# Great Black-backed Gull (*Larus marinus*) Predation on Seabird Populations at Two Colonies in Eastern Canada

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Abstract.—The increase in gull (Laridae) populations through the 20th century, largely due to an upsurge in anthropogenic food sources, has raised concerns about the effects of gulls on sympatric populations of other seabirds. In Newfoundland and Labrador, Canada, a reduction in fisheries discards due to the collapse of cod (Gadus morhua) populations and a phenological delay in the early 1990s and early 2000s in spawning capelin (Mallotus villosus) has supposedly resulted in increased seabird predation by gulls. Accordingly, the diet of Great Black-backed Gulls (Larus marinus) was quantified at two colonies (Gull Island, Witless Bay, Newfoundland, and Gannet Islands, Labrador), and the total mortality on sympatric breeding seabirds at each site was extrapolated. At the Gannet Islands, Great Black-backed Gulls primarily kleptoparasitized Atlantic Puffins (Fratercula arctica) bringing sandlance (Ammodytes sp.) to their chicks, whereas at Gull Island, seabirds formed the bulk of the gulls' diet. Great Black-backed Gulls preferred murre (Uria spp.) eggs at both sites, selecting them in far greater proportion than their abundance, consuming up to 40% of Common Murre (U. aalge) eggs laid on Gull Island. Great Black-backed Gulls also targeted Black-legged Kittiwake (Rissa tridactyla) eggs, chicks, and adults at Gull Island. Great Black-backed Gulls clearly selected certain seabird prey disproportionately to their availability, but likely have not had significant effects on the populations of other sympatric seabirds, with the possible exception of Black-legged Kittiwakes, which declined significantly from the 1970s to the early 2000s. Received 3 June 2014, accepted 7 August 2015.

**Key words.**—Gannet Islands, Great Black-backed Gull, Gull Island, *Larus marinus*, predation, seabirds, Witless Bay.

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**A**lthough Great Black-backed Gulls (Larus marinus) are considered opportunistic scavengers (Burger 1988; Buckley 1990), individuals may specialize on taking seabird eggs (Lock 1973; Regehr 1994; Massaro et al. 2000), young (McGill 1977; Mawhinney and Diamond 1999; Massaro et al. 2000), and even adults of some smaller species (Pierotti 1983; Roy 1986; Howes and Montevecchi 1993; Massaro et al. 2000). Great Blackbacked Gull populations have increased in many areas since the turn of the 20th century (Good 1998), but starting in the 1990s, the reduction of fisheries discards (Hutchings and Myers 1994), the late arrival of spawning capelin (Mallotus villosus) (Stenhouse and Montevecchi 1999; Massaro et al. 2000; Carscadden et al. 2001; Obradovich et al. 2014), and improved landfill practices may have decreased these food sources (but see Coulson 2015), and increased predation on

seabird populations in eastern Canada (Regehr 1994; Regehr and Rodway 1999; Stenhouse and Montevecchi 1999; Stenhouse *et al.* 2000).

Gulls and other predatory seabirds have been implicated in either population declines or decreased demographic rates in a variety of other seabirds though the causes and effects of gull-seabird interactions have changed considerably over time (O'Connell and Beck 2003; Oro et al. 2005; Donehower et al. 2007; Matias and Catry 2010). For example, when anthropogenic food sources were decreased in the Shetland Islands, Great Skuas (Stercorarius skua) switched to preying on seabird adults and chicks, resulting in possible population declines of other species (Furness 1981). However, when Great Skuas failed to breed because of very low levels of local forage fish abundance, Great Skua demand for food decreased,

reducing Black-legged Kittiwake (*Rissa tridactyla*) predation (Oro and Furness 2002). Long-term population effects, however, were thought to be minimal in this system (Oro and Martínez-Albraín 2007). Similarly, Western Gulls (*Larus occidentalis*) at the Farallon Islands may have played a role in the decline of Ashy Storm-petrels (*Oceanodroma homochroa*) and Cassin's Auklets (*Ptychoramphus aleuticus*) in concert with changes in Western Gull forage fish prey availability (Ainley and Boekelheide 1990; Ainley *et al.* 1994).

Here, we investigated predation of Great Black-backed Gulls on Thick-billed Murres (Uria lomvia), Common Murres (U. aalge), Atlantic Puffin (Fratercula arctica), and Razorbill (Alca torda) eggs and chicks at Gull Island, Witless Bay, Newfoundland, and the Gannet Islands, Labrador, Canada, by quantifying prey selection. We also monitored the predation of eggs, chicks, and adults of Black-legged Kittiwakes and Leach's Stormpetrels (Oceanodroma leucorhoa) at Gull Island, as they are absent or present in very low numbers at the Gannet Islands. These data were used to extrapolate and compare the total mortality caused by Great Blackbacked Gull predation of seabirds at Gull Island, where there was an available supply of human refuse and capelin, to the the situation at the remote Gannet Islands, Labrador.

