Delayed capelin (*Mallotus villosus*) availability influences predatory behaviour of large gulls on black-legged kittiwakes (*Rissa tridactyla*), causing a reduction in kittiwake breeding success

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Abstract: During 1998 and 1999, the impact of predation by herring gulls (*Larus argentatus*) and great black-backed gulls (*Larus marinus*) on breeding success of black-legged kittiwakes (*Rissa tridactyla*) at Gull Island, Witless Bay, southeastern Newfoundland, was quantified in relation to the timing of the annual arrival of capelin (*Mallotus villosus*) to spawn. The frequency of predation attempts by large gulls on kittiwakes was compared among three periods: before the mean hatching date for herring gulls, between the mean hatching date for herring gulls and the arrival of the capelin, and following capelin arrival. The frequency varied significantly among the three periods, being highest after gull chicks hatched but before the capelin arrived. The frequency of gull predation was significantly correlated with the percentage of kittiwake eggs and chicks that disappeared each week. We estimated that 43 and 30% of kittiwake eggs and chicks at Gull Island were taken by gulls in 1998 and 1999, respectively. Kittiwakes have been indirectly (through increased predation by gulls) affected by the delayed arrival and lower abundance of capelin in recent years, which underlines the need to understand multispecies interactions when interpreting the effects of human alteration of the marine environment.

Résumé : Nous avons quantifié l’impact de la prédation exercée par le Goéland argenté (*Larus argentatus*) et le Goéland à manteau noir (*Larus marinus*) sur la succès de la reproduction de la Mouette tridactyle (*Rissa tridactyla*) à l’île Gull, Witless Bay, dans le sud-est de Terre-Neuve, en relation avec le moment de l’arriveé du Capelan (*Mallotus villosus*) pour sa fraye annuelle en 1998 et 1999. Nous avous comparé la fréquence des tentatives de prédation des goélands à trois périodes diiférentes : avant l’éclosion moyenne du Goéland argenté, entre l’éclosion moyenne du Goéland argenté et l’arriveé des capelans et après l’arrivée du capelan. La fréquence des tentatives de prédation des goélands sur les mouettes différait significativement de l’une à l’autre des trois périodes et les fréquences les plus élevées ont été enregistrées après des jeunes goélands et avant l’arrivée des capelans. L’importance de la prédation par les goélands s’est avérée en corrélation significative avec le pourcentage d’oeufs et de poussins de la Mouettes tridactyle qui sont disparus en moins de 1 semaine. Nous avous estimé que 43 % des oeufs et des poussins de l’île Gull en 1998 et 30 % en 1999 ont été pris par des goélands. Les Mouettes tridactyles ont été affectées indirectement (par la prédation de plus en plus importante des goélands) par l’arrivée tardive et l’abondance réduite des capelans au cours des dernières années, ce qui démontre l’importance de comprendre les interactions entre les diverse espèces lors de l’interprétation des effets de l’intervention humaine dans les perturbations du milieu marin.

Introduction

Capelin (*Mallotus villosus*) are small circumpolar schooling fish confined to cool-temperate waters within the northern hemisphere (McAllister 1963; Jangaard 1974; Stergiou 1989). They spawn on beaches along the coast of Newfoundland, Canada, migrating inshore each spring from offshore feeding grounds (Templeman 1948). Spawning capelin are an essential food resource for many seabirds breeding in Newfoundland. During chick rearing in particular, capelin form a large component of the diet of common murres (*Uria aalge*; Burger and Piatt 1990), Atlantic puffins (*Fratercula arctica*; Brown and Nettleship 1984), and herring gulls (*Larus argentatus*; Pierotti and Annett 1987). Because of below-normal sea temperatures, the timing of peak capelin spawning on beaches has been delayed by approximately 4 weeks each year since 1991 (Shackell et al. 1994; Therriault et al. 1996). Additionally, Carscadden et al. (1997) showed that

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low water temperatures affect maturation, causing a reduction in the size of spawning capelin. In Newfoundland, delayed inshore spawning of capelin can have a devastating effect on the breeding performance of seabirds, particularly surface-feeding birds such as black-legged kittiwakes (*Rissa tridactyla*), herring gulls, and great black-backed gulls (*Larus marinus*; Regehr and Rodway 1999).

Large gulls, such as herring and great black-backed gulls, are dietary generalists that feed on marine fish and invertebrates as well as on birds and refuse (e.g., Harris 1965; Threlfall 1968; Beaman 1978). Owing to their flexible foraging behaviour, large gulls increased dramatically in number in Europe and the northwest Atlantic during the 20th century (Kadlec and Drury 1968; Harris 1970; Verbeek 1979; Furness and Monaghan 1987; Howes and Montevecchi 1993). In particular, industrial fisheries offer gulls the opportunity to feed on fish offal (e.g., Hudson and Furness 1989; Furness et al. 1992; Garthe et al. 1996), although the Eastern Canadian Groundfish Moratorium of 1992 has likely decreased this opportunity (Regehr and Montevecchi 1997).

