ACTA NATURALIA ISLANDICA

24

THE FEEDING HABITS OF GREAT BLACK-BACKED GULLS, LARUS MARINUS, AND GLAUCOUS GULLS, L. HYPERBOREUS, IN ICELAND

AGNAR INGÓLFSSON

NÁTTÚRUFRÆÐISTOFNUN ÍSLANDS
MUSEUM OF NATURAL HISTORY
REYKJAVÍK 1976

ACTA NATURALIA ISLANDICA

ISSUED BY THE ICELANDIC MUSEUM OF NATURAL HISTORY
(NÁTTÚRUFRÆÐISTOFNUN ÍSLANDS)

The Museum has published two volumes of Acta Naturalia Islandica in the period 1946–1971, altogether 20 issues. From 1972 each paper will appear under its own serial number, starting with no. 21.

ACTA NATURALIA ISLANDICA is a series of original articles dealing with botany, geology and zoology of Iceland.

ACTA NATURALIA ISLANDICA will be published preferably in English, and will appear at irregular intervals.

ACTA NATURALIA ISLANDICA may be obtained:

1) on basis of institutional exchange from Museum of Natural History, P. O. Box 5320, Reykjavík, Iceland.

2) by purchase (charges including mailing costs) from
Snaebjörn Jónsson, The English Bookshop,
Hafnarstraeti 4 & 9, Reykjavík, Iceland.

The feeding habits of Great Black-backed Gulls, Larus marinus, and Glaucous Gulls, L. hyperboreus, in Iceland

AGNAR INGÓLFSSON
Institute of Biology, University of Iceland, Reykjavík.

Abstract. The feeding ecology of Great Black-backed Gulls (*Larus marinus*) and Glaucous Gulls (*L. hyperboreus*) in Iceland was compared by means of stomach analysis and field observations. Samples of gulls were obtained throughout the year at Bulandshöfdi, western Iceland, during spring at Reykjavik, southwestern Iceland and in autumn at Sandvik, southwestern Iceland. Field observations were made throughout the year at Hvalfjördur, southwestern Iceland.

There is a considerable difference between food selection of the two species, the Glaucous Gull feeding largely on live animals obtained in the intertidal sea-shore, while the Great Black-back is a greater scavenger and a predator on birds and fishes, and depends more on nonfish refuse. However, both species feed extensively on various foods of irregular and/or periodic abundance when these are available in quantity, and usually to a similar degree.

These results indicate that the availability of foods limits the population size of these gulls. Recent trends in population size and the distrubution of the two gulls in Iceland lend additional support to this conclusion. There are indications that a divergence in size of the two species has occurred in Iceland.

INTRODUCTION

Two species, whose populations are regulated in a density-dependent manner, can only coexist if each species, when increasing, has a greater detrimental effect on itself than on the other species. This is probably identical to stating (M a c A r t h u r, 1958) that two such species are only likely to coexist indefinitely if their population size is limited by different means. Thus no two coexisting species limited by the availability of food are likely to have identical feeding habits, and one should expect differences in food selection among them to be considerable.

There have been numerous studies concerned with comparing the feeding habits of two or more species which on superficial observation or because of morphological similarity appeared to take the same food, and thus to violate the so-called competitive exclusion principle. Most of these studies, however, only cover a limited part of the year, often the breeding season. Since it is unlikely that any limiting factor will be limiting at all times, such studies should preferably cover the whole year. In fact, the early part of the breeding season may be a period when food is superabundant for many birds (L a c k, 1966; R e c h e r, 1966). Furthermore, the sampling techniques used in many of these studies are inadequate, often with the result that the data for the different species are not comparable.

The aim of the present study was to analyze the food relations over longer periods of some closely-related species of gulls occurring together in Iceland, with special reference to the role played by food in limiting the population size of these birds. The major part of the work was on the two largest species, the Great Black-backed Gull (*Larus marinus*) and the Glaucous Gull (*L. hyperboreus*), and their feeding habits will be discussed here. The feeding habits of the Lesser Black-backed Gull (*L. fuscus*) and the Iceland Gull (*L. glaucoides*) will be treated in separate papers.

GENERAL REMARKS ON THE SPECIES

Great Black-backed Gull. This is the largest of the gulls. Twenty-seven adult summer males from Iceland averaged 2165 g in weight (range 1870—2350), while 15 females averaged 1735 g (range 1570—1970) (Table 9). Relative to body size the species has a short but very stout bill when compared to other species of large gulls but its wings and tail are relatively short (details in I n g o l f s s o n, 1967). It is by far the commonest of the large gulls in Iceland. Although it is here near its northern limits, it is found breeding on all coasts as well as up to 65—70 km inland in some areas, both on lowlands and in mountains (G u d m u n d s s o n, 1954) but it breeds most abundantly on the islets of Breidafjordur in western Iceland. It is usually a colonial nester, but solitary pairs are frequently found. The nests are usually placed on fairly flat ground, but sometimes on cliffs. The adult segment of the population appears sedentary, but a portion of the immatures leave the island in winter, mainly for the Faroe Islands and the British Isles (details in I n g o l f s s o n, 1967). There is general concensus among farmers, fishermen, and others that this species has increased vastly in numbers in the last few decades. It is heavily persecuted by farmers, mainly because of its predation on Eiders (*Somateria mollissima*) but also because it is thought to kill lambs.

Glaucous Gull. Untill the recent immigration of the Herring Gull (*L. argentatus*), the Glaucous Gull was present in pure form in Iceland. The meeting of the two resulted in extensive hybridization in some areas. Before advent of the Herring Gull, Glaucous Gulls were by far most common as breeding birds in the Breidafjordur area and in northwestern Iceland. Pure Glaucous Gulls still predominate in these areas, with only about 20 per cent showing signs of Herring Gull admixture, and most of these hybrids are very close to Glaucous Gulls in appearance. The mean

„hybird indices" of populations in these areas range from 0.08 to 0.16 (Pure Glaucous Gulls = 0, pure Herring Gulls = 5). In southern and eastern Iceland, birds of hybrid origin predominate today, and pure Glaucous Gulls are scarce (I n g o l f s s o n, 1970). In pure form, Icelandic Glaucous Gulls are somewhat smaller than Great Black-backs, 40 pure or largely pure male adults taken in summer averaged 1584 g in weight (range 1250—1820), while 25 adult females averaged 1304 g (range 1090—1540) (Table 9). Compared with other large species of gulls, Glaucous Gulls have a long but slender bill relative to size, a very short tarsus but rather long middle toe and wings. Glaucous Gulls are purely coastal in habits in Iceland, all colonies being located within 5 km of the shore and the majority within 1 km. The gulls are almost exclusively colonial breeders. The populations of western Iceland typically breed on broad grassy ledges on sea-cliffs or steep mountainsides facing the sea. The birds appear largely resident although they may scatter around the island to some extent in winter but littla banding has been done. In autumn there is a large influx of Glaucous Gulls from arctic breeding grounds and these birds stay to the latter half of March at least. The Glaucous Gulls in Iceland are near the southern limits of the species, and there are recently some indications of a decline in numbers in those areas where the species is still present in a relatively pure form, although this is not marked, and the gull is also known to have commenced breeding in a few new localities in small numbers in recent years.

METHODS

The feeding habits of the two species of gulls were studied in four areas in Iceland (Fig. 1). Stomach analysis was performed on gulls shot at Bulandshöfdi, Snæfellsnessysla, western Iceland, at Reykjavik, southwestern Iceland, and at Sandvik, Gullbringusysla, southwestern Iceland.