#### METHODS

Study Sites

Gull Island, Witless Bay, Newfoundland, Canada (47° 16′ N, 52° 47′ W) is the largest island in the Witless Bay Ecological Reserve, located 2.5 km off the mainland coast, 9 km from the Bay Bulls town landfill and 40 km from the City of St. John's landfill in Robin Hood Bay. It supports a diverse seabird community, including Atlantic Puffins, Black-legged Kittiwakes, Common Murres, Herring Gulls (L. argentatus), Leach's Strompetrels, and Razorbills (Robertson et al. 2004). Our other study site was the small cluster of six islands in the Gannet Islands Ecological Reserve (53° 56' N, 56° 30' W), located approximately 50 km east of Cartwright, Labrador, Canada. The avifauna of the Gannet Islands is less diverse, with only breeding Atlantic Puffins, Common and Thick-billed murres (hereafter, murres), and Razorbills, as well as small numbers of Black-legged Kittiwakes and a few Leach's Storm-petrels and Northern Fulmars (Fulmarus glacialis) (Robertson and Elliot 2002). Differences in latitude and the subsequent 1-month difference in breeding phenology allowed us to work at both sites in the spring/summer of 2000 and 2001. We conducted field work at Gull Island from early May through late July, and at the Gannet Islands from late June through late August, which encompassed the entire breeding seasons at these locations.

#### Numbers of Seabirds Fed to Chicks

Prey delivered to Great Black-backed Gull chicks was inferred from feeding watches and chick regurgitation, and nest debris were used to determine which breeding pairs had specialized in feeding their young other seabirds (González-Solís *et al.* 1997). Three observation blinds on Gull Island, from which 28 of 90 nests could be observed, were used to record feeding bouts. Nests were selected randomly across a variety of habitat types. Two 2-hr watches were randomly assigned throughout the day (all hours of daylight) for two observers, totalling 4 hr per day per person. We used each blind in rotation to prevent one blind from being favored over any other.

At the Gannet Islands, inter-island observations were made from one observation point, using a 20-60x spotting scope, of six of the 25 total nests from the island inhabited by researchers (GC2) to the island 300 m to its west (GC1). Two-hr feeding watches were randomly assigned throughout the day as on Gull Island with the addition of an all day, continuous feeding watch once a week. The nests selected for the feeding watches were believed to be representative of the population considering the small number, low nesting density and similar habitat used by all pairs at the Gannet Islands.

Feeding watches were deemed the most reliable method for identifying items in Great Black-backed Gull chick meals because nest debris consisted mainly of non-digestible regurgitated items and egg shells, and chicks were only able to regurgitate items that had been eaten recently (Duffy and Jackson 1986). When all the diet data were combined, we characterized the chicks' broad diet category using a step-wise procedure: if there were  $\geq 10$  feeding bouts for a nest, we used the feeding watch data. If there were < 10 feeding bouts when we could not use direct observations, we used regurgitations for the remaining observations. Nest debris was used only if we did not have 10 bouts using feeding watches and regurgitations combined. Chick regurgitation and nest debris were used to identify diets at nests that were located outside the areas used in feeding watches.

## Number of Total Seabirds Taken

Feeding watches provided feeding frequency data that enabled us to quantify how many eggs, chicks, or adults of other seabirds were fed to Great Black-backed Gull chicks per 2-hr observation bout. This information was determined from the seabirds that could be seen from the blinds or observation points, and was used to extrapolate how many seabirds were being consumed by all breeding Great Black-backed Gull pairs at the

colonies. For example, if there were five pairs of Great Black-backed Gulls observed feeding each chick one Leach's Storm-petrel per feeding bout, and there were, on average, three watch bouts per day while the chicks were 10-16 days old, we concluded that at unobserved nests with storm-petrel pellets or storm-petrels in chick regurgitates, parents were feeding each 10-16 day-old chick three storm-petrels per 6 hr of daylight.

At the Gannet Islands, we were able to observe a large proportion of one island from another because of the small size and close proximity of the islands and due to the lack of visual obstruction by coniferous trees. This allowed us to set up Common and Thick-billed murre observation plots to compare how many eggs and chicks were being taken from the murre population relative to those the Great Black-backed Gulls brought back to their nests. The plots were large and contained both cliff and relatively flat, rocky habitat, which was believed to be representative of the overall colony sites. The ratio of murre eggs to Razorbill and Atlantic Puffin eggs found as nest debris was used to determine how many Razorbill and Atlantic Puffin eggs were taken from the colony. We believed this to be reliable because we assumed that a Great Black-backed Gull would have treated all eggs of the same species similarly. The total number of seabirds taken at the Gannet Islands was calculated using the following equations:

$$M_{taken} = (M_{voung} / M_{adult}) \times M_{total}$$
 (equation 1)

$$R/P_{taken} = (R/P_{found} / M_{found}) \times M_{taken}$$
 (equation 2)

where  $M_{young}$  = number of eggs or chicks taken from murre plot,  $M_{adult}$  = number of breeding murre pairs on murre plot,  $M_{total}$  = total number of murre eggs/chicks in total population,  $M_{taken}$  = total number of murre eggs/chicks taken from the population,  $M_{found}$  = number of murre eggs/chicks found at the nest site,  $R/P_{taken}$  = total number of Razorbill or Atlantic Puffin eggs/chicks taken from the population, and  $R/P_{found}$  = number of Razorbill or Atlantic Puffin eggs/chicks found at the nest site.