Large gulls depredate other seabird species, such as Atlantic puffins, common and thick-billed murres (*Uria lomvia*), and black-legged kittiwakes, and their offspring (Barrett and Runde 1980; Harris 1980; Burger and Gochfeld 1984; Schauer and Murphy 1996; Russell and Montevecchi 1996; Regehr and Montevecchi 1997; Gilchrist et al. 1998; Gilchrist 1999). Generalist foragers are known to switch their diet in response to particular nutritional requirements during the breeding cycle (Pierotti and Annett 1987) and changes in prey availability (Newton 1993). The large-scale reduction of the groundfish fisheries in Newfoundland since 1992 (Hutchings and Myers 1994; Myers and Cardigan 1995) and the shift in the timing of capelin spawning have caused an increase in predation by gulls on other seabirds (Regehr and Montevecchi 1997). After the fishing moratorium, great black-backed and herring gulls had an impact on kittiwake breeding success on Great Island in Witless Bay (Regehr 1994). Approximately 87% of 416 eggs and approximately 63% of 613 eggs disappeared in 1992 and 1993, respectively; they were most probably taken by aerial predators (Regehr 1994). In contrast, Maunder and Threlfall (1972) did not observe any predation on kittiwake eggs by herring and great black-backed gulls on Gull Island in Witless Bay, and Neuman (1994) observed herring gulls taking kittiwake eggs only twice during a study in 1990 and 1991, just prior to the moratorium.

Although it is known that herring and great black-backed gulls prey on black-legged kittiwakes, no study has quantified predation rates and their impact on kittiwake breeding success. The main objective of this study was to document the number of gull predation attempts during different phases of the kittiwake nesting cycle and in relation to the timing of capelin arrival. We predicted that predation-attempt rates would be highest when gulls were feeding their chicks and before the capelin arrived. Other specific objectives were (*i*) to compare predation-attempt rates among several kittiwake colonies of different sizes, (*ii*) to compare the frequency of predation attempts at different times of the day, (*iii*) to compare predation-attempt rates of herring and great black-backed gulls, (*iv*) to compare the frequency gull predation with the number of kittiwake eggs and chicks that disappeared, and (*v*) to measure the impact of gull predation on overall reproductive success of kittiwakes.

Methods

Study site

The study was conducted on Gull Island (47°16′N, 52°46′W), which is part of the Witless Bay Seabird Ecological Reserve off the southeast coast of Newfoundland. The island is approximately 1.6 km long and 0.8 km wide. More than 10 000 pairs of black-legged kittiwakes breed on cliffs along the edge of Gull Island (Lock et al. 1994). In 1999, there were 2794 breeding pairs of herring gulls and 115 pairs of great black-backed gulls nesting on the entire island (G.J. Robertson, unpublished data). Research on Gull Island was conducted from 24 May to 15 August in 1998 and from 16 May to 9 August in 1999.

Four west-facing kittiwake nesting cliffs at least 200 m apart were chosen as study plots. To minimize the disturbance to breeding birds, all four plots were located at the south end of the island. The heights of the cliffs in the plots ranged from about 5 to 25 m. Three of the four cliffs (N4, S5, and S1) were within protected gulches and one (P2) was an open cliff at the edge of the island. Individual study plots supported between 32 and 238 active kittiwake nests (≥1 egg was laid).

Frequency of predation attempts

During 1998 and 1999, the frequency of predation attempts was quantified on four kittiwake study plots during 2- to 4-h watches throughout the breeding season. Although the watches at study plots were not randomly selected, watches were distributed equally, both temporally and spatially, among plots. All observations were made from blinds to ensure normal, undisturbed predatory behaviour of gulls. Also, blinds were entered approximately 5 min before a watch started, to allow gulls to settle down after they were disturbed by our arrival. A predation attempt was defined as an occasion when a large gull closely approached one or more kittiwake nests, either in flight or on foot, and elicited such responses as turning towards the gull and simultaneously calling loudly, jabbing with the bill, pecking, biting, and diving at the gull on the cliff ledge, as well as while flying in close proximity to the cliff. Whether the predation attempt was made by a herring gull or a black-backed gull was recorded. For each observation period, the hourly frequency of predation attempts was calculated by dividing the number of predation attempts by the number of observation hours. Total observation times were 286 h in 1998 and 426 h in 1999. Predation-attempt rates were obtained for a total of 235 observation periods, of which 34 were directly followed by another watch at the same site. On 21 occasions, two watches were done at the same location within 1 day, but several hours apart. We categorized all watches into four time periods: (1) early morning (04:00–09:00), (2) morning (09:00–13:00), (3) afternoon (13:00–17:00), and (4) evening (17:00–22:00). We distinguished three periods within each breeding season: (1) from the start of research on the island early in the season until the mean hatching date for herring gulls, (2) from the mean hatching date for herring gulls until the arrival of the capelin, and (3) after capelin arrival.

