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THE FORAGING ECOLOGY OF THE BLACK GUILLEMOT
(Cepphus grylle)

by

DAVID KENNETH CAIRNS, B.Sc., M.Sc.

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of
Doctor of Philosophy

Department of Biology

Carleton University

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November 1984

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ABSTRACT

Breeding and foraging activities of Black Guillemots (Cepphus grylle) were investigated during the 1981-1983 nesting seasons in the Nuvuk Islands, N.W.T. ($62^{\circ}23'N$, $78^{\circ}05'W$). Guillemots laid eggs during or shortly after ice dispersal. Breeding success, egg sizes, chick growth, and attendance patterns were generally similar to results reported from other colonies.

Ninety-two percent of observed chick food was blennies (Blennioidae). Feeding rates were highest in the morning, but did not vary over the season or according to sex of the parent. Prey size increased with chick age, and daily food intake per chick peaked at about 140 g, containing about 800 kJ of energy. Most chick food was obtained in water less than 40 m deep within 2 km of the colony.

Adults fed on blennies, Arctic cod (Boreogadus saida), and mysid, amphipod, and decapod crustaceans. Birds concentrated along landfast ice edges at the beginning of the season. After ice break-up, they fed in a dispersed fashion in shallow water up to 15 km from the largest colonies in the area, with higher densities tending to occur near the colonies.

An iterative model is presented that assumes birds will choose foraging zones to minimize time required to travel to the foraging site, procure a prey item, and return to the colony. The model predicts that foraging activity, when measured as the number of visits per unit area, will be constant from the colony to a cut-off point, but that when foraging time is used as a measure intensity will gradually decline with

distance from the colony. These predictions were matched by observations of chick-feeding and self-feeding birds.

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GENERAL INTRODUCTION

The realization that optimality theory can be applied to ecological systems (Cody 1974) has spawned a heightened interest in the way that natural selection shapes animal behaviour. Optimality theory, when applied to behaviour, offers a way to identify from a set of alternatives the choice or choices that an animal should make to maximize or minimize some criterion. If there is a genetic component to such behaviour, individuals that consistently make optimal choices should be favoured by natural selection, and the genes that underlie this behaviour should increase in frequency.

Because feeding behaviour offers simple but intuitively attractive criteria for optimization (e.g. rate of energy gain, time required to meet a certain energy demand; Schoener 1971), a large part of the research on optimal behaviour has focussed on foraging. Animals that must return to a central place after capturing their prey have received particular attention since the publication of Orians and Pearson's (1979) model which dealt with prey selection at various distances from the central place.

Although the Orians-Pearson and other models have been tested by many authors with considerable success (Carlson and Moreno 1981, Jenkins 1980, Kramer and Nowell 1980, and many others), doubts have been expressed about the extent to which optimality theory can be profitably applied to the foraging behaviour of wild animals. As Zach and Smith (1981) point out, most animals feed under conditions much more complex than those found in the laboratory or in the simple field situations

where optimality models have been tested. Such complexity raises difficulties in defining and measuring the conditions under which choices are made and in specifying optimality criteria.

The purpose of this study is to determine for the Black Guillemot (Cepphus grylle), a pursuit-diving seabird, what prey adults choose for themselves and their young and where they obtain such prey, and to test predictions regarding choice of prey, feeding habitat, and distribution of feeding effort. Since it is beyond our present capability to completely assess the complex marine environment in which guillemots feed, the testing of such predictions will also be a test of whether simple models, which inevitably overlook some pertinent conditions, can nevertheless be successful in complex field situations.

In this study particular importance is attached to the question of foraging distributions. This is of practical significance because seabirds are highly susceptible to injury from oil pollution (McKnight and Knoder 1979), and oil-related activities tend to be most intense in summer when seabirds congregate near their colonies. Recent attempts to model oil spill sensitivities of seabirds (e.g. Ford et al. 1982) have brought attention to the critical need for information on foraging distributions for future sensitivity analyses (Wiens et al. 1984).

A word is in order regarding the choice of the Black Guillemot as a study species. Although alcids (Alcidae), including guillemots, are among the most vulnerable of northern seabirds to oil pollution (King and Sanger 1979), the long foraging trips of most species make direct measurement of feeding ranges difficult. This has forced investigators

to rely on indirect indicators such as duration of feeding trips (e.g. Pearson 1968, Ford et al. 1982). Although guillemots are typical alcids morphologically, they forage much closer to their colonies than other alcids, making it possible to define foraging areas by visual observation from the colony or by a network of transects across the foraging grounds. Guillemots also offer the advantages of accessible ground nesting and a method of carrying food to the young which allows identification of prey items.

The body of this thesis is divided into four parts, each of which has its own introduction and discussion. The first describes features of guillemot breeding and assesses feeding conditions in the study area in relation to the species' range as a whole. The second part deals with foraging activities directed at chick feeding, and compares choice of prey type, habitat, and prey location strategy to theoretical predictions. Part 3 deals with prey and habitat choice for adult self-feeding, and the fourth part presents a model of foraging distribution which is applicable to both chick and adult feeding. The thesis concludes with a general discussion of its major findings and a numbered list of conclusions.

STUDY AREA

Physical environment and flora

This study was conducted on the Nuvuk Islands, N.W.T. ($62^{\circ}23'N$, $78^{\circ}05'W$), and adjacent waters (Fig 1). This area lies at the juncture of Hudson Bay and Hudson Strait, and is 12 km southwest of Ivujivik, Quebec. Many geographic features of the region lack official names, so the place names used in this thesis include many local Inuit and arbitrarily coined names. The biological and physical attributes of the Nuvuk region and Hudson Bay have been described in detail by Gaston et al. (in press) and Beals (1968); this section summarizes salient details.

Landforms in the Nuvuk area are moderate in slope ($< 15^{\circ}$) and generally meet the water in rocky terraces or cobble beaches, although a few low cliffs are present. Most islands have areas of rocky debris fractured from the bedrock, and some have patches of raised boulder beach. Vegetative cover in the area is closely linked to maritime exposure. Small islands are virtually devoid of terrestrial plants, but larger ones contain elements of the tundra community found on the mainland.

Two islands were the principal sites of land-based investigation and merit further description. Pitsulak City, 300 m in length, lies 1.8 km off West Nuvuk Island (Figs. 1 and 2). A raised beach of rounded boulders runs along the central portion of the eastern side of the island, and extensive patches of tumbled rock slabs occur elsewhere in the central and southern parts of the island. The island is low

Fig. 1

Study area, showing location off northwestern Quebec (inset). Islands in the South Skerries and Pigiuliit groups are identified by numbers (e.g. South Skerries 3, Pigiuliit 5).

Fig. 2

Pitsulak City. Letters denote nesting sub-areas. The dotted line marks the boundary of the attendance count area. Locations of blinds are indicated by squares.

(maximum elevation 5.5 m), and shorelines are gently sloping except for a low cliff along the northwest margin.

Piqiuliit 5 is 4 km to the south of Pitsulak City, and resembles it in dimensions and topography. It also has patches of tumbled rock, but these cover less of the island than those of Pitsulak City.

Inshore waters to the west and south of West Nuvuk Island are shallow and are punctuated by islands and reefs. To the north of the Nuvuk Islands lies a trench 300 m deep, which is an extension of the deep basin of Hudson Strait. This trench extends west between the North and South Skerries and branches south between the South Skerries and Pitsulak City (Fig. 1).

Benthic algae are abundant throughout the area. Fucoids dominate the intertidal zone, and luxuriant beds of laminarians cover the subtidal zone to about 10-15 m.

Hudson Bay has been traditionally characterized as a biological desert (Huntsman 1954) because of low productivity caused by a lack of vertical mixing. In Hudson Strait, waters are well mixed by strong tidal currents (Barber 1968). Although oceanographic data specific to the study area are not available, the waters of the area are likely more similar to those of Hudson Strait than those of Hudson Bay, with local productivity enhanced by upwelling induced by tidal currents (Gaston et al. in press).

Nearly all of Hudson Bay and Hudson Strait is ice-covered in winter (Larnder 1968). Break-up is gradual, beginning in April and extending into July. In 1981 ice was common until mid-July, but in

1982 and 1983 most ice had dispersed by the end of June.

Summer climate of the Nuvuk area is cool, and temperature extremes are moderated by the maritime environment. Temperatures were recorded daily at 19:30 at the camp on East Nuvuk Island in 1981, and on Pitsulak City in 1982 and 1983. July and August means ($\pm$ SD, range) were 5.9° (± 2.5 , 1-13) and 6.0° (± 1.8 , 3-9) in 1981, 5.5° (± 2.0 , 2-10) and 4.0° (± 2.1 , 1-9) in 1982, and 5.0° (± 1.9 , 1-9) and 5.1° (± 1.6 , 3-9) C in 1983 respectively.

Tides in the study area are semi-diurnal, with a range of about 2 m (Anon. 1982).

Aquatic birds

Black Guillemots breed on nearly all of the islands in the Nuvuk area. Since guillemots encountered on seabird transects could thus include birds from several colonies, I censused islands in the area to identify the major sources of foraging birds (Table 1). Since some nests were undoubtedly missed in ground searches, I increased counts of nests by a factor that I subjectively estimated from the amount of search effort and the complexity of the habitat. Pitsulak City was the largest colony in the area, with 190 pairs, followed by Green Island with 100 pairs. Other islands had lesser numbers, and some birds nested non-colonially on small islets and on the mainland. Breeding populations were roughly correlated with the availability of rock crevices on each island, but all islands contained some unoccupied sites which appeared to be suitable for nesting.

Several of the islands in the study area also had small breeding

Table 1.

Estimated numbers of breeding pairs of Black Guillemots in the Nuvuk Islands area.

site	estimated population
Pitsulak City	190
Green Island	100
Yellow Island	18
Black Island	14
West Nuvuk Island	4
East Nuvuk Island	4
mainland	5
Piqiuliit 2	12
3	1
5	29
7	2
Kingituayu Island	10
Qikita Island	7
South Skerries 1	8
2	5
4	48
Piqiulik Island	3
total	460

populations of Glaucous Gulls (Larus hyperboreus) and Herring Gulls (L. argentatus). Three pairs of Herring Gulls nested on Pitsulak City in 1980 (Gaston et al. in press), but none bred in the following three years, possibly because of observer disturbance. Several Common Eiders (Somateria mollissima) attempted to nest on Pitsulak during the study years, but most of the area's eiders nested on the South Skerries, Green Island, and on West Nuvuk Island. Arctic Terns (Sterna paradisaea), Red-breasted Mergansers (Mergus serrator), and Oldsquaw (Clangula hyemalis) also bred on several islands of the study area.

Thick-billed Murres (Uria lomvia) did not breed in the study area, although they foraged in large numbers within it, mostly in deep waters offshore from Pitsulak City. These birds came from the large colonies at Digges Sound, 30 km to the northeast of the study area, whose breeding populations total some 300,000 pairs (Gaston et al. in press).

GENERAL METHODS

Field work for this study began on 18 June 1981 when a camp was established at the south end of East Nuvuk Island. This camp was used as a base for day visits to guillemot breeding islands and foraging areas. On 2 August, a second camp was set up on Pitsulak City which was continuously occupied until field work ended on 5 September.

Pitsulak City was used as the base of operations in 1982 and 1983.

- The island was occupied from 12 June to 16 September 1982 and from 13 June to 8 September 1983. The camp was located at the northeast corner of the island to reduce disturbance to nesting birds (Fig. 2).

Black Guillemots were captured in noose carpets, mist nets, and on the nest. In all years birds received coloured leg bands. In 1981 these were supplemented with patagial tags and, in some cases, radio transmitters, but since birds carrying these devices deserted their nests these methods were abandoned. In 1982 and 1983 birds were marked with wing paint and leg streamers. Wing marks were applied to the white wing patch with airplane dope in one to three vertical stripes. Streamers measured 1.5 by 22 cm, and were made of laminated vinyl supplied by the Safety Flag Co. of America, Pawtucket, Rhode Island. Streamers and wing marks were both effective in allowing individual identifications at substantial distances. Birds with wing marks and streamers did not abandon their nests and appeared to behave normally. Streamers were also useful in establishing the origin of birds seen on the water, because most of the length of each streamer was coloured a colony-specific colour, which was visible when birds flushed from the

water.

The Canadian Hydrographic Service chart that includes the study area gives little detail on the bathymetry of the area's inshore waters. More detailed charts were made from profiles traced by an echosounder (Japan Radio Company, Model NJA-155) on seabird transect routes, and on a dense network of special transects in the Pitsulak - Piquliit area.

Data were analysed with standard univariate and non-parametric techniques, including one-way and nested analyses of variance, G-tests, Pearson correlations, linear regressions, Kendall rank correlations, and Wilcoxon rank sum tests (Sokal and Rohlf 1969, Gibbons 1976).

Other methods used in this study are described in the Methods sections of the chapters which follow.

PART 1 BREEDING BIOLOGY AND BEHAVIOUR

INTRODUCTION

The breeding activities of Black Guillemots have been described from the northwestern Soviet Union (Bianki 1967, Belopol'skii 1957), Iceland (Petersen 1981), and eastern Canada (Winn 1950; Preston 1968; Cairns 1979, 1980, 1981). Despite the large number of guillemots breeding in northern North America (Brown et al. 1975), information on guillemot breeding in the Canadian arctic is scarce. In this chapter I examine breeding phenology and success, egg sizes, chick growth, and attendance patterns, and compare data on these topics from Nuvuk with results obtained elsewhere. The breeding and feeding adaptations of birds have long been known to be interrelated (Lack 1967), and each of the above features of breeding biology influences or is influenced by foraging conditions and foraging success. My purpose in this chapter is to provide essential background to the understanding of guillemot foraging ecology and to draw inferences about seasonal variation in food availability and the relative availability of food in the study area compared to the species' range as a whole.

METHODS

Timing and success of breeding in Areas C and F on Pitsulak City (Fig. 2) were monitored by nest visits at four to five day intervals. Direct visual examination was sufficient for most nest sites, but an optical fiberscope (Cairns 1983) was used to inspect deep or awkward cavities. Nest visits in 1981, 1982, and 1983 began on 24 July, 9 July, and 28 June, respectively. Because of breeding failure in Areas C and F in 1983, monitoring was extended to Areas M and N. Visits there began on 6 July for some nests, but were not conducted regularly until August. In 1983 nests were also monitored on Pigiuliit 5. Visits were made there on 19, 20, and 22 July; 3, 16, and 25 August; and 1 September.

Because visits did not always begin before laying, hatch date was used to indicate timing of breeding. Timing curves derived by this method reflect only successfully hatched eggs, and ignore those that failed to hatch. Chicks which were still damp when discovered were assumed to have hatched on that day. Hatching dates for other chicks were estimated from wingspan growth curves for known-age chicks. Wingspan was measured by laying chicks on their backs, drawing the wings away from the body, and measuring the distance between the most distal down feathers on the wing tips. Wingspan was used instead of wing length as an age indicator because it was found that it could be measured more consistently on very young chicks.

Breeding success was measured as unmodified ratios of successful to total eggs, chicks, and nests. The Mayfield method

(Mayfield 1975) was not used to estimate breeding success because this method requires that chick mortality be constant with time and that egg mortality be immediately detectable. These assumptions were not valid for guillemots breeding at Nuvuk.

Length and maximum breadth of eggs were measured with vernier calipers. Weight, wing lengths, and tarsus lengths of chicks were measured with Pesola balances, rigid rulers, and vernier calipers, respectively. Because the constants derived from logistic and other curves described by Ricklefs (1967) are poorly suited to comparing growth data where asymptotes vary as a proportion of adult weight (Hussell 1972, Gaston in press), I used maximum growth rate, measured from a smoothed graph at the inflection point, to compare growth rates. Smoothed graphs were prepared by eye from plots of mean daily weights vs. age.

Black Guillemots attending the colony were counted in 1982 and 1983 from the main blind, which was situated at the edge of Area E in 1982 and in Area M in 1983. The area counted was F Cove and those parts of Pitsulak City whose breeding birds tended to loaf in F Cove (Fig. 2). I made hourly counts in both years, and in 1982 supplemented these with counts made irregularly in the course of other duties. Both blind locations gave clear views of the count zone. Birds attending on the water posed little difficulty in counting because they generally kept close to the island, and because feeding birds rarely used the area.

RESULTS

Timing of breeding

Distributions of hatching dates for Pitsulak City 1981-1983 and for Piquliit 5 for 1983 are presented in Fig. 3. In the case of typical two-egg clutches, the curves include data from both eggs, which usually hatch two or three days apart (Petersen 1981). The 1981 hatching curve for Pitsulak City was bi-modal, with the first peak occurring in late July and the second about three weeks later. Hatching curves for 1982 and 1983 were uni-modal. Median hatching dates for 1981 and 1983 were close (30 and 31 July respectively), but median hatching did not occur until 7 August in 1982 ($P < .001$, Wilcoxon rank sum test comparing 1982 vs. 1981 and 1983 combined).

The distribution of hatching on Piquliit 5 in 1983 had the same median and a similar bi-modal form as the 1981 curve for Pitsulak City.

Breeding success

Parameters of guillemot breeding success at Pitsulak City and Piquliit 5 are presented in Table 2. Reproductive values were generally similar across year-location classes, except for the central part of Pitsulak City where monitored nests produced virtually no young in 1983.

Since the low productivity of Pitsulak City central in 1983 may have been an aberration due to ermine (Mustela erminea) visitation (see p. 43), figures from this area are excluded from the following analy-

Fig. 3

Distribution of Black Guillemot hatching dates. Scale divisions of the abscissa correspond to noon-times; vertical lines on histograms correspond to midnights.

Table 2

Black Guillemot breeding success at Pitsulak City and Pigiuliit 5.

	Pitsulak City				Pigiuliit 5	total ^a
	1981	1982	1983		1983	
			central	south		
number of nests	20	52	35	23	26	121
eggs laid	34	100	59 ^b	41 ^b	50	225
chicks hatched	19	51	1	21	31	122
chicks fledged	10	47	1	19	26	102
mean clutch ^c	1.70	1.92	1.69 ^d	1.78	1.92	1.86
chicks hatched/ egg laid ^e	0.56	0.51	0.017	0.51	0.62	0.54
chicks hatched/ nest ^f	0.95	0.98	0.029	0.91	1.19	1.01
chicks fledged/ chick hatched ^h	0.53	0.92	1.00	0.90	0.84	0.84
chicks fledged/ egg laid ⁱ	0.29	0.47	0.017	0.46	0.52	0.45
chicks fledged/ nest ^j	0.50	0.90	0.029	0.83	1.00	0.84

^aexcludes Pitsulak City central 1983.^bincludes 2 clutches with 3 eggs each, which are considered here as 2 egg clutches.^cdiffers among year-location classes ($F=3.17$, $P<.025$).