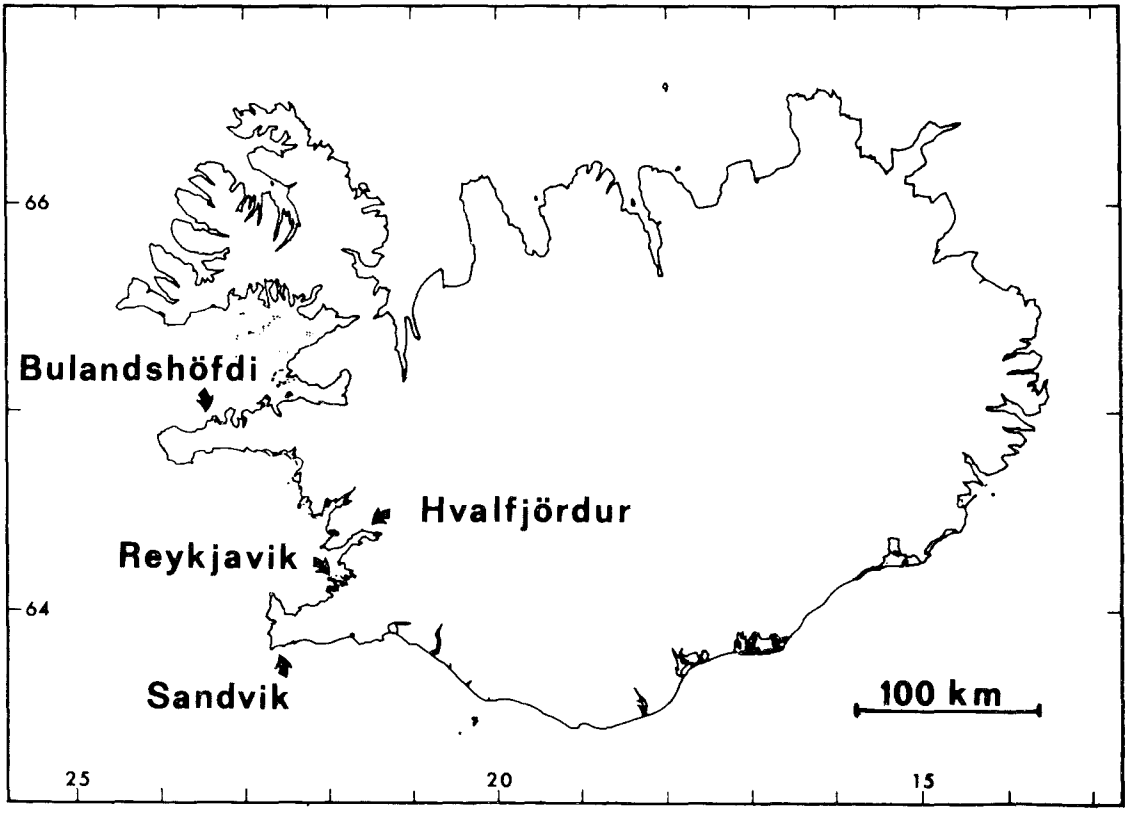

Figure 1. Outline map of Iceland, showing the study areas.

Field observations on feeding habits were made at Bulandshöfdi and surrounding areas but especially at Hvalfjördur and surrounding areas, southwestern Iceland.

There are great difficulties in adequately assessing the food of birds. Generally, the best praciticable method is to obtain random samples of the birds at frequent intervals over a period of time and analyze the stomach contents. It is, however, difficult to obtain random samples of a population with respect to food. At best, random samples may be obtained of a certain part of the population, i.e. the part frequenting the sampling area, not unlikely due to the attraction to a certain kind of food, which may be more attractive to some segments of the population than to others. Samples taken on actual feeding grounds may be particularly biased in this way. Samples taken from breeding colonies, roosts, or local flights, where any bird collected could potentially have taken food from a variety of feeding areas, will tend to give more representative results.

In this study the chief aim was to compare the feeding ecologies of the two species of gulls in order to test the null hypothesis of no difference in feeding adaptations between them. As the diet of gulls changes markedly from place to place and from time og time samples of the two species were obtained *at the same time and place*. This largely eliminated the difficulty caused by differential availability of food items at different times and places but in most other comparable studies this problem has not been adequately considered. Any differences between species when thus sampled are likely to be minimun differences. In this study samples containing both species were usually obtained by shooting from regular flights along the coast. The nature of the flights was not clearly understood but the gulls were probably flying between feeding and roosting or breeding grounds. Stomach analysis showed that birds of the same species collected from such flights within a short time interval often had been feeding on different feeding areas. I therefore think that the birds obtained were reasonably random samples of birds feeding over a rather large area. I have consequently used statistical tests requiring random sampling on these samples.

To obtain adequate samples there had to be an onshore wind of between 4 and 8 knots, as gulls were difficult to shoot under other circumstances. This somewhat limited the frequency of sampling. Adequate samples (10 individuals of each species being considered an adequate sample) were sometimes obtained in as little as 4 hours, but in other cases up to 4 days were needed.

Only the contents of the alimentary canal anterior to and including the gizzard were investigated (this part called „stomach" for convencience). Most frequently, only the gizzard and proventriculus contained food while the oesophagus was usually empty. The stomach contents were placed in isopropanol as quickly as possible after sampling. For each gull species in a sample the number of stomachs containing each kind of food was obtained and I further estimated by eye the percentage (by volume) of the various food items in each stomach, and food items were also counted when possible. These methods are simple to use and, in the case of gulls which feed on a great variety of foods with widely different digestability, give just as good if not better information than more laborious volumetric or gravimetric methods.

All food remains were identified as far as possible, but identification to genus or species was often impossible, although the remains could almost always be allotted to some more inclusive category. All remains were in addition placed into one of five groups according to where the foods had been taken, as follows:

(a) Food taken from the surface of the sea. This group includes all small fish with exception of the lumpfish (*Cyclopterus lumpus*) and the rock gunnel (*Pholis gunnellus*). A fish was arbitrarily classified as small if the largest vertebra found was less than 5 mm in diameter. Also belonging here are pelagic amphipods and euphausids, the larvae and pupae of the dipterous fly *Coelopa frigida*, and sandworms (*Nereis* sp.).

(b) Food taken alive in the intertidal zone, including lumpfish and rock gunnell and their spawn, ascideans, echinoderms, bivalves (except *Modiolus modiolus*), gastropods, decapods, sessile barnacles, isopods, and hydroids.

(c) Food washed up on the shore, eaten dead.

Included here are birds (except unfledged young), large fish (largest vertebra 5 mm or more in diameter), the horse mussel (*Modiolus modiolus*), and goose barnacles (*Lepas* spp.).

(d) Food taken from dry land, including eggs and unfledged young of birds, insects (except *Coelopa frigida*), arachnids, seeds, and berries.

(e) Refuse. This includes fish entrails without bones, and various kinds of nonfish offal (e.g. potatoes, apples, bread, meat, metal foil, plastic objects etc.)

Plants, apart from berries, seeds and vegetable refuse were not grouped into these categories, as they were probably only eaten accidentally, either together with other food or in connection with nest building. The above categories are to some extent arbitrary, and some food items can belong to several of these categories.

For statistical comparison between the two species within samples, the exact probabilities for 2×2 tables given by M a i n l a n d (1948) for comparisons of small samples ($N = 1$—20) were used when possible. When samples contained more then 20 individuals of one species chi-square was used with the precautions outlined by Mainland. The nonparametric Corner Test (O l m s t e a d and T u k e y, 1947) was used to test for correlation of the percentage occurrence of foods in the two gulls.

RESULTS

Feeding habits at Bulandshöfdi

Both species of gulls are abundant breeding birds in the area around Bulandshöfdi. No other large gulls breed in or near the area, but a small number of Lesser Black-backed Gulls and Iceland Gulls are present in summer and winter respectively.

All gulls collected were shot from the same spot on the shore at Bulandshöfdi where the rocks formed a convenient natural hide. Sixteen samples were obtained in the period April 1964 to November 1965, involving altogether 223 Great Black-backs and 244 Glaucous Gulls. Unfavourable weather conditions prevented sampling in the period December to February and in June, while sampling was most frequent in autumn. The great majority of the gulls taken were adults.

Results of the stomach analysis of the total Bulandshöfdi material are shown in Tables 1—2. For the sake of brevity, identifications to genus or species have been omitted from Table 1. Comparison between gull species can be made fairly safely on the basis of the data in these tables, as roughly similar numbers of each species were shot on each collecting date. But more reliable are the statistical comparisons done within each of the samples shown in Table 3. Comparisons have been made both between the occurrence of food genera and species in the stomachs of the two gulls, and also between the occurrence of the more inclusive categories listed in Table 1, but results of comparisons of taxonomic groups higher than genera are not shown if significant differences were found between the occurrences of genera or species of that group. Statistical comparisons of the groups listed in Table 2 are also shown. Only foods which the two species of gulls took to a significantly different degree on at least one occasion are listed.

These tables show that the Glaucous Gull took much more of its foods from the intertidal zone than the Great Black-back, this difference being significant in 7 of the 16 samples. Also, the Great Black-back took more refuse and washed-up food than the Glaucous Gull, and although food from the surface of the sea was taken extensively by both, it was taken more often by Great Black-backs. These differences were only statistically significant in a few of the individual samples (Table 3).

A closer look at some of the food species is instructive. Birds identified from gull stomachs were Eiders (*Somateria mollissima*) and Puffins (*Fratercula arctica*), but only a few identifications to species could be made. Table 1 indicates that birds are more often taken by Great Black-backs than Glaucous Gulls. The bird remains represented adults in almost all cases, and the gulls appeared to take these rather evenly throughout the year. But Great Black-backs are also known to prey extensively on ducklings of Eiders in the area, especially in June (from which month I have no sample), and I have observed this

Table 1

Stomach contents of *L. marinus* and *L. hyperboreus* shot at Bulandshöfdi, western Iceland, from April 1964 to November 1965. Total sample: 223 *L. marinus*, 208 with food in stomach, and 244 *L. hyperboreus*, 237 with food in stomach. Percentages (in brackets) are calculated on the basis of number of gulls with food in stomach. A = number (percentage) of gulls containing food in question. B = number (percentage) of gulls in which food in question amounted to 50% or more of stomach contents.

