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A STUDY OF THE BREEDING BIOLOGY OF TWO SPECIES
OF GULLS NESTING ON SABLE ISLAND, NOVA SCOTIA.

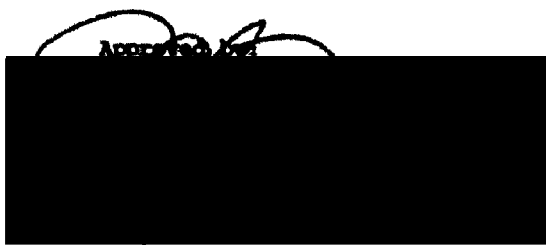
by

Anthony Lock

Submitted in partial fulfillment of the
requirements for the degree of Ph.D. at

Dalhousie University

September 24, 1973



DALHOUSIE UNIVERSITY

Date Sept. 24, 1973

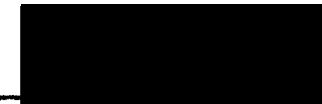
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ABSTRACT

The growth and spread of gull populations in Nova Scotia is discussed and a census of all breeding places of both species in the province was carried out.

The reproductive success of both Herring and Great Black-backed Gulls breeding on Sable Island, Nova Scotia was found to be lower than reported at any other colonies.

Great Black-backed Gulls were more successful than the Herring Gulls and proved more capable of rearing artificially enlarged broods.

The diets of adults of both species differed substantially. Fish was the chief component of diets in all cases but Herring Gulls took greater amounts of berries and invertebrates while the Great Black-backs took greater amounts of seal carrion, pelagic birds and terns and their eggs. Human waste was not a significant part of the diet of either species.

Great Black-backed Gull chicks were hand-reared and their food demands determined. A food budget for all gulls breeding on the island was constructed and it was found that due to chick mortality and adult migration food demands was uniform throughout the breeding season. It was shown that if reproductive success were as high as is typical for these species the food demand of the population would double between mid-June and mid-July.

The growth rates of chicks of both species was determined and found to be slightly less than is reported elsewhere. The rates of growth of single chicks of both species was higher (though not significantly so)

than that of chicks with siblings at the age of high food demand.

Observations of nests with broods of different ages and sizes revealed that Great Black-backed gulls spend less time foraging to feed their broods than do Herring Gulls.

ACKNOWLEDGEMENTS

I am most grateful to Dr. I. A. McLaren who supervised this study and to my wife Carolyn for her great help in all aspects of the work.

Dr. R.G.B. Brown's advice was of great value particularly in the planning of the project. To the Canadian Wildlife Service I am indebted for providing a boat and money to do the Nova Scotia survey. I am grateful also to Dr. K. Gregoire who piloted the aircraft used in the gull census.

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INTRODUCTION

In this century there have been enormous increases in the numbers of many species of gulls in the genus Larus. These increases have occurred in widely separated parts of the world and been of such magnitude and had such a profound influence on the welfare of other bird species that they have interested many investigators and been fairly well documented. For instance, Drury (1963) and Kadlec and Drury (1968a) have reviewed such increases in the eastern United States, Parslow (1967) and Harris (1970) in England and Wales, Brun (1971) in Norway, Goethe (1956, 1964) in Germany, Spaans (1972) in Holland, Salomonsen (1963) in Scandinavia and Fordham (1967) in New Zealand. These authors also report expansions of breeding range of the species they are concerned with and a broadening of the type of nesting site.

It is notable that these increases have occurred in relatively affluent, industrialised areas and that some of the heaviest concentrations of breeding colonies are close to towns with fish docks or with large populations and open dumps. This circumstance suggests that the observed population growth and present high population densities are a consequence of the availability of human wastes. The wastes of the fishing industry are a source of food for gulls but Harris (1970) points out that some British gull populations have continued to increase at times when increased processing of the catch on the fishing banks and greatly reduced fish landings have meant a decrease in food for gulls from this source. He suggests that open dumps may be more important and that a lag in learning to utilise a new resource may be responsible for asynchronies observed between creation of a food

source and population growth.

It has also been suggested that the increase is simply a recovery of the various species involved to normal levels after a period of exploitation when eggs and chicks were harvested for human food and adults were sought to supply feathers to the millinery trade.

A third hypothesis has been advanced but has been given scant attention. A significant climatic amelioration has occurred, at least in the northern hemisphere, since the eighteenth century and the effect of this change on both plant and animal communities has been quite noticeable. Crisp (1959) has reviewed the situation in northern Europe and it is apparent that changes in the breeding ranges of many species may be correlated with climatic changes. McTaggart-Cowan (1940) has reviewed the winter occurrence of summer birds on Vancouver Island and he ascribes many of the changes in bird distribution to climatic changes. The extension of the breeding range of the Herring Gull and many other bird species into Iceland has been attributed to an amelioration of the climate of the island and Drent and Guiguet (1961) suggest that longer breeding seasons allowing some species to rear two broods and mild winters reducing thermal stress and increasing food availability may explain some of the increases noted in populations of gulls and cormorants on the west coast of Canada.

This argument becomes less convincing if one considers that the increases in gull populations have occurred in this century whereas climatic amelioration has been in progress for over one hundred years. Furthermore, while these climatic changes can be correlated with range extensions of several species of plants and animals in no case have population increases of four to twenty times, which some gull species have exhibited, been ascribable to

climatic changes. Furthermore boreal birds such as the Fulmar (Fulmarus glacialis) and the Kittiwake (Rissa tridactyla) have expanded their ranges contrary to the climatic shift. These birds are constant attendants of the fishing fleets and this suggests the primacy of feeding pattern rather than climatic factors in determination of their range and numbers.

The first hypothesis has received more support than the second which is difficult to prove or to disprove as primaevial population levels are not ascertainable. These two hypotheses are not mutually exclusive and it is probable that at least the early stages of population growth after the Migratory Birds Treaty was signed in 1916, reflects a cessation of human predation and a return to earlier population levels. But many studies have shown that human wastes, particularly those of the fishing industry, make up a substantial part of the diet of many gull populations. Drury (1963), Spaans (1971), Hunt (1973), Pearson (1968), and Harris (1965) demonstrated this and Fordham (1967 and 1970) has related that the closure of a slaughter house was accompanied by a substantial decline in the numbers of Southern Black-backed Gull (Larus dominicanus) breeding in the area.

It is also instructive to note that of the other genera of Laridae in the northern Atlantic area, only the Kittiwakes (Rissa tridactyla) have shown similar large increases in range and numbers (Lock, 1972). This species commonly feeds on wastes of fishing fleets and may gain a good part of its daily ration from them. Other small gulls and terns, however, which get no part of their ration by association with man have not grown in numbers apart from an increase immediately after the introduction of protection. On the contrary, many small gulls and terns are at low population levels (Nisbet, 1973; Drury in press) primarily because they are preyed

upon by or are unable to compete for food and nesting space with the more abundant larger gulls. Thomas (1972) has reviewed the impact of gulls on other species which commonly breed near their colonies.

It is apparent that gull populations in eastern North America reached their lowest point in the late nineteenth century when many of the islands on which they now breed undisturbed were occupied by fishermen and farmers who willingly supplemented their diet with gull eggs and collected adults for their skins. Drury (1963), in examining the growth of gull populations in New England, relates that at the turn of the century when Dutcher and Norton counted 8100 pairs breeding on islands in Maine, Herring Gulls were not known to breed south of that state. The Maine population increased rapidly to a peak of 36,000 breeding pairs in 1940, declining to about 20,000 pairs in 1960. This decline is probably partially a consequence of a gull control programme begun in 1940 and described by Gross (1951). But the Maine decline also accompanied the later stages of an extension of the breeding range of the species southward to Rhode Island by 1937 and to New York state by 1940, at which time Gross (1951) estimated that 50,000 pairs bred in New England. At the same time a further 32,000 pairs of gulls bred on Kent Island in New Brunswick (Crystal, in Drury, 1963). By 1961 Drury estimated that the breeding population of New England was 58,000 pairs.

Drury's (1963) compilation of Audubon Christmas counts for the Great Lakes, Gulf coast and Atlantic coasts of the United States and Canada indicate that over this period of 60 years an increase of around 20 times took place. This seems not unrealistic in the light of censuses carried

out by Ludwig (1965) on Lakes Huron and Michigan. Here between the years 1960 and 1965 Ring-billed Gulls almost quadrupled their numbers and Herring Gulls doubled theirs. This increase is undoubtedly ascribable to immigration of gulls from other areas rather than being entirely the result of locally high reproductive success. However no great reduction in neighbouring populations has been noted and this increase exemplifies the recent increase in North American Gull populations.

In sanctuaries on the North shore of the Gulf of St. Lawrence censuses have been carried out every five years since 1925 and during this time Herring Gull numbers have increased from 1020 birds (Lewis, 1925) to 15,111 birds in 1972 when the last census was made (Nattleship and Lock in press).

No comparable data were available for Nova Scotia unfortunately, but comments of some early ornithologists indicate that the Herring Gull was never a really scarce bird here. Bryant (1857) found them nesting on most of the islands he visited off southern Nova Scotia and Downs (1888) allowed that it was very common in the province in his day. It was recorded as an uncommon bird in Bras D'Or Lakes by Dwight (1887) but even today it is not plentiful there.

The Great Black-backed Gull seems to have been only a little scarcer than the Herring Gull as Jones (1869) called it a "common species" and Allen (1895) saw "numbers" of them off the southwest coast of Cape Breton Island. However, unlike the Herring Gull, the population growth of this species in North America has not been well documented. Trotter (1904) noted that it was a common bird off southern Nova Scotia but that it was known to nest no further south than Cape Split. He was apparently unaware that Watson Bishop had collected eggs of this species at Casperess Lake in

Kings County (some 27 miles south of Cape Split) in 1889 (egg collection of Nova Scotia Museum of Science.) Before 1912 (Allen, 1915) a colony of this species was established in Lake George, Yarmouth County, increasing to around 5,000 birds by 1928 (Nova Scotia Museum of Science egg collection). Tufts (1962) reports that in 1945 there were between five and seven thousand birds on this colony but counts of adult on aerial photos taken on June 11, 1974 revealed only 2,015 birds on seven islands in the lake.

Considering the large numbers of this species breeding in the southern part of the province early in the century, it extended its range southward very slowly. Townsend (in Pettingill, 1937) saw a few around Grand Manan Island and believed a pair to be nesting at Green Island in the archipelago. Pettingill (1937) found a pair nesting at Kent Island in 1933 and considered Black-backs to have been a common nesting species in that area for only a few years. Since that time it has extended its breeding range on the Atlantic coast as far south as New York State.

Both Herring and Black-backed Gulls breed on Sable Island but it seems that they have not been long established there. Many early chronicles of the island mention the abundance of "ulls" that in breeding season supplied huge quantities of eggs to the life-saving crews quartered there. But these gulls are obviously terns or steering gulls as they were commonly called. Neither Gilpin (1858) who detailed the natural history of the island nor the diaries of the superintendents of the life-saving establishment (Public Archives of Nova Scotia) mention the large gulls and Dwight, (1895) the monographer of the Ipswich Sparrow, does not list them among the ten species of birds he found breeding there. It is certain that if any numbers of the larger gulls bred there their eggs would have been sought for food and their

presence thought worthy of mention. The terns, apparently, continued abundant throughout the nineteenth century, never having been subject to the commercial exploitation which so drastically reduced the American populations. They encountered a temporary setback from the depredations of foxes which flourished for some years on the island (Nacoun, 1899) but soon returned in large numbers.

Of all the naturalists who visited Sable Island only St. John (1921), who was on the island in 1913, attempted to estimate the numbers of terns breeding there: "After travelling over the greater part of the island and seeing the immense numbers of terns everywhere, from a rough computation of the number per acre and the average of the island we estimated that these birds alone did not fall far short of a million on the island." He makes no mention of Herring or Great Black-backed Gulls so obviously they were rare. Both Dwight (1895) and Saunders (1902) noted their presence on the island and the Herring Gulls, at least, were present in significant numbers in 1922 when F. H. Raddall was on the island (pers. comm.) At this time the terns were still present in enormous numbers and their eggs provided abundant food for the islanders. I believe that it was around 1920 that Herring Gulls began to breed on the island but between this date and the visit of J. S. Erskine in 1952 no naturalist seems to have reported the status of gulls and terns on Sable Island. In 1952 both species were breeding there (Erskine, 1954). The isolation of these colonies from areas of dense human population makes them ideal for studies of the importance of human wastes in determining gull reproductive success.

Sable Island is a crescent shaped sand bar 160 km southeast of Cape Canso, Nova Scotia at approximately 44°N, 60°W and about 45 km from the

edge of the continental shelf. It has gained some notoriety as a navigational hazard and has long excited natural scientists and dilettante historians and the voluminous literature concerning the island has been reviewed by Campbell (1963). The island is 33 km long and at no point more than 2 km wide. A spine of consolidated dunes runs along its length and long partially submerged sandbars extend to the northwest and northeast. A large salt lake, Wallace Lake, covers most of the sand flats on the south side of the island in winter, retreating to form two smaller lakes in summer. A line of dunes to the south of Wallace Lake disintegrated in the late nineteenth century, but a few, rapidly eroding remnants can be seen today.

The vegetation of the island has been described by Macoun (1899), St. John (1921) and most recently by Erskine (1954). Marram Grass (Ammophila brevigalata) and Beach Pea (Lathyrus japonicus) cover large parts of the island and only in the low, more stabilised areas around the ponds are diverse plant communities encountered. No tall shrubs or trees grow anywhere on the island. The succulent Sandwort (Arenaria peploides) occurs in large clumps on the east and west bars and to a lesser extent on the Wallace Lake sand plain.

The avifauna of the island has been described by McLaren and Ball (1972). The island is the sole breeding place of the Ipswich Sparrow (Passerculus sandwichensis princeps) and it supports a population of feral horses and is the breeding place of both Grey and Harbour seals (Halichoerus grypus and Phoca vitulina). Herring and Great Black-backed Gulls breed on all parts of the island but most of the colonies are concentrated on the dune edges on the north side of the island.

CENSUS OF NOVA SCOTIAN GULL COLONIES

Methods

Few gull colonies in Nova Scotia had been censused more than once in this century and no comprehensive list of nesting places or estimate of the size of the breeding populations of the two large gull species had ever been made. In an effort to supply this information and provide some base data that might allow future population changes to be detected, I made a survey of the entire province in the summer of 1971.

Most of the coastline of the province was examined and colonies located from the air, using a slow, two-seat, fixed-wing aircraft. Colonies were circled at around 300 feet altitude, from which height Herring and Black-backed gulls could be distinguished. The numbers of all gulls of each species were estimated by counting individuals in groups of less than about 25 gulls, by counting in fives and tens groups up to about 200 and by aerial photography of groups larger than this or groups which were unusually dense or difficult to count. Photographs were taken on 35mm Kodak Plus X film using a 135mm lens. Mosaics prepared from 5" x 7" enlargements allowed individual gulls to be identified and counted.

Ideally a population estimate should be based on nest counts, but as these are time consuming to do properly various other methods have been tried. Kadlec and Drury (1968a), working from an aircraft, counted gulls which they judged to be territorial, ignoring those loafing on the fringes of a colony or along the shore. They derived ratios, for several islands, of the number of nests and the number of attendant territorial gulls and while they found fairly constant ratios of slightly more than one adult

per nest, they varied between 0.98 and 1.45 depending on such factors as time of day and state of tide. They did not believe that population changes of less than 25% could be detected by this method.

I was unwilling to introduce a subjective element into my counts by making rapid judgements on which gulls were or were not territorial. Almost all islands in Nova Scotia on which gulls nest are small and there are never large numbers of apparently loafing or foraging birds. Nests are often built on the upper part of a shingle beach and it is not easy to distinguish between territorial and foraging birds in such circumstances. I counted all gulls on a breeding island and by doing my aerial counts were compatible with my ground counts made later. When one lands on a nesting island or approaches it closely by boat the gulls take wing in alarm and it is not possible to judge which birds are territorial and which are not. While counts thus made do not allow an exact estimate of the number of pairs breeding, future counts done either from the ground or the air will be comparable with my counts and increases or decreases should be detectable.

Sable Island presented an even greater problem. It is 20 miles long and gulls nest all over it solitarily and in colonies of various sizes, in mixed and single-species groups. The size of the island precluded nest counts. Nor could simple ratios of gulls to nests be expected to provide the basis of a good census: the very high egg and chick mortalities observed among the Herring Gulls particularly, meant that many nests had been abandoned and many pairs remaining in the colony had constructed new ones. The number of nests or even the number of full nests at any time could not be taken as an index of the number of pairs endeavouring to

breed there. However, three Herring and Black-backed Gull nesting areas had been studied intensively before the census on June the 14th and 15th and it was thought that the numbers of pairs in each area could be accurately determined by examination of nest history data.

For each colony numbers of clutches initiated were plotted against the date of initiation. While, for individual colonies, the relatively small numbers of nests and biases in deciding the exact date of laying of the first egg caused considerable irregularity in the plotted distribution, when data for all the colonies were pooled a bimodal curve approximating two overlapping normal curves was obtained. This curve was plotted on probability paper (Harding, 1949) and two separate normal curves were derived. The first and larger curve denotes the distribution in time of first clutch initiations while the second, smaller curve, represents second clutches or relays in new nests. Fitting of normal curves to these data allowed an estimate of the numbers of original nests to be made.

Another way of estimating the number of pairs in a colony was also tried. The number of nests with eggs or chicks present on the day of the census was determined. It was also noted that the mean length of time between loss of a clutch and relaying in the same nest was 15.9 days (16 examples). It was thought that the interval between clutch loss and relaying in a new nest would be somewhat longer so the number of nests which lost clutches up to ten days before the census and the number of new clutches initiated in the ten days after the census were added to the number of nests containing eggs or chicks on the census day. The former method of estimating number of breeding pairs gave 115 pairs and the latter gave 300 pairs in the three intensively studied nesting areas.

The nature of Sable Island's topography and the position of the main colonies made it impossible to distinguish these birds on territory within a colony. The largest concentrations of nesting Herring Gulls are on the dune edges on the north side of the island. The north shore is so narrow that any attempt to approach a colony results in most of the gulls in and around the colony taking flight before one is close enough to decide which are on nests and which are loafing on the periphery of the nesting area. So in the census all gulls around both the sample and censused colonies were counted. Gulls encountered away from colonies were counted separately and only numbers of gulls around colonies were used to estimate the number of pairs on the island.

A complete census occupied two days and could only be done in good visibility. The shape of the island facilitated censusing by travelling along the north and south shores of the island all birds can be seen and counted. On the first day of a census both north and south shores of one end of the island were done, the other end was done the following day.

Results

All known breeding concentrations of Herring and Great Black-backed gulls in Nova Scotia are shown in Figs. 1 and 2. Where colonies are close together it is impossible to show them as separately on maps of this scale, so these dots represent concentrations of breeding gulls perhaps in several closely spaced colonies.

All but one of the colonies was visited or surveyed from a low-flying aircraft. No count was done of Brier Island but E. L. Mills has provided me with a rough estimate of the numbers of gulls breeding there. St. Paul Island, off the northern coast of Cape Breton Island, was not visited until

Fig. 1. Concentrations of breeding Herring Gulls in Nova Scotia in 1971.

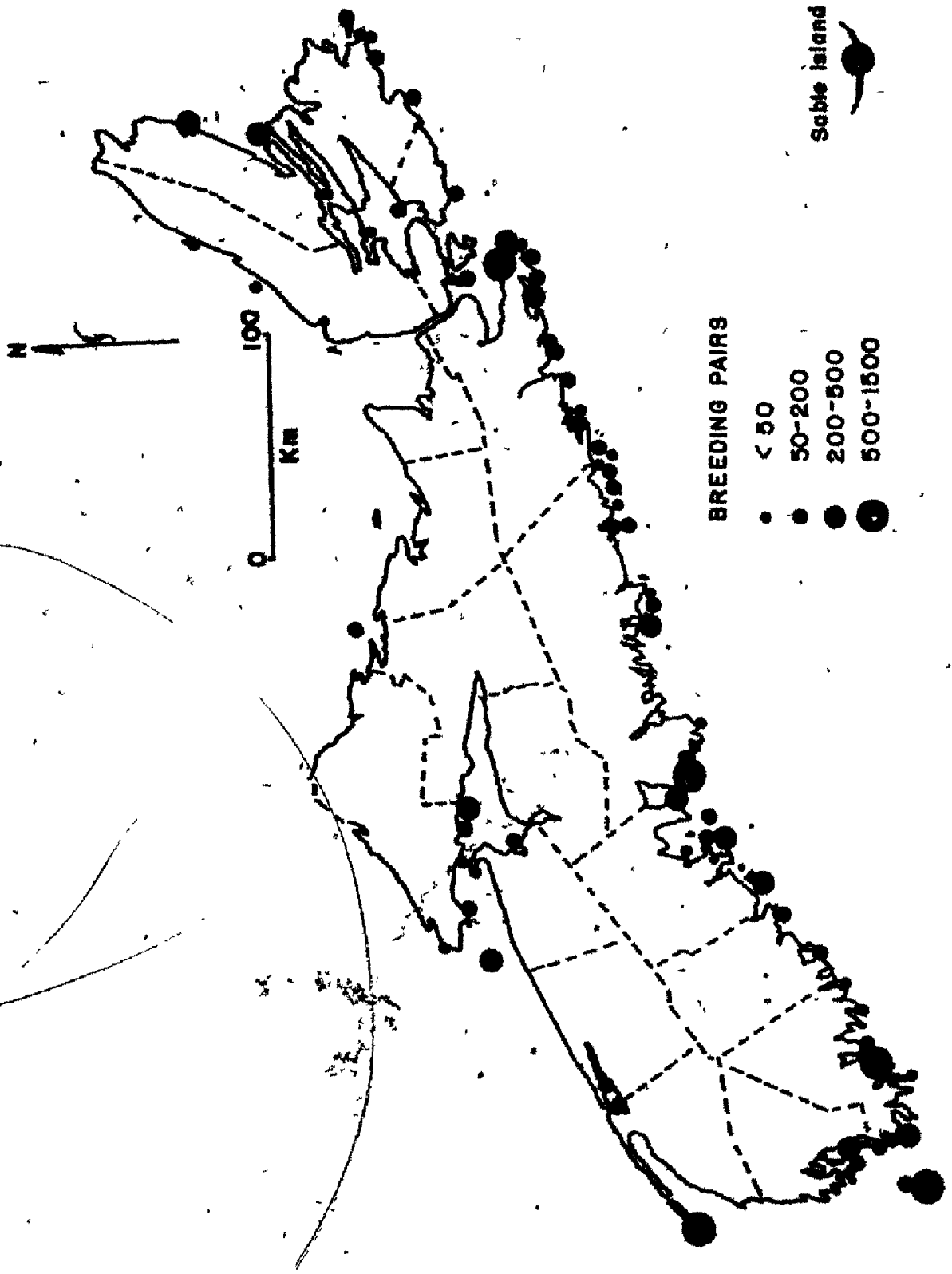
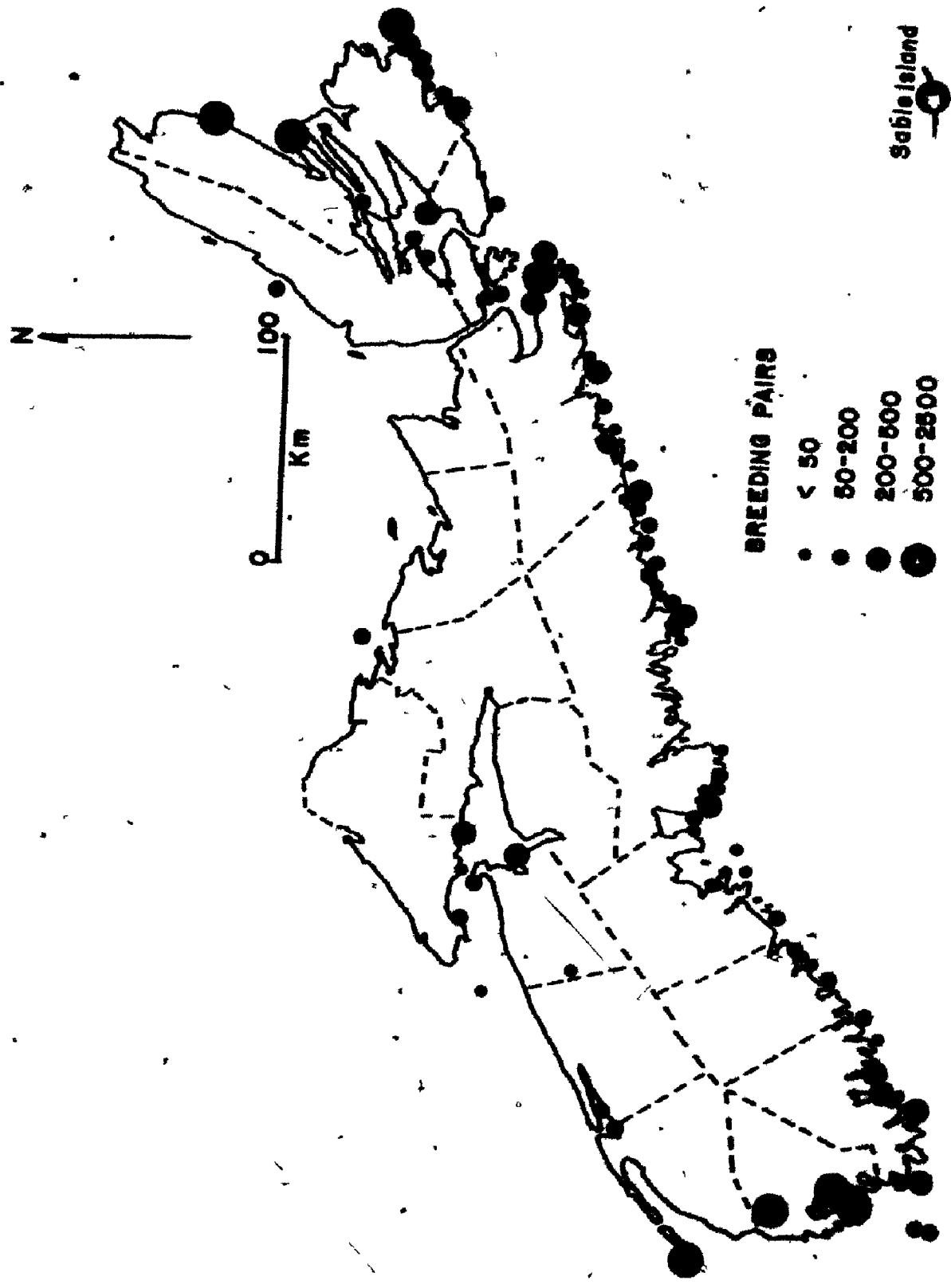


Fig. 2. Concentrations of breeding Great Black-backed Gulls in Nova Scotia in 1971.



after the breeding season and it is not known if gulls breed there. In all 111 nesting places of the Herring Gull and 141 of the Great Black-backed Gull were found in which an estimated 15,000 pairs of the Great Black-backed Gull and 14,700 pairs of the Herring gull breed. These estimates are tentative only. Kadlec and Drury (1968b) counting only suspected territorial gulls found a maximum bird to nest ratio of 1.48. As I have undoubtedly counted a few birds on each colony that they would have not considered territorial I employed a ratio of 1.5 in making these estimates.

The breeding distribution of both species of gulls is quite similar in Nova Scotia, with the greatest concentrations of breeding birds in colonies on the eastern side of the province where there is an abundance of small islands suitable for their nesting. On the western coasts of the province there are few islands and all of these which are undisturbed accommodate nesting gulls. Large concentrations of breeding birds occur around areas with large fish landings such as Yarmouth and Canso. Harris' (1970) suspicions are that urban dumps are a more important food source than fish processing plants, as modern methods of fishing and processing involve little dockside or factory waste. In Nova Scotia however, fishing is carried out from small towns all around the coast and this type of fishing does produce a significant amount of food for gulls. But there are far fewer gulls breeding near Halifax than might be expected. This may be explained by a paucity of islands immediately north of the city and a fairly regular disturbance of many of the islands immediately to the south of it.

The length of the Nova Scotia coast exceeds that of New England yet

our breeding population of Herring Gulls and Great Black-backed Gulls combined is less than 30,000 pairs, less than half that estimated by Drury (1963) for New England. This coincidence of high gull and human populations and the distribution of breeding sites in this province gives some support to the hypothesis that maintenance of high gull populations is dependent on an abundance of human wastes.

The numbers of Herring and Black-backed gulls seen on each census of Sable Island are shown in Tables 1 and 2. The numbers in these tables include gulls on colonies as well as those observed on loafing areas. For the census of June 14/15, 1970 these loafing birds were tabulated separately, though at this time there were very few: only 220 Herring and 59 Great Black-backed Gulls. Censuses were carried out on June 3 and 5, June 14 and 15, July 10 and August 22 and 23 of 1970 and on July 14 and 15 of 1971.

The locations of colonies of Herring and Great Black-backed Gulls on Sable Island are shown in Figs. 3 and 4 and the boundaries of the census areas are shown in Fig. 5.

