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Changes in nesting-habitat use of large gulls breeding in Witless Bay, Newfoundland

Gregory J. Robertson, David Fifield, Melanie Massaro, and John W. Chardine

Abstract: We counted herring gull (*Larus argentatus*) and great black-backed gull (*Larus marinus*) nests in the Witless Bay Seabird Ecological Reserve in southeastern Newfoundland, Canada, in 1999 and 2000 and compared our results with previous nest counts from the 1970s. On Gull Island, herring gull nest numbers were 27.5% (1999) and 30.0% (2000) lower than in 1979. Similarly, on Great Island, by 2000 the numbers of herring gull nests had declined 40.8% from numbers in 1979. Counts of great black-backed gull nests were more variable, but suggest a slight or no reduction since 1979. Numbers of herring gulls nesting in rocky and puffin-slope habitats were much reduced (50–70%), while numbers nesting in meadows and forests have actually increased since the 1970s. Great black-backed gulls showed a similar change in nesting distribution. For herring gulls, these changes in nesting numbers matched differences in reproductive success previously documented in these habitats. We suggest that the decline in gull numbers and the change in breeding-habitat selection were caused by changes in the food availability for gulls. Reduced amounts of fisheries offal and the delayed arrival onshore of capelin (*Mallotus villosus*), an important fish prey species for gulls, have all likely led to the decline in gull reproductive output. Gulls nesting in meadows and forests may be maintaining adequate reproductive output by focusing on alternative prey, such as adult Leach's storm-petrels (*Oceanodroma leucorhoa*), rather than scarce refuse and fish.

Résumé : Nous avons dénombré les nids de Goélands argentés (*Larus argentatus*) et de Goélands marins (*Larus marinus)* dans la réserve écologique de Witless Bay, dans le sud-est de l'île de Terre-Neuve, Canada, en 1999–2000 et comparé nos résultats à ceux de dénombrements antérieurs effectués dans les années 1970. Sur l'île Gull Island, les nids de Goélands argentés étaient de 27,5 % (1999) et de 30,0 % (2000) moins nombreux qu'en 1979. De même, dans l'île Great Island, le nombre de nids de Goélands argentés a baissé de 40,8 % entre 1979 et 2000. Le nombre de nids de Goélands marins était plus variable mais indique qu'il n'y a pas eu de réduction, ou alors très peu depuis 1979. Le nombre de Goélands argentés qui ont niché dans les habitats rocheux ou dans les habitats de macareux a beaucoup baissé (50–70 %), alors que le nombre d'oiseaux qui ont niché dans les prés et dans les forêts a augmenté depuis les années 1970. On a observé les mêmes tendances chez les Goélands marins. Les changements observés chez les Goélands argentés correspondent à des différences dans le succès de la reproduction telles que décrites antérieurement dans ces habitats. Nous croyons que la réduction du nombre de goélands et les changements dans le choix d'habitat pour la reproduction ont été causés par des changements dans la disponibilité de la nourriture. La réduction d'entrailles de poisson et l'arrivée tardive, sur les berges, des Capelans (*Mallotus villosus*), proies importantes pour les goélands, ont probablement entraîné le déclin du rendement de la reproduction. Les goélands qui nichent dans les prés ou les forêts réussissent sans doute à maintenir leur rendement en consommant d'autres proies, telles des Océanites cul-blanc (*Oceanodroma leucorhoa*) plutôt que des déchets ou des espèces peu abondantes de poissons.

[Traduit par la Rédaction]

Introduction

After suffering declines through the 19th century, many populations of large gull species increased substantially over the 20th century (Drury 1973, 1974; Blokpoel and Tessier 1986). These increases have been attributed to the ability of large gulls to utilize resources provided by humans, most notably refuse (Pons and Migot 1995) and fisheries offal and discards (Furness et al. 1992). These increases have ceased in many locations during the last two decades, and many gull populations are now stable or decreasing (Hébert 1989; Lloyd et al. 1991; Blokpoel and Tessier 1993; Chapdelaine and Rail 1997; Gilchrist and Robertson 1999). Reductions in available refuse (Pons 1992; Pons and Migot 1995) and the collapse of many fisheries, which reduces fish stocks and the amount of offal created by the fishery (Oro et al. 1995; Chapdelaine and Rail 1997), are suspected to have caused these population declines.

