INTER-COLONY AND INTERSPECIFIC DIFFERENCES IN THE ISOTOPIC NICHE OF TWO SYMPATRIC GULL SPECIES IN NEWFOUNDLAND

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ABSTRACT

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Large gulls are omnivorous predators that are typically associated with coastal environments, but gull colonies vary in their proximity to the coast. Because the diet of central-place foragers is often dictated by resource availability within range of the central place, we investigated inter-colony and interspecific differences in the diet of Great Black-backed Gulls *Larus marinus* and Herring Gulls *L. argentatus* at multiple inshore colonies (< 20 km) and one offshore colony (> 60 km; Funk Island) on the northeast Newfoundland coast, Canada. Values of δ^{15}N and δ^{13}C in whole blood of gull chicks and adults (incubating) were used to compare isotopic niche breadth (standard ellipse area) and trophic level (δ^{15}N) between species (adults and chicks) and colonies (chicks only). Herring Gull chicks had higher δ^{15}N at the offshore colony relative to inshore colonies, indicating that these chicks were provisioned with higher trophic level resources (e.g., seabird eggs/chicks) compared to lower trophic level resources (e.g., benthic invertebrates) at inshore colonies. Great Black-backed Gull chicks had higher δ^{15}N than Herring Gull chicks at all colonies, indicating they were consistently provisioned with higher trophic level resources. Isotopic niche breadth was broader for Great Black-backed Gull chicks raised inshore relative to offshore, indicating a wider variety of resources provisioned at inshore colonies relative to the offshore colony. Incubating adult Great Black-backed Gulls incorporated higher trophic level prey and had a narrower isotopic niche breadth than incubating Herring Gulls at the same inshore colony, indicating that they have a more specialized diet of higher trophic level than Herring Gulls. We suggest, based on our results, that the differential availability of food resources proximal to colonies influences the diet of these two sympatric gull species, thereby informing region-specific gull management programs.

Key words: stable isotopes, carbon, nitrogen, gulls, *Larus*, diet, isotopic niche

INTRODUCTION

Seabirds act as central-place foragers during the breeding season, whereby they forage at sea but must return to island breeding colonies (i.e., central place) to incubate or provision offspring (Orians & Pearson 1979). To efficiently provision offspring, seabirds forage within a limited range of the breeding colony (e.g., Elliott *et al*. 2009, Gulka & Davoren 2019). Therefore, breeding seabirds raising altricial offspring may maximize energy delivery to chicks by adjusting their diet according to the prey types available within ranges. Large gulls are well known dietary generalists and are observed feeding in coastal, marine, and freshwater habitats as well as landfills (Pierotti & Good 1994, Good 1998). Owing to this flexibility, the diet of large gulls can vary seasonally and annually according to the availability of high-quality prey (Gauthier *et al*. 2015, Gulka *et al*. 2017). The diets of sympatric gull species often differ, whereby larger gull species typically feed at higher trophic levels relative to smaller gulls (Washburn *et al*. 2013, Ronconi *et al*. 2014). Species-specific gull diets can also vary among colonies depending on a colony's proximity to predictable food sources (Hebert & Shutt 1999, Enners *et al*. 2018). For instance, large gulls breeding near anthropogenic food resources are often associated with human refuse facilities (e.g., landfill, fish plants) relative to birds in remote locations (O'Hanlon *et al*. 2017, Shlepr 2017). Additionally, gulls breeding on or near multi-species seabird colonies often feed on readily available seabird eggs, chicks, and even adults (Stenhouse & Montevecchi 1999, Massaro *et al*. 2000), at times resulting in the implementation of gull management programs (e.g., culling) to limit the impact of gull predation on seabirds (Guillemette & Brousseau 2001, Scopel & Diamond 2017).

