlap indicates the similarity in resource use among individuals or species (Hammerschlag-Peyer et al. 2011). The competitive exclusion principle postulates that two species with the same resource requirements cannot coexist if resources are limiting (Gause 1934). Thus, species may utilize different tactics to reduce niche overlap, with niche partitioning theory positing that if overlap occurs between species in one niche dimension, divergence is predicted in another dimension (Gause 1971). In particular, resource partitioning can result in differences in prey type (e.g. Beaulieu and Sockman 2012, Bonato et al. 2018), habitat choice (e.g. Hyrenbach et al. 2002, Nicholls et al. 2002), and foraging behaviour (Masello et al. 2010, Linnebjerg et al. 2013) among sympatric species. The ways in which niche partitioning may occur can be influenced both by species interactions and availability of resources. Species may be disparately affected by heterospecifics, known as asymmetrical competition, whereby one species may be more strongly impacted while the other species is less affected, or competitively dominant (Connell 1983).

Asymmetrical competition is common in nature and can relate to physical and behavioral traits (Dupuch et al. 2014). The abundance and distribution of food resources also plays a key role in competitive interactions, as niche overlap may only result in competition when prey is limited, with prey superabundance expected to minimize competition and, thus, the degree of niche partitioning (Giller 1984, Forero et al. 2004).

During the breeding season, seabirds act as central-place foragers, where the central place is the breeding area to which parents must return between foraging trips to incubate eggs or provision chicks (Orians and Pearson 1979). This spatial constraint restricts resource patch choice within a limited foraging range around the colony. The abundance, distribution, and predictability of prey shape foraging decisions within this range (Paiva et al. 2010). Foraging decisions also may be constrained by other species, especially when suitable breeding habitat is aggregated and many conspecifics and heterospecifics forage within the same limited range. These constraints can lead to increased overlap in resource use, causing the need for resource partitioning if resources are or become limited (Linnebjerg et al. 2013). Alcid species provide great models to examine niche partitioning, as they nest in large numbers in dense, multi-species colonies, creating a high potential for competition. In particular, the common murre (*Uria aalge*) and the razorbill (*Alca torda*) are closely related, wing-propelled, pursuit-diving auks that feed primarily on forage fish and share much of their Atlantic range (Gaston and Jones 1998, Ainley et al. 2002, Lavers et al. 2009). Although common murre (hereafter ‘murre’) and razorbills often breed on the same colonies, it is rare on the northeast Newfoundland coast, which supports regionally important breeding colonies of murre (Funk Island: 500,000 breeding pairs; South Cabot Island: 10,000 breeding pairs; Wilhelm et al. 2015) and razorbills (James Island, 300 breeding pairs; Robertson and Elliot 2002). As wing-propelled pursuit-divers, their wing design

is a compromise between efficiency of flight in air and diving underwater, resulting in high wing loading (i.e. body mass/wing area) and high energetic costs during aerial flight (Elliott et al. 2013). Murres, however, have 30% higher wing loading and larger body mass relative to razorbills and, thus, murres expend more energy during flight, but have an increased dive capacity (i.e. longer and deeper dives; Thaxter et al. 2010, Shoji et al. 2016b). As such, it is not surprising that previous studies comparing niche dynamics of breeding murres and razorbills have found differences in dive characteristics and foraging distance from the colony (Wanless et al. 1990, Thaxter et al. 2010, Linnebjerg et al. 2015). In contrast, other studies have shown a high similarity in winter and breeding season diet (Moody and Hobson 2007, Pratte et al. 2017) .

In Newfoundland, the marine system is characterized as wasp-waist with a small forage fish, capelin (*Mallotus villosus*), dominating the intermediate trophic level (Davoren et al. 2007). In coastal Newfoundland, capelin is a pulsed resource, with inshore migration during the summer to spawn (Crook et al. 2017). An influx of such a high-quality prey is of particular importance to chick-provisioning seabirds (Davoren et al. 2003, 2007, Davoren 2013a), and presents natural experimental conditions to examine niche partitioning under dramatic shifts in prey availability during the summer breeding season. Indeed, relative prey availability is low prior to the inshore arrival of spawning capelin, suggesting that niche partitioning (e.g., habitat, prey type) may be important for closely related and morphologically similar breeding seabird species, such as razorbills and murres (Gause 1934, Navarro et al. 2009), but would become less important when prey availability shifts to high. To date, studies on breeding alcids in Newfoundland have been restricted primarily to common murres (Wilhelm et al. 2003, Hedd et al. 2009, Davoren et al. 2012, Regular et al. 2013, Burke et al. 2015) and, thus, understanding resource use of razorbills in conjunction with murres can help better understand niche dynamics among these breeding

seabirds. The aims of this research were to (1) investigate partitioning in the foraging niche of murres and razorbills under low prey availability and (2) examine the impacts of varying prey availability on foraging behavior and dietary niche. We used GPS devices to track foraging trips of breeding murres and razorbills to compare foraging trip and dive characteristics, habitat selection, as well as spatial and temporal (diel) segregation of diving. We hypothesized that differences in foraging behavior and habitat selection between species were influenced by species-specific wing-loading and body size characteristics (i.e. trade-off between aerial and underwater flight). We predicted that murres would forage closer to the colony than razorbills, owing to their higher energy costs during flight, but that murres would dive longer than razorbills, owing their higher dive capabilities, thereby illustrating divergent species-specific trade-offs between horizontal and vertical space use. To investigate diet in conjunction with behavior, we used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of blood plasma and red blood cells. We predicted that razorbills would exhibit less isotopic variation than murres, as a result of their lower dive capacity and, thus, constraint to forage on prey occurring in shallower parts of the water column. Lastly, we predicted that with an increase in prey availability, both species would exhibit lower costs for foraging (e.g., shorter and less-distant trips with fewer dives), a narrowing of niche breadth and higher niche overlap between species.

Methods

Study area

Our study was conducted on South Cabot Island (N 49.1711°, W 53.3588) and James Island (N 49.5791°, W 53.7808°), on the northeastern Newfoundland coast (Fig. 1) from 14 July and 11 August, 2017. The breeding cycle of these alcids spans from late April to mid-August, with chicks hatching during mid- to late-July. Chick-rearing often corresponds with the inshore

arrival and spawning of capelin in the study area (Davoren and Montevecchi 2003), though this phenology has become highly variable in recent years (Davoren et al. 2012, Crook et al. 2017). Capelin availability in the study area was determined by monitoring persistently used beach and deep-water (14-40 m) capelin spawning sites (Fig. 1) for presence and spawning activities, based on methods in Crook et al. (2017). Monitored sites fall within the maximum foraging ranges of breeding common murre (110 km) and razorbills (78 km; Linnebjerg et al. 2015), allowing the quantification of periods of high and low capelin availability. All research was carried out in accordance with the Canadian Council of Animal Care, approved by the University of Manitoba, Fort Garry Campus Animal Care Committee.

Foraging Trip and Dive Characteristics

GPS tracking devices (Ecotone ® URIA-300) were deployed on late incubation (n=4) and early chick-rearing (n=4) common murre and early chick-rearing razorbills (n=8; 7 URIA, 1 ALLE-60) during mid- to late-July. Common murre were captured at nest sites using a telescoping noose pole and razorbills were captured in rock burrows by hand. Devices were attached to the back with subdermal sutures for long-term deployments. All loggers were <16 g, which is less than 2% of body mass for the lightest murre (840-1020 g) and less than 3% of body weight for the lightest razorbill (620-740 g). Devices recorded latitude and longitude every 10 min and dive duration was recorded when tags were submerged in water. A base station was established on each island within 30 m of nest sites of tagged birds, allowing for remote download of data via UHF.

The GPS data of foraging trip and dive characteristics were analyzed using R (version 3.3.1, R Development Core Team 2016) and ArcMap (version 10.13, ESRI), following methods

in Chapter 1. In brief, data were projected with an Azimuthal Equal Area projection, and foraging trips were characterized as birds leaving and subsequently returning to either the colony or the 250 m “splashdown area” around the colony. Short dives (<4 s) were excluded as they are not associated with foraging activities (Linnebjerg et al. 2013). Foraging trip characteristics included maximum distance from the nest (km), total trip distance (km), trip duration (h), mean dive duration (s), maximum dive duration (s), number of dive bouts, dives per bout, and mean dive efficiency. Dive bouts were categorized for each species separately using the *diveMove* package in R (Luque 2007). Bout-ending criteria of 183.8 s and 91.9 s were calculated for murre and razorbill, respectively. Dive efficiency was defined based on methods in Hedd et al. (2009). A subset of the data was used, including only foraging trips occurring during a period for which we had data from both species. REML-based general linear mixed models were used to examine differences between species in trip characteristics for all except number of dive bouts, for which we used a generalized linear model with a negative binomial distribution. Species and sex were included as fixed effects, with individual as a random effect. An analysis of variance with Satterthwaite approximation for degrees of freedom was used to examine significance of these variables. To quantify the impacts of prey availability on foraging and dive parameters, we compared the above trip characteristics between low and high prey availability periods for individuals that were tracked throughout both periods. The parameters were assessed using ANOVAs of foraging trip characteristics with individual as a fixed effect. Significant relationships were examined using Tukey Post Hoc testing. When assumptions of parametric statistics were not met, response variables were transformed as necessary, and correlation between response variables were examined.

To examine temporal variation in diving activity, the number of dives occurring during each hour of the day was determined. To standardize for differences in the number of dives by species and foraging trip, the mean percent frequency of dives for each 1 h was calculated by foraging trip and then all trips were combined by species. Differences in mean dive frequency by time of day for each species were examined using a 2-factor ANOVA. Prior to analysis, percent dive frequency was log-transformed to meet the assumptions of parametric testing.

Habitat Use and Preference

Kernel density analysis was used to characterize habitat use and to compare overlap and the total area of each species distribution, as well as changes between periods of varying prey availability. Analysis was performed in the *adehabitatHR* 0.4.14 package in R (Calenge 2006) similar to Chapter 1. In brief, a random subsample of 1000 dive locations per species was used to examine differences during low prey availability. To examine differences between prey periods, we used a random sample of 400 dive locations per individual. Non-parametric fixed kernel density analysis was used to obtain 50% and 95% volume contours representing core and overall utilization distributions, respectively. We used a fixed smoothing factor (h) of 4000 m and a cell size of 1000 m, based on the amount of estimated error in locations. The smoothing factor was chosen visually by adjusting the value calculated using reference bandwidth calculation (h_{ref}) to minimize overlap with the mainland (Pratte et al. 2017). The area of each volume contour was calculated to compare between species and prey periods.

To examine whether razorbills and murres foraged in habitats with different physical characteristics, we used mixed effects logistic regression (GLMM) and generalized additive mixed models (GAMMs) to examine foraging locations in relation to depth (m), slope (m), and

distance to land (km). As sea surface temperature and chlorophyll A did not vary greatly within foraging ranges and as these variables are not static throughout the study period, these environmental variables were not used in the habitat assessment. Dive bout locations were used as presence points, using a random subsample of 250 bout locations per species to ensure similar sample sizes. As tracking data represent presence only, we randomly generated three pseudo-absence (control) locations for every known bout location using the Data Management package in ArcMap and restricted pseudo-absence points to be ≥ 250 m away from presence points. Control locations were selected within an area of maximum foraging distance of each species based on our tracking data, excluding land (i.e. 38 km for murre, 81 km for razorbill). Control locations were randomly assigned to each individual and were weighted by the number of presence points of individuals to maintain a ratio of 3:1 pseudo-absences by individual. The *mgcv* package in R (Wood 2006) was used for binomial generalized additive mixed models (GAMM). Smoothers for environmental variables were fitted separately by species and individual was included as a random effect. To account for spatial auto-correlation, a thin-plate regression spline was included based on the longitude and latitude of points, and to prevent overfitting, knots (k) were initially restricted to 5; however, if necessary, the number was increased until diagnostic checks were satisfactory (Cleasby et al. 2015). The *gam.check* function in the *mgcv* package was used to assess k values and residual analysis was used to confirm goodness of fit. If the estimated degrees of freedom equaled 1, this indicated a linear relationship (Wood 2006) and subsequently logistic regression models were analyzed using the *lme4* package in R (Bates et al. 2015) with individual as a random effect. Chi-square distribution of deviance and residuals was used to confirm generalized linear mixed model ($p > 0.05$).

