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SEASONAL AND AGE-DEPENDENT DIETARY PARTITIONING BETWEEN THE GREAT BLACK-BACKED AND HERRING GULLS

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Abstract. Studies of seabird diets may reveal subtle ways in which sympatric species partition resources to facilitate co-existence. We studied the variability and partitioning of diets between the Herring (*Larus argentatus*) and Great Black-backed Gulls (*L. marinus*), both generalist predators, during incubation and early chick rearing on Kent Island, Bay of Fundy, Canada. We assessed diets from pellets collected around nests, regurgitates from captured birds, and stable-isotope analysis of prey items and tissues (blood and feathers) obtained from chicks and adults. Pellet analyses indicated that both species relied primarily on fish (28 to 45% of identified prey items) and crabs (15 to 43%). Stable-isotope analyses showed that the Great Black-backed Gull fed at a higher trophic level than the Herring Gull, both species fed at higher trophic levels during breeding than during nonbreeding, and both species has similar preferences for feeding inshore vs. offshore and in terrestrial vs. marine habitats. Contrary to previous research, we found that chicks were fed from a lower trophic level than where adults feed. Models of isotopic mixing estimating the proportion of assimilated diets were generally consistent with the pellet analysis for adults but revealed that both species fed their chicks more krill (>60%; *Meganyctiphanes norvegica*) and mackerel (>20%; *Scomber scombrus*) than adults consumed; adults may selectively provision their young with easily digestible prey and prey of high energy content. Our results reveal evidence of dietary partitioning between species and age classes, and highlight the strengths and biases associated with techniques for sampling gulls' diet.

Key words: *diet, gull, niche partitioning, pellets, seabirds, stable isotopes.*

Partición de la Dieta Estacional y Dependiente de la Edad entre *Larus argentatus* y *L. marinus*

Resumen. Los estudios de las dietas de aves marinas pueden revelar formas sutiles de como especies simpátricas particionan los recursos para facilitar la coexistencia. Estudiamos la variabilidad y la partición de la dieta entre *Larus argentatus* y *L. marinus*, ambas especies depredadores generalistas, durante la incubación y el periodo inicial de cría de polluelos en la isla de Kent, Bahía de Fundy, Canadá. Evaluamos las dietas a partir de pellets recogidos alrededor de los nidos, regurgitados de las aves capturadas y del análisis de isótopos estables de las presas y de tejidos (sangre y plumas) obtenidos de polluelos y adultos. El análisis de pellets indicó que ambas especies basaron su dieta principalmente en pescado (28 a 45% de las presas identificadas) y cangrejos (15 a 43%). El análisis de isótopos estables mostró que *L. marinus* se alimentó en un nivel trófico más alto que *Larus argentatus*, que ambas especies se alimentaron en niveles tróficos más altos durante el periodo de cría que durante la época no reproductiva, y que las preferencias de ambas especies por alimentarse en alta mar o frente a la costa y entre hábitats marinos o terrestres son similares. Contrariamente a las investigaciones previas, se encontró que los polluelos fueron alimentados a partir de un nivel trófico más bajo del que se alimentan los adultos. Los modelos de mezcla isotópica que estiman la proporción de la dieta asimilada fueron en general consistentes con el análisis de pellets para los adultos, pero reveló que las dos especies alimentaron a sus polluelos con más kril (> 60%; *Meganyctiphanes norvegica*) y caballa (> 20%; *Scomber scombrus*) de lo que consumen los adultos. Los adultos podrían estar aprovisionando selectivamente a sus crías con presas fáciles de digerir y con presas de alto contenido energético. Nuestros resultados revelan evidencia de una partición en la dieta entre las especies y clases de edad, y resaltan los puntos fuertes y los sesgos asociados a las técnicas para muestrear la dieta de gaviotas.

INTRODUCTION

Seabirds often nest in mixed-species colonies (Rock et al. 2007) and forage at sea in mixed flocks (Chilton and Sealy 1987, Camphuysen and Webb 1999), raising fundamental ecological questions regarding niche partitioning, competition, and co-existence (e.g., Garthe et al. 1999, Ronconi and Burger 2011). Studies of dietary choice offer insight into ways in which sympatric species may partition resources to facilitate co-existence. During conditions of changing food supply, generalist seabirds, such as gulls (family Laridae), show flexibility in niche width, which can contribute to the co-existence of competing species that rely on shared resources (González-Solís et al. 1997). The Herring (*Larus argentatus*) and Great Black-backed Gulls (*L. marinus*) are generalist predators

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and widely distributed along the coasts of the North Atlantic Ocean, offering opportunities for investigation of dietary-niche partitioning by co-existing predators.

Great Black-backed and Herring Gulls often nest sympatrically in eastern Canada (e.g., Ronconi and Wong 2003), are among the most abundant and conspicuous breeding seabirds of the region (Chapdelaine 1995), and have similar diets, predominantly of fish, fishery offal, marine invertebrates, other birds, and refuse (Pierotti and Good 1994, Good 1998). However, some studies have revealed subtle differences between these species' diets. Comparisons of their feeding habits and prey preferences suggest that the larger Great Black-backed Gull has a competitive advantage in foraging and obtaining preferred prey items over the smaller Herring Gull (Hunt and Hunt 1973, Greig et al. 1986, Hudson and Furness 1988, Rome and Ellis 2004). Great Black-backed Gulls, more so than Herring Gulls, are also known to prey on other smaller seabirds or seabird chicks (Mawhinney and Diamond 1999, Gilliland et al. 2004); a difference that increased following a decline in fishery discards (Russell and Montevecchi 1996, Stenhouse and Montevecchi 1999, Votier et al. 2004). Thus prey choice seems to be a likely means of niche partitioning between these co-nesting species.