At Gull Island, one blind was set up to evaluate the number adult Atlantic Puffins a single pair of Great Black-backed Gulls killed. Owing to time constraints and the logistics of locating and observing additional nests, we were restricted to this one pair. We estimated the number of eggs available to Great Black-backed Gulls using a Black-legged Kittiwake clutch size of 1.38 eggs/nest (Regehr 1994; Massaro et al. 2000). Three of the species, Atlantic Puffins, Common Murres, and Razorbills, lay only a single egg, so we used the number of breeding pairs as a measure of the number of available eggs. Replacement clutches can occur, however, so this is an underestimate of the number of eggs available (Harris and Birkhead 1985; Gaston and Jones 1998; Harris and Wanless 2011). Atlantic Puffin eggs were included even though the species nests in burrows because some eggs wash out after heavy rains and make up a proportion of the Great Black-backed Gull's diet. Diet data are presented as the percent frequency of occurrence. We assumed that only breeding seabirds were available to Great Black-backed Gulls, which underestimates the abundance of available birds, meaning our estimate of the effect Great Black-backed Gull predation has on seabird populations is a conservative overestimate of population impacts, especially for Atlantic Puffins and Leach's Storm-petrels where younger birds prospect at potential breeding colonies for several years (Huntington *et al.* 1996; Breton *et al.* 2006). Great Black-backed Gulls are unable to obtain more benthic prey, such as sandlance (*Ammodytes* spp.), themselves, so any sandlance observed was attributed to kleptoparasitism of Atlantic Puffins returning food to their chicks (Rice 1985).

We calculated feeding frequency by recording the time of each chick feeding over the 2-hr observation bout for each nest, and extrapolating to encompass all daylight hours to derive a rate of feedings per day. This assumes that few feedings occurred after dark, though this would be when Great Black-backed Gulls depredate adult Leach's Strom-petrels, which are nocturnal, so our estimates are again conservative and slight overestimates (Good 1998).

Finally, we calculated the electivity index for Great Black-backed Gull diet on the two islands (Ivlev 1961), determined for each prey category as:

$$E_{i} = (r_{i} - P_{i}) / (r_{i} + P_{i})$$
 (equation 3)

where  $\mathbf{r}_i$  is the percentage of prey type i in the diet, and  $\mathbf{P}_i$  is the percentage of prey type i in the environment relative to the total available resources. A value of -1 indicates a prey item that was totally ignored, and a value of +1 describes a food item that was favored (Ivlev 1961).

#### Results

# **Feeding Frequencies**

At both Gull Island and the Gannet Islands, the mean number of times Great Black-backed Gull chicks were fed per day decreased over the breeding season (Fig. 1). The sizes of the food loads given to the chicks appeared to increase over time, but it was not possible to quantify because the information was obtained through observation from a distance. In both areas, the composition of diet over time also changed, with fish becoming the predominant prey in chick meals closer to the time of fledging (Fig. 2).

#### Chick Meal Composition

At the Gannet Islands, Great Black-backed Gulls fed their chicks mostly fish (71%), which were kleptoparasitized from

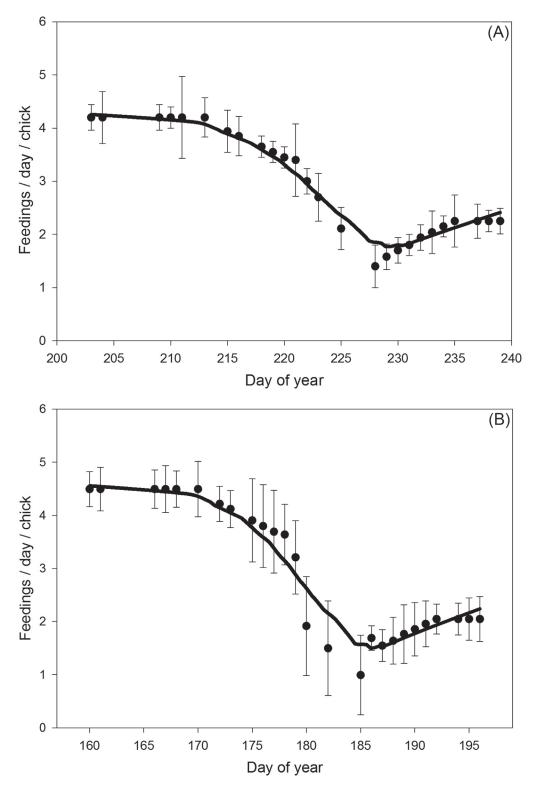


Figure 1. Great Black-backed Gull feeding frequency (number of feedings/day) over the breeding season at both the Gannet Islands (A) and Gull Island (B), Newfoundland and Labrador. Data are presented as mean  $\pm$  SD with a bi-square kernel smoothed fit.