On the northeast Newfoundland coast, Herring Gulls *Larus argentatus* and Great Black-backed Gulls *L. marinus* breed sympatrically among a variety of other seabirds in colonies located < 20 km from the shoreline (Fig. 1). The primarily inshore distribution of these colonies provides breeding gulls with readily available intertidal resources (e.g., urchins, mussels, sea stars) and land-based resources (e.g., berries, small mammals) within foraging ranges (< 50 km; Shlepr 2017, Maynard & Davoren 2018, Maynard & Ronconi 2018), in addition to marine-based resources (e.g., forage fish; Maynard & Davoren 2018). Unlike recent studies on other large gull species, which reported high use of urban habitats (O'Hanlon *et al*. 2017, Maynard & Ronconi 2018), Great Black-backed Gulls breeding at inshore colonies in this area appear to primarily forage/roost in coastal and marine habitats (Maynard & Davoren 2018), likely due to distant (80–100 km) anthropogenic food sources (e.g., landfills, urban centers). Both gull species in this area are also observed feeding on fisheries discards, primarily offal (i.e., guts, liver) of Atlantic Cod *Gadus morhua* (Maynard *et al*. 2019). An exception to the inshore distribution of gull colonies in the area is Funk Island, which is located ~60 km from the coastline and hosts breeding pairs of both Herring and Great Black-backed Gulls, along with ~500 000 breeding pairs of Common Murres *Uria aalge* (Wilhelm *et al*. 2015). Despite the access to intertidal resources along the island shoreline, the more abundant inshore intertidal resources and other inshore food sources are at the limits of gull foraging ranges from Funk Island, while seabird eggs, chicks, and adults are a highly abundant food resource (Pierotti & Good 1994, Good 1998). Although inter-colony dietary differences of large gulls have been assessed in other regions (Shlepr 2017, Enners *et al.* 2018), dietary differences between offshore and inshore colonies, associated with varying resource availability, has not been studied previously, especially in an interspecific context.

The goal of this study was to compare the isotopic niche of Herring and Great Black-backed gull chicks raised at inshore breeding colonies and an offshore breeding colony on the northeast Newfoundland coast during one year (2017) using stable isotope analysis. For each gull species, we predicted that chicks raised at the offshore colony would have a narrow isotopic niche breadth, along with a higher trophic level (i.e., higher δ^{15}N) and a more marine (i.e., higher δ^{13}C) isotopic composition, than chicks raised at inshore colonies. We also examined interspecific differences in the isotopic niche breadth and trophic position of adult Herring and Great Black-backed gulls during incubation (May–June 2017) in one inshore colony. Additionally, we predicted that Great Black-backed Gull chicks and adults would have a narrow isotopic niche breadth and higher trophic position (higher δ^{15}N) than Herring Gull chicks and adults. This study is novel because few studies have simultaneously measured interspecific and inter-colony dietary differences of sympatric gull or any seabird species. Considering that high predation pressure by gulls on seabird colonies can result in gull culling, investigating local variation in gull diet will inform gull management programs and seabird conservation.

METHODS

Study area

On the northeast Newfoundland coast, Herring Gulls (HERG) and Great Black-backed Gulls (GBBG) nest within multi-species seabird colonies, which include Common Murres, Atlantic Puffins *Fratercula arctica*, Razorbills *Alca torda*, Black Guillemots *Cepphus grylle,* Leach's Storm Petrels *Oceanodroma leucorhoa*, and Double-crested Cormorants *Phalacrocorax auratus* (Wilhelm *et al.* 2015). Most colonies host 10–50 breeding pairs of both gull species, along with 100–19 000 alcids and/or 10–8000 procellariformes (Wilhelm *et al.* 2015) and are located < 20 km from the shoreline (Fig. 1). Both gull species also breed on Funk Island, a small (400 × 800 m) island located ~60 km from the coastline that hosts ~100 breeding pairs of both Herring and Great Black-backed gulls, along with ~500 000 breeding pairs of Common Murres (Wilhelm *et al.* 2015). The closest major anthropogenic food source is a landfill ~80 km inland from the coastline near the nearest town (Gander, Newfoundland).

Capture and blood sampling

Gull chicks of both species (n = 27 GBBG; n = 16 HERG) were hand-captured nearby nests during July 2017 on a variety of inshore