Temporal and age-related variability in diet may also function as a means of niche partitioning. These co-nesting species vary their diet by season and year (González-Solís et al. 1997, Houston et al. 1983, Lindsay and Meathrel 2008, McLellan and Shutler 2009); self- and chick-provisioning also differ (Annett and Pierotti 1989, Garthe et al. 1999). Adults may partition their diet from what they feed their chicks to reduce competition for similar resources.

In addition to dietary partitioning, studies investigating the spatial and temporal variability in gull diets may reveal mechanisms associated with population trends. Prey choices and changes in food supply may, in part, be responsible for trends of the Herring and Great Black-backed Gulls' populations in eastern Canada. Throughout Atlantic Canada, gull populations, particularly of the Herring Gull, declined through the 1970s and 1980s (Hebert 1989, Chapdelaine 1995, Mawhinney et al. 1999, Boyne and McKnight 2004). These declines are thought to be in response to decreases in the abundance of fishery discards, closing of open landfills, or declines in the availability of schooling fish (Robertson et al. 2001, Boyne and Beukens 2004). Recently, however, some populations of gulls have been stable or increasing (Ronconi and Wong 2003, Boyne et al. 2006). The reasons for these recent population increases remain unknown, but changes in the availability of natural prey may be a contributing factor because local fisheries' discard rates are unlikely to have changed in recent years.

Several techniques can be used to determine gull diets. Pellet analyses examine regurgitated pellets of hard indigestible tissues of prey gathered from nests. Although pellet analysis is valuable as a noninvasive tool to assess diet, it is biased toward indigestible, identifiable parts and it does not account for prey eaten away from the nest (Votier et al. 2003, Lindsay and Meathrel 2008). A second method, stable-isotope analysis of predators' body tissues, measures $\delta^{15}N$ as an indicator of the trophic level at which a species is feeding and $\delta^{13}C$ as an indicator of inshore or offshore feeding habits as well as marine vs. terrestrial preferences (Hobson et al. 1994, Hobson and Wassenaar 1999, Knoff et al. 2002). Stable isotopes can also be used to model the contribution of different prey items in animal diets (Phillips and Gregg 2003). Moreover, different tissue types (i.e., blood and various feathers) can reflect a predator's diet at different times. Understanding temporal and age-dependent variability in stable-isotope signatures by tissue type is important to the study of dietary niche partitioning for these species.

We used analyses of regurgitated food pellets and stable-isotope analyses to answer three main questions: (1) what are the main components of and species-specific differences in Herring Gull and Great Black-backed Gull diets, (2) what are the differences in diet between age classes (adults vs. chicks), and (3) how does adults' diet vary by stage of the life cycle (nonbreeding, incubating, and chick-tending)? The Great Black-backed and Herring Gulls are widely distributed along the coasts of the North Atlantic, and both are easily sampled simultaneously from mixed-species nesting colonies. The goal of our study was to examine the intra- and inter-seasonal variability in diets of Herring and Great Black-backed Gulls nesting together during one year in the Bay of Fundy, Canada.

METHODS

STUDY SITE

Our study took place on Kent Island (44.58° N, 66.75° W) in the Grand Manan archipelago of the lower Bay of Fundy, New Brunswick, Canada, from 25 May until 7 July 2009. Kent is one of the largest seabird-breeding colonies in the region and is home to a colony of Herring Gulls (n = 5926 pairs), Great Black-backed Gulls (n = 23 pairs), Common Eiders (*Somateria mollissima*; n = 480 pairs), and several other seabird species (see Ronconi and Wong 2003 for more information on the study site). Average daily tidal flux around Kent is about 4.5 m (maximum over 6.5 m), providing gulls with ample opportunity for intertidal foraging. During incubation, Herring Gulls, tracked by satellite tags from Kent, forage at distances typically from 6 to 20 km but also up to 30 km south into the open ocean and 80 km southeast to mainland Nova Scotia (R. A. Ronconi, unpubl. data).

BIRD CAPTURE AND TISSUE SAMPLING

To collect tissues for isotope analyses, we trapped 38 adult Herring Gulls and 12 Great Black-backed Gulls during late incubation by setting square traps over their nests. We selected Herring Gull nests haphazardly from multiple locations around the island; we sampled all accessible Great Black-backed Gull

nests on Kent Island plus a few on neighboring Sheep Island. To prevent damage to eggs during trapping, we replaced eggs with wooden dummies. We banded each bird with U.S. Fish and Wildlife Service metal bands and made the following measurements: mass, tarsus length, culmen, bill depth at gonydeal angle (where the bill is deepest), total head–bill length, and wing chord. While captured, 11 Herring Gulls and 4 Great Black-backed Gulls regurgitated recent meals, which we collected and stored frozen for further identification.