Table 2 (continued)

^ddiffers from Pitsulak City 1982 (Student-Newman-Keuls (SNK) a posteriori test, $P < .05$). All other SNK comparisons are non-significant ($P > .05$).

^eproportions differ among year-location classes ($G=70.0$, $P < .005$), but not when Pitsulak City 1983 central is excluded ($G=1.84$, $P > .05$).

^fdiffers among year-location classes ($F=10.0$, $P < .001$).

^gdiffers from all other values (SNK a posteriori test, $P < .05$). All other SNK comparisons are non-significant ($P > .05$).

^hproportions differ among all year-location classes taken together ($G=14.3$, $P < .01$) and among all classes but Pitsulak City 1983 central ($G=14.3$, $P < .005$).

ⁱproportions differ among year-location classes ($G=56.6$, $P < .005$), but not when Pitsulak City 1983 central is excluded ($G=4.64$, $P > .05$).

^jdiffers among year-location classes ($F=8.2$, $P < .001$).

^kdiffers from all other values (SNK a posteriori test, $P < .05$). All other SNK comparisons are non-significant ($P > .05$).

sis. Eighty-six percent of the 121 nests of the summed year-location classes had at least two eggs, for a mean clutch of 1.86. Hatching success was 0.54 chicks hatched/egg laid, and fledging success was 0.84 chicks fledged/chick hatched. The most conspicuous departure from overall patterns was found in 1981 when chicks fledged/chick hatched on Pitsulak was only 0.53.

In order to provide a relative indication of food demand at the colony, I searched Pitsulak City thoroughly for nests in 1982, and occasionally checked nests outside the regularly monitored areas in 1982 and 1983. Numbers of nest sites producing eggs, chicks, and fledged young are given in Table 3. Nest occupancy was reduced across the island in 1983. The proportion of sites producing fledged young was also much reduced, particularly in the central part of the island. It is important to note that the figures in Table 3 provide only rough indications of breeding success, because many of the nests were visited infrequently.

Egg dimensions and chick growth

Egg lengths, diameters, and volume indices were similar on Pitsulak City in 1982 and 1983, and on Piquiliit 5 in 1983 (Table 4). Mean dimensions of 229 eggs were 58.45 x 39.63 mm, with a mean volume index of 91934 mm.

Egg volume indices showed no significant seasonal trend. Correlation coefficients between hatching date and volume index were 0.14 ($n=40$, $P>.05$) for Pitsulak City in 1982 and -0.51 ($n=26$, $P>.05$) for

Table 3

Number of nests on Pitsulak City producing eggs, chicks, or fledglings in 1982 and 1983.

area	1982			1983		
	no. nests with at least 1			no. nests with at least 1		
	egg	chick	fledgling	egg	chick	fledgling
<u>Central</u>						
C	43	26	23	35	4	3
M north	2	2	2	3	2	2
F north	17	7	7	6	0	0
E	14	11	11	7	5	4
B	40	32	25	31	15	10
total Central	116	78	68	82	26	19
<u>South</u>						
F south	4	4	4	3	3	3
D	17	14	12	11	4	4
M south	12	9	9	8	3	3
N	29	22	18	19	13	11
total south	62	49	43	41	23	21
<u>North</u>						
A	14	7	6	8	0	0
all areas	192	134	117	131	49	40

Table 4

Dimensions of Black Guillemot eggs.

	length ^a (mm)	diameter ^b (mm)	volume index ^c (L x dia ²)	n
Pitsulak City 1982	$\bar{x} \pm \text{SD}$: 58.42 $\pm$ 1.87 range: 54.4-62.3	39.78 $\pm$ 1.18 36.4-42.7	92552 $\pm$ 6618 75978-112315	104
Pitsulak City 1983	$\bar{x} \pm \text{SD}$: 58.19 $\pm$ 2.26 range: 51.6-63.3	39.65 $\pm$ 1.12 36.6-42.7	91636 $\pm$ 7494 72068-111768	74
Piquiluit 5 1983	$\bar{x} \pm \text{SD}$: 58.89 $\pm$ 1.86 range: 56.3-64.3	39.32 $\pm$ 0.87 37.2-41.2	91105 $\pm$ 5171 80019-102366	51
pooled data	$\bar{x} \pm \text{SD}$: 58.45 $\pm$ 2.01 range: 51.6-64.3	39.63 $\pm$ 1.11 36.4-42.7	91934 $\pm$ 6632 72068-112315	229

^aF=1.85, P>.05^bF=2.98, P>.05^cF=0.95, P>.05

Piqiuliit 5 in 1983.

Growth of weight, wing and tarsus of Black Guillemot chicks is plotted in Figs. 4 to 6. After an initial period of two or three days when weight growth tended to be slow, weight increased linearly until about 24 days. Weight gain then slowed until fledging at about 34 days. Maximum growth rates were 13.6, 12.4, 14.7 and 16.2 g/d for Pitsulak City 1981, 1982, 1983, and Piquliit 1983, respectively. Growth curves were similar across years and areas in the initial and linear phases. However, in the final growth phase chicks at Pitsulak in 1983 continued to grow until fledging, unlike chicks of other year-site categories whose weight stabilized at an asymptote (Fig. 7). This difference was confirmed by a comparison of the actual weights (rather than the plotted means) of chicks from the four year-site categories, measured at 30 or more days of age ($F=6.96$, $P<.001$).

Tarsus growth was roughly linear from hatching until growth stopped at about 20 days (Fig. 5). Wing growth was slow initially, but wing lengths increased linearly from about 13 days to fledging (Fig. 6).

Attendance patterns

Counts of guillemots visible from the blind at Pitsulak revealed a pattern of high attendance early in the morning, followed by afternoon troughs when very few birds were visible (Fig. 8). During the pre-laying and incubation periods, there was an additional peak of attendance in the evening. The evening peak appeared inconsistently during

Fig. 4

Weight growth of Black Guillemot chicks. Each dot is the mean weight of chicks measured at a specific age. The horizontal dotted line is the mean adult weight from Appendix 5. 1981 data are from 85 measurements of 25 chicks, 1982 data from 239 measurements of 44 chicks, 1983 Pitsulak City data from 110 measurements of 19 chicks, and 1983 Piquiluit data from 78 measurements of 28 chicks.

Fig. 5

Tarsus growth of Black Guillemot chicks. Each dot is the mean tarsus length of chicks measured at a specific age. The horizontal dotted line is the mean adult tarsus length from Appendix 5. See Fig. 4 for sample sizes.

Fig. 6

Wing length growth of Black Guillemot chicks. Each dot is the mean wing length of chicks measured at a specific age. The horizontal dotted line is the mean adult tarsus length from Appendix 5. See Fig. 4 for sample sizes.

Fig. 7

Comparison of weight growth of Black Guillemot chicks across years and sites. Curves fitted by eye from data points in Fig. 4. Horizontal line above curves is the mean adult weight from Appendix 5.

Fig. 8

Attendance of Black Guillemots at Pitsulak City. 1982 curves are based on 1 to 4 counts for 25 June - 2 July, 2 to 5 counts for 4-31 July, and 1 count for 22 August. 1983 curves are each based on single counts. The horizontal line is the number of pairs which produced at least one egg in the attendance count area. No counts made where abscissa is absent.

time

chick-rearing, and was not recorded on the two days during chick-rearing on which birds were counted.

Birds were visible near the colony throughout the night until at least mid-July. By late July non-incubating birds apparently abandoned the colony at night, since none was recorded from 00:00 to 03:00 on 31 July 1982. After this date darkness prevented night-time counts. However, the absence of visible birds at 04:00 on 18 August 1983, and their absence at first light during casual observations, suggest that guillemots did not spend the night at the colony during chick-rearing. In 1982 overall attendance levels were lower during incubation than during pre-laying and chick-rearing, but in 1983 attendance did not change between incubation and chick-rearing.

Predators

Guillemot colonies are normally free of terrestrial predators, but in 1983 Pitsulak City was visited by an ermine. I saw this animal at 09:35 on 27 June, when it emerged for about 10 s from a rock crevice in front of the main blind in Area F. Despite diligent searching and the placement of baited traps in the area, no subsequent trace of this animal was found. Since ermine seen elsewhere seemed curious of humans and often boldly explored camps, it is unlikely that the animal remained long on Pitsulak after it was sighted.

In addition to the sighting on Pitsulak City, ermine were seen in 1983 on Green and Yellow Islands, and were reported as common visitors to a biologists' camp on East Nuvuk Island and to Inuit camps else-

where. When visited late in the chick-rearing period of 1983, Yellow Island had no active or recently active nests, and Green had a single nest with one chick.

DISCUSSION

A comparison of basic features of the breeding biology of Nuvuk guillemots with those of other colonies is presented in Table 5.

Given an incubation period of about 31 d for first eggs (Petersen 1981), guillemots at Nuvuk whose eggs hatched began laying in late June (Fig. 3). At this time most crevices had been clear of ice and snow for about two weeks, indicating that readiness of nest cavities did not limit timing of laying.

In Pitsulak 1981 and Pigiuliit 1983, which were the year-site classes with the earliest laying peaks, the main period of laying was followed by a second, lower peak of activity, which probably represented relaying attempts. Presumably in later breeding years (e.g. 1982) birds do not try to replace lost clutches because the 15 d lag between clutch loss and replacement (Petersen 1981) would delay the season so much that the breeding attempt would have little chance of success.

Measures of guillemot breeding productivity vary widely among studies (Table 5), but such variation must be interpreted with caution because of the possible effects of observer disturbance on breeding success (Cairns 1980, Petersen 1981). If observer disturbance affected breeding success at Nuvuk, most of the depression probably occurred at the egg stage, because breeding loss is much greater than during chick-rearing. Most incubating birds left the nest at the distant approach of an observer. Although eggs of Pigeon Guillemots (Cephus columba) can hatch despite long gaps in incubation (Drent 1965), regu-

Table 5

Features of Black Guillemot breeding biology at Muvuk and other colonies. nd = no data.

location, latitude, source	hatching peak	chicks fledged/ nest	egg volume index	attendance pattern	maximum growth rate (g/d)	predators
Kent Island Bay of Fundy 45° Winn 1950	July	0.48	87312	nd	nd	crows, young Herring Gulls
Kent Island Preston 1968	mid July	0.85 (excludes "0 egg nests")	nd	attendance on land increases with tide height	nd	possibly crows and Herring Gulls
Brandypot I. St. Lawrence Estuary 48° Cairns 1981, unpubl.	late June	0.64	nd	attendance on land increases with tide height	15.3	none
St. Mary's I. Gulf of St. Lawrence 50° Cairns 1979, 1980, 1981, unpubl.	mid July	0.97 ("lightly disturbed" habitat)	94035	morning peak, evening peak waning at chick-rearing	15.3	none
Muvuk Is. 62° this study	late July- early August	0.84	91934	morning peak, evening peak waning at chick-rearing	12.4 to 16.2	ermine present in one year

Table 5 (continued)

location, latitude, source	hatching peak	chicks fledged/ nest	egg volume index	attendance pattern	maximum growth rate (g/d)	predators
Prince Leopold I., N.W.T. 74° A.J. Gaston pers. comm.	late July- early August	1.25	nd	peak from midnight to 06:00	13.6	none
W. Foxe Is. N.W.T. 64° F.G. Cooch pers. comm.	early August	nd	nd	nd	nd	none
Flatey I. ° Iceland 65° Petersen 1981	late June	1.29	87500	morning and evening peaks in pre-laying	15.5	rats present before start of study
Gulf of Finland 60° Bergman 1971	late June- early July	nd	nd	strong morning peak, weak evening peak	nd	fox
Denmark 56° Asbirk 1979	mid to late June	0.60	86436	morning peak throughout, evening peak in pre-laying and incubation	17.1	Herring Gulls
Kandalaksha Bay, NW U.S.S.R. 67° Blanki 1967	usually early June	nd	85358	nd	15.4	possibly fox, ermine

lar flushing of the adult from the nest must have some effect on hatching success. Perhaps more importantly, a repeatedly disturbed bird may eventually desert or incubate only sporadically. Most of the Nuvuk nests which failed to hatch seem to have been incubated infrequently.

During the first four or five days after hatching, susceptibility to disturbance probably continues at a high level, because chicks of this age need continuous brooding. After the ability to thermoregulate is established, parents spend little time in the nest, and disturbance seems to have little effect on their behaviour.

Some breeding losses may have been caused by collection of adults for stomach samples. Collected birds that might have been breeders at Pitsulak City include those shot between the northern tip of West Nuvuk Island and Ice Harbour, minus several birds which were very probably attached to the colony at Green Island, since they were collected from the early morning assemblage of birds around that island. Since no chick mortality was recorded late in chick-rearing, I also exclude birds taken after 25 August. The number of collections conforming to these criteria is 6, 12, and 5 for 1981, 1982, and 1983 respectively (Appendix 3). To calculate the heaviest potential breeding loss due to collections we may take the 12 birds collected in 1982 and double this to 24 to allow for unretrieved cripples. If the loss is evenly spread among the approximately 460 nests in the area (Table 1), the chance of a given pair suffering the death of a member due to collection would be about 5%. Since both parents participate in incubation and chick-

rearing, the loss of one of them is likely fatal to the eggs or nestlings. Thus collection activities may have downwardly biased 1982 breeding success figures by about 5%. In 1981, when fewer birds were collected, the corresponding figure is 2.6%. The downward bias in 1983 is difficult to calculate because the population that attempted to breed in the Nuvuk area decreased by a large but unknown factor in 1983 compared to the previous two years.

Guillemots breeding in the central part of Pitsulak City in 1983 suffered nearly complete breeding failure, in marked contrast to breeding performances recorded at other sites and years. This breeding collapse occurred in the same year and in the same area as the ermine sighting on Pitsulak City. Since all other known factors, including human disturbance regimes, were similar in 1983 to previous years, the ermine is the prime suspect as the cause of the 1983 breeding failure. However, the evidence for this is not conclusive because no sightings were made after the beginning of egg-laying and because no remains of ermine-killed eggs, chicks, or adults were found on Pitsulak City. If the ermine did cause the poor breeding performance, it must have done so more by frightening the birds from their nesting duties than by direct predation.

In some colonies (Preston 1968, Asbirk 1979), some pairs may suffer breeding losses because of low quality nest sites. This was not a factor at Nuvuk because well sheltered cavities that were out of reach of tides were available in excess on all breeding islands in the area.

Chick growth rates were similar in all years and sites except for Pitsulak 1983 whose chicks gained weight until fledging, unlike chicks elsewhere whose mean weight stabilized at an asymptote. The continuing growth of chicks at Pitsulak in 1983 may have reflected favourable food supplies caused by decreased demand due to low numbers of pairs raising chicks. In 1982 there were 134 pairs with chicks on Pitsulak City and about 70 on nearby Green Island. In 1983 these numbers dropped to 49 and 1 respectively. Since birds from the two colonies broadly overlap in foraging area, we can combine these figures and calculate that demand for chick food in 1983 was $(49+1)/(70+134)$, or 25% of 1982 demand. In contrast, the 1983 breeding season at Piquliit 5 appeared to be normal, with breeding parameters similar to those of Pitsulak 1981 and 1982. There is little overlap in chick-food procurement areas between Piquliit and Pitsulak-Green Island (Part 2). Thus Piquliit birds presumably had a "normal" food supply in 1983, and their chicks showed the growth pattern seen at Pitsulak in 1981 and 1982.

Chick growth rates and egg sizes from Nuvuk are close to the means reported from other colonies (Table 5, Fig. 9). If egg size and chick growth are indicators of food availability, we may postulate that food supplies at Nuvuk are similar to those exploited by guillemots elsewhere.

The distinctive attendance pattern of high morning numbers followed by low numbers in the afternoon is nearly universal in Black and Pigeon Guillemot colonies (Table 5, Cairns 1979). In the pre-laying period of 1982, numbers at Pitsulak peaked during the well-illuminated

Fig. 9

Weight growth of Black Guillemot chicks at various locations. The curved lines are growth curves and the horizontal lines are mean adult weights. The curve from Pitsulak 1983 also describes weight growth from the St. Lawrence estuary in 1976 and the Gulf of St. Lawrence in 1977. Adult weights from the St. Lawrence are similar to those of Pitsulak and Piquiliit. Icelandic growth curves are from Petersen 1981, Pitsulak and Piquiliit curves from Fig. 4, St. Lawrence curves from Cairns 1981, Danish curves from Asbirk 1979, and Prince Leopold curves from A. J. Gaston (pers. comm.). Adult weight for Pitsulak and Piquiliit is from Appendix 5, adult weight for Denmark is the mean of Asbirk's (1981) incubation and chick-rearing weights, and adult weight for Prince Leopold Island is the mean of 37 weights recorded on specimen labels of Black Guillemots that were collected in the Barrow Strait-Lancaster Sound area, and held in the National Museum of Natural Sciences, Ottawa. No adult weights are available for Iceland.

night, as they do at other Arctic colonies. By mid-July at Nuvuk nights were dimming, and the attendance peak came later. By the end of July nights were nearly dark and night-time attendance ended. At this time and subsequently, guillemots appeared at the colony at dawn.

Overall attendance levels in the incubation period of 1982 were less than half of those recorded during pre-laying (Fig. 8). This decrease in attendance probably reflects time that breeders spend hidden in their nests while incubating. It may also result from the decreased levels of courtship and other colony-based social behaviour after the beginning of laying.

In 1983, attendance in relation to breeding population was much higher than in 1982. This was undoubtedly related to the failure of many birds to breed in the central part of Pitsulak City. This had the effect of reducing the breeding population, at the same time as increasing the number of birds with free time to spend at the colony.

To summarize, the breeding biology data presented in this chapter suggest that guillemots at Nuvuk generally encounter feeding conditions which are typical for the species across its range. The 1983 season on Pitsulak City was, however, aberrant because part of the colony failed to reproduce following visitation by an ermine, and the consequent reduction in demand for food may have increased food availability.

PART 2 - FORAGING ECOLOGY: CHICK FOOD

INTRODUCTION

Although colonial breeding in seabirds is due, at least in part, to the need to choose sites devoid of mammalian predators (Lack 1967), the size and pattern of dispersion of colonies are related to feeding habits. As Ward and Zahavi (1973) pointed out, birds that feed inshore close to their colonies should have less difficulty finding their prey than offshore-feeders, which must find food far from the colony and often far from landmarks. These authors argue that information transfer may be an important role of seabird colonies, and that the large colony size typical of offshore feeding seabirds (Lack 1967) can be explained by the requirement for a large number of birds to indicate the location of prey concentrations by the formation of continuous streams of birds between the colony and the feeding site. Conversely, inshore feeders are able to breed in small colonies which are close to the food source, because foraging area is smaller and only a small number of birds is needed to maintain contact with prey locations.

