Aspects of the feeding biology of certain sea-birds

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by

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Contents.

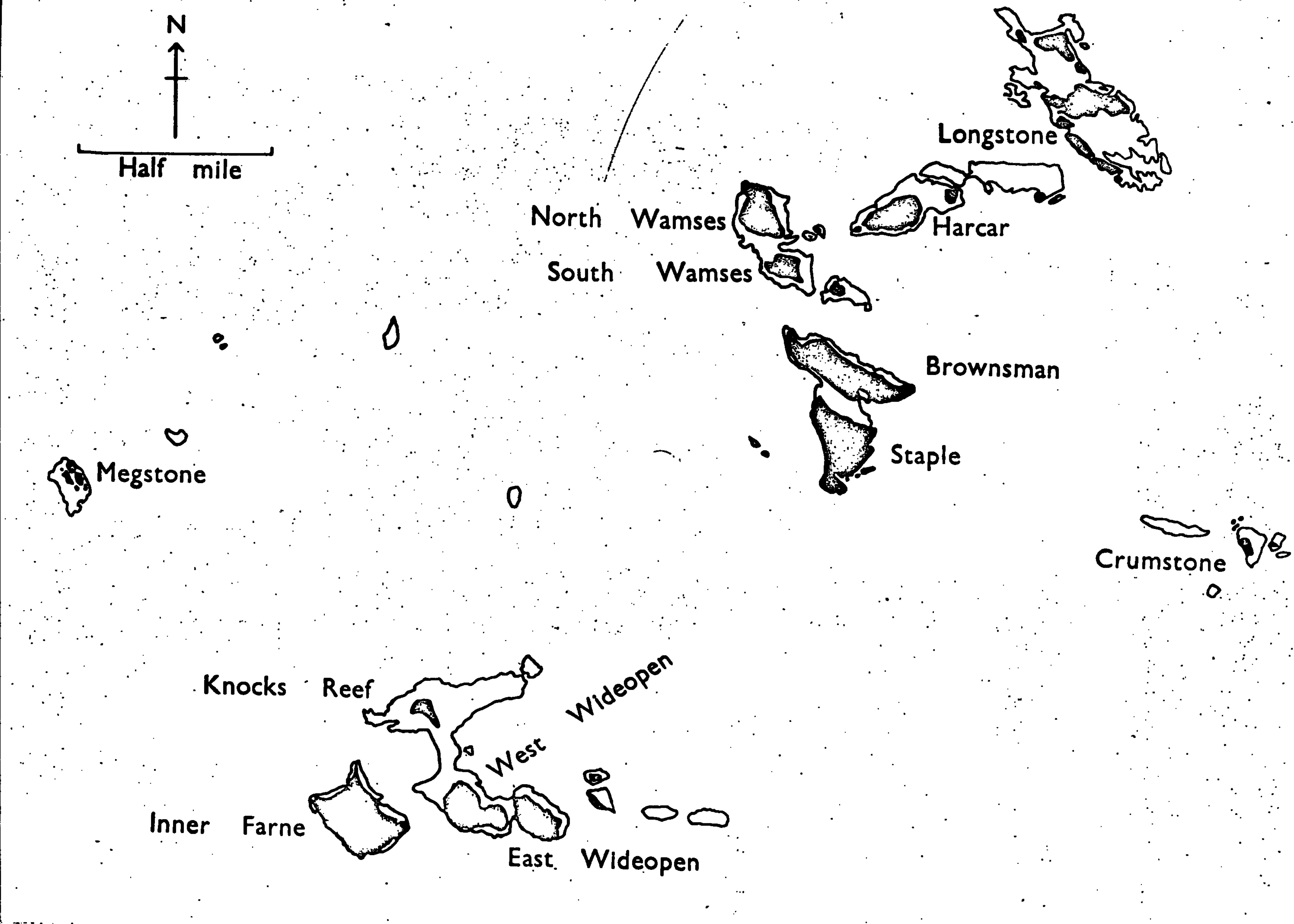
INTRODUCTION.

General perspectives.

This work presents the results of a three year study of the feeding biology of various species of sea-birds breeding on the Farne Islands, Northumberland(National Grid Reference NU220360). Very little comprehensive work has been published concerning the feeding biology of sea-birds in Britain. The diet of certain species has been examined from time to time, notably by Collinge (1925), who made a detailed study of the stomach contents of a number of species. Lumsden and Haddow (1946) and Steven (1933) described the diet of the Shag and Cormorant comprehensively. Apart from these authors however, the food of common sea-birds in Britain has received only passing mention in the literature. Moreover the interspecific feeding relationships of the colonial associations of sea-bird species breeding in this country have received little attention. Such relationships were investigated by Hartley and Fisher (1936) for a specific and specialized feeding area in Spitzbergen, and more recently Bolopolskii (1957) has reviewed in detail the synecology of the sea-birds of the Barents Sea, providing data on the feeding biology of a number of species which breed in this country. No other accounts of the synecology of

North Atlantic sea-birds have been published however, and thus the present study is designed to go some way towards filling this gap.