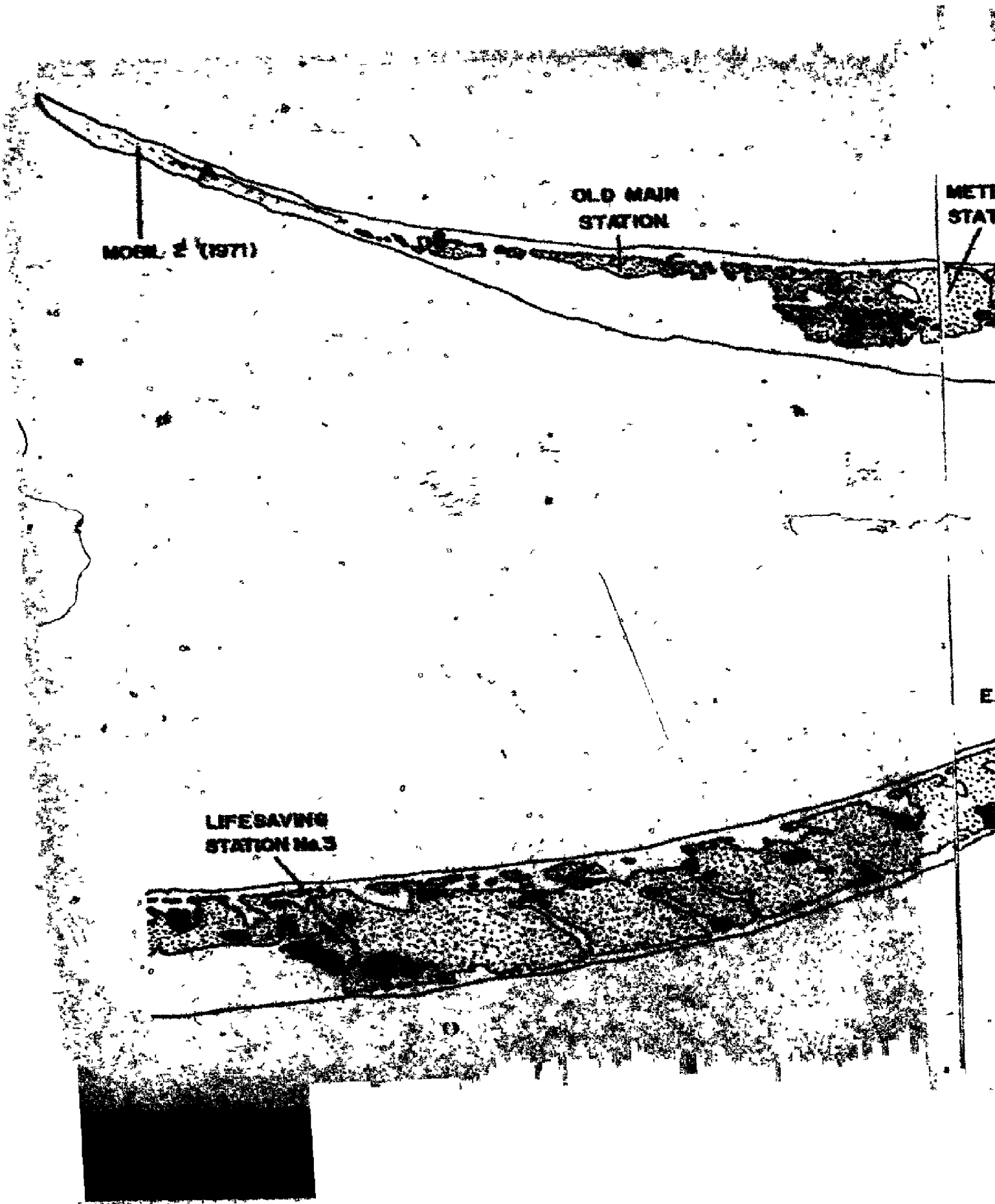
The number of breeding pairs in the Herring Gull colonies B, C and D was determined to be around 300 to 315 pairs. The numbers of birds seen on these colonies is shown in Table 3. Depending on the population assumed for these colonies the total ratio of birds to pairs was 1.41 to 1.48. The total number of birds seen on the whole island on this census was 3078, of which 66 were in loafing groups on the Wallace Lake sand flats and 154 were counted on the east and west sand bars. There were few or no Herring Gulls nesting on the East Bar, and as the numbers of Herring Gulls breeding on the West Bar were known the birds observed on these areas were omitted from the total used to calculate the numbers of breeding pairs.

Table 1. Numbers of adult Herring Gulls counted on census of Sable Island in 1970 and 1971

Area	June 3/5	June 14/15	July 10	August 22/23	July 12/15
	1970	1970	1970	1970	1971
A	71	116	75	133	93
B	133	127	99	75	110
C	240	221	123	34	115
D	14	24	22	0	37
E	471	492	212	271	218
F	367	348	264	48	304
G	200	207	191	162	175
H	21	25	14	21	26
I	79	69	59	41	72
J	71	60	64	38	90
K	90	115	245	154	311
L	62	60	204	174	186
M	425	517	347		330
N	271	263	282	217	342
O	182	164	112	219	109
P	183	188	87	48	55
Q	30	26	54		90
R	42	56	68	150	102
	2852	3078	2524	1785	2765

Table 2. Numbers of adult Great Black-backed Gulls counted on censuses of Sable Island in 1970 and 1971.

Area	June 3/5	June 14/15	July 10	August 22/23	July 12/15
	1970	1970	1970	1970	1971
A	37	30	40	110	55
B	39	40	31	8	30
C	7	13	7	2	10
D	2	0	5	0	2
E	109	83	29	35	42
F	57	44	24	8	28
G	51	65	39	38	29
H	10	10	4	1	4
I	90	83	103	33	82
J	95	103	81	603	194
K	94	43	67	76	52
L	15	9	12	51	5
M	294	279	141	262	112
N	230	251	183	281	223
O	157	142	182	15	107
P	8	5	23		17
Q	10	8	65	155	112
R	44	36	9		27
	1349	1244	1015	1878	1131



MOBL. 2 (1971)

OLD MAIN
STATION

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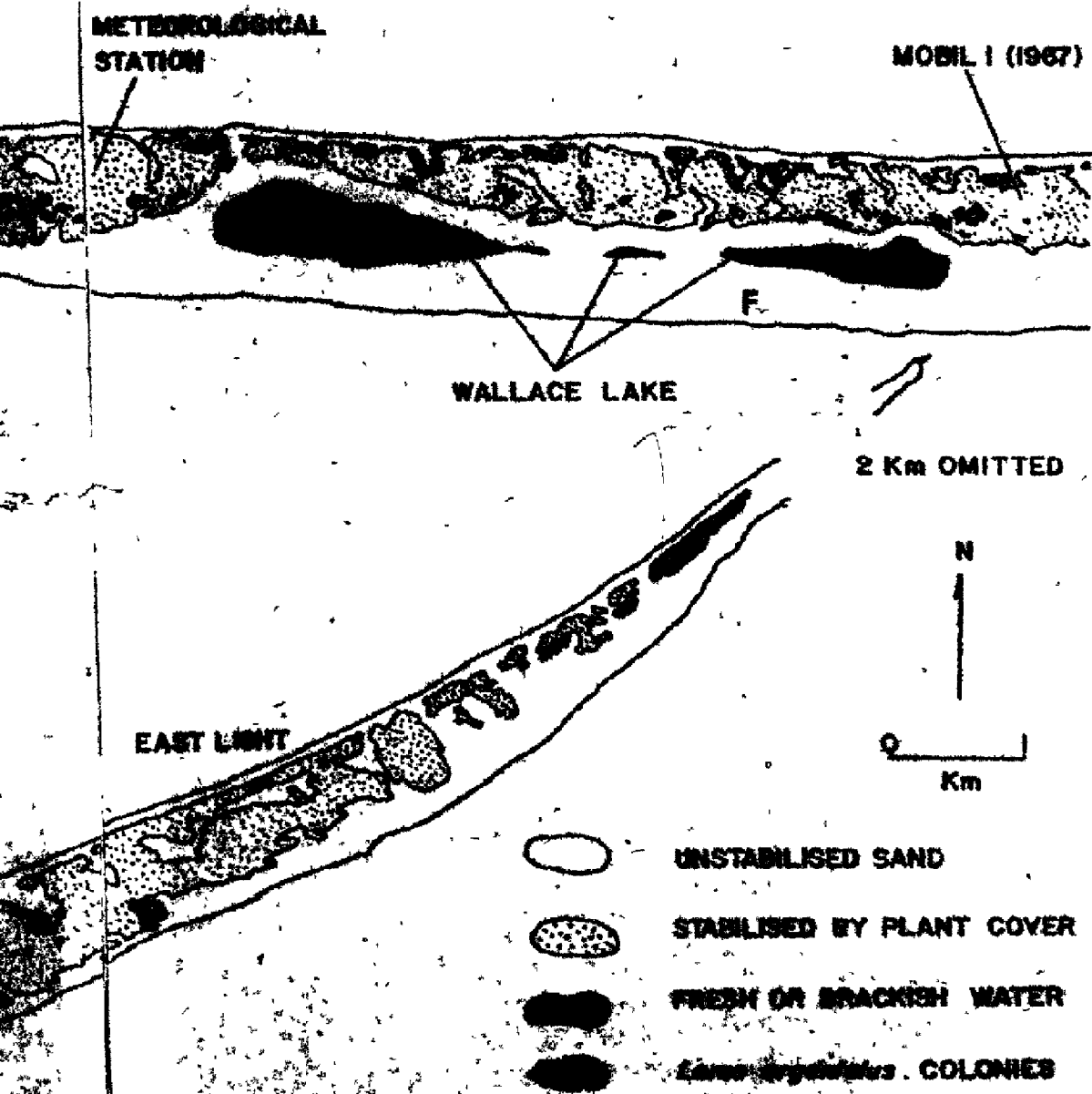


Fig. 3. The locations of colonies of Herring Gulls on Sable Island 1969-1971. Letters indicate colonies studied.

MOBL 2 (1971)

OLD MAIN
STATION

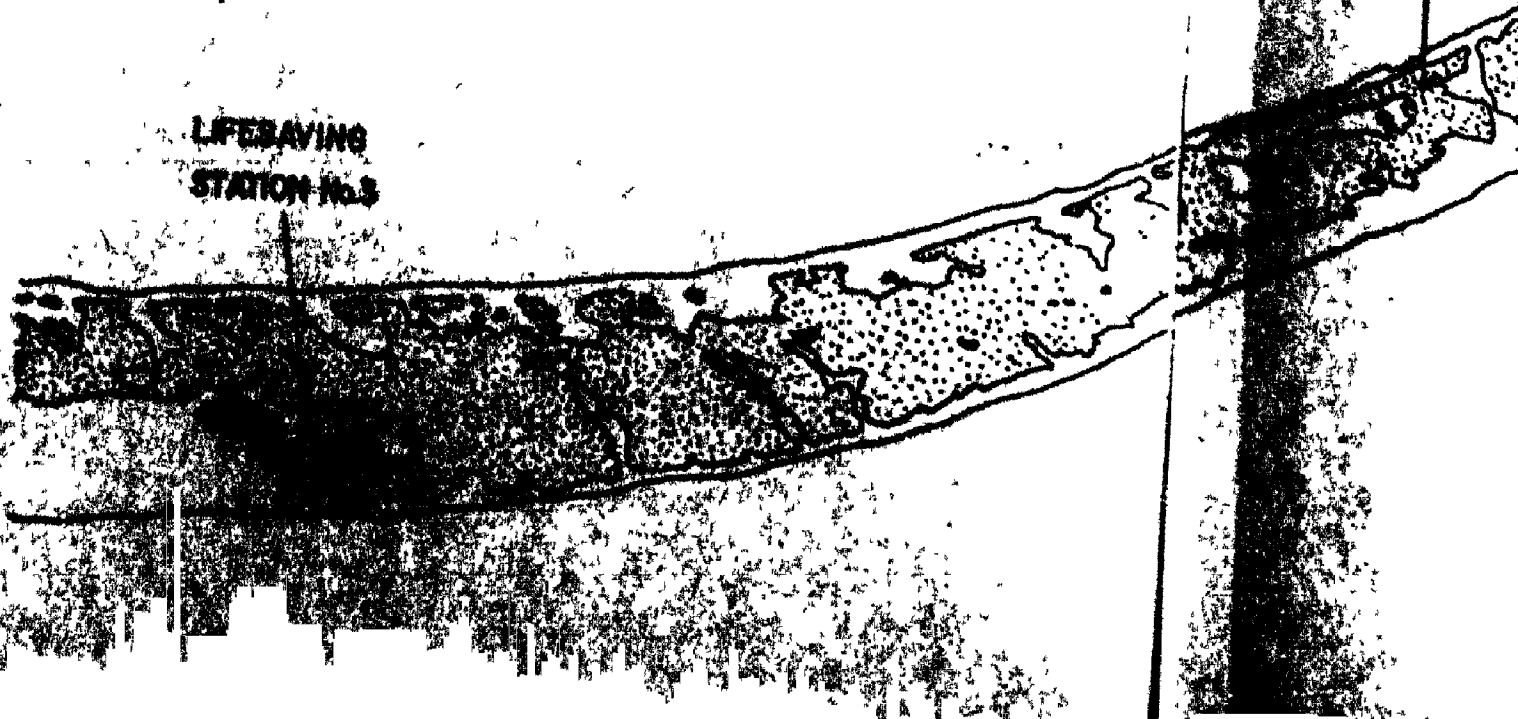
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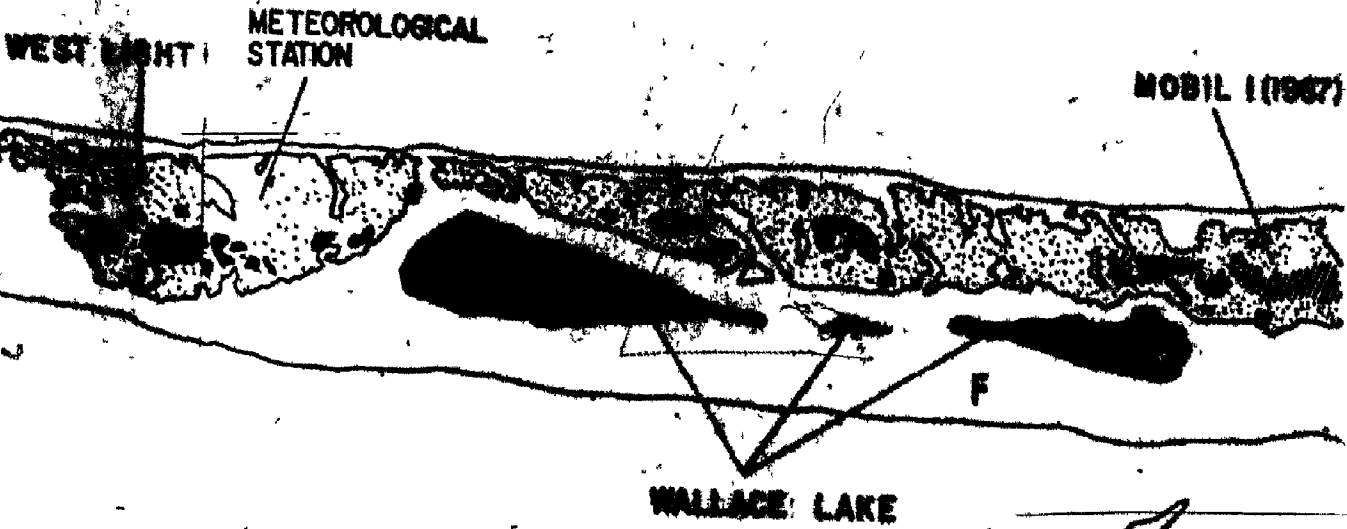
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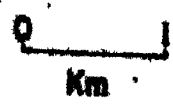
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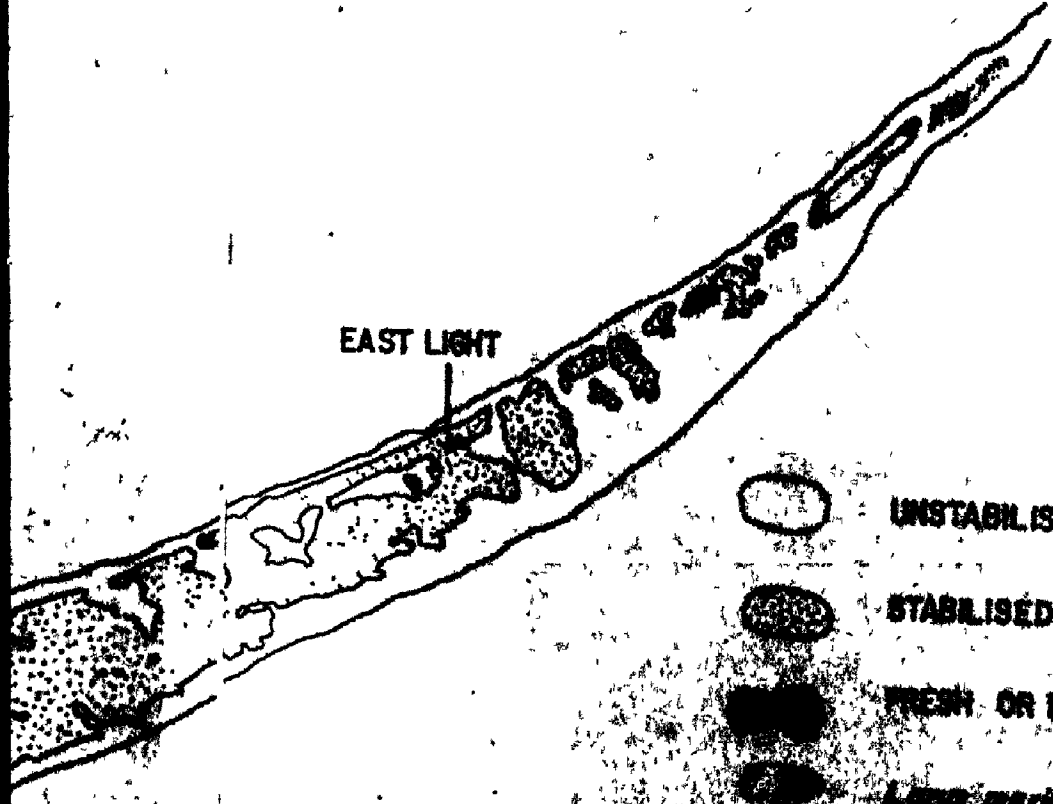
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EAST LIGHT

-  UNSTABILISED SAND
-  STABILISED BY PLANT COVER
-  FRESH OR BRACKISH WATER
-  *Lybia marinus* COLONIES






Fig. 4. The locations of colonies of the Great Black-backed Gull on Sable Island 1969-1971. Letters indicate colonies studied.

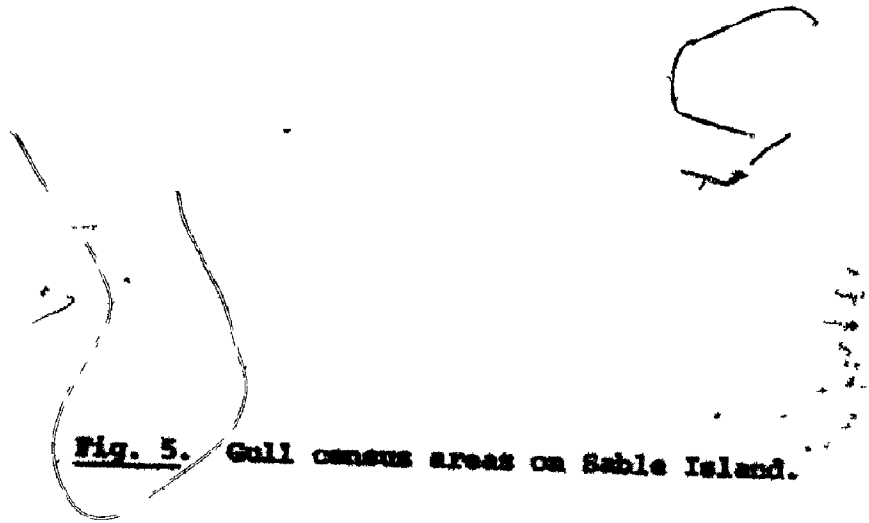


Fig. 5. Gull census areas on Sable Island.

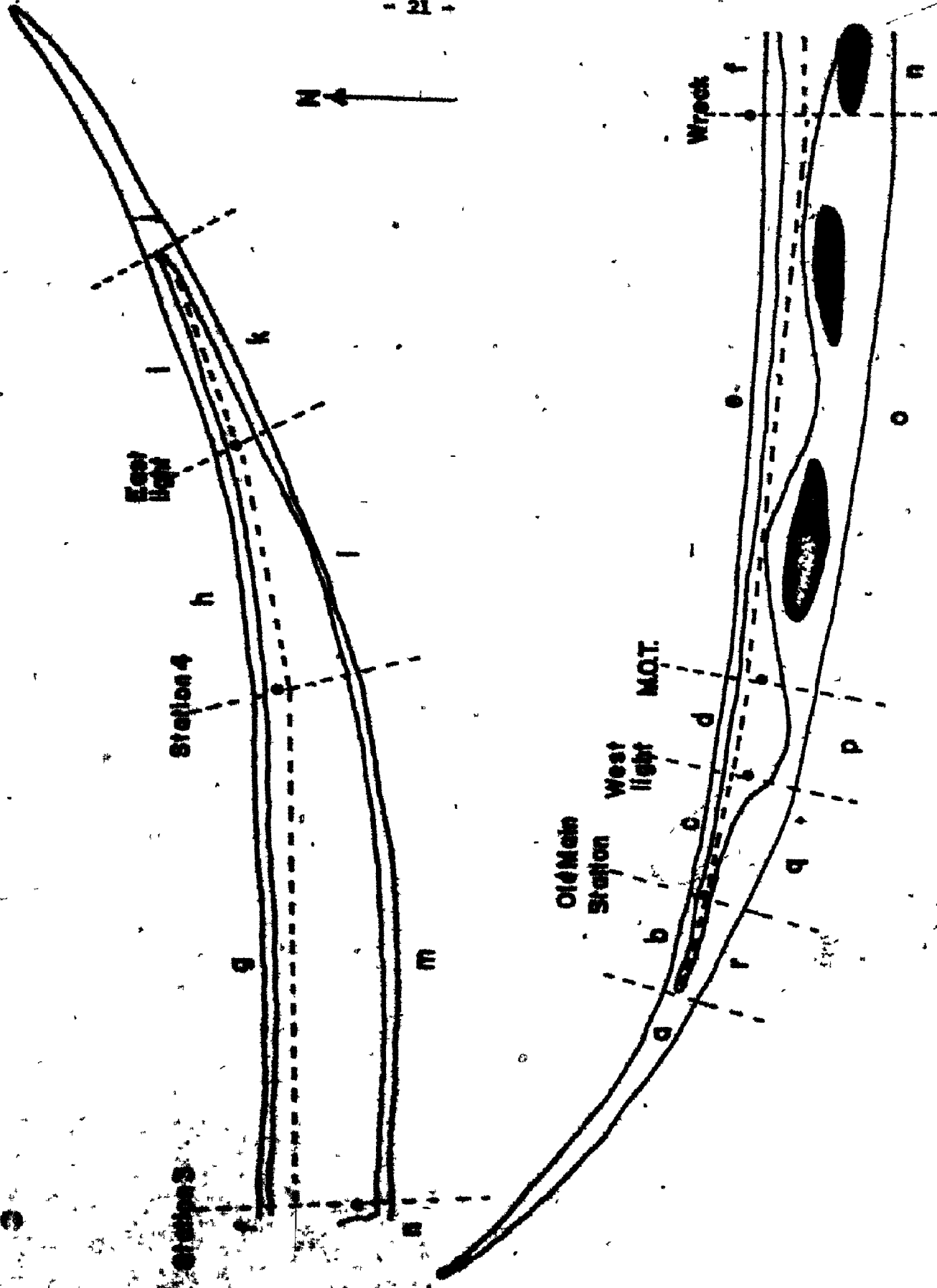


Table 3. The ratio of standing birds to breeding pairs of Herring Gulls (Larus argentatus) in three colonies on Sable Island June 14, 1970..

<u>Colony</u>	<u>Number of Breeding Pairs</u>	<u>Number of Standing Birds</u>	<u>Number of Standing Birds Per Breeding Pair</u>
B	99	142	1.432
C	108	149	1.370
D	108	154	1.426
	<u>315</u>	<u>444</u>	<u>1.409</u>

A total of 2058 Herring Gull adults were observed in the consolidated part of the island, corresponding to a breeding population of 1933 to 1998 pairs. Twenty-one nests on the West Bar were active within ten days before and after the census, so the total population of Sable Island is between 1950 to 2020 pairs.

As the egg and chick mortality of the Great Black-backed Gull is appreciably less than that of the Herring Gull, and as they relay so rarely it was thought that the best estimate of the number of breeding pairs in an area was a simple total of nests that had contained eggs at any time in the breeding season.

A total of 39 Black-backed Gull nests were found on the dunes of the island west of D. O. T. and 83 adults were on or around this area. An additional 19 were loafing on the sand flats south of the Old Main Station. A ratio of 83 : 39 or 2.128 birds per breeding pair was thus obtained. A total of 1244 adults were seen on the June 14 and 15 census; 64 of these were in loafing groups at the ends of the East and West Bars and 59 were in loafing groups on the Wallace Lake sand flats. The remaining 1121 were considered to be on or around colonies. An estimated 527 pairs result from application of an adult to nest ratio of 2.128. Seven pairs of Black-backs nested on the West Bar bringing the total to over 630 pairs.

The numbers of Herring Gulls on the island, while remaining essentially unchanged between the second and the fourteenth of June declined throughout the breeding season. Obviously, a great proportion of the birds that lose clutches leave the island sooner than those that succeed in hatching a clutch or rearing chicks. No juvenile or immature Herring

Gulls were detected on any of the breeding season censuses, but this is hardly surprising for although they migrate north in the summer to the latitude of Sable Island and beyond, they do not move far from the coast and are most unlikely to be encountered in any numbers on an island as far off shore as Sable Island. (Phillips in Brown 1967a)

Notwithstanding the lower egg and chick mortalities of the Black-backed Gull its numbers decreased no less than the Herring Gulls' between June 14 and July 12. This may indicate the presence of a population of non-breeding birds in adult plumage and the presence of 174 second and third year birds on the July count and the high adult to nest ratio of this species also point to a fair sized non-breeding population of this species. The Black-backed Gull is known to venture farther off shore than the Herring Gull (data from P.I.R.O.P., R.G.B. Brown pers. comm.) and so the presence of so many immatures on Sable Island is not too surprising.

ESTIMATES OF REPRODUCTIVE SUCCESS

Methods

Each colony was visited every four days in the course of the breeding season except where weather or transportation problems interrupted the schedule. When a nest was found containing eggs it was marked with a numbered wooden stake placed inconspicuously protruding 4 to 9 inches from the ground within 2m of the nest. Gulls often build "practice" nests in which eggs are never laid, so only those nests in which eggs were found were assigned a number and were plotted on colony maps. Eggs were marked on the pointed end with a dot of colour from a felt marking pen and different colours were used for each egg in a clutch. If colours faded appreciably they were periodically renewed.

The length and maximum diameter of each egg was measured to the nearest 1/100 inch using a vernier caliper. Roughness of the egg shell and the need for speed in order that colony visits are not unnecessarily protracted, made it impossible to make measurements of eggs with a repeatable accuracy in units of less than 1/100 inch. Metrically divided calipers allowed measurements of tenths and hundredths of a centimetre, the former being too coarse a unit and the latter too fine for the purpose.

Visits to the colony during the egg stage were made as brief as was compatible with accurate observation and on the few hot days in May and June when eggs were in the nest, colonies were not visited between noon and 16.00 hrs in order that eggs not be long exposed to hot sun.

On the first visit after hatching the chicks were marked on the ventral side with small spots of an alcoholic solution of red, yellow, blue or green

dye. The spots were small and were normally invisible from the side or from above so they could not have added to the hazards of a chick's existence. These dye spots rapidly faded but they served to identify chicks until they were large enough to bear a numbered aluminum leg band. Black-backs could not be safely banded until the age of about 12 days whereas Herring Gulls, which had a smaller band can be banded at six days.

On every visit the presence or absence of eggs or chicks was noted. If small chicks were discovered hiding in vegetation their colour code or band number was determined, often without panicking them. However, if larger chicks are disturbed they often panic or bolt. They may be quieted by hiding their heads in dense vegetation or, better, by covering with a coat. After a few minutes one may remove the coat and run quickly from the area. If treated thus, a panicked chick almost invariably remains in its territory and is soon joined by an adult. It is possible to run thus from a nest without disturbing other birds nearby because on Sable Island the colonies are strung out along the edge of dunes so that one was seldom more than 20 m from the edge of a colony.

Colony A consisted of nests of both species of gulls on the sand bar on the west end of the island. Vegetation is limited to occasional tussocks of Sandwort (Arceuthobium). Nests of both species of gull are built on the sandwort tussocks and on piles of driftwood in the central part of the whole length of the bar. Nests are seldom closer than about 25 m apart.

Colony B is concentrated on the end of the heaviest vegetated part of the island. Great Black-backs were in conspicuous positions on the

tops of the dunes and Herring Gulls occupy the steep dune sides and less commanding positions on top of the dunes. Colony C is similar in topography but only two or three pairs of Great Black-backed Gulls nest among the Herring Gulls. The colony is concentrated on the steep dune sides on the north side of the island though a few pairs nest on the flat grassy tops of some isolated dunes.

Colony D is quite different from the previous two colonies. The dunes on the south side of the island are gently sloped and there are few deep blow outs with steep, cliff-like sides. Vegetation is much sparser than in Colony C, in which thick stands of beach pea (Lathyrus japonicus) provide cover for chicks in June and July. This colony was disturbed fairly frequently in 1970 by an island resident who regularly exercised his dog within its boundaries. Colony E was also subject to some disturbances in 1970 and no more than a half dozen or so nests were laid here in that year. Only Herring Gulls breed here, nesting on the ground close to several brackish ponds which dried up in late summer.

Colony F comprises a series of isolated dunes between lake Wallace and the sea. These are the last remnants of a continuous line of dunes which once separated the lake from the sea. Black-backed Gulls nest on the grassy tops of these dunes and a few Herring Gulls breed on the sides.

Results

Herring Gulls

It is usual in gull banding studies to calculate a mean clutch size. This has little real value and Harris (1970) has pointed out that the more intense the study the closer the mean clutch size approaches

three. On Sable Island egg mortalities were so high it was not reasonable to hope that I found all eggs laid in my relatively infrequent visits and so no estimate of mean clutch size is presented.

The mortality schedules of chicks and dates of laying of all dateable eggs in both 1969 and 1970 are presented in Figs. 6 and 7 and substantial differences are immediately apparent. The laying season in 1970 was no more protracted than in 1969 but a greater proportion of the eggs were laid late in the season in 1970. These clutches I interpret as second clutches of pairs that have lost their first clutch, and the late dates of initiation of clutch as of one and two in all colonies supports this supposition. The difference in hatching success in the two years is highly significant ($\chi^2 = 17.31$, $df = 1$, $p < 0.001$) and the change in laying pattern and hatching success are undoubtedly causally linked. The causes of Herring Gull egg mortality in 1969 and 1970 are shown in Tables 4 and 5.

In gull colonies in widely separated parts of the world hatching success commonly reaches or exceeds 90%. Darling (1938) for instance recorded Herring Gull hatching successes of 86% and 96% in two years in Scotland and Faluian recorded a 90% success in one year in Denmark. In the following year, however, he recorded a hatching success of only 53.5% in the same area. Such variability is not unusual and it has not been satisfactorily explained in all cases. Certainly weather (Faluian, 1952), accumulations of toxic chemicals (Turner, 1970; Smith, 1968) and disturbances are obvious causes of egg mortality but the timing of climatic stress and disturbance are also important. Fitching (1968) has shown that disturbance during egg laying produces a significantly greater egg loss than

Fig. 6. Schedules of mortality of Herring Gull chicks in all colonies studied in 1969(a) and 1970(b). Shaded area indicates chicks whose remains were found; unshaded area indicates chicks which disappeared.

Fig. 7. Dates of laying of eggs in all Herring Gull colonies studied in 1969(a) and 1970(b).

Outer envelope: dates of laying of all eggs

Shaded-area: dates of laying of all eggs hatching

Black area: dates of laying of all eggs producing fledged young.

In 1970 Colony D was not studied beyond the hatching of chicks and so those that fledged from that colony are not included here.