Diet

To examine diet at the population-level in relation to shifting prey availability, we collected blood samples from tagged birds and additional individuals on 11 July (razorbills) and 14 July (murre) during low capelin availability and on 11 August (murre) and 14 August (razorbills), corresponding with the high capelin availability period. Approximately 1 mL of blood was sampled from the tarsus using a 25-gauge needle and syringe for genetic sex determination (one drop on FTA cards; Fast Technology for Analysis of nucleic acids; Whatman, General Electric) and stable isotope analysis of carbon and nitrogen. Blood samples were stored in EDTA tubes to prevent coagulation, kept on ice (<8 h), and centrifuged to separate plasma and red blood cells. Samples were frozen until analysis.

To identify prey species in the diet of murre and razorbill, camera traps were set up on South Cabot Island (n=1, Reconyx) and James Island (n=3, Bushnell Aggressor No-Glo) nearby nest sites, to observe prey species delivered to chicks as a proxy of adult diet. Cameras were set to trigger either daily from 0600-0900 NDT (Cabot Island, 1 picture with 2 s pause between triggers) or 0530-2100 NDT (James Island, 3 pictures with 2 s pause between triggers). From these observations, samples of capelin (*Mallotus villosus*; n=14), sandlance (*Ammodytes* sp.; n=9) and small fish including sandlance (n=19), Atlantic cod (*Gadus morhua*; n=3) and an unidentified fish (n=10) were collected using a variety of techniques (i.e., purse seines, dipnets, seabed sediment grabs, and opportunistically from fishers). Additional prey samples were collected through samples of puffin bill loads using mist-nets on James Island in mid-August, following methods outlined in Lavoie et al (2012). For fish larger than 10 cm in length, a 1-2 g sample of dorsal muscle was collected and frozen, whereas smaller fish were frozen whole.

Samples of blood plasma, red blood cells, and potential prey were kept frozen and placed into a freeze-drier for ~48 h, after which dried samples were homogenized. Prey and plasma samples were lipid-extracted, as these tissue types are ^{13}C depleted, thus variation in lipid content among individuals can introduce bias to $\delta^{13}\text{C}$ values (Post et al. 2007). Using a Soxhlet apparatus, samples were subject to lipid extraction with petroleum ether solvent for ~ 8 h, after which samples were re-dried for ~48 h and re-homogenized (Dobush et al. 1985). Lipid extraction was considered unnecessary for red blood cells due to low lipid content, as evidenced in C:N ratios < 3.5 (Bearhop et al. 2000). Samples were weighed (red blood cells: 0.4-0.6 mg, prey and plasma: 0.6-0.8 mg), placed into tin capsules and combusted using continuous-flow isotope ratio mass spectrometry (University of Windsor Laboratory, Windsor ON). Isotope ratios are expressed using delta (δ) notation as parts per thousand (per mil) relative to atmospheric nitrogen and Vienna Pee Dee Belemnite standards (Becker et al. 2007a).

Using isotopic niche as a proxy for dietary niche, the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of plasma and red blood cells were used to quantify dietary niche breadth and composition along with shifts in diet between prey availability periods of each species separately, as well as dietary overlap between species in both prey availability periods. Analysis of niche breadth and overlap were examined using the *SIBER* package in R (Jackson et al. 2011). Standard ellipse area corrected for small sample size (SEA_c) and Bayesian standard ellipse area (SEA_b) were calculated to examine differences in niche breadth between species and prey periods. Overlap of standard ellipse area and 95% ellipse area were calculated using the 'maxLikOverlap' function. To examine the percent overlap of the 95% ellipse area, we divided the area of overlap by the sum of the two species ellipse areas minus the area of overlap. To examine the potential for asymmetrical competition, we also calculated directional overlap (i.e. the amount the niche of one species

overlaps with the niche of the other) by dividing the area of overlap by the 95% ellipse area of each species separately. Univariate and multivariate assumptions were checked prior to statistical testing.

For dietary reconstruction, diet-tissue discrimination values of $-0.12 \pm 0.42\text{‰}$ for carbon and $2.49 \pm 0.30\text{‰}$ for nitrogen were applied to plasma samples, based on a study of African penguins (Barquete et al. 2013), and values of $1.10 \pm 0.30\text{‰}$ for carbon and $2.80 \pm 0.20\text{‰}$ for nitrogen were applied to red blood cell samples, based on a study of great skuas (Bearhop et al. 2002). Different studies were used for each tissue type as no study had diet-tissue discrimination values reported for both tissues separately, with most using whole blood. As razorbills and murre are closely related taxonomically, the same diet-tissue discrimination factors were applied to both species. Bayesian stable isotope mixing models in the package *MixSIAR* (Stock and Semmens 2016) were used to estimate the relative contribution of prey types in the diet of each species separately during both prey availability periods. Probability distributions for proportional contributions of different prey sources were calculated using diet-tissue discrimination factors, mean \pm SD values for prey sources, and consumer $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Moore and Semmens 2008). Potential prey included in models were restricted to those identified in previous studies or in photographs of parental prey deliveries to chicks and, thus, included large (i.e. > 10 cm) capelin and sandlance, along with small (i.e. ≤ 10 cm) fish (including sandlance, Atlantic cod, and an unidentified species). All models were run with three Markov Chain Monte Carlo chains of 3,000,000 iterations, 1,500,000 burn-in, and thinning of 500 and the median of the posterior distribution was used as the most likely proportion of each prey item. To examine sensitivity to priors, models were run both with uninformed priors and informed priors, based on photographs of parental prey deliveries to chicks. Gelman-Rubin and Geweke

diagnostic tests were used to examine chain convergence. As similar results were obtained using both uninformed and informed priors, results are reported from uninformed models, as overall, diagnostics suggested greater performance of these models

Results

Niche Metric Comparison

During the 2017 breeding season, we tracked individuals for 8-21 d and 1-29 d for murre and razorbills, respectively. Overall, we had data from six murre and four razorbills to examine differences in foraging behavior and dive characteristics (Table 1). Capelin arrival and spawning in the study area occurred from Aug 2-11, thus the period of July 28-Aug 1 was used for comparison between species during low prey availability.

There were no sex-related differences in any trip or dive characteristics ($p > 0.23$) and, thus, sex was removed from mixed models to examine species-specific differences. Most trip parameters and dive characteristics did not differ between species, but razorbills performed significantly more dives per bout and had greater dive efficiency (Table 2). In examining temporal variation in dive activities, both species performed dives throughout all hours of the day and night, with most dives performed during daylight for both species (murre: 71.7%, razorbills 93.8%), but murre foraged more at night. The mean percent dive frequency per hour peaked during the morning hours 6-9 h for both species (Fig. 2) and temporal patterns did not differ between species (ANOVA, $F_{2,155} = 1.54$, $p = 0.22$).

The 50% kernel density, representing the core foraging area, revealed complete spatial segregation between murre and razorbills (Fig. 3), with murre primarily foraging south of their

colony into Bonavista Bay, revealing one core area near the colony and another 20-30 km to the south, whereas razorbills foraged primarily between the colony and the coast and to the northwest of their colony. Spatial analysis by individual revealed that this trend was consistent across individuals. The core foraging area was larger for razorbills (281.3 km²) compared to murre (232.2 km²), and similarly the overall foraging area (i.e. 95% kernel density) was larger for razorbills (1375.9 km²) than for murre (1167.8 km²).

In examining the habitat selection of murre and razorbills, distance to shore was highly correlated with depth (Pearson's correlation =0.71) and, thus, distance to shore was excluded from analysis and comparison was focused on depth and slope. Although the available depths ranged from 0 to 450 m, both species primarily dove in areas < 50 m (Fig. 4). This use of shallow areas resulted in a significantly non-linear and generally negative response to depth for both murre (GAMM: $\chi^2_{6,91}=30.47$, $p < 0.001$) and razorbills (GAMM: $\chi^2_{3,37}=39.63$, $p < 0.001$), illustrating a preference by both species for shallow depths, which was even stronger for razorbills (Fig. 4). Slope ranged from 0 to 15 degrees though the majority of available and utilized habitat was between 0-5 degrees. Slope was a significant predictor of bird presence (GLMM: $z = 3.50$, $p < 0.001$; Fig. 4). Although species was not significant (GLMM: $z = -0.26$, $p = 0.80$), the interaction between slope and species was significant (GLMM: $z = -4.01$, $p < 0.001$; Fig. 4). Indeed, razorbills preferred (i.e. were present at) more gradual inclines, whereas murre preferred steeper slopes, between 5 and 15 degrees.

Based on Bayesian iterations, there was a high probability (0.88) that the niche breadth of plasma was larger for razorbills ($n=27$; $SEA_b = 2.24\%{}^2$) than for murre ($n=26$; $SEA_b = 1.63\%{}^2$; Fig. 5a). Red blood cell samples showed a similarly high probability (0.99) of a narrower niche breadth for murre ($n=27$; $SEA_b = 0.16\%{}^2$) than for razorbills ($n=26$; $SEA_b = 0.35\%{}^2$; Fig

6). With plasma, there was 35.9 % overlap of total shared niche between murre and razorbills, with the murre niche overlapping the razorbill niche by 57.4 % and razorbill niche overlapping the murre niche by 49.0 %. There was a similar pattern for red blood cells, whereby there was 49.9 % overlap of total shared niche between species, with murre sharing a larger percent of their niche with razorbills (86.6%) than vice versa (54.1%).

From identifiable photographs during low capelin availability (n=156 out of 238 photos with feedings), parental prey deliveries to murre chicks included 74.4% capelin, 20.5% sandlance and 5.1% that included other fish and invertebrates. For razorbills, from identifiable photos (n=11 out of 11 photos with feedings), prey deliveries included 35.7% capelin, 28.6% sandlance and 35.7% other fish. As the number of parental deliveries captured was small for razorbills, we included data from both prey availability periods. Invertebrates made up <1% of chick diet for both species and as previous studies have found both to be primarily piscivorous during the breeding season (Lilliendahl and Solmundsson 1997, Ainley et al. 2002), we did not include invertebrates in our mixing models. Using MixSIAR, all uninformed mixing models met diagnostic tests chain convergence, with all Gelman-Rubin diagnostics < 1.05 (Moore and Semmens 2008). Similarly, 0 % of Geweke z-scores were outside of +/- 1.96 for murre while 2.8 % of Geweke z-scores were outside of +/- 1.96 for razorbills, below the accepted 5% threshold. The diet composition of murre and razorbills differed in prey proportions, though capelin and sandlance comprised the majority of the diet for both species (Fig. 6c,d). During low capelin availability, murre diet was primarily comprised of capelin (53.5 %) and sandlance (44.5 %), while small fish only comprised 2.0 % of the diet. Razorbill diet was similar, with 2.0 % small fish, though had an increased proportion of sandlance (52.2 %) and a smaller proportion of capelin (45.8%).

Impacts of Prey Availability

We had concurrent tracking data from three individuals (murre: n=2, razorbill: n=1) spanning periods of both low capelin availability (July 28-Aug 1) and high availability (Aug 2-11). All three birds shifted their foraging areas closer to the colony and the razorbill shifted to more coastal areas (Fig. 7). Both murre exhibited a more substantial shift towards the colony, as dive locations no longer exhibited a bimodal distribution. When shifting from low to high prey availability, the overall foraging area for the razorbill increased from 309.0 km² to 552.3 km², whereas the areas used by the two murre decreased from 513.2 km² and 464.3 km² during low capelin availability to 88.1 km² and 227.5 km², respectively (Fig.7). Foraging areas of all three individuals were in close proximity to known capelin spawning sites (Fig. 7). As prey availability shifted from low to high, foraging trips typically became shorter in distance and duration for both species, but was only revealed in a significant decrease in maximum and total trip distance for the razorbill. In contrast, there were no obvious trends in dive characteristics for either species, although the number of dive bouts tended to decrease for murre but increased for the razorbill, whereas the number of dives per bout and dive efficiency significantly decreased for the razorbill (Table 3).