Using a geometric model, Waltz (1982) predicted that the use of colonies as information centres will be most common in species which feed far from the colony. In addition, Erwin (1978) predicted that colony size should be positively correlated with both the tendency of prey to be clumped and mobile, and with the gregariousness of feeding activity. The rationale for this is that a large colony provides more sources of information on mobile schooling prey than a small one, and that birds from a large colony should more often use social cues to

find such prey.

Diamond (1978) offered an alternative view to colony size regulation. He proposed that the larger colony sizes of offshore-feeders may be due to the larger feeding areas, and consequently greater resource bases, that offshore feeders exploit. This hypothesis does not necessarily exclude the role of social effects in influencing colony size; both may play a role.

Black Guillemots are well known as small-colony nesters which feed in inshore waters (Brown et al. 1975). If colony size and feeding distance from the colony are predictors of feeding strategies, we should expect guillemots to make little or no use of their breeding sites as information centres, and to feed on prey that is dispersed rather than clumped. In this chapter I document selection by guillemots of prey fed to chicks, and compare feeding behaviour and resource characteristics with those predicted above. I also present information on feeding rates and the role of the sexes in providing food, and discuss these findings in light of current views of chick development processes.

METHODS

Data on chick feeding were gathered by watching prey deliveries from blinds at Pitsulak City and Piquliit 5. In 1981, a small portable blind was used on Pitsulak City. Observations were made in Area B (Fig. 2) on 14 August of that year. The blind was then moved to the edge of Areas E and F for the remainder of the season. In 1982 feeding was observed at this site from a larger blind. In 1983 this blind was moved to Area M (Fig. 2) and elevated to give an uninterrupted view of birds leaving the colony. In both 1982 and 1983 this blind was accessed through a 20 m long tunnel made of steel hoops and black plastic, which allowed observers to enter the blind without being seen by the birds.

Feeding was observed at Pitsulak for 28.8 h, 136.1 h, and 113.1 h in 1981, 1982, and 1983, respectively. Observations at Piquliit in 1983 covered 23.8 h. Observers recorded the time and the recipient nest for each prey delivery, and when possible also recorded prey species, estimated prey length, and the identifying colour pattern of the delivering adult. In 1983, a second observer visually followed birds which were leaving the colony after having delivered a prey item to the nest. The following information was recorded for the departures: identity and nest of bird, route followed and splashdown site, and time from colony to splashdown.

Fish were identified in the field using Leim and Scott (1966). Identifications were later confirmed by Don McAllister of the National Museum of Natural Sciences. Nomenclature follows Leim and Scott (1966)

and Anderson (1982).

Fish used in energetic determinations were obtained at Pitsulak City in 1982 from guillemots which had been trapped in noose carpets on the way to their nests. Fish were frozen at camp in a propane refrigerator before transfer to Ivujivik, where they were stored in a freezer until they were taken south at the end of the field season.

Energetic determinations were performed at the Canadian Wildlife Service laboratory at the Bedford Institute of Oceanography, Dartmouth, Nova Scotia. Specimens were homogenized in a slurry of water in a blender for 5 - 10 min. The resulting suspension was frozen in an alcohol bath, freeze-dried for 48 h, and then weighed to 1 mg for dry weights. The material was then re-blended for 30 s. Pellets of 10 - 20 mg were made by placing the dried fish in a steel cylinder, and compressing the specimen with a piston driven by a hammer.

Pellets were stored for 48 h with a CaSO_4 desiccant before bombing in a Phillipson microbomb calorimeter (Gentry and Wiegert Ltd., Aiken, South Carolina). Pellets were placed on a platinum pan in the bomb, and secured with platinum wire which was connected to firing electrodes. After 0.1 mL of distilled water was added to the base of the bomb, the unit was pressurized with oxygen to 35 atmospheres and fired. The resulting heat rise was measured by thermocouples in the base of the unit, and recorded on a chart recorder. Energetic values of the specimens were determined by comparing heat production from fish samples to that produced during calibration runs on benzoic acid.

RESULTS

Chick diet

Species composition of chick diet is presented in Table 6. In 1981 I was unfamiliar with prey species, and identified less than one half of observed deliveries. Once learned, prey species were easy to recognize from the blind. In 1982 and 1983 failure to identify was usually due to the observer's attention being diverted to another delivery, or, occasionally, to an excessively rapid entry of the parent into the nest. Thus 1982 and 1983 data should reflect composition of chick prey in an unbiased manner. Observational data from 1981 may be biased because some species may have been more easily recognized than others.

With the exception of two crustaceans (probably decapods) and one squid, all identified items were fish. Diet was dominated by Blenni-idea (blennies), a suborder of benthic, eel-like fishes. This group comprised 91.7% of identified deliveries. Stichaeus punctatus was the most important blenny, followed by Eumesogrammus praecisus and Gymnelus viridis. Minor fish species were benthic sculpins and seasnails, and Boreogadus saida and Ammodytes sp., both of which swim pelagically but may also be found on the bottom.

Prey composition varied among years and sites (Table 6). Non-blenny species were a substantial fraction of identified deliveries at Pitsulak in 1981 and 1982 (14.2% and 11.7%), but dropped to 4% in 1983. At Pigiuliit 5 in 1983, 99.4% of identified deliveries were blennies. Stichaeus punctatus was in all cases the most numerous prey species,

Table 6

Prey items delivered by Black Guillemots to Pitsulak City and Piquillit 5^a.

taxon	Pitsulak 1981			Pitsulak 1982			Pitsulak 1983			Piquillit 1983			total		
	recovered		total	observed		no. % of those identified	observed		no. % of those identified	observed		no. % of those identified	observed		no. % of those identified
	observed	no. % of those identified		observed	no. % of those identified		observed	no. % of those identified		observed	no. % of those identified		observed	no. % of those identified	
Crustacea	1	0.9	0	0	0	0.7	1	0.1	0	0	0	0	0	0	0.1
squid	0	0	0	0	0	0	1	0.1	0	0	0	0	0	0	0.1
<i>Boreogadus saida</i> ^b (Arctic cod)	6	5.2	4	12.5	10	6.8	19	2.8	3	0.7	1	0.6	33	2.3	33
<i>Ammodytes</i> sp. (sand lance)	2	1.7	0	0	2	1.4	1	0.1	4	0.9	0	0	7	0.5	7
Blennioidea (blennies)	6	18.8					172	25.6	117	26.1	19	11.3	314	23.8 ^d	314
<i>Eumesogrammus praecisus</i> (fourline snakeblenny)	21	3.1					0	0	0	0	0	0	1	0.1	1
<i>Lampanyx maculatus</i> (daubed shanny)	17	53.1					309	45.9	197	43.9	126	75.0	649	49.1	649
<i>Stichaeus punctatus</i> (Arctic shanny)	2	6.3					58	8.6	82	18.3	17	10.1	159	12.0	159
<i>Gymnelus viridis</i> (fish doctor)	0	0					55	8.2	35	7.8	5	3.0	95	7.2	95
unidentified Blennioidea	101	87.1	26	81.3	127	85.8	594	88.3	431	96.0	167	99.4	1319	91.7	1319
total Blennioidea															

Table 6 (continued)

taxon	Pitsulak 1981			Pitsulak 1982			Pitsulak 1983			total		
	observed	no. % of those identified	recovered	no. % of those identified	total	no. % of those identified	observed	no. % of those identified	observed	no. % of those identified	no. % of those identified	total
Cottidae (sculpins)	2	1.7	2	6.3	4	2.7	48	7.1	11	2.4	0	63
<u>Myoxocephalus</u> sp.												
unidentified Cottidae	4	3.4	0	0	4	2.7	0	0	0	0	0	4
total Cottidae	6	5.2	2	6.3	8	5.4	48	7.1	11	2.4	0	67
<u>Liparis</u> sp.	0	0	0	0	0	0	9	1.3*	0	0	0	9
(seashell)												
total identified	116		32		148		673		449		168	1438
total items	248		332		280		819		518		171	1788
% identified	46.8		100		52.9		82.2		86.7		98.2	80.4

*frequency of prey classes varies with year-site category ($G=60.2$, $P<.005$). For this test prey items were classed as "pelagics" (Crustacea, squid, Boreogadus, Ammodytes), Blennioidea, and "benthics" (Cottidae and Liparis). Frequency of blennioid species also varies among year-site classes ($G=55.9$, $P<.005$). This test based on Pitsulak 1981 recovered data. Lumpenus maculatus is excluded from the comparison.

may include some Gadus ppac.

^cBlennioidea not identified to species in Pitsulak 1981 observed.

^dBlennioidea percentages in this column calculated using a total of 1322 identified items, which excludes Pitsulak 1981 observed.

comprising 44 - 53% of identified deliveries on Pitsulak. At Pigiuliit 5 in 1983, its representation was 75%.

Feeding in relation to time of day, age of brood, and sex of parent

Feeding rates varied diurnally (Fig. 10). Deliveries were most frequent in the early morning, and declined by roughly one half in the afternoon. Rates peaked again in the evening at Pitsulak in 1981 and 1982 and Pigiuliit in 1983, but not at Pitsulak in 1983.

To examine the diurnal delivery patterns of individual birds, I plotted deliveries against time for days where dawn-to-dusk observations were available. Fig. 11 is a typical example, which shows that deliveries of individual birds may be scattered across the day, or clumped in one or several bouts of repeated feeding. Most of these bouts occur early in the day, accounting for the morning peak in overall feeding rates.

Prey composition is plotted diurnally in Fig. 12 for Pitsulak 1982 and 1983 and Pigiuliit 1983. Species variation was significant on Pitsulak in both years ($G=48.4$, $P<.005$ in 1982, $G=37.9$, $P<.05$ in 1983), but diurnal changes were generally neither large nor repeated between years. One exception to this is the early morning occurrence of Eumegrammus, which was high at both years and sites.

To discover whether chick feeding activities differ between the sites, I plotted proportion of deliveries made by males and females both diurnally and in relation to the age of the brood for Pitsulak 1982 and 1983 (Figs. 13 and 14). The diurnal distribution of sexes of

Fig. 10

Guillemot prey deliveries to the nest in relation to time of day. No data available where abscissa is absent. Based on 492 deliveries in 1981, 633 deliveries in 1982, 518 deliveries for Pitsulak City 1983, and 171 deliveries for Pigiuliit 1983.

Fig. 11

Temporal pattern of chick feeding at five nests on Pitsulak City on 21
August 1983. Each dot indicates one delivery.

21 August 1983

Fig. 12

Diet of Black Guillemot chicks in relation to time of day. Based on 522 deliveries for Pitsulak 1982, 414 deliveries for Pitsulak 1983, and 163 deliveries for Piquliit 1983. Distribution of prey species varies with time of day for Pitsulak 1982 ($G=48.4$, $P<.005$) and for Pitsulak 1983 ($G=37.9$, $P<.05$), but not for Piquliit 1983 ($G=16.5$, $P>.05$).

Fig. 13.

Proportion of food deliveries made by male and female Black Guillemots in relation to time of day. Based on 628 deliveries in 1982 and 505 deliveries in 1983 to Pitsulak City. Distribution of sex of delivering bird differs with time of day in 1982 ($G=13.6$, $P<.025$) but not in 1983 ($G=1.81$, $P>.05$).

Fig. 14

Proportion of food deliveries made by male and female Black Guillemots at Pitsulak City in relation to age of brood. Based on 625 deliveries in 1982 and 506 deliveries in 1983. Distribution of sex of delivering bird independent of age of brood ($G=6.30$, $P>.05$ for 1982; $G=2.32$, $P>.05$ for 1983).

delivering birds varied significantly in 1982 ($G=13.6$, $P<.025$), but the pattern was not repeated the following year ($G=1.81$, $P>.05$). Since only five birds of each sex were observed in each year, it is possible that the observed variation in 1982 was due to individual, rather than consistent sexual, differences.

Proportions of deliveries made by males and females did not differ significantly with age of brood (Fig. 14). Nevertheless the preponderance of male deliveries to newly hatched broods at Pitsulak in 1982 suggests that sex roles might differ during the first four to five days after hatching, when chicks require brooding. The available data suggest that males brood, at least during the day, while females supply food. However this hypothesis must remain tentative given the small sample of eight deliveries to one nest, which is the basis of the initial part of the curve in Fig. 14.

Changes of prey composition with season for Pitsulak 1982 and 1983 and Pigiuliit 1983 are presented in Fig. 15. Prey composition varied significantly over the season on Pitsulak in both years ($G=83.1$, $P<.005$ for 1982, $G=29.3$, $P<.025$ for 1983). At the end of the 1982 season at Pitsulak, Stichaeus increased, and all other species but Eumesogrammus disappeared. No other seasonal trends in composition of the three chief blenny species were apparent, although observations in 1983 ended too early to detect any repetition of the Stichaeus increase of 1982. Numbers of non-blenny species are too low to confirm seasonal changes in abundance, but it may be worth noting that Boreogadus deliveries were concentrated at the beginning of observations at both years and

Fig. 15

Diet of Black Guillemot chicks in relation to season. Based on 522 deliveries to Pitsulak 1982, 414 deliveries to Pitsulak 1983, and 163 deliveries to Piquliit 1983. Distribution of prey species varies seasonally for Pitsulak 1982 ($G=83.1$, $P<.005$) and for Pitsulak 1983 ($G=29.3$, $P<.025$), but not for Piquliit 1983 ($G=0.43$, $P>.05$).

sites.

Provisioning rates and energetics of chick growth

The mean provisioning rate on Pitsulak City in 1982 was 8.04 prey items per chick per day for single chicks, and 8.74 items per chick per day for chicks raised in double broods. In 1983 on Pitsulak City, provisioning rates were 9.05 items per day for single chicks, and 9.04 items per day for double broods. The overall rate for both years and brood sizes was 8.80 feeds per day per chick. Provisioning rates did not vary significantly among years and brood sizes ($F=1.59$, $P>.05$, see Fig. 10 for sample sizes).

Daily provisioning rates are plotted against age of young in Fig. 16. Calculated delivery rates varied from day to day, particularly in 1982 when delivery rates for many days were derived from observation sessions which were only a few hours long. In 1983 most feeding observations lasted from dawn to dusk, and calculated provisioning rates were less variable. Linear regressions of provisioning rate against age of young showed no significant trends for single or double broods in either year (Fig. 16).

I collected fish of the five major prey species from Pitsulak in 1982 for energetic determinations. Unfortunately these fish thawed during transit and dried to about half their weight. Since all specimens were treated in the same way, interspecific comparisons should be valid despite the drying. However, energy densities must be viewed with caution because of the possible loss of volatile lipids.

Fig. 16

Fish delivered per day per chick at Pitsulak City in 1982 and 1983 vs. age of young. Open circles are single broods, solid circles are double broods. For 1982 single broods, $\text{deliveries/day} = 0.076 \text{ age} + 6.33$, $F=0.42$, $P>.05$, from 70 deliveries. For 1982 double broods, $\text{deliveries/day} = 0.041 \text{ age} + 8.50$, $F=0.65$, $P>.05$, from 559 deliveries. For 1983 single broods, $\text{deliveries/day} = 0.17 \text{ age} + 5.39$, $F=1.69$, $P>.05$, from 65 deliveries. For 1983 double broods, $\text{deliveries/day} = -0.014 \text{ age} + 8.82$, $F=0.02$, $P>.05$, from 453 deliveries.

Measured energy density did not vary significantly among species, and showed an overall mean of 21.4 kJ/g dry weight (Appendix 1). Measured densities were similar to those reported for blennies by Bradstreet (1983), Dunn (1975) and Koelink (1972) (using a conversion of 1 kilocalorie = 4.190 kJ).

In Fig. 17 I plot lengths of delivered fish (all species) as estimated from the blind, vs. age of brood. Estimated length increased significantly in both 1982 and 1983. The length-age relation was linear during most of chick-rearing, but chicks under five days received fish which were on the average smaller than those predicted by the regression.

Mean estimated lengths for each of the five major prey species are presented in Table 7. Mean length within species did not vary significantly by year or by site. Using length-weight regression equations derived from fish taken at Pitsulak City, I calculated weights from the estimated lengths of each fish observed, and their energy values, based on the mean energetic density of 21.364 kJ/g dry weight of fish. Means of these values for the various species vary widely; Eumesogrammus praecisus, the largest of the prey species, had nearly double the mean weight and energy content of Boreogadus saida (Table 7). Stichaeus punctatus, although similar in length to Eumesogrammus, was lighter, and contained less energy.

Weight and energy contributions of the five major prey species are plotted in Fig. 18. Because seasonal variation in composition of prey species, although significant, showed no strong and consistent trends

Fig. 17

Estimated lengths of fish delivered to Black Guillemot nests at Pitsulak City in 1982 and 1983 vs. age of young. Solid dots are means, vertical bars are standard deviations, and crossbars are standard errors. Open circles indicate a sample size of 1. From 541 deliveries in 1982 and 441 deliveries in 1983.

Table 7

Length-weight relations and estimated mean weight and energetic content of fish prey.

species	fish measured				fish observed							
	n	regression equation: weight=	year	site	n	estimated length (mm)			calculated weight (g) ^b		calculated kJ/fish ^c	
						$\bar{x}$	SD	F ^a	$\bar{x}$	SD	$\bar{x}$	SD
<u>Boreogadus</u>	6	0.000000721	1982	Pit	12	111.7	30.4		10.8	8.6	60.1	47.9
<u>salda</u>		x L 3.45	1983	Pit	3	80.0	20.0		3.1	2.4	17.3	13.4
			1983	P1q	1	80.0			2.7		14.7	
			both	both	16	103.8	30.5	1.78	8.7	8.2	49.2	45.6
<u>Eumesogrammus</u>	12	0.000000107	1982	Pit	146	134.0	16.5		17.6	6.9	97.4	38.4
<u>praecisus</u>		x L 3.38	1983	Pit	115	133.0	15.1		17.0	6.6	94.3	36.6
			1983	P1q	18	131.7	18.6		16.8	7.7	93.1	42.7
			both	both	279	133.5	16.0	0.35	17.3	6.8	95.9	37.9
<u>Stichæus</u>	32	0.000000168	1982	Pit	249	133.9	16.4		13.1	5.0	72.7	27.8
<u>punctatus</u>		x L 3.23	1983	Pit	187	137.1	18.0		14.3	6.2	79.2	34.6
			1983	P1q	120	137.2	23.8		14.9	8.6	82.8	48.2
			both	both	556	135.7	18.8	1.34	13.9	6.4	77.1	35.5
<u>Gymnelus</u>	8	0.000000453	1982	Pit	45	149.8	22.9		10.0	4.3	55.3	23.7
<u>viridis</u>		x L 2.9	1983	Pit	80	164.5	44.4		14.9	11.9	82.5	66.3
			1983	P1q	17	156.5	51.8		14.1	16.6	78.1	92.0
			both	both	142	158.9	40.2	1.85	13.2	11.0	73.2	61.3
<u>Myoxocephalus</u>	7	0.00000141	1982	Pit	43	95.6	17.6		10.0	4.9	55.8	27.4
<u>sp.</u>		x L 2.94	1983	Pit	11	102.7	15.6		12.0	4.7	66.7	26.4
			both	Pit	54	97.0	17.3	1.50	10.5	4.9	58.0	27.3

Table 7 (continued)

^a all comparisons between sites and years within species are non-significant ($P > .05$).