	L. marinus		L. hyperboreus	
	A	B	A	B
Birds	28 (13.5)	13 (6.2)	8 (3.4)	2 (0.8)
Small fish	128 (61.5)	94 (45.2)	110 (46.4)	77 (32.5)
Large fish	10 (4.8)	7 (3.4)	3 (1.3)	0
Fish spawn	1 (0.5)	1 (1.5)	0	0
Ascideans	8 (3.8)	1 (0.5)	13 (5.5)	2 (0.8)
Echinoids	6 (2.9)	0	20 (8.4)	8 (3.4)
Asteroids	4 (1.9)	1 (1.5)	9 (3.8)	3 (1.3)
Ophiuroids	1 (0.5)	0	1 (0.4)	0
Holothuriods	1 (0.5)	1 (0.5)	1 (0.4)	0
Bivalves	38 (18.3)	1 (0.5)	114 (48.1)	50 (21.1)
Gastropods	6 (2.9)	0	26 (11.0)	5 (2.1)
Decapods	14 (6.7)	6 (2.9)	63 (26.6)	26 (11.0)
Balanid barnacles	13 (6.2)	0	32 (13.5)	2 (0.8)
Isopods	0	0	2 (0.8)	0
Small pelagic crustacea	5 (2.4)	4 (1.9)	9 (3.8	7 (3.0)
Coleoptera	1 (0.5)	0	1 (0.4)	0
Diptera	19 (9.1)	10 (4.8)	27 (11.4)	15 (6.3)
Unidentified insect	1 (0.5)	0	0	0
Polychaetes	14 (6.7)	2 (1.0)	10 (4.2)	0
Hydroids	2 (1.0)	0	1 (0.4)	2
Fish offal	20 (9.6)	17 (8.2)	14 (5.9)	13 (5.5)
Nonfish refuse	14 (6.7)	6 (2.9)	2 (0.8)	1 (0.4)
Berries	13 (6.2)	9 (4.3)	9 (3.8)	2 (0.8)
Other vegtable matter	68 (32.7)	16 (7.7)	80 (33.8)	18 (7.6)
Unidentifiable matter	15 (7.2)	8 (3.8)	10 (4.2)	6 (2.5)

Table 2

Origin of food recorded from stomachs of *L. marinus* and *L. hyperboreus* shot at Bulandshöfdi, western Iceland, from April 1964 to November 1965. Total sample: 233 *L. marinus*, 208 with food in stomach and 244 *L. hyperboreus*, 237 with food in stomach. See Table 1 for further explanations.

	L. marinus		L. hyperboreus	
	A	B	A	B
Food from surface of sea	142 (68.3)	112 (53.8)	138 (58.2)	99 (41.8)
Food from intertidal zone	59 (28.4)	19 (9.1)	152 (64.1)	94 (39.6)
Washed-up food	47 (22.6)	25 (12.0)	24 (10.1)	4 (1.7)
Food from dry land	15 (7.2)	9 (4.3)	10 (4.2)	2 (0.8)
Refuse	34 (16.3)	22 (10.6)	16 (6.8)	14 (5.9)

Table 3

Statistical comparisons of food taken by *L. marinus* and *L. hyperboreus* shot at Bulandshöfdi, western Iceland. Only foods taken to a significantly different degree in at least one sample are listed. * = difference significant at the 5% level. ** = difference significant at the 1% level. Stars preceding slant lines refer to comparisons of proportions of stomachs with food in question, stars following slant lines refer to comparisons of proportions of stomachs in which the food in question amounts to 50% or more of stomach contents. Letters indicate which of the two gulls took the food more often (m = *L. marinus* h = *L. hyperboreus*).

	Mallotus villosus	*Ammodytes lancea*	*Mytilus edulis*	*Hyas araneus*	*Nereis* sp.	Fish offal	Food from surface of sea	Food from intertidal zone	Washed-up food	Refuse
15—17 April 1964										
4 *mar.*, 10 *hyp.*						*/* m				*/* m
5—8 May 1964										
14 mar., 12 *hyp.*			**/* h							
22—23 Aug. 1964										
15 *mar.*, 18. *hyp.*			*/ h							
6 Sept. 1964										
13 *mar.*, 17 *hyp.*		/** m	*/ h				*/** m	*/* h		
23 Sept. 1964										
12 *mar.*, 14 *hyp.*			**/* h					**/**h		
7 Oct. 1964										
9 *mar.*, 12 *hyp.*										
22—23 Oct. 1964										
10 *mar.*, 20 *hyp.*			**/ h					*/**h		
12 Nov. 1964										
17 *mar.*, 19 *hyp.*			*/ h	*/ h				*/**h	**/**m	
2 March 1965										
12 *mar.*, 19 *hyp.*										*/ m
16—17 March 1965										
17 *mar.*, 16 *hyp.*										
11 April 1965										
20 *mar.*, 19 *hyp.*	**/* m									
22 July 1965										
6 *mar.*, 15 *hyp.*		/* h								
20 Aug. 1965										
10 *mar.*, 5 *hyp.*			*/ h					**/ h		
3 Sept. 1965										
16 *mar.*, 16 *hyp.*			**/**h		**/ m		/* m	**/**h		
4 Oct. 1965										
13 *mar.*, 16 *hyp.*										
21 Nov. 1965										
20 *mar.*, 9 *hyp.*				**/ h				**/ h		

frequently. I have, however, no such record for the Glaucous Gull. Mr. Gunnar Gudmundsson, caretaker of the island of Melrakkaey (9 km from Bulandshöfdi) which has a large mixed colony of the two gulls and a huge colony of Puffins, informs me that he has on several occasions seen Great Black-backs grab and kill adult Puffins, while he has never seen Glaucous Gulls do so. My own limited observations from Melrakkaey are in accord with this. Although Great Black-backs may therefore at times kill healthy adult birds, most if not all birds eaten in winter are undoubtedly

found dead, sick, og injured. I have once seen a Great Black-back kill and eat an Oystercatcher (*Haematopus ostralegus*) which had been wounded by a Gyrfalcon (*Falco rusticolus*).

Both gulls take eggs extensively at times, and I have repeatedly seen both species rob the nests of Eiders. Insufficient sampling in spring is responsible for the lack of this food in the stomach analysis data.

Identified small fish from gull stomachs were mostly sand lance (*Ammodytes lancea*) and capelin (*Mallotus villosus*). The sand lance was taken to a similar degree by both gulls. It formed the main part of the diet for long periods during which little other food was taken, but at other times it was not taken at all (Fig. 2). There was a significant positive correlation between the percentage occurrence of this fish in the two gulls (quadrate sum = 14, $P<0.01$), indicating that the degree of utilization depended upon the availability of the fish. In the Bulandshöfdi area the sand lance starts to shoal near the surface in early spring and continues to do so far into the autumn. In this period the fish attracts a large number of gulls and other birds. According to local fishermen, the sand lance is rather irregular in abundance and the fish may be exceedingly abundant in some summers but scarce in others. In both summers covered by this study, the sand lance was as abundant as it ever becomes in this area. Two size classes could be distinguished in late summer and autumn by using otolith lengths (2 mm or longer and shorter than 2 mm, almost always shorter than 1.5 mm). Both gulls took the smaller fish more frequently and there was no clear indication of a difference between the two with respect to the size of the fish eaten.

The capelin is another fish which is of periodic abundance in the area, being only present from late February till April, but is then exceedingly abundant. When available it was the predominant food of both species (Fig. 2), little other food being taken. Both species appeared to feed on the fish to the same degree, although significantly more Great Black-backs than Glaucous Gulls contained the fish in the sample from 11 April 1965 (Table 3), when the fish was probably declining in abundance. The capelin has been placed in the surface-food category, and many of the fish are undoubtedly taken alive at the surface. But a great number of capelins die in early spring following spawning and countless millions may then be washed ashore where gulls often feed on them (although I did not observe this in the Bulandshöfdi area). There is furthermore an extensive commercial fishery for capelins and the gulls may obtain the fish from the nets of the boats, at piers, or at fish factories. Finally discarded entrails of larger commercial fish, often

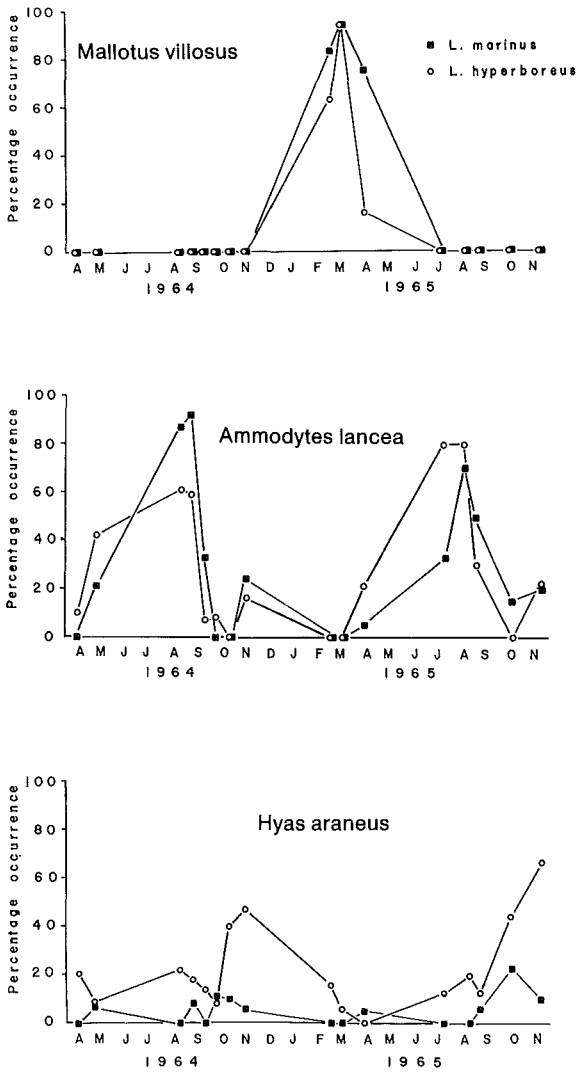

Figure 2. The percentage occurrence of capelin (*Mallotus villosus*), sand lance (*Ammodytes lancea*), and the crab *Hyas araneus* in samples of *L. marinus* and *L. hyperboreus* shot at Bulandshöfdi, western Iceland.

eaten by gulls, are frequently stuffed with capelins in the early spring. On the single occasion that I saw gulls feeding on capelins in the Bulandshöfdi area, both species were picking up apparently dead fish from the surface of the sea.

