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Gull diets reveal dietary partitioning, influences of isotopic signatures on body condition, and ecosystem changes at a remote colony

Robert A. Ronconi[1,*], Rolanda J. Steenweg[2], Philip D. Taylor[1], Mark L. Mallory[1]

[1]Department of Biology, Acadia University, Wolfville, Nova Scotia B4P 2R6, Canada
[2]Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

ABSTRACT: As top predators that feed on a wide range of prey items, gull diets may serve as important biological indicators of regional prey availability and changes in marine ecosystems. We studied the diets of herring gulls *Larus argentatus* and great black-backed gulls *L. marinus* on Sable Island, Nova Scotia, Canada, a remote colony which has shown high levels of contaminants in herring gull eggs and which has experienced significant ecological and anthropogenic change in its surrounding marine region over the past 40 yr. Analysis of regurgitated pellets suggested that current gull diets have proportionally less offshore prey (e.g. fish) and terns and tern eggs, and proportionally more molluscs, rock crabs *Cancer borealis*, and seal *Halichoerus grypus* carrion than diets sampled 40 yr ago. The composition of recent diets observed from pellet analysis is supported by stable isotope mixing models of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), which revealed that great black-backed gulls had high proportions of seals and crab in their diets, whereas herring gulls had high proportions of crab, sand lance *Ammodytes* sp., and terrestrial invertebrates. Isotopic analyses also identified dietary variability through seasonal, age-specific and body condition relationships for each species. Biometric–isotope relationships showed that larger great black-backed gulls fed at higher trophic levels, and that higher trophic level foraging in herring gulls was associated with better body condition. Collectively, these results indicate dietary partitioning within this community of sympatrically nesting gulls, and broad-scale dietary shifts since the early 1970s.

KEY WORDS: Bioindicator · Dietary shift · *Larus* · Mixing models · Scavengers · Seals · Stable isotopes

INTRODUCTION

Seabird diets are widely used as bioindicators of marine and coastal ecosystem health (Furness & Camphuysen 1997, Piatt et al. 2007) because they respond to fluctuations in prey availability (Cairns 1987, Montevecchi 2007) or quality (Diamond & Devlin 2003), changes in fish stocks (Einoder 2009, Cury et al. 2011) and environmental catastrophes (Moreno et al. 2013). Gulls (family Laridae), for example, are among the top avian predators in many marine and aquatic ecosystems, and for this reason have been successfully used to monitor environmental pollutants (Fox et al. 1990, Gauthier et al. 2008, Caut et al. 2009, Ramos et al. 2013) as well as changes in prey fish abundance (Hebert et al. 2008). However, if seabirds are to be used as effective bioindicator species, a better understanding is needed of factors influencing long-term, species-specific, and intra-specific variability in their diets.

Longitudinal studies of seabird diets have revealed broad-scale changes across several marine ecosystems and species. Seabird diets have tracked decadal changes in foraging trophic levels (Thompson et al.

*Corresponding author: rronconi@dal.ca

1995, Norris et al. 2007) and response to oceanic regime shifts (Montevecchi & Myers 1996, Montevecchi 2007). Anthropogenic activities, such as fisheries, have also been associated with gradual trophic declines in seabird diets over a century (Farmer & Leonard 2011), and sudden dietary shifts across millennia (Wiley et al. 2013). Together, these studies highlight the sensitivity and plasticity of seabird diets in changing marine ecosystems.

At the species level, competition is thought to play a fundamental role in structuring avian communities (MacArthur 1958, Lovette & Hochachka 2006), though competition among seabirds at sea has been difficult to observe and study (Maniscalco et al. 2001, Ronconi & Burger 2011). Instead, dietary studies have revealed many ways in which sympatric species partition resources during the breeding season (Rome & Ellis 2004, Rock et al. 2007) and other times of the year (Ronconi et al. 2010). At the intraspecific level, tracking studies are revealing at-sea partitioning of foraging space among neighbouring colonies (Wakefield et al. 2013, Pollet et al. 2014), but a great deal of variability in diets, and dietary partitioning, may result from individual level choices (e.g. by sex, size, age, body condition, and seasonal cycles). Sex-related partitioning is often associated with sexual dimorphism (González-Solís et al. 2000) but may also be due to differences in energetic requirements (Ludynia et al. 2013) or habitat specialization (Phillips et al. 2011). Age-related differences in diet include dominance of older birds (Greig et al. 1983) and differential provisioning of young (Schmutz & Hobson 1998, Steenweg et al. 2011), and it is thought that during poor years, young and old birds may suffer more from intra-specific competition (Pardo et al. 2013). Individuals also show seasonal changes in foraging trophic levels (Hobson 1993, Steenweg et al. 2011), and foraging trophic level can influence individuals' body condition (Ronconi et al. 2010). Together, these studies highlight the many ways in which seabirds may partition diets across species, colonies, and at the individual level.

Gulls are opportunistic foragers, feeding on a wide range of prey including fish, marine and terrestrial invertebrates, carcasses of beached marine mammals, small birds, fisheries discards, and refuse from garbage dumps (Good 1998, Pierotti & Good 1998, Steenweg et al. 2011). As generalist predators, gull diets shift in response to changes in prey availability (Gonzalez-Solis et al. 1997), and therefore are an interesting group of seabirds with which to study dietary flexibility and partitioning at various temporal scales and among species and individuals. Pellet sampling and stable isotope analysis of tissues are two effective and complementary techniques to determine gull diet (Steenweg et al. 2011, Weiser & Powell 2011), each containing certain advantages and biases in the study of seabird dietary ecology (Bond & Jones 2009). Although dietary assessment through pellet counts may be biased due to differences in prey digestibility (Barrett et al. 2007, Karnovsky et al. 2012), enumeration of pellet samples from around nest sites provides an index of recent meals during the breeding season (Weiser & Powell 2011), and when collected in the same way and compared over long time periods, pellet counts can serve as a reliable index of changes in seabird diets (Mariano-Jelicich & Favero 2006). In contrast, stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes in avian blood have a turnover rate of 12 to 15 d (Hobson & Clark 1992a), and thus indicate assimilated diets prior to collection. $\delta^{15}N$ is an indicator of the trophic level at which an individual feeds, whereas $\delta^{13}C$ is an indicator of inshore–offshore gradients in foraging habits or terrestrial vs. marine feeding preference (Hobson et al. 1994, Knoff et al. 2002). When both isotopes are considered together, and analyzed with isotopic mixing models (Phillips & Gregg 2003, Hopkins & Ferguson 2012), stable isotope signatures of predator and prey tissues can provide estimates of the contribution of prey items to diet.