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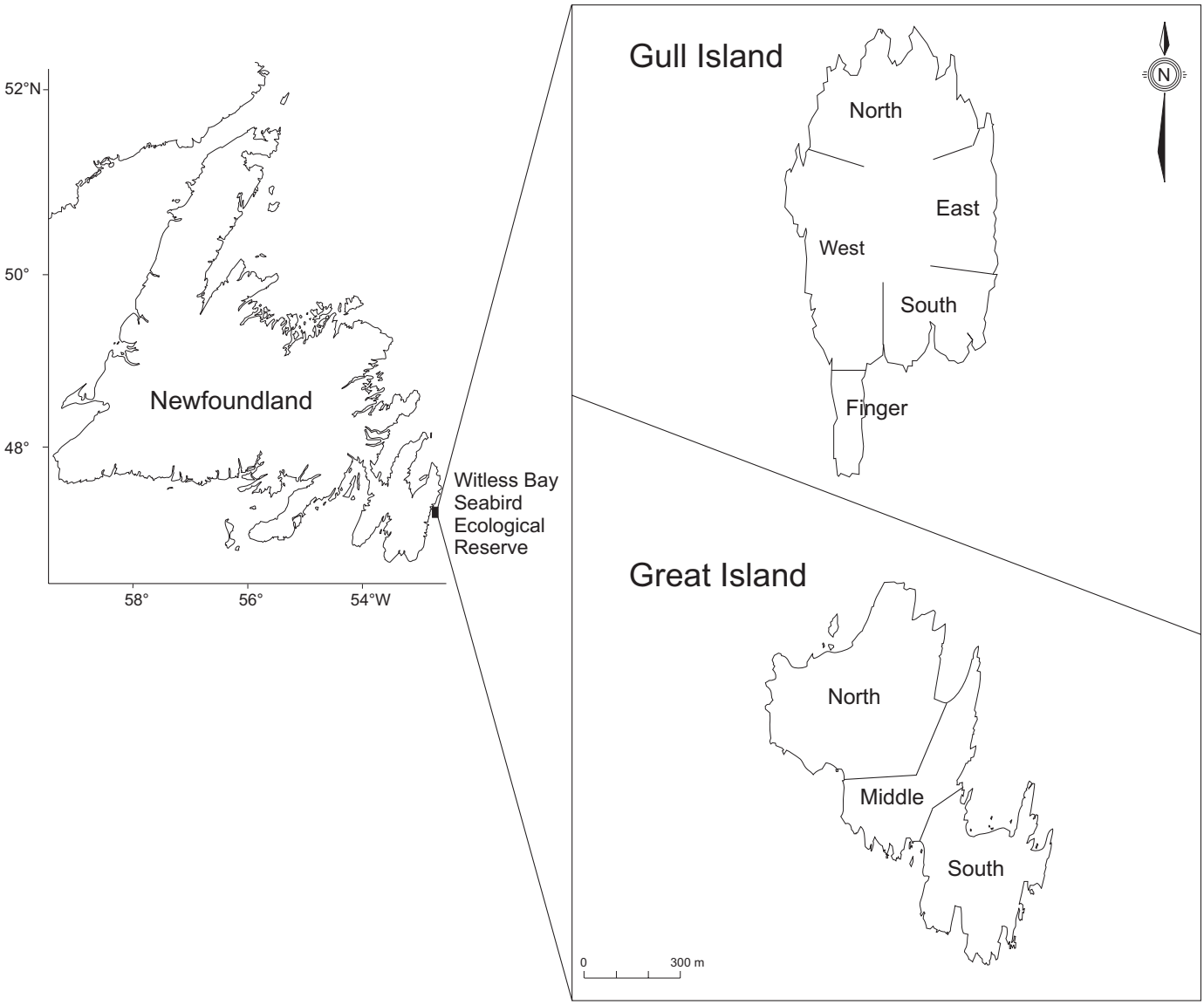
Fig. 1. The Witless Bay Seabird Ecological Reserve and its location in Newfoundland, Canada, and divisions used for pooling gull-nest counts on Gull Island and Great Island.



Between the 1970s and 1990s a number of changes occurred in Newfoundland that were expected to negatively impact breeding gulls (Howes and Montevecchi 1993; Rodway and Regehr 1999). A moratorium on groundfish fisheries was established in 1992, drastically reducing offal available to gulls. Since 1991, capelin (*Mallotus villosus*), an important food source for gulls during the breeding season, have been arriving onshore in Newfoundland much later (up to 1 month) than in previous decades (Nakashima 1996; Therriault et al. 1996; Regehr and Rodway 1999).

Nesting-habitat selection has been shown to be an important factor influencing the breeding success of large gulls (Pierotti 1982; Pierotti and Annett 1987; Rodway and Regehr 1999; but see Bosch and Sol 1998). Further, choice of nesting habitat and diet are linked in some species (Pierotti and Annett 1991). In the late 1970s an increasing population of herring gulls (*Larus argentatus*) nesting on Great Island, Newfoundland, preferred to nest in rocky habitats, and gulls were most successful in this habitat (Pierotti 1982). However, in 1992 and 1993, when breeding conditions were very poor, similar studies revealed that herring gulls nesting in meadows were more successful, although rocky habits were still heavily used (Rodway and Regehr 1999).