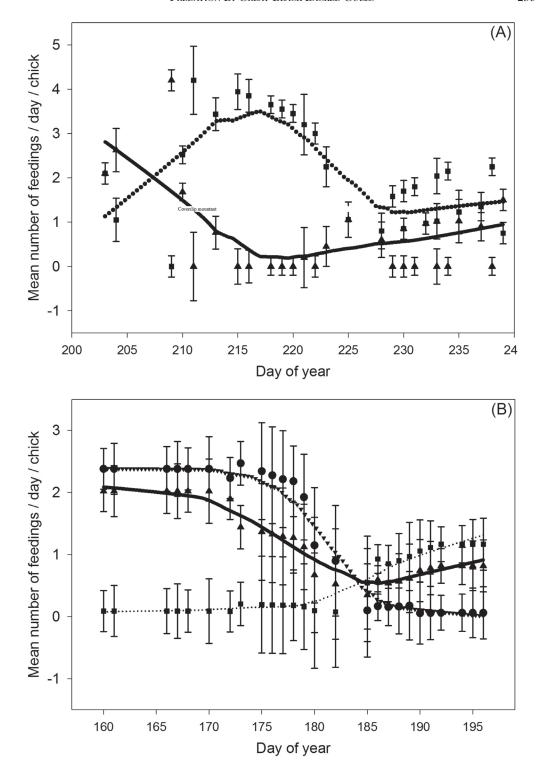


Figure 2. Changes in feeding frequencies of Great Black-backed Gulls and chick meal composition in relation to Atlantic Puffin chick hatching on the Gannet Islands (A) and capelin spawning around Gull Island (B), Newfoundland and Labrador. Data are presented as mean ± SD with a bi-square kernel smoothed fit. Fish prey: square symbols and dotted line; seabird prey: triangle symbols and solid line; garbage: diamond symbols and inverted triangle line.

Atlantic Puffins returning to their nests with sandlance, and seabirds (28%), with 1% of food items being unidentified. Gulls depredated Razorbill and murre eggs in greater proportions than were available ( $E_i = 0.49$  and 0.63, respectively; Fig. 3). Conversely, the number of Atlantic Puffin eggs and chicks taken was much lower than what

was available as prey items ( $E_i = -0.42$ ), and adult Atlantic Puffins were almost absent from chick meals at the Gannet Islands ( $E_i = -0.94$ ; Table 1).

Great Black-backed Gulls nesting on Gull Island relied heavily on garbage from local landfill sites (43%) and seabirds (39%) as sources of food for their chicks, with smaller

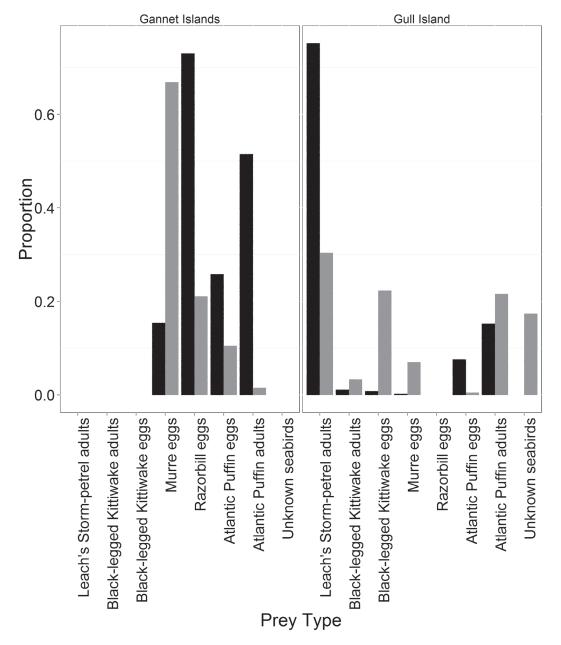


Figure 3. Available seabird prey (black bars) and Great Black-backed Gull chick meals (seabird portion only; gray bars) on the Gannet Islands and Gull Island, Newfoundland and Labrador, in 2001. Data are presented as the percent frequency of occurrence. Murres (*Uria* spp.) are grouped together.

Species	Gull Island	Gannet Islands
Leach's Storm-petrel adults	-0.25	n/a
Black-legged Kittiwake adults	0.63	n/a
Black-legged Kittiwake eggs	0.96	n/a
Common and Thick-billed murre eggs	0.98	0.63
Razorbill eggs	-1.00	0.49
Atlantic Puffin adults	-0.07	-0.94
Atlantic Puffin eggs	-0.93	-0.42

Table 1. Electivity index of seabird prey items for Great Black-backed Gulls in the Gannet Islands and on Gull Island, 2001. n/a = not applicable.

proportions of fish (15%) and invertebrates (4%, mainly snow crab discards from a nearby processing plant) (Fig. 4). Great Blackbacked Gull diet included a large number of Leach's Storm-petrels (Table 2), with roughly half as many in their diet (37%) compared with their relative availability (62%) (Fig. 3). At Gull Island, there was very high electivity for murre eggs ( $E_i = 0.98$ ) and Black-legged Kittiwake eggs and chicks ( $E_i = 0.96$ ). As at the Gannet Islands, there were proportionately more murre eggs in the Great Blackbacked Gull chick diet than what was available in the environment; this was also the case for both Black-legged Kittiwake adults and eggs (Fig. 3). Atlantic Puffin and Razorbill eggs seemed to be ignored or were unavailable (Table 1).