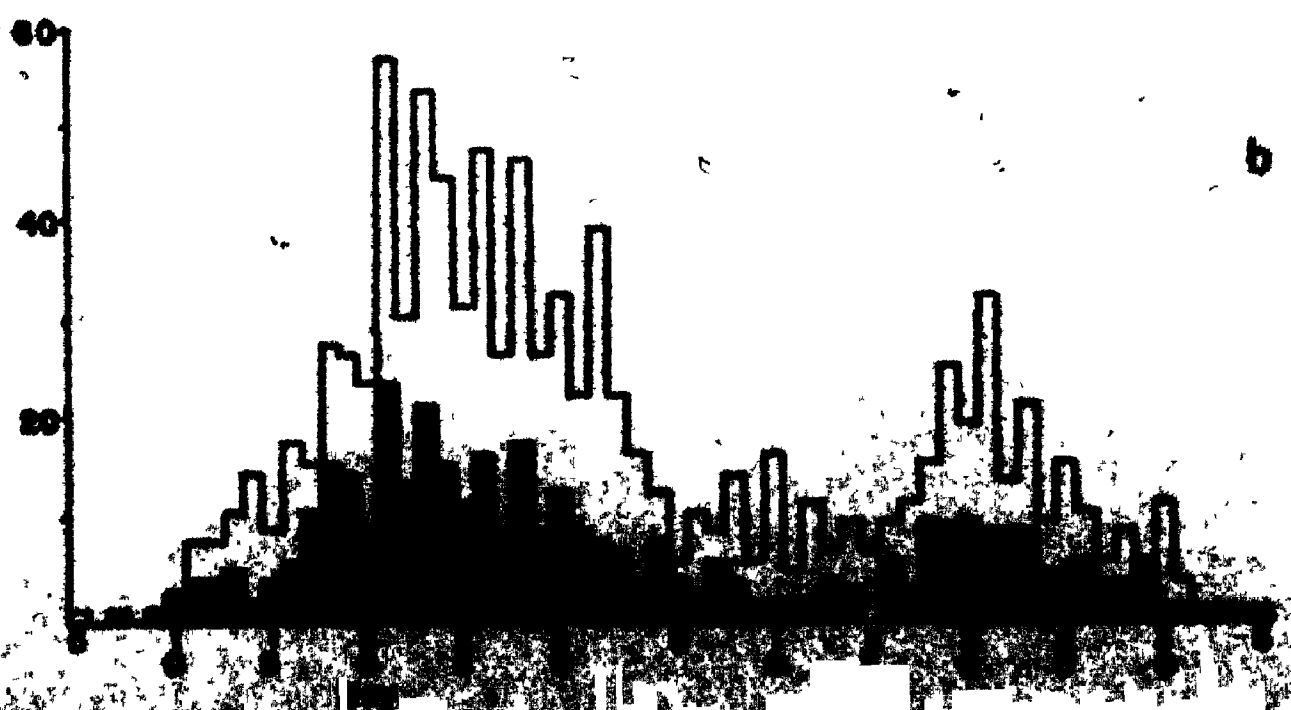
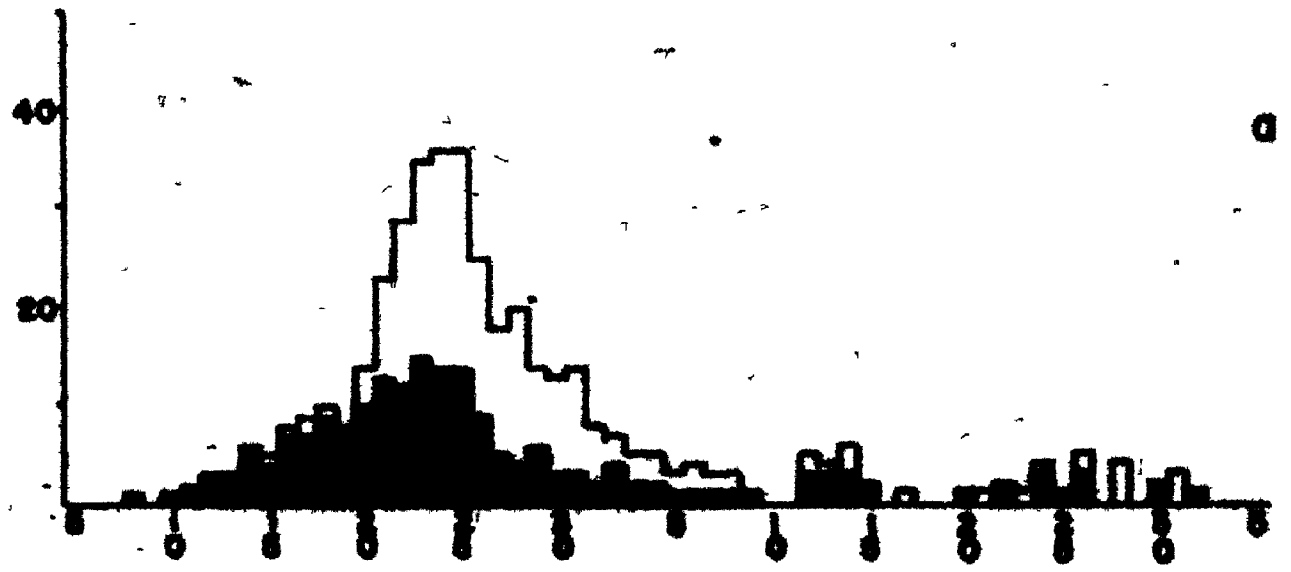
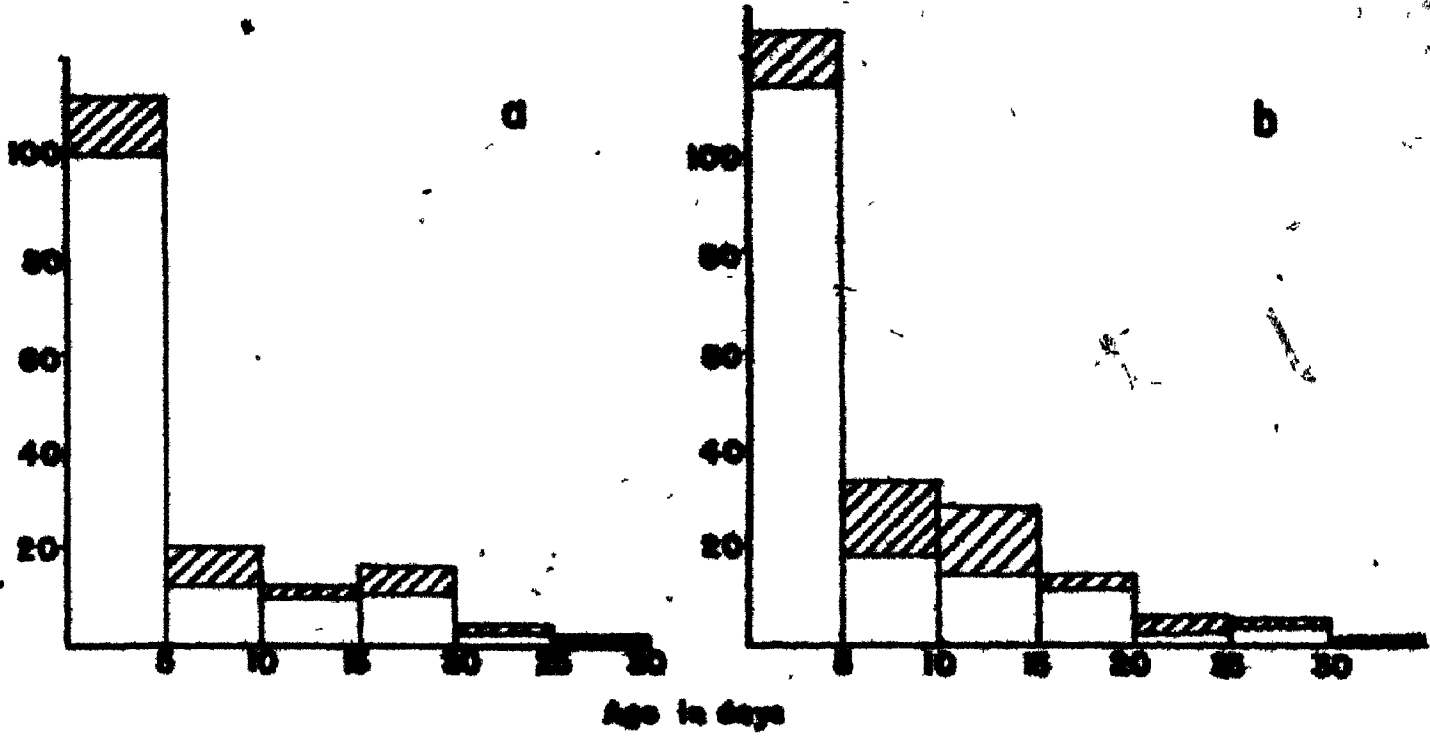


Fig 4. Egg mortality of Herring Gulls, 1969

	COLONY				Total
	A	B	D	E	
Laid	24	40	304	56	424
Disappeared	16	8	142	22	188
Broken in Nest	-	-	12	-	12
Infertile	-	1	4	3	8
Destroyed by Ravens	-	-	7	-	7
Land Slide	-	-	-	-	-
Abandoned Nest	2	3	11	-	16
Hatched	6	28	28	31	193
% Hatched	25.00	70.00	42.11	55.36	45.52

Table 5. Egg mortality of Herring Gulls, 1970

	COLONY				
	A	B	C	D	Total
Laid	79	301	343	324	1047
Disappeared	28	196	166	159	489
Broken in Nest	3	43	-	34	80
Infertile	2	9	4	3	18
Destroyed by Horses	2	11	1	5	19
Landslide	-	-	4	-	4
Abandoned Nest	-	8	21	6	31
Hatched	44	94	147	117	402
% Hatched	55.70	31.23	42.86	36.11	38.40

disturbance during incubation.

The hatching success in colonies in New England studied by Kadlec and Drury (1968) ranged from 70% to 80% in the years 1963 to 1966, in close agreement with Erwin's (1971) values of 63 and 82% in Rhode Island. Hunt (1972) however, working in colonies in Massachusetts reported hatching successes from 19 to 54%. His colonies were chosen as being different distances from sources of food and he noted an inverse correlation of hatching success with distance from food sources.

On Nable Island the hatching successes, while differing significantly between colonies, are comparable to those observed by Hunt.

Unfortunately the hatching success varies greatly in colonies and years, a χ^2 test for heterogeneity among colonies gives significant values ($P < 0.05$) in both years. There is no ready explanation for these differences but they are no greater than have been observed by other investigators. The higher hatching rate in Colony A in 1970 is particularly hard to explain as the overall hatching success for that year was lower than for 1969. The summer months of 1969 were cooler and wetter than in 1970 (Stobo, 1973) so climatic factors seem to be an unlikely explanation for the difference. The major source of egg and chick mortality is predation by other gulls and this might be affected by investigation technique. This seems unlikely to explain the differences as colony work was presumably less clumsy in the second year. However I arrived earlier in the second year. In 1969 I missed the beginning of laying and my time spent in the colonies during the laying period was less.

Nests on Colonies B and C, 1970 and Colony D, 1969, were divided arbitrarily into areas of high and low nest density, each containing

approximately equal numbers of nests. Tests revealed no significant differences in hatching or fledging success between high and low density areas. Only in Colony B was the fledging success of eggs laid in dense areas much less than that of eggs in sparse areas. In this colony the densest part of the Herring Gull colony was adjacent to the Great Black-backed Gull colony, and the large but non-significant difference in success between the areas is undoubtedly due to its proximity.

Substantial differences in hatching and fledging success of eggs laid early and late in the season have been reported. Black-headed Gulls (Larus ridibundus) Patterson (1965), and Herring Gulls (Brown, 1967b, Kadlec, Drury and Onion, 1969, Parsons, 1971) have been shown to produce most fledged young from eggs laid during the peak of laying. A decline in fledging success throughout the season has been observed for the Lesser Black-backed Gull (Larus fuscus) by Brown (1967b) and for the Herring Gull by Poynter (1949) and Kadlec and Drury (1968a). The generally greater success of early and peak clutches might be explained if one accepts that inexperienced birds may lay later (Coulson and White, 1958, 1960), being less influenced by the social stimulation which is sometimes thought to synchronize the laying of experienced birds (Darling, 1938; Coulson and White, 1960). Their inexperience presumably renders them less able to guard eggs and feed young.

If the season is divided, as in Tables 5 and 7, it will be seen that the highest hatching success in both years is found in those eggs laid before the peak. So great are the variations between colonies, however, that one must consider the differences between the time periods as being extremely small. Between years there are substantial variations as well.

Table 6. The percentage of Herring Gull eggs hatching, 1969.

Date of Laying	COLONY				Total
	A	B	D	E	
Before May 21	0	80	92	63	84
May 21-30	0	60	33	68	36
May 31-June 9	0	78	14	44	33
June 10-19	0	100	40	-	61
After June 19	50	25	56	-	48
Peak: May 21-30	0	60	33	68	37
All other times	33	76	63	44	59

Table 7. The percentage of Herring Gull eggs hatching, 1970.

Date of Laying	COLONY				Total
	A	B	C	D	
Before May 21	50	34	61	40	47
May 21-30	27	37	40	38	38
May 31-June 9	23	22	51	35	41
June 10-19	20	32	23	30	35
After June 19	11	14	43	38	37
Peak I: May 21-30	27	37	40	38	38
Peak II: June 15-25	63	41	41	48	46
All other times	67	20	51	32	37

Colony B, for instance, shows a very different pattern of hatching success in 1969 and 1970, perhaps partly reflecting the difference in coverage of the colony in the two years. In 1969 only a few nests on sand cliffs were studied while in 1970 all the nests in the colony were observed. Furthermore, as I didn't arrive on the island until May 22 in 1969, I missed the earliest egg mortality. For the differences in Colony A I have no explanation; in both years nests in similar situations were observed. Thus, while there are indications that earlier eggs may be more successful the variability between colonies and years is so great that no generalizations can confidently be made.

The data in Tables 6 and 7 are also arranged to display the hatching rate of the eggs with respect to times of peak laying. In 1969 there was no pronounced second peak of laying and hatching rates were generally higher for eggs laid outside the peak time. Colony E, which is exceptional in this year, is a small diffuse colony and there is no pronounced peak of laying, so the figures quoted for this, as well as for Colonies A and B, are probably of limited comparative value. In 1970, the numbers of nests studied was higher and reproductive success generally lower than in 1969 and it is clear that the eggs laid in the first peak, May 21 to May 30, have a lower hatching success than those laid before or after this period. On the whole those eggs laid before or after this period. On the whole those eggs laid in the second peak of laying are the most successful, though in Colony C, the most successful colony in 1970, those laid outside the peaks achieved the highest hatching rate. Though there is a disappointing variability in these results, it may be observed that in both years the early eggs are not consistently more successful than those

laid later, and in this particular the Herring Gulls breeding on Sable Island are different from most previously described populations.

In Tables 8 and 9 the fledging success of chicks hatching from eggs laid at different times is analyzed. Unhappily the overall results for the two years are quite different. In 1969, in particular, the partitioning of relatively few data results in great variations between periods. It is interesting to contrast colonies B and C in 1970. Colony B, has within it large numbers of breeding Black-backs, Colony C, very few. The percentage of chicks fledging in Colony C does not change notably or consistently as the season progresses, but Colony B shows a generally increasing success from early to late clutches. During the time when chicks from later clutches are being reared the numbers of resident Black-backs in the area is reduced. Many have lost their clutches or broods and left and others have removed their chicks from the nest area to a less crowded chick rearing territory inland and further away from the Herring Gulls.

This pattern is still detectable if the season is divided into peak and non-peak periods. Colony B, containing numerous Black-backed Gulls, enjoys its greatest chick survival in eggs laid during the second peak, while Colony C chicks are not notably more or less successful in either period. Colony D in 1969 and Colony C in 1970 were both large colonies showing peaks of laying and containing very few pairs of breeding Black-backs. Interestingly, both these colonies were the greatest success for birds hatching from peak eggs. Colony A, like Colony B containing numerous Black-backs, shows no such trend.

Tables 10 and 11 show the overall fledging success of eggs. The total fledging success in each year closely reflects the hatching success

Table 3. The percentages of hatching chicks which fledge, Herring Gulls, 1969.

Date of Laying	COLONY				Total
	A	B	D	E	
Before May 21	-	25	7	40	14
May 21-30	-	17	18	20	18
May 31-June 9	-	0	0	0	0
June 10-19	0	29	0	0	18
After June 19	0	0	0	0	0
Peak: May 21-30	-	17	18	20	18
All other times	0	16	5	25	10

Table 9. The percentage of hatching chicks which fledge, Herring Gulls, 1970.

Date of Laying	COLONY				Total
	A	B	C	D	
Before May 21	33	0	23	-	13
May 21-30	0	16	38	-	19
May 31-June 9	38	13	19	-	17
June 10-19	25	31	33	-	21
After June 19	17	60	40	-	21
Peak I: May 21-30	0	16	38	-	26
Peak II: June 16-25	25	33	38	-	33
All other times	29	18	23	-	35

Table 10. The percentage of Herring Gull eggs giving rise to fledging chicks, 1969.

Date of Laying	COLONY				Total
	A	B	D	E	
Before May 21	0	20	6	25	11
May 21-30	0	10	6	14	7
May 31-June 9	0	0	0	0	0
June 10-19	0	29	0	-	11
After June 19	0	0	0	-	0
Peak: May 21-30	0	10	6	14	7
All other times	0	12	3	12	6

Table II. The percentage of Herring Gull eggs giving rise to fledging chicks, 1970.

Date of Laying	COLONY				Total
	A	B	C	D	
Before May 21	17	0	14	-	8
May 21-30	0	6	15	-	10
May 31-June 9	23	3	10	-	10
June 10-19	20	10	8	-	11
After June 19	12	8	17	-	13
Peak I: May 21-30	0	6	15	-	10
Peak II: June 16-25	16	16	16	-	16
All other times	19	0	2	-	8

rates and the variations between colonies and years are no less. As Colonies A and B were not studied in total in 1969, the figures for Colonies B and E are of greatest interest. All fledging birds came from eggs laid before the end of May even though there were many eggs laid after this period which hatched. This contrasts strongly with 1970 when fledging rates tended to increase as the season progressed. When the data are grouped by peaks of laying, the results are somewhat inconclusive for 1969. Both Colonies B and C in 1970 show the best fledging rates for eggs laid in the second peak of laying.

The high success rate shown by Colony A for extra-peak layings is of no real consequence as it is based on small numbers and these eggs were laid by somewhat aberrant, isolated nesting gulls. Like the hatching rates observed in this study these results are quite at odds with the pattern observed in other studies. Only Harris (1969) has reported an increase in success of later clutches. He hypothesizes that as gulls are increasing rapidly in numbers, normal breeding patterns are lagging in their response to a recently improved food supply.

The causes of chick mortality are listed in Tables 12 and 13. The greatest part of this mortality is attributable to cannibalism. Chicks disappearing or dying from peck wounds accounted for 92% of the casualties in 1969 and 86% in 1970. Most of the remaining chicks whose corpses were recovered had no visible symptoms of disease or injury; these are birds dying from malnutrition, exposure or other undiagnosed ailments. The only regularly occurring but infrequent symptom of disease encountered was a gross form of constipation characterized by a hard plug of dry and sandy fecal material in the rectum. It is possible that water shortage,

Table 12. Chick mortality of Herring Gulls, 1968.

	A	B	COLONY D	E	Total
Hatched	6	28	128	31	193
Disappeared	5	21	101	16	143
Pecked	1	2	5	2	10
Underweight	-	-	-	-	-
Anal Swelling	-	-	1	1	2
No Vis. Symptoms	-	1	5	5	11
Horses	-	-	-	-	-
Fledged	0	4	23	7	27
% of Eggs Fledge	0	10	5.26	12.50	6.37
% of Hatched Fledge	0	14.29	12.50	22.58	13.99

Table 13. Chick mortality of Herring Gulls, 1970.

	COLOONY				Total
	A	B	C	D	
Hatched	44	94	147	-	285
Disappeared	30	66	66	-	162
Pecked	1	4	20	-	25
Underweight	-	-	2	-	2
Anal Swelling	-	-	-	-	-
No Vis. Symptoms	2	8	13	-	23
Resorbed	-	-	1	-	1
Fledged	11	16	45	-	72
% of Eggs Fledge	13.92	5.32	13.12	-	6.88
% of Hatched Fledge	25.00	17.02	30.61	-	25.26

which was noted by Spans (1971) as an important source of mortality, might be a contributing cause of this condition.

The characteristic pattern of gull chick mortality is of decreasing mortality rates with age (Brown, 1957b; Kadlec et al. 1969; Faludun, 1981; Parsons, 1971; Vermeer, 1963 and 1970). The histograms of chick age and deaths for each year and colony are presented as Figures 6 and 7 and in Appendix I. All show a similar pattern but, interestingly, the large colonies show the greatest concentration of chick mortality in the first ten days of life. As might be expected the proportion of chicks which disappear with no trace is highest in the first ten days, becoming less as chicks reach a size too large to be swallowed whole by other gulls.

It might also be expected that in comparison with other gull colonies there would be, on Sable Island, a relatively heavier mortality in the later stages of growth when food demand of chicks is taxing the foraging abilities of adults. Several authors have published mortality rates before and after 10 days of age and on this basis Table 14 shows a comparison of several L. fuscus, L. argentatus and L. glaucopterus colonies with Sable Island yearly totals.

West (1972) studied Herring Gulls breeding on four islands subject to different degrees of disturbance and which were varying distances from sources of garbage. His chick survival data were presented as percentages of hatched chicks which entered successive weight classes. I have reworked this to give an estimate of mean survival to ten days for each of his colonies for his two or three years of work.

Vermeer (1963) presented explicit mortality data for L. glaucopterus, a gull similar in size and habit to the Herring Gull, and his mortality

tables, which were partitioned into weeks after hatching, were interpolated graphically and ratios of pre and post ten day mortality calculated. Brown (1967b), Kadlec et al. (1969) and Parsons (1971) like Vermeer worked in situations where garbage was available to Gulls as a diet supplement but Paludan (1952) carried out his study in 1943 and 1944 on an isolated island in the Baltic Sea, presumably with no great amounts of garbage available to them. His data on reproductive success are somewhat equivocal but they were thought worthy of inclusion as a study of gulls whose demographic and trophic situation was similar to Sable Island gulls. His best estimate of chick fledging success was around 20% so the ratio of early and late mortalities for his colony has been plotted on Fig. 8 at this level.

There is a correlation between hatching success and ratios of early and late chick mortality rates but as several species of gulls are involved and many diverse factors affect the pattern of mortality and fledging success, one must expect a high degree of variability in such results. In addition the criteria for fledging are rather different in each of these studies.

Values of mortality ratio for Sable Island are shown on Fig. 8 as open circles; below them are two points representing two of Hunt's (1972) colonies. These are the two he judged to be farthest from garbage dumps and one of them was, in addition, subject to some human disturbance. His other colonies, closer to human population centres, are among the points in the upper part of the graph with mortality ratios in excess of 1.4. The mortality rates I derived from Paynter's (1949) Kent I. data are so aberrant that the ratio is not plotted on Fig. 8. Presumably the difficulties he had in locating the older chicks and the

Fig. 8. A comparison of ratio of mortalities, one to ten days and eleven days to fledging, with the percentage of chicks which fledge. Data from Table 16; open circles indicate values for Sable Island.
 $y = 0.0137x + 0.86.$

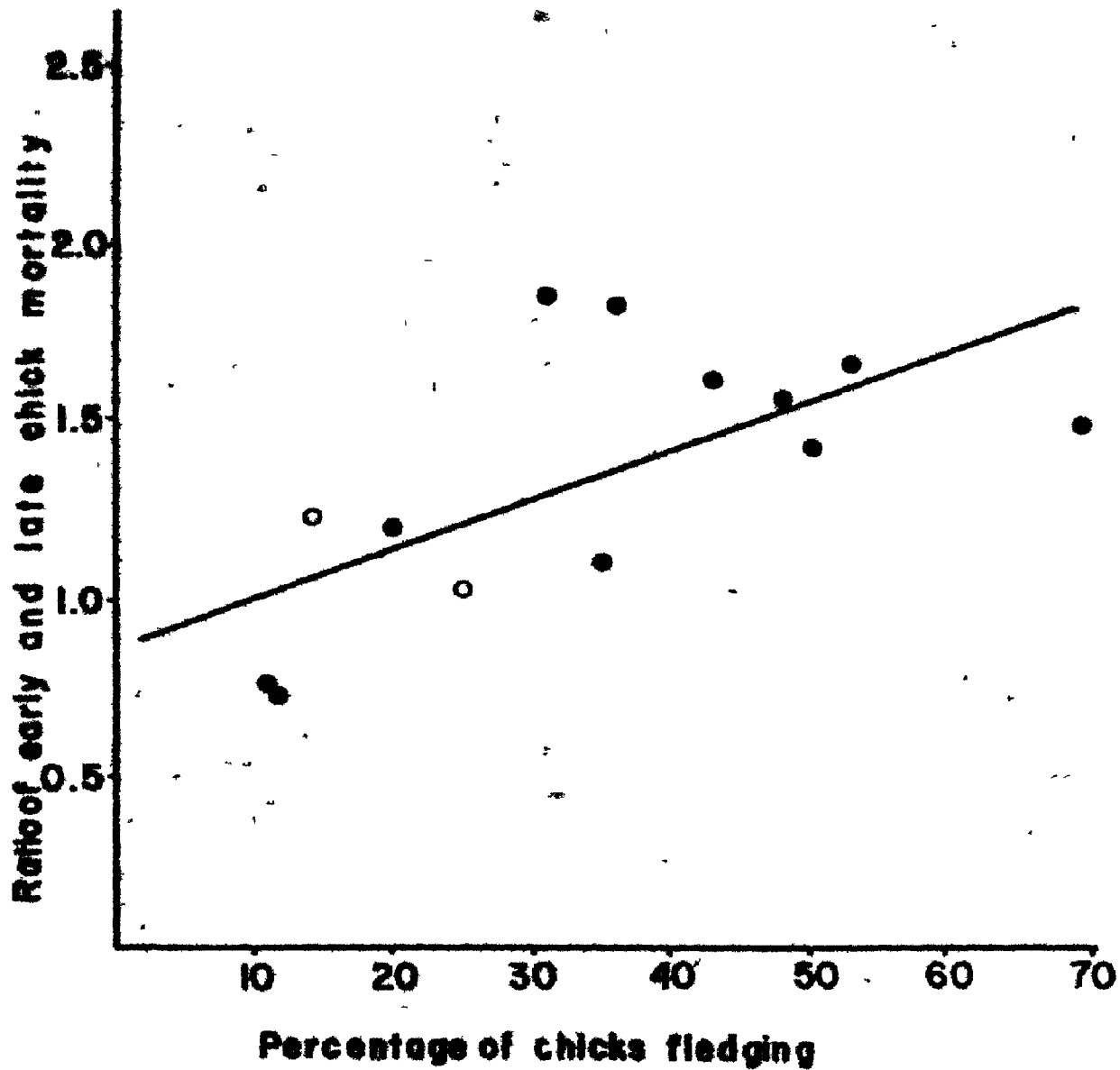


Table 14. Ratio of mortality rates of Gall chicks before and after 10 days after hatching.

Source	Species	Date	% of Chicks Fledging	Mortality Ratio
Brown (1967)	<u>L. fulvus</u>	1962-5	31	1.83
Brown (1967)	<u>L. argentatus</u>	1962-5	36	1.84
Bunt (1972)	<u>L. argentatus</u>	1968-70	43	1.53
Bunt (1972)	<u>L. argentatus</u>	1968-70	35	1.11
Bunt (1972)	<u>L. argentatus</u>	1968-70	11	0.74
Bunt (1972)	<u>L. argentatus</u>	1969-70	12	0.72
Kedlec et al. (1969)	<u>L. argentatus</u>	1965-7	51	1.88
Paludan (1961)	<u>L. argentatus</u>	1944	3-20	1.10
Parsons (1971)	<u>L. argentatus</u>	1967-9	48	1.86
Paynter (1949)	<u>L. argentatus</u>	1947	51	0.64
Vermeer (1963)	<u>L. glaucus</u>	1961	50	1.42
Vermeer (1963)	<u>L. glaucus</u>	1962	70	1.49
This study	<u>L. argentatus</u>	1969	14	1.23
This study	<u>L. argentatus</u>	1970	25	1.82

manipulations he employed to compensate for this have disturbed the results.

With such variation in technique and situation in the studies considered above, it is probably pointless to refine too much on the relationship; no more need be accepted than the general agreement on one hand of Hunt's isolated colonies with Falck's and mine, and, on the other, of colonies with access to abundant food.

Great Black-backed Gulls

Data on laying dates and egg and chick mortality are summarized in Tables 15 and 16 and in Figures 9 and 10. Data on laying dates and hatching and fledging rates are presented graphically in Appendix 2.

In 1969 only one nest was studied on area A and two in area D so data on these nests were pooled with that of the main study area, Colony B. In 1970 data for six isolated nests in Herring Gull Colonies C and D were pooled with that of Colony B.

While there are differences between colonies and years these are not as great as those observed for Herring Gulls. In 1969 I arrived on Sable Island after egg laying had started and consequently I also missed part of the egg mortality. The estimates of egg loss obtained in 1970 agree well with each other and can be considered more representative than the 1969 values. As in Herring Gulls the prime cause of chick death was predation by gulls. All other causes contribute so little to the mortality that only predation and factors affecting it are important in determining the survival of chicks of either gull species on Sable

Table 15. Egg mortality of Great Black-backed Gulls

	COLONY			COLONY			Total 1970
	AND 1969	F 1969	Total 1969	BCD 1970	A 1970	F 1970	
Laid	81	22	103	135	20	65	220
Disappeared	11	-	11	52	7	20	79
Broken in nest	6	-	6	9	3	10	22
Infertile	4	-	4	3	-	-	3
Destroyed by Horses	-	-	-	-	-	3	3
Landslide	-	-	-	-	-	3	3
Hatched	50	22	82	71	10	29	110
% Hatched	74.1	100	79.6	52.6	50.0	44.6	50.0

Table 16. Chick mortality of Great Black-backed Gulls.

	COLONY			COLONY			Total 1970
	ABD 1969	F 1969	Total 1969	BCD 1970	A 1970	F 1970	
Hatched	60	22	82	71	10	29	110
Disappeared	26	18	44	37	6	14	57
Packed	5	1	6	1	-	2	3
Underweight	2	1	3	3	-	-	3
Anal Swelling	1	-	1	2	-	1	3
No vis. Symptoms	3	-	3	3	2	4	9
Choked on Food	1	-	1	-	-	-	-
Fledged	22	2	24	25	2	8	35
% of Eggs Fledge	27.2	9.1	23.3	18.5	10.0	12.3	15.9
% of Chicks Fledge	36.7	9.1	29.4	35.6	20.0	27.6	31.8

Island. Infertility rate, as with Herring Gulls, is typical of other reported colonies.

The percentage of chicks fledging in the main study area (colonies A, B, and D in 1969 and B, C, and D in 1970) is virtually identical in the two years. Only Colony F differs greatly and I suspect that the low observed percentage of chicks fledging in this colony in 1969 is attributable to my inexperience and inability to find some of the older chicks on this colony.