We studied the diets of herring gulls *Larus argentatus* and great black-backed gulls *L. marinus* on Sable Island, a remote colony located on the Scotian Shelf, Canada, in the western North Atlantic. Situated ~160 km offshore, Sable Island is a unique gull colony because of its proximity to the continental shelf edge (~40 km), lack of coastal and intertidal influence, and isolation from anthropogenic influences such as urban areas and garbage dumps, where gulls commonly feed. In the 1970s, gulls at this site experienced low reproductive success thought to be associated with food limitations (Lock 1973), which may result in competition for resources among species (Dawson et al. 2011), colonies (Wakefield et al. 2013), or individuals (Davies et al. 2013). Since that time, Sable Island and the surrounding area has undergone significant ecological change, with the exponential increase of breeding grey seals *Halichoerus grypus*, now the largest colony in the world (Bowen et al. 2003), and has been exposed to anthropogenic activities with the development of 6 natural gas extraction platforms within 40 km of the island, where some gulls are known to forage (R. A. Ronconi unpubl. data). Moreover, levels of contaminants found in herring gull eggs at this site are higher than

at coastal breeding areas (Gebbink et al. 2011, Burgess et al. 2013); thus, understanding species- and individual-level variability in local diets may play an important role in identifying sources of contaminants in this remote ecosystem.

The goal of this study was to assess species- and individual-level variability in gull diets across seasonal, annual, and decadal time scales. Specifically, we used pellet and stable isotope analysis to (1) identify the main components and dietary partitioning between herring gulls and great black-backed gulls, (2) assess differences in diet between age classes (chicks, immatures, and adults), seasons (breeding, post-breeding, and winter) and individual body size, and (3) quantify differences in diet between now and the 1970s.

MATERIALS AND METHODS

Study site

Gulls were sampled on Sable Island, Nova Scotia (43° 56′ N, 59° 54′ W) during 2 breeding periods (7 to 14 June 2011, and 19 May to 17 June 2012), one post-breeding period (24 to 26 August 2012), and 2 winter periods (6 to 15 January 2012 and 2013). The island is 42 km long and 1.5 km across its widest point, and composed of vegetated sand dunes, sand flats, and some freshwater ponds. Approximately 2000 pairs of herring gulls and >630 pairs of great black-backed gulls were breeding on the island in 1970 (Lock 1973), though populations of both species have declined since then to approximately 900 and 500 pairs of herring and great black-backed gulls, respectively, in 2013 (R. A. Ronconi unpubl. data). On Sable Island, gulls are known to scavenge the carcasses of grey seals, whose population has increased from <300 in the 1960s to ~300 000 in 2010 (Bowen et al. 2003, DFO 2011).

Sample collection

Blood samples for stable isotope analysis were collected from adult herring gulls (n = 47) that were captured on their nests using bow nets (www.modernfalconry.com) and noose lines. Adult (n = 37) and immature (n = 17) great black-backed gulls were captured with noose carpets set around seal carcasses, and chicks (n = 10) were captured near nest sites prior to fledging. We sampled only 1 chick from each nest. A small (<1 ml) blood sample was collected by venipuncture of the tarsus or wing for stable isotope analysis. Blood samples were frozen until further processing.

Pellets and other undigested hard parts of prey items (e.g. crab carapace and claws) were sampled opportunistically around nest sites for both species of gulls, and itemised following the methods of Lock (1973). For great black-backed gulls, pellets were counted within ~2 m of individual nests. For herring gulls, all pellets and nests were counted throughout small sub-colonies (typically 5 to 30 nests each) around nests and adjacent loafing sites (e.g. dune ridges) between nests but within colonies. Prey items from pellet samples were identified in the field to the lowest taxonomic level possible, and were removed from nesting areas (or destroyed) during counting. This ensured no double counting of items, and cleared sites for recounting at later dates. Most (approx. >80%) of the nests were sampled in the western half of Sable Island; great black-backed gull nests were counted only once, and a few sub-colonies of herring gulls were counted twice. Great black-backed gull nests were sampled during late incubation and early chick-rearing. Herring gull nests were sampled during incubation and approximately 1 wk post hatching.

We calculated frequencies of occurrence as the count of a given prey type, expressed as a percentage of the total number of prey items counted (as per Lock 1973). Most pellets contained only a single prey type, but those containing 2 or more prey types were counted as separate prey items in the frequency of occurrence statistics. When possible, the total prey count included the maximum number of items that could be uniquely identified (e.g. maximum number of crab carapaces or right claws, or multiple species of fish within individual pellets; Steenweg et al. 2011). Most often, however, multiple prey items of the same prey type were counted as single records since, for example, it was not possible to count individual prey items when they were ground up within a pellet (e.g. beetle carapaces, fish bones, crab/clam shells, and vegetation). This method assumes that one pellet represents a single meal, thus underestimating the actual count (numerical frequency) of individual items within a meal. Nonetheless, the results present indices of diets from 2011 and 2012 that are comparable to those collected on Sable Island in 1969 and 1970 (Lock 1973).

Regurgitates were identified opportunistically while handling adults and chicks in the field. Fresh food regurgitated during captures for blood sampling was counted as per pellet counting above, thus

counting the total number of unique individual prey items when possible. Fish samples were retained as 'unknown fish' and processed for stable isotope analysis (see below) so that isotopic signatures could be compared to those of a reference prey collection.

Representative prey samples, based on known diet items identified from pellet analysis in this and other studies (Lock 1973, Steenweg et al. 2011), were collected to produce a reference set for stable isotope mixing models (see Table 1). Prey samples of northern short-fin squid *Illex illecebrosus*, sand lance *Ammodytes* sp., haddock *Melanogrammus aeglefinus*, capelin *Mallotus villosus*, longhorn sculpin *Myoxocephalus octodecemspinosus*, mackerel *Scomber scombrus*, Atlantic herring *Clupea harengus*, rock crab *Cancer borealis* and shrimp *Pandalus borealis* were collected during research trawl surveys within 8 to 136 km of Sable Island (mean = 63 km, n = 16 trawl sets) conducted by the Department of Fisheries and Oceans from survey vessel CCGS 'Alfred Needler' (8 July to 4 August 2012). Other prey samples gathered on Sable Island included rock crab and Atlantic surf clam *Spisula solida* found on beaches and around nests, ninespine stickleback *Pungitius pungitius* collected by dip net from freshwater ponds, sand lance collected by hand from the east tip of the island, and invertebrates (grubs, species unknown; june bugs, *Phyllophaga* sp.; amphipods, *Gammarus lawrencianus*) collected by hand from dunes, beaches and vegetation. Sub-samples of grey seal muscle, liver, and intestine tissues were collected opportunistically from adults in the summer and pups in the winter from carcasses washed ashore. These 3 tissues were selected as sub-samples from seals since we frequently observed gulls scavenging these body parts. All prey samples were stored frozen until processing for stable isotope analysis.

Stable isotope preparation

Blood samples were dried in an oven set at 40°C for 24 h. Prey samples were thawed, homogenized with a food processor or mortar and pestle, and sub-samples were dried in the oven. Whole prey items were homogenized except for crab (soft tissues were removed from the carapace, legs and claws), long-horned sculpin (thick jaw, horns and vertebrae removed prior to homogenization), clam (muscle removed from shells) and seal (sub-sample of tissues collected in field). After drying, samples were soaked in a 2:1 chloroform:methanol solution for 24 h to remove lipids from the samples, and rinsed with fresh solution (Ronconi et al. 2010), air-dried or re-dried in the oven, and then ground into a fine powder. Sub-samples of 0.25 ± 0.05 and 0.40 ± 0.05 mg (for samples analysed at University of Waterloo, UW, and University of New Brunswick, UNB, respectively), were weighed with a microbalance and folded into tin capsules. Samples were run with standards interspersed for every 8 samples, and results were corrected to these standards (nitrogen standards: ammonium sulphate; carbon standards: sugar, cellulose, or graphite). The error for standard material was ±0.2‰ for carbon and ±0.3‰ for nitrogen. Stable isotope analysis for $\delta^{13}C$ and $\delta^{15}N$ of blood and prey samples was conducted at the Environmental Isotope Laboratory (UW) and the Stable Isotopes in Nature Laboratory (UNB). Five samples were run in duplicate, 1 at each lab, showing mean absolute differences of 0.19‰ for $\delta^{13}C$ and 0.20‰ for $\delta^{15}N$ between labs; differences smaller than observed with standards (Steenweg et al. 2011 contains additional details on sample processing).