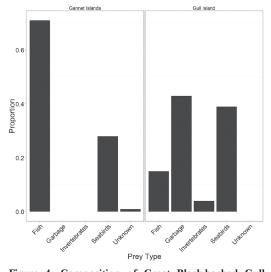


Figure 4. Composition of Great Black-backed Gull chick meals in 2001 at the Gannet Islands and Gull Island, Newfoundland and Labrador. Data are presented as the percent frequency of occurrence.

# **Total Mortality**

The level of seabird predation at the Gannet Islands was very low (Table 2), the highest being murre and Razorbill eggs taken early in the season (10.9% and 7.3% of eggs laid, respectively). The level of murre egg predation at Gull Island was the highest of all the predation seen, with 40.6% of eggs being depredated by Great Black-backed Gulls (Table 2). Black-legged Kittiwakes were also selected by Great Black-backed Gulls, with many eggs and young (22.3% of the estimated total present at the colony) and smaller numbers of breeding adults (2.2% of the population) taken (Table 2).

### DISCUSSION

The susceptibility of seabirds to predation by Great Black-backed Gulls was largely dependent upon how early in the season eggs were laid and their nesting habits (open site vs. burrow). Burrowing seabirds like Atlantic Puffins and Leach's Stormpetrels should have the lowest susceptibility to egg predation because their eggs and chicks generally remain underground until fledging, and had the lowest electivity index in this study. Razorbills should also be partially protected from egg predation by gulls because they often have protected breeding sites (Rowe et al. 2000). Cliff-nesting seabirds are the most susceptible to egg predation because their nests have little or no cover. Murres nesting on cliffs in high densities were more effective at defending their eggs than Black-legged Kittiwakes, which nest less densely along cliffs (Massaro et al. 2001). Cliff-nesting seabirds that laid eggs very early

Table 2. Estimated number of seabird prey items and level of Great Black-backed Gull predation found at two seabird colonies in eastern Canada. Population Size data are from Robertson and Elliot (2002) and Robertson et al. (2002, 2004). Population estimates are of breeding adults and number of eggs.

		Gull Island			Gannet Islands	
Prey Item	Population Size	Population Size Number Predated % of Population	% of Population	Population Size	Population Size Number Predated % of Population	% of Population
Leach's Storm-petrel adults	703,772	2,054	0.3	0	0	0
Black-legged Kittiwake adults	10,408	225	2.2	54	0	0
Black-legged Kittiwake eggs	7,182	1,603	22.3	65	0	0
Common & Thick-billed murre eggs	1,172	476	40.6	20,697	2,259	10.9
Razorbill eggs	213	0	0	808'6	713	7.3
Atlantic Puffin adults	280,858	1,202	0.4	69,224	52	0.1
Atlantic Puffin eggs	140,429	25	0.0	34,612	353	1.0

seemed to be most vulnerable to predation, since there were few conspecifics willing to stay at the nest site to defend against predators. This could differentially affect older, more established breeders, which tend to lay earlier than inexperienced, younger birds (Hedgren 1980; de Forest and Gaston 1996).

The level of seabird predation at the Gannet Islands was lower than expected, as seabirds were the only obvious source of food for Great Black-backed Gulls in that system. However, kleptoparasitism of items intended for other seabird chick meals was common. Similar to Herring Gulls (Pierotti 1983), Great Black-backed Gulls took Atlantic Puffin food loads from burrow entrances or by a brief foot chase until the puffin dropped its fish, which often occurred immediately. The apparent ease with which Great Blackbacked Gulls took food loads from Atlantic Puffins suggests that the net energy gained from kleptoparasitizing fish could be higher than depredating the seabirds themselves. Sandlance, the predominant fish item in the Great Black-backed Gull diet at the Gannet Islands, had the highest caloric value of all fish consumed by Atlantic Puffins (Russell 1999). The dominance of an easily obtained, high-energy food source is expected, as predators should concentrate on the most rewarding prey (Milinski and Parker 1991).

The level of seabird predation at the Gannet Islands was highest at the beginning of the breeding season. By the time most of the murres had laid their eggs, Great Blackbacked Gulls should have reduced predation success because the murres collectively defended the contents of their breeding sites from avian predators (Gilchrist and Gaston 1997). The slight increase in seabirds in the Great Black-backed Gull chick meals later in the season arose from predation of recently-departed murre and Razorbill chicks that are extremely vulnerable in the hours following their departure to sea with their male parent (Ainley et al. 2002; Lavers et al. 2009).