During high prey availability, there was a high probability that the niche breadth was larger for razorbills than murre using both plasma (0.95, Fig 5b) and red blood cells (0.88, Fig 6b). Additionally, there was a high probability (plasma: 1.0; RBC: 0.83) that niche breadth was narrower for murre during high prey availability (n=20; plasma: SEAb: 0.43 %²; RBC: SEAb: 0.12 %²) relative to low availability (n=27; plasma: SEAb: 1.63 %²; RBC: SEAb: 0.16 %²). A similar pattern was observed for razorbills, with a high probability (plasma: 1.0; RBC: 0.99) that niche breadth was narrower during high prey availability (n=17; plasma: SEAb: 0.76 %²; RBC:

SEAb: 0.17 %²) relative to low availability (n=27; plasma: SEAb: 2.24 %²; RBC: SEAb: 0.35 %²). This narrowing corresponded with a decrease in overlap between species from low and high prey availability for plasma (35.9% to 22.0%) and RBC (49.9% to 18.4%). The niche of murre continued to have greater overlap with that of razorbills (plasma: 50.0%; RBC: 40.4%) than vice versa (plasma: 28.2%; RBC: 25.2%). When prey availability shifted from low to high, there was a high probability (0.98) that the proportion of capelin in the diet of razorbills increased from 45.8% to 57.0% mirrored by a high probability (0.98) of decrease in sandlance from 52.2 to 38.4 % and a slight increase in small fish from 2.0 to 4.6% (probability = 0.73; Fig. 6f). Under the same shift in prey availability, murre exhibited a more dramatic increase in the amount of capelin in the diet, from 53.5 to 82.8% (probability = 1.0), while sandlance decreased to only 15.7 % (probability = 0.99), and the amount of small fish remained low at 1.7%, (probability= 0.42; Fig. 6d). These findings were supported by parental delivery observations where during high capelin availability (n=260 identifiable prey items out of 504 photos), murre parental deliveries included 98.2% capelin, 0.5% sandlance, and 1.3% other fish.

Discussion

Our findings suggest that differences in horizontal and vertical space use are the primary aspects of niche divergence between murre and razorbills, allowing for a high degree of dietary overlap. As predicted, tracking information during low prey availability indicated complete spatial separation of foraging locations, as well as differences in dive duration. Contrary to our prediction, however, foraging trip characteristics were similar, suggesting that both species forage within similar ranges from the colony regardless of differences in wing-loading. This similarity suggests that higher spatial overlap may have been observed if both species were breeding on the same island, which was further corroborated by similar habitat preferences

between species. Additionally, dietary composition was similar, and both species correspondingly responded to increased prey availability. Indeed, when local prey availability increased, foraging areas of individuals of both species shifted closer to the colony and capelin spawning sites, indicative of reduced energy costs, and dietary niche breadth narrowed while the proportion of capelin in the diet increased, as predicted, suggesting a higher reliance on this prey type. Overall, these findings suggest that murre and razorbill have phenotypic plasticity in many niche dimensions, allowing them to respond to varying resource availability, but that interspecific differences in these niche dimensions are maintained.

Niche Segregation

The most striking divergence in the niche of murre and razorbill was the complete spatial separation in foraging locations between species. This separation was surprising as the potential foraging ranges from each colony overlapped, given the proximity of the colonies (~55 km) and the maximum foraging distances of both species (murre: 110 km; razorbill: 78 km; Linnebjerg et al. 2015). Despite the potential for high spatial overlap, however, other seabirds have shown similar spatial segregation even when breeding on the same colony, such as Southern rockhopper and Magellanic penguins (Rosciano et al. 2016), and Scopoli's and Cory's shearwaters (Navarro et al. 2009). Similar to our findings, however, Cairns (1989) predicted that conspecifics or similar species of seabirds breeding on adjacent colonies would have non-overlapping foraging grounds due to competition for resources within limited foraging ranges. Indeed, this prediction has been supported for several species, whereby there is minimal overlap of foraging grounds of conspecifics breeding on adjacent colonies (e.g., Masello et al. 2010, Wakefield et al. 2013). Therefore, the complete spatial segregation may be an important

mechanism to reduce both intra- and interspecific competition while maximizing foraging trip efficiency, as predicted by Cairns (1989). Additionally, foraging grounds may be further constrained by other seabirds breeding on nearby islands in our study area. Indeed, large numbers of Atlantic puffins (~6,200 pairs) breed together with the razorbills on James Island, and a large colony of murre (Funk Island; ~500,000 pairs) resides ~50 km away from James Island and ~66 km away from our murre colony. Many other species including northern gannets, herring and black-backed gulls, and northern fulmars also breed and forage in the area (Davoren 2007, 2013a). It is also possible spatial segregation in foraging grounds did not result from competition. For instance, as nest site characteristics differ between species (Ainley et al. 2002, Lavers et al. 2009), the amount of suitable breeding habitat likely plays a role in determining the relative abundances of each species at a colony. As murre and razorbills showed similar foraging trip distances and durations, along with habitat preferences, there might have been high spatial overlap in foraging areas if breeding on the same colony. Indeed, high spatial overlap was found in previous studies on murre and razorbills breeding on the same colony (Linnebjerg et al. 2013, Pratte et al. 2017). Overall, it is difficult to determine whether the spatial segregation was primarily driven by competition or other factors.

As predicted, razorbills and murre showed interspecific differences in almost all dive characteristics examined, except mean dive duration, corresponding with previous studies showing similar differences in both dive duration and depth (Thaxter et al. 2010, Linnebjerg et al. 2013). The observed difference suggests that razorbills may use less vertical space than murre, possibly resulting in vertical niche segregation in the water column. Such vertical niche segregation has been exhibited in other seabirds (e.g. Mori and Boyd 2004), marine fish (e.g. Young et al. 2010), and marine mammals (e.g., Baird et al. 2006, Villegas-Amtmann et al. 2013).

The tendency of larger-sized murrelets to have a greater maximum dive duration than medium-sized razorbills is not surprising, given that body size is positively correlated with body oxygen storage (Piatt 1990, Elliott et al. 2013) and, thus, larger body size is related to a higher dive capacity (Schreer and Kovacs 1997, Shoji et al. 2016a). Razorbills appeared to compensate for lower dive durations by performing a greater number of short dives, as evidenced by greater number of dives per bout and higher mean dive efficiency for razorbills relative to murrelets. Razorbills also appeared to use more horizontal space than murrelets. Indeed, razorbills used a core foraging area approximately 1.2 times larger than that of murrelets, suggesting that razorbills foraged in more and different locations on any given foraging trip, relative to murrelets. Razorbills have previously been found to use a larger and more coastal area when foraging compared to murrelets, though these studies found a larger difference in space use, with razorbills utilizing an area almost twice as large as murrelets (Thaxter et al. 2010, Linnebjerg et al. 2015). Despite differences in core areas, foraging trip characteristics did not differ between species. This discrepancy may be the result of high individual variation in foraging trip characteristics, as found for murrelets (Ch 1), decreasing the probability of finding significant differences between species. Together these findings suggest a degree of vertical niche differentiation, which is coupled with a larger foraging area of razorbills, supporting an evolutionary trade-off between aerial and underwater movement (Thaxter et al. 2010).

Niche Overlap

We found evidence for a large degree of overlap in diet, diel foraging patterns, and habitat preference between murrelets and razorbills during low prey availability, though subtle differences in these dimensions were exhibited. While complete spatial segregation may suggest

different resource use, we found a large degree of overlap in the diet of murre and razorbill, with both species feeding primarily on capelin and sandlance throughout the chick-rearing season. While razorbills had a broader niche breadth and dietary overlap between species was not complete, these differences appeared to result from different proportions of the same prey types, rather than differences in prey composition. Similarly, previous studies found considerable dietary overlap of these two species in the northwest Atlantic (e.g. capelin; Pratte et al. 2017) and northeast Atlantic (e.g., sandeel, sprat; Thaxter et al. 2010, Pratte et al. 2017). Consistency between our findings and previous results suggests that there is a large degree of similarity in the diet of murre and razorbill and, thus, spatial segregation in our study may be a response to competition for the same resources. The dietary niche of razorbills tended to overlap more with that of murre than vice versa. This difference in overlap may suggest the occurrence of asymmetrical competition, whereby murre may be more competitively dominant, which is corroborated with their numerical dominance at sea in the study area (Davoren 2013a). Thus, razorbills may exhibit a higher niche breadth as a result of niche expansion to exploit alternative resources in the face of competition.

There was a high degree of similarity in diel foraging patterns of murre and razorbill. Peak foraging times and frequencies of dives were similar for both species throughout the daylight and dark periods. Additionally, both species foraged at night, likely to take advantage of diel vertical migration of their primary prey, capelin (Davoren et al. 2006). Previous studies have found murre to forage at night (Hedd et al. 2009) and have shown that the foraging behavior of many species reflects the diel vertical migration of prey (e.g., Croxall et al. 1985). Indeed, the diel vertical migration of capelin has been well documented (Davoren et al. 2006) and the dive patterns of murre have been associated with this migration pattern (Regular et al. 2010), with

peak foraging occurring during times of day when prey is more accessible in surface waters. One might predict that razorbills would forage more at night, owing to their lower dive capacity; however, murres performed ~20% more dives during dark periods at night than razorbills. As murres are deeper-diving than razorbills, they more frequently experience low-light levels at depth and, thus, may be adapted for improved visual sensitivity (Regular et al. 2011), as shown for deep-diving relative to shallow-diving pinnipeds (Levenson and Schusterman 1999).

Both species showed similar habitat preferences, both preferring to forage in shallow areas (< 50 m). This preference was mirrored by their primarily coastal foraging distributions, similar to previous findings (Pratte et al. 2017). Preference for shallower areas may be related to the primarily shallow, coastal (< 50 m) distribution of spawning capelin in the study area (Davoren et al. 2006, Davoren 2013b). Razorbills, however, showed a greater positive association with shallow areas than murres, possibly relating to their dive capabilities, as shallower habitats may allow for razorbills to use a greater proportion of the water column. In support, sympatric cormorants have differential preferences for depth relative to dive capabilities (Peck-Richardson et al. 2018). Razorbills primarily used flatter areas proportional to availability, though previous research found variation between colonies in the use of slope (Wakefield et al. 2017). In contrast, murres preferred areas of greater slope, which may relate to the available habitat as well as locations of annually persistent capelin aggregations in the study area. For instance, there is a deep-water trench within foraging ranges of murres that capelin persistently use as a pre-spawning staging area across years (Davoren et al. 2006). Additionally, annually persistent deep-water spawning sites of capelin (Fig. 1) are located in 5-10 m bathymetric trenches (Penton and Davoren 2012). Therefore, murres may be utilizing this sloped habitat to locate predictable prey (Davoren et al. 2006), supported by a higher proportion of capelin in the

diet relative to razorbills. These differences in habitat preference, however, are subtle, and, thus, likely do not represent niche dimensions with a large degree of divergence, and likely relates more to the availability of prey.

Impacts of prey availability

At the population level, we found a shift in diet when capelin availability increased, with decreased variety and an increase in the proportion of capelin in the diet. This shift was much more dramatic for murre, which coincides with previous studies on parental deliveries to murre chicks in the study area showing a primarily capelin-based diet (Davoren and Montevecchi 2003, Davoren et al. 2012). Although the diet of razorbills in this area had not been examined, prey variety in chick diets was higher for murre than razorbills in Labrador (Pratte et al. 2017), contrasting our results. Shifts in prey proportions and variety in relation to availability have been found in murre (Ainley et al. 1996) and other seabirds, such as marbled murrelets (Becker et al. 2007b) and little penguins (Kowalczyk et al. 2015). The dietary shift also corresponded with an unpredicted decrease in niche overlap between murre and razorbills, suggesting that despite an increase in the availability of capelin, razorbills remained generalist foragers with a higher proportion of the diet made up of other prey types. In contrast, murre appeared to largely specialize on capelin, despite shifts in prey availability. Similarly, Baird (1990) found different responses to changes in capelin availability among puffins, kittiwakes and gulls in Alaska, which related to accessibility and dive capabilities. Overall, murre appear to be highly reliant on the arrival and spawning of capelin (Davoren et al. 2012), but appear to also exhibit great foraging plasticity to respond to these changes in prey availability (Chapter 1, Burger and Piatt 1990, Harding et al. 2007).

