INVESTIGATION OF CAUSES AND EFFECTS OF PREDATION BY HERRING (*Larus argentatus*) AND GREAT BLACK-BACKED GULLS (*L. marinus*) ON BLACK-LEGGED KITTIWAKES (*Rissa tridactyla*) ON GULL ISLAND, NEWFOUNDLAND

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INVESTIGATION OF CAUSES AND EFFECTS OF PREDATION BY HERRING (*Larus argentatus*) AND GREAT BLACK-BACKED GULLS (*L. marinus*) ON BLACK-LEGGED KITTIWAKES (*Rissa tridactyla*) ON GULL ISLAND, NEWFOUNDLAND

© Melanie Massaro

A thesis submitted to the School of Graduate Studies in partial fulfillment of the requirements for the degree of Master of Science

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ABSTRACT OF THE THESIS

In previous studies it has been observed that herring gulls (*Larus argentatus*) and great black-backed gulls (*L. marinus*) depredated breeding black-legged kittiwakes (*Rissa tridactyla*) that nest along the southeastern coast of Newfoundland, Canada. However, the causes and effects of large gull predation on kittiwakes was never extensively investigated nor quantified. In this study, herring gull and great black-backed gull predation on black-legged kittiwakes at Gull Island, southeastern Newfoundland was quantified at four study plots in relation to the timing of the annual spawning arrival of capelin (*Mallotus villosus*), the size of kittiwake sub-colonies (number of nests), kittiwake nest-site characteristics, and wind conditions. I also investigated the impact of large gull predation on kittiwake breeding performance during 1998 and 1999.

I compared large gulls' predation attempt frequency among three periods: before mean gull hatching, between mean gull hatching and the arrival of capelin, and following capelin arrival. In both years, the frequency of gull predation attempts on kittiwakes differed significantly among the three periods, with highest levels of predation occurring after gull chicks hatched but before capelin arrival. Overall gull predation attempt levels were lower in 1999, when capelin spawned earlier, than in 1998.

Nesting density and the location on the cliff were kittiwake nest-site characteristics that affected significantly the risk of predation. Breeding success (number of successful nests) was influenced by nesting density and ledge width. Additionally, I found that both risk of predation and breeding success varied significantly among plots. Individual kittiwake nests at the smallest plot experienced a higher probability of attack by large gulls than nests at larger plots. Hence, the percentage of failed nests was highest at the smallest plot and decreased as the size of the plots increased. Regardless of wind conditions both gull species attacked nest sites located on upper parts to a higher likelihood than sites located on middle and lower parts of the cliffs. However, during calm conditions, roofs over nest sites reduced the risk of predation by herring gulls, whereas sites located on narrow ledges were less likely to be attacked by great black-backed gulls. During windy conditions, nesting density affected which sites were attacked by great black-backed gulls.

The level of gull predation behaviour was significantly correlated with the percentage of kittiwake eggs and chicks that disappeared within a week. I estimated that 43% of kittiwake eggs and chicks at Gull Island were taken by gulls in 1998 and 30% in 1999. My results demonstrated that kittiwakes have been indirectly (through increased predation by gulls) affected by the delayed arrival and lower abundance of capelin, and that kittiwake nest-site characteristics, and the size of a sub-colony were significantly correlated with the risk of depredation.

FOR MY MUM

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CHAPTER 1

Introduction

In marine ecosystems seabirds are top-predators that feed on marine fish, squid, and invertebrates and it has been shown that changes in abundance of marine prey species influence top-predators and their breeding performance. (e.g. Barrett and Furness 1990; Hamer et al. 1991; Monaghan et al. 1994; Barrett and Krasnow 1996; Harris and Wanless 1997; Boersma 1998; Bryant et al. 1999). Herring gulls (*Larus argentatus*), great black-backed gulls (*L. marinus*) and black-legged kittiwakes (*Rissa tridactyla*) are surface-feeding birds that are unable to pursue their prey under water and depend on prey to come up to the water surface. Surface-feeding seabirds appear to be more susceptible to changes in marine food webs than pursuit divers, such as puffins and murres (Baird 1990; Barrett and Krasnow 1996; Regehr and Rodway 1999).

In Newfoundland, Canada, such a change in abundance of a key marine prey species for seabirds occurred during the 1990s. Capelin (*Mallotus villosus*) migrate inshore from offshore feeding grounds to spawn on beaches along the coast of Newfoundland each spring (Templeman 1948). Spawning capelin are an important food resource for seabirds breeding along the Atlantic coast of Newfoundland and Labrador (Burger and Piatt 1990; Brown and Nettleship

1984; Pierotti and Annett 1987; Bryant and Jones 1999). Due to below-normal sea temperatures, the timing of peak capelin beach spawning has been delayed by approximately four weeks since 1991 (Shackell et al. 1994; Therriault et al. 1996). The lower water temperatures also affected maturation causing reductions in size of spawning capelin (Carscadden et al. 1997). The shift in timing of inshore spawning of capelin can have a devastating effect on the breeding performance of seabirds (Regehr and Rodway 1999; Hipfner et al. 2000).

As a result of their flexible foraging behaviour, large gulls, such as herring and great black-backed gulls, benefited from discarded fish waste by industrial fisheries (Furness et al. 1992; Garthe et al. 1996). This extra-abundant food resource easily available to large gulls caused gull populations to increase markedly during this century (e.g. Kadlec and Drury 1968; Furness and Monaghan 1987). The collapse of the northern cod (*Gadus morhua*) stocks in Newfoundland waters resulted in a moratorium that has essentially stopped the commercial cod fishery since 1992. The Eastern Canadian Groundfish Moratorium has likely decreased the opportunities for gulls to feed on fish offal (Regehr and Montevecchi 1997). The large-scale reduction of the ground-fisheries (Hutchings and Myers 1994) and the shift in the timing of capelin spawning have forced gulls to search for alternative food resources. In Newfoundland, large gulls preyed upon adult Atlantic puffins (*Fratercula* *arctica*), adult leach's storm-petrels (*Oceanodroma leucorhoa*) and eggs of black-legged kittiwakes (Nettleship 1972; Russell and Montevecchi 1996; Regehr and Montevecchi 1997; Stenhouse and Montevecchi 1999). In contrast to puffins and storm-petrels, black-legged kittiwakes nest on vertical cliffs rather than in burrows. Hence, the offspring of kittiwakes are visually 'available' to large gulls as prey. Cliff-nesting in birds evolved as an adaptation against predators, mainly mammalian species (Cullen 1957; Birkhead et al. 1985). Recent studies suggest that cliff-nesting also protected breeding thick-billed murres (*Uria lomvia*) against predation by glaucous gulls (*L. hyperboreus*) to a certain degree (Gilchrist and Gaston 1997; Gilchrist et al. 1998). Nest-site characteristics and breeding density influenced under which wind conditions glaucous gulls were able to forage successfully on murre eggs (Gilchrist et al. 1998). Compared to murres, black-legged kittiwakes build distinct nests with vegetation and hence the breeding density is lower. Kittiwakes also breed on narrower ledges than murres (Squibb and Hunt 1983). The size and density of kittiwake sub-colonies, as well as fine-scale nest-site characteristics may reduce the risk of predation by large gulls on kittiwakes. Large gulls may change their foraging tactics according to wind conditions (Gilchrist and Gaston 1997).

The objectives of my study were to test whether delayed capelin availability influences large gull predatory behaviour on black-legged kittiwakes and whether it affects the breeding performance of kittiwakes (Chapter 2) . In the third chapter I examine whether there are any relationships between kittiwake nest-site characteristics and susceptibility to predation by large gulls. A final discussion of the results of chapters 2 and 3 and general conclusions are presented in Chapter 4.

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Co-authorship Statement

For both research papers included in this thesis I am the principal author. I have designed and written the research proposal for this study. I spent several months in 1998 and 1999 on Gull Island to collect the data presented in this thesis. Finally, I analyzed the data and wrote this thesis. My co-authors, John W. Chardine, Ian L. Jones and Gregory J. Robertson (Chapter 1) were intellectually involved in this study by giving advice throughout this study and making suggestions to improve earlier drafts of the research papers.

CHAPTER 2[1]

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

2.1. Abstract

To understand causes and effects of variable foraging behaviour of large gulls I quantified the impact of herring and great black-backed gull predation on black-legged kittiwake breeding success at Gull Island, southeastern Newfoundland in relation to the timing of the annual spawning arrival of capelin during 1998 and 1999. I compared large gulls' predation attempt frequency among three periods: before mean herring gull hatching, between mean gull hatching and the arrival of capelin, and following capelin arrival. The frequency of gull predation attempts on kittiwakes differed significantly

1. This chapter has been accepted for publication as a full paper in Canadian Journal of Zoology on 'Delayed capelin (*Mallotus villosus*) availability influences large gull predatory behaviour on black-legged kittiwakes (*Rissa tridactyla*), causing a reduction in kittiwake breeding success' (Massaro M, Chardine JW, Jones IL, and Robertson GJ 2000).

among the three periods, with highest levels of predation occurring after gull chicks hatched but before capelin arrived. The level of gull predation behaviour was significantly correlated with the percentage of kittiwake eggs and chicks that disappeared within a week. I estimated that 43% of kittiwake eggs and chicks at Gull Island were taken by gulls in 1998 and 30% in 1999. Kittiwakes have been indirectly (through increased predation by gulls) affected by the delayed arrival and lower abundance of capelin in recent years, underlining the need to understand multi-species interactions when interpreting the effects of human alteration of the marine environment.

2.2. Introduction

Capelin 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. In particular, during chick rearing, capelin comprises a large component in the diet of common murres (*Uria aalge;* Burger and Piatt 1990), Atlantic puffins (Brown and Nettleship 1984) and herring gulls (Pierotti and Annett 1987). Due to below-normal sea temperatures, the timing of peak capelin beach spawning has been delayed by approximately four weeks since 1991 (Shackell et al. 1994; Therriault et al. 1996). Additionally, Carscadden et al. (1997) showed that cold water temperatures affect maturation causing reductions in size of spawning capelin. In Newfoundland delayed inshore spawning of capelin can have a devastating effect on the breeding performance of seabirds, in particular surface feeding birds, such as black-legged kittiwakes, herring gulls and great black-backed gulls (Regehr and Rodway 1999).

Large gulls, such as herring and great black-backed gulls, are dietary generalists, which feed on marine fish and invertebrates as well as birds and refuse (e.g. Harris 1965; Threlfall 1968; Beaman 1978). As a result of their flexible foraging behaviour, the numbers of large gulls have increased dramatically in Europe and in the northwest Atlantic during this 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). The Eastern Canadian Groundfish Moratorium in 1992 has likely decreased the opportunities for gulls to feed on fish offal (Regehr and Montevecchi 1997).

Large gulls prey on adults and offspring of several seabird species including Atlantic puffins, common and thick-billed murres and black-legged kittiwakes (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 diet in response to nutritional requirements during the breeding cycle (Pierotti and Annett 1987) and to changes in prey availability (Newton 1993). The large-scale reduction of the ground-fisheries in Newfoundland since 1992 (Hutchings and Myers 1994; Myers and Cardigan 1995) and the shift in the timing of capelin spawning have resulted in increased predation rates 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). In 1992, approximately 87% of 416 eggs and in 1993 approximately 63% of 613 eggs disappeared, most probably taken by aerial predators (Regehr 1994). In contrast, Maunder and Threlfall (1972) did not observe any kittiwake egg predation by herring and great black-backed gulls on Gull Island, Witless Bay, and Neuman (1994) observed herring gulls taking kittiwake eggs only twice during her study just prior to the moratorium in 1990 and 1991.

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 my study was to document the numbers of gull predation attempts during different phases of their nesting cycle and in relation to the timing of capelin arrival. I predicted that predation attempt rates would be highest when gulls were feeding their chicks and before capelin had arrived. Other specific objectives were (1) to compare predation attempt rates among several kittiwake colonies of different size, (2) to compare the frequency of predation attempts at different times of the day, (3) to compare predation attempt rates of herring and great black-backed gulls, (4) to compare gull predation behaviour frequency with the number of kittiwake eggs and chicks that disappeared and (5) to measure the impact of gull predation on overall kittiwake reproductive success.

2.3. Methods

2.3.1. Study location

The study was conducted on Gull Island (47° 16′ N, 52° 46′ W), part of the Witless Bay Seabird Ecological Reserve off the southeastern coast of Newfoundland, Canada. 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, 2794 breeding pairs of herring gulls and 115 pairs of great black-backed gulls nested on the entire island (G. J. Robertson, unpubl. data). I conducted my research on Gull Island from 24 May to 15 August in 1998, and 16 May to 9 August in 1999.

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

2.3.2. Predation behaviour frequency

During 1998 and 1999, predation behaviour frequency was quantified on four kittiwake study plots during 2-4 h watches throughout the breeding season. Although the selection of watches at study plots was not done randomly, I distributed watches equally, temporally and spatially, among plots. All observations were done from blinds to ensure normal undisturbed predatory behaviour of gulls. I also entered blinds approximately 5 min before a watch started to allow gulls to settle down after they were disturbed by my arrival. There was no evidence that predation attempts were more frequent at the beginning of a watch because of my approach to the colony. I defined a predation attempt as an occasion when a large gull closely approached, either in flight or on foot, one or more kittiwake nests, eliciting responses such as turning towards the gull and simultaneously loud calling, bill jabbing, pecking, biting and diving at a gull on the cliff ledge as well as during flight in close proximity to the cliff. For each predation attempt I recorded, whether a herring gull or black-backed gull was involved. For each observation period, hourly predation behaviour frequency 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. I obtained predation attempt rates 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 one day, but several hours apart. I categorized all watches into four different time-periods: early morning (0400 - 0900), morning (0900 - 1300), afternoon (1300 - 1700) and evening (1700 - 2200). I distinguished three periods within each breeding season: (1) from when I started my research on the island early in the season until the mean date of herring gull hatching, (2) from the mean date of gull hatching until capelin arrival, and (3) after capelin arrival.

2.3.3. 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 P2 where no breeding data were collected in 1999. In 1998 I monitored a total of 700 kittiwake nests and in 1999, 645 nests. If kittiwake chicks hatched between two watches, the date midway between the two watches was taken as the date of hatching measured to the half-day. Kittiwake chicks that survived 35 days or more were considered as fledged. In some rare occasions kittiwake chicks between the age of 30 and 35 days disappeared or I left Gull Island too early to monitor their fledging. Those chicks were assumed to fledge and were included as fledged chicks in the analysis.

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

2.3.4. Timing of gull hatching

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

The same method was used for determining the hatching dates of great black-backed gulls (1998: n = 8 nests with 18 hatched eggs; 1999: n = 10 nests with 26 hatched eggs). All observed black-backed gull nests were located at the southern end of Gull Island and were from solitary breeders, that nested with a minimum distance of 20 m to the nearest intra-species neighbour.

2.3.5. Capelin arrival

The date of first delivery of capelin by Atlantic puffins and common murres to their chicks was taken as the date for 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 (unpubl. data), who regularly collected puffin chick diet data and in 1999 by an underwater filmcrew, who dove regularly close to Gull Island. I used the terms 'inshore arrival' and 'first spawning arrival' interchangeably throughout this thesis.

2.3.6. Statistical analyses

Given my watches were not randomized, watches might not be completely independent. I was particularly concerned about the independence of back-to-back watches. In order to test whether I could include all 34 pairs of watches done back-to-back in subsequent analyses, I tested whether the number of herring and great black-backed gull predation attempts per hour occurring during the second watch of each pair was independent of the number per hour occurring in the first watch. I compared those 34 pairs of watches with the 21 pairs of observation periods which were done at one plot within a day, but several hours apart. I calculated the differences in predation attempt rates between the pairs of watches and obtained the ratio of variances. This F-ratio of a two-tailed test allowed me to test whether there was a statistically significant difference between predation attempt rates obtained from watches done back-to-back, and watches done several hours apart (Sokal and Rohlf 1995).