The low levels of seabird predation by Great Black-backed Gulls at the Gannet Islands were reflected in surveys of the seabird populations where Atlantic Puffin and Blacklegged Kittiwake numbers have remained constant, Razorbill and Thick-billed Murre numbers have increased, and Common Murre numbers have likely declined (Robertson and Elliot 2002). The apparent decline in the Common Murre population was mainly attributed to changes in the marine ecosystem in the Northwest Atlantic (Bryant and Jones 1999), Arctic fox predation, and/or a variation between surveys (Robertson and Elliot 2002) rather than Great Blackbacked Gull predation. Additionally, murres that lose their eggs early in the season can successfully lay replacement clutches and raise their chicks to fledging (Hipfner *et al.* 1999, 2001, 2003).

Although Leach's Storm-petrels made up a large part of the Great Black-backed Gull chick meals, they were not preferentially selected ( $E_1 = -0.25$ ). The large breeding population of Leach's Storm-petrels, and likely predation on prospecting pre-breeders, together formed an easily available prey for Great Black-backed Gulls. In 1997, Herring Gull predation on Leach's Storm-petrels amounted to tens of thousands of birds killed (Stenhouse et al. 2000), so the 2,000 birds consumed by Great Black-backed Gulls in the current study pales in comparison to the number depredated by Herring Gulls. The proportion of murre eggs in the diet of Great Black-backed Gulls was very high for the small numbers of breeding murres on Gull Island, and constituted 40% of the murre eggs laid. Great Black-backed Gulls mostly take murre eggs early in the breeding season, and murres are capable of laying replacement clutches and successfully raising a chick (Hipfner et al. 2001, 2003). It appears that Great Black-backed Gull predation likely does not represent a limiting factor for Common Murre populations in Witless Bay, which numbered approximately 100,000 pairs in 2011 (Canadian Wildlife Service, unpubl. data).

We found a significant level of predation of Black-legged Kittiwakes and their young at Gull Island, and the predation levels we observed have the potential to affect the long-term viability of the Black-legged Kittiwake population. The Black-legged Kittiwake population on Gull Island declined from more than 10,000 pairs in 1971 (Haycock 1973) to 4,300 pairs in 2003 (Robertson et al. 2004), and is not surprising given the high predation rates we observed. This decline was predicted by Regehr (1994), who found that Great Black-backed Gull predation of Black-legged Kittiwake eggs, in combination with low reproductive success, was likely to result in population declines. The late arrival of capelin was also linked to poor Black-legged Kittiwake productivity, which in turn made them more susceptible to Great Black-backed Gull predation by lessening their ability for communal defense (Massaro et al. 2000).

The density of Great Black-backed Gulls, as well as Herring Gulls, near Black-legged Kittiwake nest sites may have affected predation rates. Although Atlantic Puffins nesting amongst dense populations of Herring Gulls are less likely to be predated than those in low gull density areas because of interference competition (Nettleship 1972), this is unlikely to affect Black-legged Kittiwake predation rates, as Great Black-backed Gulls are more solitary than Herring Gulls, and such high nesting densities are uncommon (Good 1998). Herring Gulls seldom depredate Black-legged Kittiwakes (Pierotti 1982; A. L. Bond, unpubl. data), and Black-legged Kittiwakes that nest amongst Herring Gulls experience low levels of gull predation (Regehr 1994). Although Herring Gulls may have taken a few Black-legged Kittiwake chicks, they were very effective at deterring Great Black-backed Gulls. Given recent Herring Gull population declines (Bond et al. 2016), this could indirectly contribute to declining Black-legged Kittiwake breeding success, particularly if capelin arrival is delayed.

Great Black-backed Gulls at the Gannet Islands did not seem to have a detrimental effect on seabird populations because of a concentration on kleptoparasitizing sandlance from Atlantic Puffins rather than feeding on seabirds themselves. At Gull Island, Black-legged Kittiwakes were heavily depredated, and this may be contributing to the population decline. The continued decline in the Great Black-backed Gull breeding population at Witless Bay (Bond *et al.* 2016) means

that predation rates are not likely to affect sympatric species in the immediate future.

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## LITERATURE CITED

- Ainley, D. G. and R. J. Boekelheide. 1990. Seabirds of the Farallon Islands. Stanford University Press, Stanford, California.
- Ainley, D. G., W. J. Sydeman, S. A. Hatch and U. W. Wilson. 1994. Seabird population trends along the west coast of North America: causes and the extent of regional concordance. Studies in Avian Biology 15: 119-133.
- Ainley, D. G., D. N. Nettleship, H. R. Carter and A. E. Storey. 2002. Common Murre (*Uria aalge*). No. 666 in The Birds of North America (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania; American Ornithologists' Union, Washington, D.C.
- Bond, A. L., S. I. Wilhelm, G. J. Robertson and S. Avery-Gomm. 2016. Differential declines among nesting habitats of breeding Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*Larus marinus*) in Witless Bay, Newfoundland and Labrador, Canada. Waterbirds 39 (Special Publication 1): 143-151.
- Breton, A. R., A. W. Diamond and S. W. Kress. 2006. Encounter, survival, and movement probabilities from an Atlantic Puffin (*Fratercula arctica*) metapopulation. Ecological Monographs 76: 133-149.
- Bryant, R. and I. L. Jones. 1999. Food resource use and diet overlap of Common and Thick-billed Murres at the Gannet Islands, Labrador. Waterbirds 22: 392-400.
- Buckley, N. J. 1990. Diet and feeding ecology of Great Black-backed Gulls (*Larus marinus*) at a southern Irish breeding colony. Journal of Zoology (London) 222: 363-373
- Burger, J. 1988. Foraging behavior in gulls: differences in method, prey, and habit. Colonial Waterbirds 11: 9-23.
- Carscadden, J. E., K. T. Frank and W. C. Leggett. 2001. Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. Canadian Journal of Fisheries and Aquatic Sciences 58: 73-85.
- Coulson, J. C. 2015. Re-evaluation of the role of landfills and culling in the historic changes in the Herring Gull (*Larus argentatus*) population in Great Britain. Waterbirds 38: 339-354.
- de Forest, L. N. and A. J. Gaston. 1996. The effect of age on timing of breeding and reproductive success in the Thick-billed Murre. Ecology 77: 1501-1511.