Isotopic signatures from tissues containing keratin such as feathers, nails, and hair reflect the diet of the organism when that tissue was grown (Cherel et al. 2005), whereas signatures from blood reflect food assimilated over the previous 12–15 days (Hobson and Clark 1993). We collected ~2 cm from the tip of a newly grown primary (P1 to P3) and five contour feathers from the back of the head of each captured bird. The Herring and Great Black-backed Gulls molt their primaries during the spring breeding season (May–June) and head feathers in the winter (January–April; Ginn and Melville 1983), so isotope analysis of these tissues represents diets during the breeding (specifically incubation) and nonbreeding seasons. We confirmed that primary feathers were growing at the time of capture by scoring the state of individual feathers on a scale of 0 to 5, with 0 indicating old/worn feathers (i.e., previous year's molt), 1 the stub of a new feather, and 5 a fully grown new feather (as per Ginn and Melville 1983). Mean scores for newly grown P1, P2, and P3 were 2.0, 1.7, 0.2 for the Herring and 2.0, 1.6, 0.1 for the Great Black-backed, respectively, indicating that feathers were indeed growing at the time of sampling and thus reflecting diet during the incubation period. After breeding, from late July to early September, Herring Gulls from this region migrate to Chesapeake Bay, approximately 1000 km southwest of the Bay of Fundy (R. A. Ronconi, unpubl. data) but Great Black-backed Gulls are thought to be resident in Atlantic Canada year round (Good 1998, Farmer and Leonard 2011), so feathers from the head, molted in winter, should reflect diets at these locations. We also collected ~5 mL of blood from the brachial vein. The blood was kept on ice packs in the field for up to 4 hr, then centrifuged for 10 min to separate blood into plasma and compact red blood cells, which were stored frozen until further analysis. Blood samples collected during incubation reflect the most recent diet and should show isotopic signatures similar to those of the newly molted primaries.

When chicks were at least 2 weeks old, we captured one chick from each of 12 haphazardly selected Herring and Great Black-backed Gull nests on the island. The protocol for measuring and collecting tissue samples was identical to that for the adults, except we took feather samples only from primary feathers because head feathers were grown simultaneously and thus did not provide a "winter" signature and we collected only 1 mL of blood. We sampled the tip of the wing feather rather than feathers from the head because chicks' head feathers were not fully grown at the time of sampling.

COLLECTION OF PELLETS AND PREY SAMPLES

Beginning in early incubation for the Herring (30 May) and hatching for the Great Black-backed (26 May), and continuing each week until 5 July, we collected pellets from each of 36 haphazardly selected Herring Gull nests (n = 53 pellets, average 10 per week) and all nine Great Black-backed Gull nests that contained pellets (n = 32 pellets, average 5 per week). Many (n = 29) Herring Gull nests contained pellets only once, while the rest were sampled two or three times. All Great Black-backed Gull nests were sampled two to five times. Additionally, we collected five Herring and four Great Black-backed Gull pellet samples opportunistically from captured adults, and we collected four Herring and three Great Black-backed Gull pellet samples opportunistically from empty nests, while the rest were from the weekly nest checks.

Pellets were taken from within 30 cm of each nest so should be pellets regurgitated by the adults at that nest. During the first week of collection, we cleared nests of all pellets and thereafter collected any pellet within 30 cm of each nest. This ensured that each week of collection corresponded to the previous week of prey consumption. Pellet samples were stored frozen until further identification in the lab.

Using field guides and consulting with experts, we identified prey items found in the pellets to the lowest taxonomic level possible. We assigned prey items to categories (see Table 1 for complete list) and recorded the number that fell into each category. For each nest sample, we considered the total prey count to include individual items that could be uniquely identified (e.g., maximum number of crab shells or right claws), such as items of the same prey type from different pellets (i.e., fish from two pellets = 2) and individual items that could be identified within each pellet (i.e., bones from two fish species or four otoliths of one species = two fish each). Sometimes we considered multiple items of the same prey type (e.g., fish bones) as single records because, for instance, it was impossible to know how many fish were contained in a particular pellet. Generally, it was not possible to determine the number of individual fish from the remnants collected from nests or individual pellets, so the proportion of fish may be underestimated in diets. We collected pellets throughout the incubation period, enabling comparison with dietary composition derived from stable-isotope analysis (below).

We also collected samples of the following prey items to provide a reference dataset for stable-isotope mixing models (see Data Analysis below): one Jonah crab (*Cancer borealis*) one rock crab (*C. irroratus*), seven mussels (*Mytiloida* sp.), and six sea urchins (*Echinoida* sp.) from intertidal areas around Grand Manan and 13 northern krill (*Meganyctiphanes norvegica*) from plankton tows in the middle of the Bay of Fundy. We also included isotope values from 7 Atlantic mackerel (*Scomber scombrus*) and 115 Atlantic herring (*Clupea harengus*) collected during previous summers (2005–2009; Ronconi et al. 2010).

TABLE 1. Proportions of prey items found in pellets gathered from nests and in regurgitation samples of Herring and Great Black-backed Gulls during chick rearing and early incubation, 2009, on Kent Island, New Brunswick, Canada. Regurgitates were collected opportunistically during captures of adults.

	Herring Gull		Great Black-backed Gull	
Prey	Pellets (n = 53)	Regurgitates (n = 11)	Pellets (n = 32)	Regurgitates (n = 4)
Fish				
Herring (*Clupea harengus*)	0.04	0.36		
Mackerel (*Scomber scombrus*)				0.25
Sculpin (Scorpaeniformes sp.)			0.06	0.25
Lumpfish (*Cyclopterus lumpus*)				0.25
Unidentified fish	0.40	0.18	0.22	0.25
Marine invertebrates				
Jonah crab (*Cancer borealis*)	0.14	0.09	0.42	
Mussel (*Mytiloida* sp.)	0.09		0.01	
Urchin (*Echinoida* sp.)	0.06		0.04	
Shrimp (species unknown)		0.09		
Krill (*Meganyctiphanes norvegica*)		0.09		
Sandworm (*Nereis virens*)	0.06			
Periwinkle (Littorinidae sp.)	0.04			
Unidentified marine invertebrate	0.01			
Mammals				
Muskrat (*Ondatra zibethicus*)	0.04		0.01	
Unidentified mammal	0.01		0.06	
Birds				
Songbird	0.03			
Gull chick	0.01		0.03	
Common Eider (*Somateria mollissima*), adult			0.01	
Eider duckling			0.03	
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	0.01			
Unidentified bird	0.01	0.09	0.06	
Terrestrial invertebrates and other				
Sand flies (Diptera sp.)		0.09		
June bugs (*Phyllophaga* sp.)			0.01	
Chicken bones	0.01		0.03	
Vegetation	0.01			