Unlike the Herring Gulls, the Black-backs studied are considered representative of the whole Sable Island population and because the agreement of data is good between years data on chick survival is pooled for analysis of the effect of laying date chick survival.

In both years a greater proportion of the eggs laid before the date of the median egg hatched. In neither year is the difference significant however. The season was further partitioned into peak and non peak periods of egg laying containing approximately equal numbers of eggs in each group. In both years the chicks hatching from eggs laid at the peak of hatching (May 8-16 in 1969 and May 10-17 in 1970) produced the most fledged young: about twice as many per hatched egg as from eggs laid outside the peak in 1969, though the poor estimate of egg mortality for this year renders the fact meaningless. In both years a slightly greater proportion of chicks hatching from peak eggs fledged. In neither case was the difference significant. This pattern of success conforms well to the usual pattern of gull egg and chick mortality and indicates that this species breeds relatively normally on Sable Island.

The schedules of chick mortality in the two years are radically different (Fig. 9). The ratio of mortalities before and after ten days was a relatively normal 1.46 in 1969 but only 1.01 in 1970, the very large number of chicks between the ages of ten and twenty days dying in 1970 being responsible for shift. Of the nine birds dying in this age class whose corpses were recovered, two were underweight, four had peck wounds and three had no symptoms of disease. The mortality was fairly evenly distributed throughout the three colonies and could betoken a time when food was short. Numbers are large enough that it is unlikely that chance could produce a change of this magnitude.

Erwin (1971) observing Great Black-backed Gulls breeding in Rhode Island, found that the later clutches produced a greater proportion of fledglings than early or peak eggs. This relatively lower success of eggs laid at the peak of laying seems to indicate that these birds are breeding in marginal conditions. Gulls are generally highly synchronised breeders and where non peak eggs are more successful reproductive success is generally low, as demonstrated by Herring Gulls on Sable Island and by Black-backs in Rhode Island at the southern extreme of their breeding range.

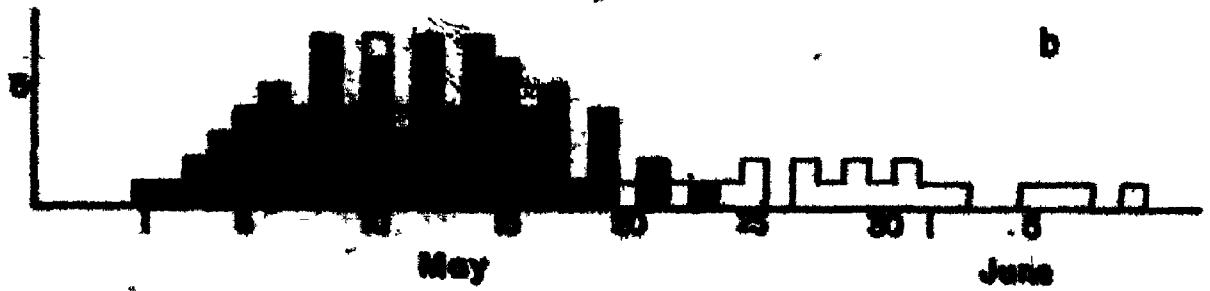
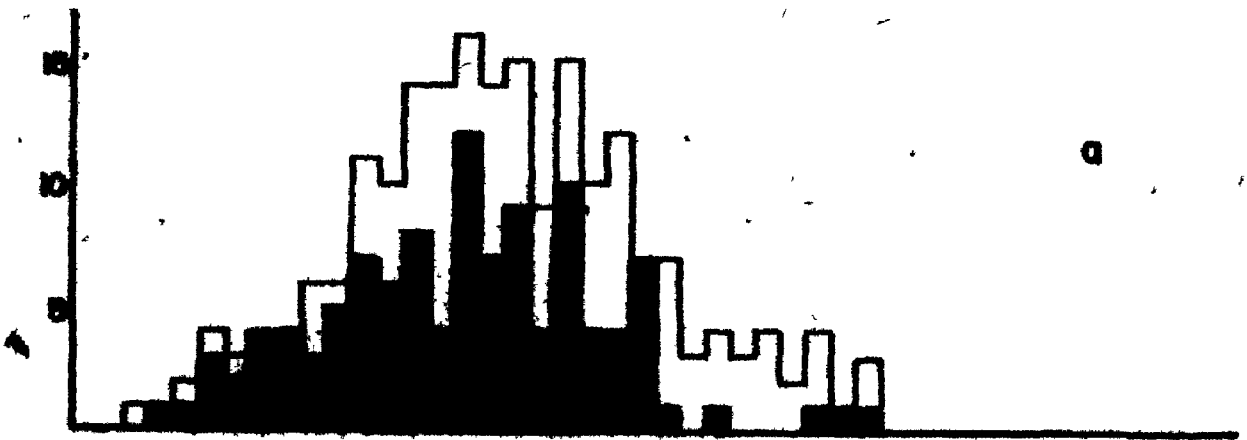
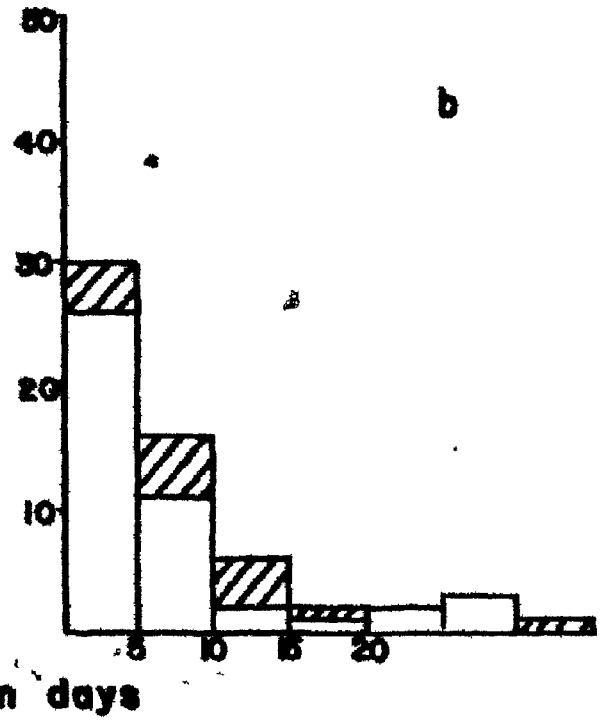
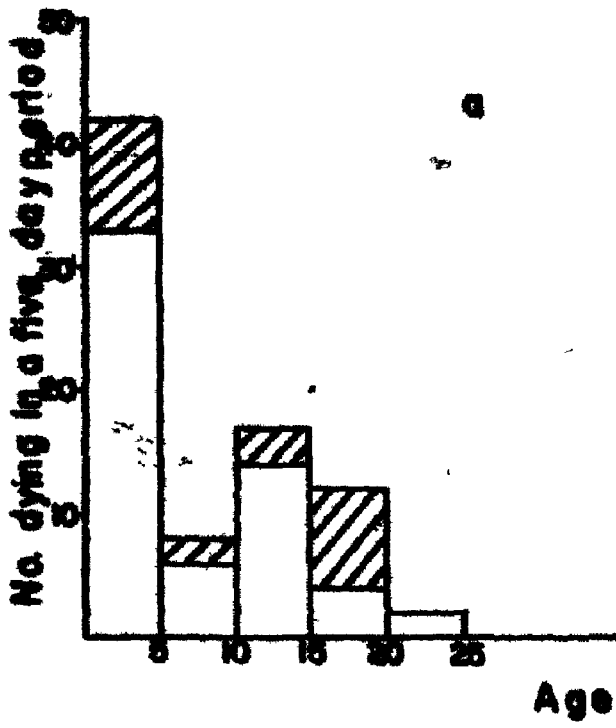
Fig. 9. Schedule of mortality of Great Black-backed Gull chicks in all colonies studied in 1969(b) and 1970(a).

Fig. 10. Dates of laying of eggs in all Great Black-backed Gull colonies studied in 1970(a) and 1969(b).

Outer envelope: dates of laying of all eggs

Shaded area: dates of laying of eggs that hatched

Black area: dates of laying of eggs producing fledging chicks



THE DIETS OF GULLS BREEDING ON SABLE ISLAND

Methods

It is very difficult to obtain a quantitative assessment of a species' diet except by killing a large sample and examining stomach contents. Even this method is not without its drawbacks, as Hartley (1948), and Lehto and Lehto (1967) have shown, and it was not considered as a method for use on Sable Island. Instead, the regurgitations of panicked chicks and food remains by the nest were examined and the contents categorized as accurately as possible. The regurgitations were not collected for analysis but were returned to the region of the nest in order that a significant part of a chick's daily ration might not be lost to it.

As the indigestible portions of a gull's diet are regurgitated, an examination of the pellets around the nest allows some information on the diet of the adults of the species to be obtained. But as the indigestible portion of different foods is so variable in amount and nature such collections cannot accurately define a species' diet. However they can be used to study the difference between areas or changes in diet over time (Spens, 1972).

On each visit the area around the nest or the habitual perching or loafing spot was searched and all food remains (regurgitations or inedible food fragments) were removed and identified. If chicks regurgitated while being handled the nature of the regurgitation was noted but the food itself was left close to the chick when I left the area. Hunt (1972) in contrast, collected samples of chick food by

inserting his finger into the oesophagus and crop of the chick and levering out their contents. This practice, like his weighing technique, must have subjected chicks to a much greater stress or disturbance than did my methods.

Results and Discussion

Diets of Chicks

In 1969 and 1970 82 regurgitations of Black-backed Gull chicks and 82 of Herring Gull chicks were examined and the occurrence of various types of food is listed in Tables 17 and 18. Substantial differences are apparent, though in both species the bulk of the diet of chicks is fish. As the regurgitations were not kept but were returned to the chick's territory, it was not possible to identify every one of the specimens. But it is suspected that many of the unidentified fish in the regurgitations were small gaffids. Of the 53 Mackerel (Scomber scombrus) identified, 5 were found between June 15 and 28 and the remaining 48 were found between June 29 and August 2. Mackerel are known not to become abundant in the surface waters of this part of the Atlantic until around the end of June (Mackay, 1967). Mackerel made up 59.3% of the regurgitations of the Black-backed Gull chicks in 1970 but only 19.7% of those of the Herring Gulls.

A majority of Black-backed Gull chicks enter their period of peak food demand at the end of June, the time Mackerel enter Nova Scotia's coastal waters. Mackerel remain near the surface until after mid July when the majority of the Herring Gull chicks enter their period of greatest food demand, but they are caught in smaller numbers by Herring

Table 17. The occurrence of various types of food in the regurgitations of Herring Gull chicks.

Type of food	1969		1970		Total	
	Number	Percent	Number	Percent	Number	Percent
Fish						
<u>Scophthalmus aquosus</u>	4	15.4	11	19.7	15	18.3
<u>Clupea harengus</u>	6	23.1	10	17.9	16	19.5
<u>Ammodytes americanus</u>	3	11.5	3	5.4	6	7.3
<u>Aequula equilla</u>	1	3.8	1	1.8	2	2.4
Unidentified fish	10	38.5	26	46.5	36	43.9
Invertebrates						
<u>Mya arenaria</u>	-	-	1	1.8	1	1.2
Unidentified squid	1	3.8	-	-	1	1.2
Polychaeta	-	-	1	1.8	1	1.2
Euphausiacea	1	3.8	-	-	1	1.2
<u>Cancer irroratus</u>	-	-	2	3.7	2	2.4
Rhubarries	-	-	1	1.8	1	1.2

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Table 19. The occurrence of various types of food in the regurgitations of Great Black-backed Gull chicks.

Type of food	1969		1970		Total	
	Number	Percent	Number	Percent	Number	Percent
Fish						
<u>Scomber scombrus</u>	3	13.1	35	59.3	38	46.3
<u>Clupea harengus</u>	6	26.1	9	15.3	15	18.3
<u>Ammodytes americanus</u>	1	4.3	-	-	1	1.2
<u>Anguilla anguilla</u>	1	4.3	2	3.4	3	3.7
<u>Pleuronectidae</u>	1	4.3	-	-	1	1.2
Unidentified fish	10	43.5	11	18.6	21	25.6
Birds (Unidentified)	1	4.3	2	3.4	3	3.7

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Gulls. Mackerel is an extremely vigorous species and fight strongly on capture; the greater weight of the Black-backed Gull gives it a substantial advantage in taking such fish.

The complete absence of invertebrates or vegetable matter in the regurgitations of Black-backed Gull chicks betokens a further difference in the foraging pattern of the adults of the two species. Similar differences are revealed by analysis of food remains left by adult birds. For comparison with the χ^2 contingency test the categories in Tables 19 and 20 were grouped into four: Mackerel, Herring, unidentified fish and other. They were found to be different beyond the 0.001 level ($\chi^2 = 34.393$, 3 df.).


There are some differences in the composition of the Great Black-backed Gull chick regurgitations between 1969 and 1970. The most notable are a decrease in the proportion of unidentified fish and a great increase in the proportion of Mackerel in 1970. These changes are probably a result of my inability to confidently identify semi-digested mackerel in the first year of the study. When tested by the χ^2 test, with the data grouped as before, the regurgitations of the two years are shown to be significantly different, ($\chi^2 = 14.588$, 3df $p < 0.01$) and the Spearman Rank Coefficient of 0.8675, $N = 7$, indicates a lack of association significant beyond the 0.05 level. The Herring Gull chick regurgitations, however, were not significantly different in the two years, showing a significant association between the two years on the Spearman Rank Coefficient test $r_s = .90$, $N = 7$, $p < 0.01$.

Diets of Adults

There are even more notable differences in food remains found around the nests of the two species. Food remains from the environs of the nests of Herring Gulls were not gathered in very large numbers or very systematically in 1969 and are not presented here; those gathered in 1970 are listed in Table 19. Tables 20 and 21 list Great Black-back food remains. Fish provide a significant part of the diet of both species but, unfortunately, most of the fish remnants were unidentifiable, the regurgitated bones being, usually, so damaged, with lateral processes broken off that even the morphology of the centra was difficult to determine. Even though Mackerel have characteristic and easily identified vertebral columns only a few were detected in each year. This is probably because the Mackerel do not appear in numbers in the waters around Sable Island until July, and almost no samples were gathered after the end of June. Great Black-backed Gulls commonly move their chicks from the region of the nest to an area as much as 100m. from the nest a week or so after the chicks have hatched. As the borders of this rearing area are not easily defined and as Herring Gulls are usually rearing chicks closely, it is difficult to be certain of the origin of remains found after this period. So while Mackerel bones were found frequently during July they were not collected or noted as parts of the diets of either species.

The food remains collected at Black-backed Gull nests in the two years shows large differences in the proportions of some constituents, particularly the tern eggs. When grouped into six categories: fish, invertebrates, birds other than terns, terns, eggs and other and tested

Table 19. The occurrence of various types of food in regurgitated pellets and food remains found near Herring Gull nests, 1970.



<u>Food Type</u>	<u>Frequency</u>	<u>Percent</u>
Fish	148	21.4
Molluscs	46	6.7
Insects	152	22.0
<u>Cancer irroratus</u>	184	26.7
Sea Cucumber	1	0.1
Other Crustacea	1	0.1
Cranberries + Crowberries	64	9.3
Leaves	4	0.6
Pelagic birds	27	3.9
Passerine birds	11	1.6
Unidentified birds	7	1.0
Terns	13	1.9
Tern eggs	4	0.6
Gull eggs	13	1.9
Seal remains	5	0.7
Garbage	10	1.4
	<hr/>	<hr/>
	703	100

Table 20. The occurrence of various types of food in regurgitated pellets and food remains found near Great Black-backed Gull nests, 1969.

Food Type	Frequency	Percent
Fish	37	19.9
Molluscs	2	1.1
CRAB Legs	8	4.3
Pelagic birds	8	4.3
Passerine birds	2	1.1
Gull chicks	1	0.5
Terns	15	8.0
Tern eggs	98	52.7
Gull eggs	1	0.5
Seal remains	11	5.9
Garbage	3	1.7
	186	100

Table 21. The occurrence of various types of food in regurgitated pellets and food remains near Great Black-backed Gull nests in 1970.

Food Type	Frequency	Percent
Fish	167	26.6
Molluscs	16	2.6
Insects	2	0.3
<u>Cancer irroratus</u>	87	13.9
Other crustacea	3	0.5
Berries	7	1.1
Pelagic birds	96	15.3
Passerine birds	17	2.7
Gull chicks	9	1.4
Terns	75	12.0
Tern eggs	43	6.9
Gull eggs	23	3.7
Seal remains	78	12.4
Garbage	4	0.6
	<hr/> 627	<hr/> 100

by χ^2 test, the difference was found to be highly significant ($\chi^2 = 168.37$, $df = 5$, $p < 0.001$). A Spearman Rank coefficient of 0.3729, $N = 10$, also reveals there is no significant relationship between the two years.

In 1969 the Black-backed Gull food remains were gathered from nests on the westmost dune of the island only. There is a large tern colony close to the gull colony and more than 2/3 of the tern eggs in the food samples came from a single gull nest close to the tern colony. In 1970 this pair, or at least the pair nesting in the same place, did not specialise on tern eggs. In 1969 the influence of this specialist pair was particularly strong as only 186 samples were gathered. In 1970, 627 samples were gathered from all the nests which were studied; consequently these are a better index to the diet of the species.

Seven hundred and three samples of food remains were gathered at Herring Gull nests in 1970 and examination of these reveals that the diet of the adults, like that of the chicks, differs significantly from that of Great Black-backed Gulls. ($\chi^2 > 200$, $d.f. = 11$, $p > 0.001$)

The proportion of garbage or other food remains attributable to human activities is less than 2% in both species. The identifiable items were such things as chop bones, sausage skins and butter papers which obviously came from the small human population of the island. Hunt (1972) in Maine and Drury (1963) in Massachusetts also report that garbage was an important item in the diet of adult birds while Brown (1967b) in Northern England recorded that a third of the identifiable items brought by Herring Gulls in courtship feeding were garbage.

Spans (1972) in his more remote colonies on Vlieland and Terschelling recorded only small amounts of garbage in the food remains at Herring Gull

nests and suggests, as did Drury in 1963, that where "natural" food is available it is preferred to garbage. Intertidal invertebrates seem to be the usual food in colonies remote from towns; Goethe (1956), Balopol'skii (1957), Ingolfsson (1967) and Spaans (1972) all report this. Marine fish seem to be almost equally important articles of diet in these areas. The great differences in the diet of this species in widely separated areas (See Harris, 1965) demonstrate a behavioural flexibility which is at the root of its success in a world where the environment is constantly changing under man's influence.

On Sable Island there are neither extensive mud or sand flats exposed at low tide nor a food rich rocky intertidal zone for foraging grounds. With the recession of Wallace Lake in summer, areas of wet sand flat are exposed which accommodate some lamellibranch molluscs and annelids, but while the Herring Gulls nesting around the lake take advantage of this temporary food supply, the majority of the gulls on the island gain little or none. Obvious sources of food are the occasional dead fish, pelagic birds and marine mammals which are cast up onto the beach and the abundant fish which are found near the surface here in summer.

There are substantial summer fisheries for Silver Hake (Merluccius bilinearis), Herring (Clupea harengus), and Cod (Gadus morhua) on Sable, Western and Emerald banks but only occasionally can the fleets come within foraging range of gulls breeding on Sable Island and certainly cannot constitute a reliable food source. Some fishing takes place between Sable Island and the mainland; on most flights to the island fleets of European fishing vessels were seen operating about 40 or 50 miles off the Nova Scotian coast but they had no attendant gull flocks. I saw no

fishing boats closer than about 50 miles from Sable Island and pilots of Air Atlantic who flew regularly to the island reported that almost all fishing activity was closer to the mainland than to the island. On clear days throughout the summer I scanned the horizon from a high point on the island but on no occasion did I see fishing boats. Few gulls forage more than 30 miles from the colony during the breeding season (Drury, 1963; Brown, 1967) and as the main fishing grounds are at least this distance from Sable Island it is doubtful if birds breeding there can obtain food from them.

Birds are a very much more important part of the Black-backed Gull's diet than the Herring Gulls. Pegaic birds such as the Great and Sooty Shearwaters (Puffinus gravis and Puffinus griseus) were the most frequently identified species but Dovakies (Plautus alle) and Puffins (Fratercula arctica) turned up regularly even as late as the beginning of July. Passerine birds were much less abundant in the diets of both species, and while identification was rarely possible it is thought that the most common passerine taken was the Ipswich Sparrow (Passerculus sandwichensis princeps). However so few of these were observed it is not thought that the gulls are in any way damaging the sparrow population.

Terns (Sterna sp.) are heavily preyed upon by Black-backed Gulls. Both adults and chicks (12% of all Black-back remains in 1970) and eggs 6.9% in 1970, 52% in 1969) are taken. Terns and tern eggs only occurred as 2.4% of Herring Gull remains in 1970. The tern population on Sable Island has dropped dramatically in the last fifty years (Lock, in press); it seems quite possible that the presence of Great Black-backed Gulls as a breeding species on the island could have been a decisive factor in

this decline. Gull chicks form a surprisingly small part of the identifiable remains of both species are pressed into a more cannibalistic feeding pattern by the difficulties of obtaining food on Sable Island.

Many of the fish remains were so fragmentary that it was not possible to identify them even to family. Bones of the Herring and the Sand Lance (Ammodytes americanus) for instance are so similar that they could not be separated, but 61 of the 149 fish remains collected from Herring Gull nests in 1970 were from these species. Bones of this type were less common in Black-back food remains, where instead, gadid skeletal fragments were most common. As only partial skeletons or disarticulated bones were usually found even assignment to family is subject to some error and 26.5% of all fish remains were not identified. Dr. W. B. Scott of the Royal Ontario Museum has identified two gadid skeletons as remains of Common Cod and Silver Hake. Both specimens, he estimated, were from fish of less than 2 lb. in weight. Fish of this size might conceivably be those which slip from trawls but, equally, they are the very size of fish that gulls are likely to be able to catch themselves. The only evidence that was found to suggest that fishing fleet wastes might be drifting to the island was the presence of small sharks and anglerfish (Lophius americanus) stranded on the north beach of the island in the summer months.

Herring Gulls make almost no use of seals as food. Black-backs, however, depend on the Harbour Seal (Phoca vitulina) population for a substantial portion of their ration; 12.4% of all food remains were from seals and most of these were tufts of the lamgo, the foetal coat of the pups. Black-backs gathered around the packs of whelping seals in May and June to feed on the placentas.

Both invertebrates and vegetable matter were more common in the Herring Gull food remains. This accords well with observations made elsewhere (Harris, 1965) and points up the Herring Gulls' greater reliance on terrestrial and littoral food sources. Berries may be less likely to leave obvious indigestible remains than other food items and their occurrence is probably underestimated by a count of food remains. Bluish-purple feces are common around Herring Gull nests indicating that Blueberries and Crowberries are a frequent item in their diets. Such purple stains were far less frequent around Great Black-backed Gull nests.

THE CONSTRUCTION OF AN ENERGY BUDGET FOR SABLE ISLAND GULLS

Methods

Two chicks were taken from nests of Black-backed Gulls approximately one day after the hatching of the one and two days after the hatching of the other. They were reared in captivity to fledging age and observations of the sequence and chronology of feather development, weight increase and food intake were made. The chicks were, at first, kept in a large indoor sand box and provided with a warm rubber water bottle wrapped in cloth as a surrogate parent. In the first week they were offered food every two to three hours during the day and no longer than six hours elapsed without food overnight. When they were capable of recognizing and taking their own food they were provided with a supply of food in their enclosure.

After the first week the chicks were kept outside in a large enclosure during the day but returned to the unheated house at night. They were not provided with hot water bottles but they used piles of newspaper and rags for sleeping on. After the second week the chicks were allowed to range freely outside and returned to the house only on wet nights. Food was made available 5 times a day and they were allowed to eat all they wished. No longer than eight hours elapsed overnight without their being offered food.

The chicks were weighed daily until the 25th day of age after which time they were weighed every second day. At all ages they were given chicken egg shells and libitum and they consumed them enthusiastically. As their food contained few bones it was thought

that the egg shells were an important part of their diet. Fresh water was available to them at all times.

Results and discussion

The two chicks were fed immediately upon capture on June 12 but their food consumption was not measured until June 13. Each was recognisable by the pattern of dots on the back of the head and they were not banded until July 9 when growth of feathers on their heads began to obscure the pattern. The development of the chicks was rapid and uninterrupted to fledging weights (Fig. 11) and both made their first hesitant flights at about 45 days of age. Chicks of this species are not usually considered to fledge until about 55 days of age (Harris, 1965; Heinroth, 1922) but the acquisition of flight in gulls is a gradual refinement of technique by progressively longer hops and glides and it is difficult to decide at which point birds are capable of self-sustaining flight. At the time of first flight their primaries were not fully grown, but by 55 days of age their flight feathers are fully developed.

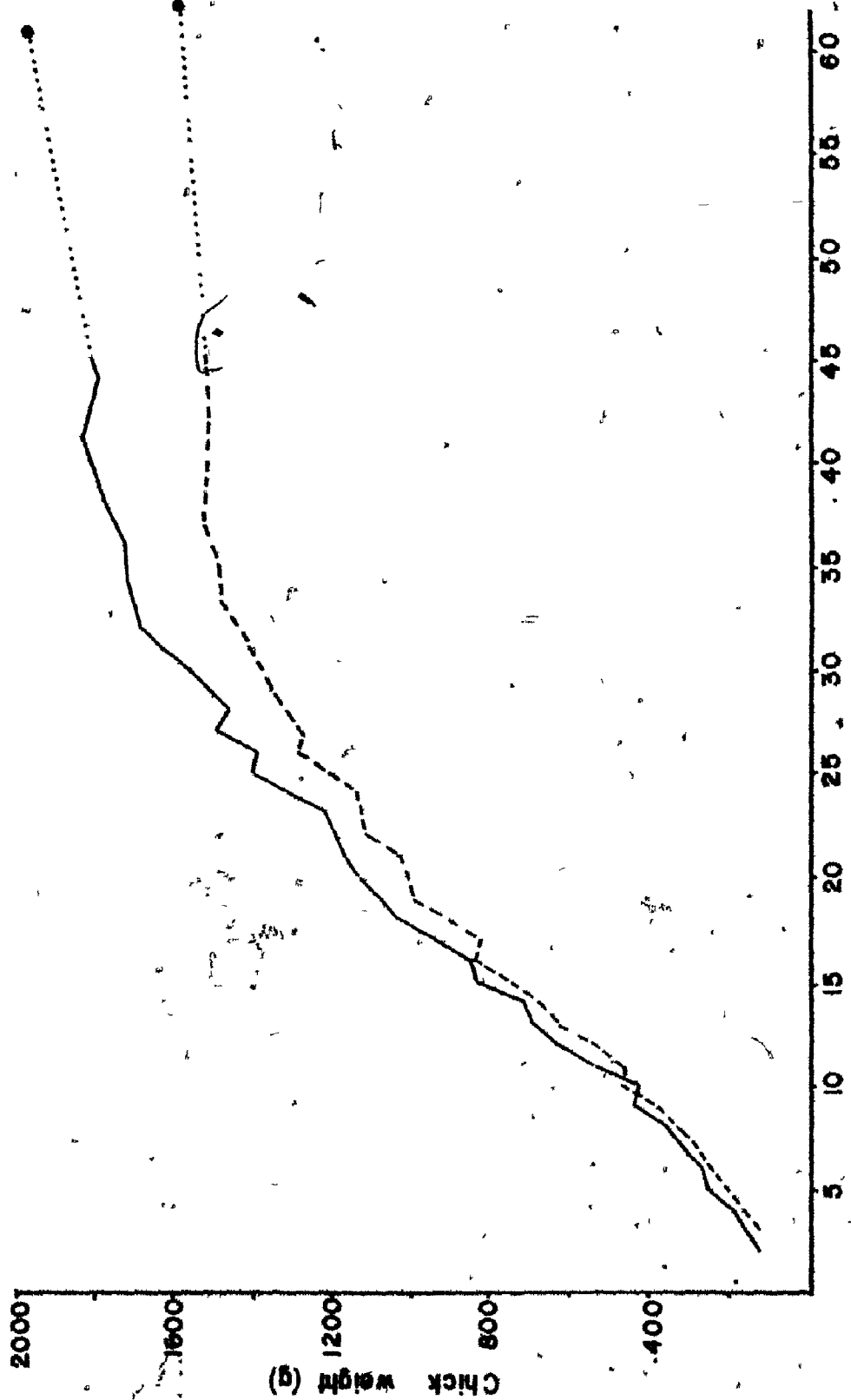
Both became very tame and took food willingly, treating their keepers as other chicks were observed to behave to their parents. They were fed a varied diet consisting primarily of beef liver, tinned cat food and fish; the total diet is listed in Table 22. The diet was the same at all ages: a mixture of all the items listed. The fish was primarily cod and haddock with the large bones, viscera and head removed. Beef liver was, like the fish and eggs, fed to them raw. The table scraps consisted of such things as bread, vegetables, gravy

Fig. 11. The growth of two hand-reared chicks of the Great Black-backed Gull (Larus marinus).