The sea-bird breeding colonies of the Farne Islands present excellent opportunities for work on the comparative ecology of their constituent species. The islands are small, thus both the numbers and extent of the colonies are restricted, making a total census of the breeding birds possible. There are major breeding colonies of the following species; Arctic Tern, Sandwich Tern, Kittiwake, Lesser Black-back Gull, Puffin, Guillemot, Shag, Cormorant and Eider Duck, together with smaller numbers of Herring Gulls, Common Terns, Fulmars, and Razorbills. Of these only the Eider Duck and the Razorbill were ommitted from the study, but the information obtained on the Herring Gull and Fulmar was very limited. Much of the work carried out during the present study took the form of preliminary investigations intended to explore the relative utility of various lines of study, thus much of the work done on the growth and food intake of chicks was exploratory rather than definative. Nevertheless the information obtained has enabled a general comparison of the feeding biology of the various species under investigation to be made.


N
Half mile
Longstone
North Wamses
Harcar
South Wamses
Brownsman
Staple
Megstone
Crumstone
Knocks Reef
West Wideopen
Inner Farne
East Wideopen

Description of the Farne Islands and the bird colonies studied.

The Farne Islands are a group of low, rocky islands lying between one and four miles from the Northumberland coast. The inner group, comprising the Inner Farne, East and West Wideopen, Megstone, and a number of small islets, lie about a mile from the coast and are separated from the outer group by a mile wide channel. The outer group comprises Staple Island and Brownsman as the two largest islands, together with North and South Wamses, the Longstone, the Harcars, and many smaller tidal or semi-tidal rocks. Map 1 shows the relative positions of the various groups of islands. Most of the present work was carried out on the Inner Farne which has large colonies of Arctic Terns and Sandwich Terns, together with some Common Terns, nesting on the top of the island, and the turf slopes and beachs to the north of the island. The cliffs on the south and west sides of the island harbour large Kittiwake colonies, together with some Shags and a small group of Guillemots. The East and West Wideopens, which are low and fairly flat, have large colonies of Lesser Black-back Gulls, together with small numbers of Herring Gulls. Their combined area is little more than half that of the Inner Farne, which itself is 16 acres in extent. There are Cormorant colonies on the Megstone in the Inner group and North Wamses in the Outer group, both containing between 100 and 170 pairs, which were visited occasionally. There were large Puffin colonies on the East and West Wideopens, and small colonies on the Inner Farne. The Outer islands have even larger colonies of the species mentioned, in particular Staple Island and Brownsman. The colonies of Guillemots and Shags on these islands are particularly numerous as compared with those on the inner islands. However it was not often possible to visit these islands for the prolonged periods necessary to conduct adequate studies.

Duration of field studies.

Observations on the breeding colonies of the birds mentioned were made between April and August in both 1961 and 1962.

Nomenclature.

A list of the species studied, together with their specific names and authorities and a list of the nomenclature of all other species mentioned in the text is given in Appendix A.

SECTION 1.

FIELD OBSERVATIONS OF THE FEEDING BIOLOGY
OF CERTAIN SEA-BIRD SPECIES.

ANALYSIS OF DIET.

A. METHODS.

The most frequently used method for assessing the diet of a sea-bird species has been by analysis of the stomach contents of dead specimens (c.f. Collinge (1925), Hartley & Fisher (1936) etc.). This can provide the investigator with a fairly accurate idea of the diet of the specimen during the few hours prior to being killed, and the cumulative data from a series of specimens will represent the overall pattern of the diet composition of the species in the area under investigation. However in the present work such an approach was not practicable, the work being carried out in protected breeding areas, and alternative methods were devised. The methods used were a) the collection and analysis of regurgitated food samples, and b) direct observation.

A major advantage inherent in these methods was that by not killing the birds the same individuals could be repeatedly observed. Thus although single observations made, or regurgitation samples obtained, do not give as much information as a complete stomach analysis, repetition of such observations allows examination of the diet of individuals over a period of time.

Stomach analyses were undertaken on thirteen Cormorants and twenty-eight Shags obtained from outside the study area.

<u>Regurgitated samples.</u>

Certain sea-bird species regurgitate the stomach contents when captured and handled. This characteristic was not common to all the species under study however, nor was it universal to all members of those species that did. It was found that Cormorant chicks regurgitated very readily upon the advent of an intruder into the colony, but that Shag nestlings did so very rarely even when handled. Adult Cormorants were not caught, but some would regurgitate on being disturbed in the breeding colony. No specimens of regurgitated food were obtained from adult Shags although many were caught and handled during ringing programmes. Of the tern species, it was found that the adults of all three species studied would regurgitate readily on handling, but amongst the chicks, Sandwich Terns alone showed a tendency to regurgitate, and then only rarely. Many hundreds of Arctic and Common Tern chicks were captured for ringing or weighing but no regurgitated food was obtained. Both the adults and young Kittiwake would occasionally regurgitate on being handled, and the chicks of the larger gulls (Herring, and Lesser Black-back) did so quite frequently.

Neither the adults nor the chicks of the auks (Puffin, Guillemot, Razorbill) showed a tendancy to regurgitate, but the chicks of the Fulmar would do so occasionally.