Other small fish were taken much less frequently. Small identifiable fish other than sand lance and capelin were recorded from 28 Great Black-backs (13.4 per cent) and 11 Glaucous Gulls (4.6 per cent). This difference appears significant, although significant differences in this respect were not seen in any individual sample. The species involved were young Gadidae (most frequently), dab (*Limanda limanda*), herring (*Clupea harengus*), sea scorpion (*Cottus scorpius*), lumpfish (*Cyclopterus lumpus*), and rock gunnel (*Pholis gunnellus*). I have on several occasions watched Great Black-backs catch dabs in shallow water but have no record for the Glaucous Gull. It is common knowledge among farmers in the area that only Great Black-backs catch the relatively large but sluggish lumpfish in rock pools or other shallow waters while Glaucous Gulls may sometimes feed on the remains of the larger gull's meals. Farmers frequently retrieve lumpfish from Great Black-backs, as the fish is relished as food.

The bivalves identified from gull stomachs were almost exclusively edible mussels (*Mytilus edulis*) and horse mussels (*Modiolus modiolus*). The edible mussel is available in the intertidal zone throughout the year. It is taken to a much greater extent by the Glaucous Gull than the Great Black-back, the difference being significant in 8 of the 16 samples. Although the mussel is constantly available, its utilization by the Glaucous Gull varied considerably (Fig. 3). At times, expecially in autumn, the mussel may be the chief food taken, but in 1965 it was hardly touched when sand lance or capelin were abundant. In August and early September 1964, however, both sand lance and mussels were recorded in a large proportion of the gulls, although the mussels were only present in small amounts in most stomachs in the August sample. The drop in the utilization of the mussel in the autumn of 1965 coincided with increasing utilization of the crab *Hyas araneus* (Fig. 2) but unfortunately nothing is known about the seasonal occurance of this crab. In contrast to gulls which had been feeding on sand lance or capelin, most Glaucous Gulls containing mussels also contained considerable amounts of other foods, mostly from the intertidal zone. This is undoubtedly due to the variety of foods available on the shore. The average length of 225 whole mussels recovered from stomachs of Glaucous Gulls was 14.0 mm (range

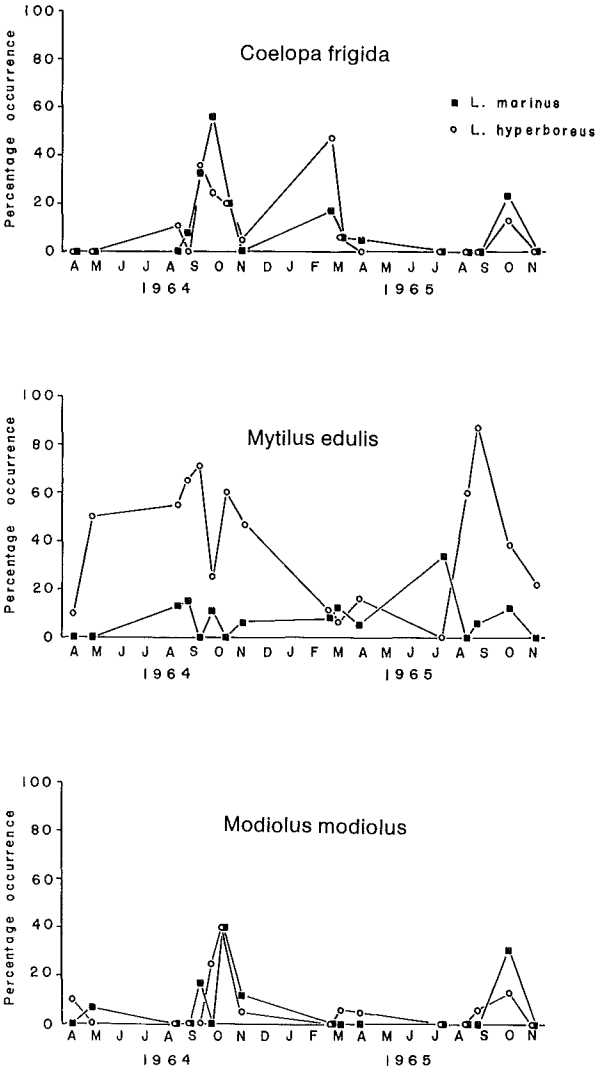

Figure 3. The percentage occurrence of larvae and pupae of the dipteron *Coelopa frigida*, the edible mussel (*Mytilus edulis*), and the horse mussel (*Modiolus modiolus*) in samples of *L. marinus* and *L. hyperboreus* shot at Bulandshöfdi, western Iceland.

2—53). Only one whole mussel was retrieved from a Great Black-back, measuring 10 mm.

In contrast to the edible mussel, the similar but larger horse mussel was taken to about the same degree by both gulls. It is a sublittoral species and is only available to the gulls at irregular intervals after storms have washed it ashore, sometimes in great quantities. The horse mussel appears to be taken largely in late autumn and early winter (Fig. 3), probably reflecting the frequent gales occurring at this season.

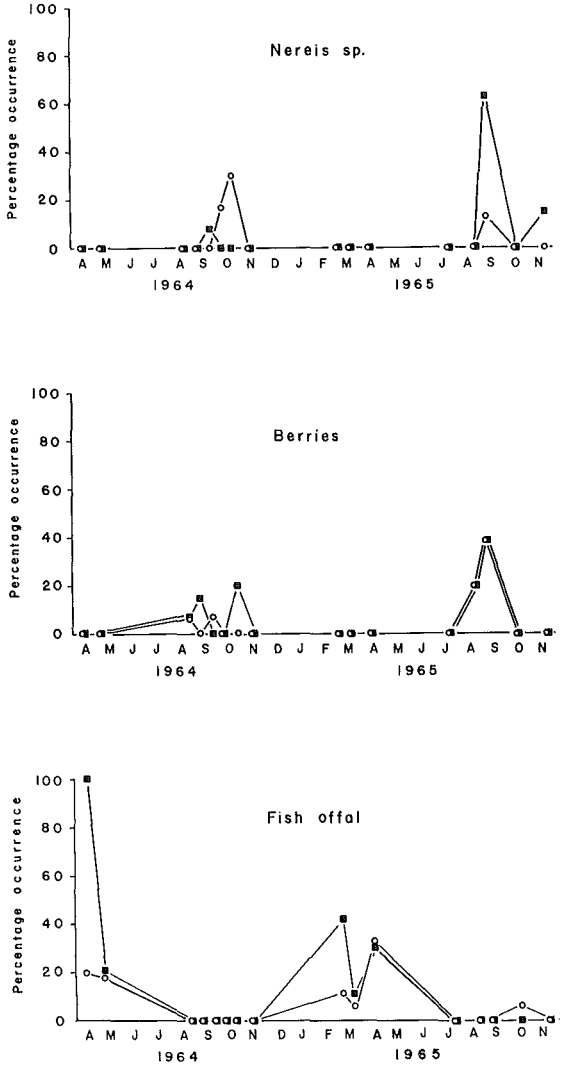

Figure 4. The percentage occurrence of sandworms (*Nereis* sp.), berries (*Vaccinium uliginosum* and *Empetrum nigrum*) and fish offal (entrails) in samples of *L. marinus* and *L. hyperboreus* shot at Bulandshöfdi, western Iceland. See Fig. 3 for symbols.

Coelopa frigida was the only diptera identified from gull stomachs, The larvae and pupae of this species are at times extremely abundant in decaying seaweeds. At high tide some of the larvae and pupae may be washed into the surf and field observations indicate that most of these insects taken by the gulls were obtained here. The insects were taken to a similar degree by both species of gulls and predominantly in autumn and winter (Fig. 3), when heaps of decaying seaweeds are especially large on the shore. There are indications of a positive correlation between the percentage occurrence of the fly in the two gulls (quadrate sum = 10, $0.1 > P > 0.05$).