The main objective of this study was to document current population sizes and trends for large gulls nesting in the Witless Bay Seabird Ecological Reserve to determine if expected population reductions have occurred. Secondly, we investigated current nesting-habitat use by gulls and compared our results with those from earlier studies to determine if nesting-habitat use has changed in concordance with the differences in reproductive output recently documented for gulls in these habitats (Rodway and Regehr 1999).

Materials and methods

The largest herring gull colonies in Newfoundland are located in the Witless Bay Seabird Ecological Reserve (Fig. 1). Of the four islands in the reserve, Gull Island is the largest at 1.6 × 0.8 km.

The margins of the island include exposed rocky habitat, which tends to be steeper on the north and east sides of the island. A rim of puffin slope surrounds the island, while flat areas near the edge of the island tend to consist of grassy meadows. The interior of the island, which forms the bulk of the habitat, is forested mainly with black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*). Great Island, 1.4 × 0.7 km, is similar but there is less forest interior and much more extensive puffin slopes that penetrate the interior of the island, and the rocky slopes tend to be steeper (for more detailed descriptions see Cairns and Verspoor 1980 and Rodway et al. 1996). Pee Pee Island is much smaller (0.4 × 0.1 km) and only has meadow and puffin-slope habitats in the middle of the island. In addition to herring gulls and great black-backed gulls (*Larus marinus*), large populations of seabirds, including 71 000 and 123 000 pairs of Atlantic puffins (*Fratercula arctica*), over 1600 and 3000 pairs of common murres (*Uria aalge*), 5200 and 24 000 pairs of black-legged kittiwakes (*Rissa tridactyla*), 213 and 120 pairs of razorbills (*Alca torda*), and 350 000 and 270 000 pairs of Leach's storm-petrels (*Oceanodroma leucorhoa*) breed on Gull Island and Great Island, respectively (Canadian Wildlife Service (CWS), unpublished data; Cairns and Verspoor 1980; Rodway et al. 1996; Stenhouse et al. 2000). As Pee Pee Island is smaller, it only harbours a small colony of 1200 breeding Atlantic puffins (Cairns and Verspoor 1980). The fourth island in the reserve is Green Island, which is surrounded by steep cliffs, where likely over 100 000 pairs of murres breed annually (Cairns et al. 1989; CWS, unpublished data). Green Island was not surveyed for gull nests, to reduce disturbance to breeding murres and danger to researchers working at this site. In 1979 this island supported at least 304 nesting herring gulls and 51 great black-backed gulls (Cairns and Verspoor 1980).

Surveys on Great Island were conducted from 3 to 6 June 2000, on Gull Island from 19 May to 1 June 1999 and from 23 to 29 May 2000, and on Pee Pee Island on 6 June 2000. We conducted a count of all gull nests on the islands to reduce error caused by sampling and to make our results comparable with those from earlier surveys (Haycock and Threlfall 1975; Cairns and Verspoor 1980; Pierotti 1982). In previous surveys Gull Island was divided into 14 sections and Great Island into 21 sections (Cairns and Verspoor 1980) and total nest counts were made for each section (Pee Pee Island was surveyed in one pass). These sections were pooled into larger areas for two reasons. Firstly, it was not always possible to delimit the exact border between sections based on the maps available, and secondly, we wished to pool sections of similar habitats for comparisons. Sections and broad descriptions of their habitats are given in the Appendix. Flagging tape was used to delimit the borders of each section prior to the nest count. One to five observers made counts. Usually we divided each section into transects and observers would walk parallel to each other, about 5–10 m apart, counting all nests to one side of them. The observer at the edge of the transect would identify the line they were walking by means of (*i*) visual landmarks such as large boulders or (*ii*) flagging tape (used extensively when surveying in the forest). Once the transect was complete, the person who walked the outermost line would retrace their path counting all nests on the other side. Further, to ensure that nests were not missed or double-counted, a small yellow stick was placed in every counted nest. All observers would call out gull species, clutch size, and habitat around the nest to a person who recorded them.