^b weights are calculated from estimated lengths of observed fish according to the regression equation for each species. Since this method assumes that lengths were estimated in the field without error, the indicated standard deviations are less than those which would be produced if error of length estimates were included.

^c based on 21.364 kJ/g dry weight (Appendix 1), and 74% water content (mean of several benthic fish species; Dunn 1975). Since calculated energetic contents are a simple multiple of estimated weights, their indicated standard deviations are also less than those which would be produced if error of length estimates were considered.

Fig. 18

Estimated daily weight and energy contribution of fish species delivered to Black Guillemot chicks. Based on estimated weights of fish of each species brought to Pitsulak City in 1982 and 1983. Energy density assumed constant across species at 5.55 kJ/g wet weight. See text for details of derivation.

(Fig. 15), I assume in this analysis that prey composition was constant over chick-rearing. The contribution of each species was based on weights calculated from estimated lengths, using lumped data from Pitsulak City 1982 and 1983. The weights of each species were scaled up according to the representation of each species in total diet (Table 6), taken as a proportion of the overall mean of 8.80 feeds per chick per day (assumed to be constant over the season).

Estimated daily food deliveries rose from 80-85 g for chicks a few days old to peak at 140 g for 25 d old chicks (Fig. 18). Weight of deliveries gradually declined from this peak until fledging. Young chicks received much more food in proportion to their body weights than older chicks. Chicks under five days received more than their own weight in food daily, whereas 25 day old chicks received about one half of their weight in food (Figs. 7 and 18).

The three species of blennies accounted for most of the food delivered to chicks, which reflects both the numerical dominance and the larger size of this group. Most of the rise in estimated weight of fish delivered was due to increasing lengths of Stichaeus punctatus, whose daily contribution increased from 42 to 74 g over the period analysed. Sizes of Eumesogrammus and Gymnelus varied little, except in the week prior to fledging when a decline in the size of Eumesogrammus was responsible for the pre-fledging reduction in overall food deliveries.

Foraging behaviour while feeding chicks

This section is based on observations of guillemots which left Pitsulak City or Pigiuliit 5 in 1983 after delivering a prey item to a nest. I assume for present purposes that these departing birds were primarily concerned with procuring another item of chick food, although this assumption was probably not valid in all cases.

Sites where departing birds splashed down are indicated in Figs. 19 and 20. All destinations of birds seen leaving Pitsulak were south or east of the island, but this may not reflect activities of birds of this colony as a whole. Guillemots were frequently encountered on the water northeast of Pitsulak (Part 3); these birds presumably came from the central and eastern parts of the colony where no feeding observations were made.

Guillemots frequently left the colony in groups of two or three. Although birds sometimes stayed close to each other for a kilometre or more, birds which left the colony together were never seen to splash down at the same destination (i.e. in the same binocular field of view). Members of a group would either separate in the air before splashdown or one bird would go to the water while others continued flying.

Mean colony to splashdown distances were similar for the two sites ($\bar{x}=677$ m, $SD=528$, $n=58$ for Pitsulak; $\bar{x}=686$, $SD=370$, $n=15$ for Pigiuliit). However, guillemots are generally known to be shallow water feeders, so analysis of destinations of departing birds must take water depth into account. A comparison of availability of depth zones vs.

Fig. 19

56 sites where Black Guillemots from Pitsulak City were observed to splash down in 1983. Each symbol represents 1 splashdown. Open triangles indicate splashdowns on 9 August, solid triangles 15 August, open squares 20-21 August, and solid squares 25-29 August.

Fig. 20

14 sites where Black Guillemots from Pigiuliit 5 were observed to splash down, 17-27 August 1983. One splashdown occurred outside the southern edge of the map.

frequency of their use indicated that depth choice was non-random ($G=45.0$, $P<.005$, Fig. 21), and that water deeper than 50 m was avoided.

Fig. 22 plots splashdown rates per unit area of the most frequently used habitat between 10 and 40 m depth for four periods during August 1983 at Pitsulak City. Birds tended to visit areas up to a certain distance after which visitation rates dropped to low levels. If the maximum regular foraging range is considered to be the largest annulus with a visitation rate at least one third as great as that of the annulus which is visited most intensively, then maximum regular foraging ranges were 0.25 km, 0.5 km, 0.5 km, and 2 km for the four time periods given in Fig. 22. This change in maximum range with date was not statistically significant (Kendall rank correlation coefficient = 0.913, $P=.08$).

On the assumption that food items brought later to the colony were obtained at the initial splashdown site, I calculated correlation coefficients between splashdown distance and estimated weight of prey that was subsequently delivered, for four time periods in 1983. Prey weights were estimated from length-weight regression formulas (Table 7). No correlations between distance and estimated weight were significant (for 9 August $n=13$, $r=0.35$; for 15 August $n=10$, $r=-0.21$; for 20-21 August $n=10$, $r=-0.35$; for 25-29 August $n=6$, $r=-0.15$; all $P's>.05$).

In some cases the assumption that birds stayed at their initial splashdown site until a chick food item was obtained was proven by following birds continuously from departure to their subsequent return.

Fig. 21

Depth preferences of Black Guillemots from 56 birds followed from Pitsulak City to splashdown in August 1988. A) Frequency of use of depth zones compared to area of zones within 2 km of the colony. B) Number of splashdowns in each depth zone divided by the area of that zone within 2 km of the colony. Frequency distribution of depth zones used differs from that which would be expected if use were proportional to area ($G=45.0$, $P<.005$).

Fig. 22

Number of Black Guillemots splashing down on the water per km² of habitat between 10 and 40 m depth vs. distance from the colony. Data from Pitsulak City 1983. Note differing ordinal scales.

But more often, birds were lost among the waves or confused with other birds soon after splashdown. In some of these cases birds may have changed locations before finding prey to deliver to the nest.

DISCUSSION

Feeding strategies

No evidence was found that Black Guillemots at Nuvuk made use of the behaviour of other birds to locate food for their chicks. This finding is consistent with the prediction that the need to use colonies as information centres and the tendency to feed in groups decline with decreasing colony size (Ward and Zahavi 1973, Erwin 1978, Waltz 1982).

In a comparison of six tern species, Erwin (1978) found that median colony size was positively correlated to distance from foraging area and gregariousness while feeding. However, unlike guillemots, all of the terns foraged in groups at least some of the time. The complete independence of guillemots while foraging for their chicks can be explained by the sedentary and non-schooling behaviour of blennies which are the major part of chick diet. Using the terms of Waltz' (1982) geometric model, the non-aggregated blennies are each a patch. Except under conditions of extraordinarily low prey density, mean inter-patch distance will be far less than twice the mean patch-central place distance, and solitary prey searching is thus expected (Waltz 1982). Of course, before a search is begun the guillemot must choose the general area in which to forage. Because blenny distributions and densities do not change rapidly, the bird's experience is an adequate guide to suitable foraging sites.

Although Black Guillemots feed solitarily, and their benthic prey has no marked activity cycle during the daylight period (J.M. Green pers. comm.), guillemots concentrate chick feeds and colony attendance

in the morning. If guillemots used social cues to locate foraging areas the morning should be the time that tracking of successful feeders, to the foraging ground should be in evidence. That no such behavior was seen suggests that the morning activity peaks serve other, perhaps social, needs.

Black Guillemots in the Nuvuk area fed their young largely on blennies. These fish have several advantages as prey for guillemot chicks, in comparison with Boreogadus and sculpins which are the main alternative prey. Blennies are larger than Boreogadus, and sculpins (Table 7), they lack the stiff spines and fins of sculpins, they are slender and hence easier to swallow than other fish of similar weight (Swennen and Duiven 1977), and they are abundant on shallow seafloors in the Nuvuk area (J.M. Green pers. comm.). Chick diet at Piquiliit 5 and Pitsulak in 1983 was nearly entirely blennies (Table 6). The higher proportion of blennies in this year at these sites may reflect a greater prey selectivity in favourable feeding conditions, as predicted by Orians and Pearson (1979). Blenny availability was probably higher around Pitsulak in 1983 than in preceeding years, because the number of chick-feeding birds was greatly reduced in that year (see Part 1), and availability around Piquiliit may be typically higher than around Pitsulak because the former is a much smaller colony. Additional evidence for a better food supply at Pitsulak in 1983 was the higher pre-fledging weights recorded in that year, despite the absence of evening feeding peaks.

In the present study no evidence was found to support Orians and

Pearson's (1979) prediction that weight (or energy value) of prey should increase with distance from which it was procured. Lessells and Stephens (1983) have recently argued that the Orians-Pearson model is flawed when it deals with single prey loaders, and that such predators ought to be unselective up to a certain critical travel time. Their formula is

$$\text{critical travel time} = \frac{\text{expected search time when unselective} \times \text{minimum prey value available}}{\text{mean prey value} - \text{minimum prey value available}}$$

Minimum and mean prey values can be calculated from size frequency distributions of fish taken by divers in the channels around East Nuvuk Island (J. M. Green, pers. comm.). For minimum and mean lengths of 117 and 134 mm, calculated weights for Stichaeus punctatus are 8.1 and 12.5 g. If an unselective forager could take a prey in a conservatively estimated 180 s, critical travel time would be 328 s and critical range would be 2361 m (assuming flight speed of 14.4 m/s). Even if an unselective guillemot could capture a blenny in 90 s, which is improbably short, critical range would be over 1 km. Thus, in the range over which most chick prey is procured, any trend of prey size with procurement distance would be weak and probably non-detectable.

Black Guillemots in other areas also depend on benthic fishes, usually blennies, for food for their young (Winn 1950; Preston 1968; Cairns 1981; Petersen 1981; Bergman 1971, 1978; Asbirk 1979; Slater and Slater 1972). Most studies also report a small pelagic component of chick diet. At Nuvuk Boreogadus and Ammodytes were the only prey that

regularly swim in pelagic schools (Quast 1974, Meyer et al. 1979, Craig et al. 1982). Guillemots are clearly capable of catching fish in mid-water; on 9 August 1983 I saw a guillemot surface with a fish after a 6 s dive in 12 m of water. However, given the general preponderance of blennies in chick diets, such captures more likely result from chance encounters than active search strategies. Such fish would not necessarily be returned to the colony if larger blennies were locally abundant.

Guillemots searching for prey for their chicks choose bottom habitat of depth less than 40-50 m, within about 2 km of the colony. Other studies (Bergman 1971, Preston 1968, Asbirk 1979, Peterson 1981, Slater and Slater 1972) have noted shallow-water feeding close to the colony, but gave poorly defined travel limits and did not describe the availability of deeper waters close to the colony. The deep water adjacent to Pitsulak City had abundant schooling organisms close to the surface (seen on echo-sounder traces) which attracted large flocks of Thick-billed Murres. That guillemots did not join these flocks indicates a strong loyalty to their benthic shallow-water feeding habitat.

Feeding energetics

Total energy intake of nestling birds typically rises after hatching to a maximum, which occurs after the midpoint of the nestling period (Dunn 1980). Gaston (in press) and Fagerstrom et al. (1983) have independently proposed that food intake is initially limited by the physiological capacity of the young to make use of the food, but

that the foraging capacity of the adults later becomes limiting. At this stage food intake can provide for maintenance energy only and growth ceases. Estimated food intake of guillemots at Pitsulak City in 1982 and 1983 rose to a peak at 25 d, to be followed by a slight decline (Fig. 18). At about the same time, chick weight growth also slowed (Fig. 7). Although chicks gain little weight in the days prior to fledging, other important processes continue, including increase in wing length (Fig. 6) and tissue maturation with concomitant water loss (Koelink 1972).

Black Guillemot chicks at the Nuvuk Islands appear to be well fed in comparison with guillemot chicks elsewhere and chicks of other alcids of similar body size. My estimated feeding maximum was 140 g of food per chick per day, containing about 800 kJ of energy, and Asbirk (1979) estimated a maximum feeding rate of 133 g per chick per day. These values contrast with that of Koelink (1972), who reported a maximum of 100 g (500 kJ) delivered daily to Pigeon Guillemot chicks. However, these figures must be interpreted with caution, because of problems in accurately measuring feeding rate, load size, and energy content. My own study is subject to the uncertainty of energetic determinations due to weight loss of samples during transportation. If energetic densities given by Dunn (1975), Koelink (1972) and Bradstreet (1983) (two values) for blennies were used, my maximum feeding rate would become 820, 700, 775, and 932 kJ per day, respectively. Spot checks showed that length estimations of delivered fish were usually accurate within 1 cm. But since the power function increases weight

sharply with length, small biases in length estimations could lead to substantial error in estimated fish weights. For example, if a 130 mm Stichaeus weighing 11.3 g was overestimated to be 140 mm long, its calculated weight would increase to 14.4 g, an error of 27%.

Koelink (1972) also used feeding frequencies and fish lengths to estimate food intake, but his lengths were measured from photographs taken by an automatically triggered camera. These lengths might thus be more accurate than mine, but his data suffer from the problem that blennies could not be identified to species from the photographs, and inappropriate length-weight equations might therefore have been used. Asbirk (1979) estimated food intake from feeding frequencies and weights of fish found at the nest. This method also has problems, because food items found at the nest may have been rejected by the chicks because they were too large to swallow. Thus resulting calculations of food intake would be overestimates.

Despite these methodological problems, it is clear from my study and the two mentioned above that guillemots alter the amount of food brought to chicks over the season. This may be done by changing the feeding rate (Petersen 1981, Slater and Slater 1972) or by changing the size of prey items brought (Asbirk 1979, Petersen 1981, Koelink 1972, Winn 1950, present study). In general, prey items delivered to nestlings in the Nuvuk Islands were larger than those reported elsewhere. The common blennies of the present study had mean weights of 13-17 g (Table 7), whereas weights from other studies were about 8 g (Petersen 1981), 4-7 g (Koelink 1972), and 12 g (Asbirk 1979).

Guillemots are the sole inshore feeders among the Atlantic Alcidæ, and contrast with the typical offshore-feeding members of the family in their larger clutch size, greater colony dispersion, and smaller colony size (Lack 1967). The material presented in this chapter also shows that guillemots differ from offshore-feeders in important features of chick provisioning and development patterns. The Atlantic Puffin (Fratercula arctica), being the Atlantic alcid closest in body size, is an appropriate example for comparison. Puffin young have lower growth rates (Gaston in press) and lower food intakes than those measured for guillemot young (Harris and Hislop 1978, Ashcroft 1979, Koelink 1972, this study), although puffin parents raise only one chick. Food intake and maximum weights of young puffins are also highly variable among years and sites compared to those of guillemots (Harris and Hislop 1978, Koelink 1972, this study).

These differences are explained by the shorter foraging distances of guillemots which their small colony size permits, and by their dependence on predictable benthic, rather than mobile schooling, prey. These differing patterns of inshore-feeding guillemots and their offshore-feeding relatives lead to an additional generalized difference between the two groups, based on sensitivity to risk of food shortage (Stephens 1981, Caraco et al. 1980). By virtue of their stable food supply, Black Guillemots are "risk-adverse", while offshore feeders which depend on unpredictable prey are "risk-prone".

PART 3 - FORAGING ECOLOGY: ADULT FOOD

INTRODUCTION

Black Guillemots have fewer constraints on the choice of food they eat themselves than on food delivered to chicks, because adult food does not have to be transported to the colony. Breeding guillemots are nevertheless subject to the important constraint that they may only visit their foraging areas, not reside there. This applies in time-scales of seconds, because of the requirement to come to the surface to breathe, and in time-scales of hours, because of the need to return to the colony and attend to breeding duties. Other factors being equal, one might expect that feeding sites would be progressively less favoured at greater distances below the surface, and at greater distances from the colony.

Bradstreet (1979, 1980) has documented the use by Black Guillemots of arctic ice edges, but little information is available on guillemot foraging in open water. The purpose of this section is to describe what adult Black Guillemots of the Nuvuk area eat and where they find it, and to explain observed choices of prey and foraging area. Particular attention is paid to selection of water depth and distance from the colony and the habitat preferences of prey species.

METHODS

Digestive tracts of birds killed for diet analysis were drenched with 70% ethanol upon collection. Within several hours, the birds were weighed, standard measurements were taken, and stomachs were removed and stored in 70% ethanol. Percent fullness of stomachs was visually estimated on dissection.

Fish remains were primarily identified by comparing otoliths to scanning electron micrographs of otoliths of known origin. No studies of otolith retention in guillemot stomachs have been performed. However, most otoliths disappear from murre (Uria spp.) stomachs a few hours after ingestion, with a small fraction persisting up to 24 h (Uspenski 1956, Sanford and Harris 1967, Bradstreet 1980). Crustaceans were identified with the help of Diane Laubitz of the National Museum of Natural Sciences.

The distribution of Black Guillemots on the water was recorded in 1982 and 1983 from an inflatable boat which was run at constant throttle along fixed routes. The boat was kept about 40 m from land or ice during coastal transects, except where shallow water impeded navigation. Open water transects were run in straight lines between landmarks, except for the route between Aulassivik Point and Aulassivik Bank. On this transect the boat followed a compass bearing until the prominent hills of Kingituayu and Aupilutu Islands came into line. Total transect coverage was 1358.3 km for the two years.

Transect information was recorded on a tape recorder. All guillemots seen on the water between 60° to the right or left of the line of

travel were recorded. The distance limit for inclusion of sightings was the distance at which guillemots could be reliably distinguished from murres, about 125 m. For each sighting, time from the start of the transect, number of birds, and presence/absence and colour of leg streamers were recorded.