LAB METHODS

In preparation for stable-isotope analysis, all prey and blood samples were dried in an oven at 38 ºC for 24 hr. Before being dried, digestible parts of each prey item were ground into a homogeneous paste. For blood, red blood cells and whole-blood samples were dried on glass-fiber filter papers (Whatman International, Maidstone, UK). We removed lipids from all prey items and feathers by soaking them in a 2:1 chloroform–methanol solution for 24 hr, then rinsing them again with fresh solution (as per Cherel et al. 2005). If some items were not adequately dried and cleaned with this procedure, they were dried, soaked, and rinsed again. Following drying, we ground each prey item into a powder with a mortar and pestle to prepare a homogeneous mixture for stable-isotope analysis.

Subsamples of ~0.250 mg of each prey item and tissue samples were weighed on a microbalance (Sartorius) and folded in a tin capsule. The Environmental Isotope Lab, University of Waterloo, analyzed the samples for ^{13}C and ^{15}N, determining their abundance ($\delta^{13}C$ and $\delta^{15}N$) in the sample in comparison to a standard as ${}^{n}X(‰) = [(R_{sample} - R_{standard})/R_{standard}) \times 1000$. (Knoff et al. 2002). Given that $\delta^{13}C$ and $\delta^{15}N$ change in predictable ways when consumers eat their prey, average isotope-fractionation values (i.e., the change in $\delta^{13}C$ and $\delta^{15}N$ between prey and consumer) are important to the interpretation of results and the development of isotopic-mixing models (below). From controlled experiments (Cherel et al. 2005, Becker et al. 2007, Williams et al. 2007), we calculated the average value of fractionation between prey and whole blood (n = 5) to be +2.75 for ^{15}N and –0.06 for ^{13}C and that between prey and feathers (n = 13) to be +4.14 for ^{15}N and +1.16 for ^{13}C.

STATISTICAL ANALYSES

Because sample sizes were unequal, we used general linear model ANOVAs (SPSS 15.0) to determine differences between the species (Great Black-backed and Herring Gulls), age groups (adult and chick), and breeding stages (breeding, primary feathers; nonbreeding, head feathers) in $\delta^{15}N$ and $\delta^{13}C$ from various tissues (primary and head feathers; red blood cells). Thus we tested the following models (Table 2) for tissues of (1) red blood cells (species, age, species × age interaction), (2) primary feathers (species, age, species × age), (3) both feathers (species, breeding stage, species × breeding stage). We assessed the differences between the species for head feathers with t tests. We used linear regression to assess within-season shifts in the Herring Gull's diet, which was possible because we collected blood over an extended period during incubation (26 May–30 June). We could not assess seasonal trends in the Great Black-backed Gull's diet because we captured that species over 6 days only (28 May–2 June).

To estimate diet composition from stable-isotope values, we used dual-isotope, multi-source mixing models (IsoSource version 1.3, as per Phillips and Gregg 2003). We selected IsoSource mixing models over other available modeling packages because comparisons of model types showed similar results for seabird diets estimated with similar prey types from the Bay of Fundy (Ronconi et al. 2010). These models require inputs of average isotope signatures in prey (Table 3) and, in predators, average signatures that have been adjusted for blood–prey fractionation values (see Lab Methods above).

TABLE 2. Results of general linear models testing the effects of species (Great Black-backed Gull [GBBG] vs. Herring Gull [HERG]), age (adult vs. chick), and breeding stage (breeding vs. nonbreeding) on difference in gull diets inferred from stable-isotope signatures. Primary feathers and head feathers used as proxies for diet during the breeding and nonbreeding periods, respectively.

Tissue type	Model and variables	Isotope	df	*F*	*P*	Interpretation
Blood	model	$\delta^{13}C$	3,69	7.23	<0.001	
		$\delta^{15}N$	3,69	15.71	<0.001	
	species	$\delta^{13}C$	1	0.42	0.52	
		$\delta^{15}N$	1	14.17	<0.001	GBBG > HERG
	age	$\delta^{13}C$	1	20.25	<0.001	adult > chick
		$\delta^{15}N$	1	35.56	<0.001	adult > chick
	species × age	$\delta^{13}C$	1	0.12	0.73	
		$\delta^{15}N$	1	0.08	0.78	
Primary feathers	model	$\delta^{13}C$	3,50	5.22	<0.01	
		$\delta^{15}N$	3,50	22.84	<0.001	
	species	$\delta^{13}C$	1	2.36	0.13	
		$\delta^{15}N$	1	17.35	<0.001	GBBG > HERG
	age	$\delta^{13}C$	1	14.80	<0.001	adult > chick
		$\delta^{15}N$	1	56.42	<0.001	adult > chick
	species × age	$\delta^{13}C$	1	0.38	0.54	
		$\delta^{15}N$	1	0.02	0.90	
Feathers (both primaries and head)	model	$\delta^{13}C$	3,77	0.71	0.55	
		$\delta^{15}N$	3,77	19.29	<0.001	
	species	$\delta^{13}C$	1	1.94	0.17	
		$\delta^{15}N$	1	11.63	0.001	GBBG > HERG
	breeding stage	$\delta^{13}C$	1	0.32	0.58	
		$\delta^{15}N$	1	25.23	<0.001	breeding > nonbreeding
	species × breeding stage	$\delta^{13}C$	1	0.49	0.48	
		$\delta^{15}N$	1	2.22	0.14	

TABLE 3. Stable-isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of selected prey items used in isotope mixing models. Data from herring and mackerel are from Ronconi et al. (2010). All other samples were collected in 2009.