Predation rates were generally distributed as a Poisson distribution, based on 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 1996) was used to compare predation attempt rates. I included the following terms in the original model: study plot, year, intra-seasonal period, time of day and all two-way interaction terms. If statistically non-significant ($p > 0.1$), high order terms were excluded from subsequent models until only significant terms remained. To reduce the risk of a type II error I used a $p < 0.1$ to allow 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.

Due to my sampling unit (number of gull predation attempts per hour) it was impossible to include an independent variable for gull species into the main analysis (see above). To be able to compare the predation attempt rates of the two gull species indirectly I chose to use herring and great black-backed gull predation attempt rates each as a response variable in two separate analyses. As in the main analysis I used a generalized linear model with a Poisson distributed response variable, including the same four independent variables. I followed the same procedure as described above for finding the best fitting model.

I used Pearson product-moment correlations to test whether percentages of kittiwake eggs and chicks that disappeared were correlated (1) with available eggs and chicks or (2) with 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.

2.4. Results

2.4.1. Timing

In 1998, schools of spawning capelin first arrived and spawned in Witless Bay on 5 July; in 1999 capelin arrived inshore on 26 June, 9 days 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. Mean hatch date of herring gulls occurred on 9 June 1999 (± 5 d). Mean first-egg laying dates for kittiwakes were 2 June in 1998 (± 7 d) and 3 June in 1999 (± 12 d). Mean hatching dates were 27 June in 1998 (± 6 d) and two days later in 1999 (29 June ± 8 d). Median laying and hatching dates of gulls and kittiwakes never differed by more than one day from mean dates (Fig. 2.1).

The period before mean herring gull hatching lasted from 4- 20 June (17 d) in 1998, and from 18 May- 9 June (23 d) in 1999. The second period, which started after mean herring gull hatching and continued until capelin arrival, was 21 June- 4 July in 1998 (14 d) and 10- 25 June in 1999 (16 d). The period after capelin arrival started on 5 July in 1998 and 26 June in 1999. In 1998, the last watch of the third period was done on 7 Aug. (34 d), and in 1999 on 25 July (29 d; Fig. 2.1).

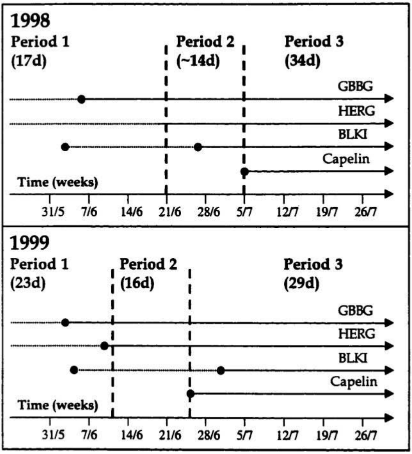


Fig. 2.1. Timing of breeding of great black-backed gulls (GBBG), herring gulls (HERG) and black-legged kittiwakes (BLKI) on Gull Island and timing of capelin arrival in Witless Bay in 1998 and 1999. Dotted lines indicate the period when birds incubated eggs and solid lines describe when birds had chicks. Mean hatching dates for all three bird species and mean first-egg laying dates for kittiwakes are indicated by big circles. The three intra-seasonal periods for each year are reported with their duration time (d = days).

2.4.2. Gull feeding territories

During the two years of my study I observed that all kittiwake plots were part of feeding territories of breeding herring and great black-backed gulls. Each kittiwake plot was defended by one or - in 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 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 both years.

2.4.3. Frequency of gull predatory behaviour on kittiwakes

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

Mean gull predation attempt rates (attempts/hour) of herring and great black-backed gulls on kittiwakes at the four study plots are presented in Figure 2.2. Whereas in 1998, mean predation attempt rate per hour in the second period (including all plots) was about 6-7 times higher (1.72 ± 1.6) than before gull hatching (0.27 ± 0.34) and after capelin arrival (0.23 ± 0.55), mean attempt rate in 1999 was only about 2-5 times higher (0.90 ± 0.97) in the second period than in the first (0.41 ± 0.66) and third period (0.19 ± 0.43).

The final generalized linear model for gull predation attempt rates included all main effects and one interaction term, year by intra-seasonal period, as predictors (Table 2.1). Gull predation attempt rates differed significantly among study plots, however there was no evidence of variation among years. Predation attempt rates were significantly different among the three intra-seasonal periods, with highest attempt rates in the second period after mean herring gull hatching, but before capelin arrival (Table 2.1). Although, mean predation attempt rates were highest early in the morning (0.76 ± 1.15), followed by attempt rates in the evening (0.59 ± 1.13) and lowest in the morning (0.46 ± 0.83) and afternoon hours (0.45 ± 0.67), those differences of attempt rates at different times of the day were not statistical significant (Table 2.1). The interaction of year and period was also insignificant in the final model (Table 2.1).

For all analyses with each gull species treated separately, all two-way interaction terms proved to be either insignificant or insufficient data were available to estimate the interaction. There was a significant year and intra-seasonal period effect in herring gull predation attempt rates (Year: $\chi^2 = 9.7$, df

$= 1$, $p = 0.0018$; Period: $\chi^2 = 54.3$, $df = 2$, $p < 0.0001$). However, for great black-backed gull predation attempt rates, I found significant plot, intra-seasonal period and time of day effects, but no significant year effect (Plot: $\chi^2 = 48.5$, $df = 3$, $p < 0.0001$; Period: $\chi^2 = 26.6$, $df = 2$, $p < 0.0001$; Time of day: $\chi^2 = 8.6$, $df = 3$, $p = 0.0351$). Mean predation attempt rates of herring gulls on kittiwakes were lower during all three periods in 1999 than in 1998. However, great black-backed gull predation attempt rates on kittiwakes were similar between years (Fig. 2.3).

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

Table 2.1. Generalized linear model of factors influencing rates of herring and great black-backed gull predation attempts 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 insignificant (p > 0.1) and dropped from the model. For the final model the tolerance for type I error was set at 0.05 for main effects. Generalized linear model with Poisson distribution and a log link function.

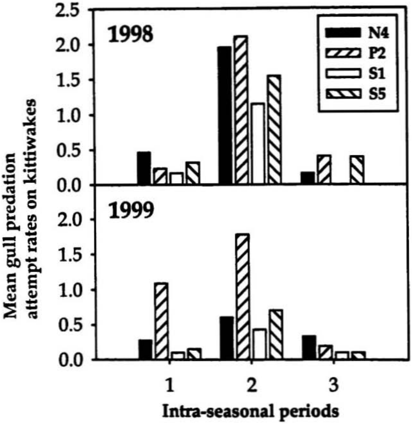


Fig. 2.2. Mean gull predation attempt rates (attempts/hour) on black-legged kittiwakes at four study plots on Gull Island within three intra-seasonal periods of 1998 and 1999. The first intra-seasonal period (1) lasted from the beginning of the season until mean herring gull hatching, the second period (2) from mean herring gull hatching until capelin arrival, and the third period (3) from capelin arrival until the end of the season.

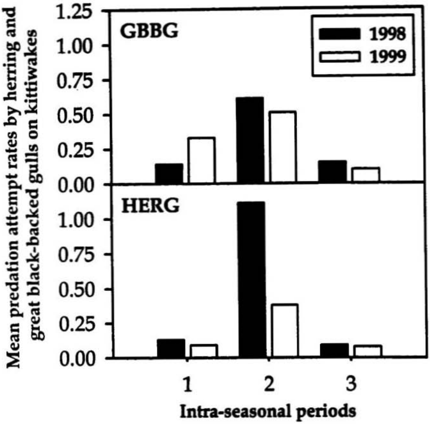
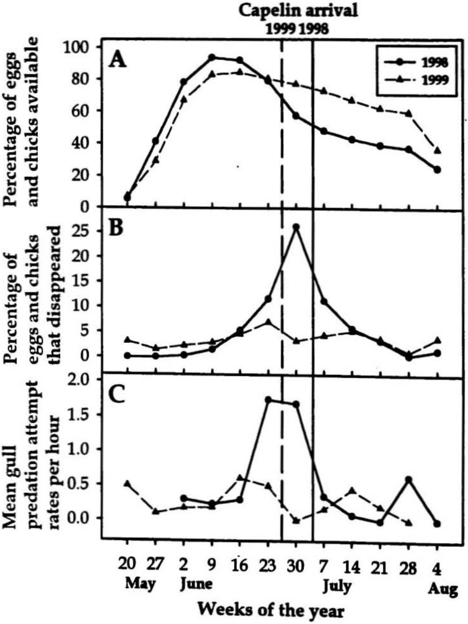


Fig. 2.3. Mean predation attempt rates (attempts/hour) of great black-backed gulls (GBBG) and herring gulls (HERG) on black-legged kittiwakes on Gull Island within three intra-seasonal periods of 1998 and 1999. The first intra-seasonal period (1) lasted from the beginning of the season until mean herring gull hatching, the second period (2) from mean herring gull hatching until capelin arrival, and the third period (3) from capelin arrival until the end of the season.

2.4.4. Gull predation attempt rates and disappearance of kittiwake eggs and chicks

I did not find any correlation between the percentage of kittiwake eggs and chicks that disappeared and available eggs and chicks in each week ($r = 0.07$, $n = 21$, $p > 0.05$). However, in both years, weekly gull predation attempt rates were positively correlated with the percentage of kittiwake eggs and chicks that disappeared within each week ($r = 0.77$, $n = 21$, $p < 0.05$; Fig. 2.4).



Capelin arrival
1999 1998
A
B
C
1998
1999
Percentage of eggs and chicks available
Percentage of eggs and chicks that disappeared
Mean gull predation attempt rates per hour
100
80
60
40
20
0
25
20
15
10
5
0
2.0
1.5
1.0
0.5
0.0
20 27 2 9 16 23 30 7 14 21 28 4
May June July Aug
Weeks of the year

2.4.5. The effect of gull predation on kittiwake breeding success

Of 700 observed kittiwake nests in 1998, 589 nests were active ($\geq$ 1 egg was laid). Of 1026 kittiwake eggs laid, 686 chicks hatched and 230 eggs disappeared. Of all chicks hatched, 367 fledged and 193 kittiwake chicks 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 (Table 2.2). A total of 423 (41.2%) kittiwake offspring disappeared and adding the 8 eggs and 8 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 due to gull predation in 1998.

In 1999, 515 nests were active of 645 monitored nests. Of 891 eggs laid, 657 chicks hatched and 158 eggs disappeared. Of 657 chicks hatched, 480 fledged and 94 disappeared. Chick survival rate per nest was 0.93 and 329 (63.9%) pairs with eggs successful fledged chicks. An average of 0.72 chicks fledged successfully per completed nest (Table 2.2). A total of 252 (28.3%) kittiwake offspring disappeared and by adding the 13 eggs and 5 chicks that were depredated 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 taken by gulls in 1999.

Table 2.2. Breeding success of black-legged kittiwakes on Gull Island in 1998 and 1999.

Kittiwake breeding performance on Gull Island	Year	
	1998	1999
Total number of observed nests	700	645
Total number of active nests (≥ 1 egg was laid)	589 (84.1%)	515 (79.8%)
Number of eggs laid	1026	891
Number of eggs that disappeared	230 (22.4%)	158 (17.7%)
Number of chicks hatched	686 (66.7%)	657 (73.7%)
Number of chicks that disappeared	193 (28.1%)	94 (14.3%)
Number of chicks fledged	367 (53.5%)	480 (73.1%)
Chick survival rate (number of fledged chicks/number of active nests)	0.62	0.93
Average number of chicks fledged per completed nest	0.52	0.72

2.5. Discussion

2.5.1. Intra-seasonal variation in gull predatory behaviour

In both years I observed striking variation in the frequency of gull predatory behaviour throughout the breeding season. At all plots predation attempt rates increased after mean herring gull hatching and decreased after capelin arrival. What caused those drastic differences in gull predation attempt rates over the breeding season?

Threlfall (1968) noted that herring gulls fed mainly on blue mussel *(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 prey-switching by herring gulls in Witless Bay from 1976 to 1978. In those years capelin arrived in Witless Bay early in June (Pierotti and Annett 1987). They found that herring gulls switched to capelin as soon as they had chicks to feed, rather than when capelin, the most profitable prey item, became available. Since the beginning of the 1990s, delayed capelin arrival and the groundfish moratorium have substantially decreased food availability at a 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, unpubl. data) and on the north shore of the Gulf of St. Lawrence (Chapdelaine and Rail 1997) since 1990 support the idea that large gulls suffered from low food availability and have been forced to find alternative food resources, such as kittiwakes, puffins and leach's storm-petrels. Stenhouse and Montevecchi (1999) found that herring gull predation on adult leach's storm-petrels decreased markedly after capelin arrival. Russell and Montevecchi (1996) suggested that kittiwake offspring and adults appear to be easier targets for gulls than adult puffins. Additionally the offspring of kittiwakes are visually 'available' during the period of high food demand compared to puffin and the nocturnal leach's storm-petrel offspring which are protected by burrows. In contrast to the situation prior to 1990, a lack of capelin after gull chicks hatched appears to have caused an increase of gull predation attempts on kittiwakes. However, as soon as spawning capelin became available to chick-rearing gulls, they once again foraged on capelin, which offers a low-risk, high-energy food resource (Pierotti and Annett 1987).

Low herring and great black-backed gull breeding success might also be a result of high rates of cannibalism in both species. It would be to great interest to investigate the levels of cannibalism prior and post capelin arrival.

2.5.2. Inter-year differences in gull predation rates

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

The inter-year difference of mean gull predation attempt rates is caused by the drastic variation of herring gull predation rates among years. However, great black-backed gull predation attempt rates on kittiwakes were similar between years. Why did predation rates by herring gulls, but not by black-backed gulls, differ among years? In both years, three of the kittiwake study plots were distinct feeding territories of great black-backed gull pairs. Spear (1993) observed that male western gulls *(Larus occidentalis)*, which had specialized in feeding on common murres and brandt's cormorants *(Phalacrocorax penicillatus)*, showed high fidelity to their feeding territories. In 1999 on Gull Island, I uniquely colour banded one male great black-backed gull, which held a feeding territory at kittiwake study plot N4. Sixty percent of all great black-backed gull predation attempts on kittiwakes at N4 were made by this individual (M. Massaro, unpubl. data). While great black-backed gulls were responsible for most predation attempts on kittiwakes during the first and third period, herring gulls pursued 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. Usually during such gull-gull interactions the resident gull approached rapidly another gull and forcing it to leave the territory by chasing and attempting to bite the intruding gull. Twenty-five (74.3%) of all intrusions were observed during the period between gull hatching and capelin arrival (M. Massaro, unpubl. data). This suggests that for most herring gulls pursuing a predation attempt in a black-backed gull territory is a risky venture, which should be avoided if other food sources are available.

2.5.3. Gull predation rate differences among study plots

Including both years, in all three periods P2, the open and more exposed cliff had the highest mean predation attempt rates. P2 was followed by N4 and lowest mean predation attempt rates were observed at S1. At S1, only herring gulls were observed as kittiwake predators. S1 was a very small cliff which could not support much more than 50 kittiwake nests. The low number of kittiwake breeding pairs at S1, and the fact that no resident great black-backed gull pair occupied S1 as a feeding territory, might explain the low predation attempt rate compared to the other study plots. Although Regehr et al. (1998) stated that large-scale cliff structure influences the predatory behaviour and success of avian predators on kittiwakes, causing differences in kittiwake breeding performance, they did not observe and compare gull predation rates among cliffs. Differences in kittiwake breeding performance among cliffs might be a result of 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 bird and large-scale cliff structure. Although P2 had the same number of resident predatory gulls as other cliffs (N4, S5), predation attempt rates were higher. I believe that due to the open cliff structure, wind conditions at P2 on most days were more favorable for gull predation than in narrow gulches, where winds are gusty and gulls cannot maneuver as easily (Gilchrist and Gaston 1997; Gilchrist et al. 1998).