Solid line, Chick # 20355

Broken line, Chick # 20356





Days after hatching of chick # 20355

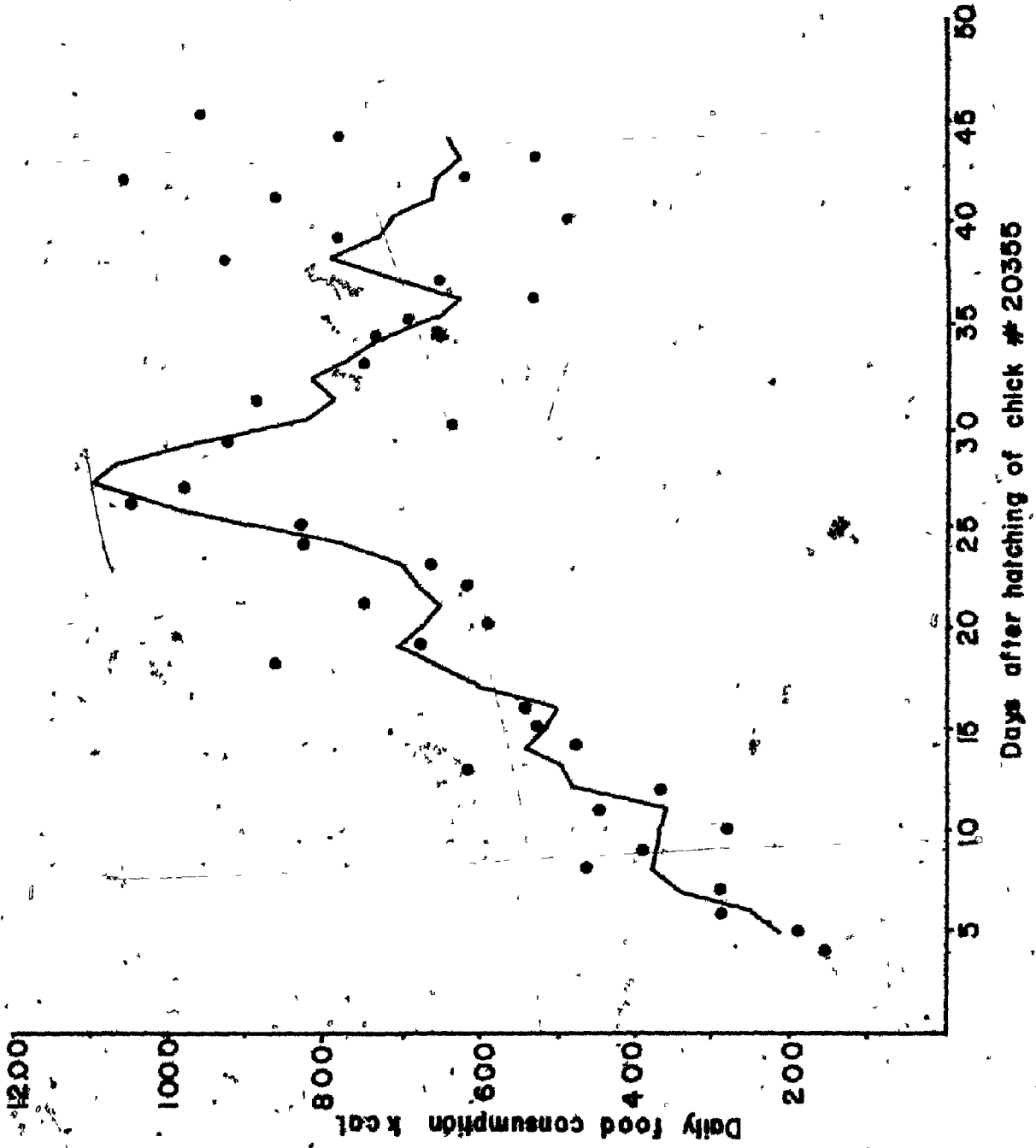
Table 22. The diet of two hand-reared Great Black-backed Gull chicks from 4 to 45 days of age.

	Wt.	Kcal/g	Total Kcal	% of Total
Cat food	9,713	1.10	10,684	39.21
Beef liver	6,359	1.32	8,394	30.81
Fish	6,136	1.0	6,136	22.52
Baby food	1,260	0.66	832	3.05
Table scraps	791	1.0	791	2.90
Hens egg	263	1.55	408	1.50
	24,522		27,245	100.

and spaghetti and this portion of their diet was judged to have a mean calorific value of 1.0 Kcal per gram. The baby food was Heinz strained vegetable, beef and liver, and the tinned cat food was Puss'n Boots fish cat food. The calorific values of these proprietary items was obtained from the manufacturers. The calorific values of the other food stuffs were obtained from Altman and Dittmer, 1968. The mean value of the diet was 1.11 Kcal per gram.

The calorific value of the food consumed each day is graphed in Fig. 12. Between days 4 and 45 a total of 27,245 Kcal were consumed corresponding to food with a wet weight of 24,522 g. Between hatching and the fourth full day of life it is reasonable to estimate a further 600 to 700 g to have been consumed bringing the total food consumption for the first 45 days to around 25,200 g or 28,000 Kcal. Food consumption leveled off at about 350 Kcal or 315 g per chick per day. Assuming that this level of consumption is equivalent to that of adults it is obvious that a chick growing to 60 days consumes 19,250 Kcal while an adult in the same period is expected to consume some 21,000 Kcal. At the peak of food demand, around the 28th day of age, a chick will consume around 550 Kcal per day, 1.57 times the adult ration. If a mated pair is rearing three chicks of this age and one bird is on territory, and only one bird is free at any time to forage, it has to gather 6.7 times its normal daily ration in the daylight hours. Furthermore, to rear three chicks to 60 days of age as well as feed themselves a pair of Great Black-backed Gulls must gather the prodigious total of around 100,000 Kcal which would correspond to almost 100 Kg of fish. However the value of 350 Kcal

Fig. 12. The calorific value of food consumed each day by two hand-reared Great Black-backed Gull chicks. Dots indicate the amounts of food consumed each day and the solid line shows a three day running average.



per day for the adult in the wild is not an exact estimate. Adults in the wild have the additional metabolic expense of flying and foraging and the extent of this energy drain has not been calculated.

The increase in weight was quite regular and the rate of gain decreased regularly to almost nil between 40 and 45 days of age (Fig. 13). In this same figure is shown the growth efficiency of the chicks calculated on 5 day intervals. The calorific value of the chicks themselves was taken as 1.97 Kcal per gram, a mean of several values obtained for Herring Gull chicks by Brisbin (1965). The efficiencies graphed are simple gross growth efficiencies.

Chicks are kept quite sheltered and warm in the first week or so of captivity, unlike wild chicks which have substantial metabolic expenses in preserving body temperature in rain and on cold nights. So the ration of these chicks in their first ten days or so might be insufficient to allow maximal growth in wild chicks.

The curve in Fig. 13 differs quite considerably from that of the Herring Gull as derived by Brisbin, in whose curve the maximum efficiency of around 40% is achieved a third of the way through the growth period. My curve has a similar value at this period and agrees closely with Brisbin's for the last two thirds of the development period. The great difference is in the first two weeks when Lehr-Brisbin records values of 24% rising to 40%. I find it difficult to believe that the warmth and shelter I provided my chicks in this period so greatly decreased their metabolic expenses that extra growth increments and efficiencies of this magnitude were obtained. The normal pattern of animal growth is of

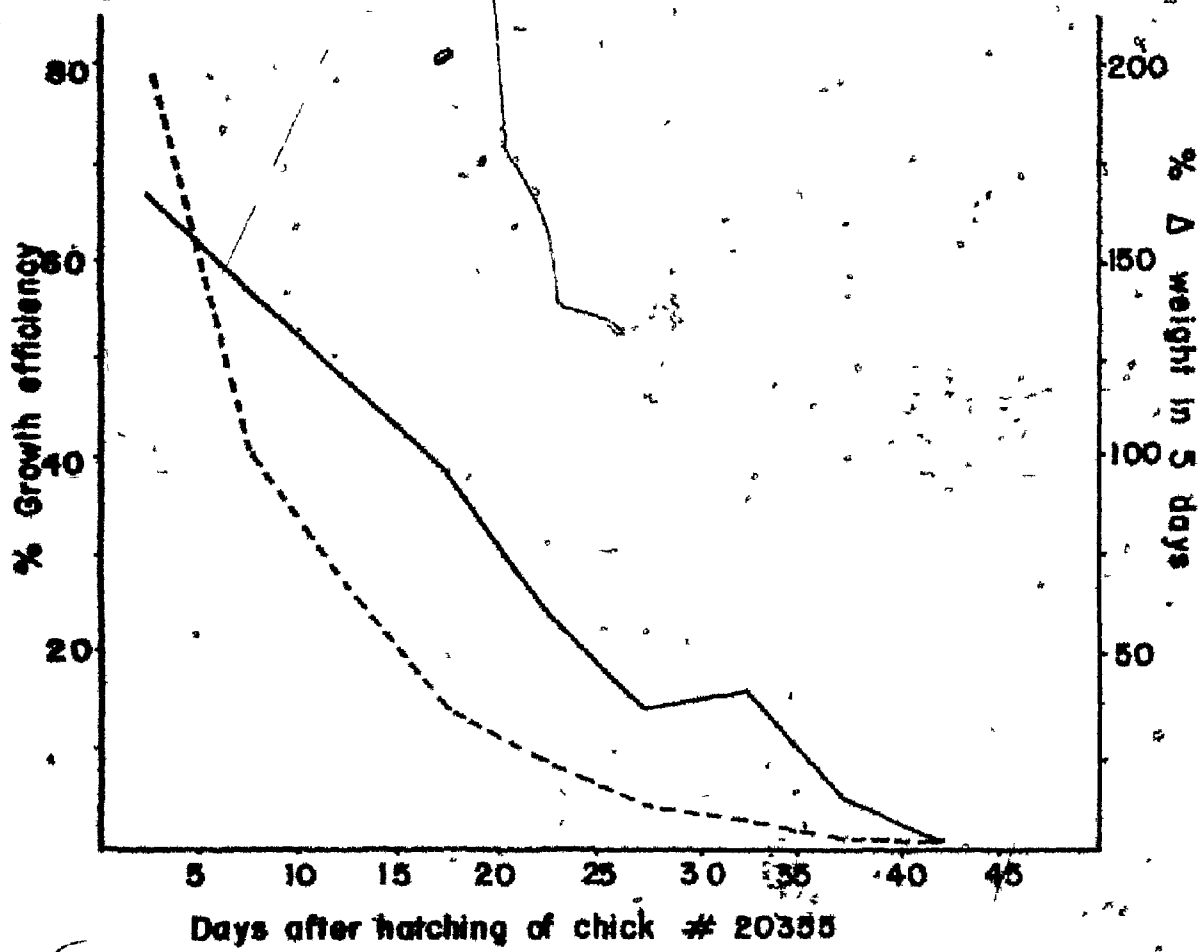
decreasing growth efficiency with age. About the disturbance of the graph in the third quarter of the growth period, I can only speculate. It may be that the rapid feather growth which occurs at this time involves a large metabolic demand with little weight increment, resulting in an apparent decrease in efficiency.

Brisbin's data are so disguised in statistical manipulations that it is not possible to reliably extract data on the amount of food needed to rear Herring Gull chicks, but Spaans (1972) reared 25 chicks of this species from hatching to fledging and has published their food requirements. Unfortunately the ages of his group of experimental birds differed by as much as 10 days and the curve of food demand is not so well defined as could be hoped. However he observed that in this species (which has a normal fledging period of 45 days) the maximal food intake of the birds occurs as early as the fourth week. In the Great Black-backed Gull chicks that I reared this peak was reached some days later, around the end of the fourth week. Spaans calculated that around 8835 g of fresh fish are required to rear a single chick to fledging weight and that between 100 and 200 g of food are required by adult Herring Gulls daily. He measured intakes of fully grown birds of 360 to 370 g of Horse Mackerel (Trachurus trachurus) and 200 to 300 g of Sprat and Herring (Sprattus sprattus and Clupea harengus) daily but in his experiment the birds gained weight, and a maintenance diet may be substantially less than this even if flying does demand an appreciable energy expense.

Spaans' estimates of adult daily ration are very inexact so to arrive at a preliminary estimate I am assuming that as the Herring

80

Fig. 13. The percentage growth efficiency calculated at five day intervals for two hand-reared Great Black-backed Gull chicks. The percentage change in weight of both chicks is shown by the dotted line. These data are plotted on the age of the younger chick.



Gull has similar morphology to the Great Black-backed Gull its daily metabolic demand will at least be approximated by the formula $Y = aW^{0.7}$, where Y is the daily food requirement, a is a constant determined to be 1.918 for Great Black-backed Gulls and assumed to be the same for Herring Gulls, and W is the weight of the gull in grammes. The daily energy requirements of an adult Herring Gull of 900 g weight would be 220 Kcal per day.

Spaans reared 25 Herring Gulls from hatching to 42 days of age on 220.87 Kg of fish. I have transformed this diet into Kcal using Altman and Dittmer's (1968) calorific values and find that a Herring Gull chick can be reared to fledging weight on 13,030 Kcal. A pair of adults rearing 3 chicks to fledging at around 42 days and for the 18 days following must gather 77,370 Kcal against 100,000 Kcal for a pair of Great Black-backed Gulls in the same period.

It is noteworthy that a Herring Gull chick is thus estimated, from Spaans' data, to consume, between hatching and 42 days of age quite as much food as a Great Black-backed Gull chick which grows to twice its weight. Though the Herring Gull pays some energetic penalty through heat loss for being small it is unlikely that this is sufficient to bring the food consumption of this species up to that of Great Black-backed Gulls. It is likely that they could have grown equally well on a much smaller ration than that used by Spaans and that a substantial portion of their food was passed through the gut unabsorbed.

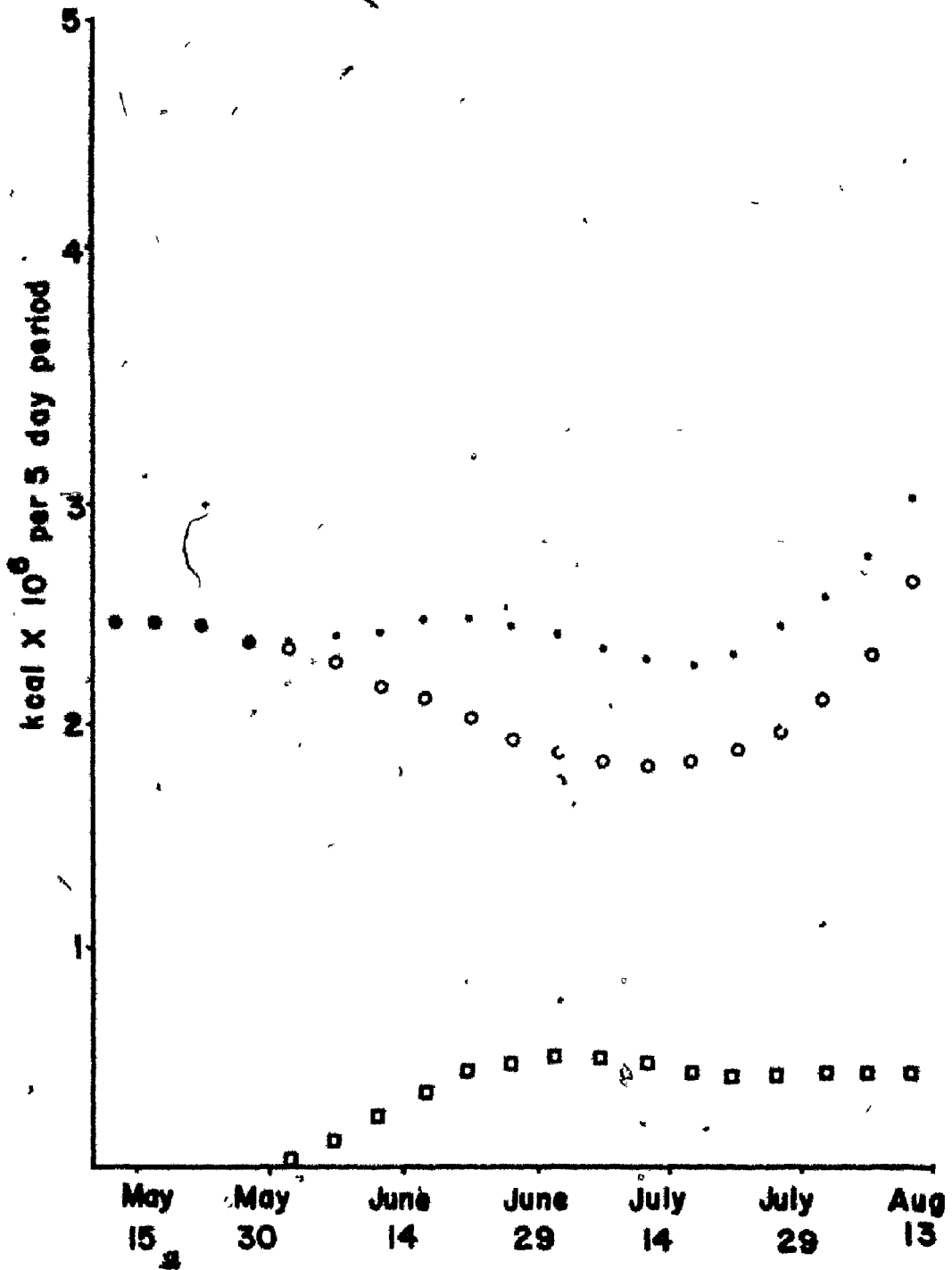
I have decided not to use Spaans' estimate of 13,030 Kcal per chick as the food requirement to fledging, instead I have constructed

a curve food demand similar to that of Black-backs with a peak of 350 Kcal at the 27th day and levelling out to 220 Kcal per day at the 45th day. The calorific value of food needed to rear a chick with such food demands is 10,300 Kcal, and a pair of adults rearing three chicks to 60 days of age would have to gather 67,200 kcal as opposed to about 100,00 Kcal of the Black-backs. But it is not usual for a breeding pair of gulls to rear a full brood of three; a fledging success of around one chick per pair is usual and on Sable Island success has been shown to be appreciably less than this.

With a knowledge of mortality schedules of chicks it is possible to construct a graph of food demand for all gulls breeding on Sable Island. For ease of calculation I have assumed that mortality of chicks was simply age dependent and independent of hatching date.

The calculations were made for five day periods and all chicks dying in each period are assumed to have done so at the end of the third day of each period. To derive a graph of Great Black-backed Gull food consumption (Fig. 14) the chick mortalities were those observed among all nests studied in 1970. Of 220 eggs laid in 77 study nests 110 hatched and 35 chicks fledged. It was estimated that over 530 pairs bred on the island and food demand was calculated to be 6.88 times that of the study nests. The calculations of food amounts of adults on the island was done by interpolating values in the table of census results for 1970. As the number of adults of this species was more than twice the number of estimated nests it was assumed that all adults on the island were within sight on the censuses.

Fig. 14. The amounts of food consumed by Great Black-backed Gulls on Sable Island in the breeding season 1970. Squares signify the consumption of chicks; open circles, that of adults and black dots show the total food consumption.



The curves of Herring Gull food demand were constructed similarly but the age specific mortality rates of the chicks was taken as that from the three quarter colony. This was the most successful colony studied and thought to be that most typical of the rest of the colonies on the island. In this colony there were differences in hatching and fledging success in the first and second layings so the survival curves for each laying were constructed separately using appropriate mortality rates. The curves in Fig. 15 describe the calculated food consumption of Herring Gulls on Sable Island in 1970. Fig. 16. shows the demands of both species separately and combined. The demand is seen to be virtually constant throughout the breeding season at around 1.4×10^6 Kcal per day; this corresponds to around 1.1 metric tons of food with a calorific value close to 1.2 Kcal/g.

It is instructive to compare this value with a hypothetical value derived assuming that both species were able to reproduce as successfully on Sable Island as they have been observed to do elsewhere. A mean clutch size of 2.827 and a hatching success of 75% were assumed; both values are representative of those observed in many studied gull populations. A chick mortality of 52.83% results in a mean fledging rate of one chick per nest. The schedule of mortality was taken from Vermeer's (1963) study of the Glaucous winged gull but is characteristic of most large gulls.

It was further assumed that chick mortality was independent of laying or hatching date and dependent only on age of the chick. As before the calculations were made for 5 day periods and it was assumed that in this relatively successful population there was no relaying as

Fig. 15. The amount of food consumed by Herring Gulls on Sable Island in the breeding season 1970. Squares signify the consumption by chicks; open circles, that of adults and black dots show the total food consumption.

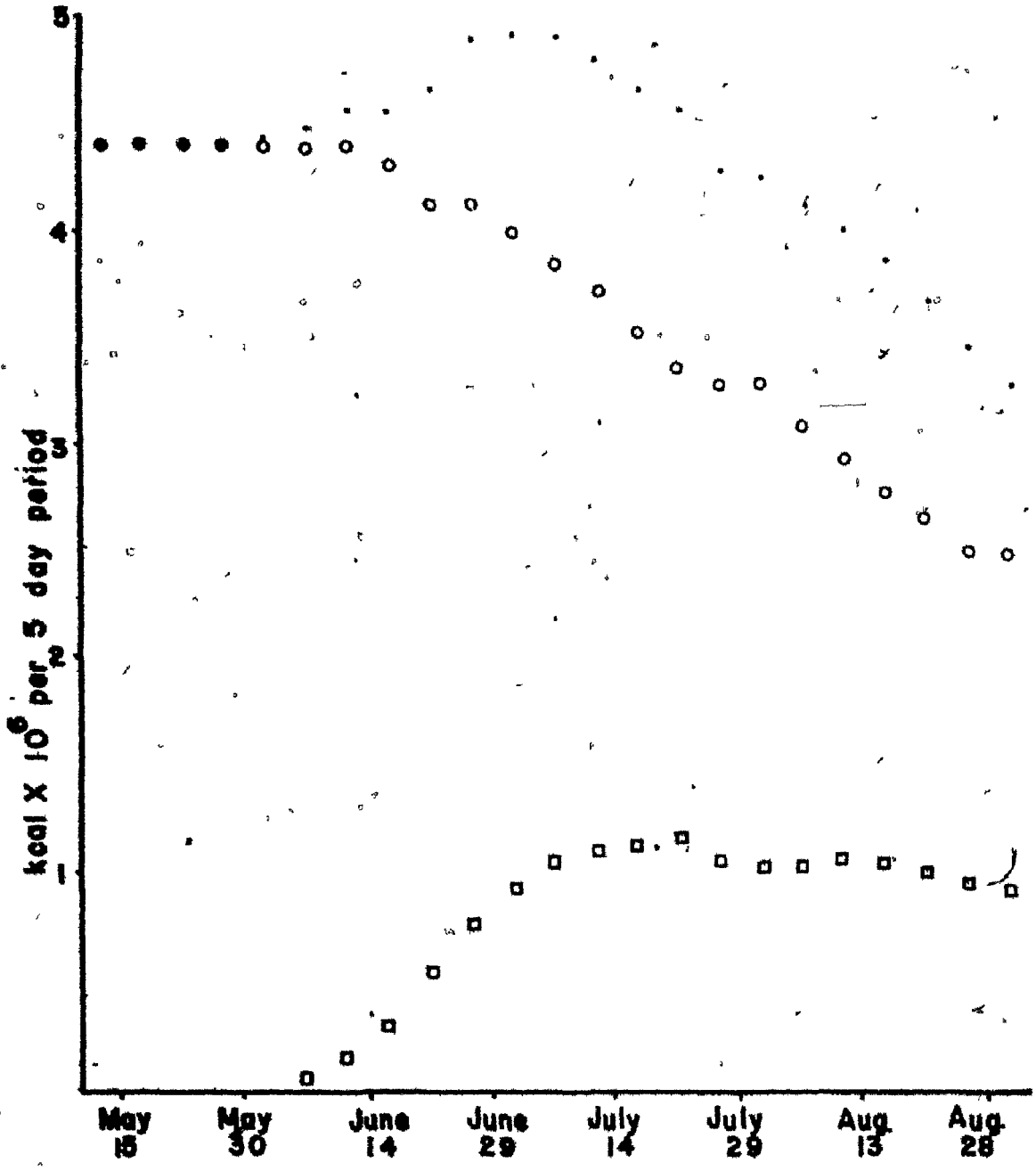
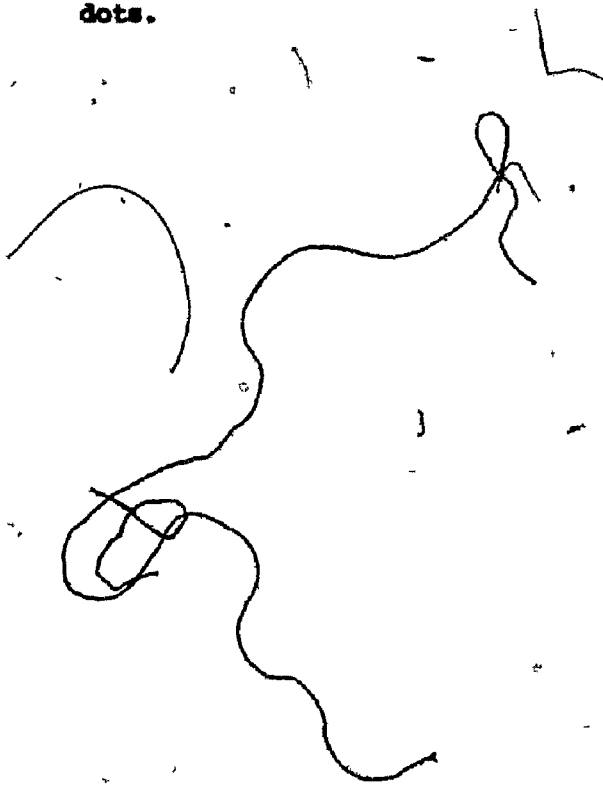
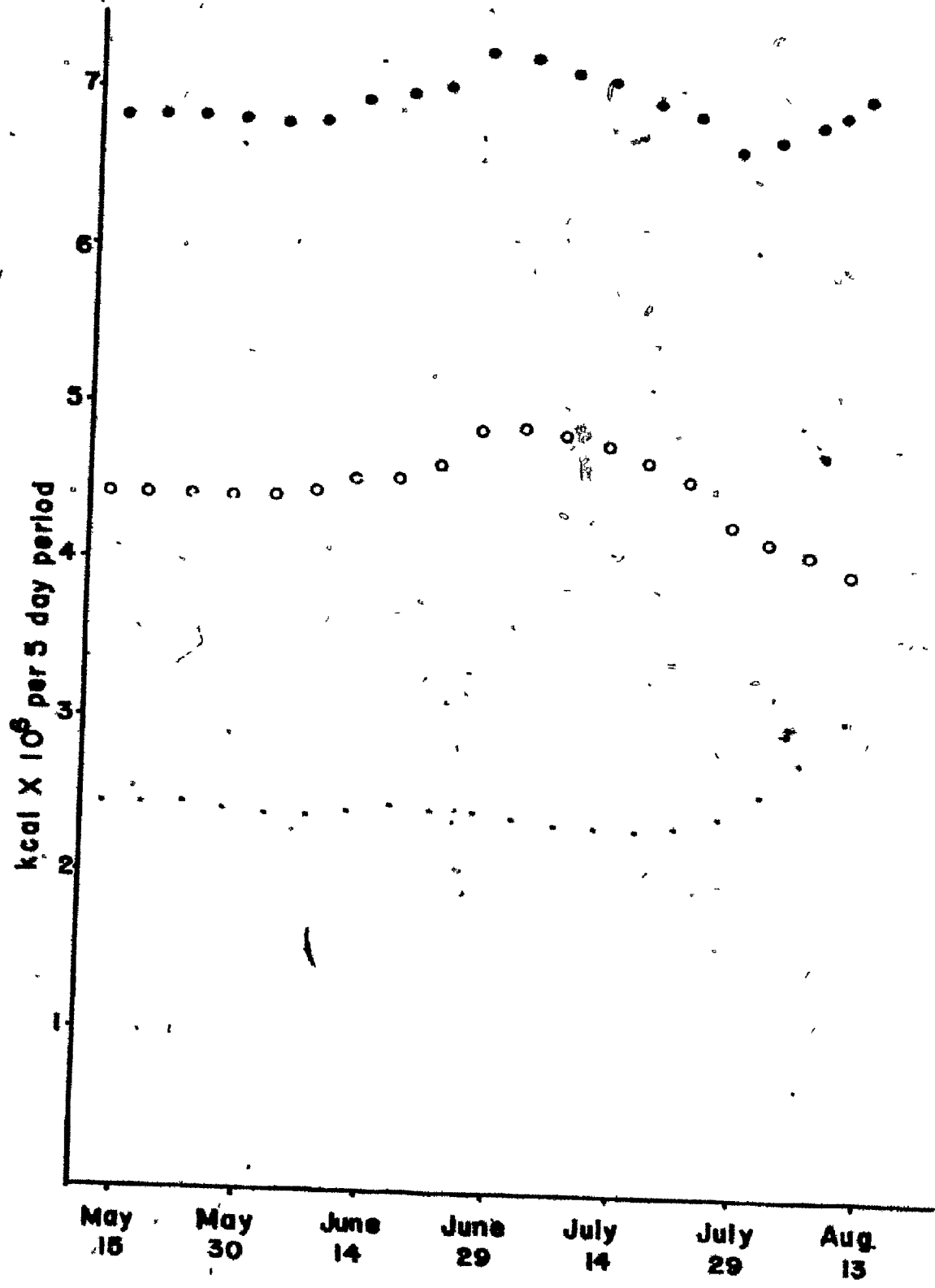


Fig. 16. The calculated calorific value of food consumed by both Herring and Great Black-backed Gulls on Sable Island. Small black dots indicate, food demand of the Great Black-backed Gulls; open circles, that of Herring Gulls and totals are shown by large black dots.



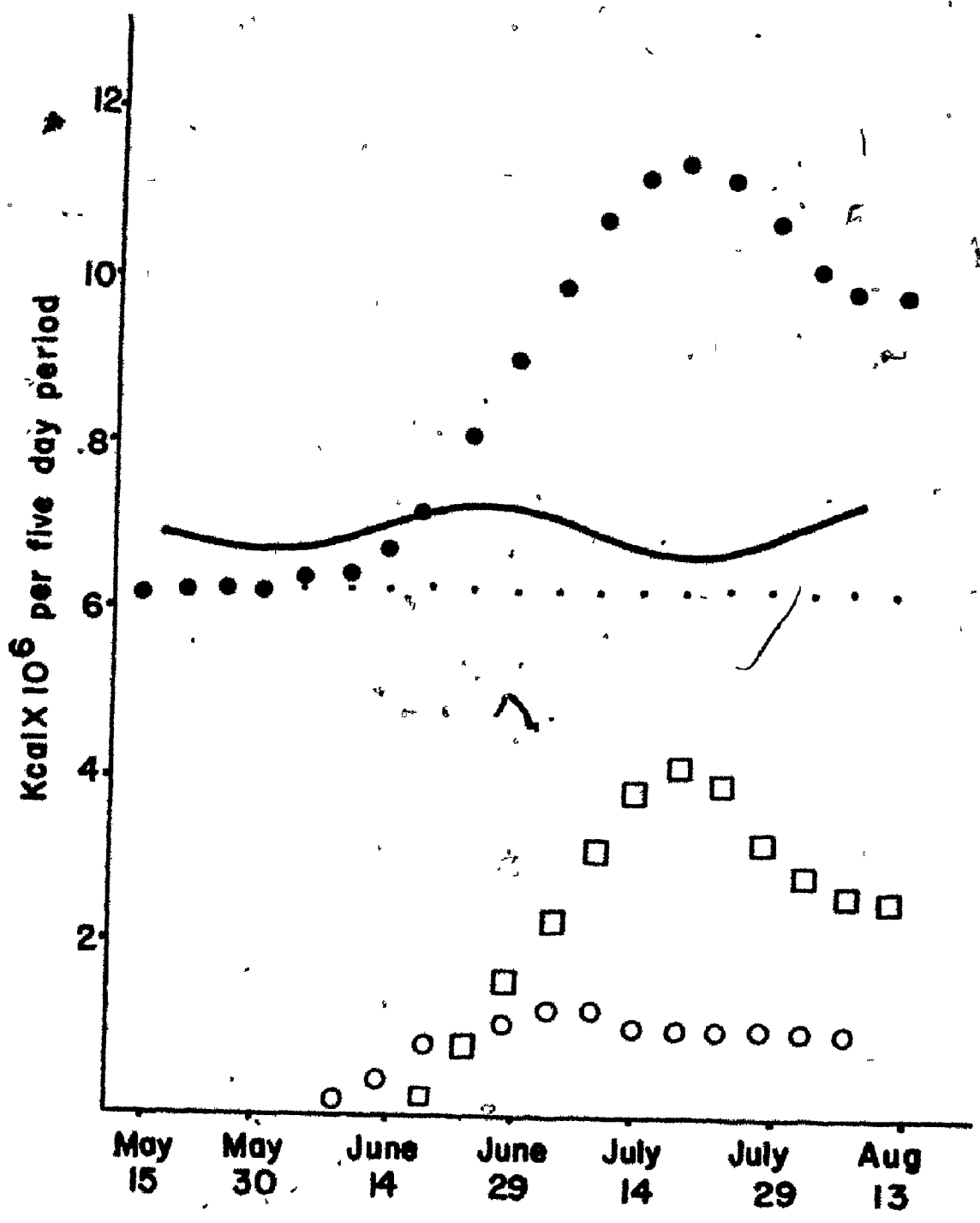


was observed in the Sable Island colonies. The laying and hatching chronology of the modelled population was identical with that of the first clutches on Sable Island. That of the Black-backs was the same of the 1970 study birds. In such a successful population there would likely not be a reduction of numbers of adults as the season progressed and their numbers were assumed to be constant throughout the summer. Fig. 17 shows the calculated food demand of such a population.