With all the species under study, it was relatively easy to catch and handle the chicks, but it was both difficult and time-consuming to capture the adults. The cliff nesting species (Kittiwake, Shags, Fulmars and Guillemots) were captured at the nest by means of a long handled fowling hook which, if carefully used, could be eased round the necks of unsuspecting birds and then drawn back to the investigator together with the bird. Puffins could be easily caught during incubation in their burrows, but the procedure tended to produce a high incidence of desertions and was abandoned in favour of mist-netting. Mist-netting was also used fairly extensively in capturing adults of all three tern species, the disadvantage being in the amount of time spent in obtaining each bird. During the incubation period, the terns could be captured more readily by placing a wire netting cage over the eggs. These cages had a single small funnel entrance at ground level, through which the birds enter. On attempting to leave, they flew upwards, and, were easily captured.

<u>Direct observation.</u>

Although adequate observation of the birds, whilst obtaining their food, was impossible due to fishing grounds being generally out of sight of the island, it was possible, from a hide, to observe the terns, Puffins and Guillemots at fairly close range when they returned from fishing. As these species carry their prey in the beak prior to feeding the chick the type and approximate size of the prey could be noted. This method, however, although providing much data on the diet of the chick, gave no indication of the adult diet.

Direct stomach analysis.

Many river boards place a bounty on the heads of Shags and Cormorants due to their alleged deleterious effects on fresh-water fish stocks, particularly Salmonidae. Such a bounty is paid at Berwick-on-Tweed by the River Tweed Commissioners, and has led to the shooting of these birds in the estuary of the river, from where several bodies were obtained. In addition, the carcasses of Cormorants shot on the estuary of the Lune and on Windermere were obtained. Stomach analyses were carried out on all such birds.

B. ANALYSIS AND PRESENTATION OF RESULTS.

Hartley (1948) discusses in detail the various methods used for the assessment of bird diets and concludes that:- "Foods may be assessed by frequency of occurence, by enumeration, by weight or by volume. The weights or volumes may be measured 'as found' or by approximations to the weight or volume of food at the time of ingestion. There is no one ideal method and the food of each species or group of species should be investigated and assessed by the methods which seem most appropriate".

In the species studied, the diet consisted almost entirely of fish, and the majority of the samples collected were to some degree decomposed. Thus assessment of weight or volume of food at the time of ingestion was difficult, but on the other hand assessment of the weights or volumes 'as found' was unsatisfactory due to the varying states of decomposition of the different samples. It was decided therefore to analyse the diet of each species in terms of the actual numbers of each prey species taken, and in terms of the estimated weight at the time of ingestion of each prey species. Where the fish taken were decomposed, the weights were to be based on the average weight of whole fish of that prey species taken by that particular bird species.

Although assessing the true volume of a badly decomposed and broken fish is difficult, this could be estimated with reasonable accuracy as a result of experience, as could the weight. However a volumetric method was not used as it was thought to have no advantages in accurate data presentation over assessment by weight, both giving a picture of the actual mass of prey taken. Moreover the presentation of the data in terms of grams weight enabled it to be used and compared with.

later information on the food intake and weight of growing chicks. In any case, the conversion of such weights to volumes on the metric system is a relatively simple procedure. Hartley (1948) discusses the difficulty, when dealing with birds of mixed diet, of estimating the relationship between the bulk and the nutritive value of the various foods ingested. In the present study, the major part of the food sampled was found to be fish, for all of the species, and only minor occurrences of other foods were recorded. Thus the nutritive value of the food taken would differ little.

In order to facilitate comparison, the weight of food is also expressed as percentages of total numbers and total weights of all species taken.

The species studied can be divided into two major groups namely 1) the surface feeders and 2) divers. For the purposes of comparison each species will be described as belonging to such a group.

C. IDENTIFICATION OF FISH SPECIES TAKEN BY THE BIRDS.

In identifying the fish species taken by the birds the descriptions of Day (1884) and Jenkins (1936) have been used. The nomenclature followed is given by Jenkins. When analysing regurgitation samples it was found that in many cases the specimens were too badly damaged to permit easy identification to species level, but it was usually possible to assign such fish to the appropriate family. It was found that with the Ammodytidae even undamaged specimens were difficult to identify specifically, as all the specimens taken were in various stages of post-larval or juvenile development without the usual adult taxonomic characteristics. The early post-larval stages of Ammodytes have been separated on the basis of pigmentation by Corbin and Vati (1949), but there are no such distinguishing marks in the juvenile stages. Corbin (pers.comm.) states that it is possible to separate the juvenile stages on the basis of scale pattern on the abdomen and on the tail, but in view of the semi-digested state of many of the specimens obtained this was not often possible. It was thus thought to be better to treat the Ammodytidae as a single group, rather than attempt an inconclusive division into species.

D. STATISTICAL METHODS USED.

The significances of variations in the diet as between species, and of the same species at different times, have been determined, where appropriate, by calculating χ^2 from contingency tables, Yates' correction being applied in those cases where the numbers compared were small.

The relationship between two variable factors has been assessed by calculating the regression coefficient (r), and basing a t-test on this coefficient to determine its significance.