We classified habitat around the nest into four categories. As in earlier studies, nests on rock slopes and ledges near the shore were classified as rocky habitat, nests on seaward-facing puffin slopes as puffin habitat, and nests on flat, open herbaceous meadows as meadow habitat (Pierotti 1982; Rodway and Regehr 1999). A fourth category, forest habitat, was added, as many nests were found in dense forest towards the interior of the island. These nests were usually found under the branches of stunted black spruce or balsam fir and often had small trails leading to them. There were only a few herring gulls and no great black-backed gulls nesting in the forest in the 1970s on Great Island (R. Pierotti, personal communication) and numbers were deemed too small to be worth including in the survey on Gull Island (Cairns and Verspoor 1980). To differentiate between herring gull and great black-backed gull nests we used a variety of clues, including egg size, nest-cup size, and the presence of a defending great black-backed gull flying overhead. Observers participating in this study had considerable experience in studying seabird colonies, and although we may have misclassified the species in the case of a few gull nests we do not feel that this error was large («5%). As misclassification of nests will not greatly impact herring gull numbers but will affect great black-backed gull estimates, the latter should be treated cautiously. Further, when gull nests were counted in 1979, great black-backed gull and herring gull nests were not classified. Species ratios were obtained by counting standing adults from a distant vantage point for each section of the survey. The species ratio of standing adults was applied to the total of nests counted. For Gull Island the counts of adults were done near the time of the survey, whereas on Great Island they were taken from early June to late July (Cairns and Verspoor 1980).

For the purposes of this paper, clutch size is the number of eggs in the nest near the end of the incubation period. This late in the nesting season the vast majority of clutches will be complete. Clutch size therefore represents the maximum number of eggs laid by the pair minus any eggs lost during incubation. Means are presented ± 1 SD. A critical α of 0.05 was used throughout and all tests were two-tailed.

Results

Timing of the survey

Generally, surveys were well synchronized with the incubation period of herring gulls. Most nests were found with just eggs, and only a few nests were found with small chicks (on Gull Island, 99.5 and 99.9% of nests contained eggs in 1999 and 2000, respectively; on Great Island, 97.1%, Pee Pee Island, 97.0%). Great black-backed gulls were more advanced in their breeding cycle when we surveyed Great Island and Pee Pee Island; we found 75.0 and 85.8% of nests containing chicks, respectively. However, the chicks in these nests were still small and could not run away. Gull Island surveys were carried out early enough that most great black-backed gulls were still incubating their clutches (96.5% of nests contained eggs in 1999 and 100% in 2000).

Population trends

The herring gull population breeding on Gull Island increased through the late 1960s and early 1970s, peaking at 3852 nesting pairs in 1979 (Table 1). The population then declined to 2794 nesting pairs by 1999 and 2698 by 2000, a reduction of 27.5 and 30.0%, respectively (Table 1). Similarly, great black-backed gull populations increased through the late 1960s and early 1970s, peaking at 118 pairs in 1979. However, the population remained at a similar level of 115 pairs by 1999 and 89 pairs by 2000.

The two gull species showed similar trends on Great Island as on Gull Island, with population increases in the 1960s and 1970s and declines by 2000. Numbers of herring gull nests declined 40.8%, from 2771 in 1979 to 1640 in 2000 (Table 1). The number of great black-backed gull nests was variable, ranging from 40 in 1976 up to 80 (possibly an overestimate) in 1979 and then down to 28 in 2000 (Table 1).

Fig. 2. Proportions of gull nests (both species) in the four types of habitat on Great Island in 1976 and on Great and Gull islands in 2000. There were fewer than 10 (*) nests in forest in 1976 on Great Island (R. Pierotti, personal communication).