2.5.4. The impact of gull predation on kittiwake breeding performance

At the population level it is essential to know the impact of large gull predation on kittiwakes and its implications on 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 due 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 with the exception of 1996 (Neuman 1994; J. W. Chardine, unpubl. data). At the Gannet Islands in Labrador, Canada, kittiwake breeding success ranged from zero to 0.77 fledged chicks per nest in 1996-98, compared to higher success in 1981-83 ranging from 0.90 to 1.13 (Hipfner et al. 2000). A similar decrease in kittiwake breeding success has been observed in southeastern Scotland and northeastern England since 1986, 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 populations of marine prey species have direct impacts 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, indirect effects, due to increasing predation of predatory bird species on other birds, have been rarely 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 difficulties in providing chicks with food but also with an increased predation pressure by gulls. Additionally, in years of food shortage kittiwakes show low adult attendance at nests with chicks, and the risk of nestlings being depredated increases (Barrett and Runde 1980). On Great Island in Witless Bay this caused a complete breeding failure of kittiwakes in 1992 (1% of pairs with eggs fledged chicks; Regehr 1994). In 1998 and 1999 on Gull Island chick survival was lower than in most other Atlantic studies [53.5% (1998) and 73.1% (1999); 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 in some studies [26% in 1976 Barrett and Runde (1980); 7% in 1992 Regehr and Montevecchi (1997)]. On Gull Island 0.52 (1998) and 0.72 (1999) chicks fledged per completed nest. Harris and Wanless (1990) reported rates for young fledged per completed nests between zero and 1.56 for 36 kittiwake colonies at the coast of England, Scotland and Ireland. In kittiwake colonies in France, Danchin and Monnat (1992) observed 1.03 fledged young per pair in a flourishing colony compared to only 0.49 young per pair in a declining colony. My estimates are below 1.03 and closer to 0.49.

Changes in 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. The predation of western gulls on common murres and brandt's cormorants were significantly higher during an El Niño year compared to the other years (Spear 1993). Gulls took 66% of all eggs laid during the El Niño year compared to 18% and 12% during years of normal food availability. Compared to Spear's study my estimates of the overall impact of gull predation on kittiwakes are high, considering that my estimates are markedly higher than 18% in two subsequent years (1998: 42.8%; 1999: 30.3%). Regehr's (1994) study suggests that the impact of gull predation on kittiwakes was even higher in the early 1990s than in 1998 and 1999. High rates of large gull predation for almost a decade now may have 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 decreasing gull predation rates on kittiwakes.

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CHAPTER 3

Relationships between black-legged kittiwake nest-site characteristics and susceptibility to predation by large gulls

3.1. Abstract

To understand how certain kittiwake site characteristics, plot variability and wind conditions affect large gulls foraging ability I quantified the relationship between black-legged kittiwake nest-site characteristics and risk of predation by great black-backed and herring gulls at Gull Island, Witless Bay, Newfoundland, Canada during 1998 and 1999. I monitored kittiwake nesting cliffs to identify sites attacked by large gulls and compared characteristics of depredated and surviving nests among four study plots. I also examined which nest sites were attacked by herring gulls and great black-backed gulls during calm (< 10 km/h) and windy conditions ($\geq$ 10 km/h). I found that individual kittiwake nests at the smallest plot were more likely to be attacked by large gulls compared to nests on larger plots. Hence, the percentage of failed nests was highest at the smallest plot and nesting success increased as the size of the plots (number of nests) increased. Nesting density and the location on the cliff

were nest-site characteristics that reduced significantly the risk of predation by large gulls. Breeding success was correlated with ledge width and nesting density and differed significantly among plots.

Regardless of wind conditions both gull species attacked nest sites located on upper parts of cliffs to a higher percentage than nests located on middle or lower parts of the cliff. However, during calm conditions, roofs over nest sites reduced the risk of predation by herring gulls, whereas sites located on narrow ledges were less likely to be attacked by great black-backed gulls. During windy conditions, nesting density affected which sites were attacked by great black-backed gulls.

Taken together, my results demonstrated a high rate of predation of kittiwake nests by large gulls at Gull Island, with striking differences among plots. I also demonstrated that kittiwake nest location, certain nest-site characteristics, and breeding density can all influence the risk of predation.

3.2. Introduction

Long-lived species that invest heavily in raising their few offspring are expected to select breeding habitat that maximizes the chances of survival for their offspring and themselves (Lack 1954; Martin 1988). Risk of predation is likely to be one of the most important factors influencing habitat selection (Martin 1993; Danchin et al. 1998; Rachlow and Bowyer 1998). In birds, the selection of cliffs as breeding habitats likely evolved as a response to predation by terrestrial mammals (Cullen 1957; Tuck 1961; Birkhead et al. 1985). However, cliff-nesting does not necessarily protect birds from avian predation. Several studies have shown that a number of species in the families Laridae and Corvidae are successful in preying upon cliff-nesting bird species (Montevecchi 1979; Maccarone 1992; Gaston and Elliott 1996; Gilchrist and Gaston 1997; Barbraud 1999).

Unlike most gulls, black-legged kittiwakes and red-legged kittiwakes (*R. brevirostris*) breed on steep, vertical cliffs rather than on the ground. Cullen (1957) proposed that as kittiwakes evolved, they switched from ground-nesting to cliff-nesting to avoid predation by terrestrial predators. With the adoption of cliff-nesting, well-developed mobbing behaviour as a group defense tactic against predators, such as observed in many species of Laridae, was lost or at least much reduced in kittiwakes (Cullen 1957; Shealer and Burger 1992; Cavanagh and Griffin 1993; Yorio and Quintana 1997). However, kittiwakes may defend their offspring against predators if faced with a high risk of predation. Whereas many kittiwake colonies, in particular in Britain and Alaska, lose few or no eggs and chicks to large gulls, ravens or crows (Coulson 1963; Maunder and Threlfall 1972; Murphy et al. 1991), other kittiwake colonies experience greater rates of avian predation (Barrett and Runde 1980; Maccarone 1992; Regehr and Montevecchi 1996). On the southeastern coast of Newfoundland, Canada, increasing populations of herring and great black-backed gulls and reduced availability of natural marine food resources and fisheries waste since the early 1990s, have caused increased predation by large gulls on kittiwakes (Regehr and Montevecchi 1996; Massaro et al. 2000).

Under conditions of high predation pressure, specific nest-site characteristics, nesting density and colony size may play a role in enhancing reproductive success. Nesting in large colonies with high nest densities may offer advantages to individual birds due to increased vigilance, group defense and predator swamping (Burger and Gochfeld 1994, Wittenberger and Hunt 1995, Gilchrist and Gaston 1997). In cliff-nesting thick-billed murres, nest-site characteristics and breeding density influenced foraging success of glaucous gulls preying on murre eggs (Gilchrist and Gaston 1997; Gilchrist et al. 1998).

Kittiwake nest-site characteristics may be particularly important in reducing predation late in the breeding season when large kittiwake chicks are often left alone by their parents, increasing their vulnerability to predation. On Baccalieu Island, Newfoundland, Maccarone (1992) found that common ravens (*Corvus corax*) were more likely to patrol along upper parts of a kittiwake cliff rather than the middle or lower parts. Kittiwake nests with chicks had larger overhangs than randomly selected nests on Great Island, Newfoundland (Regehr et al. 1998). That study used survival time of kittiwake chicks and eggs to infer which nest-site characteristics may reduce gull predation. Kittiwake colony size, specific nest-site characteristics, nesting density and wind conditions may constrain the foraging success of large gulls depredating kittiwakes.

The objective of this study was to quantify the relationship of kittiwake nest-site characteristics and susceptibility to herring and great black-backed gull predation at Gull Island, Newfoundland. I monitored nests to determine which sites were and were not attacked by large gulls. I compared characteristics of nest sites that were attacked with sites that were not to test whether plot, ledge width, roof, number of walls, nesting density or cliff part affected which sites were attacked. I also compared which nests were attacked by herring gulls and great black-backed gulls during calm and windy conditions. After identifying which nest-site characteristics reduced the risk of gull predation, I examined whether these same nest-site characteristics influenced breeding success.

3.3. Methods

3.3.1. Study location

The study was conducted from 24 May to 15 August 1998 and 16 May to 9 August 1999 on Gull Island (47° 16′ N, 52° 46′ W), the most northerly of four islands within the Witless Bay Seabird Ecological Reserve off the southeastern coast of Newfoundland, Canada (Appendix 1). Gull Island is approximately 1.6 km long and 0.8 km wide. The cliffs of Gull Island offer breeding habitat to over 10,000 pairs of black-legged kittiwakes, approximately 175 pairs of razorbills *(Alca torda)*, and 700 pairs of common murres (Lock et al. 1994). The island also supports approximately 2,800 breeding pairs of herring gulls and 115 pairs of great black-backed gulls (G.J. Robertson, unpubl. data).

3.3.2. Study plots

In order to examine the influence of nest-site characteristics on predation, I selected four west-facing kittiwake cliffs as study plots, which differed in size, height, and overall cliff structure. All four plots were located at the southern end of the island, but were at least 200 m apart (Appendix 1). Three of the four plots (N4, S5, S1) were within protected gulches (narrow inlets) and one (P2) was part of an open cliff face at the edge of the island. For all plots within a gulch I determined the opening angle towards the sea by recording the angles from the narrow end of a gulch along both cliffs enclosing a gulch.

Of all study plots, S1 was the smallest cliff with an approximate height of 5-6 m. The gulch had an opening angle of approximately 16°. P2 was the second largest cliff with a height of approximately 8-9 m and was not located within a gulch. N4 was 12-13 m high and the opening angle towards the sea was approximately 20°. Being approximately 20 m high, plot S5 was the highest cliff studied. The opening of the gulch was approximately 19°.

3.3.3. Kittiwake nest predation

In both years all nests at the four study plots were individually numbered, mapped and photographed. At all four kittiwake plots, 2-4 h watches were regularly conducted throughout the breeding season. Total observation times were 286 h in 1998, and 426 h in 1999, of which 192 h were at N4, 159 h at S5, 196 h at P2, and 165 h at S1. To ensure normal, undisturbed predatory behaviour of gulls all observations were made from blinds, and I entered blinds approximately 5 min before a watch started to allow gulls to settle down after they were disturbed by my arrival. There was no evidence that predation attempts were more frequent at the beginning of a watch due to my approach to the colony. For each herring gull or great black-backed gull predation attempt, whether successful or unsuccessful, I recorded which nest was attacked. If more than one kittiwake nest was attacked during a predation attempt I chose one of the nests randomly to ensure independence and included it in the analyses. Nests that were attacked by herring or great black-backed gulls at least once in 1998 or 1999 were classified as 'attacked' nests.

3.3.4. Nest-site characteristics

To minimize disturbance to breeding birds, nest-site characteristics were quantified during late chick rearing by observation from a distance of about 10-30 m with binoculars and a 30x75 spotting scope. For all kittiwake nest sites at each plot I recorded five characteristics with the following categories: (1) ledge width (broad, narrow), (2) roof (roof, no roof), (3) number of vertical walls (zero or one, two or three walls), (4) nesting density (low, medium or high) and

(5) cliff part (upper, middle or lower). I classified the different categories of ledge width, roof and walls following Gaston and Nettleship (1981; Figure 71). A nest was considered to be on a narrow ledge if the nest material was hanging over the edge of the seaward-oriented ledge. A nest site had a roof if the interior of a nest was overhung by rock within twice the height of an adult kittiwake. I counted the number of walls immediately surrounding the nest. Walls had to be at least the height of an adult kittiwake sitting on a nest and were at least as wide as a nest cup. For the variable 'nesting density' I counted for each nest site the number of direct neighbouring breeding pairs within a radius of three body lengths of a standing kittiwake (approximately a radius of 0.75 m; $\pi * r^2 = 1.77$ m^2) and added it to one (for the resident kittiwake pair on each site). All sites with a nesting density index (1) of one or two were classified as low density (0.6- 1.1 kittiwake pairs/m^2), (2) of three were classified as medium density (1.7 kittiwake pairs/m^2), and (3) of four and more were considered sites within high density areas ($\geq$ 2.3 kittiwake pairs/m^2). To determine whether a site was located on the upper, middle or lower part of the cliff I quantified the distance between each nest site and the upper edge of the cliff. I used a Bushnell laser range-finder to measure the distance between the observer and (1) the nest-site, (2) the upper edge of the cliff, and (3) the point on the cliff which was at eye-level, to the nearest meter. A clinometer was used to

measure the angles between those three points, and the distance of a nest to the upper edge of a cliff was calculated trigonometrically. For each kittiwake plot I calculated the median distance between all nests and the cliffs' upper edge. I defined the border between upper and middle cliff by subtracting one-half of the standard deviation from the median. By adding half a standard deviation to the median the border between the middle and lower part of the cliff was determined (Table 3.1). This procedure was used to define upper, middle and lower part of all four study plots. The number of nests and the percentage of nests with a certain nest-site characteristic are reported in Table 3.2 for each study plot. Nest-site characteristics for each individual nest site are listed in Appendix 2.

Table 3.1. Definition of the upper, middle and lower part for four study plots (S1, P2, N4 and S5) on Gull Island in 1998 and 1999. The distance of a kittiwake nest to the upper edge of a cliff defined where a nest was located relative to the upper edge of a cliff.

	Plot S1 Median = 1.70 m (± 1.03)	Plot P2 Median = 2.16 m (± 1.90)	Plot N4 Median = 4.86 m (± 2.25)	Plot S5 Median = 4.85 m (± 4.09)
UPPER PART	< 1.19 m	< 1.21 m	< 3.74 m	< 2.81 m
MIDDLE PART	1.19 - 2.21 m	1.21 - 3.11 m	3.74 - 5.98 m	2.81 - 6.89 m
LOWER PART	> 2.21 m	> 3.11 m	> 5.98 m	> 6.89 m

Note: Median nest distance to the cliff's upper edge and ± 1 SD are recorded for each plot.

Table 3.2. The number of active kittiwake nests (≥ 1 egg was laid) falling within each level of nest-site characteristic, for each of the four study plots on Gull Island in 1998 and 1999.

Nest-site characteristics		Plot S1, n = 42	Plot P2, n = 81	Plot N4, n = 268	Plot S5, n= 268
LEDGE WIDTH	broad	18 (42.9%)	24 (29.6%)	100 (37.3%)	124 (46.3%)
	narrow	24 (57.1%)	57 (70.4%)	168 (62.7%)	144 (53.7%)
ROOF	roof	15 (35.7%)	53 (65.4%)	180 (67.2%)	115 (42.9%)
	no roof	27 (64.3%)	28 (34.6%)	88 (32.8%)	153 (57.1%)
NO. WALLS	0 or 1 wall	29 (69.0%)	72 (88.9%)	219 (81.7%)	230 (85.8%)
	2 or 3 walls	13 (31.0%)	9 (11.1%)	49 (18.3%)	38 (14.2%)
DENSITY	low	18 (42.8%)	31 (38.3%)	128 (47.8%)	115 (42.9%)
	medium	21 (50.0%)	39 (48.1%)	111 (41.4%)	80 (29.9%)
	high	3 (7.1%)	11 (13.6%)	29 (10.8%)	73 (27.2)
CLIFF PART	upper part	9 (21.4%)	16 (19.8%)	92 (34.3%)	59 (22.0%)
	middle part	18 (42.9%)	31 (38.3%)	96 (35.8%)	104 (38.8%)
	lower part	15 (35.7%)	34 (42.0%)	80 (29.9%)	105 (39.2%)

3.3.5. Wind conditions

During both seasons, wind speed and direction were measured hourly by a weather station (Davis Instruments Corp., Weather Wizzard III) located on an exposed hill at the southwestern end of Gull Island (Appendix 1). The measuring device was fixed to a tree trunk approximately 1.8 m above ground. Due to a programming mistake the weather station did not collect any data for May and June 1999. To compensate, I measured wind conditions with a handheld anemometer during most predation behaviour watches at the kittiwake study plots. For 16 occasions the wind conditions during gull predation attempts were unknown and I used wind data collected by Environment Canada at the St. John's airport, located approximately 35 km to the north of the study area.