E. RESULTS.

1. The Surface Feeders.

ARCTIC TERN. Sterna paradisaea.

The Arctic Tern breeding on the Farne Islands feeds almost exclusively on small surface living marine creatures, but also occasionally takes insects on the wing. The birds seem to prefer roughened water for fishing, and in the Farne area the most favoured fishing grounds were the tide rips between the islands. These areas are where the tide is restricted to a narrow or shallow channel, thus increasing the speed of the current and the choppy turbulence at the surface even in the calmest of weather. It is possible that large numbers of fish are attracted to such areas by there being a greater abundance of zooplankton, itself attracted by a concentration of detritus swept up by tidal currents. Alternatively fish may not be more abundant in such areas but may be more readily available due to turbulence causing their white underparts to be intermittently exposed to the searching birds above, and thus increasing their vulnerability to predation. A further hypothesis is that the fish may be driven closer to the surface in these turbulent tide rips and thus be more readily available to the birds.

TABLE 1.

Arctic Tern. Analysis of diet from regurgitation samples.
(All weights in g.)

A) 1961. (77 samples).

PREY	ANALYSIS BY NO.		ANALYSIS BY WT.		
	No.	%	Wt.	%	Av.wt.of Indiv.prey
Ammodytidae sp.indet.	259	89	181	55	0.4
Clupea sprattus	4	1	45	14	11.2
Clupea harengus	6	2	25	8	4.1
Gasterosteus aculeatus	0	0	0	0	-
Gasterosteus spinachia	14	5	61	18	4.3
Pleuronectes flesus	4	1	7	2	1.8
Trachinus vipera	0	0	0	0	-
Crustacea	2	1	3	1	1.6
Cephalopoda	2	1	8	2	3.9
Insecta	0	0	0	0	-

B) 1962. (89 samples).

PREY	ANALYSIS BY NO.		ANALYSIS BY WT.		
	No.	%	Wt.	%	Av.wt.of Indiv.prey
Ammodytidae sp.indet.	104	59	131	39	1.3
Clupea sprattus	10	6	84	22	7.2
Clupea harengus	23	13	125	33	5.5
Gasterosteus aculeatus	10	6	22	6	2.2
Gasterosteus spinachia	0	0	0	0	-
Pleuronectes flesus	0	0	0	0	-
Trachinus vipera	4	2	2	1	0.6
Crustacea	0	0	0	0	-
Cephalopoda	4	2	11	3	2.7
Insecta	22	12	1	1	0.05

ANALYSIS OF REGURGITATION SAMPLES.

It was found that whereas most adult terns would regurgitate readily on capture, the Arctic Tern chicks would on no account do so. Thus investigation of the tern's diet by regurgitation was confined to adults only. In addition to specimens obtained by regurgitation, fish were often dropped by the birds in and around the colony, particularly during display behaviour during the early part of the season. These were collected whenever possible and included in the analyses. The results of these investigations are given in Tables 1 and 2. It can be seen that the monthly tables are in some cases based on small samples and thus are unreliable e.g. May and June 1962. Nevertheless their figures indicate the relative scarcity of Ammodytidae which was a feature of the diet of the Arctic Tern at that time. Thus no Ammodytidae were taken in May 1962, and they formed only 30% of the diet (by number) in June, compared with 68% in July. This scarcity of sand-eels early in the 1962 season is also reflected in the results of direct observations (see below). Table 1 shows clearly the variation in results obtained by using enumeration or weight as a basis for analysing diet. Thus the comparatively large Clupeidae form a much greater percentage of the diet by the latter method than by the former. The <u>Trachinus vipera</u> taken were young post-larval stages, seldom more than 30 mm. in length. The Crustacea taken were all the common shrimp, TABLE. 2. Arctic Tern. Monthly analysis of diet from regurgitation samples. (All weights in g.)

MONTH	PREY SPECIES	1961. No. of samples	1961. Analysis by no. No.	1961. Analysis by no. %	1961. Analysis by wt. wt.	1961. Analysis by wt. %	1962. No. of samples	1962. Analysis by no. No.	1962. Analysis by no. %	1962. Analysis by wt. wt.	1962. Analysis by wt. %
MAY	Ammodytidae sp. indet.		58	97	54	88					
	Clupeidae sp. indet.										
	Gasterosteus spinachia		2	3	7	12		2	50	12	67
	Gasterosteus aculeatus										
	Pleuronectes flesus	20					4				
	Trachinus vipera										
	Cephalopoda							2	50	6	33
	Crustacea										
	Insecta										
JUNE	Ammodytidae sp. indet.		189	91	109	60		10	30	10	57
	Clupeidae sp. indet.		4	2	13	7		1	3	6	36
	Gasterosteus spinachia		12	6	53	29					
	Gasterosteus aculeatus										
	Pleuronectes flesus	43					7				
	Trachinus vipera										
	Cephalopoda		2	1	8	4					
	Crustacea										
	Insecta							22	67	1	7
JULY	Ammodytidae sp. indet.		3	20	2	4		90	68	125	35
	Clupeidae sp. indet.		6	40	5[illegible]	83		29	21	2[illegible]4	57
	Gasterosteus spinachia										
	Gasterosteus aculeatus							10	7	22	6
	Pleuronectes flesus	14	4	27	7	11	78				
	Trachinus vipera							4	3	2	1
	Cephalopoda										
	Crustacea		2	13	3	5		1	1	5	1
	Insecta										