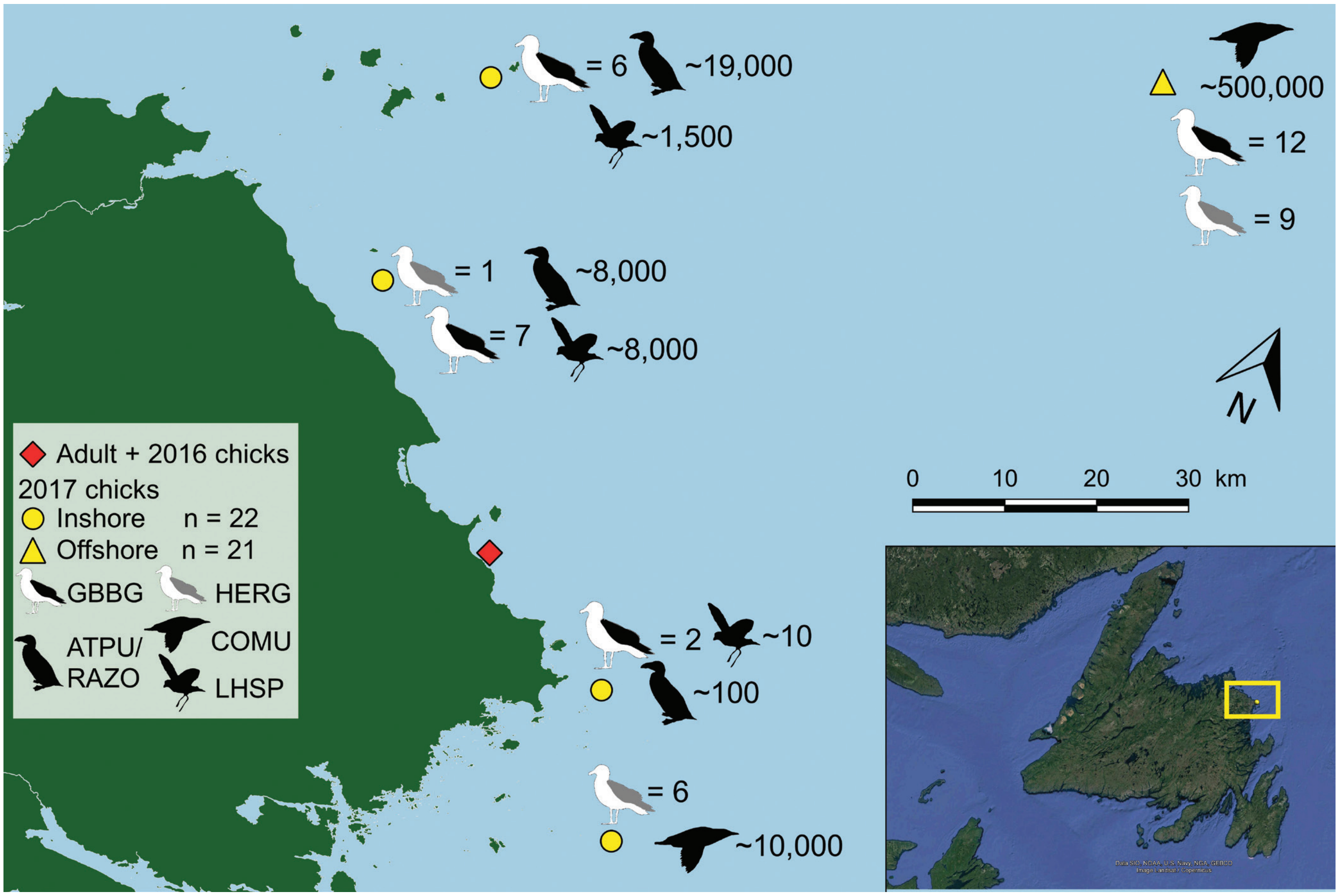

Fig. 1. Location of inshore and offshore breeding colonies where blood from Herring Gull (HERG) and Great Black-backed Gull (GBBG) was sampled during May–August 2016/2017, along with the number of adults and chicks of each species sampled per colony during each year. The number of breeding pairs of Atlantic Puffins (ATPU), Razorbills (RAZO), Common Murres (COMU), and Leach's Storm-petrels (LHSP), obtained from Wilhelm *et al.* (2015), are also shown to indicate the seabird resources available to gulls nesting at each colony.

colonies (n = 4 islands; n = 22 chicks) as well as one offshore colony, Funk Island (n = 21 chicks), on the northeast Newfoundland coast (Fig. 1). Several inshore colonies were sampled because it was difficult to locate and sample sufficient numbers of chicks of both species at one inshore colony due to varying numbers of successful nests. Chicks of similar age (~2–3 weeks old) were targeted to reduce variation of stable isotope ratios with age (Williams *et al*. 2007). The species of each chick was identified using breast feather colour, which are cream-colour in Great Black-backed Gulls and brown-grey in Herring Gulls. At one inshore colony (Southern Cat Island; Fig. 1), blood was sampled from incubating adults of Herring Gulls (n = 7, 31 May–22 June) and Great Black-backed Gulls (n = 9, 31 May–09 June) during another study (Maynard & Davoren 2018). Adults were captured using box traps and bow nets placed over the nests with eggs. We also sampled Herring and Great Black-backed gull chicks (n = 25) during 2016 (10 July–11 August) on Southern Cat Island (Fig. 1), but chicks were a variety of ages (~2–6 weeks) and thus, whole blood samples were only used to examine whether lipid extraction (described below) influenced carbon and nitrogen stable isotope ratios. Capture and handling of gulls were conducted following an approved protocol by the Canadian Council for Animal Care (F16-017/1). Birds were tagged under Canadian Bird Banding Permit #10873.