Data analysis

To determine the changes in diet since 1969–1970, we compared frequency of occurrence for prey types in pellet samples from Lock (1973) to those from this study. Change in diet was calculated by subtracting the average proportion of each prey type during the 1969 and/or 1970 diet from the average proportions in 2011 and 2012. Because Lock (1973) reported only the final percentage of prey items, and raw data by individuals nests are not available, additional statistical analysis were not possible and therefore percentage change provides only a qualitative analysis of changes in diet.

Separate general linear models were used to investigate the factors influencing variability in stable isotope signatures of $\delta^{13}C$ and $\delta^{15}N$. Great black-backed gulls typically feed at a higher trophic level than herring gulls and adults of both species may feed their chicks at different trophic levels (Steenweg et al. 2011). Thus, we tested for effects of species and age on diet. Based on plumage characteristics and date of capture, the following age classes were identified for great black-backed gulls: adult (after third year), immature (first winter until third winter), juvenile (fledged from nest and captured in August) and chicks (unfledged birds captured in June). Gull diet can also vary between winter and the breeding season (Steenweg et al. 2011) due to fluctuations in prey availability and quality (Gonzalez-Solis et al. 1997);

thus, seasonal effects were tested for great black-backed gulls that were captured during summer (breeding) and winter. Additionally, the size of a bird can influence its ability to compete for resources, with larger individuals outcompeting smaller individuals for higher quality prey (Phillips et al. 2011, Ludynia et al. 2013). Total head and bill length (head size) was used as an indicator of bird size, which, in gulls, may also be used to differentiate bird sex (males are typically larger than females; Threlfall & Jewer 1978, Evans et al. 1995). Body condition index (BCI), measured as an index of bird weight relative to bird size, may also be correlated with stable isotope signatures in seabirds (Ronconi et al. 2010), suggesting a relationship between diet and overall bird health. Residuals from a linear regression of gull mass relative to head size, calculated for each species separately, was used as a BCI. The linear models of bird mass regressed against head size were significant for both herring gulls ($F_{1,53} = 71.6$, $p < 0.001$, $R^2 = 0.574$) and great black-backed gulls ($F_{1,58} = 137.9$, $p < 0.001$, $R^2 = 0.704$). General linear models were used to evaluate the effects of age, season, head size, and BCI on stable isotope signatures.

The Bayesian stable isotope mixing model IsotopeR (Hopkins & Ferguson 2012) was used to determine proportions of prey items present in gull diets. IsotopeR uses a similar modelling process as previous stable isotope mixing models, with several important additions such as the inclusion of error estimates for discrimination factors. Using 2 isotopes, these models require 3 inputs to quantify dietary estimates: (1) isotopic signatures of individual consumers, (2) isotopic signatures of individual prey items (i.e. sources), and (3) discrimination factors (mean ± SD), representing changes in stable isotope signatures from prey ingested by consumers. Individual-level data inputs for both consumers and sources were used to calculate population-level estimates of prey consumption. We produced separate population-level estimates of diet for the following groups for which adequate sample size was available: (1) adult herring gulls in both 2011 and 2012, (2) adult and immature (combined) great black-backed gulls for winter and breeding seasons (separate), and (3) great black-backed gull chicks and juveniles (separate). With isotopic mixing models, the uncertainty in source identification increases with the number of sources/prey items considered in the model (Phillips & Gregg 2003). Therefore, based on similarity in isotope values and ecological groupings of prey types, we grouped the following prey items (Table 1): (1) 'medium offshore fish', which included large capelin (>130 g), medium haddock (>190 g), herring, mackerel, and long-horned sculpin; (2) 'small offshore fish', which included small capelin and haddock

Table 1. Measurements and stable isotope values of potential herring and great black-backed gull prey samples. Values are means (±SD). Grouping for mixing models indicates the prey types that were grouped together for isotopic mixing models; a = small offshore fish, b = medium offshore fish, c = all ages of seals combined. Shrimp and squid were excluded from the mixing model; GMM = grouping for mixing models; Excl = excluded; na = not available

Species	n	Mass (g)	Length (mm)	$\delta^{13}C$	$\delta^{15}N$	C:N ratio	GMM
Grub (species unknown)	4	0.84 (0.2)	na	–25.17 (0.2)	12.12 (0.8)	3.40	
Junebug (*Phyllophaga* sp.)	3	0.70 (0.1)	na	–24.17 (0.6)	4.41 (2.5)	3.27	
Ninespine stickleback (*Pungitius pungitius*)	4	0.59 (0.2)	45 (3.7)	–23.31 (0.2)	15.86 (0.4)	3.33	
Amphipods (*Gammarus lawrencianus*)	6	0.09 (0.07)	na	–23.24 (1.1)	9.51 (1.3)	4.03	
Atlantic surf clam (*Spisula solida*)	3	na	na	–19.45 (0.2)	10.04 (0.4)	3.72	
Rock crab (*Cancer borealis*)	12	114.0 (26.5)	96 (10.9)	–18.14 (0.4)	12.49 (0.6)	3.29	
Shrimp (*Pandalus borealis*)	6	na	na	–18.39 (0.3)	12.40 (0.3)	3.16	Excl
Northern short-fin squid (*Illex illecebrosus*)	9	76.4 (14.7)	158 (8.9)	–19.40 (0.3)	11.78 (0.3)	3.20	Excl
Sand lance (*Ammodytes* sp.)	18	8.6 (7.5)	132 (53.3)	–19.84 (0.5)	11.09 (0.3)	3.13	
Capelin (*Mallolus villosus*) – small	2	3.5 (0.8)	86 (5.7)	–20.47 (0.2)	12.15 (0.3)	3.24	a
Capelin (*Mallolus villosus*) – large	4	13.7 (1.3)	136 (4.2)	–19.59 (0.1)	12.76 (0.1)	3.11	b
Haddock (*Melanogrammus aeglefinus*) – small	3	6.8 (3.6)	82 (11.3)	–20.35 (0.2)	12.75 (0.2)	3.17	a
Haddock (*Melanogrammus aeglefinus*) – medium	3	91.6 (17.6)	213 (15.3)	–18.98 (0.1)	13.59 (0.4)	3.20	b
Atlantic herring (*Clupea harengus*)	5	162.5 (47.0)	244 (21.1)	–19.44 (0.2)	12.51 (0.2)	3.32	b
Mackerel (*Scomber scrombrus*)	4	140.0 (14.3)	243 (4.5)	–19.50 (0.2)	13.09 (0.2)	3.11	b
Longhorned sculpin (*Myoxocephalus octodecemspinosus*)	5	201.8 (177.8)	240 (67.9)	–18.50 (0.4)	14.26 (0.4)	3.32	b
Grey seal (*Halichoerus grypus*) – pups	4	na	na	–18.35 (1.0)	16.93 (0.2)	3.30	c
Grey seal (*Halichoerus grypus*) – adults	7	na	na	–18.20 (0.4)	16.39 (0.7)	3.19	c