For each gull predation attempt I classified the wind condition either as calm ($\leq$ 10 km/h) or windy (> 10 km/h). However, if wind directions were not within the opening angles of the cliffs, wind conditions were considered to be calm even if wind speed exceeded 10 km/h. For P2, only westerly (180° - 360°) winds over 10 km/h speed were considered "windy". For all other three plots only south-south-easterly to south-south-westerly winds (157.5° - 202.5°) over 10 km/h were considered "windy".

3.3.6. Breeding success of kittiwakes

Contents of all numbered nests at the four plots were monitored approximately twice per week, except at plot P2 where no breeding data were collected in 1999. For events that occurred between observation periods, such as chick hatching, the date midway between the two watches was taken as the date of the event, measured to the nearest half day. Kittiwake chicks that survived 35 days or more were considered to have fledged. On rare occasions kittiwake chicks between the age of 30 and 35 days disappeared ($n = 76$ chicks); those chicks were assumed to have fledged and were included in the analysis (9.0% of all chicks fledged). All nests where one or more chicks fledged successfully in 1998 or 1999 were considered 'successful'.

3.3.7. Statistical analyses

Only kittiwake nests that were active (≥ 1 egg was laid) in 1998 or 1999 were included in analyses. If a nest site was used by kittiwakes in 1998 and 1999, the nest site was only counted once to avoid pseudo replication. Similarly, if a kittiwake nest-site was attacked by gulls in 1998 and 1999, it was only included once in the dataset. To test whether the proportion of attacked and successful nests differed among plots, I used chi-square tests.

To be able to include density as a independent variable in the main analysis I chose randomly 300 sites (out of 659 active sites) and used these as my sample size. This procedure ensured independent samples. To test whether nest-site characteristics influenced susceptibility to large gull predation I used a generalized linear model with a binary response variable (attacked or not attacked), a logit link function and six discrete independent variables: plot, ledge width, roof, number of walls, density and cliff part. All two-way interactions were included in the original model and excluded from the final model if the probability was higher than 0.1 in the original model. To reduce the risk of a type II error, I used a $p < 0.1$ to allow 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.

I tested whether overall breeding success of certain nest sites was influenced by the same nest-site characteristics that prevented gull attacks or not. For this analysis my sample size consisted of the same 300 randomly chosen nest sites than in the main analysis (see above). I used a generalized linear model with a binary response variable (successful or not successful in raising a chick), a logit link function, and six independent variables: plot, ledge width, roof, number of walls, density and cliff part. I followed the same method for finding the best fitting model than described above.

For the next set of analyses I chose randomly 300 nests out of 617 active nests from three study plots (N4, S5 and P2). I had four response variables: attacked or not attacked (1) by herring gulls under calm conditions, (2) by great black-backed gulls under calm conditions, (3) by herring gulls under windy conditions and (4) by great black-backed gulls under windy conditions. Plot S1 was excluded from this analysis because only herring gulls foraged at this plot under calm conditions. I did four analyses, one for each response variable, with following six independent variables: plot, ledge width, roof, number of walls, density and cliff part. I used generalized linear models and logit link functions and followed the same procedure as described above for finding the best fitting model. In cases where there were no attacks on nest sites with a certain characteristic, those terms were not estimable and dropped out of the final model.

The term 'significance' is used in relation to statistical tests and does not imply biological importance.

3.4. Results

3.4.1. Differences in gull predation risk and kittiwake breeding success among plots including all nest sites

For each plot the number of active nests, the percentage of attacked nests and successful nests is reported in Table 3.3. The proportion of nests attacked differed significantly among plots ($\chi^2 = 53.11$, df = 3, $p < 0.0001$). Plot S1 had the highest percentage of attacked nest sites, followed by P2, N4 and S5 (Table 3.3). I received the same results in the analysis including 300 randomly chosen sites (see below). The percentage of successful nests in 1998 or 1999 varied significantly among plots ($\chi^2 = 40.58$, df = 3, $p < 0.0001$). Plot S1 which had the highest proportion of attacked nests (see above), also had the lowest percentage of sites that raised chicks (33.3%, 14/42), followed by plot P2 with 55.6% (45/81) , and plots S5 and N4 had the highest percentage of 72.4% (194/268) and 76.6% (205/268) respectively (Table 3.3). I also received the same results in the analysis including 300 randomly chosen sites (see below).

Table 3.3. Nest numbers, percent nests attacked by herring or great black-backed gulls and percent nests successful in raising at least one chick in four kittiwake plots on Gull Island in 1998 and 1999.

Kittiwake study plot	Number of nests that were active (eggs laid) in 1998 or 1999	% nests attacked (attacked nests/ active nests)	% nests successful (successful nests/ active nests)
S1	42	59.5	33.3
P2	81	45.7	55.6
N4	268	20.1	76.6
S5	268	19.0	72.4

3.4.2. Gull attacks and nest-site characteristics

In the main analysis including 300 randomly chosen nest sites, plot, density and cliff part had a significant effect on which nest sites were attacked by gulls (Table 3.4). Nest sites in medium density areas were more likely to be attacked (33.0%; 38/115) than sites in high (30.4%; 14/46) or low (15.8%; 22/139) density areas. Sites at upper parts of cliffs had a higher likelihood of being attacked by large gulls (45.2%; 38/84) compared to nest sites located at middle (20.5%; 23/112) or lower parts of the cliff (12.5%; 13/104).

3.4.3. Kittiwake breeding success and nest-site characteristics

Plot, ledge width and density affected significantly where chicks fledged (Table 3.5). Of 300 randomly chosen nests, sites on narrow ledges had a higher likelihood of succeeding in raising chicks (73.0%; 135/185) than sites on broad ledges (59.1%; 68/115). Sites located in high density areas had a higher success rate in raising chicks (73.9%; 34/46) than sites in medium (68.7%; 79/115) or low (46.3%; 90/139) density areas.

Table 3.4. Generalized linear model of kittiwake nest-site characteristics that reduced the risk of predation attacks by herring or great black-backed gulls on Gull Island in 1998 and 1999 (n = 300 randomly chosen sites).

Source	df	F	p
PLOT	3	11.63	< 0.0001
LEDGE WIDTH	1	0.15	0.70
ROOF	1	0.51	0.48
NO. WALLS	1	0.97	0.33
DENSITY	2	3.54	0.03
CLIFF PART	2	14.81	< 0.0001

Note: Only active kittiwake nests ($\geq$ 1 egg was laid) were included in the analysis. Higher order terms not present were insignificant ($p > 0.1$) and dropped from the model. For the final model the tolerance for type I error was set at 0.05 for main effects. Generalized linear model with a binary response variable and a logit link function.

Table 3.5. Generalized linear model of kittiwake nest-site characteristics that influenced the breeding success of kittiwakes on Gull Island in 1998 and 1999 (n = 300 randomly chosen sites).

Source	df	F	p
PLOT	3	7.32	< 0.0001
LEDGE WIDTH	1	10.11	0.0016
ROOF	1	0.32	0.57
NO. WALLS	1	0.37	0.55
DENSITY	2	3.04	0.05
CLIFF PART	2	0.44	0.64

Note: Only active kittiwake nests ($\geq$ 1 egg was laid) were included in the analysis. Higher order terms not present were insignificant ($p > 0.1$) and dropped from the model. For the final model the tolerance for type I error was set at 0.05 for main effects. Generalized linear model with a binary response variable and a logit link function.

3.4.4. Comparison of foraging decisions of herring gulls and great black-backed gulls in relation to wind conditions

During calm conditions, roofs over nest sites, the location on the cliff as well as ledge width reduced the risk of herring gull attacks on kittiwakes (Table 3.6). Of all nest sites without roofs, 14.0% (18/129) were attacked, however only 6.4% (11/171) of all nest sites with roof were attacked. Nest sites on upper parts of cliffs had a higher likelihood of being attacked by herring gulls (15.9%; 13/82) than sites on middle (11.0%; 12/109) or lower parts (3.7%; 4/109). There was a significant interaction effect among plots and ledge width. Whereas at plot S5, sites located on narrow ledges experienced a higher risk of predation by herring gulls during calm conditions (16.9%; 11/65; compared to sites on broad ledges: 7.4%; 4/54), sites on broad ledges had a higher risk of predation at plot P2 and N4 [P2: sites on broad ledges: 20.0% (2/10); sites on narrow ledges: 6.3% (2/32); N4: sites on broad ledges: 13.7% (7/51); sites on narrow ledges: 3.4% (3/88)].

During calm conditions, plot, ledge width and cliff part affected significantly which nest sites were attacked by great black-backed gulls (Table 3.6). Nineteen percent of nest sites at plot P2 were attacked by great black-backed gulls (8/42), however only 7.9% (11/139) at plot N4 and 3.4% (4/119) at plot S5. Sites on broad ledges experienced a higher risk of predation by great black-backed gulls (13.0%; 15/115) than sites on narrow ledges (4.3%; 8/185). Nest sites on upper parts of cliffs had a higher likelihood of being attacked by great black-backed gulls (17.1%; 14/82) than sites on middle (4.6%; 5/109) or lower parts (3.7%; 4/109).

During windy conditions, the location on the cliff affected the risk of predation by both herring and great black-backed gulls (Table 3.6). Sites located on upper parts of cliffs had a higher likelihood of being attacked by herring and great black-backed gulls [12.2 % (10/82) and 13.4% (11/82), respectively] than sites on middle [0.9% (1/109) and 1.9% (2/109), respectively] and lower parts [1.9% (2/109) and 3.7% (4/109), respectively]. However, density also affected the risk of predation by great black-backed gulls in windy conditions (Table 3.6). Sites in medium density areas had a higher likelihood of being attacked by great black-backed gulls (10.5%; 12/114) than sites in low (2.1%; 3/140) or high density areas (2.2%; 1/46).

Table 3.6. Four generalized linear models, testing whether certain kittiwake nest-site characteristics influenced which sites were attacked by (1) herring gulls (= HERG) during calm conditions, (2) great black-backed gulls (= GBBG) during calm conditions, (3) herring gulls during windy conditions, and (4) great black-backed gulls during windy conditions.

Nest-site characteristics	**Calm conditions**		**Windy conditions**	
	HERG	**GBBG**	**HERG**	**GBBG**
PLOT	ns	0.0015	-	-
LEDGE WIDTH	ns	0.0052	ns	ns
ROOF	0.018	ns	ns	ns
NO. WALLS	ns	-	ns	ns
DENSITY	ns	ns	-	0.0055
CLIFF PART	0.0253	0.0046	0.0017	0.0033
PLOT * LEDGE WIDTH	0.0137	-	-	-

Note: In cases where there were no attacks on nest sites with a certain characteristic, those terms were not estimable and dropped out of the final model. Only significant p- values are reported.

3.5. Discussion

3.5.1. The effect of plot size and nesting density on nest predation and kittiwake breeding success

I found significant differences in the proportions of kittiwake nests attacked by gulls and kittiwake breeding success among plots. On Gull Island, individual kittiwake nests at the smallest plot S1 experienced a higher probability of being attacked by herring or great black-backed gulls than at larger plots. Hence, the percentage of failed nests was highest at plot S1 and decreased as the size of the plots (number of nests) increased. The number and foraging ability of resident breeding gulls, which occupied kittiwake nesting cliffs as feeding territories, might explain the variability of nest predation among plots. Although I observed study plots for many hours, there was some evidence that I might have monitored the foraging behaviour of only a few large gulls. In 1999 on Gull Island, we uniquely colour banded one male great black-backed gull, which held a feeding territory at kittiwake study plot N4. Sixty percent of all great black-backed gull predation attempts on kittiwakes at N4 were made by this individual (M. Massaro, unpubl. data).

In bird species that show mobbing behaviour as a defense strategy against predators, nesting in large, dense colonies offers advantages against predators (Wittenberger and Hunt 1985). Several studies have shown that if the risk of predation is high, cliff-nesting black-legged kittiwakes defend their nests by vigorous mobbing against avian predators (Andersson 1976; Montevecchi 1979; Maccarone 1992). During this study I frequently observed that kittiwake eggs and chicks were not only defended by their own parents, but also by cooperative mobbing of prospectors as well as failed nesters. Several times I observed that kittiwakes made physical contact with an attacking great black-backed gull in order to hinder the gull from landing or remaining on the ledge. At a declining thick-billed murre colony glaucous gulls were more likely to forage on foot on broad ledges, where, because of population declines, murres nested at lower densities (Gilchrist 1999). However, at highly populated and dense murre colonies glaucous gulls were given less opportunity to forage on foot than in low density murre ledges. Surprisingly in this study, nest sites with two active neighbours (medium density) were more likely to be attacked than sites with less or more active neighbours. Breeding success (percentage of successful nests) was highest in high density areas and lowest in low density areas. This suggests that it is most advantageous for a kittiwake pair to breed in a high nesting density area within a large sub-colony where predation pressure per individual sub-colony member was lower than in small sub-colonies, increasing the chance of reproductive success. However, two questions remain unanswered: (1) Why were gulls more likely to attack nests in medium density areas than in low density areas? and (2) Why was breeding success substantially lower in low density areas than in medium density areas, although predation pressure is paradoxically higher in medium density areas? Foraging decisions of gulls might be influenced by the trade-off between maximizing energy gain and minimizing risk of injury (Stein 1977; Gilchrist et al. 1998). Gulls may have found the optimum foraging tactic by attacking sites in medium density areas, where the level of mobbing behaviour is tolerable and the possible energy gain, in case the gull succeeded in landing on the ledge, substantially higher than in low density areas. The low breeding success in low density areas could be attributable to the lower quality of birds breeding at the edge of a sub-colony (Coulson 1968) or to a lower level of social stimulation that may cause low breeding success (Danchin 1988).

Viewed in a broader perspective, a high percentage of failed nesting attempts experienced by a small sub-colony can have long-term effects on recruitment. First-time breeding kittiwakes as well as adults choose their nesting location based partly on their own reproductive success and that of conspecific nesters during the previous breeding season (Danchin and Monnat 1992; Cadiou et al. 1994; Danchin et al. 1998). Low average reproductive success at small sub-colonies, such as S1, might provide an indication to pre-breeding kittiwakes on the local quality of the sub-colony, causing recruiting kittiwakes to choose larger cliffs (Danchin et al. 1998). Further confirmation of this possibility at Gull Island would require replicated small versus large plot comparisons.

3.5.2. Relationships between kittiwake nest-site characteristics, gull predation and kittiwake breeding success

Besides a significant plot and density effect, I found that nest sites at the upper parts of cliffs experienced a higher probability of being attacked than sites located at the middle or lower parts of cliffs. Similarly, Maccarone (1992) observed that ravens on Baccalieu Island, Newfoundland, hunted along the upper third of a kittiwake nesting cliff on 49% of all patrols, 33% along the middle and 18% along the lower third of the cliff. At a thick-billed murre colony, Gaston and Elliot (1996) found that 68% of all predation attempts by ravens occurred in the upper 30% of the cliff, although all nesting sites were almost evenly distributed in relation to the distance from the upper edge of the cliff. They also observed that within the top 30% of the cliff, peripheral sites were more likely to be attacked than central sites. In an earlier study on Great Island, Witless Bay, kittiwake nest-site position relative to the periphery of the colony did not differ between nests with chicks and random nests (Regehr et al. 1998). Instead they found that nests with chicks had larger overhangs than random nests. In this study, an overhang (roof) over a nest site reduced only the risk of predation by herring gulls during calm conditions.

When I tested whether breeding success of certain nest sites was influenced by the same nest-site characteristics that reduced the risk of gull attacks, I found that plot and density also affected breeding success. Whereas, gull attacks were aimed more likely at sites located on upper parts of cliffs, I did not find any breeding success differences among upper, middle and lower parts. However, ledge width influenced the breeding success rate of nests, whereby sites on narrow ledges showed a higher percentage of success.