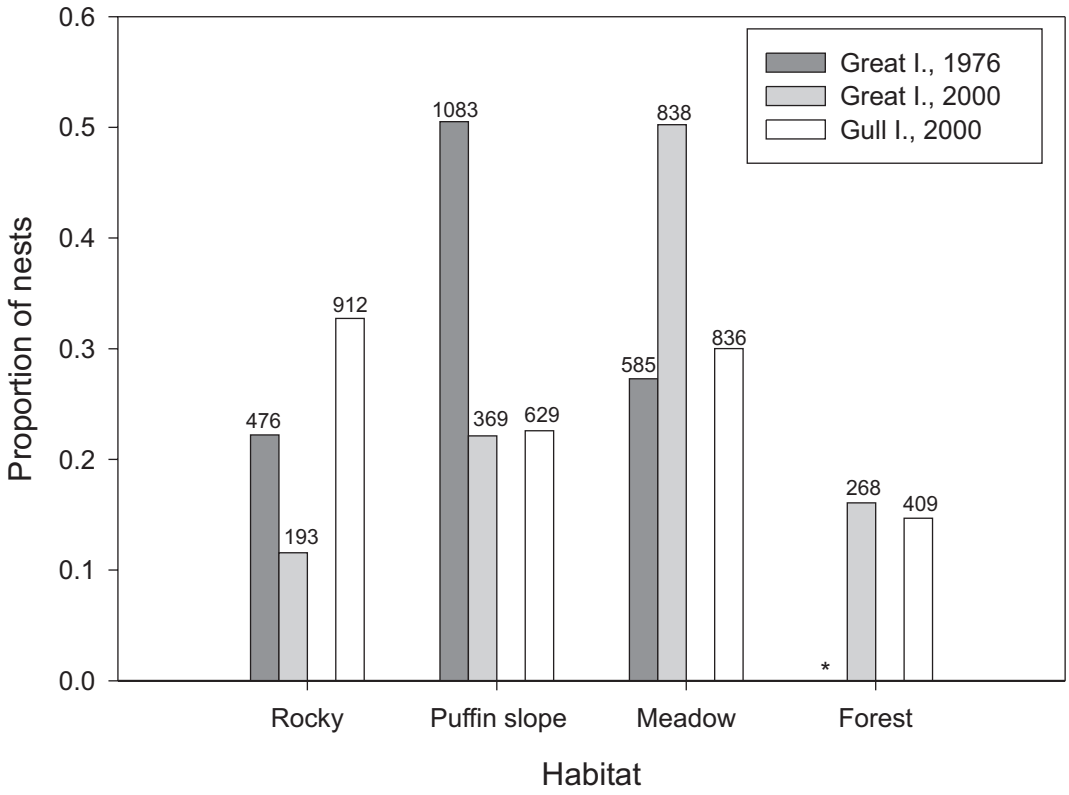


Table 1. Results of previous nest surveys of herring gulls, *Larus argentatus* (HERG), and great black-backed gulls, *Larus marinus* (GBBG), in Witless Bay, Newfoundland.

	Gull Island		Great Island		Pee Pee Island	
Year	HERG	GBBG	HERG	GBBG	HERG	GBBG
1968	1983[a]	—	1500[b]	40[b]	—	—
1969	2033[a,c]	36[a,c]	—	—	—	—
1970	2544[a,c]	40[a,c]	—	—	—	—
1971	2663[a]	—	—	—	—	—
1976	—	—	2104[d]	40[d]	—	—
1979	3852[e]	118[e]	2771[e]	80[e]	—	—
1984	—	—	—	—	75[f]	3[f]
1999	2794[g]	115[g]	—	—	—	—
2000	2698[g]	88[g]	1640[g]	28[g]	134[g]	7[g]

[a] From Threlfall (1978).
[b] From Nettleship (1972); rough estimate for late 1960s only.
[c] From Haycock (1973).
[d] From Pierotti (1982); the exact ratio of HERG to GBBG is not known, estimated ~40 pairs of GBBG and the rest HERG.
[e] From Cairns and Verspoor (1980). Note that GBBG counts on Great Island may be biased, as counts of standing adults were taken as late as 28 July, more than 6 weeks later than the survey dates.
[f] From Cairns et al. (1989).
[g] From this study.

Only two surveys are available for Pee Pee Island; although numbers of nesting herring and great black-backed gulls are small, they have actually increased at this colony since 1984 (Table 1).

Habitat use

Patterns of nesting-habitat use by herring gulls changed on Great Island between 1976 and 2000. Overall the population declined 22.2% between these years, yet the number of gulls nesting in rocky and puffin habitats declined 59.4 and 65.9%, respectively (Fig. 2). The number of gulls nesting in meadow habitats increased 43.2% and nest numbers in forest habitats increased from <10 to 268 nests. Meadows and forests now harbour the bulk of the breeding population.

Similar patterns were seen at larger, but coarser, scales on Gull Island and Great Island between 1979 and 2000 (Table 2). A reduction of >50% in herring and great black-backed gull nest numbers occurred on the east and south sides of Gull Island, areas composed predominantly of puffin and rocky habitats. Slight reductions in herring gull numbers and increases in great black-backed gull numbers occurred in the northern part of the island, which is a mixture of all habitats, while both species showed slight declines on the finger, a mixture of rocky and meadow habitats. Both species increased their numbers on the predominantly forested west side of Gull Island (Table 2). On Great Island, the two species showed similar patterns (although sample sizes were low for great black-backed gulls). The greatest reductions occurred in the rocky habitat – puffin habitat area at the south end of the island, moderate declines in the puffin habitat – meadow habitat areas in the middle of the island, and modest increases at the forested north end of the island (Table 2).

Clutch size

Herring gulls

There was no evidence that clutch size varied among habi-

Table 2. Numbers of nests of herring gulls (HERG) and great black-backed gulls (GBBG) in different areas of Gull and Great islands in 1979, 1999, and 2000.