For purposes of analysis, transects were divided into 100 m segments. The depth at the midpoint of each segment was measured from echo-sounder tracings. Sighting times were converted into locations assuming a constant travel speed, and assuming that birds were 50 m ahead of the boat when recorded.

Weights and measures were taken of both collected and captured adult guillemots. Whole birds and pectoral muscles were weighed on a triple beam balance. Other measurements were made with vernier calipers and flat steel rulers as appropriate.

RESULTS

Adult diet

Stomach contents of the 76 guillemots collected are listed in Appendix 3. Since stomachs of birds collected at or near colonies were empty or nearly so, analysis is limited to stomachs of the 68 birds collected on their presumed feeding grounds.

Breeders and non-breeders contained similar spectra of food remains (Table 8). Fish remains were present in stomachs of 95.7 and 95.5% of breeders and non-breeders, respectively. Most fish material was bones, bits of flesh, and small otoliths which could not be identified. Of identified fish, Boreogadus saida and Stichaeus punctatus appeared most frequently. Most stomachs containing fish remains had evidence of the presence of one to several individuals, although two exceptional stomachs of non-breeders contained 200 and 460 small otoliths, and must have had at least 100 and 230 individual fish. Fish larvae were found in three stomachs, and egg masses in two stomachs.

Lengths of Boreogadus were estimated from an equation regressing body and otolith length (Appendix 3). Mean of the estimated lengths from the 18 stomachs containing measurable Boreogadus otoliths was 114 mm. Using the length-weight formula given in Table 7, a fish of this length would weigh 9.0 g. Most of the numerous small unidentified otoliths presumably came from fish much smaller than this, because the stomachs containing large numbers of small otoliths could hardly have accommodated corresponding numbers of medium or large fish.

Crustaceans were represented in 56.5 and 54.5% of stomachs of

Table 8

Minimum numbers of prey items in stomachs of 22 non-breeding and 46 breeding Black Guillemots.

prey taxon	number (and %) of stomachs containing given numbers of items					mean number of items of a taxon/stomach		
	≥1	0	1-4	5-9	10-49	≥50	for stomachs containing taxon	for all stomachs
<u>Non-breeders</u>								
<u>Fish</u>								
<u>Boreogadus</u>	8 (36.4)	14 (63.6)	4 (18.2)	3 (13.6)	1 (4.5)	0 (0)	4.1	1.5
<u>saia</u>								
<u>Eumesogrammus</u>	2 (9.1)	20 (90.9)	2 (9.1)	0 (0)	0 (0)	0 (0)	1.5	0.14
<u>praciscus</u>								
<u>Stichæus</u>	4 (18.2)	18 (81.8)	4 (18.2)	0 (0)	0 (0)	0 (0)	1.3	0.23
<u>punctatus</u>								
<u>unidentified</u>	15 (68.2)	7 (31.8)	11 (50.0)	0 (0)	2 (9.1)	2 (9.1)	26.9	18.3
<u>all fish</u>	21 (95.5)	1 (4.5)	12 (54.5)	4 (18.2)	3 (13.6)	2 (9.1)	21.1	20.2
<u>Crustaceans</u>								
<u>Mysidae</u>	3 (13.6)	19 (86.4)	2 (9.1)	0 (0)	1 (4.5)	0 (0)	6.0	0.82
<u>Amphipoda</u>	9 (40.9)	13 (59.1)	6 (27.3)	2 (9.1)	0 (0)	1 (4.5)	16.6	6.8
<u>Decapoda</u>	1 (4.5)	21 (95.5)	1 (4.5)	0 (0)	0 (0)	0 (0)	2.0	0.09
<u>unidentified</u>	3 (13.6)	19 (86.4)	0 (0)	0 (0)	2 (9.1)	1 (4.5)	32.7	4.5
<u>all Crustaceans</u>	12 (54.5)	10 (45.5)	4 (18.2)	3 (13.6)	3 (13.6)	2 (9.1)	22.3	12.18
<u>Polychaetes</u>	7 (31.8)	15 (68.2)	6 (27.3)	1 (4.5)	0 (0)	0 (0)	2.6	0.82
<u>Gastropods</u>	3 (13.6)	19 (86.4)	1 (4.5)	2 (9.1)	0 (0)	0 (0)	4.7	0.64

Table 8. (continued)

prey taxon	number (and %) of stomachs containing given numbers of items					mean number of items of a taxon/stomach	
	>1	0	1-4	5-9	10-49	>50	for all stomachs containing taxon
<u>Breeder</u>							
<u>Fish</u>							
<u>Boreogadus</u>	15 (32.6)	31 (67.4)	10 (21.7)	4 (8.7)	1 (2.2)	0 (0)	3.5
<u>salda</u>							1.1
<u>Eumegarrhinus</u>	5 (10.9)	41 (89.1)	5 (10.9)	0 (0)	0 (0)	0 (0)	1.2
<u>praeceus</u>	13 (28.3)	33 (71.7)	13 (28.3)	0 (0)	0 (0)	0 (0)	1.3
<u>punctatus</u>	30 (65.2)	16 (34.8)	28 (60.9)	0 (0)	2 (4.3)	0 (0)	2.3
unidentified	4 (95.7)	2 (4.3)	35 (76.1)	5 (10.9)	4 (8.7)	0 (0)	3.1
<u>all fish</u>							
<u>Crustaceans</u>							
<u>Mysidae</u>	14 (30.4)	32 (69.6)	5 (10.9)	2 (4.3)	6 (13.0)	1 (2.2)	23.1
<u>Amphipoda</u>							
<u>Decapoda</u>	8 (17.4)	38 (82.6)	6 (13.0)	1 (2.2)	1 (2.2)	0 (0)	5.0
unidentified	5 (10.9)	41 (89.1)	5 (10.9)	0 (0)	0 (0)	0 (0)	2.2
<u>all Crustaceans</u>							
<u>Polychaetes</u>	7 (15.2)	39 (84.8)	6 (13.0)	0 (0)	0 (0)	1 (2.2)	15.4
<u>Gastropods</u>	26 (56.5)	20 (43.5)	12 (26.1)	5 (10.9)	7 (15.2)	2 (4.3)	18.6
unidentified	12 (26.1)	34 (73.9)	10 (21.7)	2 (4.3)	0 (0)	0 (0)	2.7
<u>all Polychaetes</u>							
<u>Gastropods</u>	5 (10.9)	41 (89.1)	3 (6.5)	1 (2.2)	0 (0)	1 (2.2)	17.6

number of fish or polychaete items = number of otoliths or jaws/2, rounded up to the nearest individual.

breeders and non-breeders, respectively. Mysids (probably all Mysis spp.) were the most numerous identified crustaceans. Amphipods were slightly less numerous and were represented by at least six genera and seven species. Decapods were also diverse (at least four species) but less common; only 12 individuals were found in the the combined sample of 68 stomachs.

Polychaete mandibles were found in 26.1% of breeders' stomachs and 31.8% of non-breeders' stomachs. No Polychaete remains other than mandibles were ever identified. Gastropods were represented in stomachs by shells and opercula, which were present in 10.9% of breeders' stomachs and 13.6% of non-breeders' stomachs. Other items occasionally found in stomachs were pebbles, pieces of algae, and small, unidentified worms.

At the beginning of each season, some birds were shot near ice. Seven of the eight birds collected near ice in 1981 and 1982 had stomach contents dominated by Boreogadus. In the eighth, a female with a fully developed egg, stomach contents were mostly snail remains. The dominance of Boreogadus in collections made near ice was not repeated in 1983. Five of the six birds shot near ice in 1983 had both fish and crustacean remains, and only one of these had recognizable Boreogadus otoliths. One of the six birds contained only amphipods.

Distribution while foraging

Use of ice edges. Casual observations in all years suggested that guillemots concentrate along edges of landfast ice. On 27 June -1

July 1983 I quantified guillemot use of ice edge habitat with transects along the mainland coast between Ice Harbour and Nuvuk Point, and in Nuvuk Harbour (Figs. 23-25). By late June of this year free ice in the area was restricted to scattered floes, so open water habitat was also available for guillemot foraging. On 27 and 29 June, guillemots were abundant along the ice edge that formed the inner boundary of Nuvuk Harbour (Fig. 23). Sightings of guillemots on the water totalled 174 and 225 birds for these days respectively. By 1 July a channel had opened through the ice, but birds were still abundant along its edges (Fig. 24). Two hundred sixty-five guillemots were recorded on the water on that day.

On 24 June 1983 I noticed many guillemots along the ice edge across the entrance to Ice Harbour. By 28 June, the ice edge had retreated deep into the harbour and transects conducted then and the following day recorded only a few birds (Fig. 25). Use of ice edges at the entrances to the channel between Aupilutu Island and the mainland persisted slightly longer. I recorded 6 and 30 birds at the southern end on 28 and 29 June, and 32 and 35 birds at the northern end on 29 June and 1 July. Landfast ice throughout the general area disappeared in the first few days of July, and no further concentrations of birds at these sites were noted.

Birds foraging along the mainland ice edges presumably included some from Pitsulak City. Nine guillemots were marked with streamers on Pitsulak City up to 29 June 1983, and one of these was seen at the ice edge between Aupilutu and Nuvuk Point on this date. It is less clear

Fig. 23

Mean sighting frequencies of Black Guillemots along ice edges in Nuvuk Harbour from surveys on 27 and 29 June 1983. The transect route is the line paralleling the Nuvuk Harbour ice edge. Where histogram columns are absent along this line, no birds were sighted.

Fig. 24

Distribution of Black Guillemots along ice edges in Nuvuk Harbour, 1
July 1983. See explanation in Fig. 23.

Fig. 25 .

Coastal distribution of Black Guillemots from Ice Harbour to Nuvuk Point, 28 June - 1 July 1983. Sighting frequencies averaged from one complete survey and two partial ones. Partial surveys ran from the south side of Ice Harbour to the southern tip of Aupilutu Island, and along the ice edge between Aupilutu Island and Nuvuk Point. See explanation in Fig. 23.

whether Pitsulak birds used the ice edges of Nuvuk Harbour. No streamered birds were seen there, but this may have been due to the low number of marked birds early in the season. Since only a few pairs of guillemots breed around Nuvuk Harbour (Gaston et al. in press), most of the birds using the ice edge there must have come from elsewhere. The majority of these birds were presumably breeders, since 10 of 11 birds shot there early in the 1982 and 1983 seasons had brood patches. Some of these birds may have come from the North Skerrie Fairway Island, or Digges Sound. However, the colonies at Pitsulak City and Green Island are more populous and just as close (Gaston et al. in press), and so may well have contributed many of the birds utilizing the Nuvuk Harbour ice edge.

Use of open water. Open water transects were run between Boulder Point and Kingituayu Island (the Nuvuk area) in 1982. In 1983 these transects were repeated and the network extended south of Kingituayu (the Aulassivik area). Guillemot distributions in these areas are summarized in Figs. 26 and 27. Transect lengths, schedules, and guillemot distribution maps for short time periods are given in Appendix 4.

Guillemots were distributed across most of the area sampled, with all areas regularly used except for waters beyond the 40 m contour and the area south of Aulassivik Point. Generally they did not form concentrations on their feeding grounds; the area near Boulder Cove on West Nuvuk Island is an exception. A mean of 3.6 birds was recorded within 200 m of the end of the transect running from Pitsulak City to

Fig. 26

Distribution of Black Guillemots in the Nuvuk area. Straight lines are transect routes. Sighting frequencies are averaged from surveys 22 June - 7 September 1982 and 21 June - 27 August 1983. See Appendix 4 for survey schedules.

Fig. 27

Distribution of Black Guillemots in the Aulassivik area. Sighting frequencies are averaged from surveys 21 June - 27 August 1983. See Appendix 4 for survey schedules.

Boulder Cove. Concentrations of birds also occurred near colonies.

In order to examine choice of water depth more closely, I plotted sighting frequencies against depth for zones of various distance from Pitsulak City (Fig. 28). To avoid including birds loafing near their breeding sites, I exclude sightings of birds within 200 m of a colony from this and subsequent analyses. Guillemots occurred consistently in waters of 10 to 30 m depth. Areas less than 10 m deep were used in the three zones closest to Pitsulak City, but no birds were recorded in this depth category in the two most distant zones. Few guillemots were sighted in waters deeper than 40 m in the two closest zones. Beyond 4 km from the colony the transects did not cover enough deep water to test preference for this habitat.

In 1982 and 1983 guillemots from all parts of Pitsulak City (except area N in 1982, Fig. 2) were marked with streamers, which could be easily seen on transects as birds were flushed by the boat. Birds given streamers were all known breeders except a few which were caught early in the season before the brood patch had developed. If distribution of Pitsulak City guillemots on their foraging areas is similar to the distribution of guillemots as a whole, then the proportion of birds sighted on transects that carried streamers should be approximately uniform in all areas, and not vary with distance from the colony. Since patterns of foraging distance from the colony did not vary systematically with season (see below), the proportion of streamered:unstreamered birds, from data summed over each season, should be independent of the number of birds carrying streamers. Numbers of

Fig. 28 .

Number of Black Guillemots seen on the water per 100 m of transect in relation to depth, for five distance categories from Pitsulak City. Numbers of 100 m transect segments run in each depth-distance category are given at base of columns. No data available where abscissa is absent.

streamered birds could not be determined for any given time because of gradual streamer loss.

Streamered birds were represented in all transect areas except the vicinity of the South Skerries (Figs. 26 and 27). Guillemots were regularly seen around the Skerries, but were apparently all attached to colonies there. The proportion of marked guillemots showed no consistent trend with distance from the colony (Fig. 29), suggesting that transect sightings approximately reflected the distribution of Pitsulak City guillemots in areas other than the South Skerries.

The transect network used in 1983 probably covered most of the area used by Pitsulak City guillemots. Pitsulak birds apparently did not penetrate the channel between East and West Nuvuk Islands and the mainland or utilize the waters of Nuvuk Harbour during the ice-free season, because no streamered birds were ever seen in these areas during many trips to Ivujivik. Guillemots from Pitsulak did use the coastal waters northeast of Boulder Cove as far as the deep bay which bisects East Nuvuk Island from the north, because streamered birds were seen in this area. Guillemots were only seen close to land in this area, and it is unlikely that they ever used the very deep channel which separates the Nuvuk Islands from the North Skerries and Fairway Island.

One other probable foraging area is worthy of note. The area west and southwest of Kingituayu Island was likely used by guillemots, because birds were often seen flying southwest near the south end of the transect between South Skerries 4 and Pigiuliit 7. The area to

Fig. 29

Percent of Black Guillemots sighted on the water between 10 and 30 m depth that were marked. Colony distance refers to distance from Pitsulak City. Sightings over 4 km from the colony are lumped to increase sample size. From 4 marked birds among 315 sightings in 1982 and 20 marked birds among 928 sightings in 1983.

which these birds must have been flying was only partly covered by the transect between Aulassivik Bank and Kingituayu Island.

Frequencies at which guillemots were sighted on water over the consistently utilized depths of 10 to 30 m are plotted against distance from Pitsulak City in Fig. 30. Sighting frequencies for each distance zone varied with date in an irregular fashion. No consistent seasonal trends in the use of zones of varying distance from the colony were evident.

The limits of foraging distance from Pitsulak City were only established in the second and third sampling periods of 1983, because guillemots were recorded up to the outer limits of previous surveys. These 1983 transects showed that guillemots occurred regularly to 13 km from Pitsulak City, with a small number found as far as 15 km. The overall shape of the sighting frequency - distance curve can best be seen in the lumped data plotted in Fig. 31. Sighting frequencies tended to be highest within 5 km of Pitsulak, and then decreased to the limit of foraging range.

Changes in the condition of adults during breeding

Individual and collective weight changes of breeding Black Guillemots are plotted in Fig. 32. Weight records of individual birds which were known to be incubating or raising a clutch between weighings showed inconsistent trends (Fig. 32 A). Three birds stayed about the same weight, while five lost weight and one gained. All birds in the collective weighing sample (Fig. 32 B) had brood patches, but some might have been failed breeders. After a drop in mean weights from the

Fig. 30

Number of Black Guillemots seen on the water per 100 m of transect in areas between 10 and 30 m depth during seven periods in 1982 and 1983. Distance from the colony means distance from Pitsulak City. Numbers of 100 m transect segments run in each distance category are given at base of columns.

Fig. 31

Number of Black Guillemots seen on the water per 100 m of transect in areas between 10 and 30 m depth, summed for 1982 and 1983. Distance from the colony means distance from Pitsulak City. Numbers of 100 m transect segment run in each distance category are given at base of columns.

Fig. 32

Weights of breeding Black Guillemots in relation to date. A) Weight changes of individual birds. B) Means, standard errors, and standard deviations of bird weights measured over the breeding season, from 239 weighings. Data are averaged over seven day periods. Means differ among dates ($F=2.62$, $P<.025$).

initial sample of late June, mean weights of birds remained fairly steady.

Mean weights of males, females, breeders and non-breeders were very close (Appendix 5). Overall mean weight of 258 birds was 404.8 g.

DISCUSSION

Prey and habitat choice

This study confirms the Black Guillemot as a specialist in two types of foraging habitats: a) ice edges, and b) shallow open water. Guillemot concentrations along edges of landfast ice have been documented in the Canadian high arctic (Bradstreet 1979, 1980, 1982; Bradstreet and Cross 1982), and the species is also known to winter in northern pack ice (Divoky 1979, Renaud and Bradstreet 1980). The enhancement of feeding opportunities at ice edges in the spring appears to be primarily due to release of microscopic algae from the melting under-ice surface and the resulting attraction of primary and secondary consumers (Horner 1977, Cross 1982, Bradstreet and Cross 1982). When ice is present Boreogadus saida and several amphipod species concentrate under it, and these species dominate diets of locally feeding Black Guillemots (Bradstreet 1980). The principal foods found in guillemots collected at ice edges in the Nuvuk area were Boreogadus and the amphipod Gammarus setosus, both members of the under-ice community (Bradstreet 1980).

Ice-inhabiting algae seem to bloom earlier than those in open water (Horner 1977), which may have an important effect in providing food at the beginning of the guillemot breeding season. The availability of concentrated food at ice edges may explain the higher weights of birds measured at the beginning of the season (Fig. 32) (although early season weight loss might also be due to recrudescence of reproductive tissue, Ricklefs 1977; or function to reduce the cost of locomotion).

tion, Norberg 1981). However, despite the heavy use of ice edges along the mainland and in Nuvuk Harbour, some birds used open waters early in the season (Appendix 4).