These results suggest that although reproductive performance of a pair of kittiwakes was likely influenced by nest-site characteristics reducing the risk of predation, also a wider variety of factors, including quality of the pair, age, and parasite abundance may influence breeding success.

3.5.3. Relationships of wind conditions and foraging decisions of gulls

If foraging decisions are influenced by the trade-off between possible energy gain and the risk of injury (Gilchrist et al. 1998), in particular, opportunistic foragers, such as herring and great black-backed gulls should be confronted frequently by those decisions, as they are capable of switching to different prey (Pierotti and Annett 1987). Conditions that constrain the foraging ability of predators are highly dynamic due to changes in prey availability, competition among predator species, and environmental conditions (Verbeek 1977; Baird 1990; Van Heezik 1990; Anderson and Hodum 1993; Gilchrist et al. 1998). Several studies have shown that avian predators respond to differential wind conditions by changing their foraging tactics (Spear and Anderson 1989; Young 1994; Gilchrist and Gaston 1997). Although both herring gulls and great black-backed gulls have a wing loading of 48 N/m^2 (Pennycuick 1987; Spear and Ainley 1997), their foraging tactics differ due to their size. Regehr (1994) observed that kittiwakes usually left their nests when a great black-backed gull soared above them and 15% of eggs taken were depredated by hunting this way. However herring gulls never took any eggs this way (Regehr 1994). On Gull Island, I observed that breeding kittiwakes usually stayed on their nests even when a great black-backed gull soared above. Regardless of wind conditions, herring and great black-backed gulls attacked to a greater percentage nest sites located at the upper parts of cliffs than at middle and lower parts. However, herring gulls had more difficulty foraging on nest sites with roofs during calm conditions. Herring gulls were observed to start most of their foraging attacks on kittiwakes from the upper edge of the cliff. From that position they either tried to walk into the kittiwake colony or they jumped into the air flying in a small 180° semi-circle before attacking a site. Usually herring gulls stole kittiwake eggs or chicks by supporting their own weight by rapid wing beating and lowering their feet on the kittiwake ledge. Sometimes herring gulls removed adult kittiwakes from the nest before nest contents were taken. The foraging effort of great black-backed gulls was constrained by narrow ledges during calm wind conditions. In contrast to herring gulls, great black-backed gulls started most of their attacks by flying circles along the kittiwake nesting cliff. Usually they lowered their flight speed and then tried to land on one of the kittiwake ledges. Once they landed successfully on a ledge, great black-backed gulls walked within the kittiwake colony robbing all nests they could reach on the ledge.

Windy conditions likely increased the aerial maneuverability of both gull species. Great black-backed gulls were able to land more successfully on kittiwake ledges and then attack nests on foot. They chose to attack a significant higher proportion of sites within medium density areas than sites in low or high density areas. However, herring gulls, being more vulnerable to kittiwake defense behaviour due to their smaller size, were observed to forage on the wing, almost standing still in mid-air over a kittiwake cliff, and perform sudden attempts to steal an egg or chick from a nest without landing on a ledge. Monitoring individual gull foraging behaviour and measuring wind conditions including up and down drafts at different elevations of a cliff might give more clues as to why large gulls prefer to forage on certain nest sites.

In conclusion, among my study plots at Gull Island, nests at smaller kittiwake sub-colonies experienced a higher risk of being depredated by gulls than nests at larger cliffs, resulting in a lower breeding success at small cliffs. Gull attacks were more frequent on sites in medium density areas than on nest sites in low or high density areas. Nests located at the upper part of the cliff experienced a higher probability of being attacked than nests at the middle or lower part of the cliff. Breeding success was correlated with ledge width and density and varied significantly among plots. Wind conditions influenced which nest-site characteristics reduced the risk of predation. Further investigation on how physical cliff structures constrain the foraging ability of avian predators should focus on three main issues: (1) large scale cliff characteristics, including a larger sample size of nesting cliffs, (2) wind conditions at different elevations of the cliff, and (3) predator dynamics, such as breeding density, competition, and foraging range.

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CHAPTER 4

Final Discussion and Conclusions

The main objective of this study was to investigate the causes and effects of herring and great black-backed gull predation on kittiwakes. I approached the topic of this study from two different angles: (1) from a coarse scale perspective including inter-trophic relationships and the implications of large gull predation on kittiwake populations in Witless Bay and (2) from a fine scale perspective examining kittiwake plot differences, nesting density, nest-site characteristics, local wind conditions as well as the risk of predation for any individual kittiwake nest.

In ecosystems where one species, such as capelin, is a predominant prey item for seabirds, inter-trophic relationships are relatively clear and hence offer an opportunity to study the effects of reduced availability of a marine prey species on seabird populations. The results of this study strongly suggest that the timing of inshore spawning of capelin influenced the predatory behaviour of large gulls on kittiwakes and hence kittiwake breeding performance. Kittiwakes have been affected by the delayed arrival of capelin in recent years both indirectly (due increased predation by gulls) and directly (due to reduced food availability; Regehr 1994). Commercial fishing or abiotic factors, such as change in water or air temperatures, often cause reduced marine prey availability and decrease seabird breeding performance (e.g. Springer et al. 1984; Hatch 1987; Anderson 1989; Baird 1990; Hamer et al. 1991 and 1993; Murphy et al. 1991). For example, kittiwake populations in Alaska showed higher reproductive success in breeding seasons following warm springs and reduced success following cold springs (Murphy et al. 1991). The spring of 1999 was one of the warmest of this decade in Newfoundland. In 1999, when capelin arrived 9 days earlier to spawn, kittiwake breeding success on Gull Island was 53.3% higher than in 1998. Warm spring temperatures may give breeding kittiwakes an indication of the food availability during this season and may affect egg-laying and clutch size.

In my study, large gull predation was highest when gulls had small chicks to feed but capelin was not available. In 1998, an inland kittiwake plot (not included in this study) on Gull Island was about a week delayed in breeding in comparison to other kittiwake plots (J. W. Chardine, unpubl. data). It seemed that this plot benefited from this delay, because only a small proportion of kittiwake eggs were laid in the period of high gull predation. In years of late capelin availability, it could be advantageous for kittiwakes to delay breeding. However, in the study of Coulson and Thomas (1984) breeding success declined if eggs were laid after the first third of the breeding season. In

1969 and 1970 mean egg-laying dates for kittiwakes on Gull Island were 3 June and 29 May, respectively (Maunder and Threlfall 1972). Mean egg laying occurred around the same time in 1998 and 1999, suggesting that kittiwakes did not delay breeding due to later capelin availability. It is questionable how quickly and efficiently seabirds can adapt their life history strategies to large scale environmental changes.

In chapter 2 and chapter 3 I looked at differences among plots on Gull Island: mean gull predation attempt rates were lowest at plot S1, the smallest kittiwake nesting aggregation, however the highest percentage of nests were attacked at plot S1. Predators are attracted to seabird colonies because a large concentration of food is available (Wittenberger and Hunt 1985). Whereas, on Gull Island, the smallest kittiwake plot S1 was occupied by only one herring gull pair, the largest plot S5 was occupied by one great black-backed gull pair and one herring gull pair. It appears that larger kittiwake sub-colonies attracted more and larger predators (great black-backed gulls versus herring gulls), which require a larger feeding territory to be able to adequately feed their young. However, clearly the predation pressure for an individual kittiwake nest decreased as the size of the sub-colony increased. The percentage of nests where chicks fledged was more than twice as high at large plots (N4 and S5, compared to plot S1). The results of this study suggest that predators were attracted to larger sub-colonies than smaller ones, however the predation risk per individual colony member is decreased in larger sub-colonies.

The effect of increased populations of large gulls on other seabirds has been controversial for several decades. There is a widespread opinion among the general public in Newfoundland that gulls are pest species due to their huge presence near landfill sites and around fishing operations. Whereas several studies have shown that large gulls have been responsible for declining seabird populations (e.g. Hatch 1970; Gilchrist 1999; Whittam and Leonard 1999), other studies point out that even when gull predation or kleptoparasitism is evident it has little negative effect on prey populations (e.g. Pierotti 1983; Rice 1985; Cavanagh and Griffin 1993; Howes and Montevecchi 1993). For Gull Island, I estimated that gulls took 43% and 30% of all kittiwake eggs laid in 1998 and 1999 respectively. However, it is unknown whether gull predation has an overall negative effect on kittiwake populations in Witless Bay. As pointed out earlier, it appeared that only a few resident breeding gull pairs were responsible for most kittiwake predation. When predatory gulls were removed in a study of golden plovers (*Pluvialis apricaria*), plover numbers did not increase (Parr 1993). I predict a similar effect on Gull Island if resident breeding gulls were removed. After removing resident gull pairs, predation rates might decrease for a few weeks, but I predict other gulls, in particular recruiting gulls, would soon occupy the feeding territory and prey upon kittiwakes. If gull predation becomes an evident problem for seabird populations in Newfoundland, I suggest approaching the problem at the source and trying to alter human behaviour instead of 'blaming' gulls. In Newfoundland this may require a change in managing fish and household waste and reducing the quota for the annual capelin fishery.

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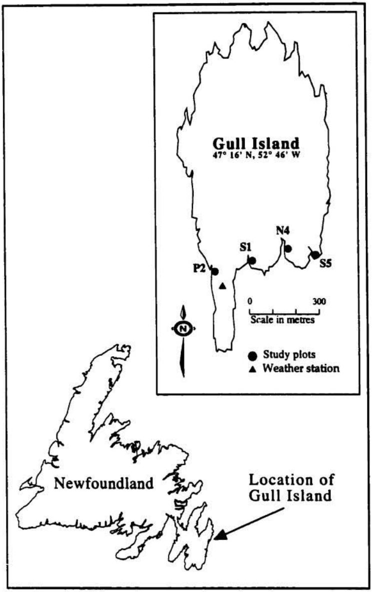

Gull Island
47° 16' N, 52° 46' W
N4
S1
P2
S5
0
300
Scale in metres
N
Study plots
Weather station
Newfoundland
Location of
Gull Island

Appendix 2. Kittiwake nest-site characteristics for each nest site at four study plots (S1, P2, N4 and S5) on Gull Island in 1998 and 1999; P = Plot, NS = Nest Site, LW = Ledge Width, R = Roof, W = No. of Walls, D = Density, CP = Cliff Part, and A = Active. Last column indicates whether at least one egg was laid in this nest site in 1998 or 1999 (active nest site = 1) or not (= 0). Please see for further detailed definitions of nest-site characteristics section 3.3.4. Nest-site characteristics on p. 60.

P	NS	LW	R	W	D	CP	A	P	NS	LW	R	W	D	CP	A
S1	1	broad	None	2+	medium	medium	0	S1	28	narrow	None	2+	medium	medium	1
S1	2	broad	Roof	2+	medium	upper	1	S1	31	broad	Roof	1-	low	medium	0
S1	3	broad	Roof	2+	medium	medium	0	S1	32	narrow	Roof	2+	medium	medium	1
S1	4	narrow	Roof	2+	medium	medium	1	S1	34	broad	None	2+	low	medium	1
S1	5	broad	None	1-	low	lower	0	S1	35	broad	None	1-	medium	lower	1
S1	6	broad	None	1-	medium	lower	0	S1	36	broad	None	1-	medium	lower	1
S1	7	broad	Roof	2+	low	medium	0	S1	37	narrow	None	2+	low	lower	0
S1	8	narrow	Roof	1-	medium	medium	1	S1	38	broad	None	1-	low	lower	1
S1	9	narrow	Roof	1-	medium	medium	0	S1	39	narrow	None	1-	medium	lower	1
S1	10	broad	Roof	1-	medium	medium	1	S1	40	broad	None	1-	low	lower	1
S1	11	broad	Roof	1-	medium	upper	1	S1	41	broad	Roof	1-	high	upper	1
S1	12	broad	None	1-	low	medium	1	S1	42	broad	None	2+	low	medium	1
S1	13	narrow	Roof	1-	medium	upper	1	S1	43	narrow	None	1-	low	medium	1
S1	14	narrow	None	1-	high	upper	1	S1	44	narrow	None	1-	low	medium	1
S1	15	narrow	Roof	2+	low	medium	1	S1	45	narrow	Roof	1-	low	lower	1
S1	16	narrow	None	1-	medium	medium	1	S1	46	broad	Roof	2+	low	lower	1
S1	17	narrow	None	1-	medium	medium	1	S1	47	narrow	None	2+	low	lower	1
S1	18	narrow	None	1-	high	medium	0	S1	48	narrow	Roof	2+	low	lower	1
S1	19	broad	None	1-	medium	medium	1	S1	49	narrow	Roof	1-	medium	medium	1
S1	20	broad	None	1-	medium	medium	1	S1	50	narrow	None	1-	high	medium	1
S1	21	narrow	None	2+	medium	upper	1	S1	51	broad	None	1-	low	upper	1
S1	22	broad	None	1-	low	medium	1	S1	52	broad	None	1-	medium	upper	1
S1	23	narrow	Roof	2+	medium	lower	1	S1	53	broad	None	1-	medium	lower	0
S1	24	narrow	None	1-	medium	lower	1	S1	60	narrow	Roof	1-	medium	upper	0
S1	25	narrow	None	1-	medium	lower	1	S1	61	narrow	None	1-	low	lower	1
S1	26	broad	Roof	2+	low	lower	1	S1	62	broad	None	1-	low	medium	0
S1	27	broad	None	1-	high	lower	0	S1	63	narrow	None	1-	low	upper	1

P	NS	LW	R	W	D	CP	A	P	NS	LW	R	W	D	CP	A
S1	64	narrow	None	1-	medium	upper	0	P2	36	narrow	Roof	2+	medium	lower	1
S1	65	narrow	None	1-	low	lower	1	P2	37	narrow	Roof	2+	medium	lower	1
S1	66	broad	None	1-	medium	upper	0	P2	38	narrow	Roof	1-	medium	medium	1
S1	69	broad	None	1-	low	lower	0	P2	39	narrow	Roof	1-	low	medium	1
P2	1	narrow	Roof	1-	low	upper	1	P2	40	narrow	None	1-	high	medium	1
P2	2	narrow	Roof	1-	medium	upper	1	P2	41	broad	None	1-	high	medium	1
P2	3	narrow	Roof	1-	low	upper	1	P2	42	broad	Roof	1-	high	medium	1
P2	4	narrow	None	1-	low	medium	1	P2	43	broad	Roof	1-	medium	medium	1
P2	5	broad	None	1-	low	medium	1	P2	44	broad	Roof	1-	medium	medium	1
P2	6	broad	None	1-	low	medium	0	P2	45	broad	Roof	1-	medium	medium	1
P2	7	narrow	Roof	1-	medium	upper	1	P2	46	broad	Roof	1-	medium	medium	1
P2	8	broad	Roof	1-	high	upper	1	P2	47	broad	Roof	1-	medium	medium	1
P2	9	broad	None	1-	high	upper	1	P2	48	narrow	Roof	1-	low	medium	0
P2	10	narrow	Roof	1-	high	upper	1	P2	49	narrow	None	1-	low	medium	1
P2	11	narrow	Roof	1-	high	upper	1	P2	50	narrow	Roof	1-	low	lower	1
P2	12	narrow	Roof	1-	medium	medium	1	P2	51	narrow	Roof	1-	low	lower	1
P2	13	narrow	None	1-	low	medium	1	P2	52	narrow	Roof	1-	medium	lower	1
P2	14	narrow	None	1-	medium	medium	1	P2	53	narrow	Roof	1-	low	lower	1
P2	15	narrow	None	1-	low	medium	1	P2	54	narrow	Roof	1-	low	lower	1
P2	16	broad	None	1-	low	lower	1	P2	55	narrow	Roof	1-	medium	lower	1
P2	17	narrow	Roof	2+	medium	lower	1	P2	56	narrow	Roof	1-	medium	lower	1
P2	18	narrow	None	1-	medium	lower	1	P2	57	narrow	Roof	2+	low	lower	0
P2	19	narrow	None	1-	low	lower	1	P2	58	narrow	Roof	1-	medium	lower	1
P2	20	narrow	Roof	1-	medium	medium	1	P2	59	narrow	None	1-	medium	lower	1
P2	21	narrow	Roof	1-	medium	medium	1	P2	60	narrow	Roof	1-	medium	lower	1
P2	22	broad	Roof	1-	medium	medium	1	P2	61	narrow	None	2+	low	lower	1
P2	23	broad	Roof	1-	high	medium	1	P2	62	narrow	Roof	2+	low	lower	1
P2	24	broad	Roof	1-	high	medium	1	P2	63	broad	None	1-	low	lower	1
P2	25	broad	Roof	1-	medium	medium	1	P2	64	broad	None	1-	low	lower	1
P2	26	narrow	None	1-	low	lower	1	P2	65	narrow	None	1-	low	medium	1
P2	27	narrow	Roof	1-	low	medium	1	P2	66	narrow	None	1-	medium	upper	1
P2	28	narrow	Roof	2+	low	lower	1	P2	67	narrow	None	1-	medium	upper	1
P2	29	narrow	Roof	1-	low	lower	1	P2	68	narrow	None	1-	medium	upper	1
P2	30	broad	Roof	1-	medium	medium	1	P2	69	narrow	None	1-	medium	upper	1
P2	31	broad	Roof	1-	low	medium	1	P2	70	narrow	None	1-	medium	upper	1
P2	32	broad	Roof	1-	high	lower	1	P2	71	narrow	None	1-	medium	upper	1
P2	33	narrow	Roof	2+	low	lower	1	P2	72	narrow	Roof	1-	low	medium	1
P2	34	narrow	Roof	2+	medium	lower	1	P2	73	narrow	Roof	1-	medium	medium	0
P2	35	narrow	Roof	2+	medium	lower	1	P2	74	narrow	Roof	1-	medium	medium	1