At the individual level, both species shifted foraging areas closer to the colony as prey availability increased, resulting in a decrease in foraging area for the two murrelets, while the area used by the razorbill increased. Interestingly, foraging locations overlapped with known capelin deep-water and beach spawning sites (Penton and Davoren 2012), which represented areas of both high predictability and densely aggregated capelin during August. Additionally, individuals tended to decrease foraging trip parameters, indicative of reduced energy costs in foraging. These results are similar to previous studies of alcids (Monaghan et al. 1994, Uttley et al. 1994, Litzow et al. 2002) as well as other species (Suryan et al. 2002, Paiva et al. 2010, Garthe et al. 2011). However, despite the presence of super-abundant prey, complete spatial segregation between species remained. Additionally, we observed only minimal changes in dive characteristics between prey availability periods, with a decrease in dives per bout and efficiency for the razorbill. As dive depth and duration relates directly to physiology, it may be that dive characteristics, particularly dive duration and depth, are more constrained and, thus, do not vary with prey availability (Linnebjerg et al. 2013). Dive effort may be more flexible, however, as previous studies have found birds exhibiting lower dive effort (i.e. number of dives, percent of trip spent diving) with higher prey availability (Monaghan et al. 1994, Litzow and Piatt 2003, Paiva et al. 2010, Regular et al. 2014). Thus, horizontal trip characteristics, diving effort, and diet may be more flexible over the short-term than dive characteristics.

Conclusion

By simultaneously examining foraging behavior, space and habitat use, along with diet of common murrelets and razorbills, we were able to examine multiple niche dimensions concurrently. This multifaceted approach allowed a better understanding of foraging niche

dynamics and mechanisms of coexistence among similar species. Niche divergence appeared to be greatest in horizontal and vertical foraging space, which is supported by differences in morphometric characteristics (e.g. wing-loading, body size) and physiology (e.g. dive capacities) of murre and razorbill. This spatial separation contrasted high similarities in foraging trip duration and distance as well as diet, suggesting the exploitation of the same prey types but in differing proportions. Overall, coupling GPS data with diet information allowed a more comprehensive examination of niche partitioning between these two morphometrically similar species. By extending beyond trip and dive characteristics, understanding variation in space, time, and habitat selection allowed for a more holistic view of the possible ways these species may partition their n-dimensional niche.

Seabirds and marine systems face many potential threats, the greatest of which may be climate change, affecting all trophic levels both directly and indirectly (Lauria et al. 2012). Environmental change occurs quickly, so response time of species and individuals is of great concern (Gaston and Woo 2008). Behavioral traits have greater potential for plasticity than morphological or physiological traits and, thus, behavioral responses are likely to immediately follow environmental change (Linnebjerg et al. 2013). In coastal Newfoundland during recent decades, the inshore arrival and spawning of capelin has become highly variable (Crook et al. 2017), as these dynamics appear to be largely influenced by seasonal sea ice (Buren et al. 2014). Therefore, the potential influence of climate change on sea ice dynamics may have a large impact on breeding seabirds. While both individual and population-level responses in our study suggest behavioral flexibility with changing resource availability, our findings also suggest some niche dimensions may not be flexible, which could lead to higher niche overlap between species and an increase in competition. The degree of capelin reliance varied by species, but may also

vary by availability of capelin, presence of alternative resources, breeding stage, and likely other dynamics as well (Burger and Piatt 1990, Limmer and Becker 2009, Garthe et al. 2011, Scioscia et al. 2014). Murres appear to be more heavily reliant on capelin (Davoren and Montevecchi 2003, Davoren et al. 2012, this study), which may suggest that they are more vulnerable to negative impacts, whereas razorbills with a more generalist strategy may be more flexible in the face of change, or may be more greatly impacted by the availability of other prey species (e.g. sandlance). Further investigation is needed to better understand the impacts of changing resources for seabirds, not only in terms of foraging ecology, but survival and reproductive success, along with expanding beyond these two species to the entire seabird assemblage in coastal Newfoundland to better understand both inter and intra-specific dynamics.

References

- Ainley, D.G., Nettleship, D.N., Carter, H.R., and Storey, A.E. 2002. Common Murre (*Uria aalge*). In *The Birds of North America*. Edited by P.G. Rodewald. Ithaca, New York.
- Ainley, D.G., Reyes, P., Observatory, B., Beach, S., Reyes, P., Observatory, B., Beach, S., and Allen, S.G. 1996. Temporal and spatial patterns in the diet of the common murre in California waters. *Condor* **98**(4): 691–705.
- Baird, P.H. 1990. Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. *Scand. J. Ornithol.* **21**(3): 224–235.
- Baird, R.W., Webster, D.L., McSweeney, D.J., Ligon, A.D., Schorr, G.S., and Barlow, J. 2006. Diving behaviour of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales in Hawai'i. *Can. J. Zool.* **84**: 1120–1128.
- Barquete, V., Strauss, V., and Ryan, P.G. 2013. Stable isotope turnover in blood and claws: a case study in captive African penguins. *J. Exp. Mar. Bio. Ecol.* **448**: 121–127.
- Bates, D., Machler, M., Bolker, B., and Walkter, S. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**(1): 1–48.
- Bearhop, S., Teece, M.A., Waldron, S., and Furness, R.W. 2000. Influence of lipid and uric acid on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of avian blood: implications for trophic studies. *Auk* **117**(2): 504–507.
- Bearhop, S., Waldron, S., Votier, S.C., and Furness, R.W. 2002. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiol. Biochem. Zool.* **75**(5): 451–458.
- Beaulieu, M., and Sockman, K.W. 2012. One meadow for two sparrows: resource partitioning in a high elevation habitat. *Oecologia* **170**(2): 529–540.

- Becker, B.H., Newman, S.H., Inglis, S., and Beissinger, S.R. 2007a. Diet–feather stable isotope ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$) fractionation in common murrelets and other seabirds. *Condor* **109**(2): 451.
- Becker, B.H., Peery, M.Z., and Beissinger, S.R. 2007b. Ocean climate and prey availability affect the trophic level and reproductive success of the marbled murrelet, an endangered seabird. *Mar. Ecol. Prog. Ser.* **329**: 267–279.
- Bonato, K.O., Burrell, E.D., Fialho, C.B., and Armbruster, J.W. 2018. Resource partitioning among syntopic Characidae corroborated by gut content and stable isotope analyses. *Hydrobiologia* **805**(1): 311–324.
- Buren, A.D., Koen-Alonso, M., Pepin, P., Mowbray, F., Nakashima, B., Stenson, G., Ollerhead, N., and Montevecchi, W.A. 2014. Bottom-up regulation of capelin, a keystone forage species. *PLoS One* **9**(2): e87589.
- Burger, A.E., and Piatt, J.F. 1990. Flexible time budgets in breeding common murrelets: buffers against variable prey abundance. *Stud. Avian Biol.* **14**: 71–83.
- Burke, C.M., Montevecchi, W.A., and Regular, P.M. 2015. Seasonal variation in parental care drives sex-specific foraging by a monomorphic seabird. *PLoS One* **10**(11): e0141190.
- Cairns, D.K. 1989. The regulation of seabird colony size: A Hinterland Model. *Am. Nat.* **134**(1): 141–146.
- Calenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Modell.* **197**: 516–519.
- Chase, J.M., and Leibold, M.A. 2003. Ecological niches: linking classical and contemporary approaches. The University of Chicago, London.
- Cleasby, I.R., Wakefield, E.D., Bodey, T.W., Davies, R.D., Patrick, S.C., Newton, J., Votier,

- S.C., Bearhop, S., and Hamer, K.C. 2015. Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Mar. Ecol. Prog. Ser.* **518**: 1–12.
- Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* **122**(5): 661–696.
- Crook, K.A., Maxner, E., and Davoren, G.K. 2017. Temperature-based spawning habitat selection by capelin (*Mallotus villosus*) in Newfoundland. *ICES J. Mar. Sci.* **74**(6): 1622–1629.
- Croxall, J.P., Everson, I., Kooyman, G.L., Ricketts, C., and Davis, R.W. 1985. Fur seal diving behaviour in relation to vertical distribution of krill. *J. Anim. Ecol.* **54**(1): 1–8.
- Davoren, G.K. 2007. Effects of gill-net fishing on marine birds in a biological hotspot in the northwest Atlantic. *Conserv. Biol.* **21**(4): 1032–1045.
- Davoren, G.K. 2013a. Distribution of marine predator hotspots explained by persistent areas of prey. *Mar. Biol.* **160**(12): 3043–3058.
- Davoren, G.K. 2013b. Divergent use of spawning habitat by male capelin (*Mallotus villosus*) in a warm and cold year. *Behav. Ecol.* **24**(1): 152–161.
- Davoren, G.K., Anderson, J.T., and Montevecchi, W.A. 2006. Shoal behaviour and maturity relations of spawning capelin (*Mallotus villosus*) off Newfoundland : demersal spawning and diel vertical movement patterns. *Can. J. Aquat. Sci.* **63**: 268–284.
- Davoren, G.K., May, C., Penton, P., and Reinfort, B. 2007. An ecosystem-based research program for capelin (*Mallotus villosus*) in the Northwest Atlantic : Overview and Results. *J. Northwest Atl. Fish. Sci.* **39**: 35–48.
- Davoren, G.K., and Montevecchi, W.A. 2003. Signals from seabirds indicate changing biology of capelin stocks. *Mar. Ecol. Prog. Ser.* **258**: 253–261.

- Davoren, G.K., Montevecchi, W.A., and Anderson, J.T. 2003. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. *Mar. Ecol. Prog. Ser.* **256**: 229–242.
- Davoren, G.K., Penton, P., Burke, C., and Montevecchi, W.A. 2012. Water temperature and timing of capelin spawning determine seabird diets. *ICES J. Mar. Sci.* **69**(7): 1234–1241.
- Dobush, R., Davison, C., and Ankney, C.D. 1985. The effect of apparatus, extraction time, and solvent type on lipid extractions of snow geese. *Can. J. Fish. Aquat. Sci.* **63**: 1917–1920.
- Dupuch, A., Bertolo, A., Magnan, P., and Dill, L.M. 2014. Indirect effects of asymmetrical competition among top predators determine spatial patterns of predation risk for prey. *Aquat. Sci.* **76**(4): 543–552.
- Elliott, K.H., Ricklefs, R.E., Gaston, A.J., Hatch, S. a., Speakman, J.R., and Davoren, G.K. 2013. High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Proc. Natl. Acad. Sci. U. S. A.* **110**(23): 9380–9384.
- Forero, M.G., Bortolotti, G.R., Hobson, K.A., Donazar, J.A., Bertelotti, M., and Blanco, G. 2004. High trophic overlap within the seabird community of Argentinean Patagonia: A multiscale approach. *J. Anim. Ecol.* **73**(4): 789–801.
- Garthe, S., Montevecchi, W.A., and Davoren, G.K. 2011. Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator. *Limnol. Oceanogr.* **56**(3): 802–812.
- Gaston, A.J., and Jones, I.L. 1998. *The auks: Alcidae*. Oxford University Press, New York.
- Gaston, A.J., and Woo, K. 2008. Razorbills (*Alca Torda*) Follow Subarctic Prey Into the Canadian Arctic: Colonization Results From Climate Change? *Auk* **125**(4): 939–942.
- Gause, G.F. 1934. Experimental analysis of Vito Volterra's Mathematical Theory of the struggle

- for existence. *Science* **79**: 16–17.
- Gause, G.F. 1971. *The struggle for existence*. Dover Publications, Inc., Meneola, New York.
- Giller, P.S. 1984. *Community structure and the niche*. Chapman and Hall Ltd, New York.
- Hammerschlag-Peyer, C.M., Yeager, L.A., Araújo, M.S., and Layman, C.A. 2011. A hypothesis-testing framework for studies investigating ontogenetic niche shifts using stable isotope ratios. *PLoS One* **6**(11): e27104.
- Harding, A.M. a, Piatt, J.F., Schmutz, J. a, Shultz, M.T., Van Pelt, T.I., Pelt, V., Kettle, A.B., and Speckman, S.G. 2007. Prey density and the behavioural flexibility of a marine predator: the common murre (*Uria aalga*). *Ecology* **88**(8): 2024–2033.
- Hedd, A., Regular, P.M., Montevecchi, W.A., Buren, A.D., Burke, C.M., and Fifield, D.A. 2009. Going deep: common murres dive into frigid water for aggregated, persistent and slow-moving capelin. *Mar. Biol.* **156**(4): 741–751.
- Hutchinson, G.E. 1978. *An introduction to population biology*. Yale University Press, New Haven, CT.
- Hyrenbach, K.D., Fernández, P., and Anderson, D.J. 2002. Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Mar. Ecol. Prog. Ser.* **233**: 283–301.
- Jackson, A.L., Inger, R., Parnell, A.C., and Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* **80**(3): 595–602.
- Kowalczyk, N.D., Reina, R.D., Preston, T.J., and Chiaradia, A. 2015. Environmental variability drives shifts in the foraging behaviour and reproductive success of an inshore seabird. *Oecologia* **178**(4): 967–979.