Crangon vulgaris, and the Cephalopoda were Sepiola atlantica, the little cuttle and Loligo forbesi, the common squid. The insects taken in 1962 were Diptera of the families Dorcylor-idae and Tachinidae and a beetle of the Anobiidae family. In addition to these, Arctic Terns were seen hawking for moths on a number of occasions, notably in mid-June 1961, when there was an influx of Noctuid moths to the island, these being taken by many terns. No specimens were taken in the food samples however, and they have thus been excluded from the diet analyses.

ANALYSIS OF DIRECT OBSERVATION RESULTS.

As none of the chicks of the Arctic Terns would regurgitate, the only reasonable methods for assessing their diet was by direct observation at the nest. The adult tern carries the prey transversely in its bill, usually only one fish being carried. Thus it is relatively easy to observe the prey being fed to the chick by undertaking a series of watches from a hide. The majority of chicks regularly observed were within 10 feet of the hide, at which distance the approximate size and type of prey fed to the chicks could be readily noted with reasonable accuracy. To check on this, the birds were occasionally startled into dropping their prey, which was then collected and its actual size and species compared with those estimated by observation. In no case was the observers' record found to be incorrectly identified or the estimation of approximate size to be erroneous. The prey were identified into one of the following main groups; Ammodytidae (Sand-eels), Clupeidae (Young herring and sprats), Gasterosteidae (Sticklebacks), Gadidae (Young codling and whiting), Crustacea (Shrimps), Cephalopoda (Squids), and 'Fry'. This latter group consisted of very small (less than 1 inch) silvery fish only one example of which was ever obtained for examination. This proved to be the fry of Trachinus vipera, the Lesser Weever, similar to those identified from regurgitation results. Whether the other 'fry' noted, of a similar size and colour, were of the same species it is impossible to assess.

The Ammodytidae taken in 1962 varied in size from under 25mm. to over 150mm., but the most commonly taken size group was 50-70mm., the corresponding weight being between 1 and 1.5g. In 1961, the average size of these fish taken was smaller, between 25 and 50mm., weight approximately 0.5g. The size frequencies for both years are given in histogram form in Figure 1. The Sprats taken were generally between 70 and 100mm. long, weighing approximately 10g. and the young Herring slightly smaller at between 50 and 70mm. or about 5g. weight. The average size of these fish did not vary much in the two years. The young Gadidae and Gasterosteidae were similar in size and weight to the young Herring apart from the Fifteen-spined Stickleback (Gasterosteus

FIGURE 1.

Size frequencies of Ammodytidae taken by Tern species.

X = Number of specimens recorded.

Y = Length of fish (in mm.).

a = Arctic Tern 1961 measured specimens.

b = Arctic Tern 1962 measured specimens.

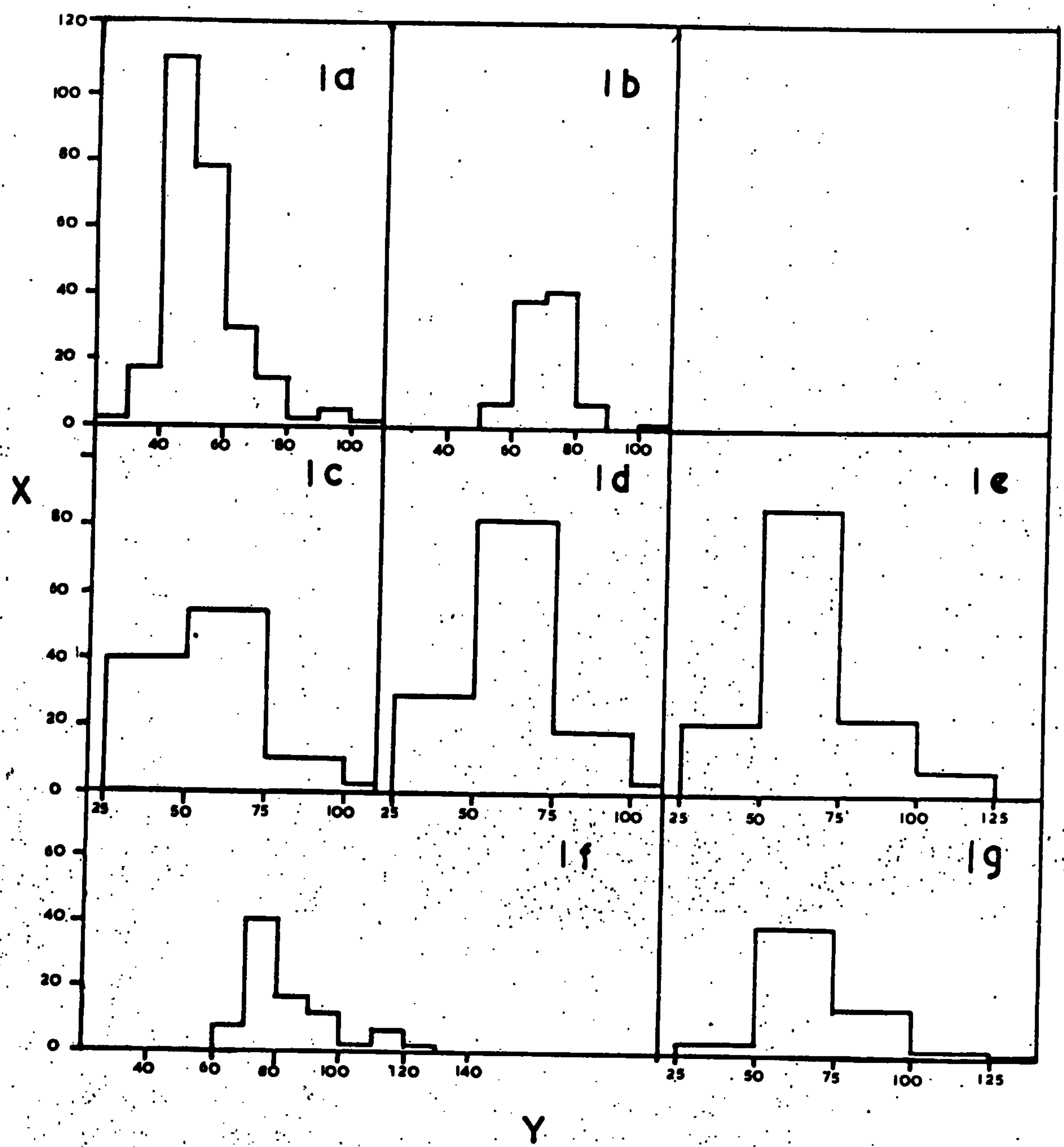
c = Arctic Tern 1961 Estimates sizes from observations.