Polychaetes (*Nereis* sp., probably mostly *N. pelagica*) were only recorded from the gulls in autumn (Fig. 4) but were then taken rather extensively. In the sample from 3 September 1965 a significantly greater portion of Great Black-backs than Glaucous Gulls had taken the worms, while in the previous autumn a trend in the opposite direction was indicated (Table 3). Most of the worms were undoubtedly taken at the surface of the sea when swarming, and large quantities were often taken at such times. Remains of 15—40 worms (judged from number of jaws) per gull were usual, the record being at least 214 worms, probably averaging around 10 cm in length.

Berries (*Vaccinium uliginosum* and *Empetrum nigrum*) were also only taken in the autumn and to a similar extent by both gulls. According to local people, the summer of 1965 produced a much better crop of berries than the previous summer, and the data from the gulls may reflect this (Fig. 4).

Under the heading fish offal I have included only the entrails of fish, the most common type of offal. This is quickly digested beyond recognition and is undoubtedly taken more often than the data indicate. In the Bulandshöfdi area fish offal is available in greatest quantities during the winter fishing season (January—May) and it is taken by gulls chiefly at this time (Fig. 4). In one sample (15—17 April 1964) a significantly greater number of Great Black-backs than Glaucous Gulls had taken fish offal, but the remaining stomach analysis data do not indicate any dif-

ference (Table 3). However, results from three counts made on the northern shore of the Snaefellsnes peninsula (Table 4) showed that a significantly larger proportion of Glaucous Gulls than Great Black-backs were feeding on fish offal in two of the counts while in the third count the reverse was true. In all three counts a significantly greater proportion of Glaucous Gulls were roosting close to fish factories.

There is a constant supply of nonfish refuse at the village dumps in the area but this kind of refuse did not appear to be of major importance to the gulls, judging from the analysis of stomach contents. Although there is no significant difference in any sample, the overall results indicate that the Great Black-backs took nonfish refuse to a greater extent than the Glaucous Gulls (Table 1). Furthermore, in two of the three counts made in the area (Table 4), a significantly greater proportion of Great Black-backs than Glaucous Gulls were feeding at dumps (no gulls so engaged in the third count) and similarily a larger proportion of Great Black-backs were roosting close to dumps in two counts (no gulls roosting in such locations in the third count).

Feeding habits at Reykjavik

Of the two gulls, only the Great Black-back breeds in the area around Reykjavik, but the Glaucous Gull is common in winter. The wintering Glaucous Gull population has a hybrid composition similar to that of the Bulandshöfdi birds, about 20 per cent showing signs of Herring Gull admixture. The migratory Lesser Black-backed Gull also breeds commonly in the area, while the Iceland Gull is common in winter.

Altogether 6 samples were taken at Reykjavik between 12 February and 18 April 1966, involving 92 Great Black-backs and 87 Glaucous Gulls. All gulls were shot from a jeep parked on the same spot on the island of Örfirisey bordering Reykjavik harbour. Both Lesser Black-backed and Iceland Gulls were taken as well.

Results of the stomach analysis of the total material are shown in Tables 5—6 and statistical comparison within the samples in Table 7. The results agree well with those obtained at Bulandshöfdi, except that the differences between the two gulls are even more distinct here. Glaucous Gulls had taken significantly more food from the intertidal zone than the Great Black-

Table 4

Number of *L. marinus* and *L. hyperboreus* in three counts made on the northern shore of Snaefellsnes Peninsula, western Iceland, between Hellisandur and Stykkishólmur. Percentage of total numbers are shown in brackets. The counts were made from the main highway between the two villages, using a 40x telescope.

	28—29 August 1964		29 September 1964		12—13 February 1965	
	L. marinus	L. hyperboreus	L. marinus	L. hyperboreus	L. marinus	L. hyperboreus
Roosting						
Near fish factories	183 (9.7)	169 (16.6)	125 (16.3)	362 (57.3)	753 (15.8)	430 (27.3)
Near dumps	203 (10.8)	3 (0.03)	133 (17.3)	9 (1.4)	0	0
Elsewhere	1,430 (75.9)	316 (31.0)	323 (42.2)	247 (39.1)	1,073 (22.7)	96 (6.1)
Eating						
Fish offal	59 (3.1)	95 (9.3)	100 (13.2)	0	2,700 (57.1)	1,020 (64.5)
Other refuse	0	0	80 (10.5)	3 (0.4)	200 (4.4)	30 (0.2)
On shore	8 (0.1)	435 (42.7)	5 (0.6)	11 (1.7)	0	0
By robbing eiders	0	2 (0.02)	0	0	0	0
Total	1,883	1,020	766	632	4,726	1,576

backs in all 6 samples. The chief intertidal food was the edible mussel (34 whole mussels from Glaucous Gull stomachs ranged from 3—29 mm in length, averaging 11.1 mm, as against 14.0 mm for 225 mussels from Bulandshöfdi gulls), but echinoids (*Strongylocentrotus droebachiensis*), asteroids (*Asterias rubens*) and decapods (mostly *Hyas araneus* and *Carcinus maenas*) were also taken extensively. Great Black-backs took more food from „the surface of the sea" than Glaucous Gulls (difference significant in one sample). However, the chief food in this category, the capelin, was undoubtedly taken to some extent as offal at piers and fish factories where gulls were seen feeding at times. In addition, Table 6 indicates that Great Black-backs took more refuse than the Glaucous Gulls, although the difference is not significant in any one sample.

It was surprising that neither sand lance, the immature stages of *Coelopa frigida*, nor *Nereis* were ever taken to any extent by the two species at Reykjavik, as all of these were taken extensively

Table 5

Stomach contents of *L. marinus* and *L. hyperboreus* shot at Reykjavik, southwestern Iceland, from 19 February to 25 April 1966. Total sample: 82 *L. marinus*, 72 with food in stomach and 80 *L. hyperboreus*, all with food in stomach. See Table 1 for further explanations.

	L. marinus		L. hyperboreus	
	A	B	A	B
Birds	8 (11)	5 (7)	0	0
Small fish	44 (61)	33 (47)	27 (34)	12 (15)
Ascideans	0	0	3 (4)	0
Echinoids	7 (10)	4 (6)	21 (26)	10 (12)
Asteroids	1 (1)	0	21 (26)	12 (15)
Cephalopods	1 (1)	0	0	0
Bivalves	21 (29)	5 (7)	59 (74)	23 (29)
Gastropods	0	0	11 (14)	2 (2)
Decapods	4 (6)	1 (1)	26 (32)	12 (15)
Balanid barnacles	5 (7)	0	6 (7)	0
Diptera (imm. stages)	2 (3)	2 (3)	2 (2)	0
Polychaetes	9 (12)	0	10 (12)	1 (1)
Fish offal	8 (11)	7 (10)	3 (4)	0
Nonfish refuse	11 (15)	6 (8)	5 (6)	0
Vegetable matter	15 (21)	3 (4)	5 (6)	1 (1)
Unidentifieable matter	4 (6)	2 (3)	1 (1)	1 (1)

Table 6

Origin of food recorded from stomachs of *L. marinus* and *L. hyperboreus* shot at Reykjavik, southwestern Iceland, from 19 February to 25 April 1966. Total sample: 82 *L. marinus*, 72 with food in stomach and 80 *L. hyperboreus*, all with food in stomach. See Table 1 for further explanations.

	L. marinus		L. hyperboreus	
	A	B	A	B
Food from surface of sea	49 (68)	36 (50)	34 (42)	14 (17)
Food from intertidal zone	28 (39)	11 (15)	72 (90)	61 (76)
Washed-up food	12 (17)	6 (8)	17 (21)	4 (5)
Refuse	18 (25)	13 (18)	7 (9)	1 (1)

Table 7

Statistical comparisons of food taken by *L. marinus* and *L. hyperboreus* shot at Reykjavik, southwestern Iceland, in 1966. See Table 3 for further explanations.

	Mallotus villosus	Echinoids	Asteroids	*Mytilus edulis*	Decapods	Food from surface of sea	Food from intertidal zone
12—14 Feb.							
8 *mar.*, 7. *hyp.*							*/ h
19—21 Feb.							
15 *mar.*, 20. *hyp.*		*/ h			*/ h		*/**h
1 March							
15 *mar.*, 15 *hyp.*							*/**h
4—5 April							
19 *mar.*, 21 *hyp.*	**/**m		**/ h	**/* h	*/ h	*/* m	**/**h
12 April							
12 *mar.*, 11 *hyp.*				**/* h			*/**h
18. April							
10 *mar.*, 11 *hyp.*			*/ h	**/ h			*/**h

at times at Bulandshöfdi. These foods were obviously available at Reykjavik, as many Iceland Gulls shot at the same time had been feeding on them. Probably, these organisms were not present in sufficient quantities to attract the larger gulls, while the smaller and more agile Iceland Gull could utilize these foods without too much expenditure of energy. This view is supported by the following observation: In the Bulandshöfdi area, gulls were frequently seen feeding in very dense flocks on sand lance, the fish shoals being obviously very compact; at Reykjavik, the gulls feeding on sand lance were scattered over a large area (in both areas feeding gulls were shot to identify the food taken). Although many Iceland Gulls had been feeding on sand lance the fish rarely made up more than half of their stomach content, whereas this was the rule for the Bulandshöfdi birds. This observation also holds for *Coelopa frigida*, although the difference is not as marked here. As for *Nereis* sp., most Iceland Gulls contained less than five of these worms (maximum 16), while 15—40 were usual numbers for the two larger species at Bulandshöfdi (maximum 220).