- Lauria, V., Attrill, M.J., Pinnegar, J.K., Brown, A., Edwards, M., and Votier, S.C. 2012. Influence of climate change and trophic coupling across four trophic levels in the Celtic Sea. *PLoS One* **7**(10): e47408.
- Lavers, J., Hipfner, J.M., and Chapdelaine, G. 2009. Razorbill (*Alca torda*). In *The Birds of North America*. Edited by P. Rodewald. Ithaca, New York.
- Lavoie, R. A., Rail, J.F., and Lean, D.R.S. 2012. Diet composition of seabirds from Corossol Island, Canada, using direct dietary and stable isotope analyses. *Waterbirds* **35**(3): 402–419.
- Levenson, D.H., and Schusterman, R.J. 1999. Dark adaptation and visual sensitivity in shallow and deep-diving pinnipeds. *Mar. Mammal Sci.* **15**(4): 1303–1313.
- Lilliendahl, K., and Solmundsson, J. 1997. An estimate of summer food consumption of six seabird species in Iceland. *ICES J. Mar. Sci.* **54**(4): 624–630.
- Limmer, B., and Becker, P.H. 2009. Improvement in chick provisioning with parental experience in a seabird. *Anim. Behav.* **77**(5): 1095–1101.
- Linnebjerg, J.F., Fort, J., Guilford, T., Reuleaux, A., Mosbech, A., and Frederiksen, M. 2013. Sympatric breeding auks shift between dietary and spatial resource partitioning across the annual cycle. *PLoS One* **8**(8): e72987.
- Linnebjerg, J.F., Reuleaux, A., Mouritsen, K.N., and Frederiksen, M. 2015. Foraging ecology of three sympatric breeding alcids in a declining colony in southwest Greenland. *Waterbirds* **38**(2): 143–152.
- Litzow, M. a., and Piatt, J.F. 2003. Variance in prey abundance influences time budgets of breeding seabirds: evidence from pigeon guillemots *Cephus columba*. *J. Avian Biol.* **34**: 54–64.

- Litzow, M.A., Piatt, J.F., Prichard, A.K., and Roby, D.D. 2002. Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey. *Oecologia* **132**(2): 286–295.
- Luque, S.P. 2007. Diving behaviour analysis in R. In R News.
- Masello, J.F., Mundry, R., Poisbleau, M., Demongin, L., Voigt, C.C., Wikelski, M., and Quillfeldt, P. 2010. Diving seabirds share foraging space and time within and among species. *Ecosphere* **1**(6): 1–28.
- Monaghan, P., Walton, P., Wanless, S., Uttley, J.D., and Burns, M.D. 1994. Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge*. *Ibis* **136**: 214–222.
- Moody, A., and Hobson, K.A. 2007. Alcid winter diet in the northwest Atlantic determined by stable isotope analysis. *Mar. Ornithol.* **35**: 39–46.
- Moore, J.W., and Semmens, B.X. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. *Ecol. Lett.* **11**(5): 470–480.
- Mori, Y., and Boyd, I.L. 2004. Segregation of foraging between two sympatric penguin species: does rate maximisation make the difference? *Mar. Ecol. Prog. Ser.* **275**: 241–249.
- Navarro, J., Forero, M.G., González-Solís, J., Igual, J.M., Becares, J., and Hobson, K.A. 2009. Foraging segregation between two closely related shearwaters breeding in sympatry. *Biol. Lett.* **5**: 545–548.
- Nicholls, D.G., Robertson, C.J.R., Prince, P.A., Murray, M.D., Walker, K.J., and Elliott, G.P. 2002. Foraging niches of three *Diomedea* albatrosses. *Mar. Ecol. Prog. Ser.* **231**: 269–277.
- Orians, G.H., and Pearson, N.E. 1979. On the theory of central place foraging. *In* *Analysis of Ecological Systems*. Edited by J. Horn, G.R. Stairs, and R. Mitchell. Ohio State Press.

- pp. 155–177.
- Paiva, V.H., Geraldes, P., Ramírez, I., Meirinho, A., Garthe, S., and Ramos, J.A. 2010. Foraging plasticity in a pelagic seabird species along a marine productivity gradient. *Mar. Ecol. Prog. Ser.* **398**: 259–274.
- Peck-Richardson, A.G., Lyons, D.E., Roby, D.D., Cushing, D.A., and Lerczak, J.A. 2018. Three-dimensional foraging habitat use and niche partitioning in two sympatric seabird species, *Phalacrocorax auritus* and *P. penicillatus*. *Mar. Ecol. Prog. Ser.* **586**: 251–264.
- Penton, P.M., and Davoren, G.K. 2012. Physical characteristics of persistent deep-water spawning sites of capelin: Importance for delimiting critical marine habitats. *Mar. Biol. Res.* **8**: 778–783.
- Piatt, J.F. 1990. The aggregative response of common murre and Atlantic puffins to schools of capelin. *Stud. Avian Biol.* **14**: 36–51.
- Polito, M.J., Trivelpiece, W.Z., Patterson, W.P., Karnovsky, N.J., Reiss, C.S., and Emslie, S.D. 2015. Contrasting specialist and generalist patterns facilitate foraging niche partitioning in sympatric populations of *Pygoscelis* penguins. *Mar. Ecol. Prog. Ser.* **519**: 221–237.
- Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., and Montaña, C.G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**(1): 179–189.
- Pratte, I., Robertson, G.J., and Mallory, M.L. 2017. Four sympatrically nesting auks show clear resource segregation in their foraging environment. *Mar. Ecol. Prog. Ser.* **572**: 243–254.
- Regular, P.M., Davoren, G.K., Hedd, A., and Montevecchi, W.A. 2010. Crepuscular foraging by a pursuit-diving seabird: tactics of common murre in response to the diel vertical migration of capelin. *Mar. Ecol. Prog. Ser.* **415**: 295–304.

- Regular, P.M., Hedd, A., and Montevecchi, W.A. 2011. Fishing in the dark: A pursuit-diving seabird modifies foraging behaviour in response to nocturnal light levels. *PLoS One* **6**(10): e26763.
- Regular, P.M., Hedd, A., and Montevecchi, W.A. 2013. Must marine predators always follow scaling laws memory guides the foraging decisions of a pursuit-diving seabird. *Anim. Behav.* **86**: 545–552.
- Regular, P.M., Hedd, A., Montevecchi, W.A., Robertson, G.J., Storey, A.E., and Walsh, C.J. 2014. Why timing is everything: energetic costs and reproductive consequences of resource mismatch for a chick-rearing seabird. *Ecosphere* **5**(12): 155.
- Robertson, G.J., and Elliot, R.D. 2002. Changes in seabird populations breeding on Small Island, Wadham Islands, Newfoundland. Canadian Wildlife Service Technical Report Series No. 381. Atlantic region. pp1-26.
- Rosciano, N.G., Polito, M.J., and Rey, A.R. 2016. Do penguins share? Evidence of foraging niche segregation between but not within two sympatric, central-place foragers. *Mar. Ecol. Prog. Ser.* **548**: 249–262.
- Schreer, J.F., and Kovacs, K.M. 1997. Allometry diving capacity. *Can. J. Zool.* **75**: 339–358.
- Scioscia, G., Raya Rey, A., Saenz Samaniego, R.A., Florentin, O., and Schiavini, A. 2014. Intra- and interannual variation in the diet of the Magellanic penguin (*Spheniscus magellanicus*) at Martillo Island, Beagle Channel. *Polar Biol.* **37**(10): 1421–1433.
- Shoji, A., Aris-Brosou, S., and Elliott, K.H. 2016a. Physiological constraints and dive behavior scale in tandem with body mass in auks: a comparative analysis. *Comp. Biochem. Physiol. -Part A Mol. Integr. Physiol.* **196**: 54–60.
- Shoji, A., Aris-Brosou, S., Owen, E., Bolton, M., Boyle, D., Fayet, A., Dean, B., Kirk, H.,

- Freeman, R., Perrins, C., and Guilford, T. 2016b. Foraging flexibility and search patterns are unlinked during breeding in a free-ranging seabird. *Mar. Biol.* **163**(4): 1–10.
- Stock, B., and Semmens, B. 2016. MixSIAR GUI user manual. Version 3.1 (March): 1–59.
- Suryan, R.M., Irons, D.B., Kaufman, M., Benson, J., Jodice, P.G.R., Roby, D.D., and Brown, E.D. 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the black-legged kittiwake *Rissa tridactyla*. *Mar. Ecol. Prog. Ser.* **236**: 273–287.
- Thaxter, C.B., Wanless, S., Daunt, F., Harris, M.P., Benvenuti, S., Watanuki, Y., Grémillet, D., and Hamer, K.C. 2010. Influence of wing loading on the trade-off between pursuit-diving and flight in common guillemots and razorbills. *J. Exp. Biol.* **213**: 1018–1025.
- Uttley, J.D., Walton, P., Monaghan, P., and Austin, G. 1994. The effects of food abundance on breeding performance and adult time budgets of guillemots *Uria aalge*. *Ibis* **136**(2): 205–213.
- Villegas-Amtmann, S., Jeglinski, J.W.E., Costa, D.P., Robinson, P.W., and Trillmich, F. 2013. Individual foraging strategies reveal niche overlap between endangered Galapagos pinnipeds. *PLoS One* **8**(8): e70748.
- Wakefield, E.D., Bodey, T.W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R.G., Green, J.A., Grémillet, D., Jackson, A.L., Jessopp, M.J., Kane, A., Langston, R.H.W., Lescroëil, A., Murray, S., Nuz, M. Le, Patrick, S.C., Péron, C., Soanes, L.M., Wanless, S., Votier, S.C., and Hamer, K.C. 2013. Spatial segregation without territoriality in gannets. *Science* **341**: 68–71.
- Wakefield, E.D., Owen, E., Baer, J., Carroll, M.J., Daunt, F., Dodd, S.G., Green, J.A., Guilford,

- T., Mavor, R.A., Miller, P.I., Newell, M.A., Newton, S.F., Robertson, G.S., Shoji, A., Soanes, L.M., Votier, S.C., Wanless, S., and Bolton, M. 2017. Breeding density, fine-scale tracking, and large-scale modeling reveal the regional distribution of four seabird species. *Ecol. Appl.* **27**(7): 2074–2091.
- Wanless, S., Harris, M.P., and Morris, J.A. 1990. A Comparison of Feeding Areas Used by Individual Common Murres (*Uria aalge*), Razorbills (*Alca torda*) and an Atlantic Puffin (*Fratercula arctica*) during the Breeding Season. *Colon. Waterbirds* **13**(1): 16–24.
- Wilhelm, S.I., Mailhiot, J., Arany, J., Chardine, J.W., Robertson, G.J., and Ryan, P.C. 2015. Update and trends of three important seabird populations in the western North Atlantic using a Geographic Information System approach. *Mar. Ornithol.* **43**: 211–222.
- Wilhelm, S.I., Robertson, G.J., Taylor, P.A., Gilliland, S.G., Pinsent, D.L., Waterbirds, S., International, T., Biology, W., Sep, N., Wilhelm, S.I., Robertson, G., Taylor, P.A., Gilliland, S.G., and Pinsent, D.L. 2003. Stomach contents of breeding common murres caught in gillnets off Newfoundland. *Waterbirds* **26**(3): 376–378.
- Wood, S.N. 2006. Generalized additive models: an introduction with R. *J. R. Stat. Soc. A* **170**(1): 388.
- Young, J.W., Lansdell, M.J., Campbell, R.A., Cooper, S.P., Juanes, F., and Guest, M.A. 2010. Feeding ecology and niche segregation in oceanic top predators off eastern Australia. *Mar. Biol.* **157**(11): 2347–2368.