Prey Item	*n*	$\delta^{13}C$ (SD)	$\delta^{15}N$ (SD)
Urchin (*Echinoida* sp.)	6	–15.9 (0.3)	4.9 (0.2)
Mussel (*Mytiloida* sp.)	6	–17.9 (0.2)	6.0 (0.2)
Krill (*Meganyctiphanes norvegica*)	13	–18.6 (0.6)	7.9 (0.6)
Crab (*Cancer borealis* and *C. irroratus*)	2	–17.1 (0.4)	9.1 (0.2)
Herring (*Clupea harengus*)	115	–18.5 (0.8)	11.7 (0.8)
Mackerel (*Scomber scombrus*)	7	–19.3 (0.5)	12.7 (0.3)

We used post-hoc comparisons to assess whether each prey item differed from each other item in values of at least one of the two isotopes. Good separation in the isotopic signatures of prey is important for the estimation of diets with mixing models. We developed mixing models for adults and chicks of both the Herring and Great Black-backed Gulls separately. Moreover, because Herring Gulls were sampled over 36 days, and isotope in blood turn over about every 12–15 days (Hobson and Clark 1993), we subdivided the Herring Gull samples into two periods: early to mid-incubation (26 May–10 June) and late incubation (13–30 June). This subdivision allowed for further assessment of dietary shifts within the season and comparison with pellet samples collected synoptically.

RESULTS

STABLE-ISOTOPE SIGNATURES AND MIXING MODELS

Overall, general linear models (Table 2) showed significant differences in $\delta^{15}N$ for all tissue types (for all models, $P < 0.001$; Fig. 1a), suggesting differences in trophic level by species, age class, and breeding status. Levels of $\delta^{15}N$ were significantly higher for adult Great Black-backed Gulls than for adult Herring Gulls in blood tissue ($P < 0.001$), primaries ($P < 0.001$), and head feathers ($t = 3.24$, d.f. = 47, $P = 0.002$). Higher values of $\delta^{15}N$ in the Great Black-backed Gull were

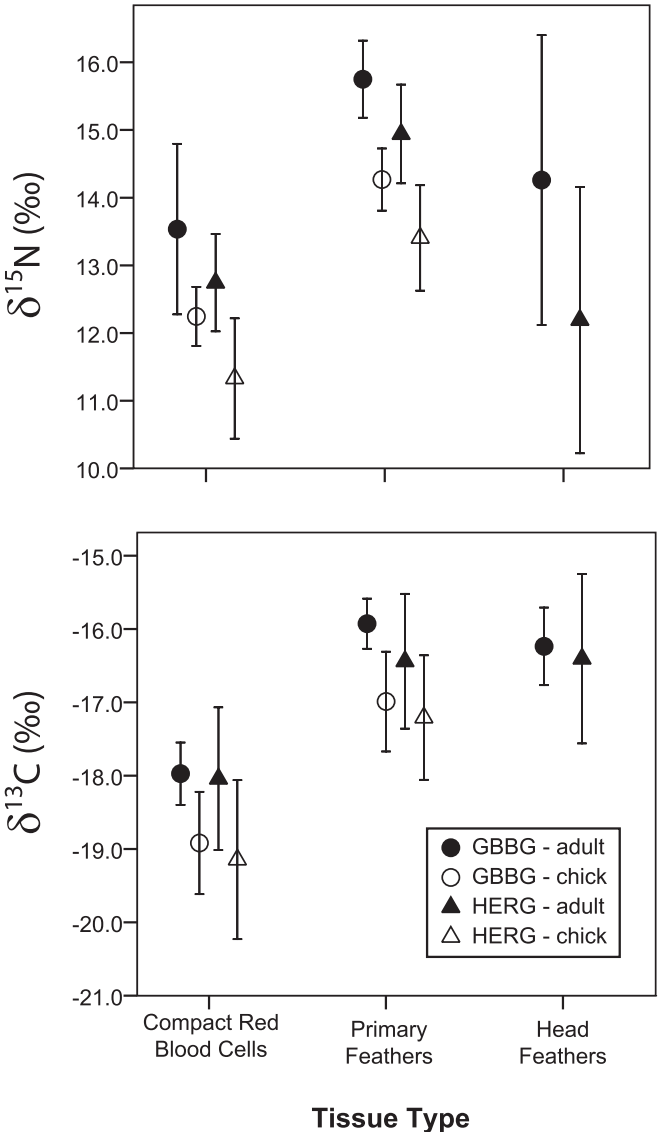

FIGURE 1. Variability in stable-isotope signatures (mean ± SE) from various tissues of adults and chicks of the Great Black-backed Gull (GBBG) and Herring Gull (HERG).

consistent for both adults and chicks, as indicated by the nonsignificant age × species interaction (Table 2) for both primaries ($P = 0.896$) and red blood cells ($P = 0.785$). Adults of both species had levels of $\delta^{15}N$ significantly higher than those of the chicks (age effect, $P < 0.001$; Table 2). Finally, comparison of head and primary feathers revealed dietary differences by breeding stage; $\delta^{15}N$ values were higher during breeding than during nonbreeding periods (primary vs. head feathers, respectively; $P < 0.001$). The direction of the seasonal effect—higher $\delta^{15}N$ values during breeding—was consistent for both species (species × breeding stage, $P = 0.140$; Fig. 1).