P	NS	LW	R	W	D	CP	A	P	NS	LW	R	W	D	CP	A
P2	75	broad	None	1-	medium	lower	1	N4	14	narrow	Roof	2+	medium	upper	1
P2	76	narrow	Roof	1-	low	medium	1	N4	15	broad	Roof	1-	medium	upper	1
P2	77	narrow	Roof	1-	low	lower	1	N4	16	broad	Roof	1-	medium	upper	1
P2	78	narrow	Roof	1-	low	lower	0	N4	17	broad	Roof	1-	medium	upper	1
P2	79	narrow	Roof	1-	medium	medium	0	N4	18	narrow	Roof	1-	medium	upper	1
P2	80	broad	Roof	1-	high	lower	0	N4	19	broad	Roof	1-	medium	upper	1
P2	81	broad	Roof	1-	high	lower	0	N4	20	broad	Roof	1-	medium	upper	1
P2	82	narrow	Roof	1-	low	lower	0	N4	21	narrow	Roof	1-	low	upper	1
P2	83	broad	Roof	1-	medium	lower	0	N4	22	narrow	Roof	1-	medium	upper	1
P2	84	narrow	Roof	1-	low	lower	1	N4	23	narrow	Roof	1-	medium	upper	1
P2	85	narrow	None	1-	medium	medium	0	N4	24	narrow	Roof	1-	low	upper	1
P2	86	narrow	Roof	1-	medium	medium	0	N4	25	broad	Roof	1-	medium	upper	1
P2	87	broad	Roof	1-	medium	lower	1	N4	26	broad	Roof	1-	medium	upper	1
P2	88	broad	Roof	1-	high	medium	0	N4	27	narrow	Roof	2+	low	upper	1
P2	90	narrow	None	1-	low	medium	1	N4	28	broad	Roof	1-	medium	upper	1
P2	91	narrow	None	1-	medium	upper	1	N4	29	narrow	Roof	1-	low	upper	1
P2	92	narrow	Roof	1-	low	medium	0	N4	30	narrow	Roof	1-	medium	upper	1
P2	93	narrow	Roof	1-	low	lower	1	N4	31	narrow	Roof	1-	medium	upper	1
P2	94	narrow	None	1-	low	medium	0	N4	32	broad	Roof	1-	medium	medium	1
P2	95	broad	None	1-	high	medium	0	N4	34	narrow	Roof	1-	medium	upper	1
P2	96	narrow	Roof	1-	low	lower	0	N4	35	narrow	Roof	1-	low	upper	1
P2	97	broad	None	1-	high	medium	0	N4	36	narrow	Roof	1-	medium	upper	1
P2	98	broad	None	1-	high	medium	0	N4	37	narrow	Roof	2+	low	upper	1
P2	99	narrow	None	1-	medium	medium	0	N4	39	broad	Roof	1-	medium	medium	1
P2	100	narrow	Roof	2+	low	lower	0	N4	40	broad	Roof	1-	medium	medium	1
P2	101	narrow	None	1-	medium	upper	0	N4	41	narrow	Roof	2+	low	medium	1
P2	102	broad	Roof	1-	high	lower	1	N4	42	broad	None	1-	low	lower	0
P2	103	broad	Roof	1-	medium	upper	1	N4	43	broad	Roof	1-	medium	lower	1
P2	104	narrow	None	1-	medium	lower	1	N4	44	broad	Roof	1-	medium	lower	1
N4	1	broad	None	1-	low	upper	0	N4	45	broad	Roof	1-	medium	lower	1
N4	2	broad	Roof	1-	low	upper	1	N4	46	broad	Roof	1-	medium	medium	1
N4	3	narrow	Roof	1-	low	upper	0	N4	47	narrow	Roof	1-	medium	lower	1
N4	5	narrow	Roof	1-	low	upper	1	N4	49	narrow	Roof	1-	medium	lower	1
N4	6	broad	Roof	1-	low	upper	1	N4	52	narrow	None	2+	medium	medium	1
N4	7	broad	Roof	1-	low	upper	1	N4	53	broad	Roof	1-	medium	medium	1
N4	10	narrow	Roof	1-	low	upper	0	N4	56	narrow	Roof	1-	low	medium	1
N4	11	narrow	Roof	1-	low	upper	1	N4	58	narrow	Roof	1-	medium	medium	1
N4	12	narrow	Roof	1-	medium	upper	1	N4	60	broad	None	1-	medium	lower	1
N4	13	narrow	Roof	1-	low	upper	1	N4	62	broad	None	1-	low	lower	1

P	NS	LW	R	W	D	CP	A
N4	65	narrow	None	2+	low	lower	1
N4	66	narrow	None	1-	low	lower	1
N4	67	narrow	None	1-	low	lower	1
N4	68	narrow	Roof	1-	low	lower	1
N4	70	narrow	None	1-	low	lower	0
N4	76	narrow	None	1-	low	upper	1
N4	77	broad	None	1-	low	upper	1
N4	80	narrow	Roof	1-	low	medium	1
N4	81	narrow	Roof	1-	high	upper	1
N4	82	narrow	Roof	1-	medium	upper	1
N4	83	narrow	None	1-	low	upper	1
N4	84	narrow	None	1-	low	upper	1
N4	86	narrow	Roof	1-	low	upper	1
N4	87	narrow	None	1-	low	upper	1
N4	88	broad	None	1-	medium	upper	1
N4	89	broad	None	1-	medium	upper	1
N4	90	narrow	None	1-	medium	upper	1
N4	91	broad	None	2+	low	medium	1
N4	92	broad	Roof	2+	medium	medium	0
N4	94	broad	Roof	1-	medium	medium	1
N4	95	broad	None	1-	high	upper	1
N4	96	narrow	None	1-	medium	upper	1
N4	97	narrow	None	1-	medium	upper	1
N4	98	broad	Roof	1-	medium	upper	1
N4	99	broad	None	1-	medium	upper	1
N4	100	broad	None	1-	medium	upper	1
N4	101	broad	None	1-	medium	upper	1
N4	102	broad	Roof	1-	low	upper	1
N4	103	broad	Roof	1-	medium	upper	1
N4	104	broad	Roof	1-	low	upper	0
N4	105	broad	None	1-	low	upper	1
N4	106	narrow	None	1-	medium	lower	1
N4	107	broad	Roof	1-	medium	upper	1
N4	108	broad	Roof	1-	medium	upper	1
N4	109	narrow	Roof	1-	low	upper	1
N4	110	narrow	Roof	1-	low	upper	1
N4	111	narrow	Roof	1-	low	upper	1
N4	113	narrow	Roof	1-	low	upper	1
N4	114	narrow	Roof	1-	medium	upper	1
N4	115	narrow	Roof	1-	medium	medium	1
N4	116	broad	Roof	1-	low	medium	1
N4	117	broad	Roof	1-	low	upper	0
N4	118	narrow	None	1-	low	medium	1
N4	119	narrow	Roof	1-	low	medium	1
N4	120	narrow	Roof	1-	medium	medium	1
N4	121	narrow	Roof	1-	low	medium	1
N4	122	narrow	Roof	1-	low	medium	1
N4	123	narrow	None	1-	low	medium	1
N4	125	narrow	None	1-	low	lower	1
N4	126	narrow	None	1-	medium	lower	1
N4	127	narrow	None	1-	low	lower	1
N4	128	narrow	None	1-	low	lower	1
N4	129	narrow	Roof	1-	medium	lower	1
N4	130	narrow	None	2+	medium	lower	1
N4	131	narrow	None	1-	low	lower	1
N4	132	narrow	Roof	2+	low	medium	1
N4	133	narrow	Roof	1-	medium	medium	1
N4	134	broad	Roof	1-	medium	medium	1
N4	136	narrow	None	1-	low	medium	1
N4	137	narrow	None	1-	low	lower	1
N4	138	broad	None	1-	low	upper	1
N4	140	broad	None	1-	medium	upper	1
N4	141	narrow	Roof	2+	low	upper	1
N4	142	narrow	Roof	1-	low	upper	1
N4	143	broad	None	1-	low	medium	1
N4	144	narrow	None	1-	low	medium	1
N4	145	broad	Roof	1-	medium	upper	1
N4	146	narrow	Roof	2+	low	lower	0
N4	147	broad	Roof	2+	low	lower	0
N4	148	broad	Roof	2+	low	lower	1
N4	150	broad	Roof	1-	low	lower	0
N4	151	broad	Roof	1-	low	lower	1
N4	152	broad	Roof	2+	medium	upper	1
N4	153	broad	None	1-	medium	upper	1
N4	154	broad	None	2+	low	lower	0
N4	155	broad	None	1-	low	upper	1
N4	156	broad	Roof	1-	medium	upper	1
N4	159	broad	Roof	1-	low	upper	1

P	NS	LW	R	W	D	CP	A	P	NS	LW	R	W	D	CP	A
N4	161	broad	Roof	1-	low	upper	1	N4	202	narrow	Roof	1-	medium	lower	1
N4	162	broad	None	1-	low	lower	0	N4	203	narrow	Roof	1-	medium	lower	1
N4	165	narrow	None	1-	low	upper	1	N4	204	narrow	Roof	1-	low	medium	1
N4	166	broad	Roof	1-	low	upper	0	N4	205	narrow	None	2+	low	lower	1
N4	167	broad	Roof	2+	medium	medium	0	N4	206	narrow	Roof	2+	low	medium	1
N4	168	broad	Roof	2+	low	medium	1	N4	207	narrow	Roof	1-	medium	medium	1
N4	169	broad	Roof	1-	medium	medium	1	N4	208	narrow	None	1-	low	medium	1
N4	170	narrow	Roof	2+	low	upper	1	N4	209	narrow	None	1-	high	medium	1
N4	171	broad	Roof	1-	medium	medium	0	N4	210	narrow	Roof	1-	high	medium	1
N4	172	broad	Roof	1-	medium	upper	0	N4	211	broad	Roof	1-	high	medium	1
N4	173	broad	None	1-	medium	lower	1	N4	212	narrow	None	1-	medium	medium	1
N4	174	narrow	None	1-	low	medium	1	N4	213	narrow	None	1-	low	upper	1
N4	175	broad	Roof	2+	low	lower	1	N4	214	narrow	None	1-	medium	medium	1
N4	176	broad	None	1-	medium	medium	0	N4	215	narrow	None	1-	high	medium	1
N4	177	narrow	Roof	1-	low	lower	0	N4	216	narrow	None	1-	medium	medium	1
N4	178	narrow	Roof	1-	low	medium	0	N4	217	narrow	None	2+	low	medium	1
N4	179	narrow	None	1-	low	upper	1	N4	218	narrow	None	2+	low	medium	1
N4	180	broad	Roof	1-	low	medium	1	N4	219	narrow	Roof	1-	low	medium	1
N4	181	broad	Roof	1-	medium	medium	1	N4	220	narrow	Roof	2+	low	medium	1
N4	182	broad	Roof	1-	medium	medium	1	N4	221	narrow	Roof	2+	low	upper	1
N4	183	broad	Roof	1-	medium	medium	1	N4	222	narrow	Roof	1-	low	upper	1
N4	184	broad	Roof	1-	medium	medium	1	N4	223	narrow	Roof	2+	low	upper	1
N4	185	broad	Roof	1-	medium	medium	1	N4	224	narrow	None	1-	low	upper	1
N4	186	broad	Roof	1-	medium	medium	1	N4	225	broad	Roof	1-	low	upper	1
N4	187	broad	Roof	1-	medium	medium	1	N4	226	broad	Roof	1-	medium	upper	1
N4	188	broad	Roof	1-	medium	medium	1	N4	227	broad	Roof	1-	high	upper	1
N4	189	broad	Roof	1-	medium	medium	1	N4	228	broad	None	1-	medium	upper	1
N4	190	narrow	Roof	1-	medium	medium	1	N4	229	narrow	None	1-	medium	upper	1
N4	191	narrow	Roof	1-	medium	medium	1	N4	230	narrow	Roof	2+	medium	upper	1
N4	192	narrow	Roof	1-	medium	medium	1	N4	231	narrow	Roof	2+	medium	upper	1
N4	193	narrow	Roof	1-	medium	medium	1	N4	232	narrow	None	1-	high	upper	1
N4	194	narrow	Roof	2+	low	medium	1	N4	233	narrow	None	1-	high	medium	1
N4	195	broad	None	1-	low	lower	0	N4	234	narrow	None	1-	high	medium	1
N4	196	broad	None	1-	low	lower	0	N4	235	narrow	None	1-	low	upper	1
N4	197	narrow	Roof	2+	low	lower	1	N4	236	broad	Roof	2+	high	medium	1
N4	198	narrow	None	1-	medium	lower	1	N4	237	broad	Roof	1-	high	medium	1
N4	199	narrow	None	1-	medium	lower	1	N4	238	broad	None	1-	medium	medium	1
N4	200	narrow	None	2+	low	lower	1	N4	239	broad	None	1-	medium	medium	1
N4	201	narrow	Roof	1-	low	medium	1	N4	240	broad	None	1-	medium	medium	1