- Donehower, C. E., D. M. Bird, C. S. Hall and S. W. Kress. 2007. Effects of gull predation and predator control on tern nesting success at Eastern Egg Rock, Maine. Waterbirds 30: 29-39.
- Duffy, D. C. and S. Jackson. 1986. Diet studies of seabirds: a review of methods. Colonial Waterbirds 9: 1-17.
- Furness, R. W. 1981. The impact of predation by Great Skuas *Catharacta skua* on other seabird populations at a Shetland colony. Ibis 123: 534-539.
- Gaston, A. J. and I. L. Jones. 1998. The auks: Alcidae. Oxford University Press, New York, New York.
- Gilchrist, H. G. and A. J. Gaston. 1997. Effects of murre nest site characteristics and wind conditions on predation by Glaucous Gulls. Canadian Journal of Zoology 75: 518-524.
- González-Solís, J., D. Oro and V. Pedrocchi. 1997. Bias associated with diet samples in Andouin's Gulls. Condor 99: 773-779.
- Good, T. P. 1998. Great Black-backed Gull (*Larus marinus*). No. 330 in The Birds of North America (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania; American Ornithologists' Union, Washington, D.C.
- Harris, M. P. and T. R. Birkhead. 1985. Breeding ecology of the Atlantic Alcidae. Pages 155-204 in The Atlantic Alcidae: the Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas (D. N. Nettleship and T. R. Birkhead, Eds.). Academic Press, London, IJ K
- Harris, M. P. and S. Wanless. 2011. The puffin. T. & A. D. Poyser, London, U.K.
- Haycock, K. A. 1973. Ecological studies on Gull Island, Witless Bay, with particular reference to avifauna. M.S. Thesis, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador.
- Hedgren, S. 1980. Reproductive success of guillemots *Uria aalge* on the island of Stora Karlsö. Ornis Fennica 57: 49-57
- Hipfner, J. M., A. J. Gaston and A. E. Storey. 2001. Nestsite safety predicts the relative investment made in first and replacement eggs by two long-lived seabirds. Oecologia 129: 234-242.
- Hipfiner, J. M., A. J. Gaston, D. L. Martin and I. L. Jones. 1999. Seasonal declines in replacement egg-layings in a long-lived, Arctic seabird: costs of late breeding or variation in female quality? Journal of Animal Ecology 68: 988-998.
- Hipfner, J. M., A. J. Gaston, G. R. Herzberg, J. T. Brosnan and A. E. Storey. 2003. Egg composition in relation to female age and relaying: constraints on egg production in Thick-billed Murres (*Uria lomvia*). Auk 120: 645-657
- Howes, L.-A. and W. A. Montevecchi. 1993. Population trends and interactions among terms and gulls in Gros Morne National Park, Newfoundland. Canadian Journal of Zoology 71: 1516-1520.
- Huntington, C. E., R. G. Butler and R. A. Mauck. 1996. Leach's Storm-petrel (*Oceanodroma leucorhoa*). No. 233 in The Birds of North America (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia,