For both adults and chicks, < 1 mL of blood was sampled from the median metatarsal vein or the cutaneous ulnar vein in the wing using puncture needles (size = 25G) and capillary tubes. Whole blood samples represent the last 12–15 d, thereby representing short-term diet relative to other tissue types (e.g., feathers; Hobson & Clark 1993). Samples were stored in microcentrifuge vials, put on ice, and later frozen (within 8 h). To aid in the interpretation of stable isotope ratios, spontaneous regurgitations were opportunistically collected and later identified, and pellets were collected around nests of captured adults during incubation. To obtain stable isotope ratios of these and other potential prey types, prey samples were then collected opportunistically at colonies during June–August 2016/17, in collaboration with fishers in the study area. Prey samples consisted of a Common Murre chick (n = 1; from gull predation), a Leach's Storm Petrel adult (n = 1; found dead), spawning capelin *Mallotus villosus* (n = 15), sandlance *Ammodytes* sp. (n = 9), a fly (Diptera; n = 1), blue mussels *Mytilus edulis* (n = 3), and green sea urchin *Stronglyocentrotus droebachiensis* (n = 4). We also sampled prey discarded during fishing activities in the area that gulls have been observed to exploit, including Atlantic herring *Clupea harengus* (n = 15, 180–340 mm) used as bait in a local lobster fishery and Atlantic cod stomach tissue (n = 3) discarded at wharfs, which has similar δ^{13}C and δ^{15}N values to cod liver (Carvalho & Davoren 2019).

Stable Isotope Analysis

Whole blood samples were lyophilized at -56 °C for 48 h and homogenized by crushing samples into powder. Whole blood samples from gull chicks sampled during summer 2016 were divided in half, with one half not lipid-extracted and the other half lipid-extracted for eight hours using petroleum-ether solution in a Soxhlet apparatus (Elliott *et al*. 2017). Lipid-extracted samples were then oven-dried for 48 h at 60 °C. Whole blood samples from adults and chicks sampled during 2017 were not lipid extracted. Dried and homogenized subsamples were weighed (0.4–0.6 mg) and placed in tin capsules. For the prey samples, muscle plugs were sub-sampled from bird and fish samples, whereas a number of flies were used in one bulk sample, and soft body tissue was sub-sampled from mussels and urchins. All prey samples were lipid-extracted as above. All samples were analyzed using a Thermo Finnigan Delta^{Plus} mass spectrometer (Therno Finnigan, San Jose, CA, USA) coupled with an elemental analyzer (Costech, Valencia, CA, USA) at the Chemical Tracers Laboratory, Great Lakes Institute for Environmental Research, University of Windsor (Windsor, ON, Canada). Reference standards (Vienna PeeDee belemnite for ^{13}C, atmospheric air for ^{15}N) were used to quantify stable isotope ratios, which were expressed in delta (δ) notation as parts per thousand (per mil; ‰) using $X = [(R_{standard}/R_{standard})-1]$, where X is ^{13}C or ^{15}N and R is the corresponding ratio (i.e., $^{13}C/^{12}C$ or $^{15}N/^{14}N$). Instrumental accuracy was based on certified values of the United States Geological Survey (USGS) 40 for δ^{13}C and Urea for δ^{15}N; instrumental accuracy was similar in both years for δ^{15}N (2016: 0.01 ‰; 2017: 0.06 ‰) and δ^{13}C (2016: 0.04 ‰; 2017: 0.03 ‰). Instrumental precision was quantified as the standard deviation of replicates of four standards (NIST1577c, internal lab standard [tilapia muscle], USGS 40, and Urea) spaced throughout runs and was similar in 2016 and 2017 for both δ^{15}N (≤ 0.16 ‰ and ≤ 0.17 ‰, respectively) and δ^{13}C (≤ 0.17 ‰ and ≤ 0.12 ‰, respectively).