(<100 g); and (3) 'seal', which included both adults and pups. Thus mixing models considered up to 10 prey items including 4 terrestrial sources (*Gammarus*, junebugs, grubs, and sticklebacks) and 6 marine sources (clam, crab, sand lance, small offshore fish, medium offshore fish, and seal). Grub, junebug and stickleback were excluded from the winter diet mixing models as they are not available to gulls on Sable Island during the winter. Discrimination factors were obtained from controlled feeding experiments with fish-eating birds (Hobson & Clark 1992b, Bearhop et al. 2002, Cherel et al. 2005, Becker et al. 2007, Williams et al. 2007). We used average (±SD) values of fractionation between lipid extracted prey and whole blood (n = 5): +2.75 ± 0.40 for $\delta^{15}N$ and −0.06 ± 0.71 for $\delta^{13}C$, which were previously used for isotopic mixing models with herring and great black-backed gulls (Steenweg et al. 2011) and which are very similar to the discrimination values for 'birds' obtained from a meta-analysis (Caut et al. 2009). Isotopic mixing model outputs reported were the mean solutions and standard deviation.

All statistical analyses were performed using program R (R Development Core Team 2013) and descriptive statistics throughout are reported as mean values ± SD.

RESULTS

Pellet analysis

Herring gull diets were assessed from over 1690 pellets examined across 3 yr (Table 2). Compared to 1970, the current composition of diet had lower proportions of fish and crab but higher proportions of molluscs and seal remains. Great blacked-back gull diets were assessed from over 940 pellets examined over 4 yr (Table 2). Proportions of fish and tern eggs/chicks were lower and proportions of molluscs, crab and seal remains were higher than they were 40 yr ago. Direction of change in dietary proportion (Fig. 1) was similar between both gull species for the main prey items, including fish (declined), molluscs and seal remains (increased), but not crabs (increased for great black-backed gulls and decreased for herring gulls). Within recent years, 2011 and 2012 pellet sampling suggested differences in diet between species: there was a higher occurrence of molluscs for herring gulls and higher occurrence of crabs and seal remains for great black-backed gulls. Many of the main prey items were widely consumed among individual nests, suggesting broad scale consumption rather than individual specialization: 68% of

Table 2. Proportion of food types found in pellets (n) collected from herring gull *Larus argentatus* and great black-backed gull *L. marinus* nests during the summers of 1969–1970 (historical; from Lock 1973), and 2011–2012 (contemporary; this study). Number of nests sampled in each year are indicated in parentheses but were not reported for the 1969–1970 sampling periods. Herring gull pellets were not sampled in 1969. (–) indicates prey types not previously reported during historical surveys

Food type	Herring gull			Great black-backed gull			
	1970 (n = 690)	2011 (72) (n = 539)	2012 (147) (n = 462)	1969 (n = 186)	1970 (n = 627)	2011 (20) (n = 143)	2012 (36) (n = 173)
Fish	0.21	0.03	0.08	0.20	0.27	0.06	0.02
Molluscs	0.07	0.80	0.36	0.01	0.03	0.29	0.14
Insects	0.22	0.02	0.17	0	<0.01	0.06	0.03
Cancer irroratus	0.27	0.04	0.20	0.04	0.14	0.19	0.29
Sea cucumber	<0.01	0	0	0	0	0	0
Other crustacea	<0.01	<0.01	0	0	<0.01	0	0
Cranberries and crowberries	0.09	0.01	0.05	0	0.01	0	0
Leaves	0.01	0	<0.01	0	0	0.01	0
Pelagic birds	0.04	<0.01	0.01	0.04	0.15	0.03	0.02
Passerine birds	0.02	0.01	0.01	0.01	0.03	0.01	0
Unidentified birds	0.01	0	<0.01	0	0	0	0
Terns	0.02	0	0	0.08	0.12	0.01	0.01
Tern eggs	0.01	0	0	0.53	0.07	0	0
Gull chicks	0	0	0	0.01	0.01	0	0
Gull eggs	0.02	0	0	0.01	0.04	0	0
Seal remains	0.01	0.09	0.12	0.06	0.12	0.29	0.49
Garbage	0.01	0	0	0.02	0.01	0.03	0
Seaweed	–	<0.01	<0.01	–	–	0	0
Horse	–	0	0	–	–	0.02	0

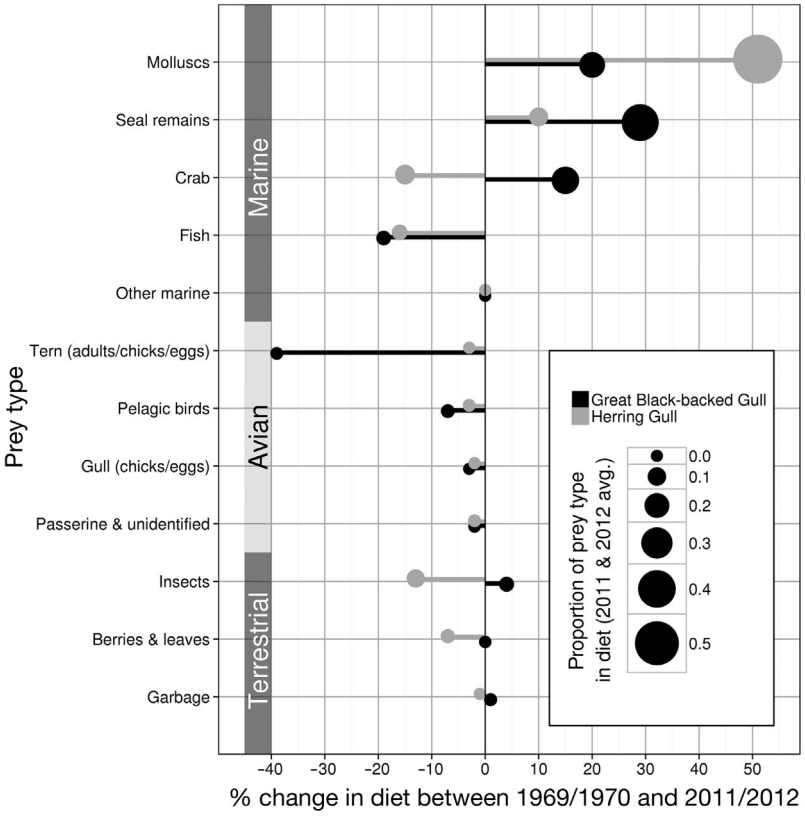

Fig. 1. *Larus argentatus* and *L. marinus*. Change in percentage points of the composition of dietary items found in regurgitated pellets of herring and great black-backed gulls on Sable Island, Nova Scotia, Canada. Change is measured as the difference between mean historical diets (1969–1970) and mean contemporary diets (2011–2012) from data presented in Table 2 with some prey types grouped together. Dot size represents mean proportion of prey item in contemporary diets (averaged between 2011 and 2012)

great black-backed gull nests (n = 47 in 2011–2012) had pellets with seal remains compared with other commonly consumed prey such as crabs (57% of nests), molluscs (57%), and fish (13%). Comparable estimates among individual herring gull nests are not available because pellets were enumerated by subcolonies rather than individual nests.