For $\delta^{13}C$ values, models (Table 2) found significant effects of predictor variables on some tissues (red blood cells and primary feathers, both $P < 0.001$; Fig. 1) but not on others (head feathers or head vs. primary feathers, $P = 0.551$). There were no significant differences in $\delta^{13}C$ between the species for any tissue (species effect, Table 2), including head feathers ($t = 0.52$, d.f. = 47, $P = 0.603$). Breeding stage also had no effect on $\delta^{13}C$ levels ($P = 0.576$). Age class was the only significant predictor of $\delta^{13}C$ levels, $\delta^{13}C$ being higher for adults than for chicks of both species in both primary feathers and blood samples (both $P < 0.001$).

We tested for changes in stable isotopes within the breeding season, from early to late incubation, only in the Herring Gull (see above). In red blood cells, $\delta^{15}N$ levels did not change significantly ($r^2 = 0.278$, $P = 0.24$; Fig. 2), but $\delta^{13}C$ levels decreased through the incubation period ($r^2 = 0.432$, $P = 0.001$; Fig. 2).

Both $\delta^{15}N$ and $\delta^{13}C$ varied significantly by prey item (ANOVA: $\delta^{15}N$, $F_{5,143} = 194.5$, $P < 0.001$; $\delta^{13}C$, $F_{5,143} = 19.58$, $P < 0.001$; Table 3). Post-hoc comparisons showed that each prey item differed from each other item in at least one of the two stable-isotope values.

Mixing models of prey contributions to Herring Gull diets estimated that herring (31% of diet) and mackerel (18%) were the primary prey consumed by adults, that krill (67%) and mackerel (20%) were the primary prey items for chicks (Table 4). For the Great Black-backed Gull, they estimated that herring (54%) and crab (30%) were present in the highest proportions for adults, while, as for the Herring Gull, that krill (61%) and mackerel (34%) were the primary prey items for chicks (Table 4). For adult Herring Gulls, the models also implied a marked change in diet between the early/mid and late incubation periods (Table 4), with crab consumption decreasing from 64% to 10% and mackerel consumption increasing from 8% to 32%.

PELLET AND REGURGITATION SAMPLES

Pellets collected from Herring Gull nests contained an average of 1.3 (SD 0.7) prey items per pellet, those from Great Black-backed Gull nests an average of 2.4 (SD 1.3) prey items per pellet. The dominant food items found in Herring Gull pellets were fish (45% of prey items), crabs (15%), and other marine invertebrates (12%), and the dominant prey in their regurgitates ($n = 11$) was herring (Table 1). Similarly, the dominant prey types found in Great Black-backed Gull pellets were crabs (43%) and fish (28%) but also birds (15%; Table 1). Regurgitates ($n = 4$) contained an equal amount of herring, mackerel, lumpfish (*Cyclopterus lumpus*), and an unidentified fish (Table 1). Fish constituted 100% of Herring Gull diets during early incubation but then decreased each week thereafter to a low of 13% during the final week of sampling. The percentages of crabs and mammals in the diet increased over this time (Table 5). For the Great Black-backed Gull, weekly pellet samples were dominated by fish (20–40%) and crab (29–55%; Table 5) with little evidence of seasonal trends.

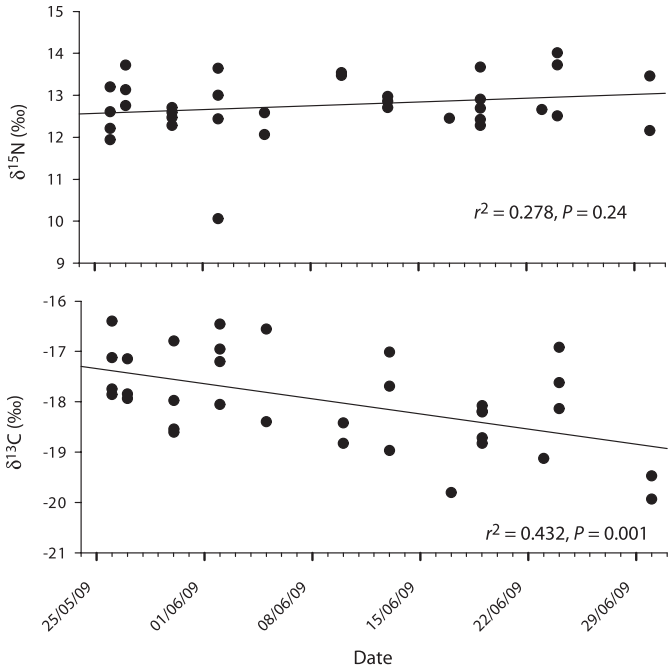

FIGURE 2. Changes in stable-isotope values in Herring Gull blood collected during the incubation period at Kent Island, New Brunswick, Canada.

DISCUSSION

DIFFERENCES BETWEEN SPECIES AND AGE CLASSES

Stable-isotope analyses provide indices of assimilated diets that are easily compared, without biases, by age class and species (Williams et al. 2008, Ronconi et al. 2010). Elevated $\delta^{15}N$ values in all sampled tissues of Great Black-backed Gulls indicated that this species fed at a trophic level consistently higher than that of Herring Gulls both in provisioning themselves and their young, during both the breeding and nonbreeding seasons. These results are consistent with other diet and behavioral studies showing that the Great Black-backed is the dominant species at gull colonies (Hunt and Hunt 1973, Greig et al. 1986), outcompeting the Herring Gull and forcing it to feed at a lower trophic level (Rome and Ellis 2004). This inference assumes, however, that prey from a higher trophic level is of better quality and is preferred by Herring Gulls, which may not always be the case. There may also be trade-offs between energy content and handling time (Brodman and Reyer 1999). For example, the long handling times of "shelled" prey may make these less desirable prey items depending on how easily they are found. This trade-off may explain why the presumably dominant Great Black-backed Gull consumes fewer mussels and urchins (this study) and selects larger crabs (Rome and Ellis 2004) than does the Herring Gull. Together these results suggest ways in which these species partition diets; however, the overlap between adult Herring Gulls' diet and Great Black-backed Gull chicks' diet (Fig. 1) still suggests some potential for competition.