Most food items were taken rather evenly throughout the short period of the Reykjavik study. However, the utilization of capelins by both species decreased sharply in April (this was also true for the other two species of gulls studied), as the fish obviously became unavailable. Glaucous Gulls then turned to the edible mussel to a much greater extent than before, while the Great Black-back seemed to increase its utilization of fish offal.

Feeding habits at Sandvik

The material gathered at Sandvik, Gullbringusysla, southwestern Iceland, in the autmns of 1964 and 1965 is meager and has been discussed elsewhere to some extent (Gudmundsson and Ingolfsson, 1967; Ingolfsson, 1970). The data are generally in good agreement with the data from Bulandshöfdi and Reykjavik. In the autumn of 1965, however, both species were feeding to a large and equal extent on goose barnacles(*Lepas* spp.) which were excessively common at that time due to special circumstances.

Field observations at Hvalfjördur

Systematic field observations of feeding habits of the two species were carried out in Hvalfjördur, near Reykjavik, southwestern Iceland. Hvalfjördur is a long fjord (Fig. 5) with most of its human settlements concentrated around an American military base, where there is a dump. A whaling station nearby was operated from May to late September, producing quantities of offal in this period. There are several estuaries with

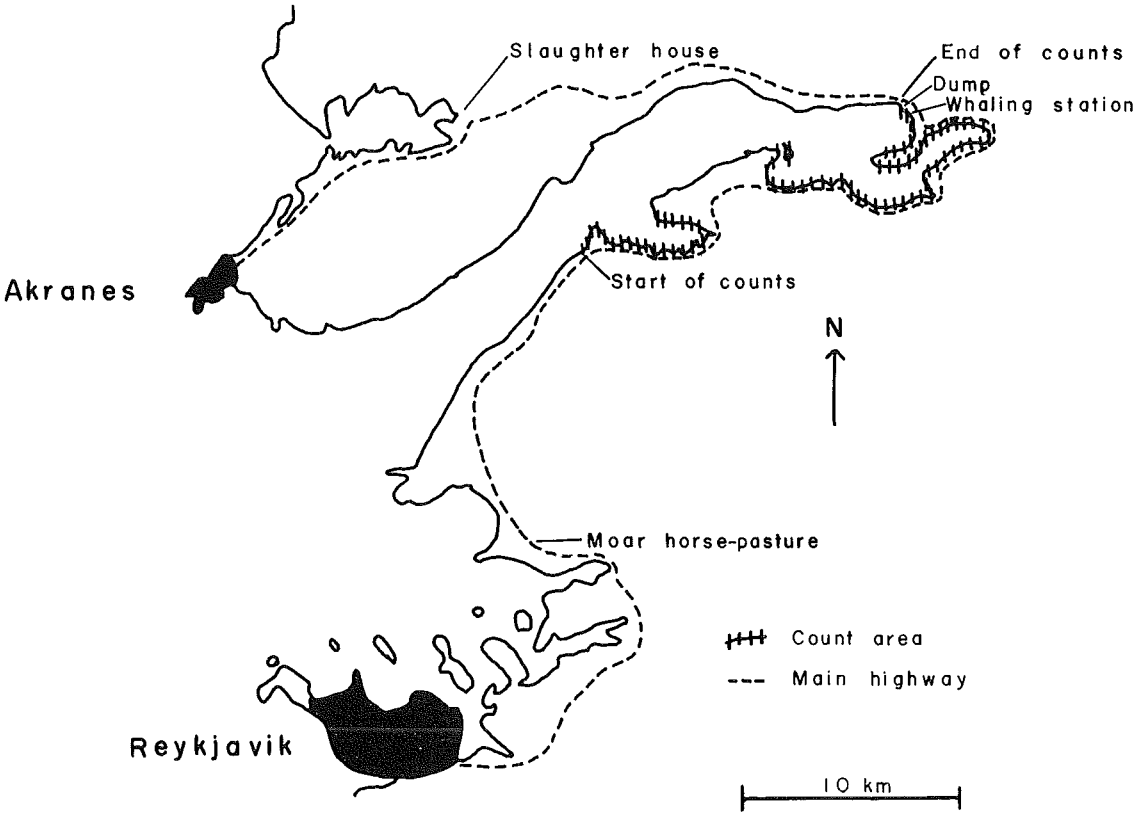

Figure 5. Outline map of Hvalfjördur, southwestern Iceland, and surrounding areas, showing the count route and points mentioned in the text.

extensive tidal flats in the area. Both species of gulls are present in some numbers throughout the year, but only the Great Black-back breeds in the area. Glaucous Gulls are common in winter but less so in summer when only immatures are present. Lesser Black-backs also breed in the area and are common in summer.

Thirteen counts were made in Hvalfjördur at approximately monthly intervals from August 1964 to October 1965. All gulls were counted from a car on the main highway using a 40x telescope (Fig. 5). Each count started 1 hour before slack low tide and was completed in about 2 hours. In addition to the 13 low-tide counts, five counts made from August 1964 to January 1965 were started 1 hour before slack high tide. The gulls observed were grouped into five categories according to their activities as follows: (a) Roosting, bathing, etc. This category included birds that were sleeping or standing on or near the shore, drinking, bathing, and preening as well as other birds that were not engaged in any feeding activity. (b) Feeding on the shore, mostly in the intertidal zone. (c) Feeding on refuse at the dump.(d) Feeding on offal at the whaling station. (e) Associating with Eiders.

The results (Table 8) agree with the stomach contents data in showing that the Glaucous Gull is to a much greater extent an intertidal feeder than the Great Black-back. Even at high tide an appreciable portion of the Glaucous Gulls was feeding on the shore. Glaucous Gulls also robbed food from Eiders more often than did the Great Black-backs. Most of the food obtained in this way was probably edible mussels, and as expected more gulls were associating with Eiders at high tide than low tide (see Ingolfsson, 1969). On the other hand, Great Black-backs

Table 8

Total Number of *L. marinus* and *L. hyperboreus* in 18 counts made from 18 August 1964 to 7 October 1965 in Hvalfjördur, southwestern Iceland. Percentages of total number are shown in brackets.

	L. marinus	L. hyperboreus
Low-tide counts (13)		
Roosting, bathing, etc.	3,140 (74.6)	342 (7.4)
Feeding on shore	622 (15.7)	3,966 (86.0)
Robbing eiders	4 (0.1)	254 (5.5)
Feeding at whaling station	208 (4.9)	13 (0.3)
Feeding at dump	194 (4.6)	36 (0.8)
Total	4,208	4,611
High-tide counts (5)		
Roosting, bathing, etc.	700 (83.5)	661 (41.1)
Feeding on shore	54 (6.4)	759 (47.2)
Robbing eiders	33 (3.9)	183 (11.4)
Feeding at whaling station	9 (1.1)	0
Feeding at dump	42 (5.0)	5 (0.3)
Total	836	1,608

took more of the food provided by man than did Glaucous Gulls. The above differences were found to be statistically significant in most of the individual counts.

Only 23.9 per cent of the Great Black-backs observed were feeding, while the corresponding percentage for Glaucous Gulls was 80.8. More than half of the Great Black-backs were seen in the relatively small area around the dump and whaling station, but even here they were much less often seen feeding than the Glaucous Gulls, which were scattered much more evenly throughout the area. Thus the Great Black-back fed on a very concentrated food source and needed much less energy in food gathering than the Glaucous Gull. In addition, a substantial portion of Great Black-backs may have been feeding outside the Hvalfjördur area, using it only for roosting, preening and drinking, and in summer, for breeding. Large numbers of Great Black-backs were thus seen feeding just outside the count area, for example at a slaughter house (Fig. 5) when that was in operation (late September to late November). On 7 October 1965 the routine count was extended to include the slaughter house as well as the coastline extending from it to the city of Akranes where fish offal was available in quantity. There were almost three times as many Great Black-backs (but no Glaucous Gulls) around the slaughter house as in the whole of the usual count area(413 vs. 151). The count also showed a greater proportion of Glaucous Gulls than Great Black-backs feeding on fish offal, supporting the evidence from Bulandshöfdi. In October 1964 large numbers of gulls were seen feeding on earthworms in horse dung in a pasture at Moar south of the count area (Fig. 5). These were almost all Great Black-backs (19 October count: 403 Great Black-backs, 4 Glaucous Gulls at Moar, compared with 178 Great Black-backs and 483 Glaucous Gulls in the usual count area). This was the only instance where the two gulls were seen feeding on earthworms, and earthworms were never recorded from stomachs.