Breeding success

In both years, all kittiwake nests at the four study plots were numbered and mapped. Nest contents at all four plots were monitored approximately twice a week, except for site P2, where no breeding data were collected in 1999. A total of 700 kittiwake nests were monitored in 1998 and 645 nests in 1999. If kittiwake chicks hatched between two watches, the date midway between the two watches, measured to the half day, was taken as the hatching date. Kittiwake chicks that survived for 35 d or more were considered fledged. On rare occasions, kittiwake chicks between the ages of 30 and 35 d disappeared or the observers left Gull Island too early to monitor their fledging. These chicks were assumed to have fledged and were included in the analysis.

If kittiwake eggs or chicks were lost between two watches, the date midway between the two watches, measured to the half day, was taken as the date of disappearance. All kittiwake eggs and chicks that were found to be missing between two nest checks were classified as disappeared. Eggs found broken, dead chicks in the nest, and complete nests that were missing after heavy rains were classified as egg or chick loss. The percentage of eggs and chicks that disappeared was calculated for each week of the year. We tested whether this disappearance rate was positively correlated with weekly mean predation-attempt rates. To estimate the percentage of kittiwake offspring lost to gull predation, the number of kittiwake eggs and chicks that were seen to be taken by gulls was added to the number of offspring that disappeared, and this number was divided by the number of eggs laid.

Timing of gull hatching

In 1999, 50 herring gull nests, distributed over the southern part of Gull Island, were randomly chosen and checked every 3 d until all eggs hatched. If chicks hatched between two checks, the day midway between checks, measured to the half day, was considered to be the hatching date. From a total of 46 nests with 101 hatched eggs, the mean date of hatching for herring gulls was calculated. Unfortunately, the exact date was not determined for 1998. However, by 21 June, most chicks had hatched (M. Massaro, personal observation) and this date was used to denote the beginning of herring gull chick rearing in that year.

The same method was used to determine the hatching dates for great black-backed gulls ($n = 8$ nests with 18 hatched eggs in 1998; $n = 10$ nests with 26 hatched eggs in 1999). All black-backed gull nests observed were those of solitary breeders and were located at the southern end of Gull Island.

Capelin arrival

The date of first delivery of capelin by Atlantic puffins and common murres to their chicks was taken as the date of inshore capelin arrival. In both years, an abrupt increase in humpback whale (*Megaptera novaeangliae*) numbers in Witless Bay was observed simultaneously with the first delivery of capelin by breeding auks. Furthermore, in both years, the date of capelin arrival was confirmed by other observers: in 1998 by S. Baillie (unpublished data), who regularly collected puffin chick diet data, and in 1999 by an underwater film crew, who regularly dove close to Gull Island.

Statistical analysis

Given that our watches were not randomized, they might not be completely independent. We were particularly concerned about the independence of back-to-back watches. To test whether all 34 pairs of watches done back-to-back could be included in subsequent analyses, we tested whether the number of predation attempts per hour made by herring and great black-backed gulls during the second watch of each pair was independent of the number made per hour during the first watch. These 34 pairs of watches were compared with the 21 pairs of watches done at one plot within a day but several hours apart. The differences in predation-attempt rates between these pairs of watches were calculated and a ratio of variances was obtained. This F ratio of a two-tailed test allowed us to determine whether there was a statistically significant difference between predation-attempt rates obtained from watches done back-to-back and from watches done several hours apart (Sokal and Rohlf 1995).

Predation rates generally followed a Poisson distribution, based on a graphical examination of the data and variance-to-mean ratios that approached 1.0. A generalized linear model with a Poisson distributed response variable (PROC GENMOD; SAS Institute Inc. 1996) was used to compare predation-attempt rates. The following terms were included in the original model: study plot, year, intraseasonal period, time of day, and all two-way interaction terms. If they were statistically nonsignificant ($P > 0.1$), high-order terms were excluded from subsequent models until only significant terms remained. To reduce the risk of a Type II error, $P < 0.1$ was used to allow the interaction terms to remain in the model. However, for the final model, the tolerance for Type I error was set at 0.05 for main effects.

Because of the sampling unit (number of gull predation attempts per hour), it was impossible to include an independent variable for gull species in the main analysis (see above). In order to compare the predation-attempt rates of the two gull species indirectly, we chose to use the predation-attempt rates of herring and great black-backed gulls each as a response variable in two separate analysis. As in the main analysis, a generalized linear model with a Poisson distributed response variable was used and the same four independent variables were included. We followed the procedure described above for finding the best fitting model.

We used Pearson's product-moment correlations to test whether the percentages of kittiwake eggs and chicks that disappeared were correlated with (*i*) the number of eggs and chicks available or (*ii*) weekly mean observed predation-attempt rates.

Except during the process of finding the best models, the tolerance for Type I error was set at 0.05 for all other statistical tests. All tests were two-tailed and all means are reported with ±1 SD.

Results

Timing

In 1998, schools of capelin first arrived and spawned in Witless Bay on 5 July; in 1999, capelin arrived inshore on 26 June, 9 d earlier than in 1998.

Mean hatching dates for great black-backed gulls were 6 June (±4 d) in 1998 and 2 June (±7 d) in 1999. The mean hatching date for herring gulls was 9 June 1999 (±5 d). For kittiwakes, mean first-egg laying dates were 2 June in 1998 (±7 d) and 3 June in 1999 (±12 d), and mean hatching dates were 27 June in 1998 (±6 d) and 2 d later in 1999 (29 June ± 8 d). Median laying and hatching dates for gulls and kittiwakes never differed by more than 1 day from mean dates (Fig. 1).