d = Arctic Tern 1962 Estimated sizes from observations.

e = Common Tern 1962 Estimated sizes from observations.

f = Sandwich Tern 1962 measured specimens.

g = Sandwich Tern 1962 Estimated sizes from observations.



1a
1b
1c
1d
1e
1f
1g
X
Y
120
100
80
60
40
20
0
40
60
80
100
25
50
75
100
125
120
140

spinachia) which, although similar in weight, were much more elongated.

TABLE 3.

ARCTIC TERNS. Analysis of the composition of the diet from observations in 1961 and 1962.

GROUP	1961 Prey fed to chicks under observation. No.	%	1961 Prey carried by birds in flight. No.	%	1962 All Observations. No.	%
Ammodytidae	103	67	444	64	477	61
Clupeidae	26	17	196	28	190	24
Gasterosteidae	2	1	0	0	4	0.5
Gadidae	0	0	0	0	48	6
'Fry'	0	0	0	0	51	7
Crustacea	15	10	35	5	3	C.4
Cephalopoda	7	5	19	3	4	0.5
Totals	153		694		777	

In addition to the observations on individual chicks, hourly or half-hourly counts were taken at various times during the day of the relative numbers of the various types of prey being carried into or across the area under observation. Data obtained from these watches and counts is presented in Table 3, in terms of the number seen of each type of prey, and the percentage of the total numbers formed of each type. The total numbers of the various groups of prey fed to 8 chicks under observation throughout the various periods of watching in 1961, and the total of the hourly counts taken of various types of prey carried across the field of view during the same watching periods are given. A comparison of this data shows no significant difference in the numbers of Ammodytidae taken, as assessed from observations of prey carried by birds in flight, and of prey fed to chicks under direct observation ($P>0.5$). The difference in the numbers of Clupeidae taken, as assessed by the two methods of observation does, however, differ significantly ($P<0.01$), suggesting that the identification of this group of fish when carried by birds in flight may be unreliable. The identification of the other groups would appear to be reliable however, there being no significant difference in the results obtained by the two methods.

In 1962 the data from the continuous watches on individual chicks and from hourly counts of all prey-carrying birds were combined to give the results shown. These results are broadly similar to those of 1961, except in the inclusion of 'fry' and Gadidae, which were not evident the previous year. There was no significant difference between the numbers of Ammodytidae, or the numbers of Clupeidae, taken in 1961 and in 1962 ($P<0.2$ and $P<0.8$ respectively).

Table 4 breaks down the counts for 1961 and 1962 into

TABLE 4. Observations of prey carried by Arctic Terns. Periodic counts on different days. (Percentages given as percentage of total number of prey seen on each count).