- Pennsylvania; American Ornithologists' Union, Washington, D.C.
- Hutchings, J. A. and R. A. Myers. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Canadian Journal of Fisheries and Aquatic Sciences 51: 2126-2146.
- Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut.
- Lavers, J. L., J. M. Hipfner and G. Chapdelaine. 2009. Razorbill (*Alca torda*). No. 635 in The Birds of North America Online (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. http://bna.birds.cornell. edu/bna/species/635, accessed 6 June 2014.
- Lock, A. R. 1973. A study of the breeding biology of two species of gulls nesting on Sable Island, Nova Scotia. Ph.D. Thesis, Dalhousie University, Halifax, Nova Scotia.
- Massaro, M., J. W. Chardine and I. L. Jones. 2001. Relationships between Black-legged Kittiwake nest-site characteristics and susceptibility to predation by large gulls. Condor 103: 793-801.
- Massaro, M., J. W. Chardine, I. L. Jones and G. J. Robertson. 2000. Delayed capelin (*Mallotus villosus*) availability influences predatory behaviour of large gulls on black-legged kittiwakes (*Rissa tridactyla*), causing a reduction in kittiwake breeding success. Canadian Journal of Zoology 78: 1588-1596.
- Matias, R. and P. Catry. 2010. The diet of Atlantic Yellow-legged Gulls (*Larus michahellis atlantis*) at an oceanic seabird colony: estimating predatory impact upon breeding petrels. European Journal of Wildlife Research 56: 861-869.
- Mawhinney, K. and A. W. Diamond. 1999. Using radiotransmitters to improve estimates of gull predation on Common Eider ducklings. Condor 101: 824-831.
- McGill, P. A. 1977. Breeding ecology and competition between Great Black-backed and Herring Gulls. Ph.D. Thesis, Cornell University, Ithaca, New York.
- Milinski, M. and G. A. Parker. 1991. Competition for resources. Pages 137-168 in Behavioural Ecology: an Evolutionary Approach (J. R. Krebs and N. B. Davies, Eds.). Blackwell Scientific Publications, Oxford, U.K.
- Nettleship, D. N. 1972. Breeding success of the Common Puffin (Fratercula arctica L.) on different habitats at Great Island, Newfoundland. Ecological Monographs 42: 239-268.
- Obradovich, S. G., E. H. Carruthers and G. A. Rose. 2014. Bottom-up limits to Newfoundland capelin (*Mallotus villosus*) rebuilding: the euphausiid hypothesis. ICES Journal of Marine Science 71: 775-783.
- O'Connell, T. J. and R. A. Beck. 2003. Gull predation limits nesting success of terns and skimmers on the Virginia barrier islands. Journal of Field Ornithology 74: 66-73.
- Oro, D. and R. W. Furness. 2002. Influences of food availability and predation of survival of kittiwakes. Ecology 83: 2516-2528.
- Oro, D. and A. Martínez-Albraín. 2007. Deconstructing myths on large gulls and their impact on threatened sympatric waterbirds. Animal Conservation 10: 117-126.

- Oro, D., A. de León, E. Minguez and R. W. Furness. 2005. Estimating predation on breeding European stormpetrels (*Hydrobates pelagicus*) by yellow-legged gulls (*Larus michahellis*). Journal of Zoology (London) 265: 491-499
- Pierotti, R. 1982. Habitat selection and its effect on reproductive output in the Herring Gull in Newfoundland. Ecology 63: 854-868.
- Pierotti, R. 1983. Gull-puffin interactions on Great Island, Newfoundland. Biological Conservation 26: 1-14.
- Regehr, H. M. 1994. Breeding performance of Blacklegged Kittiwakes on Great Island, Newfoundland, during periods of reduced food availability. M.S. Thesis, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador.
- Regehr, H. M. and M. S. Rodway. 1999. Seabird breeding performance during two years of delayed capelin arrival in the Northwest Atlantic: a multi-species comparison. Waterbirds 22: 60-67.
- Rice, J. 1985. Interactions of variation in food supply and kleptoparasitism levels on the reproductive success of Common Puffins (*Fratercula arctica*). Canadian Journal of Zoology 63: 2743-2747.
- Robertson, G. J. and R. D. Elliot. 2002. Population size and trends of seabirds breeding in the Gannet Islands, Labrador. Technical Report Series No. 393, Canadian Wildlife Service, Atlantic Region, Mount Pearl, Newfoundland and Labrador.
- Robertson, G. J., J. Russell and D. A. Fifield. 2002. Breeding population estimates for three Leach's Storm-petrel colonies in southeastern Newfoundland. Technical Report Series No. 380, Canadian Wildlife Service, Atlantic Region, Mount Pearl, Newfoundland and Labrador.
- Robertson, G. J., S. I. Wilhelm and P. A. Taylor. 2004. Population size and trends of seabirds breeding on Gull and Great Islands, Witless Bay Islands Ecological Reserve, Newfoundland, up to 2003. Technical Report Series No. 418, Canadian Wildlife Service, Atlantic Region, Mount Pearl, Newfoundland and Labrador.
- Rowe, S., I. L. Jones, J. W. Chardine, R. D. Elliot and B. G. Veitch. 2000. Recent changes in the winter diet of murres (*Uria* spp.) in coastal Newfoundland waters. Canadian Journal of Zoology 78: 495-500.
- Roy, N. A. 1986. The breeding biology and behaviour of Great Black-backed Gulls (*Larus marinus*) in Newfoundland. M.S. Thesis, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador.
- Russell, J. 1999. Chick diet and nestling condition among Atlantic Puffins at three Northwest Atlantic colonies. M.S. Thesis, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador.
- Stenhouse, I. J. and W. A. Montevecchi. 1999. Indirect effects of the availability of capelin and fishery discards: gull predation on breeding storm-petrels. Marine Ecology Progress Series 184: 303-307.
- Stenhouse, I. J., G. J. Robertson and W. A. Montevecchi. 2000. Herring Gull Larus argentatus predation on Leach's Storm-petrel Oceanodroma leucorhoa breeding on Great Island, Newfoundland. Atlantic Seabirds 2: 35-44.