P	NS	LW	R	W	D	CP	A
N4	241	broad	None	1-	high	medium	1
N4	242	broad	None	1-	high	medium	1
N4	243	broad	None	1-	medium	medium	1
N4	244	broad	Roof	1-	high	medium	1
N4	245	broad	None	1-	medium	medium	0
N4	246	broad	Roof	1-	medium	medium	1
N4	247	narrow	Roof	1-	low	medium	1
N4	248	narrow	Roof	1-	low	lower	1
N4	249	narrow	Roof	1-	low	medium	1
N4	250	narrow	Roof	1-	low	medium	0
N4	251	narrow	Roof	1-	medium	medium	1
N4	252	narrow	Roof	1-	high	medium	1
N4	253	narrow	None	1-	high	medium	1
N4	254	narrow	Roof	1-	high	medium	1
N4	255	narrow	Roof	1-	high	medium	1
N4	256	narrow	Roof	2+	high	medium	1
N4	257	narrow	None	1-	high	medium	1
N4	258	narrow	None	1-	high	medium	1
N4	259	narrow	Roof	1-	medium	medium	0
N4	260	narrow	Roof	2+	low	medium	1
N4	261	narrow	Roof	1-	low	medium	1
N4	262	narrow	Roof	2+	medium	lower	1
N4	263	narrow	Roof	1-	low	lower	1
N4	264	narrow	Roof	1-	low	lower	1
N4	265	narrow	Roof	2+	low	lower	1
N4	266	narrow	Roof	2+	low	lower	1
N4	267	narrow	Roof	1-	medium	lower	1
N4	268	narrow	Roof	1-	low	lower	1
N4	269	narrow	None	1-	low	lower	1
N4	270	broad	None	1-	medium	lower	1
N4	271	broad	Roof	2+	medium	lower	1
N4	272	broad	None	1-	high	lower	1
N4	273	narrow	Roof	1-	high	lower	1
N4	274	broad	None	1-	medium	lower	1
N4	275	broad	None	2+	medium	lower	1
N4	276	narrow	Roof	1-	medium	lower	1
N4	277	narrow	Roof	1-	medium	lower	1
N4	278	narrow	Roof	1-	medium	lower	1
N4	279	narrow	Roof	2+	low	lower	1
N4	280	narrow	Roof	1-	low	lower	1
N4	281	narrow	Roof	1-	low	lower	1
N4	282	narrow	None	1-	low	lower	1
N4	283	narrow	Roof	2+	low	lower	1
N4	284	narrow	Roof	2+	medium	lower	1
N4	285	narrow	None	1-	medium	lower	1
N4	286	narrow	None	1-	medium	lower	1
N4	287	narrow	Roof	1-	medium	lower	1
N4	288	narrow	Roof	1-	low	lower	1
N4	289	narrow	Roof	2+	low	lower	1
N4	290	narrow	Roof	1-	low	lower	1
N4	291	narrow	Roof	2+	low	lower	1
N4	292	narrow	Roof	1-	low	medium	1
N4	293	narrow	Roof	2+	low	medium	1
N4	294	narrow	Roof	1-	low	lower	1
N4	295	narrow	Roof	1-	low	medium	1
N4	296	narrow	Roof	1-	low	medium	1
N4	297	narrow	Roof	1-	low	lower	1
N4	298	narrow	Roof	1-	low	lower	1
N4	299	narrow	Roof	1-	low	lower	1
N4	300	narrow	Roof	2+	low	lower	1
N4	301	narrow	Roof	2+	low	lower	1
N4	302	narrow	Roof	1-	low	lower	0
N4	303	broad	Roof	1-	low	lower	1
N4	304	narrow	None	1-	low	lower	1
N4	305	broad	Roof	1-	low	lower	0
N4	306	broad	Roof	1-	low	lower	1
N4	307	broad	Roof	1-	low	lower	1
N4	308	broad	Roof	1-	low	lower	1
N4	309	broad	Roof	1-	medium	medium	1
N4	310	broad	Roof	2+	medium	lower	1
N4	311	broad	None	1-	high	lower	1
N4	312	narrow	Roof	2+	low	upper	1
N4	313	narrow	Roof	1-	low	upper	1
N4	314	narrow	Roof	1-	low	upper	1
N4	315	narrow	Roof	1-	low	upper	1
N4	316	broad	Roof	2+	high	upper	1
N4	317	broad	None	1-	low	lower	0
N4	318	broad	Roof	1-	low	lower	1

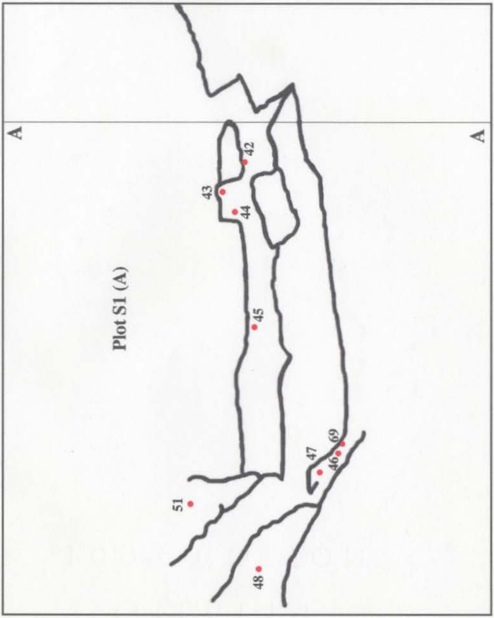
P	NS	LW	R	W	D	CP	A	P	NS	LW	R	W	D	CP	A
N4	319	narrow	None	1-	low	lower	1	S5	12	narrow	Roof	2+	low	upper	1
N4	321	narrow	Roof	1-	low	lower	0	S5	13	broad	None	1-	low	medium	1
N4	322	broad	Roof	1-	medium	medium	1	S5	14	narrow	None	2+	low	upper	1
N4	323	broad	Roof	1-	medium	medium	0	S5	15	narrow	Roof	1-	low	medium	1
N4	324	narrow	Roof	1-	medium	medium	1	S5	16	narrow	Roof	2+	low	medium	1
N4	325	broad	Roof	1-	medium	medium	0	S5	17	narrow	Roof	2+	low	medium	1
N4	326	broad	Roof	2+	high	medium	1	S5	18	narrow	Roof	1-	low	medium	1
N4	327	broad	Roof	2+	low	lower	1	S5	19	narrow	None	1-	low	medium	1
N4	328	narrow	None	1-	low	medium	1	S5	20	narrow	Roof	1-	low	medium	1
N4	331	narrow	Roof	1-	low	lower	0	S5	21	narrow	Roof	1-	low	medium	1
N4	332	broad	Roof	1-	low	lower	1	S5	22	narrow	Roof	1-	low	medium	1
N4	333	narrow	Roof	1-	medium	medium	0	S5	23	narrow	Roof	1-	low	medium	1
N4	335	narrow	None	2+	low	upper	0	S5	24	narrow	None	1-	low	upper	1
N4	336	broad	None	1-	low	lower	0	S5	25	narrow	Roof	1-	medium	upper	1
N4	337	narrow	None	1-	medium	medium	0	S5	26	narrow	None	1-	low	upper	1
N4	338	broad	None	1-	high	upper	1	S5	27	narrow	Roof	2+	medium	upper	1
N4	339	narrow	None	1-	high	medium	1	S5	28	narrow	Roof	2+	medium	upper	1
N4	340	narrow	Roof	2+	low	upper	1	S5	29	narrow	Roof	1-	high	upper	1
N4	341	broad	None	1-	high	medium	0	S5	30	narrow	Roof	1-	high	upper	1
N4	342	broad	None	1-	low	medium	0	S5	31	narrow	Roof	1-	low	medium	1
N4	343	broad	None	1-	low	medium	0	S5	32	broad	Roof	1-	medium	medium	1
N4	344	narrow	Roof	1-	medium	lower	0	S5	33	broad	None	1-	high	lower	1
N4	345	broad	None	1-	low	lower	1	S5	34	narrow	None	1-	low	medium	1
N4	347	broad	None	1-	low	medium	0	S5	35	broad	None	1-	high	medium	1
N4	348	broad	Roof	1-	medium	medium	0	S5	36	broad	None	1-	medium	lower	1
N4	350	broad	None	1-	medium	upper	0	S5	37	narrow	Roof	1-	medium	medium	1
N4	351	narrow	None	1-	medium	medium	1	S5	38	narrow	Roof	1-	high	medium	1
N4	352	broad	Roof	1-	medium	medium	1	S5	39	narrow	Roof	1-	high	medium	1
S5	1	narrow	Roof	2+	medium	upper	1	S5	40	narrow	Roof	1-	high	medium	1
S5	2	narrow	Roof	1-	high	upper	1	S5	41	narrow	Roof	1-	medium	medium	1
S5	3	narrow	Roof	1-	medium	upper	1	S5	42	narrow	Roof	1-	high	medium	1
S5	4	narrow	None	2+	high	upper	1	S5	43	narrow	Roof	1-	high	medium	1
S5	5	narrow	None	1-	high	upper	1	S5	44	narrow	None	1-	high	medium	1
S5	6	narrow	None	1-	medium	upper	1	S5	45	narrow	Roof	2+	high	medium	1
S5	7	narrow	Roof	1-	medium	upper	1	S5	46	narrow	Roof	1-	medium	medium	1
S5	8	narrow	Roof	1-	low	upper	1	S5	47	narrow	Roof	1-	low	medium	1
S5	9	narrow	None	2+	low	upper	1	S5	48	narrow	Roof	1-	medium	medium	1
S5	10	broad	None	2+	low	upper	1	S5	49	narrow	None	1-	low	medium	1
S5	11	broad	None	1-	low	upper	1	S5	50	narrow	Roof	1-	high	upper	1

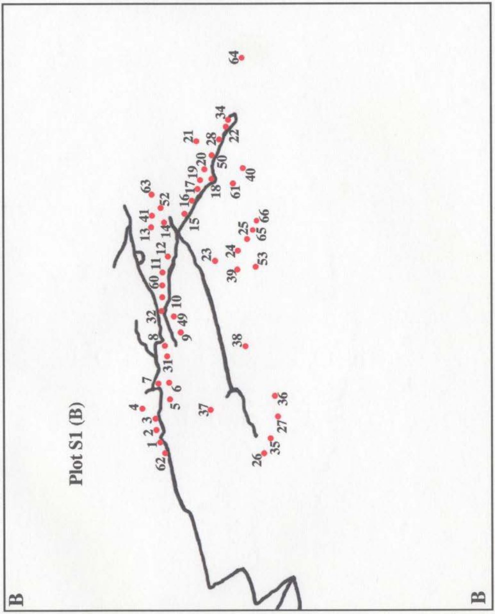
P	NS	LW	R	W	D	CP	A	P	NS	LW	R	W	D	CP	A
S5	51	narrow	None	2+	high	upper	1	S5	90	broad	None	1-	low	upper	1
S5	52	narrow	Roof	1-	high	upper	1	S5	91	broad	None	1-	low	upper	1
S5	53	narrow	Roof	2+	high	upper	1	S5	92	narrow	Roof	1-	low	lower	1
S5	54	narrow	None	1-	high	upper	1	S5	93	broad	None	1-	medium	lower	1
S5	55	narrow	None	1-	medium	upper	1	S5	94	broad	None	1-	high	lower	1
S5	56	narrow	None	1-	low	upper	1	S5	95	broad	None	1-	high	lower	1
S5	57	broad	None	1-	low	upper	1	S5	96	broad	None	1-	high	lower	1
S5	58	narrow	None	1-	low	lower	1	S5	97	broad	None	1-	high	lower	1
S5	59	narrow	None	1-	medium	lower	1	S5	98	broad	None	1-	high	lower	1
S5	60	narrow	None	1-	low	lower	1	S5	99	broad	None	1-	high	lower	1
S5	61	broad	None	1-	low	lower	1	S5	100	broad	None	1-	high	lower	1
S5	62	broad	None	1-	high	lower	1	S5	101	broad	None	1-	high	lower	1
S5	63	broad	None	1-	high	lower	1	S5	102	broad	Roof	1-	high	lower	1
S5	64	broad	None	1-	high	lower	1	S5	103	broad	Roof	1-	high	lower	1
S5	65	broad	None	1-	high	lower	0	S5	104	broad	None	1-	high	lower	1
S5	66	broad	None	1-	medium	lower	1	S5	105	broad	Roof	1-	high	lower	1
S5	67	broad	None	1-	medium	lower	1	S5	106	broad	Roof	1-	high	lower	1
S5	68	broad	None	1-	medium	lower	1	S5	107	broad	Roof	1-	high	lower	1
S5	69	broad	None	1-	medium	lower	1	S5	108	broad	Roof	1-	high	lower	1
S5	70	broad	None	1-	medium	lower	1	S5	109	broad	Roof	1-	high	lower	1
S5	71	broad	None	1-	medium	lower	1	S5	110	broad	None	1-	high	lower	1
S5	72	broad	Roof	1-	low	lower	1	S5	111	broad	None	1-	high	lower	1
S5	73	broad	Roof	1-	medium	lower	1	S5	112	broad	None	1-	high	lower	1
S5	74	broad	None	1-	high	medium	1	S5	113	broad	None	1-	high	lower	1
S5	75	broad	None	1-	low	medium	0	S5	114	broad	None	1-	high	lower	1
S5	76	broad	Roof	1-	medium	medium	1	S5	115	broad	None	1-	medium	lower	1
S5	77	broad	Roof	1-	high	medium	1	S5	116	narrow	Roof	1-	low	lower	1
S5	78	broad	Roof	1-	high	medium	1	S5	117	narrow	Roof	1-	medium	lower	1
S5	79	broad	Roof	1-	medium	medium	1	S5	118	narrow	Roof	1-	low	lower	1
S5	80	broad	Roof	2+	medium	medium	1	S5	119	narrow	None	1-	low	lower	1
S5	81	broad	None	2+	high	medium	1	S5	120	narrow	None	1-	low	lower	1
S5	82	narrow	Roof	2+	medium	medium	1	S5	121	narrow	None	1-	medium	lower	1
S5	83	broad	Roof	2+	low	medium	1	S5	122	narrow	None	1-	low	lower	1
S5	84	broad	None	1-	medium	medium	1	S5	123	broad	None	1-	low	lower	0
S5	85	narrow	None	1-	low	medium	1	S5	124	narrow	Roof	2+	low	lower	1
S5	86	narrow	Roof	1-	low	medium	0	S5	125	narrow	Roof	1-	low	lower	1
S5	87	broad	Roof	1-	low	medium	1	S5	126	broad	Roof	1-	low	lower	1
S5	88	broad	None	1-	low	medium	1	S5	127	broad	Roof	1-	low	lower	1
S5	89	broad	None	1-	low	upper	0	S5	128	narrow	Roof	2+	low	lower	1

P	NS	LW	R	W	D	CP	A	P	NS	LW	R	W	D	CP	A
S5	129	broad	None	1-	low	lower	1	S5	168	narrow	None	1-	medium	medium	1
S5	130	narrow	None	1-	low	lower	1	S5	169	narrow	None	1-	medium	medium	1
S5	131	broad	None	1-	medium	lower	1	S5	170	broad	None	1-	low	medium	1
S5	132	narrow	Roof	2+	low	lower	1	S5	171	broad	None	1-	low	upper	1
S5	133	narrow	None	1-	low	lower	1	S5	172	broad	None	1-	high	medium	1
S5	134	narrow	None	1-	low	lower	1	S5	173	narrow	None	1-	medium	medium	1
S5	135	narrow	None	1-	medium	lower	1	S5	174	broad	None	1-	high	medium	1
S5	136	narrow	None	1-	low	medium	1	S5	175	broad	None	1-	high	medium	1
S5	137	narrow	None	1-	low	medium	1	S5	176	broad	None	1-	medium	upper	1
S5	138	narrow	None	1-	low	medium	1	S5	177	broad	None	1-	high	upper	0
S5	139	narrow	None	1-	medium	medium	1	S5	178	broad	None	1-	medium	upper	1
S5	140	narrow	None	1-	low	medium	1	S5	179	broad	None	1-	medium	upper	1
S5	141	broad	None	1-	low	medium	1	S5	180	broad	None	1-	high	upper	1
S5	142	broad	None	1-	medium	medium	1	S5	181	broad	None	1-	high	upper	1
S5	143	broad	None	1-	low	medium	1	S5	182	broad	None	1-	medium	upper	1
S5	144	narrow	None	1-	low	medium	0	S5	183	broad	None	1-	low	upper	1
S5	145	narrow	Roof	1-	low	medium	0	S5	184	broad	None	1-	high	medium	1
S5	146	narrow	None	2+	low	medium	1	S5	185	broad	Roof	1-	low	medium	1
S5	147	narrow	None	1-	low	medium	0	S5	186	broad	None	2+	low	upper	1
S5	148	narrow	None	1-	low	medium	1	S5	187	narrow	None	1-	medium	upper	1
S5	149	narrow	Roof	2+	low	medium	1	S5	188	narrow	None	1-	medium	upper	1
S5	150	broad	None	1-	high	medium	1	S5	189	narrow	None	1-	low	medium	1
S5	151	broad	None	1-	medium	medium	1	S5	190	narrow	Roof	2+	low	medium	1
S5	152	broad	None	1-	low	medium	1	S5	191	narrow	Roof	1-	medium	medium	1
S5	153	narrow	None	2+	medium	upper	1	S5	192	broad	Roof	1-	low	upper	1
S5	154	narrow	None	1-	medium	medium	1	S5	193	broad	Roof	1-	medium	upper	1
S5	155	narrow	None	1-	low	medium	1	S5	194	narrow	None	1-	low	upper	1
S5	156	narrow	None	2+	medium	medium	1	S5	195	narrow	Roof	1-	low	lower	1
S5	157	narrow	None	1-	medium	medium	1	S5	196	narrow	Roof	1-	low	lower	1
S5	158	narrow	None	1-	medium	medium	1	S5	197	narrow	Roof	1-	medium	lower	1
S5	159	narrow	None	1-	medium	upper	1	S5	198	narrow	Roof	2+	low	medium	1
S5	160	narrow	None	1-	medium	upper	1	S5	199	narrow	Roof	1-	low	medium	1
S5	161	narrow	None	1-	medium	upper	1	S5	200	narrow	Roof	1-	medium	medium	1
S5	162	broad	None	1-	high	upper	1	S5	201	narrow	None	1-	medium	medium	1
S5	163	broad	None	1-	high	upper	1	S5	202	narrow	None	1-	medium	medium	1
S5	164	broad	None	1-	high	upper	1	S5	203	narrow	Roof	1-	medium	medium	1
S5	165	broad	None	1-	high	upper	1	S5	204	narrow	Roof	1-	medium	medium	0
S5	166	broad	None	1-	medium	upper	1	S5	205	narrow	Roof	1-	low	medium	1
S5	167	broad	None	1-	medium	medium	1	S5	206	narrow	Roof	1-	low	medium	1