Tables and Figures

Table 1. Summary of individual common murre (*Uria aalge*) and razorbills (*Alca torda*) tracked during 2017 in northeastern Newfoundland, and data used in analysis including the sex of individuals, the number of foraging trips, the total number of dives, and the total number of dive bouts. Foraging trips include only the number of complete trips. Values represent those during low capelin availability (July 28-Aug 1) while values in parentheses represent those during high capelin availability (Aug 2-11).

Species	Id	Sex	No. of Trips	No. of Dives	No. of Dive Bouts
Common murre	URE03	F	1	19	5
	URE06	F	4	378	87
	URE07	M	3	261	43
	URE08	F	3 (4)	189 (292)	68 (47)
	URE09	M	4 (5)	290 (277)	50 (59)
	URI11	F	2	669	81
Razorbill	ALL11	F	1	64	14
	URI03	M	5 (20)	1139 (1685)	49 (339)
	URI13	F	4	1331	75
	URI14	F	5	1513	77

Table 2. Summary of foraging trip and dive characteristics of common murre (COMU) and razorbills (RAZO) from South Cabot Island and James Island, Newfoundland respectively, during chick-rearing 2017. Values for each species include mean \pm standard error.

Variable	COMU	RAZO	df	t (z)	p-value
Maximum distance (km)	16.9 \pm 3.4	19.7 \pm 3.5	546	0.57	0.57
Total distance (km)	44.1 \pm 8.7	49.8 \pm 8.9	30	0.45	0.66
Trip durations (h)	15.1 \pm 2.4	10.3 \pm 2.8	30	-1.29	0.21
Maximum dive duration (s)	122.2 \pm 10.8	66.1 \pm 8.1	1	-3.02	0.16
Mean dive duration (s)	36.4 \pm 3.1	32.0 \pm 2.8	5	-1.02	0.36
Number of Dive Bouts	19.6 \pm 4.2	14.3 \pm 3.6	-	(-1.14)	0.26
Mean Dives per bout	4.3 \pm 4.0	18.8 \pm 4.2	30	3.86	<0.001
Mean Dive Efficiency	0.44 \pm 0.02	0.65 \pm 0.02	6	5.37	0.001

Table 3. Mean \pm SE foraging trip and dive characteristics under low and high capelin availability for individual common murre (n=2) and razorbills (n=1) breeding on South Cabot Island and James Island, Newfoundland respectively, during chick-rearing (July-August) 2017. Bolded values represent significant differences between low and high capelin availability periods, with level of significance indicated as $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$.

Variable	ID	Common Murre		Razorbill	
		Low	High	Low	High
Maximum distance (km)	1	27.9 \pm 5.2	7.9 \pm 2.7	15.4 \pm 2.6	3.8 \pm 1.2 **
	2	27.0 \pm 5.5	5.8 \pm 0.3		
Total distance (km)	1	81.7 \pm 13.0	28.9 \pm 12.0	41.9 \pm 9.1	15.5 \pm 4.6 *
	2	85.0 \pm 19.6	22.5 \pm 1.7		
Duration (h)	1	32.2 \pm 2.8	26.1 \pm 11.4	7.2 \pm 3.1	6.5 \pm 1.6
	2	25.8 \pm 3.6	12.9 \pm 0.9		
Maximum dive duration (s)	1	116.2 \pm 2.7	97.8 \pm 9.0	58.0 \pm 2.7	88.0 \pm 10.2
	2	111.0 \pm 6.4	89.8 \pm 8.4		
Mean dive duration (s)	1	57.7 \pm 4.0	48.0 \pm 1.5	33.1 \pm 1.7	30.2 \pm 1.8
	2	36.5 \pm 3.3	30.3 \pm 2.7		
Number of Dive Bouts	1	31.6 \pm 4.1	13.2 \pm 4.0	9.8 \pm 4.1	16.1 \pm 3.7
	2	24.7 \pm 4.6	10.8 \pm 2.6		
Dives per bout	1	4.3 \pm 1.7	4.6 \pm 0.8	25.6 \pm 9.0	3.6 \pm 0.7 ***
	2	5.2 \pm 0.6	4.9 \pm 0.5		
Mean Dive Efficiency	1	0.47 \pm 0.05	0.55 \pm 0.02	0.70 \pm 0.01	0.55 \pm 0.02 *
	2	0.47 \pm 0.03	0.44 \pm 0.01		

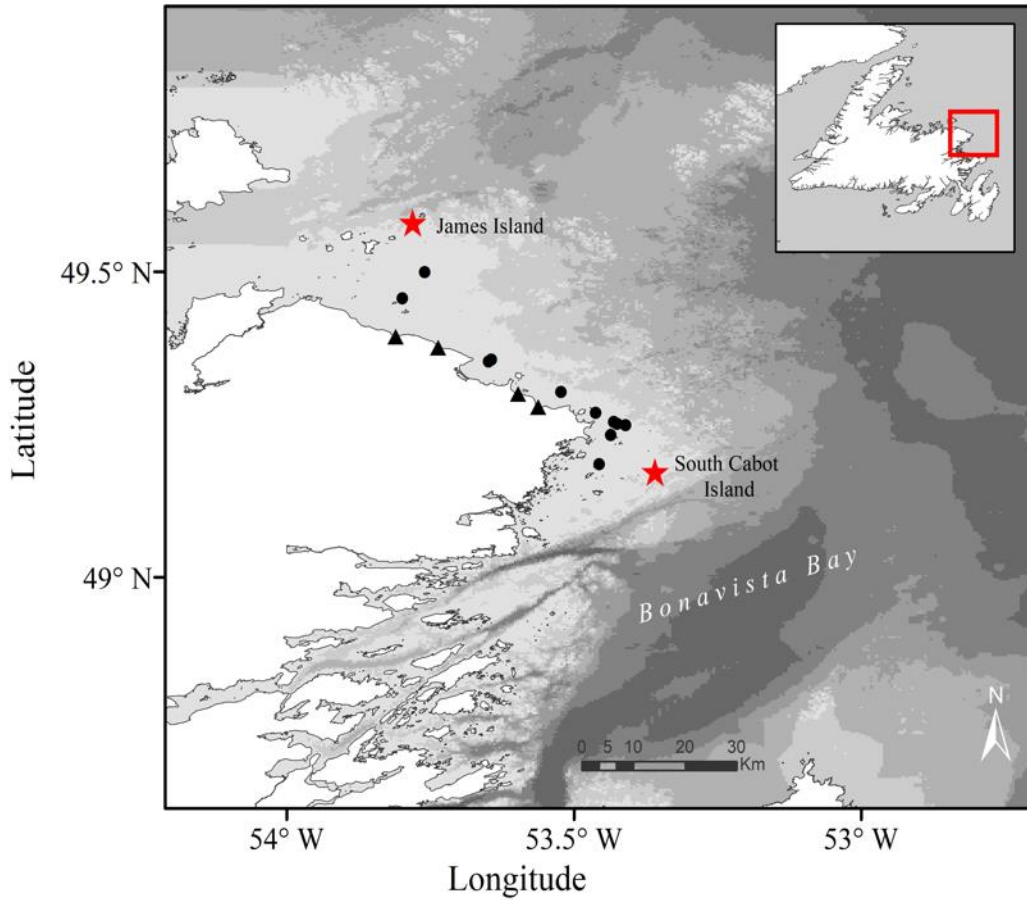


Figure 1. Study area in northeastern Newfoundland including the common murre colony on South Cabot Island, the razorbill colony of James Island (red stars), and beach (triangle) and deep-water (circle) capelin spawning sites.

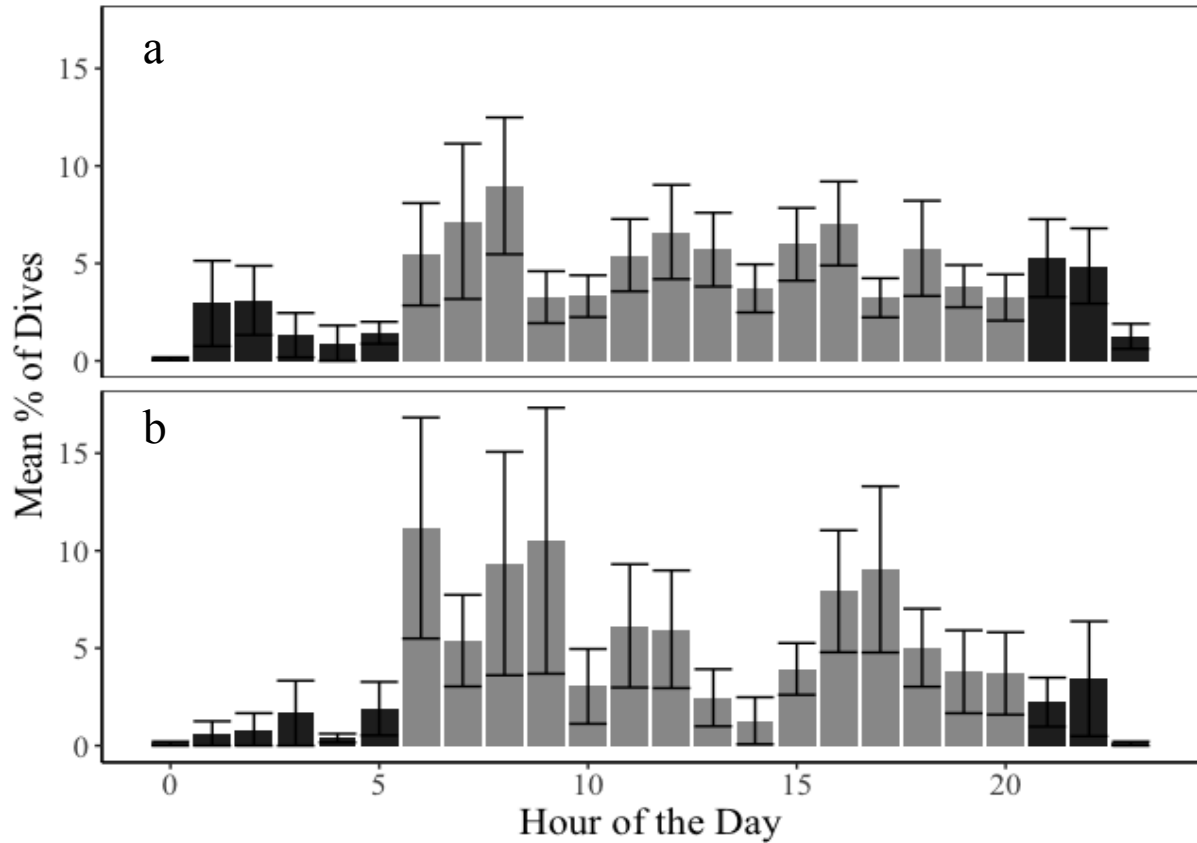


Figure 2. Mean frequency (% , \pm SE) of dives occurring during each hour of the day for common murre (a) and razorbills (b) in northeastern Newfoundland during chick-rearing 2017. Dives occurring between sunset and sunrise (black) and during daylight hours (grey) are indicated.