Regurgitated prey

Regurgitated prey from adult herring gulls (n = 4) and great black-backed gulls (n = 1) included one or more fish from each adult and grubs from one of the herring gulls. A total of 10 prey items were identified from regurgitates of 7 great black-backed gull chicks, including fish (2), seal remains (5), crab (1), junebugs (1), and clams (1). One regurgitated fish was identified in the field as a sand lance; others were too degraded for proper identification. Stable isotope signatures of the 5 unknown fish showed their isotopic signatures to be closest to herring (1), herring or mackerel (1), mackerel or medium-sized haddock (1), small capelin (1), and long-horned sculpin (1) (Table 1).

Stable isotope analysis and mixing models

There were strong differences in stable isotope signatures between species (Table 3, Fig. 2), with herring gulls having significantly lower values of $\delta^{13}C$ (–19.3 ± 0.6, range –20.6 to –17.7; t_{109} = 8.32, p < 0.001) and $\delta^{15}N$ (14.3 ± 0.9, 12.1 to 16.1; t_{109} = 11.37, p < 0.001) compared with great black-backed gulls ($\delta^{13}C$ = –18.4 ± 0.5, –19.3 to –17.7; $\delta^{15}N$ = 16.4 ± 1.0, range 11.3 to 18.0); hereafter, species were considered separately. One immature great black-backed gull had an anomalously low $\delta^{15}N$ signature of 11.25‰, which was less than all herring gull values and a full trophic level lower than the next highest great black-backed gull value (14.31‰). We report this value here as it may represent extremely

Table 3. Stable isotope values for adult, chick, juvenile and immature age classes of herring gulls *Larus argentatus* and great black-backed gulls *L. marinus* during winter and breeding seasons. Birds were aged by plumage characteristics: juvenile (fledged young sampled in August), immature (first year to third year birds), adult (after third year)

Species Season	Age	n	$\delta^{13}C$ (SD)	$\delta^{15}N$ (SD)
Herring gull				
2011	Adult	15	–18.99 (0.54)	14.63 (0.76)
2012	Adult	32	–19.40 (0.62)	14.16 (0.87)
Great black-backed gull				
Breeding	Chick	10	–18.72 (0.38)	16.00 (0.53)
	Juvenile	6	–18.56 (0.22)	16.98 (0.56)
	Immature	5	–18.22 (0.61)	16.38 (1.27)
	Adult	20	–18.11 (0.32)	16.93 (0.62)
Winter	Immature	5	–18.37 (0.16)	16.13 (1.4)
	Adult	18	–18.33 (0.27)	16.09 (0.65)
Great black-backed gull				
All	All	64	–18.34 (0.38)	16.45 (0.84)

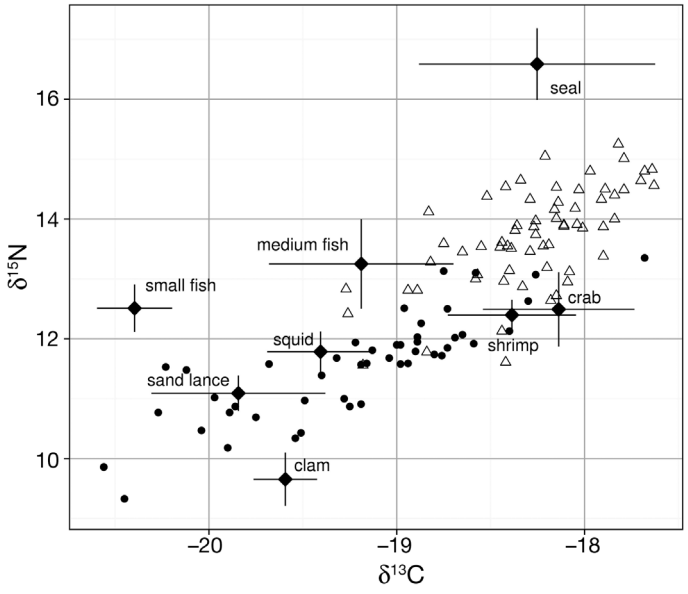

Fig. 2. *Larus argentatus* and *L. marinus*. Stable isotope signatures of individual herring gulls (●) and great black-backed gulls (△) from Sable Island in relation to potential prey items (means ± SD). See Table 1 for details of prey types (note terrestrial prey types not shown; all $\delta^{13}C$ values <−22‰). Gull isotope values are from whole blood and have been adjusted (−2.75 for $\delta^{15}N$, +0.06 for $\delta^{13}C$) to account for discrimination factors between consumer and prey (see 'Materials and methods: Data analysis' for details)

low trophic foraging of immature birds, however, this value produced spurious results during preliminary analysis, and was therefore omitted from statistical and isotopic mixing-models.

$\delta^{15}N$ in herring gulls was influenced by year (higher values in 2011) and was higher for birds in better body condition, but $\delta^{13}C$ was not significantly influenced by these parameters (Table 4; model adjusted R^2 = 0.059 and 0.118 for $\delta^{13}C$ and $\delta^{15}N$, respectively). Effects of BCI on $\delta^{15}N$ indicated that birds in better condition were also feeding at higher trophic levels (Fig. 3). There were no significant effects of bird size or day of year on either isotope.

Within the breeding season, there were differences in isotope signatures among some age classes for great black-backed gulls (ANOVA; $\delta^{13}C$: $F_{3,37}$ = 7.12, p < 0.001; $\delta^{15}N$: $F_{3,37}$ = 4.66, p = 0.007). Chicks had lower $\delta^{13}C$ values than adults (Tukey's HSD post-hoc tests: p < 0.001) and immatures (p = 0.084), and juveniles had lower values than adults (p = 0.053) but not chicks or immature birds. Chicks also had lower $\delta^{15}N$ than adults (p = 0.008) and juveniles (p = 0.048), but no other pairwise comparisons were significant. Chicks and juveniles were omitted from further analysis because they were still growing, and therefore head size and BCI measures were not comparable with adults and immature great black-backed gulls. During winter, there were no significant differences between adult and immature age classes for either $\delta^{13}C$ ($F_{1,21}$ = 0.07, p = 0.79) or $\delta^{15}N$ ($F_{1,21}$ = 0.008, p = 0.93).