P	NS	LW	R	W	D	CP	A
S5	207	narrow	Roof	1-	low	medium	1
S5	208	narrow	Roof	2+	medium	medium	1
S5	209	narrow	Roof	1-	medium	medium	1
S5	210	narrow	Roof	2+	medium	medium	1
S5	211	narrow	Roof	2+	low	medium	1
S5	212	broad	Roof	1-	medium	medium	1
S5	213	broad	None	1-	medium	medium	1
S5	214	narrow	Roof	2+	low	medium	1
S5	215	narrow	None	1-	low	medium	1
S5	216	narrow	Roof	1-	low	lower	1
S5	217	narrow	Roof	1-	low	lower	1
S5	218	narrow	Roof	1-	medium	lower	1
S5	219	narrow	Roof	2+	low	lower	1
S5	220	narrow	Roof	1-	low	lower	1
S5	221	narrow	Roof	2+	low	lower	1
S5	222	narrow	Roof	1-	low	lower	1
S5	223	narrow	Roof	1-	low	lower	1
S5	224	narrow	None	1-	low	lower	1
S5	225	broad	Roof	1-	low	lower	1
S5	226	broad	Roof	1-	low	lower	1
S5	228	broad	Roof	1-	low	lower	1
S5	229	broad	Roof	1-	low	lower	1
S5	230	broad	Roof	1-	low	lower	1
S5	231	broad	Roof	1-	medium	lower	1
S5	232	broad	Roof	1-	medium	lower	1
S5	233	broad	Roof	1-	high	lower	1
S5	234	broad	Roof	1-	high	lower	1
S5	235	narrow	Roof	1-	high	lower	1
S5	236	broad	Roof	1-	high	lower	1
S5	237	broad	Roof	1-	high	lower	1
S5	238	broad	None	1-	high	lower	1
S5	239	narrow	Roof	1-	high	lower	1
S5	240	narrow	Roof	1-	low	lower	1
S5	241	narrow	None	1-	medium	lower	1
S5	243	narrow	None	1-	medium	lower	1
S5	244	broad	None	1-	low	lower	1
S5	245	broad	None	1-	low	lower	1
S5	246	broad	None	1-	high	lower	1
S5	247	broad	None	1-	high	lower	1
S5	248	broad	None	1-	high	lower	1
S5	249	broad	None	1-	high	lower	1
S5	250	broad	Roof	1-	low	lower	1
S5	251	broad	Roof	1-	low	lower	1
S5	252	narrow	None	1-	low	lower	0
S5	253	narrow	None	1-	low	lower	1
S5	254	narrow	None	1-	medium	upper	0
S5	255	broad	None	1-	medium	upper	1
S5	256	broad	None	1-	low	upper	1
S5	257	broad	None	1-	low	upper	0
S5	258	broad	None	1-	low	upper	0
S5	259	broad	Roof	1-	low	upper	1
S5	260	narrow	Roof	1-	low	medium	1
S5	261	broad	None	1-	medium	medium	1
S5	262	broad	None	2+	medium	medium	1
S5	263	broad	None	1-	medium	medium	1
S5	264	broad	None	1-	medium	medium	1
S5	265	narrow	None	1-	low	medium	1
S5	266	narrow	None	2+	low	medium	1
S5	267	narrow	Roof	1-	high	medium	1
S5	268	narrow	None	1-	high	upper	0
S5	269	broad	None	1-	medium	medium	1
S5	270	narrow	None	1-	low	medium	0
S5	271	narrow	None	1-	low	medium	0
S5	272	narrow	None	1-	low	medium	1
S5	273	narrow	Roof	1-	low	lower	0
S5	274	broad	None	1-	high	upper	1
S5	275	broad	None	1-	medium	medium	0
S5	276	narrow	Roof	1-	low	lower	1
S5	277	broad	None	1-	low	medium	1
S5	278	narrow	None	1-	low	lower	1
S5	279	broad	None	1-	high	lower	1
S5	280	narrow	Roof	2+	low	lower	1
S5	281	broad	None	1-	high	lower	0
S5	282	narrow	None	1-	low	medium	1
S5	283	narrow	Roof	2+	low	upper	1
S5	285	narrow	None	1-	high	medium	0
S5	287	narrow	Roof	2+	low	lower	1
S5	288	narrow	None	1-	medium	upper	0

P	NS	LW	R	W	D	CP	A
S5	289	narrow	None	1-	low	lower	1
S5	290	broad	None	1-	high	lower	0
S5	291	narrow	None	1-	medium	upper	0
S5	292	narrow	None	1-	medium	upper	0
S5	293	broad	None	1-	low	upper	0
S5	294	narrow	None	1-	medium	lower	1
S5	295	broad	None	1-	high	lower	0
S5	301	narrow	None	1-	low	upper	1
S5	302	broad	None	1-	high	medium	1
S5	303	narrow	Roof	1-	low	lower	0
S5	304	narrow	None	1-	low	lower	0
S5	305	narrow	None	1-	high	medium	0
S5	306	narrow	None	1-	low	medium	1
S5	311	broad	None	1-	medium	medium	1


Plot S1 (A)
A
A
42
43
44
45
46
47
48
51
69


Plot S1 (B)
B
B
62
1
2
3
4
5
6
7
31
8
32
9
49
10
60
11
12
13
41
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63
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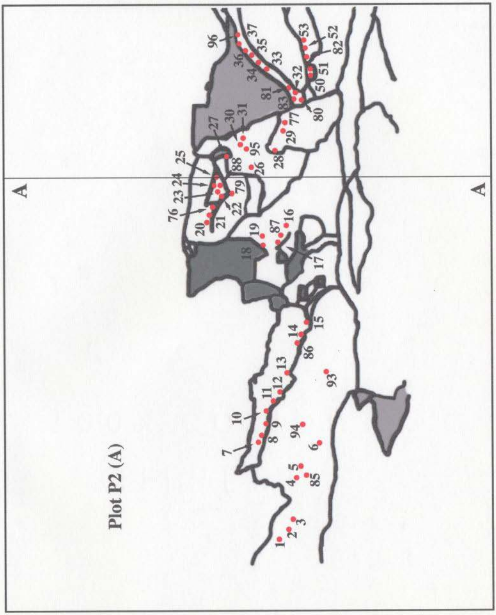
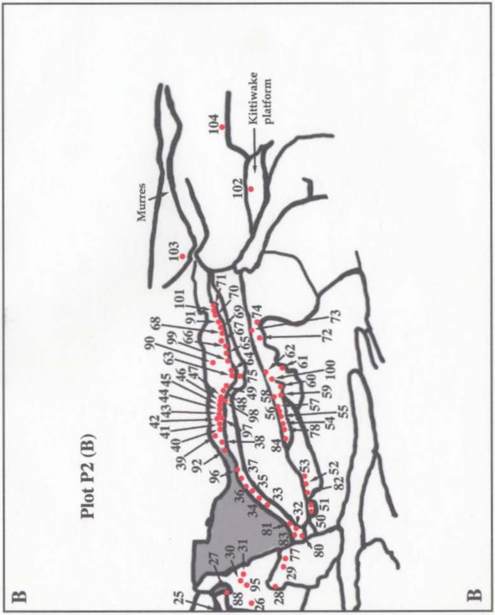
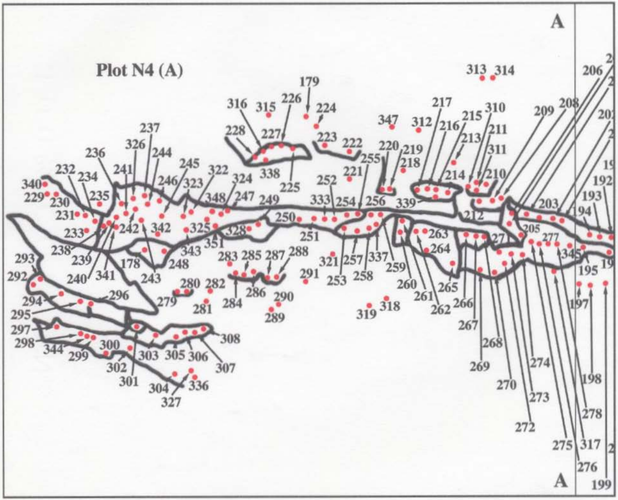
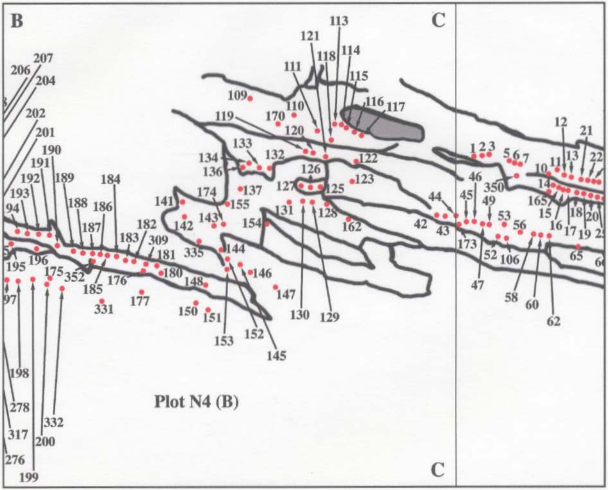
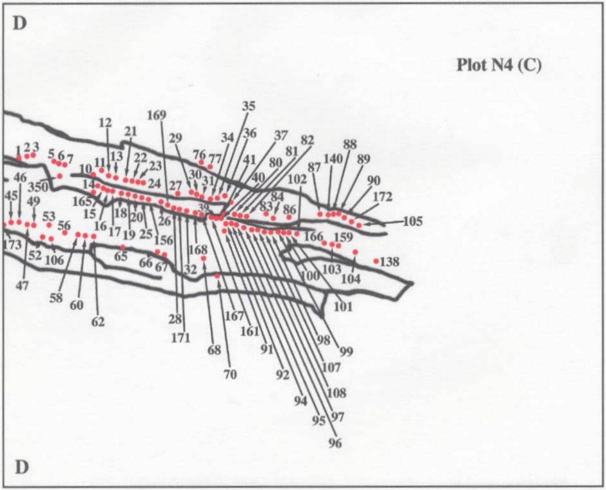

Plot P2 (A)
A
A


Plot P2 (B)
B
B
Murres
Kittiwake
platform


Plot N4 (A)
A
A


B
C
Plot N4 (B)
C


D
Plot N4 (C)
1 2 3
5 6 7
46
350
45
49
53
56
173
52
106
47
58
60
62
10
11
12
13
21
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23
24
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165
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156
169
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76
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66
67
32
168
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171
68
70
167
161
91
92
94
95
96
97
98
99
107
108
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84
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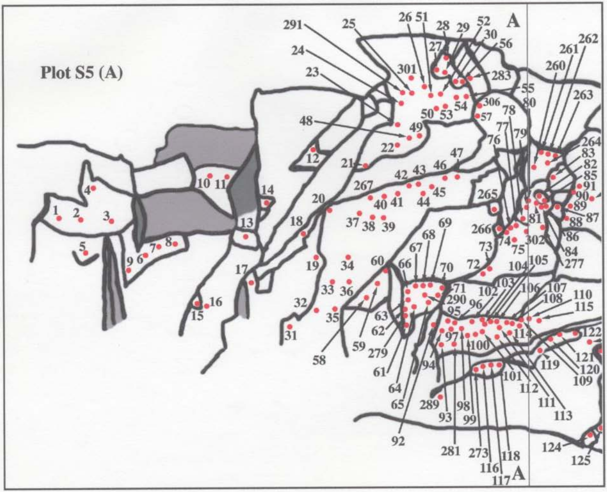
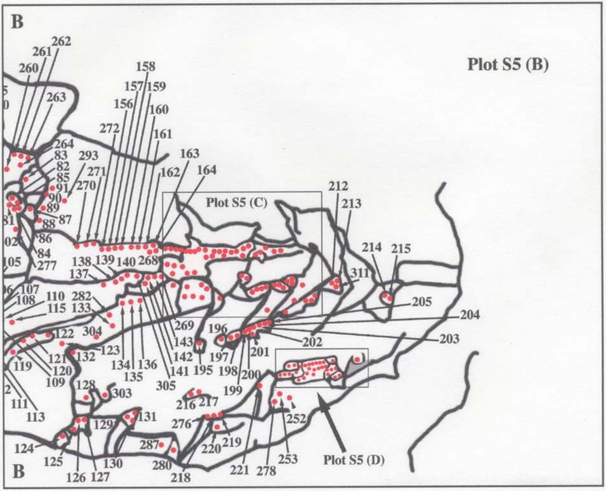
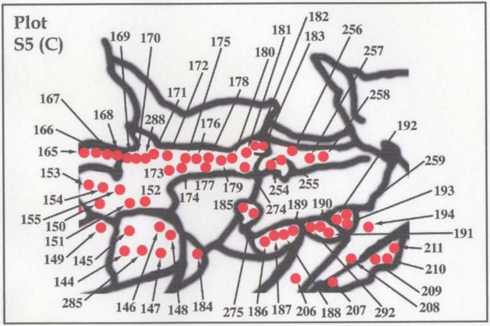
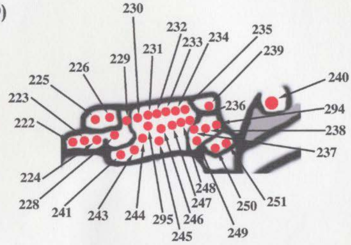
87
102
140
88
89
90
172
105
166
159
103
104
100
101
138
D


Plot S5 (A)
A
A


B
Plot S5 (B)
Plot S5 (C)
Plot S5 (D)
B


Plot
S5 (C)
169 170 175 172 171 178 181 182 183 180 256 257 258
167 168 288 176 166 165 192 259
153 173 177 179 154 152 174 254 255 193
155 150 185 274 189 190 194
151 191 211 149 145 210 144 209
285 146 147 148 184 275 186 187 206 188 207 292 208

Plot
S5 (D)



7394 21