In contrast to the results for $\delta^{15}N$, we found no significant difference in $\delta^{13}C$ levels between the species, suggesting that adult Herring and Great Black-backed Gulls feed at similar distances from shore, likely a result of both species being generalist predators that take advantage of offshore and coastal prey in similar proportions. This is evident from the error bars for blood (Fig. 1), which span the $\delta^{13}C$ values of coastal (crabs, –17.1; mussels, –17.9) and offshore prey (krill, –18.6; herring, –18.5; mackerel, –19.1). The similarity in $\delta^{13}C$ values may also indicate a consistently marine diet and lack of terrestrial food sources for both species. In the 1980s and 1990s, at other local colonies closer to the mainland, gulls consumed human refuse (Gilliland et al. 2004, Rome and Ellis 2004), but we found little indication of human refuse in their current diets at Kent Island. Long-term trends in $\delta^{13}C$ values for the Great Black-backed Gull show no clear evidence of shifts between terrestrial or offshore foraging habits (Farmer and Leonard 2011), suggesting that coastal foraging is likely the norm for this species in Atlantic Canada.

TABLE 4. Estimated proportion of prey types in diets of adults and chicks of the Herring and Great Black-backed Gulls during incubation and early chick rearing, 2009, on Kent Island, New Brunswick, Canada. Adult Herring Gulls' diet is also divided into early (26 May–10 June) and late incubation (13–30 June). Values are means ± SD derived from dual-source isotope mixing models (IsoSource 1.3; Phillips and Gregg 2003). See Table 3 for scientific names of prey types.

	Herring Gull				Great Black-backed Gull	
	Adult					
Prey type	Overall	Early incubation	Late incubation	Chick	Adult	Chick
Mussel	0.04 ± 0.03	0.01 ± 0.01	0.10 ± 0.07	0.09 ± 0.08	0 ± 0	0.03 ± 0.03
Urchin	0.10 ± 0.07	0.02 ± 0.02	0.07 ± 0.05	0	0.02 ± 0.03	0
Crab	0.10 ± 0.14	0.64 ± 0.06	0.11 ± 0.08	0	0.30 ± 0.09	0
Herring	0.31 ± 0.18	0.24 ± 0.10	0.26 ± 0.18	0.04 ± 0.04	0.54 ± 0.17	0.02 ± 0.02
Krill	0.05 ± 0.04	0.01 ± 0.01	0.14 ± 0.09	0.67 ± 0.13	0.01 ± 0.01	0.61 ± 0.04
Mackerel	0.18 ± 0.12	0.08 ± 0.07	0.32 ± 0.15	0.20 ± 0.06	0.12 ± 0.11	0.34 ± 0.02

TABLE 5. Intraseasonal variation in prey remains found in pellets of the Herring and Great Black-backed Gulls during incubation and early chick rearing on Kent Island, 2009. Values are percentages of prey items in pellets; *n* = number of pellets collected in each interval.

	Herring Gull				Great Black-backed Gull				
	30 May–2 Jun (*n* = 4)	5–9 Jun (*n* = 21)	15–19 Jun (*n* = 18)	28–30 Jun (*n* = 8)	26 May–2 Jun (*n* = 6)	8–9 Jun (*n* = 7)	15 Jun (*n* = 6)	22–23 Jun (*n* = 5)	28 Jun (*n*=6)
Crab	0	13	12	38	47	40	50	29	56
Mussel	0	3	19	0	0	0	0	6	0
Urchin	0	7	8	0	13	0	0	6	0
Fish	100	53	38	13	20	40	25	29	22
Other marine invertebrate	0	1	15	13	0	0	0	0	0
Terrestrial invertebrate	0	0	0	0	0	7	0	0	0
Mammal	0	3	4	25	7	0	8	12	11
Bird	0	10	4	13	13	13	17	18	11

Chicks of both species had $\delta^{15}N$ and $\delta^{13}C$ levels lower than those of adults, suggesting that chicks are fed prey items different from and from a lower trophic level than those adults eat. These results are not consistent with work on other seabird species, which found adults feeding their chicks from the same (Williams et al. 2008) or higher (Hobson 1993, Schmutz and Hobson 1998) trophic level than that at which they feed themselves. The differences between adult consumption and chick provisioning may also reflect trade-offs between food quality, handling time, and digestibility. Krill, for example, have relatively high energy content per unit weight (Brown et al. 1981, Gilliland et al. 2004), but the time required to catch sufficiently large quantities of krill may also be high. Nevertheless, the high digestibility of this soft-bodied prey may make it desirable as food for gull chicks (Gilliland et al. 2004; this study). The tendency of gulls to provision young with foods of higher lipid and energy content (Pierotti and Annett 1987, Annett and Pierotti 1989, Garthe et al. 1999) may also explain the high proportion of mackerel in estimates of chicks' diet. The complete lack of crabs in chick diets estimated by the mixing models (see also Gilliland et al. 2004) suggest the low importance of this prey item, likely due to low energy content and difficulty of handling and digestion for young. Adults may also partition their diet from their chicks' to reduce competition for resources between adults and their young. Regardless of differences between gull species or trade-offs associated with prey choice for young, in 2009 there was no evidence of food limitation at this colony since we observed very few starved or abandoned chicks.