For great black-backed gulls, isotopic signatures were significantly influenced by the characteristics of birds and sampling period (Table 4; model adjusted R^2 = 0.139 and 0.239 for $\delta^{13}C$ and $\delta^{15}N$, respectively). Seasonal effects were the strongest, whereby winter isotope signatures were significantly lower than during the breeding season for $\delta^{13}C$ (p = 0.005) and $\delta^{15}N$ (p < 0.001). Head size was positively correlated with $\delta^{13}C$ (p = 0.021) and $\delta^{15}N$ (p = 0.011), suggesting that larger birds (presumably males) fed on different prey types and at higher trophic levels (Fig. 4). Effects of body condition, age class and an Age × Season interaction were not significant. Based on these results,

Table 4. General linear models results of the effects of year, age, season, head size, body condition index (BCI) on gull diets as inferred from stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope signatures

Species Model and variables	Isotope	df	*F*	p	Interpretation
Herring gull					
Model fit	$\delta^{13}C$	2,42	1.72	0.163	
	$\delta^{15}N$	2,42	2.54	0.054	
Year (2011 vs. 2012)	$\delta^{13}C$	1	−1.63	0.110	
	$\delta^{15}N$	1	−1.77	0.084	2011 > 2012
Head Size	$\delta^{13}C$	1	0.35	0.731	
	$\delta^{15}N$	1	0.46	0.645	
BCI	$\delta^{13}C$	1	1.45	0.154	
	$\delta^{15}N$	1	2.49	0.017	+ correlation
Day of Year	$\delta^{13}C$	1	0.35	0.731	
	$\delta^{15}N$	1	0.02	0.986	
Great black-backed gull					
Model fit	$\delta^{13}C$	5,42	2.43	0.050	
	$\delta^{15}N$	5,42	3.96	0.005	
Age	$\delta^{13}C$	1	−0.24	0.813	
(immature vs. adult)	$\delta^{15}N$	1	−0.73	0.468	
Season	$\delta^{13}C$	1	−2.94	0.005	Winter < summer
(breeding vs. winter)	$\delta^{15}N$	1	−4.10	<0.001	Winter < summer
Age × Season	$\delta^{13}C$	1	0.27	0.792	
	$\delta^{15}N$	1	0.92	0.364	
Head size	$\delta^{13}C$	1	2.39	0.021	+ correlation
	$\delta^{15}N$	1	2.67	0.011	+ correlation
BCI	$\delta^{13}C$	1	0.33	0.739	
	$\delta^{15}N$	1	1.02	0.315	

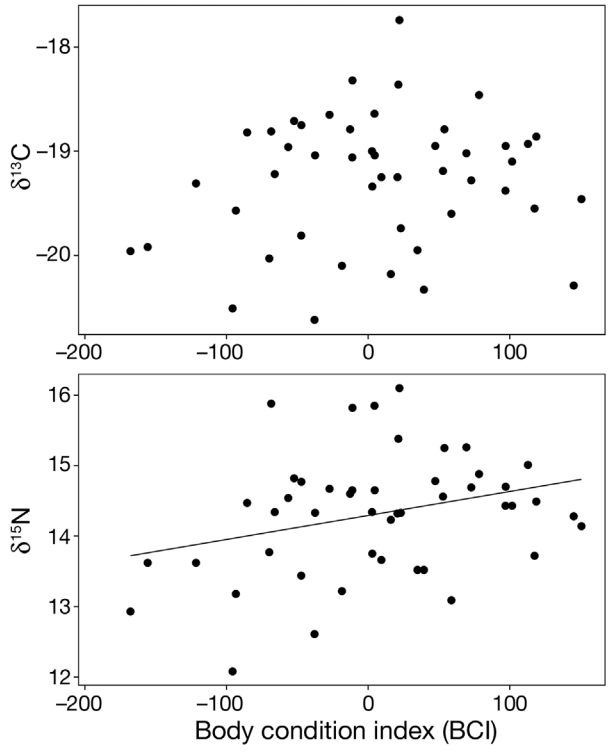

Fig. 3. *Larus argentatus*. Body condition index (BCI) versus stable isotope signatures for herring gulls. Regression line fit for significant correlation between BCI and $\delta^{15}N$. BCI values are residuals of bird mass (g) regressed against head size (head + bill)

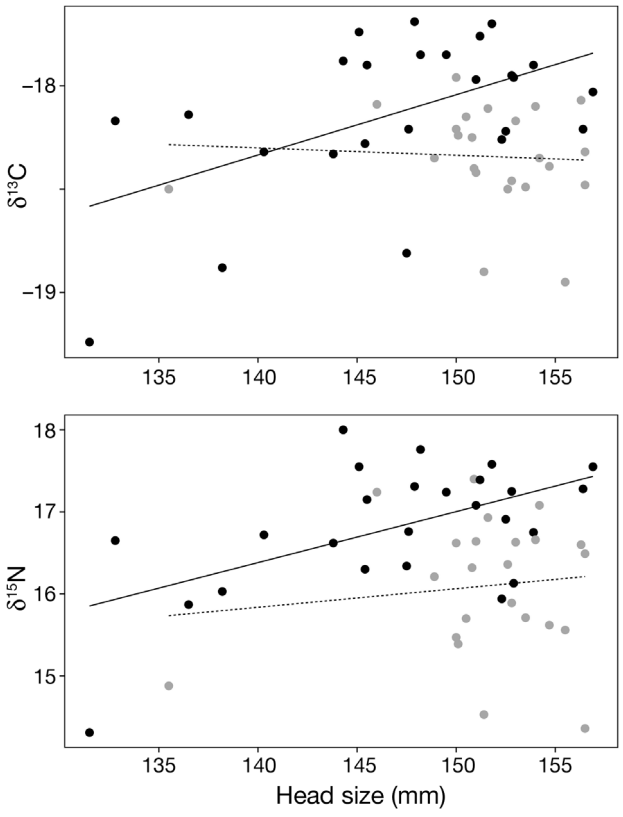

Fig. 4. *Larus marinus*. Effects of season and head size stable isotope signatures for great black-backed gulls. Regression lines fit separately for seasons: winter (grey symbols, dashed line) and summer (black symbols, solid line)

for mixing model estimates of great black-backed gull diets, we pooled adult and immature age classes to create separate estimates for winter and breeding season.

Stable isotope values for prey showed strong separation between marine and terrestrial prey types: terrestrial organisms were distinct by both $\delta^{13}C$ and $\delta^{15}N$, marine invertebrates (crab, clams) and seals separated by either $\delta^{13}C$ or $\delta^{15}N$, but with considerable overlap for many of the fish species except sand lance (Table 1, Fig. 2). Isotopic signatures of shrimp and squid overlapped with crabs and fish, respectively, but these prey types were not found in pellets or regurgitates for this gull population (Lock 1973, this study), and therefore were excluded as prey sources from the mixing models.

For herring gulls, model estimates from 2 summers showed crabs (38 to 70%) and sand lance (20 to 52%) to be the primary prey items, with modest dietary contribution from terrestrial sources (*Gammarus* and junebugs, <8% combined) and negligible contributions from other marine prey types (Table 5). In both summer and winter, adult/immature great black-backed gull diet was estimated to consist primarily of crab (61 to 82%) and seal remains (14 to 36%) with only marginal contributions from other prey sources (<5% from all fish types and clams combined; Table 5). In contrast, chicks sampled in June and post-fledging juveniles sampled in August had much more varied diets, which included seal remains, medium offshore fish, crabs, clams, and sand lance (listed in order of relative importance; Table 5). Terrestrial prey sources were not important prey items in great black-backed gull diets (typically 0% estimated for all age classes).