	HERG				GBBG			
	1979	1999	2000	Change (%)[a]	1979	1999	2000	Change (%)[a]
Gull Island								
Finger (rocky–meadow)	508	394	373	–26.6	59	64	52	–11.9
South (rocky–puffin)	1259	623	608	–51.7	29	11	12	–58.6
East (puffin)	1048	400	377	–64.0	28	13	8	–71.4
North (mix)	653	585	579	–11.3	2	18	9	+350
West (forest–puffin)	384	792	761	+98.2	0	9	7	+∞
Great Island								
South (puffin–rocky)	1666	—	774	–53.5	66[b]	—	14	–78.8
Middle (meadow–puffin)	788	—	456	–42.1	8[b]	—	7	–12.5
North (forest)	317	—	410	+29.3	6[b]	—	7	+16.7

Note: Data for 1979 are from Cairns and Verspoor (1980).
[a]From 1979 to 2000.
[b]GBBG counts on Great Island may be biased, as counts of standing adults were taken as late as 28 July, more than 6 weeks later than the survey dates.

Table 3. Clutch sizes of herring gulls in different habitat types on Great Island.

	1976[a]	1977[a]	1978[a]	1992[b]	1993[b]	2000[c]
Rocky	2.44 ± 0.72 (66)	2.65 ± 0.56 (117)	2.60 ± 0.62 (120)	2.06 ± 0.78 (85)	1.89 ± 0.69 (78)	2.51 ± 0.65 (191)
Puffin	2.27 ± 0.73 (72)	2.72 ± 0.54 (134)	2.67 ± 0.61 (137)	1.82 ± 0.73 (109)	1.91 ± 0.56 (59)	2.57 ± 0.63 (366)
Meadow	2.16 ± 0.72 (88)	2.51 ± 0.63 (98)	2.51 ± 0.73 (94)	2.14 ± 0.75 (97)	2.08 ± 0.67 (77)	2.58 ± 0.63 (812)
Forest	—	—	—	—	—	2.63 ± 0.60 (265)

Note: Values are given as the mean ± 1 SD. Numbers in parentheses are sample sizes.
[a]Data from Pierotti (1982).
[b]Data from Rodway and Regehr (1999).
[c]Data from this study.

tat types on Great Island in 2000 ($F_{[3,1630]} = 1.32$, $p = 0.265$; Table 3). On Gull Island, however, there was a significant difference in clutch size among habitats ($F_{[3,1630]} = 5.98$, $p = 0.0005$), gulls in forest habitats having larger clutches (2.68 ± 0.55, $n = 405$) than those in meadow (2.54 ± 0.68, $n = 782$), puffin (2.51 ± 0.69, $n = 607$), and rocky (2.52 ± 0.69, $n = 904$) habitats. Further, clutch size increased on Gull Island from 2.39 ± 0.73 in 1999 to 2.55 ± 0.67 in 2000 ($F_{[1,5491]} = 67.8$, $p = 0.0001$). On Great Island, clutch size has varied over time. In the mid-1970s and 2000, clutches ranged from 2.5 to 2.7 eggs, while in the early 1990s they ranged from 1.8 to 2.1 eggs (Table 3).

There was no detectable difference in clutch size between Gull, Great, and Pee Pee islands in 2000 (Great Island: 2.58 ± 0.63, $n = 1634$; Pee Pee Island: 2.64 ± 0.61, $n = 134$; $F_{[2,4455]} = 1.22$, $p = 0.29$, controlling for habitat).

Great black-backed gulls

There was no evidence that clutch size varied among habitats ($F_{[3,112]} = 0.90$, $p = 0.44$) or between Gull Island and Great Island ($F_{[1,114]} = 1.01$, $p = 0.32$) in 2000 (Pee Pee Island was not included, owing to small sample sizes). Clutch size was 2.53 ± 0.69 ($n = 116$) eggs for Great and Gull islands in 2000. There was also no evidence of a difference in the size of great black-backed gull clutches on Gull Island between 1999 (2.63 ± 0.61, $n = 115$) and 2000 (2.57 ± 0.67, $n = 88$) ($F_{[1,201]} = 0.54$, $p = 0.46$).

Discussion

Interpretation of survey results

Our survey appeared to be well timed, with few chicks hatching and no indication of chicks leaving the nests before they were counted. However, our gull nest numbers and mean clutch sizes could have been biased if there was partial or total clutch predation while we were present in the colony. Previous studies on single-species or mixed gull colonies reported high levels of offspring loss due to intraspecific or intrageneric predation (Parsons 1971; Davis and Dunn 1976; Burger 1979; Velarde 1992). With the exception of a few incidents when otters (*Lutra canadensis*) took gull offspring in Witless Bay, gulls are the major predators of eggs and chicks of members of their own genus. However, during incubation herring gulls appear to be much more intent on defending their nests than on attempting to steal the eggs of other gulls and we observed no incident of partial or total clutch loss due to our disturbance during our survey. This no longer holds after hatching has begun and chicks are mobile, and observer disturbance can greatly increase predation rates on young gull chicks (Brown and Morris 1995). Great black-backed gulls will actively take herring gull eggs and chicks, especially while their own chicks are hatching (Pierotti 1987); fortunately, our survey was made before great black-backed chicks hatched in any numbers.