Data analysis

A paired t-test was used to examine the influence of lipid extraction on δ^{13}C and δ^{15}N values of whole blood ($\alpha = 0.05$) from chicks sampled during 2016, whereby the mean difference in δ^{13}C and δ^{15}N values was compared separately between the lipid-extracted and non-lipid-extracted sub-samples. For whole blood samples of adults and chicks in 2017, isotopic niche breadth was quantified using standard ellipse area (SEA), whereby ellipses are drawn from the standard deviation of δ^{13}C and δ^{15}N values around the bivariate mean. Standard ellipses encompass approximately 40% of the data point and, thus, represent the core niche (Jackson *et al*. 2011). The SEA was calculated using both a correction factor curve to account for small sample size (SEAc) and a Bayesian model (SEAb), with 10 000 repetitions and three Markov chain Monte Carlo (MCMC) algorithms using the *SIBER* (Jackson *et al*. 2011) package in R (R Development Core Team 2018). Priors for the Bayesian analysis were set as uninformed and we used the mode of the posterior distribution to indicate the most likely SEAb. Samples from inshore colonies were pooled due to low sample sizes per colony and, thus, ellipses were quantified for each species at the offshore colony as well as all inshore colonies combined. Additionally, two-factor ANOVAs were used to compare means of δ^{15}N and δ^{13}C separately between species and colonies (and their interaction) for chick samples, whereas t-tests were used to compare means of δ^{15}N and δ^{13}C separately between species for adult samples. Post-hoc Tukey tests were used to differentiate means when the interaction (species:colony) was significant in ANOVAs. A discrimination factor (Ringed-bill Gull chicks *L. delawarensis*; Hobson & Clark 1992) was added to the prey δ^{13}C and δ^{15}N values to interpret chick and adult δ values in relation to their prey. Isotopically similar prey types were averaged together, including Atlantic herring and capelin ('forage fish'), as well as mussels and urchins ('benthic invertebrates'). All graphics and analysis were done using R version 3.5.3 (R Development Core Team 2018) and QGIS version 3.4.1 (QGIS Development Team 2018).

RESULTS

During adult capture, regurgitations and pellets were collected and were comprised of a diversity of prey types, including birds (Leach's Storm Petrel), mammals (Meadow Vole *Microtus pennsylvanicu*), large fish (sculpin *Myoxocephalus* sp.), forage fish (capelin and Atlantic herring), and benthic fish (sandlance and rock gunnel *Pholis gunnellus*; Table 1). During chick capture, chicks regurgitated birds (Common Murre chicks), large fish (sculpin), forage fish (capelin and Atlantic herring), benthic fish (sandlance and rock gunnel), insects (flies and dragonflies), and marine invertebrates (Atlantic rock crab *Cancer irroratus*; Table 1).

Lipid-extracted and non-lipid extracted whole blood for gull chicks (2016) did not differ significantly for δ^{13}C (difference: -0.07 ± 0.05 ‰; t_{24} = -1.36, P = 0.19), but did differ for δ^{15}N (difference: 0.10 ± 0.04 ‰; t_{24} = 2.56, P = 0.02). Because the difference in δ^{15}N is below the analytical precision for δ^{15}N (0.16 ‰), this difference is likely not biologically relevant.

When comparing δ^{13}C of chicks between species and colony locations relative to shore, δ^{13}C was different between species and colony locations (interaction; F = 11.01; P = 0.002). A post-hoc Tukey test showed that δ^{13}C was significantly lower for Herring Gull chicks raised at inshore colonies relative to the offshore colony (P = 0.02), as well as Great Black-backed Gull chicks at both inshore and offshore colonies ($P < 0.001$; Table 2, Fig. 2a). Herring Gull chicks raised at the offshore colony also had significantly lower δ^{13}C than Great Black-backed Gull chicks raised at inshore colonies (P = 0.002), but there was no difference in δ^{13}C in Herring Gull chicks compared with offshore Great Black-backed Gull chicks (P = 0.1; Table 2, Fig. 2a). An analysis of variance showed that δ^{15}N in chicks also differed between species and colonies (interaction; F = 6.86; P = 0.01). Herring Gull chicks raised inshore had lower δ^{15}N compared to all other levels of chicks (GBBG inshore and offshore; HERG offshore; $P < 0.001$). Values of δ^{15}N

TABLE 1

Number of regurgitations and pellets containing a particular prey type from Great Black-backed and Herring gull chicks and adults at multiple inshore colonies and a single offshore colony (Funk Island)

	Inshore – Adults		**Inshore – Chicks**		**Offshore – Chicks**	
Prey	**GBBG**[a] (***n*** **= 5)**	**HERG**[a] (***n*** **= 5)**	**GBBG (*n* = 4)**	**HERG (*n* = 8)**	**GBBG (*n* = 3)**	**HERG (*n* = 4)**
Large fish	2	1	2			
Forage fish		1	2	2	1	1
Benthic fish		3		2		
Insects				2		
Unknown fish				1	1	
Marine invertebrates	1			1		
Birds	1				1	3
Mammals	1					