The only great change in the potential food supply for Gulls breeding on Sable Island is the annual appearance of fish, mackerel particularly, in the surface waters towards the end of June and the importance of these fish has been shown in the section on the diets of gulls.

This annual migration is correlated with changes in sea-surface temperature (Sette, 1950) and the chronology of gull reproduction is well adapted to it. The peak of food demand of a hypothetical, successful breeding population coincided exactly with the appearance of mackerel in waters around Sable but the graph of food demand of the gull population breeding there does not show a prominent peak at this time as might be expected. Herring Gulls account for the greater part of the food demand on Sable Island but mackerel forms a relatively small part of their diet probably because they are too small to deal successfully with mackerel of the size occurring around the island. Consequently the presence of these fish is of less consequence to the Herring Gulls than to the Great Black-backed Gulls and their presence does not allow the Herring Gulls to greatly reduce their hunting time

Fig. 17. The calculated caloxific value of food consumed by Herring and Great Black-backed Gulls on Sable island if chick survival were as high as is in some mainland colonies. Open squares and circles indicate the food demands of Herring Gull and Great Black-backed Gull chicks respectively while the small black dots show the total food demand of adults of both species. Large black dots show the total food demand. The solid line shows the food demand of gulls on Sable Island calculated using observed chick mortality rates and adult numbers.



and, concomitantly, increase the amount of time they can spend on territory.

Fig. 17 shows that in order to allow a reproductive success comparable with that on other studied colonies the gulls on Sable Island would have to be able to double, between mid-June and mid-July, the amount of food they take from the environment. This the Herring Gull is less able to do than is the Great Black-backed Gull and consequently their reproductive success is lower.

In the forgoing considerations, no account has been taken of the feedback of energy to adult gulls in the consumption of the eggs and chicks of other gulls. Certainly some birds, Blackbacks particularly, exploit the foraging efforts of other gulls by consuming their young, but the amount of energy so gained by them is small. If the energy content of the eggs and chicks disappearing on Sable Island is approximated it is around 3.5×10^6 Kcal, sufficient to supply the food demands of the Gulls on Sable Island for sixty hours.

GROWTH RATES OF WILD CHICKS

Methods

As weighing a chick often causes it to panic, all chicks found were not weighed on every trip. Whenever a chick was found in the open it was weighed and returned carefully to cover and calmed by being covered by a coat. Chicks were weighed on one of three simple, hand-held balances weighing to 350 g, 1000 g and 2200 g, accurate to 2 g, 5 g and 10 g respectively. Chicks were placed in opaque plastic bags, suspended from the balance hook and the sliding weight was adjusted until the balance beam was horizontal (level was checked by sighting against the oceanic horizon which was almost always in view). That chicks usually remained quiet in the bag and could be replaced in their hiding places without being panicked attests the success of this method.

Hunt (1972) whose study of gull reproductive success is closest to mine in intention, time and space, weighed Herring Gull chicks on a spring balance, suspending them by inserting the hook between the aluminum band and the chick's leg. This practice would seem to be more disturbing to the chicks than the methods I employed.

Results and discussion

Herring Gulls

Most published accounts of Herring Gull growth have been quite unanalytical and the only data with which useful comparisons can be made are those of Spans (1971) and Hunt (1972). Both authors fitted regression lines to plots of Herring Gull chick growth between the

ages of five and twenty-five days. Unfortunately, Spaans neglected to publish the variance of his determination of growth rates and his data are of limited use, in consequence. Hunt (1972) only accepted weights from chicks which were weighed at least twice at over 125 g and, to allow statistical comparison with his data I have adopted this criterion also, and the growth rates quoted in Table 2 were calculated by fitting a straight line regression to weights of chicks five to twenty-five days old.

As weighing involves an extra disturbance of chicks only those found moving about in the open were weighed in 1969 and very few weights were obtained. In 1970 Colony C was selected for chick weighing as it contained an abundance of cover to which released chicks could retreat.

The mean growth rate of all chicks for which sufficient data were available was 26.04 g per day, almost identical with the 26.72 g per day that Hunt reports for Sloop I., a colony that he judged to be farther from garbage food sources than any other he studied. Hunt reported significant differences between growth rates of fledging and non-fledging chicks. Similar differences were noted on Sable Island, and when tested by t test (Nather, 1943) were found to be highly significant ($0.01 > p > 0.002$). While multiple tests of a single block of data require more stringent significance limits than the usual 0.05 level, the difference referred to above must be judged significant.

Hunt follows Kallos et al (1969) in believing that underweight chicks are more susceptible to disease, predation and chilling.

Table 23. Growth rates of Herring Gull chicks between the ages of five and twenty-five days, Colony C, 1970.

	No. of Weights	No. of Chicks	Grammes per day	Variance
All chicks weighed	197	65	26.04	0.74
Chicks not fledging	58	21	22.76	2.11
Chicks fledging	139	44	27.54	1.08
Chicks fledging from eggs laid before June 9	112	32	26.59	1.17
Chicks fledging from eggs laid after June 9	27	12	33.36	7.36
Chicks fledging with no sibs at 20 days of age	60	21	29.59	1.93
Chicks fledging with one or more sibs at 20 days of age	79	23	26.15	2.58

Probably the inability of younger chicks in a brood to compete successfully for food with their older and stronger siblings results in slow growth and weakness rendering them more vulnerable to the predatory attacks of gulls. Certainly the chick hatching last in a clutch has the lowest chances of survival to fledging (Parsons, 1971) and the fact that slow growth may lead to difficulties with heat loss is less important than its effect on a chick's abilities to escape other gulls.

Spaans (1971) found that chicks hatching from late clutches grew more slowly than those from early clutches. He hypothesized that less favourable hot weather during the growth period of the later chicks results in water shortages retarding normal growth. On Sable Island those chicks hatching from eggs laid in the first peak of hatching grew at a substantially lesser rate than those hatching from eggs laid later. The difference ($t = 2.32, 0.05 < p < 0.02$) can be taken as significant even though the data are subdivided twice for t tests, and it is presumably ascribable to a difference in the amount of food available to gulls throughout the season. Certainly the number of gulls competing for food is lower later in the season though the food demand of gulls breeding on the island is not (Fig. 16). Probably, the presence of Mackerel and Herring in the surface waters in July makes it easier for the gulls to feed their broods in July. This increased growth rate late in the season is correlated with a high breeding success of late nests. Possibly a part of the reason for this is that gulls are habit feeders to some degree, and feeding habitually on fish in late summer are less likely to prey

on gull chicks.

It is expected that on Sable Island, particularly, adults may be able to feed a single chick at its peak of food demand but have trouble providing food for two or three chicks at this stage. It was observed that chicks without a sibling at the age of twenty days (at which time food demand approaches its peak) grew faster than chicks with a sibling. This difference is not significant however ($p > 0.1$). Varmeer (1963), Harris (1964), Fordham (1964) and Spaans (1971) all report a faster growth of single chicks but only Spaans has done analysis to show that the difference is in some cases significant. It was not expected that the difference between growth rates of single and multiple chick broods would be larger on Sable Island than elsewhere. The extra time needed by adults to gather food for a large brood (see following) results in an extra exposure of chicks to predation. The consequent reduction of brood size to that which can be adequately fed by the parents means that one cannot expect the great differences in growth rate correlated with brood size that one would expect in a species subject to little or no chick predation.

Great Black-backed Gulls

This species, with its longer development period, shows a linear growth phase between the ages of six and thirty days of age. In Table 24 are shown the growth rates calculated from data obtained in 1969 and 1970 by fitting a straight line regression to weights of chicks in this age group. As with the Herring Gulls, the difference between those birds fledging which had one or more siblings at the age of

Table 24. The growth rates of Great Black-backed Gull chicks between the ages of six and thirty days.

	No. of Weights	No. of Chicks	Grammes per day	Variance
Chicks not fledging	91	29	39.83	5.93
Chicks fledging	197	52	45.87	2.55
Chicks fledging with sibs at 20 days of age	152	36	44.64	3.62
Chicks fledging with no sibs at 20 days of age	45	16	50.43	7.00
Hand reared chick # 20355	22	1	57.08	0.45
Hand reared chick # 20356	22	1	51.64	0.20

twenty days and those which did not is not significant ($P > 0.05$). However, the difference between those fledging and those not fledging is sufficiently large that it must be considered meaningful. ($t = 2.074$, $0.05 > p > 0.02$). The growth rates of the hand-reared chicks are appreciably larger than the mean of any subgroup of the wild population. While this can imply nothing about the level of nutrition of the wild birds it does reveal that hand-reared chicks do not show the abnormally low growth which normally characterises hand-reared gulls (Kadlec et al. 1969).

ESTIMATES OF REPRODUCTIVE SUCCESS WITH ARTIFICIALLY ENLARGED BROODS

Introduction

In the examination of the biology of bird species it is of interest to ascertain whether the most frequently observed clutch size is that which, on the average, gives rise to the greatest number of fledgelings. This is particularly worthy of attention in species whose numbers are changing or whose environment is changing. For instance, Nelson (1964) has added chicks to the nests of Gannets (Sula bassana) and found that they can commonly rear two chicks even though their clutch is almost invariably a single egg, a circumstance that suggests that the clutch size of this species was selected for at a time when conditions were quite different from those today. Similar brood enlargements experiments have been carried out on the Glaucous-winged Gull (Larus glaucescens), another increasing species, with similar results (Vermeer, 1963). Harris and Plumb (1965) did brood enlargements with Herring and Lesser Black-backed Gulls in colonies in Wales and here too the larger than normal broods resulted in larger than normal fledging success. I thought that similar experiments carried out on Sable Island would be an important part of an attempt to elucidate the relationships between gull reproductive success and food availability.

Methods

In order to contain the chicks added to gull nests, to reduce the time needed to find the chicks to monitor their daily weight changes

Harris and Plumb (1965) erected low wire-mesh enclosures around study nests. I used this method on Sable Island: around each experimental nest enclosures about five metres square were made from 18 inch wide strips of one inch mesh galvanised "chicken wire". Usually the area thus enclosed contained little cover for the chicks so I added wooden boxes, tree branches and piles of vegetation for refugiums. Enclosures were erected as soon as the first egg in a clutch was pipped and additions were of hatching eggs, chicks of one or two days of age. All chicks were marked for identification with dye spots on the ventral side and the enclosure was checked daily.

Results and discussion

a. Herring Gulls

Nine enclosures were built in Colony D. Here the terrain is relatively flat and enclosures are easily built. The experiment was carried out in mid-July and so these were probably second nests of the pairs involved. However the experiment is not invalidated by the consideration that these are nests of unsuccessful and therefore inexperienced or "inferior" adults. Examination of the fledging rates of Herring Gulls in the Colonies A, B, and C show that second clutches are quite as successful as first clutches.

One of the nine experimental nests was broken up and all eggs lost before any of the eggs hatched but in the remaining nests hatching eggs or chicks were added to bring the brood size up to four and in one case to five. In five of these enclosures all chicks disappeared or were found dead within five days, in the others some chicks survived beyond

this time. To two of the more successful enclosures additional chicks added as casualties were noted but in no case did a brood of four chicks survive to ten days of age.

It was noted in these experiments that where one chick was appreciably smaller than the others in an enlarged brood it gained weight less quickly than was normal and less quickly than its broodmates. Obviously in the struggle for the limited amount of food that can be brought by a parental pair the smaller chicks compete unsuccessfully with larger siblings.

While his supernormal broods were more successful than these, Spaans (1971) thought it probable that in the Wadden Sea area, Herring Gulls were not capable of rearing larger than normal broods in spite of the presence of large amounts of human wastes in their diets. He contrasts this situation with that reported by Harris and Plumb (1965): they found that even in the absence of garbage, Lesser Black-backed Gulls can rear super-normal broods. Spaans does not attempt to explain this, but it seems likely that the amounts of food available per gull pair on Skomer and the nearby rocky coasts of Wales far exceeded that available per pair in the sandy area around the Wadden Sea. On Sable Island the situation is even more extreme for on Sable Island's beaches there is no intertidal fauna such as that supplying some food to Spaans' gulls, not is there any significant amount of garbage.

Vermeer's (1963) enlarged broods of L. glaucescens were successful presumably because adults were within foraging range of long stretches of rocky shoreline and a source of garbage.

b. Great Black-backed Gulls

Five enclosures were placed around Black-back nests in 1970; all had their clutches augmented to five chicks. Three lost most of their chicks within five days and were abandoned but the remaining two were somewhat more successful. Enclosure J had two chicks hatch and two chicks and a hatching egg were added on June 10. This egg or its hatchling disappeared almost immediately but the four remaining chicks matured to between 25 and 28 days before three of them were killed by adults from an adjacent territory. While one chick, # 20303, showed a growth rate comparable to that of the hand-reared chicks, the growth rates of the other three in the brood differ from it markedly after the fourteenth day of age. At this time the four chicks can be expected to demand around 1200 Kcal of food a day. It appears that the foraging ability of the adults is hard pressed at food demands greater than this because on July 4 when the chicks averaged around 25 days of age and the food demand of the whole family was estimated to be around 2500 Kcal per day, the chicks were unattended for as much as 40% of the daylight hours. This food demand is close to the maximum for such a brood and that demand cannot be met after the fourteenth day of age of such a brood is shown by the departure of the growth curves of three of the four chicks from that of the Hand-reared chicks.

In enclosure 116 two chicks were added to the two native hatchlings on June 9. Two died within two weeks of introduction leaving only two to develop to thirty days of age when they were released. These two showed abnormally poor growth rates so it is possible that by being kept inside an enclosure the chicks are prevented from following an adult about the

territory and importuning it for food. Possibly the adults, able to escape from the chicks, tend to forage less food than adults which are constantly stimulated by the begging of hungry chicks. This consideration casts doubt on the validity of brood enlargement experiments employing enclosures.

NEST ATTENDANCE OF ADULT GULLS

Methods

In an effort to determine the time required for adult gulls to gather food for their broods, nests were observed from a hide. The hide was erected the day before observations were due to start and left in position overnight. Preliminary observations located the habitual lounging and roosting spots of the adult gulls and on the eve of the first observations methylene blue and a proprietary red clothes dye were spread on the vegetation near the roosts. The dye crystals were mixed into a paste with flour and water to make it adhere to vegetation. Most gulls picked up smudges of dye which enabled the observer to identify them later.

The hide could be sited within a few metres of the nests of Herring Gulls without undue disturbance but the Black-backs proved very wary of a hide set up closer than 50 m from the boundaries of their nest territory. Watches were started as soon as it was light enough to see and only ended when it became too dark or foggy to observe clearly or when human disturbance was great enough to render further observations fruitless.

Results and discussion

a. Herring Gulls

On the three days July 28, 29 and 30, 1971 five Herring Gull nests were observed during the daylight hours. These nests were on dune sides on the north side of the island about a mile east of the

N.O.T. establishment. Activities of the Mobil Oil Company's seismic crew made work impossible on July 31. Attempts were made to resume observations on August 1 and 2 but observations were suspended around noon each day due to the continuing disturbance. The seismic work finally scattered the gull families and observations could not be resumed.

The attendance of adults at nest and times of feedings were noted and absences of more than five minutes were recorded. Absences of less than five minutes were ignored as the bird was assumed to have been in the vicinity of the nest in this period. As estimates of the daily food consumption of adults and chicks of different ages were available the daily food demand of adults and chicks in each of the observed nests was easily calculated (Table 25) and compared to Black-back food demands in Table 26. The results of the hide observations are presented in Table 27, and the following figures 18 to 20 show the same data graphically.

Fig. 18 shows a strong correlation between the food demand of a gull family and the amount of time that the nest is left unattended. There is a substantial variation in the results as can be expected of behavioural data when the performances of several individuals are combined. However, the regression is highly significant ($p < 0.01$) and demonstrates that the food demands of two or three half-grown chicks may force the adults to leave the territory unguarded for more than a third of the time.

As Herring Gull adults were successfully dyed and individually recognizable it is possible to plot the amount of time spent by each adult individually at the nest as a function of food demand. There

Table 25. The food demand of observed nests of Herring Gulls.

Nest	D	C	E	A	B	I	2
No. of chicks	0	1	1	1	3	2	2
Age (days)	-	5	15	18	15	27	27
Food demand Kcal/day	440	520	650	690	1070	1150	1150

Table 26. The food demand of observed nests of Great Black-backed Gulls.

Nest	26	116	5	51	J
No. of chicks	2	2	3	3	4
Age (days)	4	25	38	36	26
Food demand Kcal/day	1000	1575	1700	1700	2500

Table 27. The percentage of observation time during which adult Herring Gulls were present at the nest.

Nest	Food demand Kcal./day	Date of Observation	# hours Observed	Nest Unattended	Percent of observed time		
					Adult # 1 Present	Adult # 2 Present	Both adults Present
D	440	29/7	14.08	16.55	60.83	53.85	32.43
D	440	30/7	15.00	7.56	53.85	84.00	77.00
C	520	28/7	13.33	1.63	52.51	65.02	19.13
C	520	29/7	14.08	0.71	74.79	24.14	1.67
C	520	30/7	15.00	17.00	57.22	53.11	27.33
E	650	28/7	13.33	5.88	39.98	83.27	29.13
E	650	29/7	14.08	28.52	25.80	45.68	0
E	650	30/7	15.00	14.33	85.67	15.22	15.22
A	690	28/7	13.33	11.75	70.64	22.51	4.63
A	690	29/7	14.08	2.25	53.61	44.62	0.47
A	690	30/7	15.00	1.00	41.44	74.00	16.44
B	1070	28/7	13.33	53.76	38.76	17.00	9.50
B	1070	29/7	14.08	93.37	3.43	2.01	0
B	1070	30/7	15.00	91.78	6.33	1.78	0
1	1150	1/8	7.66	41.60	8.49	71.66	8.49
1	1150	2/8	7.75	40.53	20.44	38.74	2.36
2	1150	1/8	7.60	14.82	85.30	0	0
2	1150	2/8	7.75	34.65	8.83	52.92	0.65

is, as expected, a strong inverse relationship between them and it is obvious that at a daily food demand of about 750 Kcal/day each adult will be able to spend only around 50% of its time at the nest. As food demands exceed this value chicks will, perforce, be left on undefended territories for greater periods of time.

Fig. 20 relates the amount of time that both parents are at the nest with food demand. The relationship is similar to that displayed for Great Black-backs in Fig. 22 with the important difference that Herring Gulls gathering around 1000 Kcal/day will tend to be together at the nest less than 20% of the time while Black-backs with a proportionate food demand (a little over 4.5 adult rations) might be expected to be at the nest together 35% of the time.

Unfortunately these interesting relationships are not a simple explanation of the high chick mortalities on Sable Island. The highest Herring Gull mortality occurs, as is normal for Gull colonies, in the first few days of life. Over 60% of the chicks that hatched died or disappeared within 10 days. (Fig. 6). Mortality rate declines with age but takes a sharp drop after the age of 20 days suggesting that the increase of food demand at the time when chicks are in the 20 to 40 day old age group has no significant effect on the mortality schedule. This circumstance is consonant with the curve of food demand for Sable Island (Fig. 16) which shows that the watering of chicks on the island causes no great increase in the food demand curve. There is a degree of circularity in a discussion of this sort and an attempt will be made to resolve it in the final discussion.

Fig. 19. The proportion of observation time during which the nest was unattended plotted against the food demand of the family, Larus argentatus.

$$Y = 0.0579X - 28.6794. \quad 0.002 < p < 0.01.$$

Fig. 20. The proportion of observation time during which each individual adult is present plotted against the food demand of the family, Larus

argentatus. $Y = -0.0500X + 82.3029. \quad 0.02 < p < 0.01$

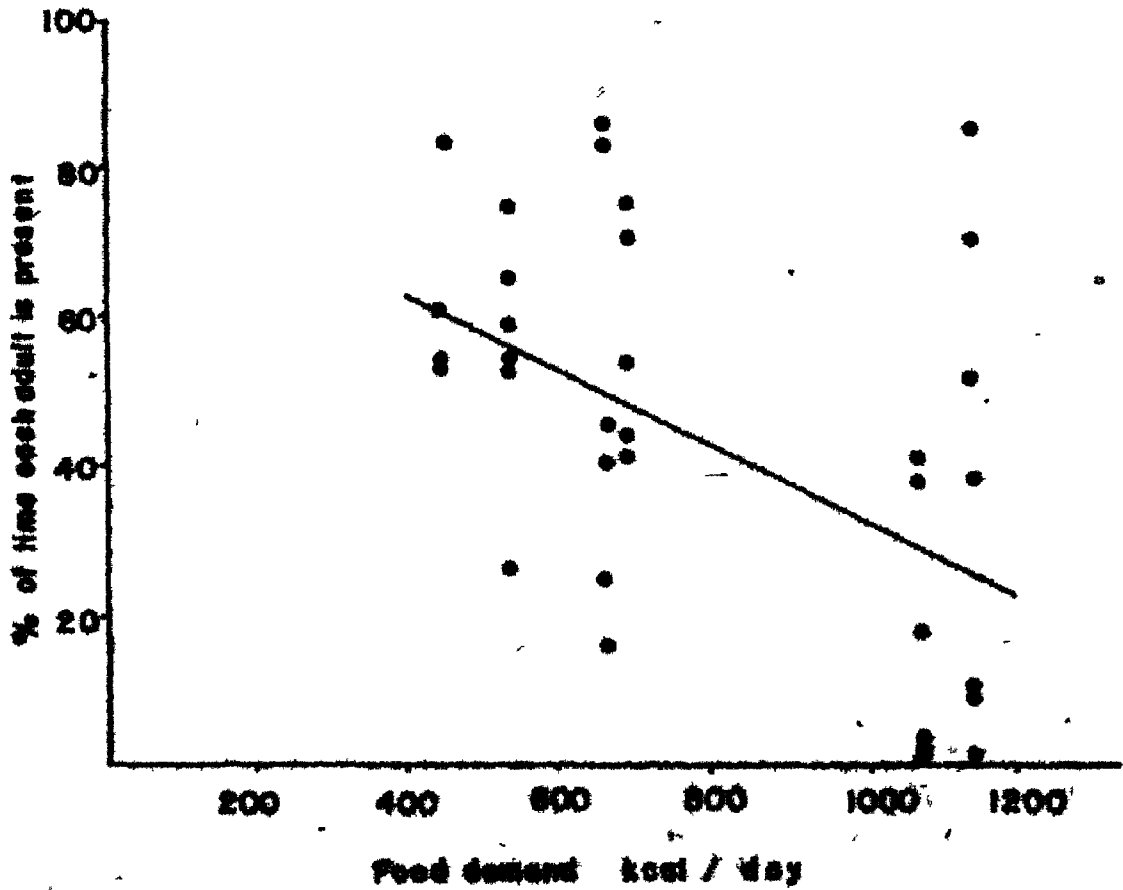
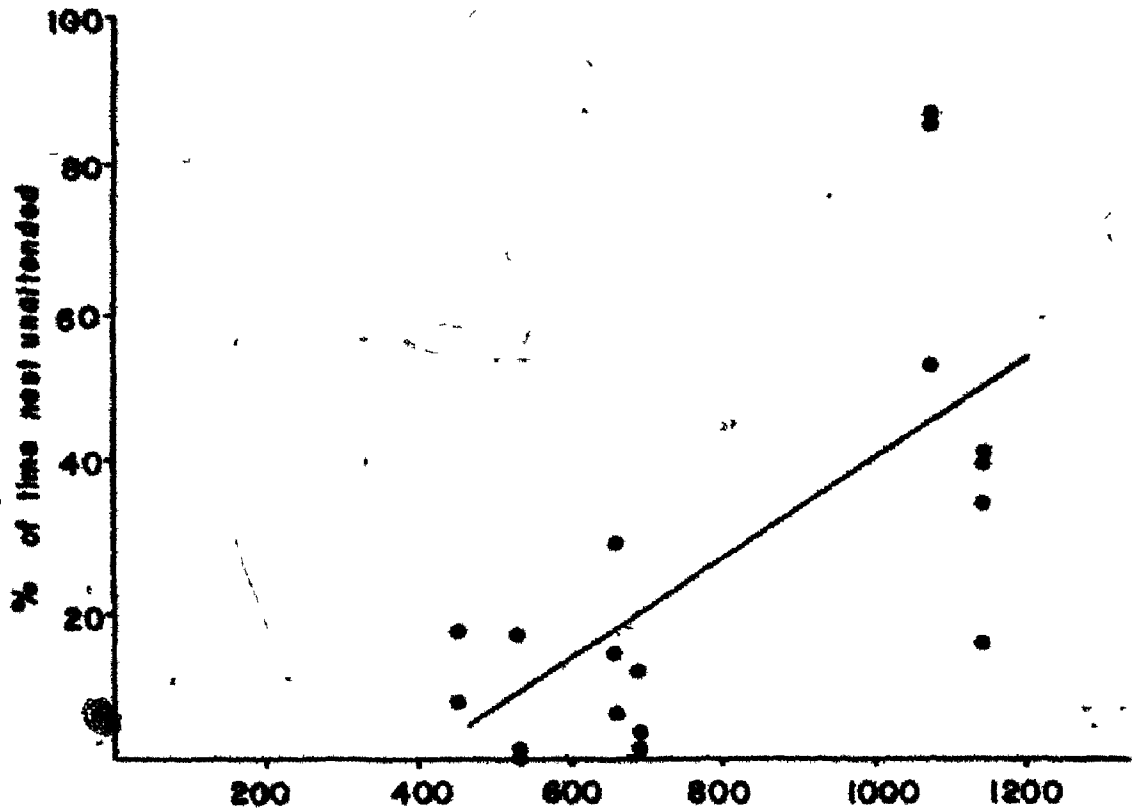
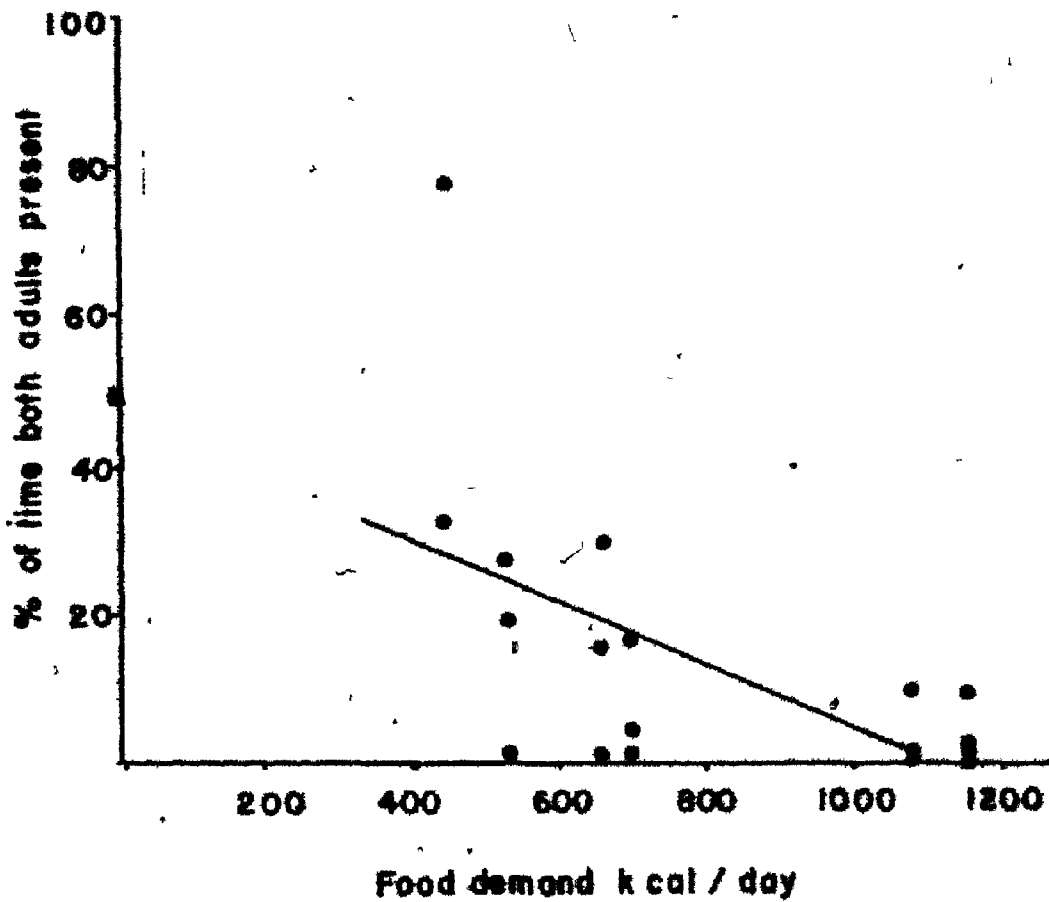


Fig. 20. The proportion of observation time during which both adults were present at the nest plotted against food demand of the family, Larus argentatus. $Y = 0.0410X + 46.0803$. $0.02 < p < 0.01\%$



b. Great Black-backed Gulls

As the adults of this species breed solitarily or in looser colonies than the Herring Gulls it proved difficult to keep several nests under observation simultaneously. Their more wary natures force an observer to keep at least 40 to 50 metres from their nest or chick-rearing territory and as these territories are larger than those of Herring Gulls and contain several habitual lookout points or roosting places, it was less easy to dye them for identification or to keep them under observation. Even though individual adults were not always individually identifiable behavioural clues allowed identification of the adults associated with each territory.

The results of the observations on Black-backed Gull nests are shown in Table 29 and Figs. 21 and 22. It is apparent at first inspection that the amount of data gathered are not sufficient to outweigh the variability of individual responses to the food demand of chicks.

Regressions are plotted on the data and while there are not significant, there is a strong suggestion that there are behavioural differences between gull pairs subject to light and heavy food demands. This great variability in the data is also observable in the Herring Gull results and presumably reflects differences in foraging skill, possibly between experienced and inexperienced pairs. Furthermore, gulls are scavengers which often find their food in large lumps, so mere chance encounter with a large food item can influence daily attendance at the nest to a great extent.