The period before the mean hatching date for herring gulls lasted from 4 to 20 June (17 d) in 1998 and from 18 May to 9 June (23 d) in 1999. The second period, which started after the mean hatching date for herring gulls and continued until the capelin arrived, was from 21 June to 4 July in 1998 (14 d) and from 10 to 25 June in 1999 (16 d). The period after the capelin arrived started on 5 July in 1998 and 26 June in 1999. The last watch of the third period was done on 7 August in 1998 (34 d) and 25 July in 1999 (29 d) (Fig. 1).

Gull feeding territories

During the 2 years of the study, all kittiwake plots were observed to be part of the feeding territories of breeding herring and great black-backed gulls. Each kittiwake plot was defended by one or, in the case of S5, two breeding resident gull pairs against other intruding gulls. Study plots P2, N4, and S5 were each part of a feeding territory of a different resident great black-backed gull pair, and S1 and S5 were

Fig. 1. Timing (day/month) of breeding of great black-backed gulls (GBBG), herring gulls (HERG), and black-legged kittiwakes (BLKI) on Gull Island, and timing of capelin arrival in Witless Bay, in 1998 and 1999. The dotted lines indicate the period when birds incubated eggs and the solid lines indicate when chicks fledged. Mean hatching dates for all three species and the mean first-egg laying date for kittiwakes are indicated by solid circles. Data for and duration (d) of three intraseasonal periods are reported: (1) from the beginning of the season until the mean hatching date for herring gulls, (2) from the mean hatching date for herring gulls until the capelin arrive, and (3) from capelin arrival until the end of the season.

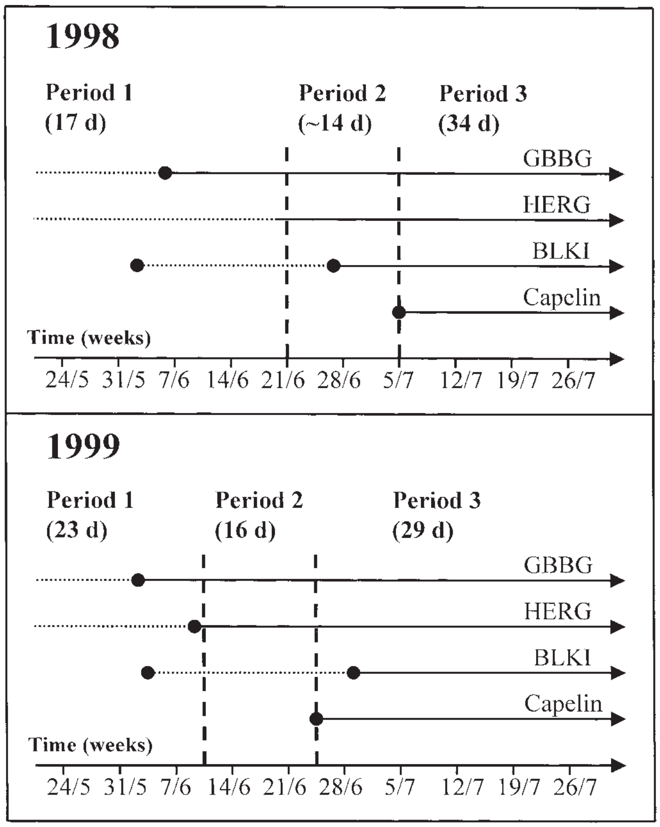
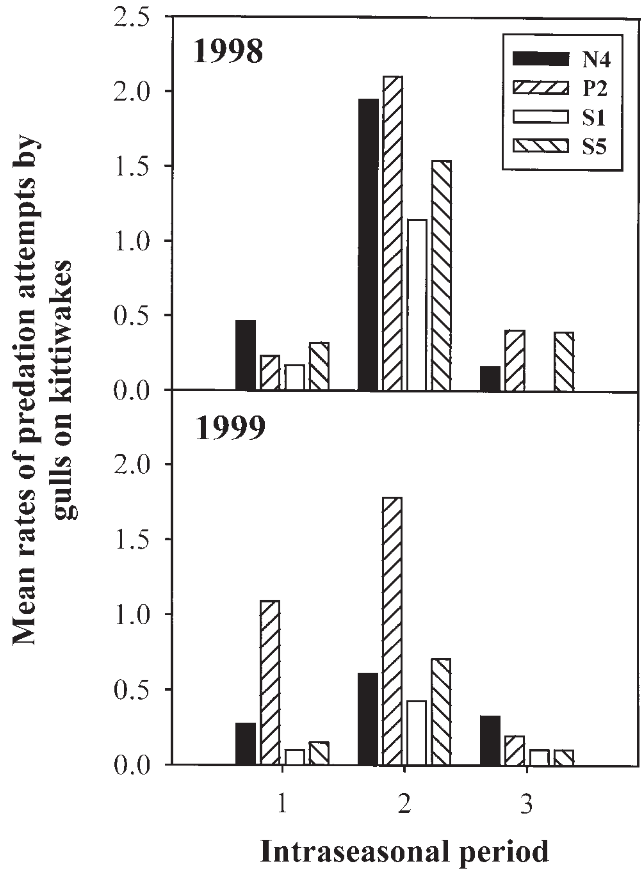