[a] GBBG = Great Black-backed Gull; HERG = Herring Gull

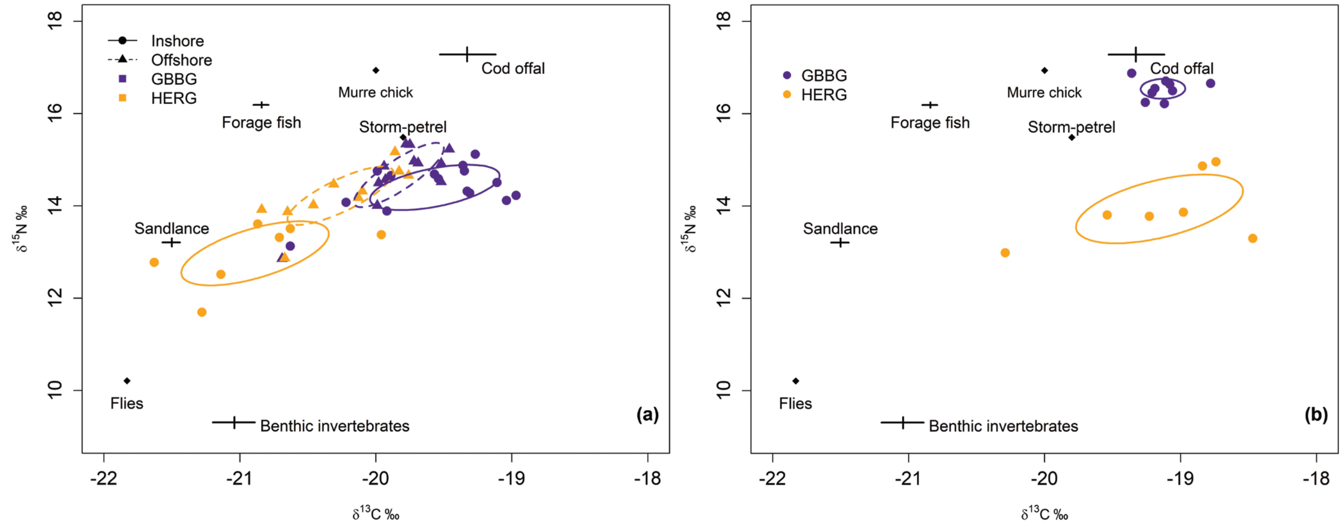

Fig. 2. Values of δ^{15}N and δ^{13}C (‰) from Great Black-backed Gull (GBBG; purple) and Herring Gull (HERG; yellow) whole blood samples, along with standard area ellipses corrected for small sample sizes, for gull chicks at inshore (circle; thick line) and offshore (triangles; dashed) colonies (a), as well as gull adults at an inshore colony during incubation (b). Prey δ^{13}C and δ^{15}N are represented by the bivariate mean and standard error.

in Great Black-backed Gull chicks did not differ between colony locations ($P = 0.7$; Table 2, Fig. 2a).

Comparing isotopic niche breadth (SEAc, SEAb) between species at the inshore and offshore colonies, inshore Herring Gull chicks had a broader isotopic niche relative to inshore Great Black-backed Gull chicks, but in only 40% of the model runs for the SEAb (Table 2). In contrast, Herring Gull chicks raised offshore had a broader isotopic niche than Great Black-backed Gull chicks raised offshore (77% of the model runs; Table 2). Herring Gull chicks from inshore colonies had a broader isotopic niche than Herring Gull chicks from the offshore colony in only 47% of the model runs for SEAb, whereas isotopic niche breadth of inshore-raised Great Black-backed Gull chicks was broader than for offshore Great Black-backed Gull chicks (83% of the model runs; Table 2). A *t*-test revealed that δ^{15}N values were significantly higher in adult Great Black-backed Gulls relative to Herring Gulls at the same inshore colony ($t_7 = 9.04$; $P < 0.001$; Fig. 2b), and Great Blacked-back Gulls also had a narrower isotopic niche than Herring Gulls (100% of the model runs; Table 2, Fig. 2b). Values of δ^{13}C were not different between adult Great Black-backed and Herring gulls ($t_7 = 0.11$; $P = 0.92$; Table 2, Fig. 2b).