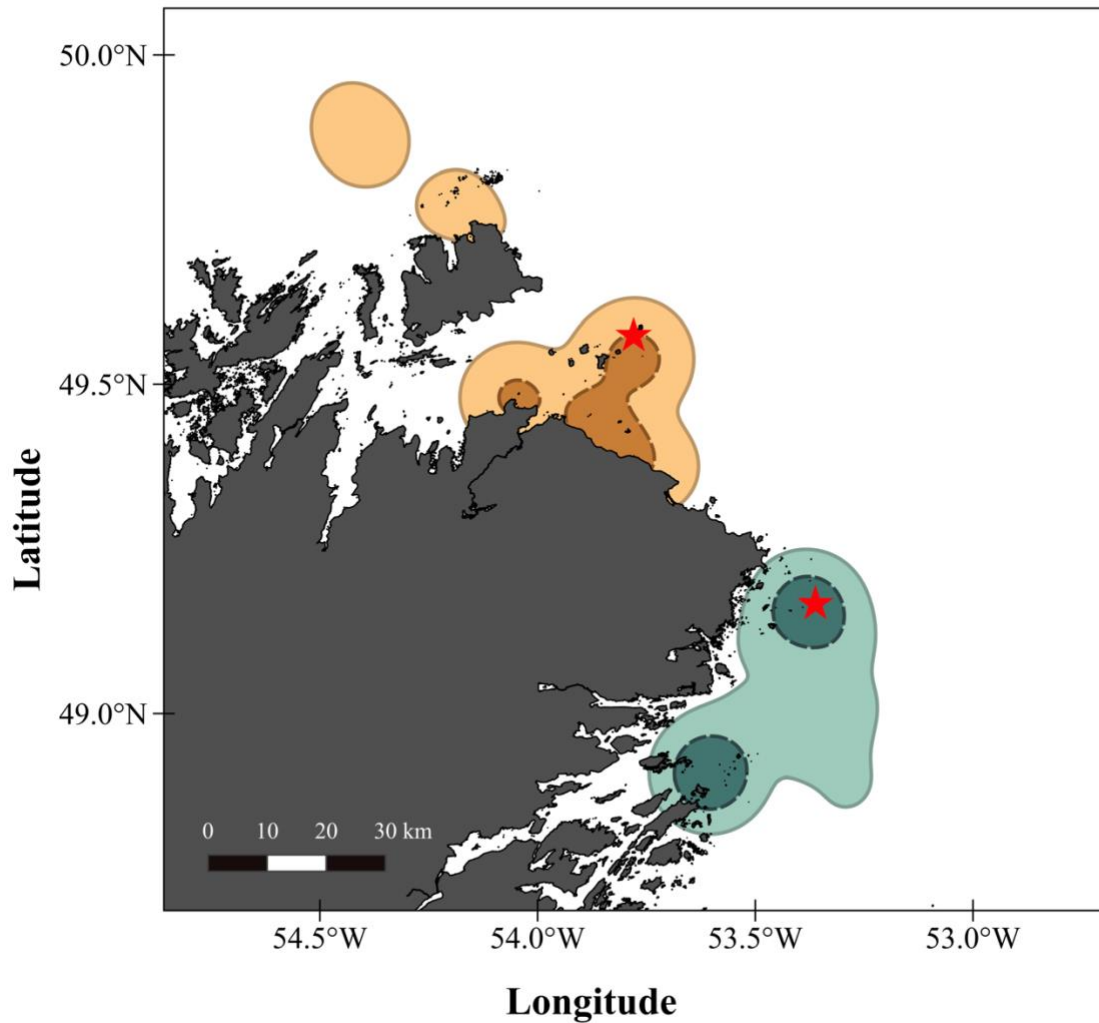


Figure 3. Kernel density analysis of dive locations of common murre (green) and razorbill (orange) from South Cabot Island and James Island (red stars), Newfoundland respectively, during chick-rearing 2017. Areas represent overall foraging areas (95% kernel, light solid) and core foraging area (50% kernel, dark dashed).

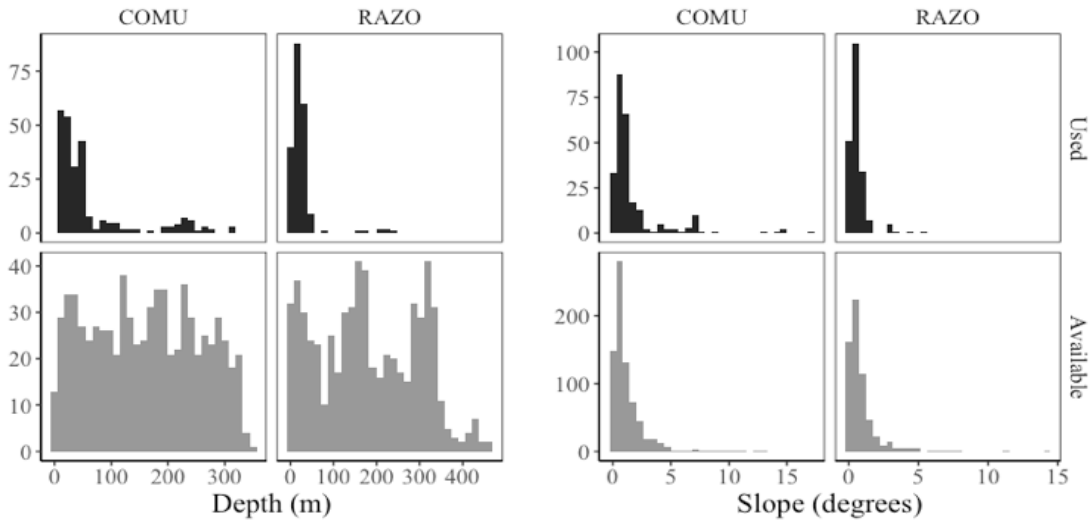


Figure 4. Foraging habitat use versus availability for common murre and razorbill during chick-rearing in northeastern Newfoundland, 2017. Values bathymetric depth (m) and bathymetric slope (degrees) based on dive bout locations (used; top) and pseudo-absences (available; bottom) within maximum foraging ranges of birds from the breeding colony.

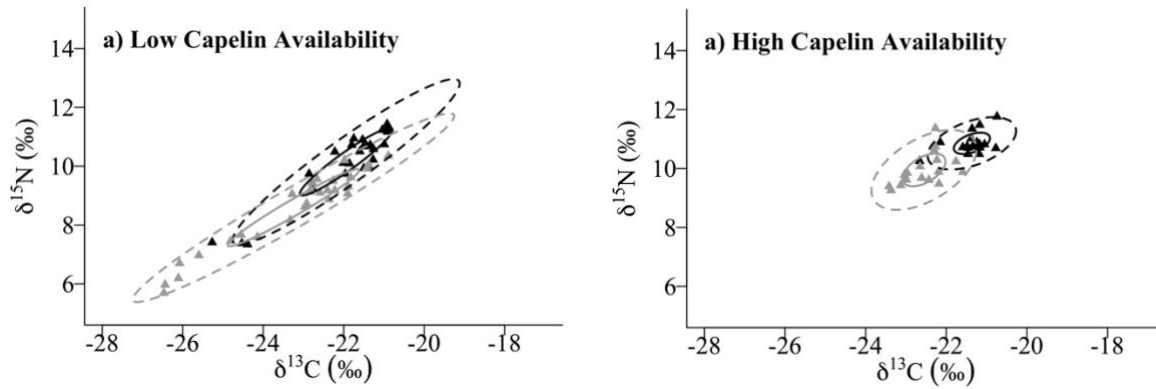


Figure 5. Stable isotope ratios of common murre (black) and razorbill (grey) of short-term integrated diet of plasma along with standard ellipse area (SEAc; solid line) and 95% ellipse area (dashed line) during low (a) and high (b) capelin availability.

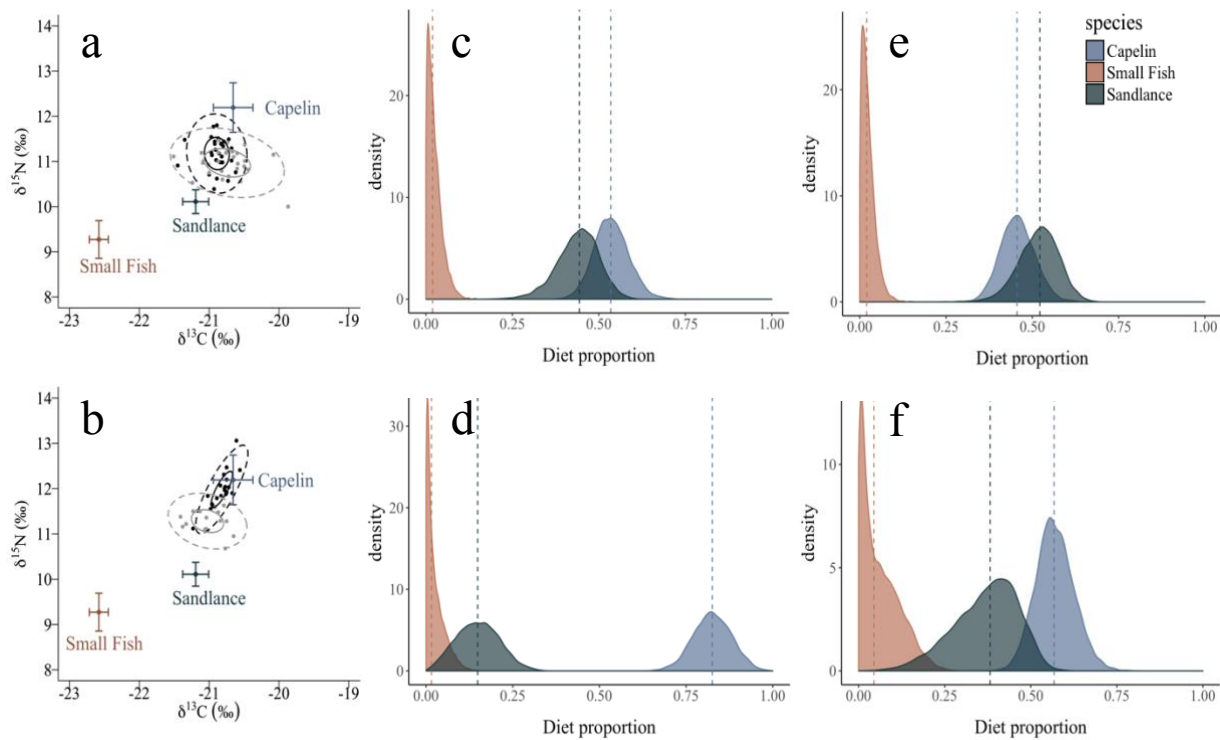


Figure 6. Isotopic niche and diet composition of chick-rearing common murres and razorbills in northeastern Newfoundland, 2017 with shifting prey availability. Isotopic niche breadth for red blood cell samples represented by $SEAc$ (solid line) and 95% ellipse area (dashed line) for murres (black) and razorbills (grey) during low (a) and high (b) capelin availability. Values are shown in relation to potential prey values (mean \pm SD) and have been adjusted to account for discrimination between consumer and prey. Diet proportion estimates represented by posterior distributions of Bayesian estimates for prey species in the diet during low capelin availability for murres (c) and razorbills (e) and during high availability for murres (d) and razorbills (f). Prey included are capelin (blue), sandlance (green) and small fish (pink). Dashed lines represent the median values of posterior estimates.