Feeding habits outside Iceland

The literature on the feeding habits of the two species outside Iceland has been reviewed in detail by Ingolfsson (1967). On the whole the records are in agreement with the findings in Iceland. In many areas the Glaucous Gull is an intertidal feeder to a large degree, but it may be more of a predator on birds and mammals in arctic regions (north of the range of the Great Black-back) than it is in Iceland. This may,

however, entirely be due to lack of suitable avian or mammalian prey, such as Little Auks (*Alle alle*) and lemmings, in Iceland. In most areas Great Black-blacks prey heavily on young birds in summer, and even on adults in one area, but fish is also taken extensively. It is difficult to evaluate fully the difference in feeding adaptions of the two species outside Iceland, as they have not elsewhere been studied together.

DISCUSSION

The data from stomach analysis show that the two species of gulls utilize several food items to a similar degree. Thus both species feed extensively on capelin and sand lance when these are available in abundance, and at such times there may be little difference in their diet. Both fish are of periodic and somewhat irregular availability, and this is true also of all other food items which the gulls utilize to a similar extent and simultaneously (*Modiolus modiolus*, *Lepas*, *Coelopa frigida*, and berries). Pronounced differences between the two appear when more stable food sources are considered. These foods include birds (mostly dead or injured), most small fish other than capelin and sand lance, large fish, and nonfish refuse taken more often by Great Black-backs; and intertidal animals taken predominantly by the Glaucous Gull. Some of these food items, of course, show some periodic changes in availability, but these are not as marked or irregular as in the case of the foods utilized similarily by the two gulls.

These findings are in agreement with the hypothesis that the population size of these gulls is limited by the availability of food. If such food-limitation exists, the critical factor would be the availability of the more stable food sources on which the populations would rely in the absence of the abundant but more periodic and irregular foods. Two species which have coexisted for a long time could therefore be expected to differ in their choice of these stable foods, each having become specially adapted to feed on certain of these. When the more periodic or irregular foods become abundant they may, because of their great availability, be preferred by the gulls although they are ignored when present in smaller quantities. Since they are available in addition to the more stable foods, on which the gulls could fall back, they can be said to be superabundant relative to the needs of the birds, and there appears no reason why two coexisting species could not utilize such a source in a similar manner.

All superabundant foods cannot of course be expected to be utilized to a similar degree by both species of gulls. Since they are adapted to feed on largely different stable food sources, there will be superabundant foods which only one of the species can utilize efficiently. Thus the lumpfish, a fish of periodic and somewhat irregular availability, is taken predominantly by the Great Black-back, presumable because the smaller Glaucous Gull is unable to cope with this large fish. Any superabundant littoral food can similarly be expected to be utilized mainly by Glaucous Gull, as the Great Black-back only rarely searches for food in the intertidal zone.

Superabundant foods can, however, be expected to influence population size to some degree. Gulls may be able to accumulate great amounts of fat when such food is available, resulting in better survival during a subsequent period of food scarcity. Also, stable food sources may be spared when superabundant foods are present, perhaps allowing the former subsequently to support a larger number of gulls.

The two species of gulls divided up the suitable stable food sources between them largely by habitats rather than by selecting different foods from the same habitat. When the Lesser Black-back and Iceland Gull are considered also (I n g - o l f s s o n, 1967) the division of the resources by habitats among the four species becomes even more striking. These species are so similar in morphology that the range of foods that could be utilized efficiently would undoubtedly overlap very broadly if they fed in the same habitat, and it would seem doubtful that they could coexist under such circumstances.

Marked differences in feeding habits among related coexisting species of birds have been demonstrated in numerous studies (e.g. B e l o-

pol'skii, 1961; Harris, 1965 working on gulls; Steven, 1933, Hartley, 1953; Gibb, 1954; Betts, 1955; MacArthur, 1958; Carrick, 1959; Ehlert, 1964; Murton *et al.*, 1964; Ashmole and Ashmole, 1967; Newton, 1967; Snelling, 1968; Weeden, 1969; Ashmole, 1970; Dina and Eltringham, 1974, working with other birds). In several studies, related species were found to take superabundant foods to a similar degree, while differing in their choice of the more stable food sources, and in most of the studies quoted above the species were found to divide up the resources between them largely by habitats. The agreement among these studies in showing marked differences in feeding habits among related species is by itself strong evidence that availability of food is limiting the size of bird populations, as has been pointed out by Lack (1954). If food were not limiting (that is, if food were always superabundant) two or more sympatric species should frequently have identical or closely similar feeding habits, as has been found to be true of the Glaucous and Herring Gulls in Iceland (Ingolfsson, 1970). These two forms, although hybridizing extensively in Iceland at the present time, differ considerably in morphology, including bill size. There are a few studies in which little or no difference in feeding habits among closely-related coexisting species of birds has been discovered, implying that the availability of food might not be a limiting factor, but a closer look at these studies shows that this is not the inevitable conclusion. Thus, the several species of gulls studied by Smith (1966) in the eatern Canadian Arctic were evidently utilizing temporarily superabundant food supplies. Sladen (1955) found that the two penguins *Pygoscelis adeliae* and *P. antarctica* both fed exclusively on the euphausid *Euphausia superba* throughout the breeding season. However, *adeliae* fed in the pack ice far from the colonies while *antarctica* fed much closer to land. Thus feeding habitats differed markedly, and it seems certain that in the absence of the superabundant euphausids, differences between the two would appear. Their feeding habits in winter are unknown. The feeding habits of four species of sandpipers (*Calidris alpina*, *C. melanotus*, *C. pusillus*, and *C. bairdii*) studied in Alaska overlap markedly (Holmes and Pitelka, 1968). A possibility here is that the food of these sandpipers may often be superabundant during their short stay in northern Alaska, their population size being limited primarily by the availability of food on wintering grounds, where their feeding habits remain to be compared. Evans (1964) concluded that there was no evidence of a significant difference in the kind of food taken by three species of sparrows (*Pooectes gramineus*, *Spizella pusilla*, and *S. passerina*) studied in Michigan in summer, but the data appear too scanty to give such a conclusion much weight.

There is additional, indirect evidence that the population size of gulls is limited by the availability of food. Several species of large gulls have increased enormously in numbers in this century, coinciding with increasing availability of refuse on which these gulls often feed. In Iceland, the great increase in numbers of the Great Black-backs as opposed to the stability of the Glaucous Gull population, may be correlated with the observation that the Black-backs are more attracted to refuse dumps than are the Glaucous Gulls. In addition, the densities of Glaucous Gulls in different parts of Iceland seem to be correlated with food availability. This species is by far most abundant in Breidafjördur and northwestern Iceland where conditions are particularily favourable for an intertidal feeder due to the very extensive intertidal region here (Ingolfsson, 1975). Also, more than half of the Eider population of Iceland is concentrated in the Breidafjördur area (Fiskiskyrslur og hlunninda, 1920—1940). Not only do Glaucous Gulls prey to some extent on the eggs (and perhaps chicks) of the Eider, but frequently rob these ducks of their food (Ingolfsson, 1969). The presence of the large Eider population in the Breidafjördur area may also partially explain the abundance there of Great Black-backs which prey extensively on the Eider chicks and eggs. Lack (1954) discusses further evidence for food limitation in birds in general, some of which being admittedly rather circumstantial.

Table 9

Average body weight (g) (±2 SE) of sympatric and allopatric populations of *L. marinus* and *L. hyperboreus* adults collected in summer (April—August). Data for Northern Canada and Greenland were obtained from museum skin labels. Data for Britain are from Harris (1964). Sample size is shown in brackets.

		L. hyperboreus	L. marinus
Northern Canada and Greenland	♂♂	1,747 ± 50 (35)	
	♀♀	1,465 ± 73 (25)	
Iceland (Bulandshöfdi)	♂♂	1,584 ± 40 (40)	2,165 ± 50 (27)
	♀♀	1,304 ± 38 (25)	1,735 ± 58 (15)
Britain	♂♂		1,713 ± 31 (106)
	♀♀		1,486 ± 25 (130)

Competition for food can be said to occur between two species if the removal of one immediately results in increasing survival of the individuals of the other. Competition can undoubtedly be quite severe for some time after two similar species meet for the first time. But if coexistence proves possible the feeding habits of the two are then likely to diverge. Measurments of allo- and sympatric populations of Glaucous and Great Black-backed Gulls indicate that such a divergence may have occurred in Iceland. The difference in weight between the two species there is thus greater than between neighbouring allopatric populations of the two (Table 9). Linear measurements (e.g. of bill size) show similar trends, although the data are here less comparable due to the differences in the ways in which workers take their measurements. Of course, competition with other species of gulls could also be expected to influence the evolution of the two species in question. In particular, the large size of Glaucous Gulls in many areas outside Iceland may also be related to competition with smaller species (Herring, Thayer's (*L. thayeri*) and Iceland Gulls) in those areas.