YEAR	DATE	TIME OF DAY (Hours)	AMMODYTIDAE No.	AMMODYTIDAE %	CLUPEIDAE No.	CLUPEIDAE %	GADIDAE No.	GADIDAE %	OTHER FISH No.	OTHER FISH %	CRUSTACEA No.	CRUSTACEA %	CEPHALOPODA No.	CEPHALOPODA %
1962	6 May	1430-1500	3	5	30	48	0	0	8	13	0	0	22	35
	18 June	1500-1530	37	47	28	35	0	0	10	13	0	0	4	5
	3 July	0900-0930	28	80	7	20	0	0	0	0	0	0	0	0
	18 July	2100-2130	10	30	7	21	11	33	2	6	2	6	1	3
	22 July	1500-1530	36	43	45	54	1	1	2	2	0	0	0	0
	22 July	1630-1700	79	70	17	15	6	5	11	10	0	0	0	0
	22 July	1900-1930	46	49	16	17	16	17	12	13	2	2	2	2
	23 July	0520-0550	52	59	23	26	7	8	6	7	0	0	0	0
	23 July	0720-0750	81	49	70	42	5	3	9	5	0	0	1	<1
	25 July	1215-1245	61	91	1	1	0	0	4	6	0	0	1	1
	25 July	1345-1415	47	96	1	2	0	0	1	2	0	0	0	0
	25 July	1935-2005	37	59	13	21	2	3	11	17	0	0	0	0
1961	12 July	0650-0750	64	62	27	26	0	0	0	0	11	11	1	1
	12 July	0830-0930	78	68	28	24	0	0	0	0	9	8	0	0
	14 July	0830-0930	19	37	31	61	0	0	0	0	1	2	0	0
	14 July	0930-1030	16	67	6	25	0	0	0	0	0	0	2	8
	15 July	1400-1500	23	33	37	61	0	0	0	0	1	2	0	0
	15 July	1600-1700	45	52	34	39	0	0	0	0	3	3	4	5
	26 July	0645-0745	38	64	11	19	0	0	0	0	3	5	7	12
	26 July	1330-1430	23	88	1	4	0	0	0	0	2	8	0	0
	28 July	2015-2115	138	82	21	12	0	0	0	0	5	3	5	3

the composite hourly counts for the various dates and times of day. Nearly all counts were undertaken during July, this being the month during which the chicks were being fed. Comparative analyses of the variation in numbers of the different types of prey taken at varying times of day are given in Table 5. Counts taken in May and June have been omitted from these analyses in order that they might be more strictly comparable.

In the early morning period, i.e. before 0900 hours, the prey consisted of 56.5% Ammodytidae, 31.9% Clupeidae, 5.5% non-fish groups (Crustacea and Cephalopoda) and 6.9% other fish. In the late morning period, from 0900 hours until 1230 hours the percentage of Ammodytidae taken rose, and the percentage of Clupeidae taken fell, both differences being highly significant ($P < 0.001$). During the early afternoon the converse occurred, the percentage of Ammodytidae taken falling off significantly, with a corresponding highly significant rise in the numbers of Clupeidae taken. At the same time there was a significant drop in the numbers of non-fish groups taken ($P < 0.01$). During the late afternoon period there was a significant drop in the numbers of Clupeidae taken ($P < 0.01$), but the numbers of Ammodytidae and non-fish groups remained at approximately the same level, there being an increase in the numbers of other types of fish taken during this period (see Table 4). In the evening

TABLE 5. Arctic Tern. Comparative analysis of numbers of different types of prey taken at various periods throughout the day, during the month of July.

TYPE OF PREY		Before 0900	0900-1230	1230-1530	1530-1830	After 1830
All Prey.	Total No. taken	416	213	218	209	432
Ammodytidae	No. taken	235	163	129	124	266
	Percentage	56.5	76.5	59.2	59.3	61.6
	Significance of change since previous period	$P>0.05$	$P<0.001$	$P<0.001$	$P>0.05$	$P>0.05$
Clupeidae	No. taken	131	36	82	51	94
	Percentage	31.5	16.9	37.6	24.4	21.8
	Significance of change since previous period	$P<0.01$	$P<0.001$	$P<0.001$	$P<0.01$	$P>0.05$
Non-fish gps (Crustacea & Cephalopoda)	No. taken	23	10	3	7	20
	Percentage	5.5	4.7	1.4	3.3	4.6
	Significance of change since previous period	$P>0.05$	$P>0.05$	$P<0.01$	$P>0.05$	$P>0.05$

Period before 0900 hours compared with period after 1830 hours.

period (after 1830 hours) there was no significant change in the relative numbers of any of the major groups being taken. A further comparison of the early morning period with the late evening period shows no significant change in the numbers of Ammodytidae or non-fish groups being taken ($P > 0.05$ in both cases), but a significant increase in the numbers of Clupeidae taken ($P < 0.01$), at the expense of the types of fish other than Ammodytidae (see Table 4).

OVERALL DIET. (Average of combined chick and adult diets).

Table 6 shows the total figures for the diet of the Arctic Tern, being an average of the direct observation results and regurgitation results for both years. Table 7 gives the total results broken down into monthly tables.

In these tables the results are expressed in terms of both numbers and weights, the weights being estimated from the average weight of individual prey species taken over both years.

F. DISCUSSION.

For the purposes of this discussion comparison will be based on the figures of percentage occurrence by number, unless stated otherwise.

Comparison of the diet of young and adult birds.

The diet of the adult birds, as shown by analysis of regurgitation samples is broadly similar to that of the

TABLE 6.

Average diet of Arctic Tern. (Weights in g.)