Use of open water by Black Guillemots has been poorly studied, although the paucity of offshore records (Brown et al. 1975) firmly designates the species as an inshore feeder. Habitat choice is strongly influenced by depth, and the same preference for shallow water was found both in birds assumed to be searching for food for their chicks and in those recorded on boat transects (Figs. 21 and 28). Depth limitations apply only in open water; large numbers of guillemots used ice edges over deep water in Nuvuk Harbour (Fig. 23 and 24), as did birds recorded by Bradstreet (1979) and McLaren (1982) at offshore ice edges in the high arctic.

The diet of adult Black Guillemots is much more diverse than that of their chicks. Three species of fish and 11 species of crustaceans were identified from guillemot stomachs, but the true number of species present was probably higher than this, because many prey left remains that could not be identified. In particular most of the numerous small otoliths did not appear to be any of the identified species, but their lack of distinctive features precluded reliable identification. Some of the apparent diversity may also have been due to organisms in the digestive tracts of prey species. Copepods are prey for some larger crustaceans (Bradstreet and Cross 1982) and polychaetes are a major part of Eumesogrammus diet in the Nuvuk area (J. M. Green pers. comm.).

Adult diets were found to be much more diverse than chick diets in

this study. This can be understood in the context of Orians and Pearson's (1979) prediction that prey selectivity should increase with travel distance, because self-feeding adult guillemots must return to the "central place" of the surface to breathe. Since travel times between the surface and the bottom may be several orders of magnitude shorter than travel time from the foraging grounds to the colony, we would expect self-feeding to be much less selective than chick-feeding. This is indeed what happens; chick diet was over 90% blennies, whereas adults took a wide variety of both fish and invertebrates.

The assignment of guillemot foraging preference within the water column on the basis of stomach contents is risky, because habitat choice of many of the prey species is poorly known and probably variable. Of the fish species consumed Eumesogrammus and Stichaeus are indisputably benthic, while Boreogadus may use both benthic and mid-water habitats (Bradstreet 1980, Green and Steele 1975). Bradstreet's (1980) epibenthic tows included Hyperia galba and Mysis oculata, both of which were found in stomachs of birds shot in open water, and members of Lebbeus, Onisimus and Gammarus. In contrast, his studies suggested that Themisto libellula preferred midwater habitats.

It is plausible that some, perhaps many, of the prey guillemots took for themselves at Nuvuk were obtained in the water column. This could easily occur as guillemots descended to and returned from the bottom. However, if guillemots regularly remained in mid-water during their dives without continuing to the bottom, it becomes difficult to explain why deeper waters were rarely visited. The deep water near

Pitsulak City must have contained abundant prey at least some of the time, because the area was often used by large flocks of Thick-billed Murres. These birds were actively feeding, but were never joined by guillemots. It is unlikely that the larger murres excluded guillemots from this habitat by interference competition, a mechanism postulated for some other seabirds (Wiens in press), because no behavioural interactions between the two species were ever witnessed.

Other studies have also shown a diverse diet for adult guillemots. Storer's (1952) compilation of early work showed stomachs contained fish, crustaceans, polychaetes, snails, and pebbles, all of which were found in Nuvuk birds. Belopol'skii (1957) and Petersen (1981) reported fish and crustaceans as the major components of guillemot diets. The closest available data on guillemot diet come from southeast Baffin Island, where Smith and Hammill (1980) found most stomachs contained cottid and liparid fish larvae, with Themisto libellula and mysids occurring in lesser frequency. Fish larvae were rare in Nuvuk birds, occurring only in three stomachs.

The general picture obtained from Nuvuk and other data is that guillemots favour ice edges and ice-associated prey when ice is present, but when ice is absent they feed opportunistically in shallow water. Guillemots feed on the bottom, but the extent to which mid-water habitats are also exploited remains uncertain.

Foraging range

Black Guillemots were regularly sighted up to 13 km from Pitsulak

City in 1983. Interpretation of the foraging pattern depicted in Fig. 31 must consider the presence of other guillemot colonies, and pre-breeders and failed breeders. Since most guillemot feeding occurred in the band of shallow water parallel to the coast, it seems fair to lump Pitsulak City with Green and Yellow Islands, which lie directly to the east. Distance from the colony along a north-south axis is the same for all of these sites. The main alternative source of birds found in the coastal band of shallow waters are the colonies on Kingituayu, Qikita, and the Piquiliit Islands. Population estimates for these islands total 61 pairs, whereas the Pitsulak area colonies contained an estimated 308 pairs (Table 1). The Kingituayu area birds thus composed 17% of the region's total breeding population. This area is about 4 km south of Pitsulak City, so if birds at the limit of foraging range were from this area, they must have travelled about 10 km. The presence of streamered birds at the foraging limit indicates that at least some birds feeding there were from Pitsulak City.

Some birds sighted on the water were undoubtedly pre-breeders, and many others were failed breeders (including streamered birds). The proportion of failed breeders was abnormally high in 1983, following the visitation of several colonies by ermine. On Pitsulak City the number of pairs producing eggs was reduced and the number hatching chicks was severely reduced from the previous year (Table 3). Most nests used the previous two years on Green Island were found to be empty on 21 July 1983, and only a single chick was found there on 23 August. On Yellow Island, which is close to the mainland, ermine may

have completely prevented breeding because no evidence of nest sites having been used was found on a visit in early September. Despite the breeding failures guillemots were seen in large numbers in the morning near these islands, and attendance at Pitsulak City was as high as during the previous year (Fig. 8). Although they maintained normal attendance patterns at the colony, the large number of failed breeders may nevertheless have foraged at greater than normal distances because they did not need to return for incubation or chick-feeding. The transect period which offered the closest approach to a normal situation was mid-July 1983, when most guillemots with eggs at Pitsulak were still incubating. The frequency of sightings vs. distance from the colony at this time was similar to that recorded during the August chick-rearing period (Fig. 30), when few birds in the Pitsulak City area were still actively engaged in breeding activities.

Part 4 - MODELLING THE USE OF SPACE BY FORAGING GUILLEMOTS

INTRODUCTION

The previous chapters have shown that Nuvuk guillemots, like most seabirds, travel considerable distances to obtain their food. Since the presumed advantage of distant feeding is greater food availability at distant sites, patterns of foraging distribution will be influenced by depletion of prey by foragers and by the natural distribution patterns of the prey.

Only one model has been published to date which predicts the relation between foraging intensity and distance from the central place at a given moment in time. This model, due to Evans (1982), assumes that foragers prey on patchily distributed food sources which appear irregularly, and predicts that foraging intensity per unit area should decline monotonically with distance from the colony. This distribution of foraging intensity was matched by Evans' (1982) observations of Black-billed Gulls (Larus bulleri), but such a foraging distribution is not general among colonial seabirds. Foraging distributions around three colonies of Thick-billed Murres in the Canadian Arctic were distinctly hump-shaped, with densities peaking 25 - 85 km from the colony (Gaston and Nettleship 1981, Gaston and Smith 1984). Seabird surveys around the Pribilof Islands showed hump-shaped, monotonically decreasing, and concave foraging distributions for the six species and the eight transect tracks covered (Hunt et al. 1980, Kinder et al. 1983).

Evans' (1982) model is not appropriate for Black Guillemots at

Nuvuk because their prey do not appear sporadically. In this section I model the interactions of guillemots and their benthic, sedentary prey. My goal is to make robust predictions, insensitive to variation in input values, of the form of the relation between foraging intensity and distance from the colony.

STRUCTURE OF THE MODEL

Consider a colony of seabirds occupying an island of negligible size in the centre of a sea of constant depth. Birds leave the colony to forage on prey items of uniform size which are distributed randomly on the seafloor. The birds choose their foraging sites on the basis of concentric rings or annuli, whose centre is the colony. In doing so the predators attempt to minimize trip time, which is defined as the time required to fly to the foraging site, capture a prey item, and return to the colony.

If the predator can be considered to "sweep" the seafloor at a constant speed and capture any prey item within a certain detection radius, the time required to capture a prey item (procurement time) is inversely proportional to prey density. Thus procurement time, and consequently trip time, will increase as prey are removed by predation.

In the model these changes are accommodated by an iteration, whose steps are listed in Table 9. The model allows birds to choose foraging zones daily, after prey densities have been updated to account for prey removed the previous day (to account for the effects of rapid change in prey densities at the beginning of exploitation, the iteration cycles five times a day until at least six annuli are being exploited). Because birds are assumed to have imperfect knowledge of their environment, they do not forage solely in the annulus with the lowest trip time; other zones whose trip times are within 10% of the minimum are also utilized. Because trip times for all exploited annuli are similar, the model implicitly assumes Andersson's (1978) contention that

Table 9

Steps in the foraging distribution model.

1. For each annulus, calculate trip times as the sum of travel time and procurement time, where

$$\text{travel time} = 2 \frac{(\text{distance from colony to midpoint of annulus})}{\text{flight speed}}$$

$$\text{area swept} = (\text{swimming speed} \times \text{dive time} - 2 \text{ depth}) 2 \text{ detection radius}$$

$$\text{procurement time} = \frac{\text{dive time} + \text{surface time}}{\text{area swept} \times \text{prey density}}$$

2. Designate annulus with the lowest trip time, and all other annuli with trip times within 10% of this minimum, as foraging zones.
3. Reduce prey populations in these zones by the daily prey consumption. Reduction in each annulus is proportional to its area.
4. Recalculate prey densities.
5. Return to Step 1.

predators should forage in such a way that no exploited area becomes more or less attractive than any other.

PREDICTIONS

For convenience I have used input values which are plausible for Nuvuk guillemots (Appendix 6). Foraging intensity can be measured in two ways, and the shape of the curve that relates foraging intensity to colony distance varies with the units used. In Fig. 33 the left histograms indicate the number of visits birds make to each zone, whereas the right histograms indicate the summed foraging time birds spend in each zone. Both of these measures of foraging intensity are standardized for area.

The simulations predict that some annuli close to the colony would not be used on some days, which reflects sensitivity to changes in procurement time in zones with low travel times. In nature prey depletion, which controls procurement time, is continuous rather than periodic. I have therefore presented predicted foraging distributions as continuous to the edge of foraging range.

Fig. 33 plots foraging distributions for the simplest situation in which all of the area around a colony is available for foraging. At the start of the simulation all birds forage in the zone adjacent to the colony. As nearby prey are depleted, birds extend their range to more distant zones, but retain use of nearby zones. Near and distant zones are used simultaneously because foragers are trading off travel time against resource abundance (Hamilton and Watt 1970). Distant zones have low procurement times because their prey has been little depleted, but they require high travel times. Close zones have low travel times, but procurement times are high because of heavy prey

Fig. 33

Predicted distribution of Black Guillemot foraging effort with respect to distance from the colony. At the beginning of the simulation prey densities are assumed to be uniform, and the entire area around the colony is available for foraging. Other input values are listed in Appendix 6.

depletion. Because the birds renew their choice of foraging zones at short intervals, and because prey removal is proportional to area, trip times are similar among exploited zones at any given time.

Foraging intensity as measured by visits per unit area is constant out to the maximum foraging range (left histograms, Fig. 33) because foraging zones have similar trip times, and therefore attract birds equally. In contrast, time spent by birds at the foraging site declines with distance from the colony (right histograms, Fig. 33), because distant zones with high prey densities require less time to procure a prey item. This decline in foraging intensity is approximately linear.

Because only part of the area around Pitsulak City is water of suitable depth for guillemot feeding, I ran a second simulation using areas between 10 and 30 m depth for annuli centred on Pitsulak City (Fig. 34). Areas within 2 km of Pitsulak City were measured by planimeter from bathymetric charts prepared from sounder traces. Areas beyond this were assumed to include only a coastal strip stretching south along the coast.

Despite the change in foraging area, predicted foraging intensities changed with distance from the colony and with time in a similar manner to that found in Fig. 33.

To test the sensitivity of the model to changes in input values, I compared predicted distributions of bird-time per area for various values of prey detection radius and initial prey density (Figs. 35 and 36). Changing these parameters affected the slope of the foraging

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Fig. 34

Predicted foraging distribution at ten-day intervals when only part of the area around the colony is assumed to be available for foraging. Exact areas and other input values are given in Appendix 6.

Fig. 35

Sensitivity of the foraging distribution model to changes in prey detection radius. Only part of the area around the colony is assumed to be available for foraging. Exact areas and other input values are given in Appendix 6.

Fig. 36

Sensitivity of the foraging distribution model to changes in initial prey density. Only part of the area around the colony is assumed to be available for foraging. Exact areas and other input values are given in Appendix 6.

intensity-distance relation, but did not alter its monotonically decreasing form.

The simulations described above assume that guillemots have a previously unexploited prey population available to them at the beginning of each breeding season. This is simplistic for sedentary organisms such as blennies, because depletion of populations by predation would carry over from year to year. A more realistic view is to consider guillemot predation on blennies as a short pulse within a long ice-free season during which blennies recruit into the population of harvestable prey. To simulate the carry-over of prey depletion between years, I have taken the prey densities from day 70, Fig. 34, and used them as initial values for a subsequent season. The ensuing prediction (Fig. 37) shows a stabilization in patterns of foraging intensity in comparison with the first year. This can be attributed to the fact that birds were exploiting larger areas in the second year, and so reduced prey densities by smaller proportions.

Growth of prey organisms during the breeding season would provide an additional stabilizing influence for foraging distributions, because fewer of the larger prey would be required to meet a constant energetic demand. This is simulated in Fig. 37 for a daily increment of 0.5% of prey weight at the beginning of the season. Foraging range increased over the season despite the smaller number of food items required, but the increase was slower than that predicted by the simulation which assumed constant prey size.

Fig. 37

Predicted foraging distribution at ten-day intervals when initial prey densities are those predicted for day 70, Fig. 34. For "prey size increasing" columns food value of prey is assumed to increase daily by 0.5% of its value at the beginning of the simulation. Only part of the area around the colony is assumed to be available for foraging. Exact areas and other input values are given in Appendix 6.

DISCUSSION

The two units of foraging intensity used in model predictions are comparable to the two ways in which foraging distributions were recorded at Nuvuk. Observations of chick-feeding birds followed to splashdown correspond to visits per unit area. Frequencies of birds sighted on the water during transects correspond to foraging time, because sighting frequencies in foraging areas should be proportional to foraging time spent there. In three of four observation periods, visitation rates were approximately constant until the limit of foraging (Fig. 22), as predicted by the model. In the case of foraging time per unit area, sighting frequencies during incubation and chick-rearing tended to be highest near the colony and decline to the limit of foraging (Fig. 30), also as predicted by the model.

The foraging distribution model predicts that foraging range should increase as prey are depleted over the season. No evidence for such an increase was found in this study. To understand why this might be so, the second-year simulations of Fig. 37 are more useful than those which started with uniform prey densities. Seasonal changes in predicted foraging patterns in the second year simulations were small. If changes such as those predicted did occur in the foraging distribution of Nuvuk birds, they would probably not have been detectable above the fluctuations of sampling error. Reduced prey consumption because of prey growth may also have contributed to the apparent stability of foraging distributions.

Since prey depletion has not been demonstrated in this study, it

may be instructive to examine the consequences of removing the assumption of depletion from model simulations. Since the inshore waters of the Nuvuk area do not differ systematically in depth or other biological and physical factors in respect to distance from the guillemot colonies, we may consider that the densities of an unexploited blenny population would also not vary with colony distance. Given a uniform prey distribution, and assuming no prey depletion, the model predicts that birds will forage only in the zone adjacent to the colony and that the foraging range will never extend beyond this zone. Since this is clearly not the case for Nuvuk guillemots, we must postulate some mechanism which can produce and maintain a prey gradient that is capable of explaining why birds forage both near and far from the colony. The model outlined in this chapter, when it includes the assumption of prey depletion, provides such a mechanism.

The model presented in this section is applicable to central place foragers where the following conditions are met; a) prey is sedentary and is not detectable from a distance, b) habitat factors which influence prey density do not vary systematically with distance from the central place, c) recruitment of prey into exploitable size-classes within the foraging area is unrelated to previous prey density, d) prey do not complete their life cycles in times which are short relative to the observation periods, and e) choice of foraging areas is not influenced by social effects or avoidance of predation.

These conditions are unlikely to be met by most seabirds, because most species probably use social cues to locate their prey, which is

usually mobile and schooling. A closer approximation to these conditions may be found in ground-feeding passerines. Foraging time per unit area in Seaside Sparrows (Ammodramus maritima, Post 1974) and Ovenbirds (Seiurus aurocapillus, Zach and Falls 1979) decreased linearly with distance from the central place except for near and distant annuli. Deviations from linearity close and far from the nest in passerines may be due to a violation of e) above, since birds may preferentially remain close to the nest to defend it, or spend a disproportionate amount of time far from it in order to maintain territorial boundaries (Andersson 1981).

GENERAL DISCUSSION

In this thesis I have compared theoretically predicted choices of prey type, feeding strategy, and foraging distributions to observed results, and found that predicted and observed patterns were similar. However, comparisons between field data and predicted "optimal" behaviour do not prove the validity of theory, because observations may match predictions for reasons other than those assumed by the theory (Aronson and Givnish 1983). Similarly, failure to perform as models predict does not necessarily refute optimality (Zach and Smith 1981).

Since theories of optimal behaviour can neither be proven nor disproven by field tests, they are useful only if we assume a priori that natural selection does indeed push behaviour toward optimal patterns. Given this assumption, it is useful to distinguish between behaviour patterns and the logical processes by which they are determined. It is the behaviour itself, rather than the logical processes, which is subject to selection. Since it is unreasonable to expect animals to duplicate the complete knowledge of the environment and the complex calculations inherent in most models, animals may adopt other, simpler, rules which produce something close to optimal behaviour under typical conditions. In this context correspondence between observed results and those predicted by models makes no statement on the proximate mechanisms by which animals choose their behaviour patterns. Rather, such correspondence provides support, but not proof, for the hypothesis that the assumptions and the algorithms of the model are valid predictors of behaviour patterns which we

assume, a priori, are most beneficial to the animal.

Although various optimality criteria have been proposed for breeding birds (Hixon 1982, Fagerstrom et al. 1983), I have considered guillemots to be time minimizers. Guillemots and their young in the study area did not appear to be under any substantial food stress, as indicated by food delivery rates compared to other colonies and the maintenance of adult body weights during the breeding season. Thus guillemots would be unlikely to be under strong pressure to acquire more food. Adults should, however, tend to try to reduce the time spent procuring food, because this frees more time for social activities at the colony which may enhance retention of mates and nest sites (Nelson 1982) and hence improve reproductive prospects in future years. Displays between members of pairs are frequent at Black Guillemot colonies (Preston 1968, pers. obs.).