ACKNOWLEDGEMENTS

This paper is based on a Ph. D. dissertation submitted in the Depertment of Zoology, the University of Michigan, Ann Arbor. I wish to express special thanks to my chairman, Dr. Robert W. Storer, who has assisted me in innumerable ways. Dr. Finnur Gudmundsson granted working facilities in the Museum of Natural History, Reykjavík and assisted in numerous other ways. The many stimulating discussions I have had with Dr. Gudmundsson have been especially helpful. I am deeply grateful to my wife, Linda, who acted as my assistant throughout the period of study. Acknowledgements are due to many other persons, too numerous to mention here.

During the period of this study I received financial aid from the Icelandic Science Fund (Vísindasjódur Íslands), Reykjavík and from the Chapman Memorial Fund and Mae P. Smith Gull Fund, American Museum of Natural History, New York. I was also the recipient of a Edward C. Walker Scholarship and a Rackham Predoctoral Fellowship from the University of Michigan, and a NATO Science Fellowship, during the period of this study. To all those concerned I am deeply grateful.

REFERENCES

Ashmole, M. J. 1970. Feeding of western and semipalmated sandpipers in Peruvian winter quarters. Auk, 87:131—135.

Ashmole, N. P. and Ashmole, M. J. 1967. Comparative feeding ecology of sea birds of a tropical oceanic island. Peabody Mus. Nat. His., Bull. 24:1—131.

Belopol'skii, L. O. 1961. Ecology of sea colony

birds of the Barents sea. Jerusalem, Israel Program for Scientific Translations.

Betts, M. M. 1955. The food of titmice in oak woodland. J. Animal Ecol., 24: 282—323.

Carrick, R. 1959. The food and feeding habits of the Straw-necked Ibis, *Threskiornis spinicollis* (Jameson) and the White Ibis, *T. mollucca* (Cuvier) in Australía. CSIRO Wild. Res., 4: 69—92.

Dina, N. A. and Eltringham, S. K. 1974. Ecological seperation between white and pink-backed pelicans in Ruwenzori National Park, Uganda. Ibis, 116: 28—51.

Ehlert, W. 1964. Zur Ökologie und Biologie der Ernahrung einiger Limicolen-Arten. J. Orn., 105: 1—53.

Evans, F. C. 1964. The food of Vesper, Field and Chipping Sparrows nesting in an abandoned field in Southeastern Michigan. Amer. Midl. Naturalist, 72: 57—75.

Fiskiskyrslur og hlunninda. 1920—1940. Reykjavik, Hagstofa Islands.

Gudmundsson, F. 1954. Islenzkir fuglar X. Svartbakur (*Larus marinus* L.) (Icelandic birds X. The Great Black-backed Gull [*Larus marinus* L]. Natturufrædingurinn, 25: 24—35.

Gudmundsson, F. and Ingolfsson, A. 1967. Helsingjanef á Surtseyjarvikri (Goose barnacles [*Lepas* spp.] on Surtsey pumice). Natturufrædingurinn, 37: 222—235.

Harris, M. P. 1964. Measurments and weights of Great Black-back Gulls. Brit. Birds, 57: 71—75.

„ 1965. The food of some *Larus* gulls. Ibis. 107: 43—53.

Hartley, P. H. T. 1953. An ecological study of the feeding habits of the English titmice. J. Animal Ecol., 22: 261—288.

Holmes, T. R. & Pitelka, F. A. 1968. Food overlap among coexisting sandpipers on northern Alaskan tundra. Syst. Zool. 17: 305—318.

Ingolfsson, A. 1967. The feeding ecology of five species of large gulls (*Larus*) in Iceland. Unpublished Ph. D. dissertation, Ann Arbor, Michigan.

„ 1969. Behavior of gulls robbing eiders. Bird Study, 16: 45—52.

„ 1970. Hybridization of Glaucous Gulls *Larus hyperboreus* and Herring Gulls *L. argentatus* in Iceland. Ibis, 112: 340—362.

„ 1975. Lífríki fjörunnar (Life on seashores). Rit Landverndar, 4: 61—99.

Lack, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press.

„ 1966. Population studies of birds. Oxford, Clarendon Press.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology, 39: 599—619.

Mainland, D. 1948. Statistical methods in medical research I. Canadian J. Res., Sec. E. Med. Sci., 2: 1—166.

Murton, R. K. Westwood, N. J. and Isaacson, A. J. 1964. The feeding habits of the Woodpigeon *Columba palumbus*, Stock Dove *C. oenas* and Turtle Dove *Streptopelia turtur*. Ibis, 106: 174—188.

Newton, I. 1967. The adaptive radiation and feeding ecology of some British finches. Ibis, 109: 33—98.

Olmstead, P. S. and Tukey, J. W. 1947. A corner test for association. Ann. Math. Stat., 18: 495—513.

Recher, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology, 47: 393—407.

Sladen, W. J. L. 1955. Some aspects of the behaviour of Adelie and Chinstrap Penguins. Proc. 11th Intern. Ornithol. Congr.: 241—247.

Smith, N. G. 1966. Evolution of some arctic gulls (*Larus*): An experimental study of isolating mechanisms. Ornithol. Monogr., 4.

Snelling, J. C. 1968. Overlap in feeding habits of Redwinged Blackbirds and Common Grackles nesting in a cattail marsh. Auk, 85: 560—585.

Steven, G. A. 1933. The food consumed by Shags and Cormorants around the shores of Cornwall (England). J. Mar. Biol. Ass. U. K., 19: 277—292.

Weeden, R. B. 1969. Food of Rock and Willow Ptarmigan in Central Alaska with comments on interspecific competition. Auk, 86: 271—281.

ACTA NATURALIA ISLANDICA

Volume I:

1. Tr. Einarsson: Origin of the Basic Tuffs of Iceland. 75 pp. 1946.
2. J. Áskelsson: A Contribution to the Geology of the Kerlingarfjöll. A Preliminary Report. 15 pp. 1946.
3. S. Steindórsson: Contribution to the Plant-Geography and Flora of Iceland IV. The Vegetation of Ísafjarðardjúp, North-west Iceland. 32 pp. 1946.
4. I. Davíðsson: Notes on the Vegetation of Árskógsströnd, North Iceland. 20 pp. 1946.
5. S. H. Pétursson: Die Herkunft der Milchsäurelangstäbchen des isländischen Speisequarks. 8 pp. 1946.
6. Ó. B. Bjarnason: The Component Acids of Icelandic Herring Oil. 9 pp. 1946.
7. H. Einarsson: The Post-larval Stages of Sand-eels (Ammodytidae) in Faroe, Iceland and W-Greenland Waters. 75 pp. 1951.
8. H. Lister, R. Jarvis, M. McDonald, I. W. Paterson and R. Walker: Sólheimajökull. Report of the Durham University Iceland Expedition 1948. With an Introduction by J. Eythórsson. 41 pp. 1953.
9. R. Dearnley: A Contribution to the Geology of Loðmundarfjörður. 22 pp. 1954.
10. T. Tryggvason: On the Stratigraphy of the Sog Valley in SW-Iceland. 35 pp. 1955.

Volume II:

1. H. Einarsson: On the Post-larval Stages of Ammodytes lancea Cuvier. 7 pp. 1955.
2. S. Thorarinsson: The Öræfajökull Eruption of 1362. 99 pp. 1958.
3. J. Áskelsson: Fossiliferous Xenoliths in the Móberg Formation of South-Iceland. 30 pp. 1960.
4. S. Steinthórsson: The Ankaramites of Hvammsmúli, Eyjafjöll, Southern Iceland. 32 pp. 1964.
5. E. Wenk, H. Schwander und H.-R. Wenk: Labradorit von Surtsey. 29 pp. 1965.
6. S. Jakobsson: The Grímsnes Lavas, SW-Iceland. 30 pp. 1966.
7. K. Saemundsson: Vulkanismus und Tektonik des Hengill-Gebietes in Südwest-Island. 105 pp. 1967.
8. K. Nakamura: En Echelon Features of Icelandic Ground Fissures. 15 pp. 1970.
9. G. Jónsson: Fasciation inflorescentielle et fasciation végétative. 15 pp. 1970.
10. N. Hald, A. Noe-Nygaard & A. K. Pedersen: The Króksfjörður Central Volcano in North-west Iceland. 29 pp. 1971.

No. 21. I. Munda: General Features of the Benthic Algal Zonation around the Icelandic Coast. 36 pp. 1972.

No. 22. T. W. Johnson, Jr.: Aquatic fungi of Iceland: Uniflagellate species. 38 pp. 1973.

No. 23. T. W. Johnson, Jr.: Aquatic fungi of Iceland: Biflagellate species. 40 pp. 1974.

No. 24. A. Ingólfsson: The feeding habits of Great Black-backed Gulls, Larus marinus, and Glaucous Gulls, L. hyperboreus, in Iceland. 19 pp. 1976.

AVAILABLE FROM:

SNAEBJÖRN JONSSON & CO. H.F. — THE ENGLISH BOOKSHOP

Hafnarstraeti 4 & 9, Reykjavík — Iceland,