DISCUSSION

Long-term dietary changes

Several studies have recently shown long-term changes in seabird diets associated with natural or anthropogenically induced ecosystem changes (Thompson et al. 1995, Montevecchi 2007, Norris et al. 2007, Farmer & Leonard 2011). Though our results

Table 5. Model estimates of the contribution of prey types to herring gull *Larus argentatus* and great black-backed gull *L. marinus* diets using a Bayesian stable isotope mixing model (IsotopeR; Hopkins & Ferguson 2012). See Tables 1 & 3 for details of prey types included in the mixing model and sample size for gull groups. Values are mean (±SD) proportion of diet. (–) indicates prey items not included in the mixing model for winter diets because these prey types are not available to gulls in the winter

Source	Herring gull		Great black-backed gull			
Prey type	Adult: 2011	Adult: 2012	Chicks	Juv. post-fledging	Adult: Breeding	Adult: Winter
Terrestrial						
Gammarus	0.06 (0.08)	0.03 (0.06)	0	0	0	0
Grub	0	0	0	0	0	–
Junebug	0.02 (0.04)	0.03 (0.04)	0	0.01 (0.02)	0.00 (0.01)	–
Ninespine stickleback	0.00 (0.01)	0.01 (0.01)	0.00 (0.01)	0.00 (0.01)	0.00 (0.01)	–
Marine						
Clam	0.00 (0.01)	0.00 (0.02)	0.15 (0.21)	0.00 (0.01)	0.01 (0.03)	0.01 (0.02)
Crab	0.70 (0.17)	0.38 (0.27)	0.18 (0.21)	0.43 (0.30)	0.61 (0.08)	0.82 (0.11)
Sandlance	0.20 (0.24)	0.52 (0.38)	0.06 (0.12)	0.06 (0.11)	0.00 (0.01)	0.01 (0.01)
Small offshore fish	0.00 (0.02)	0.02 (0.04)	0.02 (0.06)	0.01 (0.03)	0	0.01 (0.02)
Medium offshore fish	0.01 (0.03)	0.00 (0.02)	0.36 (0.41)	0.21 (0.24)	0.01 (0.02)	0.02 (0.04)
Seal	0.01 (0.02)	0	0.23 (0.21)	0.29 (0.21)	0.36 (0.07)	0.14 (0.09)

from pellet counts present only qualitative change from 2 distinct time periods, this provides some evidence of broad changes occurring in this isolated offshore island over 40 yr. Most notable were increases in seal remains and molluscs, declines in fish, near absence of terns, and variable changes in the proportion of crab contributions to recent diets.

The higher occurrence of seal remains in gull pellets was expected given that the seal population on Sable Island has increased exponentially since the 1960s (Bowen et al. 2003), providing ample opportunity for scavenging on carcasses year-round. An abundance of carcasses provides an energy-rich food source of protein and lipids, which is easily obtained with low energy expenditure compared with offshore foraging trips for fish. Other prey items obtained from scavenging along Sable Island shorelines are molluscs and crab, both of which have increased in the diets of one or both gull species. It is not clear if the availability of clams or crabs have changed on Sable Island since the 1970s, but increased reliance on these prey items may be associated with decreased reliance on other prey types such as offshore fish. Both herring and great black-backed gulls showed a >15% decline in the proportion of fish in pellets on Sable Island. Reasons for this decline are unclear, but may be related to changes in local fish availability, perhaps through declining scavenging from fisheries offal (Farmer & Leonard 2011), or through broad-scale ecosystem changes (Montevecchi & Myers 1996, Montevecchi 2007). However, without continuous, long-term records of gull diets from Sable Island, it is impossible to speculate on the timing of, or reasons for, the declining reliance on fish in this colony. Nevertheless, fish were commonly found in regurgitates of adult gulls and chicks on Sable Island during this study, suggesting that fish are an available prey item and that pellet counts may underestimate the contribution of fish in their diets.

When marine prey sources are scarce, gull diets may shift towards greater consumption of other bird species (Russell & Montevecchi 1996, Stenhouse & Montevecchi 1999). In contrast, we observed decreased proportions of all bird types in gull pellets, and especially strong declines in terns and tern eggs. The low proportions of terns in recent gull diets may be an artefact of the timing and biases of sampling from both recent and historical data. These biases might include earlier nesting of great black-backed gulls than occurred historically (R. A. Ronconi unpubl. data), lack of gull pellet sampling during the tern chick-rearing period (this study), and sampling of an apparent tern-specialist (67% of the tern eggs recorded in pellets in 1969 were from a single great black-backed gull nest; Lock 1973). Such individual specialization is known to occur in gulls (Pierotti & Annett 1991), and disproportionate sampling of specialists may introduce biases for population level dietary analysis. Alternatively, reduced gull predation pressure on terns may be a response to increased availability of seal carcasses, or to the recent growth of Sable Island's tern population (Sable Island Preservation Trust 2009) since large tern colonies are better able to defend themselves from predators (Hernández-Matías & Ruiz 2003).

Without historical blood samples from Sable Island gulls, it is not possible to determine long-term dietary shifts from stable isotope signatures, but analysis of feathers and eggs suggest long-term changes in other parts of Atlantic Canada. Temporal trends in $\delta^{15}N$ of herring gull eggs between the 1970s and 2008 showed declines in foraging trophic level in 3 of 4 coastal colonies in eastern Canada, but no significant declines on Sable Island (Burgess et al. 2013). Likewise, throughout Atlantic Canada, feather $\delta^{15}N$ values of great black-backed gulls have declined over the past 110 yr (Farmer & Leonard 2011). In our study, mean blood sample values of $\delta^{15}N$ were ~14.5 and 16.9 for herring and great black-backed gulls, respectively, suggesting a high foraging trophic level for both species at this colony compared to other regions of Atlantic Canada (Farmer & Leonard 2011, Steenweg et al. 2011, Burgess et al. 2013). This suggests that Sable Island gulls have a strong reliance on high trophic level prey (such as seal carcasses), or that $\delta^{15}N$ baseline values of other prey (such as fish and crabs) are higher around Sable Island compared to coastal areas (see Steenweg et al. 2011, their Table 3; $\delta^{15}N$ values 3.4, 0.8, and 0.4‰ higher on Sable Island for crab, herring, and mackerel, respectively). Though pellet counts suggest long-term changes in gull diets on Sable Island (this study), unchanged egg $\delta^{15}N$ over 4 decades (Burgess et al. 2013) may reflect greater dietary flexibility from a wider range in high trophic level prey types available to Sable Island gulls relative to mainland gulls, where foraging trophic level has declined (Farmer & Leonard 2011, Burgess et al. 2013). Alternatively, differences in baseline $\delta^{15}N$ values in the ecosystem may be important when accounting for differences in diets among seabird colonies (Moreno et al. 2011, Brasso & Polito 2013), but baseline stable isotope data are unknown for this 40 yr period on the Scotian Shelf. Together, these studies highlight the need to examine colony-specific patterns in diet since regional patterns may not reflect true local change. This is especially true when nearby colonies show spatial segregation in foraging ranges (Wiley et al. 2012, Pollet et al. 2014).