Another potentially confounding factor in interpreting survey results occurs when adult gulls do not breed in a given year (Kadlec and Drury 1968; Pierotti and Annett 1995; Calladine and Harris 1997), as these birds will not be included in nest counts. If rates of nonbreeding adults vary drastically among years, then differences in nest counts may not reflect a true population change. Unfortunately, we were not able to evaluate this potential error in this study.

Comparison with earlier surveys

The breeding population of herring gulls has decreased substantially in Witless Bay since the late 1970s. Changes have occurred in Newfoundland since then that have likely reduced the amount of food available to breeding gulls. Since 1992, there has been a moratorium on all groundfish fisheries on the east coast of Newfoundland, reducing the availability of fisheries offal to gulls. Additionally, the arrival of capelin to spawn onshore was delayed by up to 1 month in the 1990s (Nakashima 1996). Of these factors, the delayed capelin arrival has probably caused the most severe reduction in the reproductive performance of gulls. Even in the late 1960s and 1970s, refuse and fisheries offal did not form a large part of the diet fed to gull chicks in Witless Bay (Haycock and Threlfall 1975; Pierotti and Annett 1987, 1991), and chicks fed on garbage tend to have the poorest reproductive success (Pierotti and Annett 1987, 1991). Therefore, reductions in amounts of refuse and offal have probably not impacted the nesting success of gulls in Witless Bay to a great degree. However, reductions in refuse and fisheries offal may be a factor in reducing the survival of postfledging chicks. It is suspected that over-winter survival rates of young gulls were increased by the presence of these food sources (Spear et al. 1987; Pierotti and Good 1994).

The delay in the arrival of capelin onshore is likely to have had a large impact on gulls breeding in Newfoundland. Capelin are a high-energy food source and seabirds utilize them to feed their chicks as soon as they become available (Montevecchi and Tuck 1987; Rodway and Regehr 1999). Traditionally, capelin were already available when herring gulls chicks hatched (Pierotti and Annett 1987, 1991). In recent years capelin have been arriving up to 3 weeks after herring gulls chicks hatch (Massaro et al. 2000). Herring gulls have responded to this food shortage during the early chick-rearing period by focusing their foraging efforts on other seabirds and their young. This increased predation on seabird young has caused significant declines in reproductive success, especially among kittiwakes (Regehr and Montevecchi 1997; Massaro et al. 2000); predation has been particularly heavy on adult Leach's storm-petrels (Stenhouse and Montevecchi 1999; Stenhouse et al. 2000). In spite of this increased predation on seabirds, however, herring gull reproductive success has been low (Regehr and Rodway 1999). Gulls that feed their chicks seabirds still switch to capelin when they arrive, which suggests that fish is still the best food for chicks (Pierotti and Annett 1987, 1991). A population-level response to low productivity would not be expected immediately, as herring gulls are long-lived (Coulson and Butterfield 1986; Pierotti and Good 1994), but after a decade of low productivity a reduction in the breeding population would be expected (Pons and Migot 1995).

Interestingly, the nesting great black-backed gull population has shown a mixture of patterns, with some increases and decreases over the years, but has never become large compared with herring gull populations. Great black-backed gulls have different foraging habits than herring gulls. First of all, they are more pelagic than other gulls and can acquire food offshore (Good 1998). Also, they are more predatory than other gulls and are very proficient at killing other seabirds and their young (Russell and Montevecchi 1996; Good 1998). Lastly, as a result of their large size, great black-backed gulls are probably dominant when obtaining limited food from landfills. Great black-backed gulls certainly feed on capelin when available, but appeared to have been able to compensate for the absence of capelin by resorting to other food sources in the 1990s (Regehr and Rodway 1999). Across their range, great black-backed gull populations are increasing, even where local herring gull populations are in decline (Ewins et al. 1992; Chapdelaine 1995). Nevertheless, it is difficult to draw any firm conclusions concerning gull populations in Witless Bay, as the trends on the three islands monitored were different and the great black-backed gull population is small, so any observed changes may simply be the result of demographic stochasticity or other processes.