DISCUSSION

Our results indicate that the diet of Herring Gulls, but not Great Black-backed Gulls, differs with colony location, which results in intercolony differences in interspecies dietary overlap. Indeed, Herring Gull chicks raised offshore have higher δ^{15}N values and lower δ^{13}C values than chicks raised at colonies closer to the coast, but these inshore–offshore differences were not evident for Great Black-backed Gull chicks. These findings indicate that inshore Herring Gulls provision their chicks with lower trophic level, coastal prey, such as benthic invertebrates found in the intertidal areas, whereas offshore Herring Gulls provision their chicks with higher trophic level, marine-based prey, such as seabirds and fish. In contrast, minimal variation in δ values in Great Black-backed Gull chicks raised inshore and offshore indicate that chicks were provisioned at the same trophic level (marine-based resources) despite varying proportions of available resource types among colonies. Isotopic niche breadth was broadest for gull chicks of both species raised at inshore colonies, which may indicate that inshore parents provisioned chicks with a greater variety of prey types relative to the offshore colony. Incubating adult Great Black-backed Gulls had higher δ^{15}N values and narrower isotopic niche breadth than adult Herring Gulls, indicating that Herring Gulls consistently consumed a varied diet of lower trophic level prey than Great Black-backed Gulls while incubating at the same inshore colony. These interspecific differences were similar for chicks raised inshore, but they were not evident for chicks raised offshore. Although some of this variation in δ values may be related to slight age variation in the chicks, as growth affects δ values by influencing metabolic processes and fractionation (Williams *et al*. 2007, Gorokhova 2017), the larger differences in δ values likely reflect inter-colony and interspecific dietary differences.

For Herring Gulls, higher δ^{13}C and δ^{15}N values in chicks raised at the offshore relative to inshore colonies was not surprising due to variation in the proportion of available resource types within typical foraging ranges (< 50 km; Shlepr 2017, Enners *et al*. 2018). Indeed, the availability of coastal resources is much lower at the offshore colony relative to the availability of seabird resources. Similarly, Enners *et al*. (2018) found that adult Herring Gulls breeding at colonies farther from the coast had higher δ^{13}C and δ^{15}N values. Although seabirds are considered high-quality prey for gulls (Gilliland *et al*. 2004), they may only become a primary prey in coastal Newfoundland when other food sources, such as capelin, are not highly available (Stenhouse & Montevecchi 1999, Massaro *et al*. 2000). The high availability of seabird eggs/chicks on Funk Island (~500 000 pairs of Common Murres; Wilhelm *et al*. 2015) may provide gulls with plentiful food resources to provision chicks farther from the coast. The importance of seabirds in the diet is supported by the presence of Common Murre chicks in three out of the four regurgitations of Herring Gull chicks raised at the offshore colony. Additionally, Herring Gulls are known to kleptoparasitize fish from alcids on foraging grounds or at colonies, when parental alcids return to feed their chicks with fish in their bills (Thompson 1986). Kleptoparasitizing fish could provide another highly

TABLE 2

Isotopic ratio and isotopic niche breadth among chicks and adults at multiple inshore colonies and one offshore colony

		δ^{13}C ‰			δ^{15}C ‰				
Colony location	**Species**[a]	**Mean**	**Std. dev.**		**Mean**	**Std. dev.**		**SEAc**[c]	**SEAb**[d]
Gull chicks									
Inshore	GBBG	-19.57	0.47	& [b]	14.4	0.49	& [b]	0.66	0.71
	HERG	-20.89	0.54	*	12.97	0.69	#	1.11	0.64
Offshore	GBBG	-19.83	0.33	& #	14.67	0.69	&	0.43	0.34
	HERG	-20.26	0.39	#	14.22	0.63	&	0.51	0.69
Adult Gulls									
Inshore	GBBG	-19.13	0.16	&	16.54	0.21	&	0.12	0.16
	HERG	-19.16	0.61	&	13.94	0.74	#	1.44	2.23

[a] GBBG = Great Black-backed Gull; HERG = Herring Gull

[b] Symbols refer to significant differences between factor levels, where different symbols indicate significant differences between two factor levels.

[c] SEAc = standard ellipse area corrected for small sample size

[d] SEAb = mode of the Bayesian standard ellipse area

available food source for gulls breeding offshore, which could explain the observed increase in trophic level in the assimilated diet. In contrast, seabird resources are much less available at inshore colonies, where inshore breeding pairs of alcids are far fewer (Wilhelm *et al*. 2015), possibly explaining the lower trophic position of inshore Herring Gull chicks. Additionally, Herring Gull chicks raised inshore had lower δ^{13}C values, consistent with a more terrestrial or intertidal diet (Hobson *et al*. 1994), which was further supported by regurgitations consisting primarily of prey found in the intertidal and terrestrial habitats (e.g., benthic invertebrates, terrestrial insects). Intertidal and terrestrial food resources are often the dominant prey types in Herring Gull diet (Ronconi *et al*. 2014, Shlepr 2017), especially in regions where availability of marine food resources is lower (O'Hanlon *et al*. 2017, Enners *et al*. 2018). Overall, our results support previous studies, where proximity to highly available food resources affects diet and foraging locations in Herring Gulls (O'Hanlon *et al*. 2017, Enners *et al*. 2018).