Individual- and species-level variability in diet

Stable isotope signatures of $\delta^{13}C$ and $\delta^{15}N$ in predator tissues represent assimilated diets which lack the biases associated with pellet sampling (Barrett et al. 2007, Karnovsky et al. 2012), thus inference is more reliable when comparing diets between time periods, groups, and individuals. In this study, we observed differences among species, seasons, and age classes, in addition to high variability among individuals which was associated with bird size and body condition.

Species-specific dietary differences are sometimes obscure among sympatrically-nesting species (Rock et al. 2007, Weimerskirch et al. 2009); however, assessments of diets and foraging tactics have consistently shown differences between co-nesting great black-backed and herring gulls, suggesting a competitive advantage for preferred prey by great black-backed gulls (Hunt & Hunt 1973, Greig et al. 1986, Rome & Ellis 2004, Steenweg et al. 2011). Likewise in this study, stable isotope analysis, isotopic mixing models, and pellet samples showed dietary differences between herring and great black-backed gulls. Some of this difference may be explained by inshore–offshore feeding preferences; great black-backed gulls fed more on offshore fish while herring gulls consumed more sand lance and terrestrial prey. Differences in scavenging preferences on the island may also account for niche partitioning; great black-backed gulls had higher proportions of seal remains in their diets. Though seal carrion is relatively abundant on Sable Island, herring gulls were less frequently observed at carcasses, and great black-backed gulls were often observed aggressively displacing herring gulls from foraging opportunities. Mixing models showed crab to be important prey for both gull species, though differences observed in pellet counts may also be a result of competitive exclusion by great black-backed gulls (Rome & Ellis 2004). As a result, herring gulls may be forced to feed on smaller, less profitable prey items such as molluscs, terrestrial invertebrates, and sand lance, items which are less prevalent or absent in great black-backed gull diets. This suggests several ways in which these 2 species of gull partition their diet in this ecosystem.

Great black-backed gulls also showed marked differences in diet among age classes. In other gull species, adults may displace immature birds from foraging opportunities (Greig et al. 1983), but we observed no difference in stable isotope signatures between immature and adult great black-backed gulls during the summer or winter. However, during the breeding season, the stable isotope signatures of adult gulls differed from that of juveniles and chicks. Adults had a more restricted diet at a higher trophic level compared to chicks; presumably adults were selectively provisioning chicks with easily digestible prey of high energy content (Pierotti & Annett 1987, Steen-

weg et al. 2011). Post-fledging juveniles sampled in August also showed a greater diversity in dietary items compared to adults, though main items were similar to adults and included scavenged prey, such as crabs and seal, which may be the easiest items to obtain as they learn to forage on their own. Little is known about the learning of foraging in post-fledging seabirds, but differences in experience and energetic demands likely play a role in divergent foraging strategies between fledglings and adults (Gutowsky et al. 2014).

Among seasons, dietary shifts should be expected due to changes in seasonally available prey and reduced energetic demands post breeding. We observed decreased foraging trophic level ($\delta^{15}N$) and lower $\delta^{13}C$ values in great black-backed gulls sampled during the winter, which was consistent with other studies comparing breeding and non-breeding diets of gulls (Hobson 1993, Steenweg et al. 2011). This result, however, was contrary to what was expected since the winter period on Sable Island presents increased scavenging opportunities of high trophic level prey when gulls are foraging on placenta and dead pups during the grey seal breeding season. The decreased $\delta^{15}N$ values during winter may be explained by the timing of gull sampling, which occurred in early January (only 1 or 2 wk into the pupping season), when the 2 to 3 wk turnover rate for blood isotope values (Hobson & Clark 1992a) would not yet have resulted in $\delta^{15}N$ enrichment from seal contribution to the diet. Nevertheless, the $\delta^{15}N$ signature in winter was still a trophic level higher than mainland colonies (Steenweg et al. 2011), suggesting high trophic level foraging for great black-backed gulls year-round at Sable Island.

We also observed high individual-level variability in both $\delta^{15}N$ and $\delta^{13}C$ stable isotope signatures which spaned more than a full trophic level for each gull species. Although gulls are typically regarded as generalist predators due to their broad diets, individual specialization may be common within a population (Pierotti & Annett 1991). For great black-backed gulls, individual level variability in blood $\delta^{15}N$ and $\delta^{13}C$ were positively correlated with head size, indicating that larger birds (presumably males) foraged at higher trophic levels and on higher $\delta^{13}C$ prey types (e.g. seals). Great black-backed gulls are highly sexually dimorphic with males on average ~20% heavier than females (Good 1998), which may account for the observed size-related differences in prey choice since larger birds (i.e. males) exclude smaller birds from preferred prey (Greig et al. 1985) such as seal carcasses. Sex-specific foraging behaviours are also explained by sexual dimorphism in other seabird species (González-Solís et al. 2000, Weimerskirch et al. 2009). The lack of head-size effect for herring gulls may indicate less sexual segregation in diet for this species, and in some seabird species, sexes may partition resources through habitat specialization (Phillips et al. 2011).

For herring gulls, blood $\delta^{15}N$ values were positively correlated with a BCI which suggested that those individuals feeding at higher trophic levels were also in better condition. For other seabirds, positive correlations between body condition and $\delta^{15}N$ have been observed (Ronconi et al. 2010), higher quality prey may influence body condition and growth in juveniles (Janssen et al. 2011), and higher trophic level foraging may result in increased breeding performance for adults (Norris et al. 2007). On Sable Island, the individual herring gulls with higher $\delta^{15}N$ values had stable isotope signatures more similar to great black-backed gulls, suggesting their diets consisted of higher proportions of seal remains, an energy-rich food source which may improve body condition. During the breeding season, gull body condition may become depleted from the energetic demands of egg-laying (Houston et al. 1983) and mate-feeding (Hario et al. 1991), thus, dietary choice and individual specialization may play an important role in the replenishment and maintenance of body reserves after energetically demanding periods. In our study, herring gulls were sampled closer to egg-laying, compared with great black-backed gulls sampled during chick-rearing, which may explain the effect of trophic level on body condition during a period when herring gull energetic reserves would have been depleted post egg-laying.

CONCLUSIONS

On Sable Island, pellet sampling in 2011–2012 documented changes in gull diets since sampling 4 decades earlier; blood $\delta^{15}N$ values suggested that this population forages at a high trophic level in comparison with historical and current diets of mainland colonies, and stable isotopes identified seasonal, species-level, age-class and individual level dietary partitioning. Together, these results highlight the complexity and dynamics of gulls using the marine food-web around Sable Island. Moreover, because contaminant exposure in gulls is linked with prey choices, this study provides clues to potential dietary pathways for contaminants in this remote ecosystem (Gebbink et al. 2011, Burgess et al. 2013). Collec-

tively, the results of this study suggest dietary partitioning within this community of co-nesting gulls and that broad-scale dietary shifts have occurred since the early 1970s, thus laying a strong foundation for using gulls as bioindicators of marine ecosystem health and change in the offshore waters of Atlantic Canada.

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