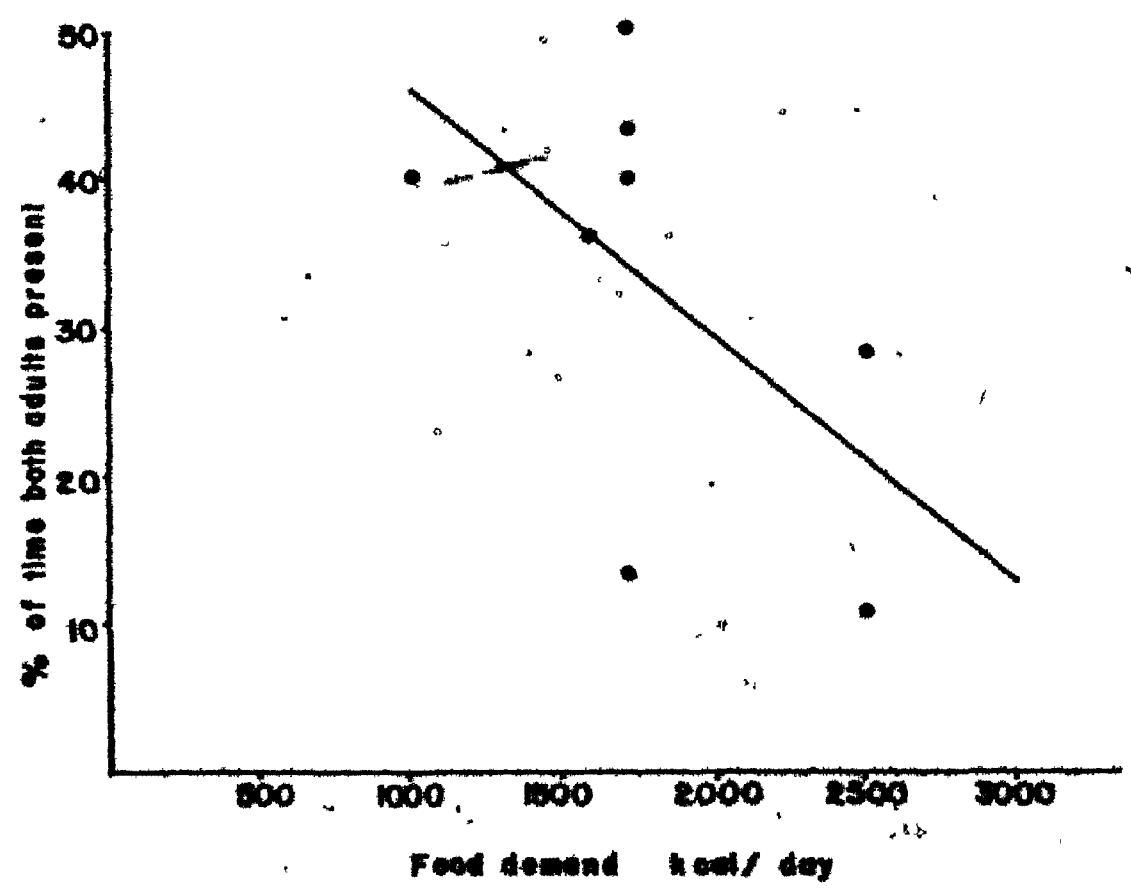
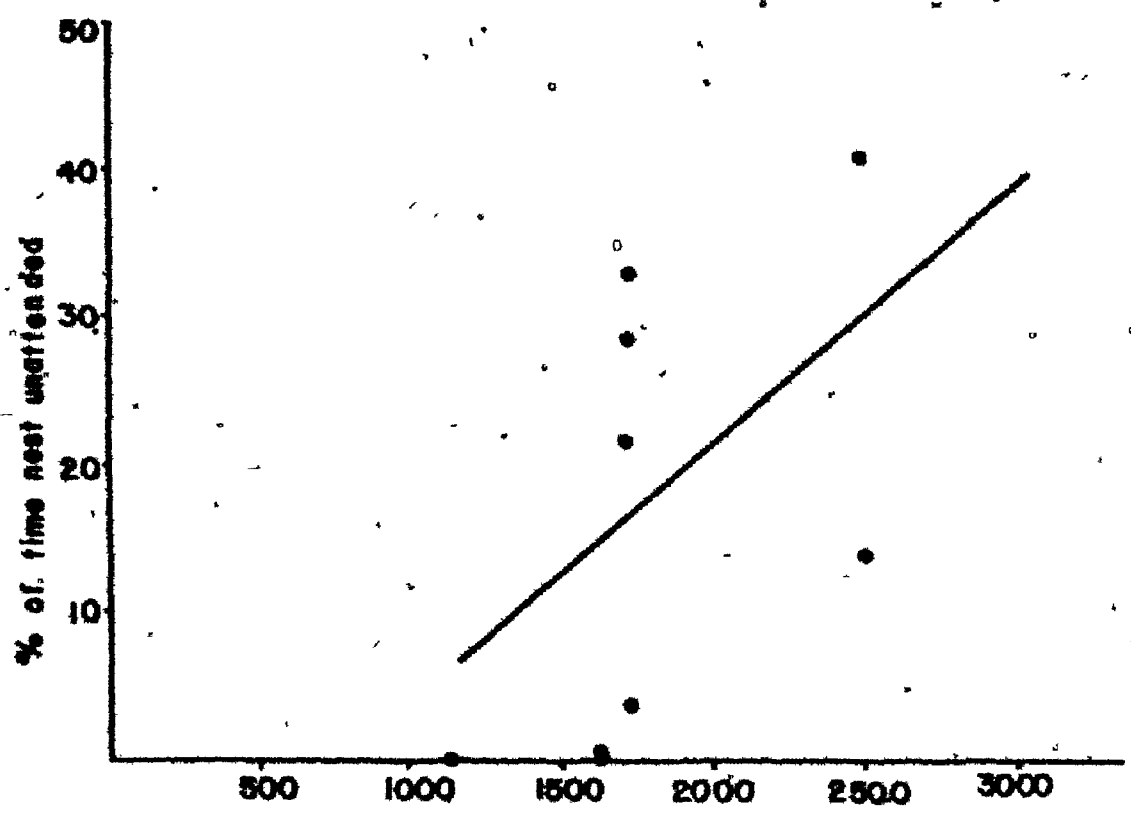
Two full days of observation were done on a pair whose brood had been artificially enlarged to four. This pair had reared the chicks

Table 28. The percentage of observation time during which adult Great Black-backed Gulls were present at the nest.

Nest number	Family Food demand Koal/day	Date of Observation	# Hours Observed	Percent of observation time		
				Nest Unattended	One adult Present	Two adults Present
26	1000	30/6	7.90	0	58.86	41.14
116	1575	4/7	13.50	0	63.60	36.40
5	1700	18/7	15.13	28.19	31.50	40.31
5	1700	23/7	15.00	3.33	53.22	43.44
51	1700	18/7	15.13	21.70	29.19	51.12
51	1700	23/7	15.00	32.77	53.88	13.33
J	2500	2/7	14.58	40.50	46.60	10.87
J	2500	4/7	13.50	13.60	58.50	27.90

Fig. 21. The proportion of observation time during which both adults were absent from the nest plotted against food demand of the family, Larus marinus. $Y = 0.0174X - 13.6969$. $p > 0.1$.

Fig. 22. The proportion of observation time during which both adults were present at the nest plotted against food demand of the family, Larus marinus. $Y = -0.0163X + 62.4311$. $p > 0.1$.



to the age of around 25 days when observations were started. Unfortunately, early in the third day of observations 3 of the chicks were killed and eaten by an adult on a neighbouring territory. However in the 28.08 hours of observation it became clear that these four large chicks, whose food demands were equivalent to about six adults, only slightly strained the food gathering abilities of the adult pair who were absent from the territory for only 27.6% of the time. Compared with the other observed Black-back nests which were unattended for an average of 15.87% of the time the difference is not substantial. In fact their closeness is interesting when compared to the performance of Herring Gulls.

The amount of time when both birds are at the nest together decreases, predictably, with increasing food demand. There is probably only a slight biological significance in this relationship but it does reflect the more important inverse correlation between food demand and the attendance of individual birds at the nest. Also if there is a general disturbance in the colony, as when horses run through it, chicks are dispersed often into adjacent territories. The presence of both adults will reduce the danger to chicks from such disturbances.

It seems that a Black-backed Gull pair gathering 2500 Kcal per day may leave the nest unguarded no longer than a Herring Gull pair gathering only around 1000 Kcal per day. Even if the slightly greater energy demands of the larger species is taken into account it is obviously a more efficient forager than the Herring Gull. When food demand is greatest a Herring Gull pair may have to gather something

over 1400 Kcal per day and at this level of demand it is to be expected that the nest would be guarded only around 30% of the time. A Great Black-backed Gull pair, in contrast, gathering its normal maximum of around 2350 Kcal per day might be expected to be present at the nest for more than 70% of the time.

DISCUSSION

Gull population growth has been less in Nova Scotia in this century than in New England; this fact supporting the hypothesis that increases in range and numbers of the large gulls are, to some extent, due to their use of human wastes as food. Great Black-backed and Herring Gulls only began nesting on Sable Island after 1920 when the eastern North American populations were already at a high level (Drury, 1963), implying that Sable Island is not an optimal breeding area.

The reproductive success of both species is lower on Sable Island than in most other investigated colonies through the exceptionally low success of Herring Gulls here is paralleled by that of non garbage-feeding populations studied by Hunt (1972) and Paludan (1952). Ludwig (1966), examining banding data from Herring Gulls breeding on the Great Lakes, concluded that an annual production of 0.67 chicks per pair was sufficient to maintain the population size; there is no reason to think that the post-fledging mortality of the Atlantic coast population is radically different. Colony C was thought to be most representative of the Herring Gull colony on Sable Island, here 108 pairs laid an average of 3.18 eggs per pair and reared 43 fledged chicks, an average of rather less than 0.42 chicks per pair. This is below the number needed to maintain population size, and it is probable that the Sable Island population is maintained by immigration from the more successful mainland colonies.

The pattern of chick mortality on Sable Island (Fig. B) sets this population among populations breeding with an insufficient food supply

and the fact that eggs laid earliest or at the peak of egg laying are not the most successful differentiates it from all except Harris' (1969) colony on Skokholm in Wales. Presumably the advantages which accrue to highly synchronized nesters are annulled by the somewhat peculiar breeding situation on Sable Island.

Erwin (1971) reported that Herring Gulls nesting near Great Black-backed Gulls enjoy a lower success than those not so placed. On Sable Island the Herring Gull Colonies B and C were topographically similar, differing mainly in the greater number of breeding Black-backs in the Colony B. The percentage of eggs producing fledging young in Colony C in 1970 was more than twice as great as Colony B. The predatory predilections of the Black-backs in a mixed colony and Herring Gull breeding success. The effect of Black-backs on Herring Gulls in Erwin's (1972) colonies is quite small compared with the effect on Sable Island, possibly because at the southern extreme of its range in Rhode Island they enjoy less of a competitive advantage.

It is certain that disturbance by the investigator contributes significantly to both egg and chick mortality and that survival in an unstudied colony is higher than in a study colony. A colony where food is scarce may be more sensitive to disturbance if more adults are away from the colony foraging and those remaining possibly more

likely to prey on gull chicks. Studies on Sable Island will thus give less accurate estimates of breeding success than will investigations carried out in a colony with an abundant food supply. However as my colonies have been subject to no greater disturbance by the investigator than any other, results are comparable. In such situations as Sable Island quite small environmental perturbations might be expected to have large demographic consequences and minor changes in weather, investigation technique, or the number of Black-backed Gulls nesting near-by have a disproportionate effect and account for the rather large variations in egg and chick mortality noted in the different colonies studied.

Where two or more taxonomically close seabird species are sympatric, competition may be demonstrably reduced by morphological differences, staggering of breeding seasons or partition of feeding and breeding areas. Cormorant species employ all these strategies (Ross, 1973) while the auks though not staggering their breeding seasons, do differ in feeding behaviour, area and apparatus (Cody, 1973, for summary). The two species of large gull breeding on Sable Island are morphologically similar but the Herring Gull is only about 50% of the weight of the Black-backed Gull. There is no obvious modification of bill morphology as in the auks (Bedard, 1969a, b) and little obvious partitioning of the breeding areas. Certainly the Black-backs tend to nest on the more commanding spots in mixed colonies but there is little competition for space on Sable Island and both species nest in similar situations.

The larger, Black-backed Gulls commence breeding earlier than the Herring Gulls and it is to be expected that this would ensure a temporal

displacement of peaks of food demand of the two species. In fact the slower development of the larger species more or less annuls this and the curves of food demand overlap considerably and their peaks are only about a week apart. Competition between these species seems to be reduced mainly by differences in weights, each species, as a consequence of its size, feeding in different areas and to some extent taking different prey. Differences in diets (Tables 21 to 23) show this and it seems that the great Black-backed Gull's breeding schedule is adapted to the availability of a specific food source: the schooling mackerel and herring. That this species renests less often than the Herring Gull supports the contention that it is adapted to a food source of short duration. Herring Gulls, in contrast, do reneest and their breeding season is more protracted, as might be expected of a shore scavenger whose food supply does not peak in abundance at a predictable time of year.

Erwin (1971) noted that Great Black-backed Gulls exhibited a more protracted laying period than the Herring Gulls in Rhode Island. In this area laying of both species is about two weeks earlier than on Sable Island and it is possible that at this latitude where seasonal extremes and effects are less pronounced the Black-backs (which have only recently begun to breed in the area) have a different feeding pattern. This supposition is supported by the fact that Herring Gulls are more successful than Black-backs at this latitude. Erwin prefers to explain the observed differences in nesting pattern and breeding success in purely societal and behavioural grounds.

The curve of food demand of a normal population of gulls increases

substantially about the time when the chicks hatching from eggs laid at peak of laying reach their fourth week of growth. It is demonstrated that food demand, in fact, would double in the period between the time when the peak eggs hatch and the chicks reach their fourth week. The fact that the calculated curve of food demand on Sable Island does not peak is of great interest. It cannot be argued that there is an unsurpassable limit to the amount of food that can be taken from the waters around the island because there is a demonstrable increase in the food supply when the mackerel and herring arrive at the surface in late June. As a normally reproducing population increases its food demand about the time that this increased food supply appears, the unescapable conclusion is that food is already insufficient for the population before the majority of chicks enter their fourth week of growth and before food demand increases drastically. The hatching rate of eggs on Sable Island is exceptionally low; as gulls are not crowded physically on the island one must accept that they are crowded trophically, and that the stress of seeking food and guarding a clutch of eggs proves to be too much for many of them. The short food supply probably further increases the likelihood of eggs and chicks being an attractive prey and as gulls are habit feeders the pattern of feeding, once established, is not readily abandoned even if a new food source does appear.

The birds, mainly Herring gulls, leaving the island even at the time that food is becoming more plentiful are those birds which have failed in their attempt at breeding. Their migration is in response to conditions created by an earlier food shortage and results in the curve of food demand being flat even though food available does increase in

mid-summer.

The greater rate of growth of both Herring and Black-backed Gull chicks without siblings at 20 days of age is a further evidence of the crucially short food situation on Sable Island. The differences in growth rates were, in both cases, substantial but so great is the variability of measures of this kind that in neither case was the difference significant. Most interesting was the demonstration that, in 1970, Colony C, the most generally successful and representative Herring Gull colony studied, the growth rate of chicks hatching from eggs laid late in the season was significantly higher than that of chicks from eggs laid in the first peak of laying. Spaans (1971) found the opposite. Presumably the increased availability of food later in the season allows this enhanced growth. This higher growth rate and relatively greater reproductive success of late clutches of Sable Island compared with other reported Herring Gull colonies suggests that the appearance of another food source was of paramount importance in determining breeding success.

The lesser ability of Herring Gulls than Black-backs to rear enlarged broods on Sable Island is explained by an examination of the relative abilities of the two species to gather sufficient food to rear their chicks. Herring Gulls must spend a larger part of their time than Black-backs foraging to feed their broods. While Black-backs have the weight and strength to exploit the schooling mackerel and the terns breeding on the island are well adapted to exploit the abundant Ammodytes in the waters around the island, neither food species is efficiently taken by a bird the size of a Herring Gull and the greater amount of time

they must spend foraging means that their chicks are unguarded for longer periods as they approach their period of maximum growth. During this critical time mortality is higher on Sable than in colonies with abundant natural or man made food supplies, demonstrating the importance of human wastes to breeding gull populations.

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APPENDIX I

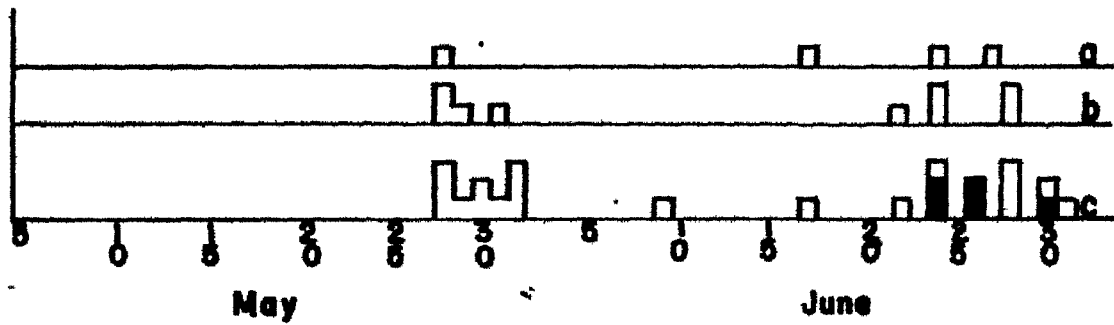
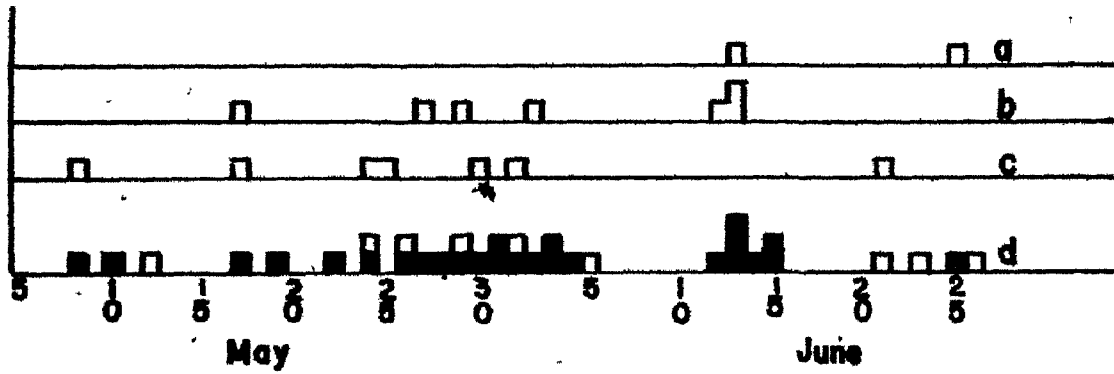
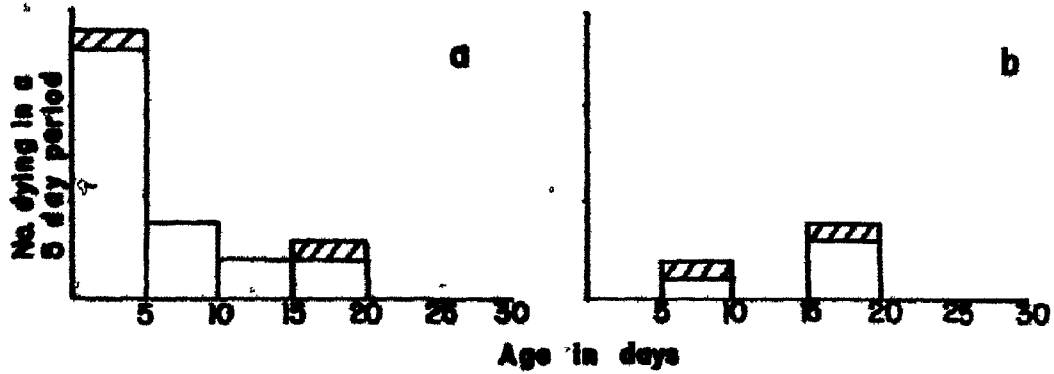
Schedules of Herring Gull chick mortality, dates of laying of eggs and dates of initiation of clutches of varying size.

In the figures that follow shaded areas on the schedules of chick mortality indicate chicks whose remains were found. On the histograms of egg laying, all datable eggs laid in a colony are shown by the outer envelope. The cross-hatched areas indicate eggs which hatched and the black areas indicate eggs producing fledglings.

APPENDIX Ia. Schedules of mortality of Herring Gull chicks in Colony B, 1969 (a) and Colony A, 1969 (b).

APPENDIX Ib. Herring Gulls, Colony B, 1969. Dates of initiation of clutches of one (c), two (b) and three (c) eggs and dates of laying of all eggs (d).

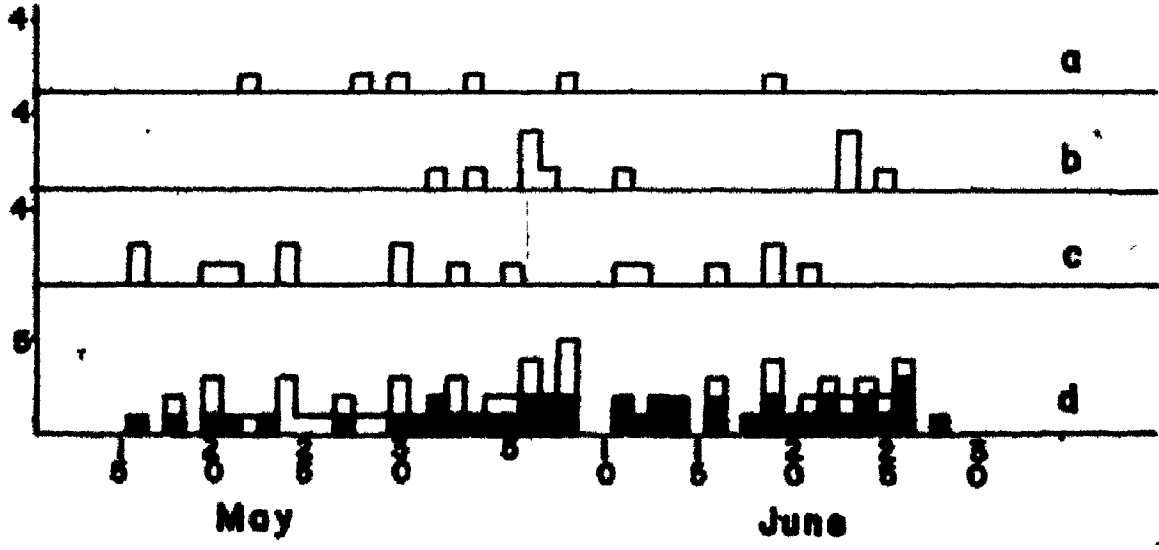
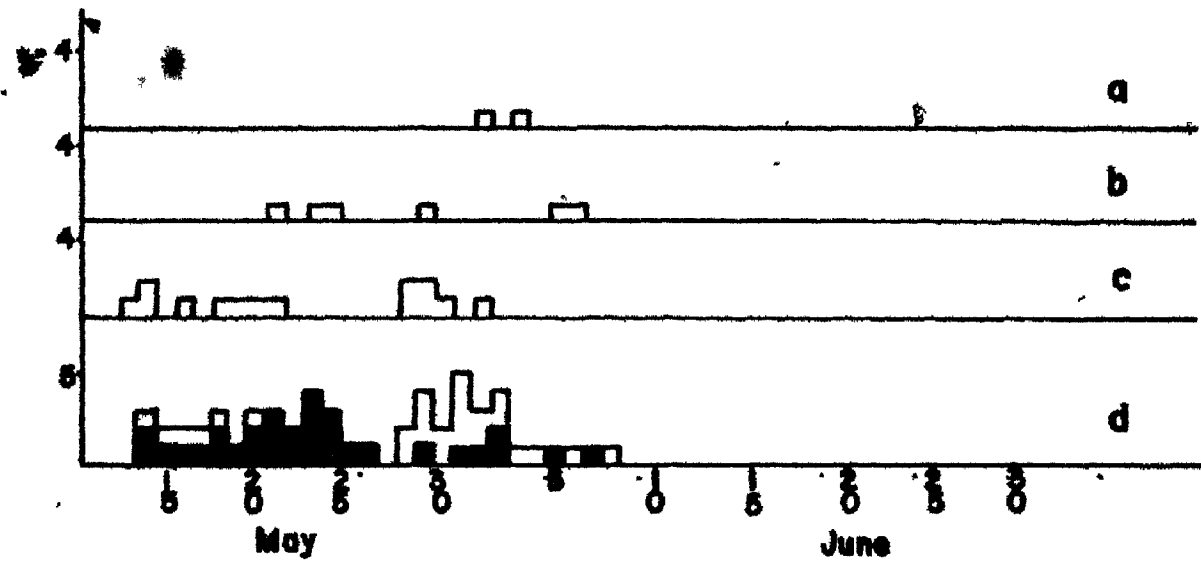
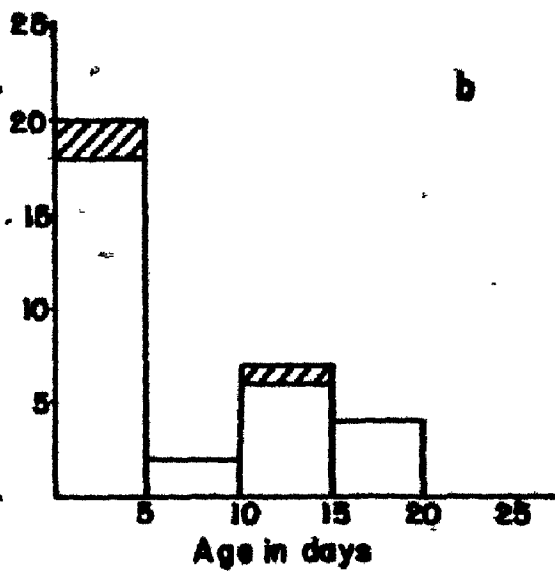
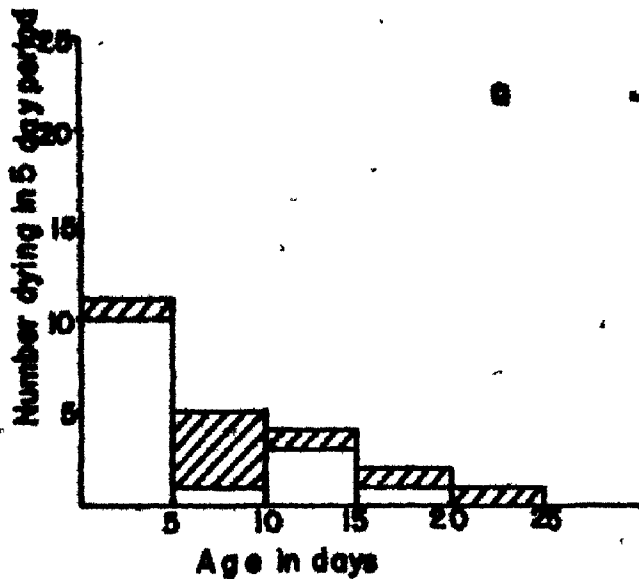
APPENDIX Ic. Herring Gulls, Colony A, 1969. Dates of initiation of clutches of one (a) and two (b) eggs and dates of laying of eggs (c).



APPENDIX Id. Schedules of mortality of Herring Gull chicks in Colony E, 1969 (a) and Colony A, 1970 (b).

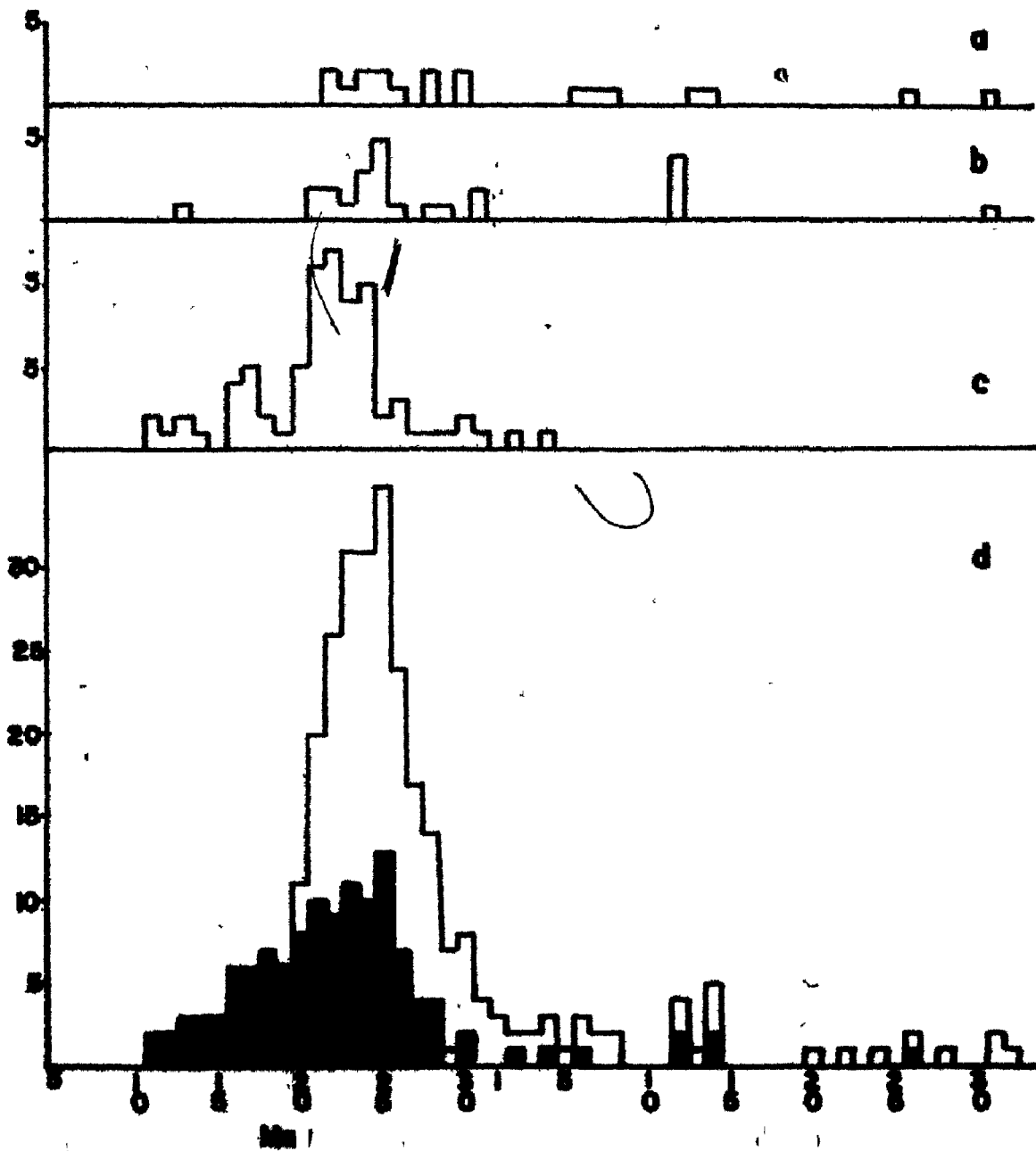
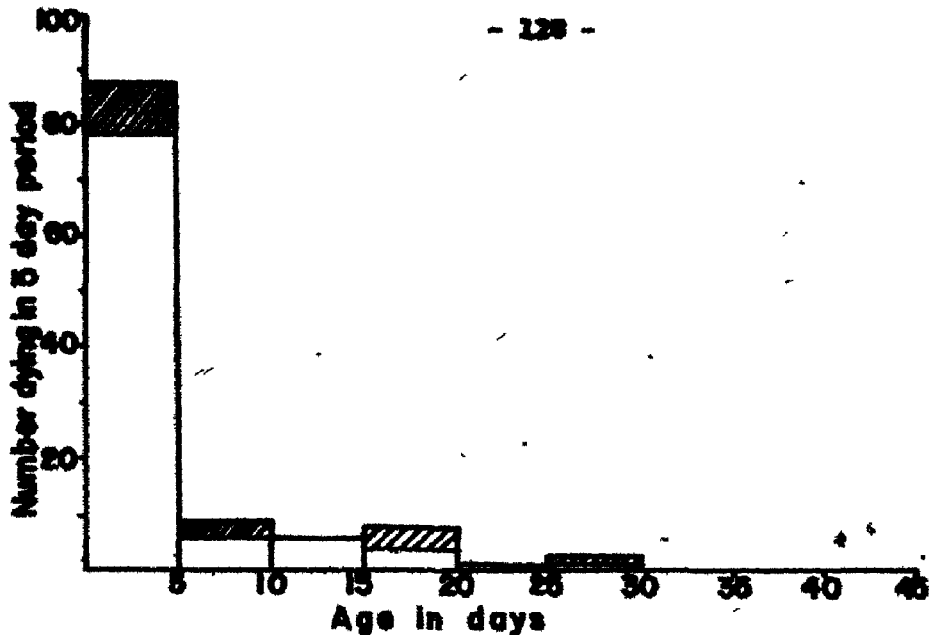
APPENDIX Ie. Herring Gulls, Colony E, 1969. Dates of initiation of clutches of one (a), two (b); and three (c) and dates of laying of eggs (d).