The question remains why self-feeding occurred at greater distances from the colony than chick-feeding. In the model presented in Part 4, birds choose foraging zones on the basis of the sum of travel and prey procurement times. The simulation runs assume the simplest situation of a predator that finds one prey item and then returns to the colony. If the predator takes several prey items before returning, procurement time becomes relatively more important in comparison to travel time, and distant zones with high prey densities and low procurement times will be favoured. Guillemots probably do take several prey items per trip while self-feeding, but they are single prey loaders while chick-feeding, in which case the relative

importance of travel times would favour close feeding zones.

The non-uniformity in distribution of feeding effort that was predicted and observed in this study has also been found, in various forms, for other seabirds (Gaston and Nettleship 1981, Gaston and Smith 1984, Hunt et al. 1980, Kinder et al. 1983). Although this lack of uniformity has important implications for the energetics of marine communities around seabird colonies, published models of seabird energetics have assumed that birds evenly exploit their environment to the edge of the foraging range (Wiens and Scott 1975, Furness 1978, Furness and Cooper 1982). Future modelling efforts clearly ought to geographically define predicted impacts on prey sources, a task which has been attempted in a preliminary way by Wiens (in press).

Non-uniformity of seabird distribution patterns is also important in predicting impacts of oil spills on seabird populations, a topic of increasing interest as oil exploration and transportation expands in areas used by marine birds. Ford et al.'s (1982) oil spill sensitivity model predicts effects of spills at various distances from the colony, but requires that densities of foraging birds or prey productivity be previously measured throughout the foraging range of the colony. Since it is impractical to obtain such information for most seabird colonies which are vulnerable to oil spills, models that make general predictions about foraging ranges and the form of foraging distributions are required. For most seabirds, such models will have to simulate the complex movements of mobile shoaling prey which often have rapid reproduction rates and short life spans. The foraging

distribution model presented in this thesis deals with the much simpler situation of a predator of benthic sedentary prey, and is but a first step in this direction.

CONCLUSIONS

(1) Data on nesting success, egg size, chick growth and colony attendance of Black Guillemots breeding in the Nuvuk Islands suggest that food is at least as abundant there as elsewhere in the species' range.

(2) Guillemots fed their young benthic, sedentary prey, primarily Stichaeus punctatus and other blennies, which they obtained in shallow water within 2 km of the colony. Guillemots foraged in a solitary fashion, without reference to the behaviour of conspecifics. These choices of prey and foraging strategy accord with predictions for seabirds which breed in small colonies.

(3) Adults altered the size of prey delivered in the course of chick-rearing, with energy delivery peaking at 25 d post-hatch when chicks received about 800 kJ/d.

(4) Adult diet was more diverse than chick diet, and consisted mostly of blennies, crustaceans and Boreogadus saida. Guillemots fed heavily along landfast ice until the ice melted. Food fed to chicks and adults was obtained in similar water depth, but adults tended to travel much greater distances from the colony for food for themselves than for chick food.

(5) A model which considers the interactions between guillemots and benthic fish prey predicts that the rate of foraging visits with respect to distance from the colony should be constant up to a certain cut-off, but that time spent foraging should decline monotonically with distance from the colony. Distributions of birds recorded on transects

and visually followed to their splashdown sites, respectively, corresponded approximately to these predictions.

(6) The observed and predicted distribution patterns of Nuvuk guillemots and distributional data recorded for other seabirds suggest that prey exploitation and foraging effort often vary greatly within a colony's foraging range. It is suggested that such variation ought to be considered in models of seabird energetics and oil-spill sensitivity.

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Appendix 1

Dry weights, wet weights, and caloric determinations in kJ/g dry weight of fish collected at the Nuvuk Islands.

species	fish no.	dry wt. (g)	wet wt. (g)	wet dry wt. (g) wet wt.	kJ/g dry weight						mean within species
					trial				within fish		
					A	B	C	D	mean	SD	
<u>Boreogadus saida</u>	27	3.54	23.6	0.15	24.840	25.728	26.812	24.530	25.478	1.024	26.524
	28	2.31	14.3	0.16	27.930	26.741	28.244	27.365	27.570	0.662	
<u>Eumesogrammus praecisus</u>	13	1.65	11.2	0.15	20.628	21.989	22.504	20.578	21.425	0.972	20.337
	14	1.49	11.1	0.14	20.013	20.494	18.966	20.859	20.083	0.821	
	15	1.35	10.7	0.13	20.126	19.519	18.531	19.837	19.503	0.694	
<u>Stichæus punctatus</u>	2	1.79	14.7	0.12	22.852	26.021	25.117	21.637	23.907	2.017	22.446
	3	4.27	26.1	0.16	20.951	22.056	20.913	22.722	21.661	0.884	
	4	1.79	12.2	0.15	23.107	20.536	21.076	18.728	20.862	1.802	
	5	2.76	12.0	0.23	21.290	23.555	22.420	22.207	22.368	0.931	
	6	2.67	12.6	0.21	24.296	22.316	24.011	23.103	23.432	0.901	
	16	3.73	n/a	n/a	19.829	20.942	20.880	21.637	20.822	0.746	
<u>Gymnelus viridis</u>	17	1.86	11.3	0.16	23.815	23.304	21.688	21.231	22.510	1.244	22.723
	18	2.92	13.2	0.22	26.013	24.041	24.300	24.991	24.836	0.881	
<u>Myoxocephalus sp.</u>	21	0.54	4.7	0.12	16.257	18.552	20.834	19.263	18.727	1.902	17.181
	22	1.11	10.7	0.10	15.479	14.980	14.164	15.893	15.129	0.744	
	23	1.63	11.9	0.14	17.074	17.920	17.434	19.891	18.080	1.256	
	26	0.66	6.2	0.11	17.107	16.710	14.775	18.568	16.790	1.563	

Appendix 1 (continued)

mean of all trials	21.364
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^a $F=2.61$, $P>.05$.

^bcaloric values differ among fish of a species, but not among species ($F=6.04$, $P<.001$ for variance among fish within a species; $F=3.20$, $P>.05$ for variance among species (nested anova, Sokal and Rohlf 1969)).

Appendix 2

Caloric determinations in kJ/g ash-free dry weight of fish collected at the Nuvuk Islands.

species	fish no.	kJ/g ash-free dry weight				within fish		mean within species
		trial				mean	SD	
		A	B	C	D			
<u>Boreogadus</u> <u>saida</u>	27	27.105	28.671	30.078	27.110	28.241	1.429	29.166
	28	30.145	29.178	31.104	29.940	30.092	0.793	
<u>Eumesogrammus</u> <u>praecisus</u>	13	23.886	26.444	25.602	23.036	24.742	1.558	24.568
	14	24.015	23.919	24.024	25.158	24.279	0.588	
	15	24.618	24.815	23.995	25.309	24.684	0.544	
<u>Stichaeus</u> <u>punctatus</u>	2	25.406	n/a	26.856	23.856	25.258	1.333	25.616
	3	27.457	24.786	24.430	27.939	26.153	1.801	
	4	27.160	23.371	24.874	24.283	24.922	1.615	
	5	24.070	26.444	25.598	26.306	25.604	1.088	
	6	25.225	25.142	27.239	26.268	25.969	0.990	
<u>Gymnelus</u> <u>viridis</u>	16	22.739	24.350	21.897	24.208	23.298	1.185	25.477
	17	27.114	26.322	24.669	23.940	25.511	1.461	
	18	28.382	26.327	27.570	28.202	27.620	0.930	
<u>Myoxocephalus</u> <u>sp.</u>	21	21.713	20.553	23.467	24.091	22.456	1.620	22.285
	22	20.976	21.516	21.068	21.256	21.204	0.238	
	23	22.299	21.943	22.914	25.397	23.138	1.558	
	26	23.434	22.257	19.577	24.103	22.343	1.995	
mean of all trials								25.031

Appendix 3

Stomach contents of Black Guillemots. See notes on p. 192.

	specimen number				
	1-81	2-81	3-81	4-81	5-81
collected: date	11 July	11 July	11 July	11 July	20 July
time	1645	1700	1700	1715	
location	KI, I	KI, I	KI, I	KI, I	MI, O
sex and breeding status	M, N	M, N	M, B	F, B	M, B
stomach % full	75			100	1
FISH					
<u>Boreogadus saida</u> :					
intact remains	-	-	-	4	-
no. otoliths	10	15	2	21	2
oto. length: mean	5.6	5.3	2.4	4.0	
SD	1.0	1.3	2.7, 2.4	0.7	
n	4	5	2	14	
estimated fish length	136	130	69	103	
<u>Eumesogrammus praeceus</u> :					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
<u>Stichaeus punctatus</u> :					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
unidentified and other					
no. otoliths	-	-	1	2	-
oto. length: mean			2.6		
SD					
n			1		
other remains	bones,	bones	-	bones,	-
	flesh			flesh	
CRUSTACEANS					
Mysidae	-	-	-	-	-
Amphipoda	-	-	-	-	-
Decapoda	-	-	-	-	-
unidentified and other	-	-	-	-	-
POLYCHAETES					
	-	-	-	-	-
GASTROPODS					
	-	-	-	-	-
OTHER					
	1 worm,	-	1 pebble	1 pebble	2 pebbles
	algae fragments		algae fragments		

Appendix 3 (continued)

	specimen number				
	6-81	7-81	8-81	9-81	10-81
collected: date	20 July	30 July	30 July	30 July	30 July
location	MI,0	MI,0	MI,0	MI,0	MI,0
sex and breeding status	M,B	M,N	F,B	M,B	M,B
stomach % full			100	50	100
FISH					
<u>Boreogadus saida:</u>					
intact remains	1	-	-	1	-
no. otoliths	17	19	2	10	-
oto. length: mean	4.5	4.6	3.9	5.3	
SD	1.0	1.1	3.8, 4.0	1.6	
n	11	11	2	7	
estimated fish length	113	115	101	130	
<u>Eumecogrammus praecius:</u>					
intact remains	-	-	-	-	-
no. otoliths	1 (prob.)	-	-	1 (prob.)	-
oto. length: mean	2.9			2.4	
SD					
n	1			1	
<u>Stichaeus punctatus:</u>					
intact remains	-	-	-	-	-
no. otoliths	2	2	3	-	2
oto. length: mean	4.3	6.9	1.5		4.3
SD	4.3, 4.3	6.9, 6.9	0		4.3, 4.3
n	2	2	3		2
unidentified and other					
no. otoliths	-	-	-	-	-
oto. length: mean	-	-	-	-	-
SD					
n					
other remains	soupy flesh	soupy flesh	a few bones	many bones	bones, flesh
CRUSTACEANS					
Mysidae	-	-	124	1	-
Amphipoda	-	1 G	-	-	-
Decapoda	-	-	1 Lp, 2 L	-	-
unidentified and other	-	-	-	-	-
POLYCHAETES					
	-	-	-	2 jaws	18 jaws
GASTROPODS					
	-	-	-	-	-
OTHER					
	-	-	algal fragment	-	-

Appendix 3 (continued)

	specimen number				
	11-81	12-81	13-81	14-81	15-81
collected: date	30 July	30 July	13 Aug.	13 Aug.	13 Aug.
time			1600	1600	1600
location	MI,0	MI,0	IH,0	IH,0	IH,0
sex and breeding status	M,N	M,B	F,B	M,B	M,N
stomach % full	5	20	40	10	100
FISH					
<u>Boreogadus saida:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	9	2	-	2
oto. length: mean		4.0			7.6
SD		1.1			
n		3			1
estimated fish length		103			178
<u>Eumesogrammus praecius:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	1	-	-
oto. length: mean			2.4		
SD					
n			1		
<u>Stichaeus punctatus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	2	-	-
oto. length: mean			2.2		
SD					
n			1		
unidentified and other					
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
other remains	bones	bones	part of body	bones	bones, flesh
CRUSTACEANS					
Mysidae	-	2	-	-	-
Amphipoda	-	-	3, 1 Am	-	-
Decapoda	-	-	-	-	-
unidentified and other	-	-	-	-	-
POLYCHAETES					
	4 jaws	-	-	2 jaws	-
GASTROPODS					
	-	-	-	-	-
OTHER					
	-	1 worm	-	-	3 pebbles

3 3

OF / DE

Appendix 3 (continued)

	specimen number				
	16-81	17-81	18-81	19-81	20-81
collected: date	13 Aug.	13 Aug.	28 Aug.	28 Aug.	28 Aug.
time	1600	1600	1500	1500	1500
location	IH,O	IH,O	MI,O	MI,O	MI,O
sex and breeding status	M,B	M,B	N	N	N
stomach % full	1	15	5	2	25
FISH					
<u>Boreogadus saida:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	4	-	-
oto. length: mean			3.5		
SD			0.2		
n			4		
estimated fish length			92		
<u>Eumesogrammus praecisus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
<u>Stichaeus punctatus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	1 (prob.)	-	-
oto. length: mean			3.1		
SD					
n			1		
unidentified and other					
no. otoliths	-	-	4	-	3
oto. length: mean	-	-	0.5	-	0.3
SD			0.2		0
n			4		3
other remains	-	bones, some flesh	bones	bones	bones
CRUSTACEANS					
Mysidae	-	-	-	-	-
Amphipoda	-	-	-	-	-
Decapoda	-	-	-	-	1 Ef, 1 pos. decapod
unidentified and other	-	-	-	-	-
POLYCHAETES					
	6 jaws	-	-	-	3 jaws
GASTROPODS					
	-	-	-	-	-
OTHER					
	-	-	-	1 pebble	-

Appendix 3 (continued)

	specimen number				
	21-81	22-81	1-82	2-82	3-82
collected: date	28 Aug.	28 Aug.	2 July	2 July	2 July
time	1500	1500	1630	1650	1740
location	MI,0	MI,0	NC,0	NC,0	NC,0
sex and breeding status	B	B	F,N	M,N	F,B
stomach % full	75	25	20	10	35
FISH					
<u>Boreogadus saida:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	9	-	-
oto. length: mean	-	-	5.3	-	-
SD	-	-	0.48	-	-
n	-	-	4	-	-
estimated fish length	-	-	130	-	-
<u>Eunesogrammus praecisus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	1	-	1	-
oto. length: mean	-	2.9	-	2.9	-
SD	-	-	-	-	-
n	-	1	-	1	-
<u>Stichaeus punctatus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	3	1	-
oto. length: mean	-	-	3.9	4.2	-
SD	-	-	-	-	-
n	-	-	1	1	-
unidentified and other					
no. otoliths	-	1	-	3	-
oto. length: mean	-	0.6	-	1.1	-
SD	-	-	-	-	-
n	-	1	-	1	-
other remains	bones,	bones,	bones	bones	bones
		flesh			
CRUSTACEANS					
Mysidae	49	4	-	-	36
Amphipoda	-	1 (prob.)	-	-	-
Decapoda	-	-	-	-	-
unidentified and other	many exoskel-	-	-	-	-
	etal fragments				
POLYCHAETES					
	6 jaws	13 jaws	-	-	-
GASTROPODS					
	-	-	-	-	-
OTHER					
	-	-	-	-	-

Appendix 3 (continued)

	Specimen number				
	4-82	5-82	6-82	7-82	8-82
collected: date	2 July	3 July	3 July	3 July	3 July
time	1750	1250	1315	1415	1425
location	NC,O	NC,O	NC,O	NH,I	NH,I
sex and breeding status	M,N	F,B	M,B	F,B	M,B
stomach % full	25	30	20	65	80
FISH					
<u>Boreogadus saida:</u>					
intact remains	1 headless	-	-	-	1 headless
no. otoliths	-	-	-	12	4
oto. length: mean				3.7	4.3
SD				0.6	0.7
n				4	4
estimated fish length				97	109
<u>Eumesogrammus praecisus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
<u>Stichaeus punctatus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	2	-	-
oto. length: mean			3.8		
SD					
n			1		
unidentified and other					
no. otoliths	2	3	4	-	-
oto. length: mean	3.0	2.6	1.2	-	-
SD	3.0, 3.0	1.0	0.31		
n	2	3	4		
other remains	bones	1 large piece of flesh	-	bones	bones
CRUSTACEANS					
Mysidae	-	32	3	-	-
Amphipoda	-	-	2 ?T	-	-
Decapoda	-	1 ?Eg, 1Sp	-	-	-
		1 ?Sp, 1 ui	-	-	-
unidentified and other	-	-	-	-	-
POLYCHAETES					
	-	-	-	-	-
GASTROPODS					
	-	-	-	-	-
OTHER:					
	-	-	1 pebble, 1 worm piece of kelp	-	-

Appendix 3 (continued)

	specimen number				
	9-82	10-82	11-82	12-82	13-82
collected: date	3 July	3 July	21 July	21 July	21 July
time	1430	1445	1700	1715	1720
location	NH,I	NH,I	NC,O	NC,O	NC,O
sex and breeding status	M,B	F,B	M,B	F,B	M,B
stomach % full	95	20	12	15	5
FISH					
<u>Boreogadus saida:</u>					
intact remains	3 headless	-	-	-	-
no. otoliths	6	-	-	-	-
oto. length: mean	6.3	-	-	-	-
SD	1.0	-	-	-	-
n	6	-	-	-	-
estimated fish length	151	-	-	-	-
<u>Eumesogrammus praecisus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	4	-	-
oto. length: mean	-	-	2.3	-	-
SD	-	-	0.3	-	-
n	-	-	4	-	-
<u>Stichaeus punctatus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	3	-	1
oto. length: mean	-	-	2.7	-	3.7
SD	-	-	0.8	-	-
n	-	-	3	-	1
unidentified and other					
no. otoliths	6	1	3	1	-
oto. length: mean	-	-	1.1	1.0	-
SD	-	-	0.1	-	-
n	-	-	3	1	-
other remains	-	-	bones	bones	bones
CRUSTACEANS					
Mysidae	-	-	-	6	-
Amphipoda	-	-	3 ui	-	-
Decapoda	-	-	-	-	-
unidentified and other	-	-	fine remains	fine remains	-
POLYCHAETES					
	-	-	-	1 jaw	-
GASTROPODS					
	-	3 shells, 79 opercula	-	-	2 opercula
OTHER					
	-	4 pebbles	-	-	2 pebbles