Fig. 2. Mean predation attempt rates (attempts/h) of herring gulls and great black-backed gulls on black-legged kittiwakes at four study plots (N4, P2, S1, and S5) on Gull Island during three intraseasonal periods in 1998 and 1999 (see Fig. 1).



each occupied by one breeding pair of herring gulls. These feeding territories of three great black-backed gull pairs and two herring gull pairs were consistent over the 2 years.

Frequency of gull predation attempts on kittiwakes

There was no difference between predation-attempt rates obtained from watches done back-to-back and watches done several hours apart at the same plot within a day ($F_{[33,20]}$ = 1.14, $P > 0.05$). This result allowed all 34 pairs of watches done back-to-back to be included in the main analysis comparing gull predation attempt rates.

The mean gull predation attempt rates of herring and great black-backed gulls on kittiwakes at the four study plots are presented in Fig. 2. In 1998, the mean predation attempt rate in the second period (1.72 ± 1.6 attempts/h (including all plots)) was about 6–7 times higher than in the first period (0.27 ± 0.34 attempts/h) and third period (0.23 ± 0.55 attempts/h), while in 1999, the mean predation attempt rate in the second period (0.90 ± 0.97 attempts/h) was only about 2–5 times higher than in the first period (0.41 ± 0.66 attempts/h) and third period (0.19 ± 0.43 attempts/h).

The final generalized linear model for gull predation attempt rates included all main effects and one interaction term, year by intraseasonal period, as predictors (Table 1). Gull predation attempt rates differed significantly among study plots, but there was no evidence of variation among years. Predation-attempt rates varied significantly among the three intraseasonal periods, with the highest attempt rates in the second period, i.e, after the mean hatching date for herring gulls but before the capelin arrived (Table 1). Although predation attempt rates were highest early in the morning (0.76 ± 1.15 attempts/h), lower in the evening (0.59 ± 1.13 attempts/h), and lowest in the morning (0.46 ± 0.83 attempts/h) and afternoon (0.45 ± 0.67 attempts/h), these differences for different times of the day were not statistically significant (Table 1). The interaction of year and period was also not significant in the final model (Table 1).

For all analyses in which each gull species was treated separately, all two-way interaction terms either proved to be nonsignificant or insufficient data were available to estimate the interaction. There was a significant year and intraseasonal period effect on herring gull predation attempt rates (year: χ^2 = 9.7, df = 1, P = 0.0018; period: χ^2 = 54.3, df = 2, $P < 0.0001$). However, for great black-backed gull predation attempt rates, significant effects were found for plot,

Table 1. Generalized linear model of factors influencing rates of predation attempts by herring and great black-backed gulls on kittiwakes on Gull Island in 1998 and 1999.

Source	df	χ^2	*P*
Plot	3	19.7	0.0002
Year	1	0.8	0.3682
Period	2	72.5	<0.0001
Time of day	3	6.8	0.0770
Period × year	2	5.1	0.0775

Note: Higher order terms not present were nonsignificant ($P > 0.1$) and were dropped from the model. For the final model, a generalized linear model with a Poisson distribution and a log link function, the tolerance for Type I error was set at 0.05 for main effects.

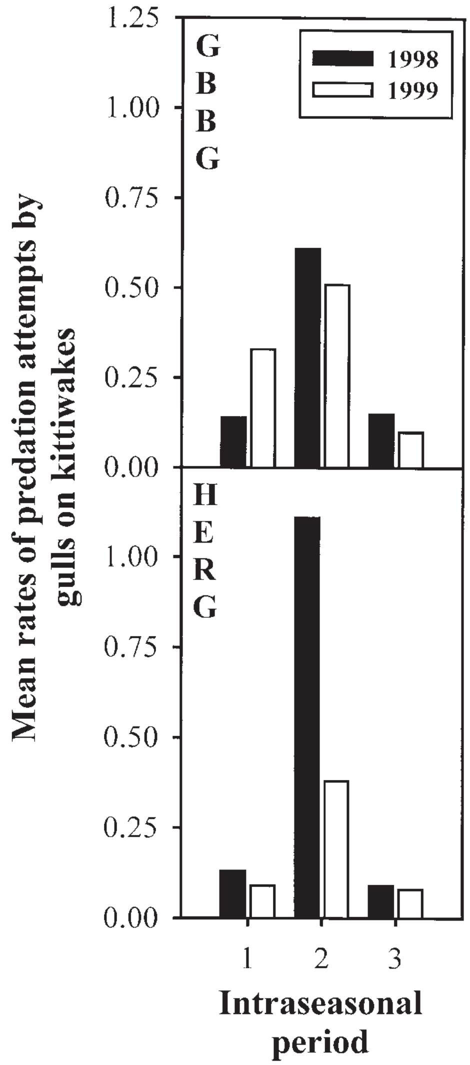
intraseasonal period, and time of day, but not for year (plot: $\chi^2 = 48.5$, df = 3, $P < 0.0001$; period: $\chi^2 = 26.6$, df = 2, $P < 0.0001$; time of day: $\chi^2 = 8.6$, df = 3, $P = 0.0351$). In 1999, mean predation attempt rates of herring gulls on kittiwakes were lower during all three periods than in 1998. However, predation-attempt rates of great black-backed gulls on kittiwakes were similar between years (Fig. 3).