VARIABILITY BETWEEN BREEDING STAGES

For both species, levels of $\delta^{15}N$ increased from the nonbreeding to the breeding season, indicating that the birds were feeding at higher trophic levels during incubation (spring) than during the winter. This result is consistent with previous work showing that breeding seabirds feed on prey from trophic levels higher than do nonbreeding birds (Hobson 1993). Gulls' diet may change seasonally because of changes in food availability and/or because of differences in energy requirements by breeding stage. During winter, intertidal prey, typically lower in $\delta^{15}N$, are more common in gull diets (Annett and Pierotti 1989), which may explain the lower $\delta^{15}N$ levels of gulls during winter when they are away from their offshore breeding grounds (Pierotti and Good 1994).

In contrast, $\delta^{13}C$ did not differ between the incubation period and winter. When breeding, gulls are central-place foragers, so their movements and diets are inextricably tied to coasts near nesting colonies. The lack of change in $\delta^{13}C$ during nonbreeding periods suggests that both species remained coastal and neither species wintered exclusively offshore or inland. Fitting of Herring Gulls from Kent Island with satellite tags confirms that the birds typically forage within 20 km of the colony during incubation and chick rearing and migrate to the coastal waters of Chesapeake Bay in the winter (R. A. Ronconi, unpubl.data). Their prey choices during this time are unknown, but they may feed on inshore fish with low $\delta^{15}N$ values. The movements of Great Black-backed Gulls from Kent Island remain unknown but that species is likely resident in Atlantic Canada year round (Farmer and Leonard 2011) and is frequently sighted in coastal areas.

MAIN COMPONENTS OF DIET AND BIASES OF SAMPLING TECHNIQUE

Pellet analyses showed that fish were a consistently prevalent prey of both species. The proportion of fish in Herring Gull pellets declined from a peak of 100% during nest building and early incubation to a low of 12% by hatching. In contrast, the proportion of fish in Great Black-backed Gull pellets remained high from late incubation through to hatching**.** Pellet analyses also indicated that crab was prevalent in the diet of both species, particularly the Great Black-backed Gull. In Maine, Rome and Ellis (2004) found that crabs were the dominant prey in pellets of both species, but the proportion of fish was higher for the Great Black-backed than for the Herring Gull. Thus for pellets the results of these two studies are consistent,

suggesting that direct comparisons of pellets among colonies and regions may be widely applicable.

Detected in pellets, birds of various species that nest on the island made up a small but consistent contribution to the diets of both gulls. They included gull chicks, Leach's Storm-Petrels (*Oceanodroma leucorhoa*), passerines (likely Savannah Sparrows, *Passerculus sandwichensis*, the most abundant passerine on the island; predation of Savannah Sparrows, by both gulls has been previously observed by other researchers), and Common Eider ducklings. Likewise, Gilliland et al. (2004) found that eider ducklings made up a small (<1%) but consistent proportion of the diet of Great Black-backed Gull chicks in the Bay of Fundy. At a colony of 350 pairs of Great Black-backed Gulls, Gilliland et al. (2004) estimated that 147 ducklings were fed to chicks and extrapolated (from chick diets) that 775 ducklings were consumed by adults during the breeding season of 1989. This equates to ~2.5 ducklings depredated per gull pair but is almost certainly an overestimate since our study demonstrated that adults' and chicks' diets differ significantly. Nevertheless, there remains concern that Great Black-backed Gulls may reduce eider recruitment by consuming a large quantity of ducklings (Mawhinney and Diamond 1999), particularly as gull populations increase (Mawhinney et al. 1999). Large gulls may feed on small seabirds more readily when other prey sources become scarce (Russell and Montevecchi 1996, Stenhouse and Montevecchi 1999, Votier et al. 2004), so continued monitoring of gull diets for avian prey may be an important tool for detecting broad-scale changes in the prey base of marine ecosystems.

Although collected pellets and other prey remains may reflect seabird diets generally (Pierotti and Annett 1990), there are still inherent biases with this approach since they do not represent assimilated food and they are biased toward prey of low digestibility (Votier et al. 2003). By synoptically sampling pellets concurrently with sampling the blood used for stable-isotope mixing models, we are able to compare the techniques. The results from pellets and isotopes were broadly consistent, both showing crab and fish to be the dominant prey types. However, the seasonal mixing models for the Herring Gull showed an increase in fish and a decrease in crab toward late incubation—a pattern that was reversed in the pellet data. Great Black-backed Gull chicks' diets of fish and krill according to isotopic mixing models (this study) and regurgitate samples from other studies (Gilliland et al. 2004) are highly consistent. However, neither pellet nor isotope analysis was able to assess reliance on fishery discards, which may be an important food source (Gilliland et al. 2004). Isotopic mixing models also failed to detect birds as prey items, because stable-isotope signatures of these prey were not available and not included in the suite of potential prey items. Therefore, a blend of techniques, combining pellet sampling, regurgitates from chicks, and isotopic mixing models may produce the most reliable method to for monitor gull diets. Additionally, this study only focused on the intra- and inter-seasonal variation in gulls' diet in one year. Further studies should obtain samples over several years and other seasons (i.e., post-breeding dispersal) in order to assess the true breadth and partitioning of these sympatric generalist predators' niches.

CONCLUSIONS

We found that the Herring and Great Black-backed Gulls foraged at different trophic levels and consumed prey types in different proportions, suggesting some partitioning. For both species, diets of adults and chicks differed, chicks were fed at lower trophic levels, and diets differed by season (the breeding-season diet was at a higher trophic level). Within the breeding season, the Herring Gull's diet also shifted from early to late incubation with consumption of crabs decreasing and that of offshore prey (fish and krill) increasing. Together these results underscore the versatility of these generalist predators. As generalist feeders, gulls could be used as indicators for fluctuations in a wide range of marine fish and invertebrates, though this will require more information on the functional response between diet and prey density (e.g., Montevecchi 2007, Hebert et al. 2009).

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