Appendix 3. (continued)

	specimen number				
	14-82	15-82	16-82	17-82	18-82
collected: date	21 July	21 July	21 July	10 Aug.	10 Aug.
time	1755	1805	1830	1650	1702
location	NC,0	NC,0	NC,0	NC,0	NC,0
sex and breeding status	M,N	F,B	F,B	M,B	M,N
stomach % full	8	10	20	10	5
FISH					
<u>Boreogadus saida:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
estimated fish length					
<u>Eumesogrammus praecisus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
<u>Stichaeus punctatus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
unidentified and other					
no. otoliths	1	-	1	1	-
oto. length: mean	2.0	-	1.6	1.5	-
SD					
n	1		1	1	
other remains	bones	bones, fine flesh	bones	bones	bones
CRUSTACEANS					
Mysidae	4	13	10	-	-
Amphipoda	2 ui	-	1 Tl	-	1 hyperiid
Decapoda	-	-	-	-	-
unidentified and other	fine remains	fine remains	fine remains	-	fine remains
POLYCHAETES	2 jaws	-	-	-	-
GASTROPODS	-	-	-	-	-
OTHER	-	-	-	-	-

Appendix 3 (continued)

	specimen number				
	19-82	20-82	21-82	22-82	23-82
collected: date	10 Aug.	10 Aug.	13 Aug.	10 Aug.	30 Aug.
time	1710	1825	1030	1031	1724
location	NC,O	NC,C	NC,O	NC,C	NC,O
sex and breeding status	F,B	M,N	M,B	F,B	M,B
stomach % full	40	100	100	15	90
FISH					
<u>Boreogadus saida:</u>					
intact remains	1 tail	-	1 headless	-	-
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
estimated fish length					
<u>Eumesogrammus praecisus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
<u>Stichaeus punctatus:</u>					
intact remains	-	-	-	-	1
no. otoliths	1	-	-	-	2
oto. length: mean	3.2				4.9
SD					4.8, 5.0
n	1				2
unidentified and other				<u>small</u> <u>large</u>	
no. otoliths	1	6	1	45 2	-
oto. length: mean	1.1	0.39	4.2	0.56 2.9	-
SD		0.11		0.31 2.9, 2.9	
n	1	6	1	45 2	
other remains	bones	1 larva	bones, flesh	bones	bones, flesh
CRUSTACEANS					
Mysidae	-	-	-	-	-
Amphipoda	-	2 T1, 2T 2 Ag	-	-	-
Decapoda	-	-	-	-	-
unidentified and other	-	fine remains	-	fine remains	-
POLYCHAETES					
	-	18 jaws	2 jaws	3 jaws	2 jaws
GASTROPODS					
	-	5 shells, 5 opercula	-	-	-
OTHER					
	-	2 pebbles	-	1 pebble	1 pebble

Appendix 3 (continued)

	specimen number				
	24-82	25-82	26-82	27-82	28-82
collected: date	30 Aug.	30 Aug.	30 Aug.	30 Aug.	30 Aug.
time	1740	1800	1830	1845	1920
location	NC,0	NC,0	NC,0	NC,0	NC,0
sex and breeding status	M,B	F,B	M,B	M,B	M,B
stomach % full	90	30	90	45	60
FISH					
<u>Boreogadus saida:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	3
oto. length: mean	-	-	-	-	7.0
SD	-	-	-	-	-
n	-	-	-	-	2
estimated fish length	-	-	-	-	165
<u>Eumesogrammus praecisus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean	-	-	-	-	-
SD	-	-	-	-	-
n	-	-	-	-	-
<u>Stichaeus punctatus:</u>					
intact remains	1 headless	-	-	-	-
no. otoliths	4	-	1	1	3
oto. length: mean	4.6	-	5.2	3.7	4.4
SD	4.5, 4.6	-	-	-	0.99
n	2	-	1	1	3
unidentified and other					
no. otoliths	-	-	2	1	-
oto. length: mean	-	-	2.3	-	-
SD	-	-	2.1, 2.5	-	-
n	-	-	2	-	-
other remains	bones	bones	about 500 eggs, 1 piece of flesh	pieces of flesh, bones	1 piece of flesh
CRUSTACEANS					
Mysidae	-	38	-	-	-
Amphipoda	-	-	-	-	-
Decapoda	-	-	-	-	-
unidentified and other	exoskeletal fragments	1 ? copepod	-	-	-
POLYCHAETES					
GASTROPODS					
OTHER					
	-	1 pebble	-	-	3 pebbles, piece of algae

Appendix 3 (continued)

	specimen number				
	1-83	2-83	3-83	4-83	5-83
collected: date	27 June	27 June	27 June	27 June	27 June
time	1430	1430	1430	1430	1430
location	NH,I	NH,I	NH,I	NH,I	NH,I
sex and breeding status	F,B	M,B	F,B	M,B	F,B
stomach % full	10	20	10	15	20
FISH					
<u>Boreogadus saida:</u>					
intact remains	-	-	-	-	1 piece of flesh
no. otoliths	-	-	-	-	6
oto. length: mean					2.3
SD					0.6
n					6
estimated fish length					67
<u>Eumesogrammus praeceus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
<u>Stichaeus punctatus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
unidentified and other					
no. otoliths	-	-	1	2	-
oto. length: mean	-	-	3.4	4.6	-
SD				4.2, 4.9	
n			1	2	
other remains	bones, flesh	bones	bones	-	bones, flesh
CRUSTACEANS					
Mysidae	-	-	5	1	-
Amphipoda	-	-	-	-	8 Gs
Decapoda	-	1 ui	-	1 ui, 1 Eg	-
unidentified and other	exoskel. fragments	exoskel. fragments	exoskel. fragments	-	exoskel. fragments
POLYCHAETES					
	-	-	-	3 jaws	-
GASTROPODS					
	-	1 operculum	-	-	-
OTHER					
	-	-	1 pebble	-	1 pebble

Appendix 3 (continued)

	specimen number				
	6-83	7-83	8-83	9-83	10-83
collected: date	27 June	12 July	12 July	12 July	13 July
time	1430	1630	1730	1745	1530
location	NH,I	NC,O	NC,O	NC,O	NC,O
sex and breeding status	M,N	M,B	F,B	M,N	F,N
stomach full	90	75	10	8	25
FISH					
<u>Boreogadus saida:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
estimated fish length					
<u>Eumesogrammus praecisus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	3	-
oto. length: mean				(pos. S. punct.)	
SD				3.7	
n				1	
<u>Stichaeus punctatus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean					
SD					
n					
unidentified and other					
no. otoliths	-	-	-	-	small large
oto. length: mean	-	-	-	-	4 2
SD					1.0 2.3
n					0.11 2.3,2.3
other remains	-	1 headless	-	bones	bones
		body, bones,			
		fine flesh			
CRUSTACEANS					
Mysidae	-	-	-	-	-
Amphipoda	123 Ga	-	1 T1, 3 T	-	1 T1, 2 T
			1 Hg, 15 ui		
Decapoda	-	-	-	-	-
unidentified and other	-	amphipod	exoskel.	-	fragments
		or decapod	fragments		
		fragments			
POLYCHAETES					
	-	-	-	1 jaw	-
GASTROPODS					
	-	-	5 shells	-	7 opercula
OTHER					
	-	-	2 pebbles	1 pebble	-

Appendix 3 (continued)

	specimen number				
	11-83	12-83	13-83	14-83	15-83
collected: date	13 July	13 July	16 July	16 July	16 July
time	1630	1630	0450	0530	0545
location	NC, O	NC, O	GI, O	GI, O	GI, O
sex and breeding status	F, N	M, B	M, B	M, B	M, B
stomach % full	25	20	0	1	5
FISH					
<u>Boreogadus saida:</u>					
intact remains	-	-	-	-	-
no. otoliths	2	-	-	-	-
oto. length: mean	2.2	-	-	-	-
SD	2.2, 2.2	-	-	-	-
n	2	-	-	-	-
estimated fish length	65	-	-	-	-
<u>Eumesogrammus praecisus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean	-	-	-	-	-
SD	-	-	-	-	-
n	-	-	-	-	-
<u>Stichaeus punctatus:</u>					
intact remains	-	-	-	-	-
no. otoliths	-	-	-	-	-
oto. length: mean	-	-	-	-	-
SD	-	-	-	-	-
n	-	-	-	-	-
unidentified and other					
no. otoliths	1	-	-	-	-
oto. length: mean	1.7	-	-	-	-
SD	-	-	-	-	-
n	1	-	-	-	-
other remains	bones, fine flesh	bones	-	-	-
CRUSTACEANS					
Mysidae	13	-	-	-	-
Amphipoda	1 On, 1 Ta	1 T	-	-	-
Decapoda	-	-	-	-	-
unidentified and other	exoskel. fragments	exoskel. fragments and flesh	-	-	exoskel. fragments, mostly amphipods
POLYCHAETES					
GASTROPODS					
OTHER					
	1 pebble	-	-	2 pebbles	-

Appendix 3 (continued)

	specimen number					
	16-83	17-83	18-83	19-83	20-83	
collected: date	22 Aug.	22 Aug.	22 Aug.	22 Aug.	22 Aug.	
time	1200	1245	1300	1330	1900	
location	NC,0	NC,0	NC,0	NC,0	NC,0	
sex and breeding status	M,N	M,N	M,N	F,B	M,B	
stomach % full	30	12	12	30	15	
FISH						
<u>Boreogadus saida:</u>						
intact remains	-	-	-	-	-	
no. otoliths	-	-	-	-	-	
oto. length: mean	-	-	-	-	-	
SD	-	-	-	-	-	
n	-	-	-	-	-	
estimated fish length	-	-	-	-	-	
<u>Eumesogrammus praecisus:</u>						
intact remains	-	-	-	-	-	
no. otoliths	-	-	-	-	-	
oto. length: mean	-	-	-	-	-	
SD	-	-	-	-	-	
n	-	-	-	-	-	
<u>Stichaeus punctatus:</u>						
intact remains	-	-	-	-	-	
no. otoliths	-	-	-	-	-	
oto. length: mean	-	-	-	-	-	
SD	-	-	-	-	-	
n	-	-	-	-	-	
unidentified and other						
	small	large		small	large	
no. otoliths	39	2	460	200	1	3
oto. length: mean	0.4-1.6	2.3	0.59	1.58	2.1	0.54
SD		2.3, 2.3	0.09	0.09		0.10
n	39	2	20	20	1	3
other remains	1 headless body (sculpin?), 1 body	bones, fine flesh	bones, fine flesh	1 body (sculpin?) bones, eggs, flesh		bones
CRUSTACEANS						
Mysidae	-	-	-	-	-	-
Amphipoda	3 gammaridians	-	-	-	-	-
	4 ui	-	-	-	-	-
Decapoda	-	-	-	1 prob.	-	-
unidentified and other	-	about 20 copepods	12 copepods	about 100 copepods, fragments	3 copepods, fragments	3 copepods
POLYCHAETES						
	-	-	1 jaw	1 jaw	-	-
GASTROPODS						
	-	2 shells, 1 operculum	-	1 shell	-	-
OTHER						
	-	-	1 piece algae	-	1 pebble	-

Appendix 3 (continued)

	specimen number					
	21-83	22-83	23-83	24-83	25-83	26-83
collected: date	22 Aug.	27 Aug.	2 Sep.	2 Sep.	3 Sep.	3 Sep.
time	1915	0712	0725	0755	0755	0820
location	NC,0	PC,0	PC,0	PC,0	PC,0	PC,0
sex and breeding status	M,N	M,B	F,B	M,B	F,B	M,B
stomach % full	100	2	8	3	1	6
FISH						
<u>Boleogadus saida:</u>						
intact remains	-	-	-	-	-	-
no. otoliths	-	-	-	-	-	-
oto. length: mean						
SD						
n						
estimated fish length						
<u>Eumesogrammus praecisus:</u>						
intact remains	-	-	-	-	-	-
no. otoliths	-	-	-	-	-	-
oto. length: mean						
SD						
n						
<u>Stichaeus punctatus:</u>						
intact remains	-	-	-	-	-	-
no. otoliths	-	-	-	-	-	-
oto. length: mean						
SD						
n						
unidentified and other						
no. otoliths	-	-	6	1, prob. <u>S. punct.</u> or <u>E. praec.</u>	-	-
oto. length: mean	-	-	0.32	-	-	-
SD			0.12			
n			6			
other remains	33 larvae	-	3 larvae,	bones	-	bones
	bones,		bones,			
	flesh		flesh			
CRUSTACEANS						
Mysidae	1	-	5	-	-	-
Amphipoda	4	-	-	-	-	-
Decapoda	-	-	-	-	-	-
unidentified and other	about 60	1	frag-	-	-	-
	copepods	copepod,	ments			
		fragments				
POLYCHAETES	4 jaws	-	-	-	-	2 jaws
GASTROPODS						
OTHER	-	-	-	3	1	1
				pebbles	pebble	pebble

Appendix 3: Notes

Suffix of specimen number gives year of collection.

Location codes: KI = near Kingituyu Island; MI = near Midway Island, 6 km north of Ivujivik; IH = near Ice Harbour; NC = near northern entrance to channel between East and West Nuvuk Islands; GI = near Green Island; PC = Pitsulak City; I = near ice edge; O = open water.

Sex and breeding status: Breeding status determined by presence or absence of brood patch. M = male, F = female, B = breeder, N = non-breeder.

Fish contents: Intact remains are body parts sufficiently well preserved to identify. Mean lengths of otoliths are from unbroken specimens.

When $n = 2$, ranges are given instead of standard deviations. Estimated lengths of Boreogadus saida are derived from the mean otolith length and the formula total length = 20.8 otolith length + 19.55 (D. Noble and A. J. Gaston, pers. comm.). All otolith and fish lengths are in mm.

Crustaceans:

Mysidae: Probably all Mysis spp. Only a few specimens were identified to species; these were all M. oculata and M. mixta.

Amphipoda: G = Gammarus sp., Cs = G. setosus, Am = Ampelisca macrocephala, T = Themisto sp., Tl = T. libellula, Ta = T. abyssorum, Ag = Apherusa glacialis, Hg = Hyperia galba, On = Oniscus nanseni.

Decapoda: L = Lebbeus sp., Lp = L. polaris, E = Eualus sp., Ef = E. fabricii, Eg = E. gaimardi, Sp = Spirontocaris phippii.

Other abbreviations: pos. = possible, prob. = probable, ui = unidentified, nr = not recorded or not relevant, - = none present. ? before the abbreviation of a taxon indicated identification is uncertain.

Appendix 4, Part A

Route numbers of seabird transects.

Appendix 4, Part B (continued)

Appendix 4, Part B (Continued)

transect number	number of times transects were run						transect length (km)	total distance run (km)
	1982				1983			
	22 June- 5 July	21-25 July	1-4 August	3-7 September	21 June- 3 July	9-22 July		
coastal:								
60: land edge								6.1
ice edge								3.8
total					0	3 ^a	3	9.9
71					0	2	2	2.0
72					0	3	3	0.8
73					0	1	1	2.1
74					0	1	1	1.1
total	37	40	13	41	68	98	116	88.8
							282	1358.3

^aincludes two incomplete runs.

Appendix 4, Part C

Distribution of Black Guillemots in the Nuvuk and Aulassivik areas for seven time periods in 1982 and 1983. Survey schedules are given in Part B.

Appendix 5

Weights and measurements of Black Guillemots.

	breeders			non-breeders			total		
	males	females	total ^a	males	females	total ^a	males	females	total ^a
weight (g)									
mean	409.8	414.8	405.0	410.4	415.7	403.8	410.0	414.9	404.8
SD	28.6	34.8	30.7	34.1	36.7	36.4	30.0	34.6	31.5
range	341-464	350-493	310-499	356-485	365-473	341-485	341-485	350-493	310-499
n	45	28	220	18	6	38	63	34	258
wing length (mm)									
mean	169.5	169.5	169.8	166.8	168.8	167.5	168.7	169.4	169.4
SD	4.3	3.3	3.8	4.0	3.5	4.1	4.3	3.3	3.9
range	158-177	165-177	158-179	159-173	162-172	159-175	158-177	162-177	158-179
n	45	28	215	18	6	38	63	34	253
tarsus length (mm)									
mean	31.3	31.3	31.4	31.1	30.5	30.9	31.2	31.2	31.3
SD	1.2	1.4	1.2	1.8	1.4	1.6	1.4	1.4	1.3
range	29.1-33.8	27.8-33.3	27.8-33.8	27.0-34.1	29.5-32.1	27.0-34.1	27.0-34.1	27.8-33.3	27.0-34.1
n	29	18	8	16	3	21	45	21	102
culmen length (mm)									
mean	27.4	26.9	27.0	27.4	26.5	27.3	27.4	26.8	27.0
SD	1.4	0.96	1.5	1.5	0.55	1.4	1.4	0.91	1.5
range	24.2-29.7	25.1-28.3	22.9-30.6	24.1-29.3	25.9-26.9	24.1-29.3	24.1-29.7	25.1-28.3	22.9-30.6
n	29	18	81	14	3	19	43	21	100
pectoral muscle weight (g)									
mean	91.0	90.0	90.7	90.4	77.5	87.8	90.8	88.0	89.9
SD	8.1	8.3	8.0	6.4	17.7	9.8	7.4	10.4	8.5
range	76-107	73-98	73-107	80-98	65-90	65-98	76-107	65-98	65-107
n	16	10	26	8	2	10	24	12	36

^amales, females, and unsexed birds

Appendix 6

Input values used in simulation runs of the foraging distribution model^a.

parameter	simulation presented in Figure:				
	33	34	35	36	37
annulus width (km)	1	1	1	1	1
flight speed (m/s)	14.4	14.4	14.4	14.4	14.4
dive time (s)	74	74	74	74	74
surface time (s)	42	42	42	42	42
depth (m)	20	20	20	20	20
swimming speed (m/s)	1.75	1.75	1.75	1.75	1.75
prey detection radius (m)	0.2	0.2	0.04, 0.2, 1	0.2	0.2
initial food density (prey items/ha)	100	100	100	20, 100, 500	from day 70, Fig. 34
prey consumption (items/d)	40000	5000	5000	5000	5000
areas of annuli	full ^c	partial ^d	partial ^d	partial ^d	partial ^d

^aSources for input values are as follows. Flight speed is from Bradstreet (1982). Dive and surface times were averaged from 93 dives and 56 inter-dive intervals observed from Pitsulak City in 1983. Water depth was typical of areas used by guillemots observed from the blind and recorded on transects in the Nuvuk area (Figs. 21 and 28). Swimming speed is the mean of two values reported by Uspenski (1956). Prey detection radii, initial food density and prey consumption were assigned arbitrary values.

^bfor "prey size increasing" simulation, daily consumption is $5000/(1 + \text{number of days} \times 0.005)$

^call of annulus available for foraging.

^dfor the first three annuli, areas are 132, 273, and 440 ha, respectively; thereafter 600 ha.

END

2	8	H	1	0	H	8	5
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FIN