APPENDIX If. Herring Gulls, Colony A, 1970. Dates of initiation of clutches of one (a), two (b), and three (c) eggs and dates of laying of eggs (d).



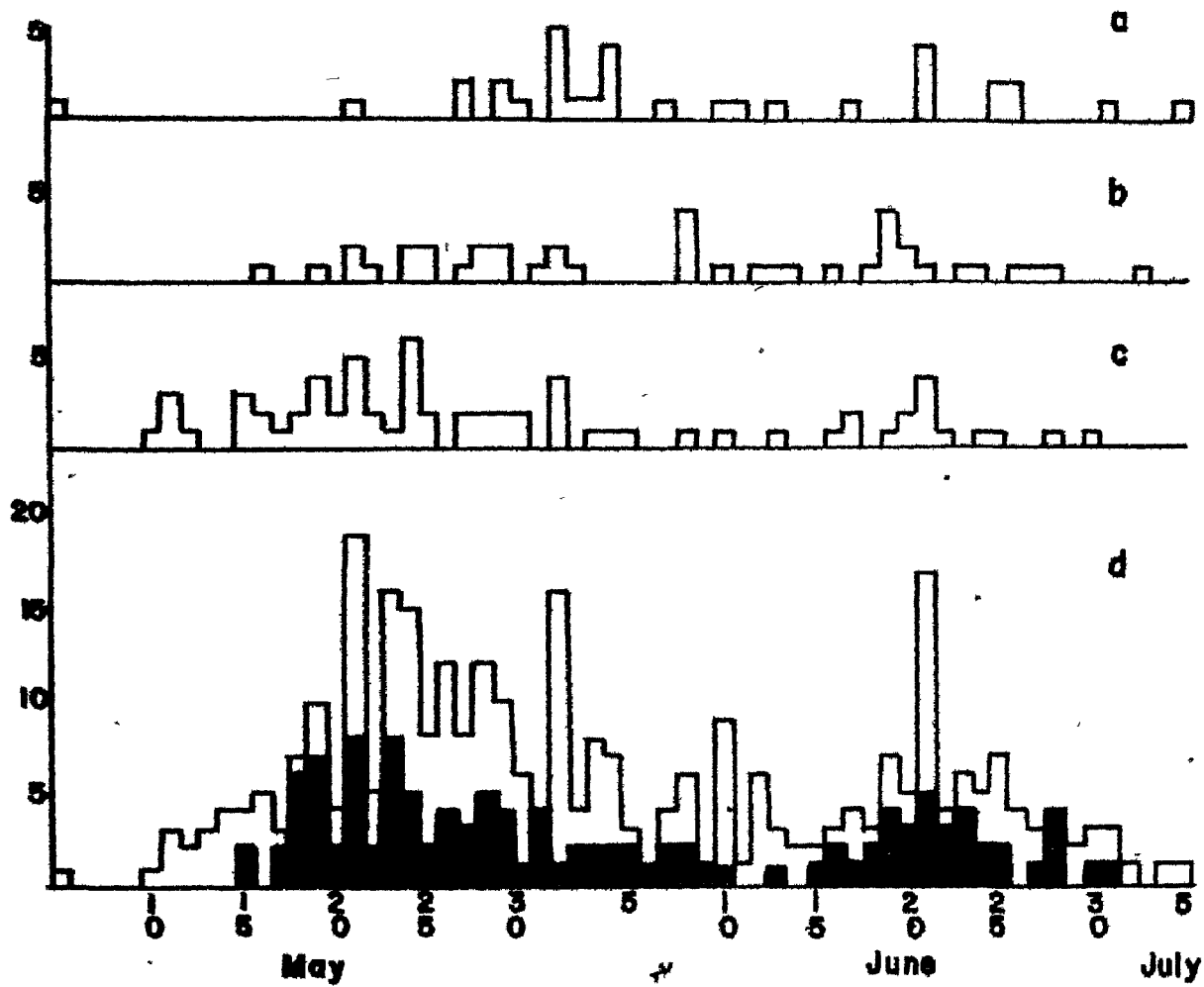
APPENDIX Ig. Schedule of mortality of Herring Gull chicks in Colony D,
1969.

APPENDIX Ih. Herring Gulls, Colony D, 1969. Dates of initiation of
clutches of one (a), two (b), and three (c) eggs and dates of laying
of eggs (d).



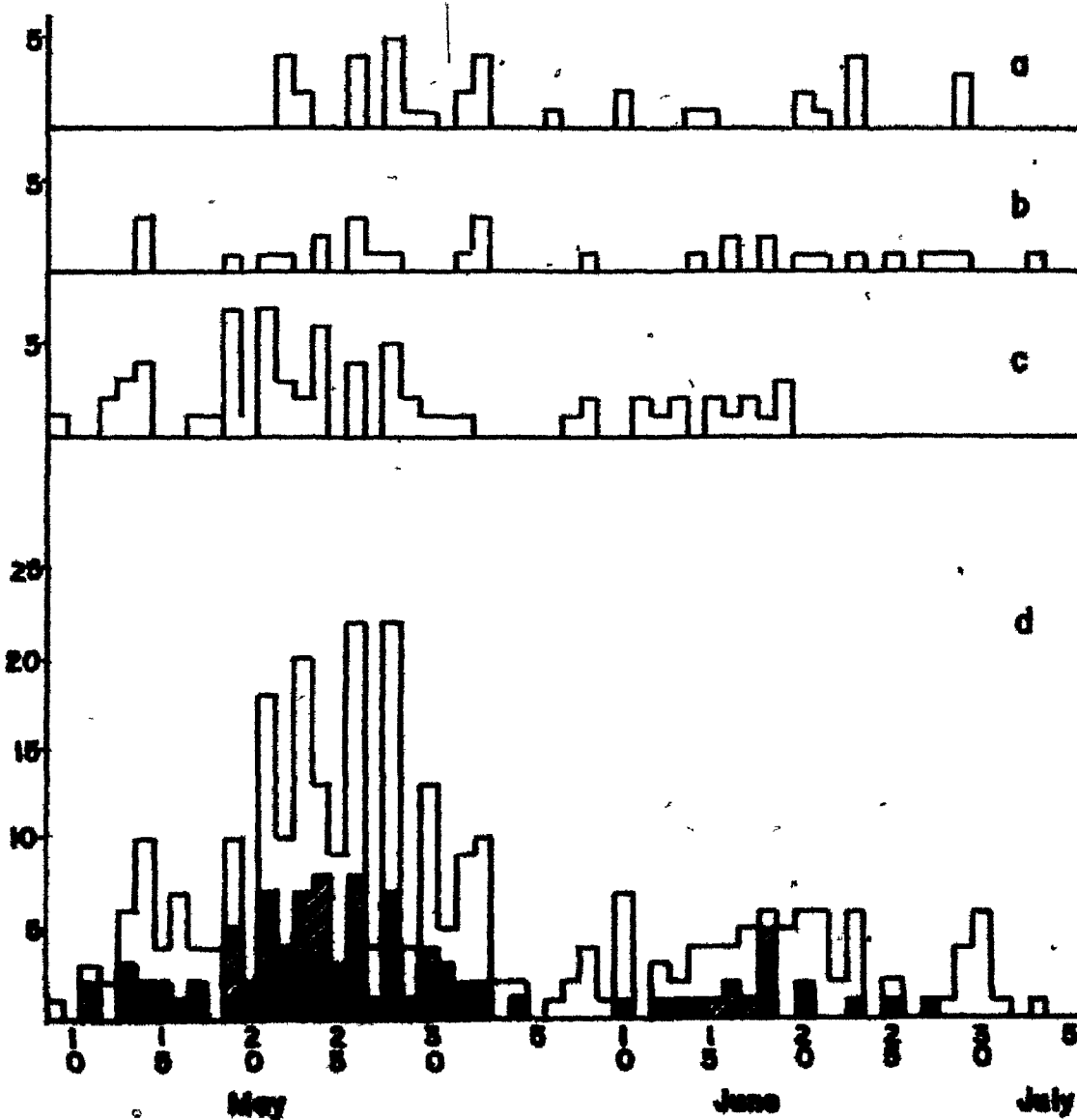
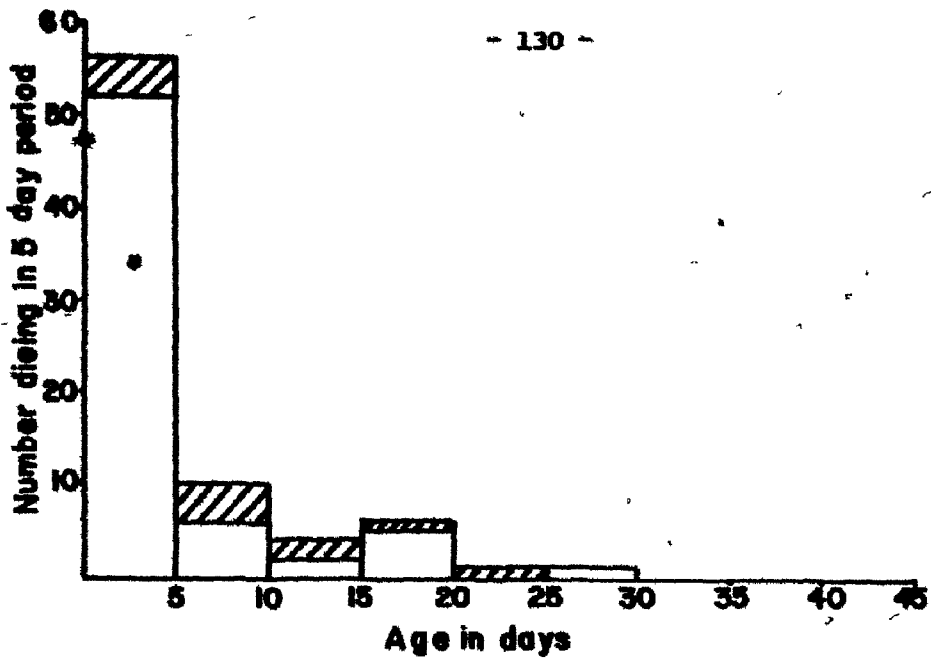
APPENDIX II: Herring Gulls Colony D, 1970. Dates of initiation of clutches of one (a), two (b), and three (c) eggs and dates of laying of eggs (d).

(1)



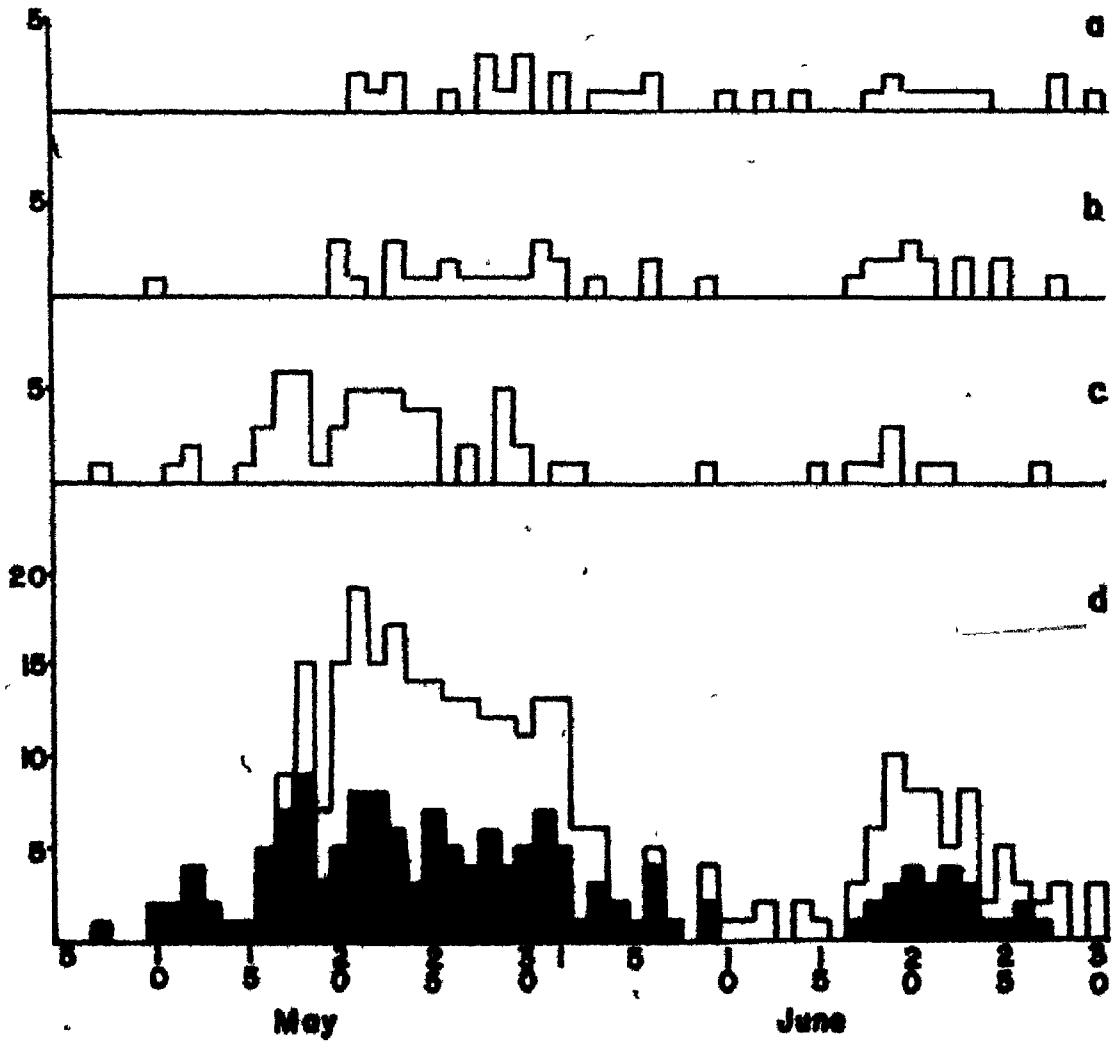
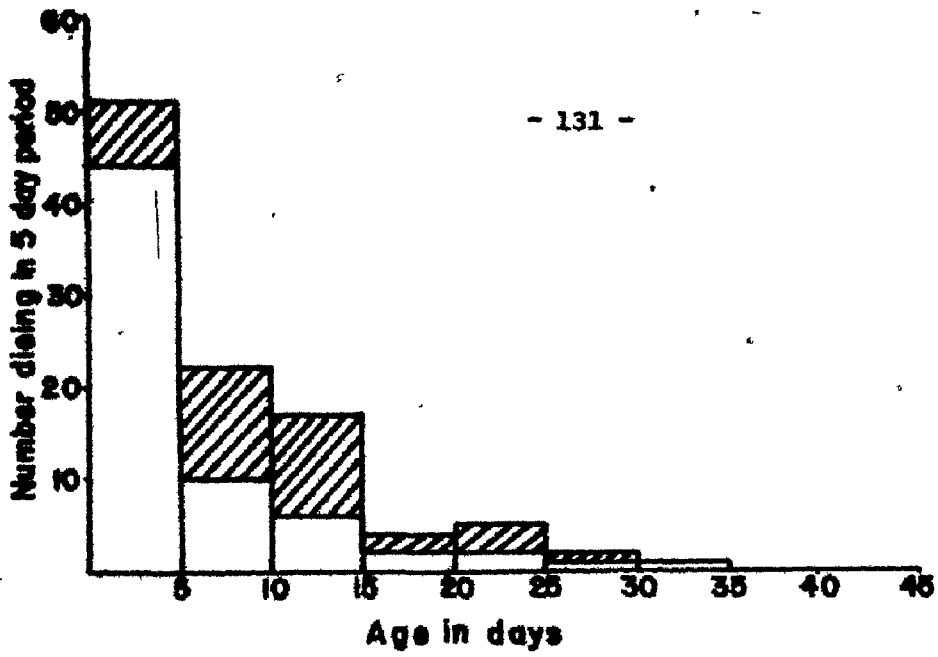
APPENDIX Ij. Schedule of mortality of Herring Gull chicks in Colony B,
1970.

APPENDIX Ik. Herring Gulls, Colony B, 1970. Dates of initiation of
clutches of one (a), two (b), and three (c) eggs and dates of laying of
eggs (d).



APPENDIX II. Schedule of mortality of Herring Gull chicks in Colony C,
1970.

APPENDIX Im. Herring Gulls, Colony C, 1970. Dates of laying of clutches
of one (c), two (b), and three (c) eggs and the dates of laying of eggs
(d).



APPENDIX II

Schedules of Great Black-backed Gull chick mortality, dates of laying of eggs and dates of initiation of clutches of varying size.

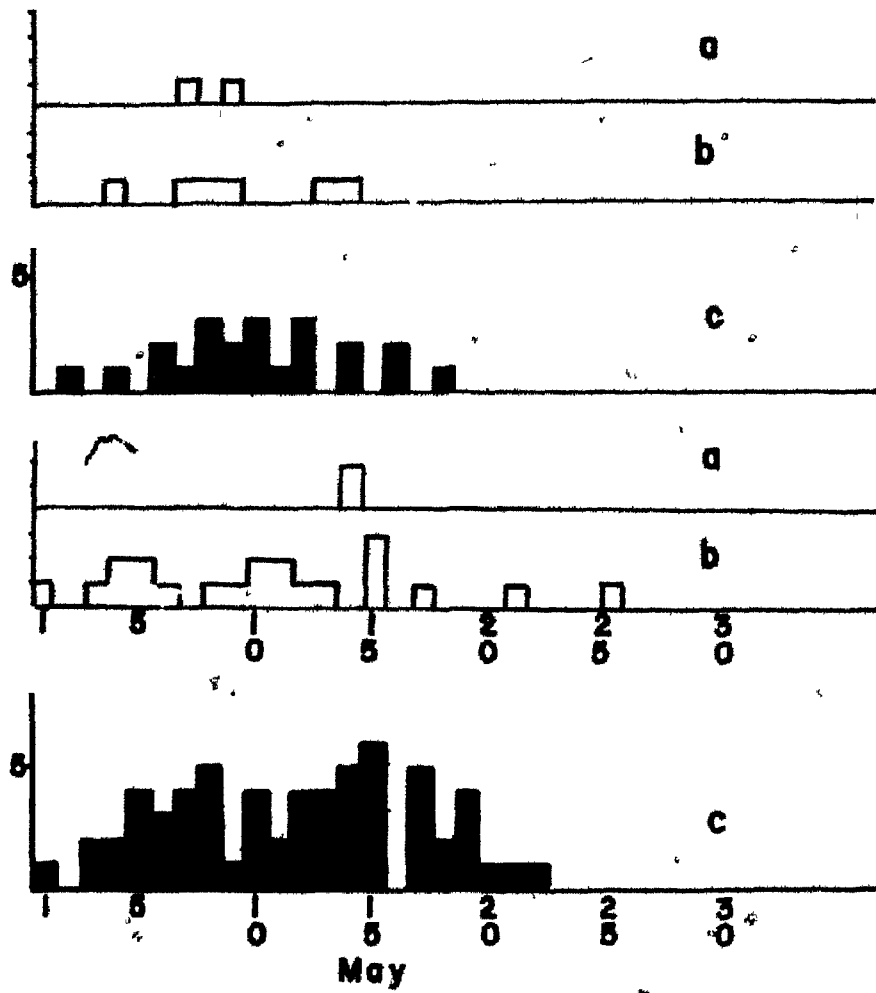
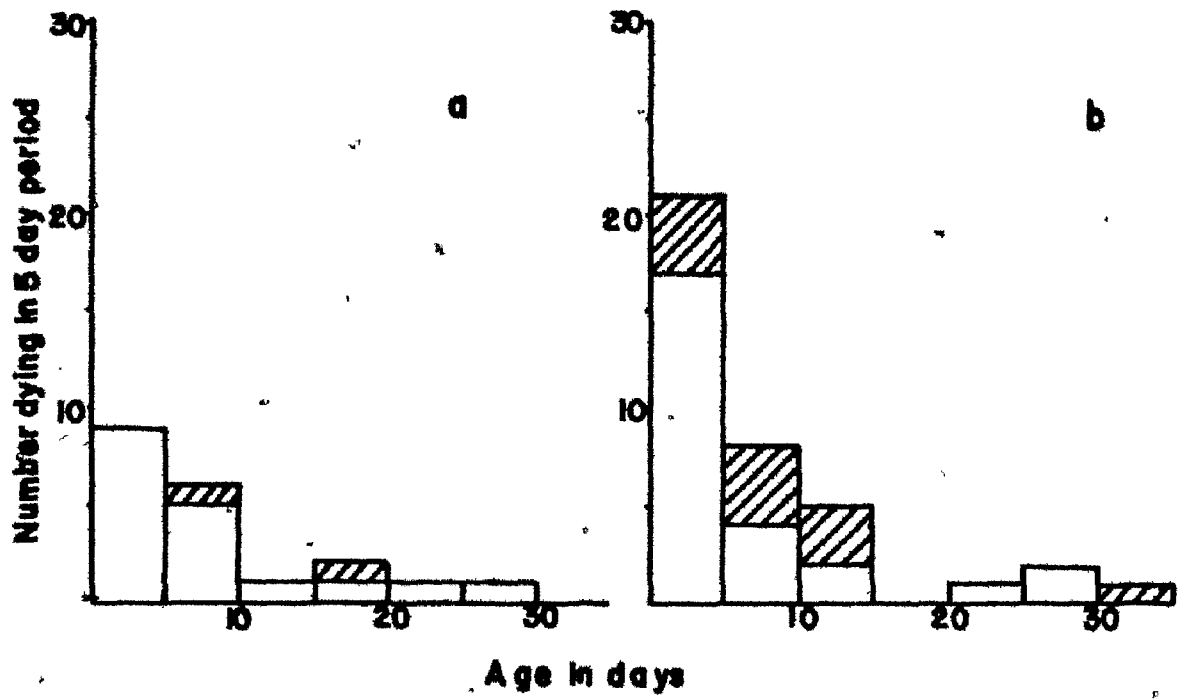
In the figures that follow shaded areas on the schedules of chick mortality indicate chicks whose remains were found. On the histograms of egg laying, all datable eggs laid in a colony are shown by the outer envelope. The cross-hatched areas indicate eggs which hatched and the black areas indicate eggs which produce fledglings.

APPENDIX IIa. Schedules of mortality of Great Black-backed Gull chicks

On Colonies F (a) and B (b) in 1969.

APPENDIX IIb. Great Black-backed Gulls, Colony F, 1969. Dates of initiation of clutches of two (a) and three (b) eggs and dates of laying of eggs (c).

APPENDIX IIc. Great Black-backed Gulls, Colony B, 1969. Dates of initiation of clutches of two (a) and three (b) eggs and dates of laying of eggs (c).

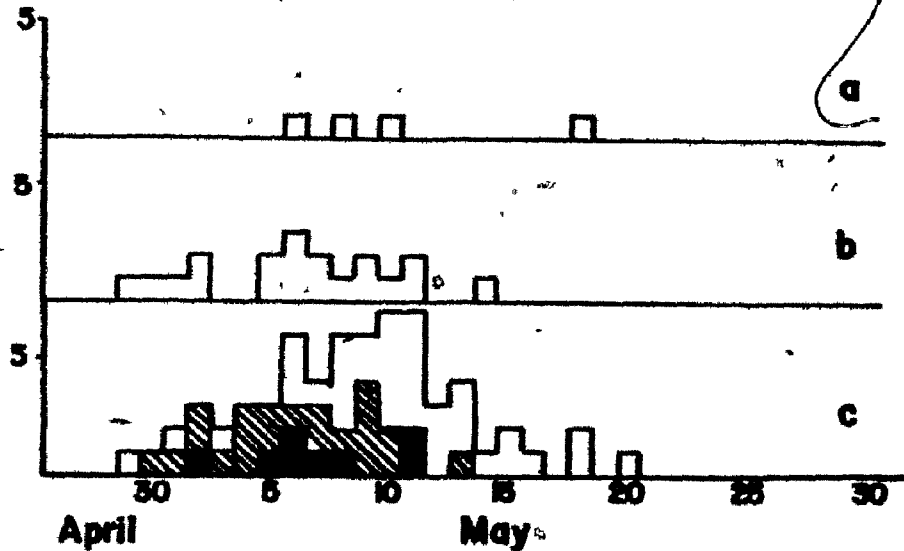
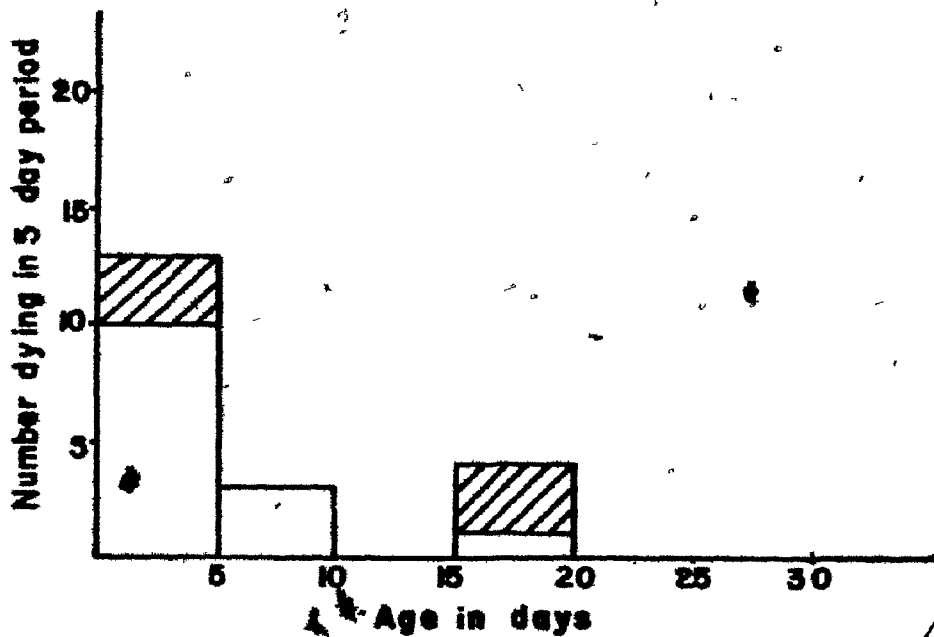
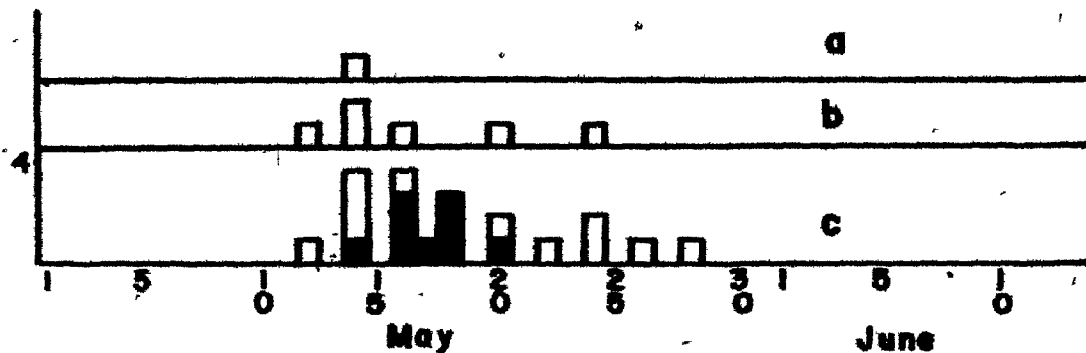
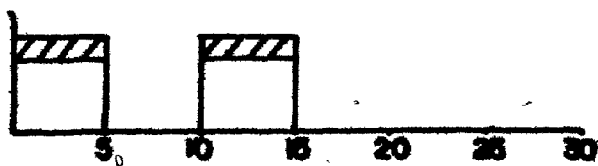


APPENDIX IIId. Schedule of Great Black-backed Gull chick mortality in
Colony A, 1970.

APPENDIX IIe. Great Black-backed Gulls Colony A, 1970. Dates of laying
of clutches of two (a) and three (b) eggs and dates of laying of eggs (c).

APPENDIX IIIf. Schedule of Great Black-backed Gull chick mortality in
Colony F, 1970.

APPENDIX IIg. Great Black-backed Gulls, Colony F, 1970. Dates of laying
of clutches of two (a) and three (b) eggs and dates of laying of eggs (c).



APPENDIX IIh. Schedule of mortality of Great Black-backed Gull chicks
in Colony B, 1970.

APPENDIX III. Great Black-backed Gulls Colony B, 1970. Dates of initiation of clutches of one (a), two (b), and three (c) eggs and dates of laying of eggs (d).