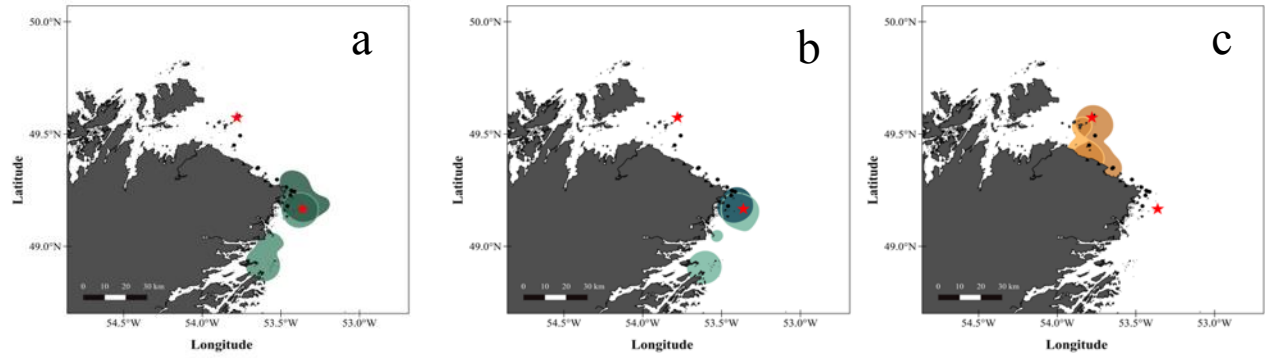


Figure 7. Individual foraging areas represented by 95% volume contours of kernel density analysis of dive locations of two common murre (a,b) and an individual razorbill (c) with a shift in prey availability from low (light color) to high (dark color) in relation to beach (triangle) and deep-water (circle) capelin spawning sites. Data collected during chick-rearing 2017.

Synthesis Discussion

Intra- and inter-specific interactions drive many aspects of the ecology of species. Understanding variation among individuals, populations and species under varying environmental conditions can help us understand each level's sensitivity to change. In this study, we found evidence of flexibility at the individual and the population level to changes in resource availability on multiple temporal scales, both inter-annually and within a breeding season. Common murrelets exhibited a large degree of within-individual variation in foraging behavior, and this variation remained high even as availability of their primary prey (capelin) varied inter-annually (Chapter 1). On the shorter temporal scale of the breeding season, this behavioral flexibility appeared to allow for responses to local prey availability, whereby individuals shifted foraging locations closer to the colony and capelin spawning sites and increased the proportion of capelin in the diet as availability increased (Chapter 2). While we were unable to examine individual-level foraging behavior of razorbills, behavioral and dietary shifts were observed under varying prey availability, suggesting that razorbills also respond to changes in resources. Razorbills exhibited a more varied diet, even when capelin availability was high, suggesting that flexibility in prey choice may be the primary response of razorbills to environmental change, with birds switching to alternative prey when capelin availability is low. In contrast, murrelets appear to specialize on capelin to a large degree regardless of relative availability, but exhibit a high degree of behavioral flexibility, suggesting that changes in foraging trip characteristics and time budgets may be the primary response of murrelets to changing resources. Owing to these different responses to resource availability, changes in resource availability may not increase competition between these two similar species, but rather result in greater divergence in niche dimensions.

Without information on breeding success, it is difficult to ascertain whether behavioral and dietary changes would buffer potential impacts of a reduction in capelin availability on breeding outcomes. For instance, how might switching to alternative prey, such as sandlance, impact chick growth and survival? As sandlance and similar species (i.e. sandeels) are a primary food source for many seabirds in the northeast Atlantic (Lilliendahl and Solmundsson 1997, Anderson et al. 2014), if suitable alternative prey remain available, prey switching may not have a negative impact on reproductive success. In contrast, behavioral responses to changes in capelin availability, such as increased trip distance and duration, to continue exploiting capelin may compromise chick feeding rates (Uttley et al. 1994), which at some point may begin to negatively impact breeding success (Cairns et al. 1987). Thus these different responses may have alternative outcomes, and could result in lower impacts on razorbills to extreme changes in capelin availability compared to murre.

There may also be other factors contributing to individual- and, thus, population-level variation in behavior and foraging choices. Increasingly, there is an interest in the impacts of temperament on individual-level foraging decisions (e.g. how shy and bold individuals differ in behavior), which is likely directly affected by interactions both among conspecifics and heterospecifics. For instance, previous studies have found measures of boldness to correspond with both reproductive success and foraging behavior in albatross (Patrick and Weimerskirch 2014, 2015). Sex may also play a role, as many studies have found differences in foraging and dive behavior (e.g., Lewis et al. 2002, Phillips et al. 2004, Peck and Congdon 2006), habitat use (e.g., Cleasby et al. 2015), and diet (e.g., Phillips et al. 2011, Carle et al. 2015) between males and females in different seabird species. While we controlled for sex in our analyses when possible, sample sizes may have been too small to detect any differences. Age is another factor

influences individual-level foraging behavior, as senescence and previous experience may also play a role in variation and flexibility of behavior. For instance, previous studies of thick-billed murre and Cory's shearwaters have found evidence of differences in diving and foraging activity with age (Catry et al. 2011, Cunningham et al. 2017), whereas little penguins have been found to spatially segregate by age (Pelletier et al. 2014). Thus, in the case of razorbills and murre, these may be additional factors affecting both individual variation and population-level niche partitioning, as bold and shy individuals, males and females and young and old individuals may respond differently to changes in prey availability, which in turn may impact niche partitioning.

During our study, we found evidence for both niche segregation and overlap within and between species, indicating that many niche dimensions integrate to determine patterns in resource exploitation. While we aimed to examine as many niche dimensions as possible, especially between species, many more subtle aspects of the n-dimensional hypervolume of the niche were not examined. In particular, we used dive duration as a proxy of dive depth to examine vertical segregation in foraging habitat between murre and razorbills. With increases in technology during the course of my program, however, it is already possible to incorporate temperature-depth recorders (TDRs) and accelerometers into GPS tags, allowing future researchers to examine many more aspects of foraging behavior simultaneously. With TDRs, depth profiles of dives as well as temperature characteristics of the water column can be quantified (Daunt et al. 2003), while accelerometers provide information on small-scale three-dimensional movement (Chimienti et al. 2017), thereby allowing researchers to examine search behavior both above and underwater as well as prey capture rates. In addition, while we found evidence for a high degree of similarity in the diet between species, more subtle differences in

dietary niche dimensions might exist between murre and razorbill. For instance, it may be insightful to examine the size class of prey and consistency over multiple time scales. With a better understanding of trophic discrimination in bird plasma, it may be possible to reconstruct dietary composition on the scale of both days and weeks. In addition, using feathers molted during the non-breeding season paired with geolocators would also allow us to examine niche partitioning beyond the breeding season and, thus, changes throughout the annual cycle.

Understanding non-breeding foraging behavior and diet would help provide greater insight into the flexibility of species in both the degree and mechanisms by which they avoid interspecific competition.

The degree of change in prey availability is also an important aspect to consider. Timing of the inshore arrival of spawning capelin varies among years as does the inshore biomass. Therefore, it is likely not as simple as categorizing prey availability into 'low' and 'high' as these categories may differ among years. While we examined 'low' capelin availability, this prey state likely did not represent extreme conditions of reduced prey availability and, thus, there may be niche dimensions that did not diverge between murre and razorbill that might have with a greater reduction in prey. For instance, although we concluded that habitat preference and diurnal foraging patterns do not represent dimensions of great niche divergence between species, we might observe more obvious differences in these dimensions as the necessity to reduce competition increases under an extreme shortage in prey. Additionally, while we found evidence for individual-level responses to short-term changes in prey availability, sample sizes were small. To better understand responses to shifting prey availability, future studies should collect a greater number of samples over multiple years to better understand how individuals and populations respond to relative differences in capelin availability. By continuing to examine these changes

over multiple years, researchers could address more specific questions related to relative prey biomass rather than coarse periods of prey availability, as well as how the timing of capelin arrival and spawning in the area impacts the foraging ecology of breeding seabirds.

Overall, this thesis has demonstrated that common murre and razorbill breeding in northeastern Newfoundland exhibit plasticity in foraging behavior and diet at both the individual and population level and that spatial segregation is the main aspect of niche divergence between these species, presumably allowing high dietary overlap. These results contribute to understanding the dynamics of this marine ecosystem and the potential sensitivity of these top marine predators to changes in capelin availability in the future. Understanding these dynamics is important because the timing of arrival and spawning as well as biomass of capelin in the area is high, which is likely to persist into the future. Future management should take into consideration these findings to inform both the conservation of seabird populations and the management of capelin fisheries in the area.

References

- Anderson, H.B., Evans, P.G.H., Potts, J.M., Harris, M.P., and Wanless, S. 2014. The diet of common guillemot *Uria aalge* chicks provides evidence of changing prey communities in the North Sea. *Ibis* **156**(1): 23–34.
- Cairns, D.K., Bredin, K.A., and Montevecchi, W.A. 1987. Activity budgets and foraging ranges of breeding common murre. *Auk* **104**: 218–224.
- Carle, R.D., Beck, J.N., Calleri, D.M., and Hester, M.M. 2015. Temporal and sex-specific variability in rhinoceros auklet diet in the central California Current system. *J. Mar. Syst.* **146**: 99–108.
- Catry, P., Granadeiro, J.P., Ramos, J., Phillips, R.A., and Oliveira, P. 2011. Either taking it easy or feeling too tired: old Cory's shearwaters display reduced activity levels while at sea. *J. Ornithol.* **152**(3): 549–555.
- Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I.M., Travis, J.M.J., and Scott, B.E. 2017. Taking movement data to new depths: Inferring prey availability and patch profitability from seabird foraging behavior. *Ecol. Evol.* **00**: 1–14.
- Cleasby, I.R., Wakefield, E.D., Bodey, T.W., Davies, R.D., Patrick, S.C., Newton, J., Votier, S.C., Bearhop, S., and Hamer, K.C. 2015. Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Mar. Ecol. Prog. Ser.* **518**: 1–12.
- Cunningham, J.T., Le Vaillant, M., Gaston, A.J., Ropert-Coudert, Y., Kato, A., Jacobs, S.R., and Elliott, K.H. 2017. Reduced activity in middle-aged thick-billed murre: evidence for age related trends in fine-scale foraging behaviour. *Anim. Behav.* **126**: 271–280.
- Daunt, F., Peters, G., Scott, B., Grémillet, D., and Wanless, S. 2003. Rapid-response recorders reveal interplay between marine physics and seabird behaviour. *Mar. Ecol. Prog. Ser.* **255**:

283–288.

- Lewis, S., Benvenuti, S., Dall-Antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S., and Hamer, K.C. 2002. Sex-specific foraging behaviour in a monomorphic seabird. *Proc. R. Soc. B Biol. Sci.* **269**(1501): 1687–1693.
- Lilliendahl, K., and Solmundsson, J. 1997. An estimate of summer food consumption of six seabird species in Iceland. *ICES J. Mar. Sci.* **54**(4): 624–630.
- Patrick, S.C., and Weimerskirch, H. 2014. Personality, foraging and fitness consequences in a long-lived seabird. *PLoS One* **9**(2): e87269.
- Patrick, S.C., and Weimerskirch, H. 2015. Senescence rates and late adulthood reproductive success are strongly influenced by personality in a long-lived seabird. *Proc. R. Soc. B Biol. Sci.* **282**: 20141649.
- Peck, D.R., and Congdon, B.C. 2006. Sex-specific chick provisioning and diving behaviour in the wedge-tailed shearwater *Puffinus pacificus*. *J. Avian Biol.* **37**(3): 245–251.
- Pelletier, L., Chiaradia, A., Kato, A., and Ropert-Coudert, Y. 2014. Fine-scale spatial age segregation in the limited foraging area of an inshore seabird species, the little penguin. *Oecologia* **176**(2): 399–408.
- Phillips, R.A., McGill, R.A.R., Dawson, D.A., and Bearhop, S. 2011. Sexual segregation in distribution, diet and trophic level of seabirds: Insights from stable isotope analysis. *Mar. Biol.* **158**(10): 2199–2208.
- Phillips, R.A., Silk, J.R.D., Phalan, B., Catry, P., and Croxall, J.P. 2004. Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc. R. Soc. B Biol. Sci.* **271**(1545): 1283–1291.

Uttley, J.D., Walton, P., Monaghan, P., and Austin, G. 1994. The effects of food abundance on breeding performance and adult time budgets of guillemots *Uria aalge*. *Ibis* **136**(2): 205–213.