In contrast to Herring Gulls, Great Black-backed Gull chicks raised at both inshore and offshore colonies had similar δ^{13}C and δ^{15}N values, indicating dietary composition remained at similar trophic levels from similar habitats regardless of proximity to the coast (Hobson *et al*. 1994). This was expected, as Great Black-backed Gulls in Newfoundland appear to mainly feed on seabirds (Stenhouse & Montevecchi 1999, Massaro *et al*. 2000) or fish stolen from other seabirds (Veitch *et al*. 2016) and, thus, do not typically rely on coastal food sources. In contrast, diet studies from other regions of North America reveal that Great Black-backed Gulls feed mainly on large fish such as Atlantic herring (Gilliland *et al*. 2004, Steenweg *et al*. 2011) and frequently integrate coastal and inland prey (Ronconi *et al*. 2014, Maynard & Ronconi 2018). Interestingly, regurgitations of chicks raised inshore contained large fish species, likely from discarded lobster bait and Atlantic cod offal that are primarily available to gulls at wharfs or near-shore during fisheries activities. In contrast, chicks raised offshore primarily regurgitated seabird chicks and small pelagic fish that may have been kleptoparasitized from other seabirds. The similar trophic level occupied by these large fish and seabirds could explain the similar δ values of chicks raised at different colonies despite dietary differences. Values of δ^{13}C, however, differed among these prey types, possibly explaining the slight isotopic variation between colonies. Dietary differences were also supported by the slightly broader isotopic niche breadth of chicks raised inshore relative to offshore, indicating that a higher variety of prey types are used to provision chicks at the inshore colonies. Overall, these findings indicate that the diet of Great Black-backed Gull chicks is primarily composed of higher trophic level prey, but prey types may shift under varying availability within their foraging range.

Interspecies differences in isotopic niche breadth and δ^{15}N values was high for adults but minimal for chicks, especially at the offshore colony. Great Black-backed Gull adults showed lower trophic diversity and a higher trophic level isotopic composition (δ^{15}N) relative to adult Herring Gulls breeding at the same inshore colony, indicating that Great Black-backed Gulls have a more specialized diet of higher trophic level prey than Herring Gulls. As mentioned above, this was expected, as Great Black-backed Gulls rely less on coastal food sources (Good 1998) and typically feed at higher trophic levels (Steenweg *et al*. 2011, Westerberg *et al*. 2019). Differences in species-specific isotopic niche breadth of chicks was only evident at the offshore colony, which indicates that the trophic diversity provisioned to Herring Gull chicks is higher than that provisioned to Great Black-backed Gulls, as seen in adults. Interestingly, neither δ^{13}C nor δ^{15}N at the offshore colony reflected this interspecies difference. This is likely due to the increased incorporation of higher trophic level prey (i.e., seabirds, fish) by Herring Gulls, resources that they share with Great Black-backed Gulls. At the inshore colony, interspecies differences were evident in both higher δ^{13}C and δ^{15}N values in Great Black-backed Gull chicks relative to Herring Gull chicks. This supports the assumption that Great Black-backed Gulls do not incorporate coastal resources into their diet to the same extent as Herring Gulls, which is contrary to recent North American studies comparing the diet of both species (Steenweg *et al*. 2011, Ronconi *et al*. 2014). It also suggests dietary differences between species, and it is potentially indicative of dietary partitioning and reduced species interactions at inshore locations. As gulls are known dietary generalists at the population level (Pierotti & Good 1994, Good 1998), a similar broad variation in diet among individuals has been observed in other studies (Steenweg *et al.* 2011, Ronconi *et al*. 2014).

Overall, the δ^{13}C and δ^{15}N values and isotopic niche breadth of gull chicks differed between inshore and offshore colonies as well as between two sympatric species of large gulls, which resulted in smaller interspecies dietary difference at the offshore colony. In coastal Newfoundland, capelin used to be the main prey for Herring Gull chicks from hatching to fledging (Pierotti & Annett 1987). Since the crash in the Newfoundland capelin population during the early 1990s (Buren *et al*. 2019), our results indicate that Herring Gulls have diversified their diet to incorporate less capelin. However, further depletion in capelin could potentially increase interspecific competition for available resources within the foraging range. Investigating local variation in gull diets will be important for seabird and gull conservation and will inform region-specific gull management programs.

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