Habitat

Although herring gull populations in Witless Bay have declined, the declines were not evenly distributed over the nesting habitats used. Overall, they were steepest in rocky and puffin habitats, while increases were seen in meadows and forests. Herring gulls in Witless Bay now commonly nest in dense forest. In the 1970s, rocky habitats were preferred and gulls nesting there showed the highest breeding success (Pierotti 1982), while in the early 1990s, gulls nesting in meadows were the most successful (Rodway and Regehr 1999). The difference in breeding success among these habitats may be related to two factors. Firstly, rocky habitat is relatively limited and gulls nest at high densities in this habitat. At these high densities intraspecific competition and territorial defense can lead to chick mortality (Pierotti 1982, 1987), reducing breeding success. Secondly, nesting habitat and diet are related: gulls nesting in rocky habitats tend to consume fish and intertidal invertebrates, those on puffin slopes consume discards, and those in meadows consume petrels (Pierotti and Annett 1991). With the delay in capelin arrival through the 1990s, capelin are no longer readily available until late June to early July. This is about 2–3 weeks after the chicks hatch, too late for gulls that rely extensively on capelin (i.e., breeders in rocky habitat) to feed their chicks. However, petrels, the major food of gulls nesting in meadows (Pierotti and Annett 1991), are available throughout the breeding season. Similarly, gulls nesting in the forest consume a large number of petrels (Stenhouse et al. 2000). The numbers of gulls nesting in meadows and forests have increased since 1979. Gulls nesting in the forest also had larger clutches on Gull Island (but not on Great Island). Forest habitat provided substantial cover for nests (and chicks), and the larger clutches may reflect the absence of partial clutch depredation by conspecifics and (or) great black-backed gulls.

What is not known is whether the change in nesting distribution is the result of individual breeding gulls moving to

new breeding habitat (and presumably changed foraging habits) or differential recruitment. Breeding gulls, especially males, tend to show high nest-site fidelity, so most adults probably do not shift breeding habitats once they have begun nesting (Pierotti and Good 1994). Natal philopatry is inversely related to nest density (Coulson and Butterfield 1986; Pierotti and Good 1994), so at high nest densities some natal dispersal is inevitable (see also Spear et al. 1998). A plausible scenario is that meadow-nesting gulls have been enjoying higher reproductive success and are recruiting more young into the meadows and subsequently the adjacent forests. Since male gulls tend to retain the foraging habits of their parents (Annett and Pierotti 1999), and meadow-nesting gulls tend to be petrel-specialists (Pierotti and Annett 1991), these new recruits into the meadows and forests are also likely taking petrels. Alternatively, young prospecting gulls evaluate the habitat by examining the breeding success of conspecifics and preferentially recruit into successful breeding habitats, as is seen in black-legged kittiwakes (Boulinier and Danchin 1997; Boulinier et al. 1997). Herring gulls in third-summer plumage are seen in Witless Bay during the late chick-rearing period (G.J. Robertson, personal observation). Regardless of the mechanism, this study demonstrates that differential reproductive success among habitats could lead to the expected changes in population sizes in these habitats.

Similar patterns were seen in the small great black-backed gull population, although data are only available for the coarse-level analysis. It is not known what has caused these changes in the nesting distribution of great black-backed gulls. They may be moving with the shifting herring gull populations, as they are predators of their young (Pierotti 1982; Good 1998). Unlike herring gulls, great black-backed gulls have not moved in to the dense forest. They possibly do not perceive the forest as appropriate nesting habitat, owing to their size and wingspan, which leave them with less maneuverability in forest habitat.

Summary

On the two largest islands in Witless Bay, overall numbers of breeding herring gulls have decreased to less than two-thirds of the numbers recorded in 1979. Concurrently, both herring gulls and great black-backed gulls changed their nesting distribution: numbers of gulls nesting in rocky and puffin habitats were much reduced, while numbers nesting in meadows and forests have actually increased since the 1970s. Breeding-habitat selection is likely to be affected by dietary specialization as well as the risk of predation by other gulls. Further investigations on why gulls have changed their nesting distribution should focus on (*i*) levels of intraspecific predation, (*ii*) gull breeding success, and (*iii*) dietary specialization of individual gulls, and compare all three aspects among the four habitats.

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Appendix

Table A1. Description of sections and their habitats.

	Sections pooled	Description of area
Gull Island		
Finger	1, 2	Exposed rocky habitat and open meadow
South	4, 5, 6	Mix of rocky habitat, puffin slopes, and forest margin
East	7, 8	Large expanse of puffin slope with some rocky ledges and forest margin
North	9, 10, 11, 12, 13	Steep cliffs and degraded puffin slopes; mix of all four habitats
West	3, 14	Large forest-covered ridge with some degraded puffin slopes and rocky ledges
Great Island		
South	1a, 1b, 3a–3d, 2a–2e	Mostly puffin slopes (some degraded) and rocky ledges
Middle	1c, 1d, 3e, 3f	Section of meadows and puffin slope
North	1e, 4a–4d	Forested north end of island

Note: Section numbers are from Cairns and Verspoor (1980).