By comparing the number of attempts made by each gull species in each intraseasonal period, we found that most predation attempts in the first and third periods were made by great black-backed gulls (70.3% of all attempts in the first period and 57.6% in the third). However, during the second period, 55.3% of all predation attempts were made by herring gulls and only 44.7% by great black-backed gulls.

Gull predation attempt rates and disappearance of kittiwake eggs and chicks

We found no correlation between the percentage of kittiwake eggs and chicks that disappeared and the number of eggs and chicks available each week ($r = 0.07$, $n = 21$, $P > 0.05$; Fig. 4). However, in both years, weekly gull predation attempt rates were positively correlated with the percentage of kittiwake eggs and chicks that disappeared each week ($r = 0.77$, $n = 21$, $P < 0.05$; Fig. 4).

Fig. 3. Mean predation attempt rates (attempts/h) of great black-backed gulls (GBBG) and herring gulls (HERG) on black-legged kittiwakes on Gull Island within three intraseasonal periods in 1998 and 1999 (see Fig. 1).



Effect of gull predation on kittiwake breeding success

Of 700 kittiwake nests observed in 1998, 589 (84.1%) were active (≥1 egg laid). Of 1026 kittiwake eggs laid, 686 (66.7%) hatched and 230 (22.4%) disappeared. Of all kittiwake chicks hatched, 367 (53.5%) fledged and 193 (28.1%) disappeared. In 1998, chick survival rate per nest was 0.62 (number of fledged chicks/number of active nests), and 302 (51.3%) kittiwake pairs that laid eggs fledged chicks. An average of 0.52 chicks fledged per completed nest (number of fledged chicks/number of completed nests). A total of 423 (41.2%) kittiwake offspring disappeared and, adding the eight eggs and eight chicks seen to be taken by herring and great black-backed gulls, 42.8% (23.2% of all eggs and 29.3% of all chicks) of all kittiwake offspring were lost to gull predation in 1998.

Of 645 nests monitored in 1999, 515 (79.8%) were active. Of 891 eggs laid, 657 (73.7%) hatched and 158 (17.7%) disappeared. Of 657 chicks hatched, 480 (73.1%) fledged and 94 (14.3%) disappeared. In 1999, the chick survival rate per nest was 0.93, and 329 (63.9%) kittiwake pairs that laid eggs fledged chicks. An average of 0.72 chicks fledged per completed nest. A total of 252 (28.3%) kittiwake offspring disappeared and, adding the 13 eggs and five chicks that were seen to be taken by herring and great black-backed gulls, 30.3% (19.2% of all eggs and 15.1% of all chicks) of all kittiwake offspring were lost to gull predation in 1999.

Discussion

Intraseasonal variation in gull predatory behaviour

In both years, striking variation in the frequency of gull predation attempts was observed throughout the breeding season. At all plots, predation-attempt rates increased after the mean hatching date for herring gulls and decreased after the capelin arrived. What caused these drastic differences in gull predation attempt rates over the breeding season?

Threlfall (1968) noted that herring gulls fed mainly on blue mussels (*Mytilus edulis*) in Witless Bay during May and June and changed to capelin as a major food source later in the season. Pierotti and Annett (1987) examined the diet and timing of

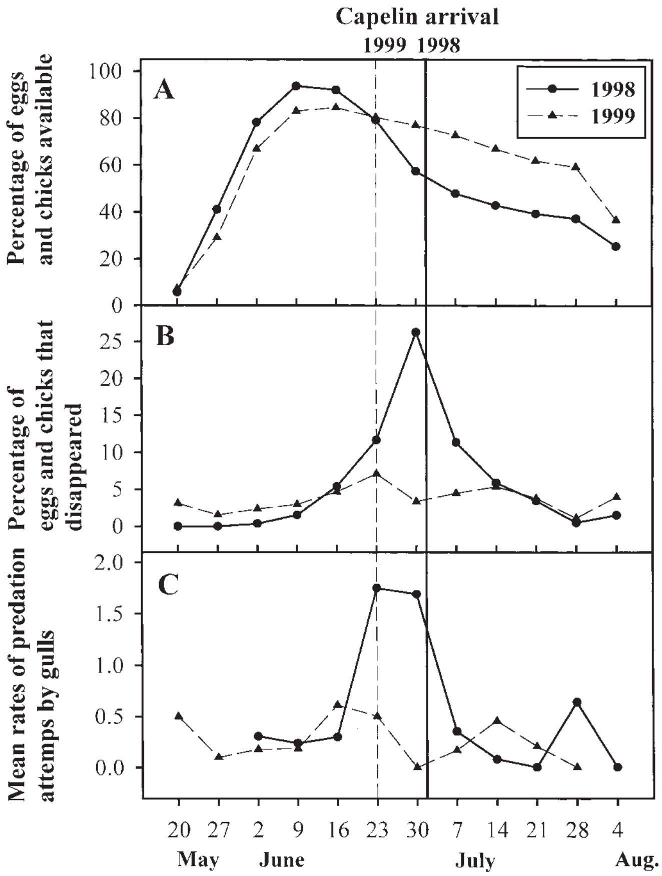


Fig. 4. Percentages of kittiwake eggs and chicks available (number of kittiwake eggs or chicks/total number of eggs laid) (A), percentages of kittiwake eggs and chicks that disappeared (B), and mean gull predation attempt rates (C) on Gull Island each week in 1998 (solid line) and 1999 (broken line). The vertical lines denote the arrival of the capelin on 5 July 1998 (solid vertical line) and 26 June 1999 (broken vertical line).

prey-switching by herring gulls in Witless Bay from 1976 to 1978, years when the capelin arrived in Witless Bay early in June. Those authors found that herring gulls switched to capelin as soon as they had chicks to feed, rather than when the capelin, the most profitable prey item, became available. Since the beginning of the 1990s, the delay in capelin arrival and the groundfish moratorium have substantially decreased food availability at the crucial time when gulls have small chicks to feed. Low gull breeding success in Witless Bay (Neuman 1994; Regehr and Montevecchi 1997; J.W. Chardine, unpublished data) and on the north shore of the Gulf of St. Lawrence (Chapdelaine and Rail 1997) since 1990 supports the idea that large gulls have suffered because of low food availability and have been forced to find alternative food resources, such as kittiwakes, puffins, and Leach's storm petrels (*Oceanodroma leucorhoa*). Stenhouse and Montevecchi (1999) found that herring gull predation on adult Leach's storm petrels decreased markedly after the capelin arrived. Russell and Montevecchi (1996) suggested that kittiwake offspring and adults appeared to be easier targets for gulls than adult puffins. Additionally, kittiwake offspring are more visually "available" during the period of high food demand than offspring of puffins and the nocturnal Leach's storm petrels, which are protected by burrows. In contrast to the situation prior to 1990, the lack of capelin after gull chicks hatched appears to have led to an increase in gull predation attempts on kittiwakes. However, as soon as spawning capelin became available to chick-rearing gulls, they once again foraged on capelin, a low-risk high-energy food resource (Pierotti and Annett 1987).

Interyear differences in gull predation rates

Although no significant difference in predation-attempt rates between years was detected in the main analysis, higher mean gull predation attempt rates were observed in all three periods in 1998 than in 1999, except during the first period at P2 and the third period at N4. This suggests that overall food availability was greater in 1999 than in 1998. Earlier capelin arrival, a longer period of capelin availability (M. Massaro, personal observation), and a 53.3% increase in kittiwake breeding success support this suggestion. Although spawning capelin arrived in Witless Bay 9 d later in 1998 than in 1999, we did not observe that the period between the mean gull hatching date and the arrival of the capelin was longer in 1998. Because the exact hatching date for herring gulls in 1998 is not known, the period between that date and capelin arrival might have been longer than was assumed in this study (>14 d). However, based on casual observations, we doubt that the mean hatching date for herring gulls was significantly earlier than 20 June.

The interyear difference between mean gull predation attempt rates is caused by the drastic variation in herring gull predation rates among years. However, rates of great black-backed gull predation attempts on kittiwakes were similar between years. Why did the predation rates of herring gulls, but not of great black-backed gulls, differ among years? In both years, three of the kittiwake study plots were distinct feeding territories for great black-backed gull pairs. Spear (1993) observed that male western gulls (*Larus occidentalis*) that specialized in feeding on common murres and Brandt's cormorants (*Phalacrocorax penicillatus*) showed a high degree of fidelity to their feeding territories. In 1999 on Gull Island, we uniquely colour banded one male great black-backed gull that held a feeding territory at kittiwake study plot N4. This individual was responsible for 60% of all great black-backed gull predation attempts on kittiwakes at N4 (M. Massaro, unpublished data). While great black-backed gulls were responsible for most predation attempts on kittiwakes during the first and third periods, herring gulls made more predation attempts during the second period. On only one occasion was a great black-backed gull observed to intrude on the feeding territory of another great black-backed gull. However, on 34 occasions, we observed territorial defense behaviour in which herring gulls were the intruders. Furthermore, 74.3% (25) of all intrusions were observed during the period between gull hatching and capelin arrival (M. Massaro, unpublished data). This suggests that for most herring gulls, making a predation attempt in a black-backed gull territory is a risky venture, to be avoided if other food sources are available.

Differences in gull predation rates among study plots

During both years and in all three periods, mean predation attempt rates were highest at P2, the open and more exposed cliff. P2 was followed by N4, and the lowest rates were observed at S1. At S1, only herring gulls were observed to be kittiwake predators. S1 was a very small cliff that could not support many more than 50 kittiwake nests. The small number of kittiwake breeding pairs at S1 and the fact that no resident great black-backed gull pair used S1 as a feeding territory might explain the low predation attempt rate here compared with the other study plots. Although Regehr et al. (1998) stated that large-scale cliff structure influences the predatory behaviour and predation success of avian predators on kittiwakes, causing differences in kittiwake breeding performance, they did not observe or compare gull predation rates among cliffs. Differences in kittiwake breeding performance among cliffs might be due to a variety of factors interacting with each other, such as exposure of the cliff to wind, the number of resident predatory gulls, ectoparasite abundance, quality of breeding birds, and the presence of large-scale cliff structure. Although the number of resident predatory gulls was the same at P2 as at other cliffs (N4 and S5), predation-attempt rates were higher. We believe that because of the open cliff structure, wind conditions on most days were more favourable for gull predation at P2 than in the narrow gulches, where winds were gusty and gulls could not maneuver as easily (Gilchrist and Gaston 1997; Gilchrist et al. 1998).

Impact of gull predation on kittiwake breeding performance

At the population level, it is essential to know the impact of predation by large gulls on kittiwakes and its implications for kittiwake breeding performance. The demonstrated relationship between gull predation attempt rates and the number of kittiwake offspring that disappeared supports the assumption that most missing kittiwake eggs and chicks were lost to gull predation. During two seasons of intensive observations of kittiwake colonies, only one egg and four chicks were seen to fall out of a nest in the absence of a predation attempt. Kittiwake reproductive success in Newfoundland has been low since at least 1990, except in 1996 (Neuman 1994; J.W. Chardine, unpublished data). At the Gannet Islands in Labrador, Canada, kittiwakes bred less successfully in 1996–1998 (0–0.77 chicks fledged per nest) than in 1981–1983 (0.90–1.13 chicks fledged per nest) (Hipfner et al. 2000). Similar decreases in kittiwake breeding success have been observed in southeastern Scotland and northeastern England since 1986, which are explained by large-scale industrial fisheries for sandeels (*Ammodytes marinus*), a major prey item for kittiwakes in the North Sea (Harris and Wanless 1990, 1997). It has been shown that changes in the populations of marine prey species have a direct impact on seabird breeding success (e.g., Vermeer et al. 1979; Baird 1990; Hamer et al. 1993; Barrett and Krasnov 1996; Harris and Wanless 1997); however, the indirect effects of an increase in predation by predatory bird species on other birds have rarely been studied (Hamer et al. 1991; Spear 1993; Stenhouse and Montevecchi 1999). In years of low food availability in Witless Bay, kittiwakes are confronted not only with the difficulty of providing chicks with food but also with increased predation pressure from gulls. Additionally, in years of food shortage, adult attendance at kittiwake nests with chicks is reduced and the risk of predation on nestlings increases (Barrett and Runde 1980). On Great Island in Witless Bay, this caused complete breeding failure among kittiwakes in 1992 (1% of pairs with eggs fledged chicks; Regehr 1994). In 1998 and 1999 on Gull Island, the chick survival rate was lower than that found in most other Atlantic studies (53.5% in 1998 and 73.1% in 1999, this study; 88%, Cullen 1957; 87%, Coulson and White 1958; 81% in 1969 and 73% in 1970, Maunder and Threlfall 1972; 56% in 1973 and 75% in 1974, Barrett and Runde 1980; 68% in 1993, Regehr and Montevecchi 1997) but higher than that found in some studies (26% in 1976, Barrett and Runde 1980; 7% in 1992, Regehr and Montevecchi 1997). On Gull Island, 0.52 (in 1998) and 0.72 (in 1999) chicks fledged per completed nest. Harris and Wanless (1990) reported numbers of young fledged per completed nest of 0–1.56 for 36 kittiwake colonies on the coasts of England, Scotland, and Ireland. In kittiwake colonies in France, Danchin and Monnat (1992) observed 1.03 young fledged per pair in a flourishing colony compared with only 0.49 young fledged per pair in a declining colony. Our estimates are below 1.03 and closer to 0.49 young fledged per pair.

Changes in the abundance of marine prey species caused by fishing activities or climate change (Stergiou 1991) have indirect effects on the predation pressure imposed by large gulls on other seabirds. Predation by western gulls on common murres and Brandt’s cormorants was significantly higher during an El Niño year than in other years (Spear 1993). Gulls took 66% of all eggs laid during an El Niño year compared with 18 and 12% during 2 years of normal food availability. Compared with Spear’s (1993) study, our estimates of the overall impact of gull predation on kittiwakes are high, considering that our estimates are markedly above 18% for 2 subsequent years (42.8% in 1998; 30.3% in 1999). Regehr’s (1994) study suggests that the impact of gull predation on kittiwakes was even greater in the early 1990s than in 1998 and 1999. High rates of predation by large gulls for almost a decade now may have had an impact on the growth rate of kittiwake populations in Newfoundland. However, the relatively good season for kittiwakes in 1999 suggests that the overall food situation is improving and so gull predation rates on kittiwakes are decreasing.

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