PREY.	Analysis by No. No.	%		Average weight of Individual	Analysis by Wt. Wt.	%
Ammodytidae	1580	67	[illegible]1.6	0.8	1372	22
Clupeidae	535	22	21.8	7.0	3749	63
Gadidae	51	2	2.1	6.1	357	6
Gasterosteidae	48	2	2.0	3.2	148	2
Pleuronectidae	4	<1	0.2	1.8	7	<1
'Fry' (incl. <u>Trachinus vipera</u>)	90	4	3.7	0.6	54	1
Crustacea	55	2	2.2	1.6	88	2
Cephalopoda	62	2	2.5	3.3	204	3
Insecta	22	1	0.9	0.05	1	<1
Totals	2447		100.0		5976	

TABLE 7.

Average monthly diet of Arctic Tern. (Weights in g.)

PREY	MAY By No. No.	%	By Wt. Wt.	%	JUNE By No. No.	%	By Wt. Wt.	%	JULY By No. No.	%	By Wt. Wt.	%
Ammodytidae	61	48	51	13	236	74	198	38	1250	63	1050	21
Clupeidae	32	25	224	58	33	10	231	44	477	24	3339	66
Gadidae									51	3	357	7
Gasterosteidae					22	7	71	14	16	1	52	1
Pleuronectidae									4	<1	7	<1
'Fry' (incl. T.v.)									90	5	54	1
Crustacea									55	3	88	2
Cephalopoda	24	19	79	21	6	2	20	4	31	2	102	2
Insecta	10	8	32	8	22	7	1	<1				
Totals	127		386		319		521		1974		5049	

TABLE 8.

Arctic Tern.

Comparison of diets of chicks and adults in terms of the major food groups (percentage occurrence by number).

FOOD GP.	1961 CHICK No.	1961 CHICK %	1961 ADULT No.	1961 ADULT %	1962 CHICK No.	1962 CHICK %	1962 ADULT No.	1962 ADULT %
Fish	771	88.9	287	98.7	770	99.1	151	85.3
Crustacea	50	7.4	2	0.7	3	0.4	0	0
Cephalopoda	26	3.6	2	0.7	4	0.5	4	2.3
Insecta	0	0	0	0	0	0	22	12.4
Totals	847	99.9	291	100.1	777	100.0	177	100.0

		1961	1962
Comparison of diets of chicks and adults in each year.	χ^2	17.99	78.0
	P	<0.001	<0.001

Comparison of chick diet in 1961 and 1962	χ^2	54.4
	P	<0.001
Comparison of adult diet in 1961 and 1962.	χ^2	32.5
	P	<0.001

χ^2 with 1 degree of freedom in each case.

chicks shown by direct observation. Table 8 shows a comparison of the composition of the diets of young and adult birds in respect of the major food groups taken. In 1961, the chicks were fed significantly more non-fish prey than the adults, whilst in 1962 they were fed significantly less, ($P < 0$[illegible] in both cases) but the amount of the differences are small in any case. The 1962 figure for adults is however distorted due to the relatively large number of insects. These form a very small proportion (0.3) by weight of the diet, and are thus comparatively unimportant in relation to the total food intake. If these insects are omitted in considering the adult diet then there is no significant difference between the diet of chicks and of the adults in that year ($p > .05$).

The fact that the chicks were fed relatively more non-fish food than that taken by the adults in 1961 appears to be at variance with the observations of Belopolskii (1957), who found that young Arctic Terns of the Seven Islands (Barents Sea) population were fed predominantly more fish than the adults (80.2% as opposed to 50.6%) and that although the adults took 28.6% crustaceans, this group was not found in the stomachs of chicks. However Belopolskii's sample of young birds (18) was small and may not reflect the true range of diet of the young birds. It must be noted that the percentage of fish taken by the chicks on the Farne Islands is higher than that of the chicks in the Arctic, and that there was a greater difference in the diet of the adults between the two regions. In nearly all species of sea-birds investigated in the Barents Sea, Belopolskii found that a higher percentage of fish was fed to the young than used by the adults. He suggests that the greater nutritional value of fish, for a given weight ingested, is important for the growing birds. It is possible that in the Arctic seas the terns search specifically for fish when feeding young, and ignore the relatively abundant Crustacea, Pteropods etc., whereas in the Farne Islands area small fish are extremely abundant during the breeding season, and the other planktonic groups much less so, enabling the birds to support both themselves and their progeny on fish.

Seasonal changes in diet.

Figures 2 a, b, and c, show the variation from month to month of the diet as assessed by collecting samples and as observed from counts. In 1961 counts of birds carrying prey were made during July only, thus variation over the summer cannot be assessed. It can be seen that the 1962 results for both methods show similar trends i.e. a very low percentage of Ammodytidae early in the season, which later rose rapidly, reaching a peak in early July, followed by a slight drop. The percentage of Clupeidae does not show as great a seasonal fluctuation, but tended to be

FIGURE 2.

Seasonal variation in the diet of the Arctic Tern, as the average percentage of each prey group taken per month.

a = Based on regurgitation samples, 1961.

b = Based on regurgitation samples, 1962.

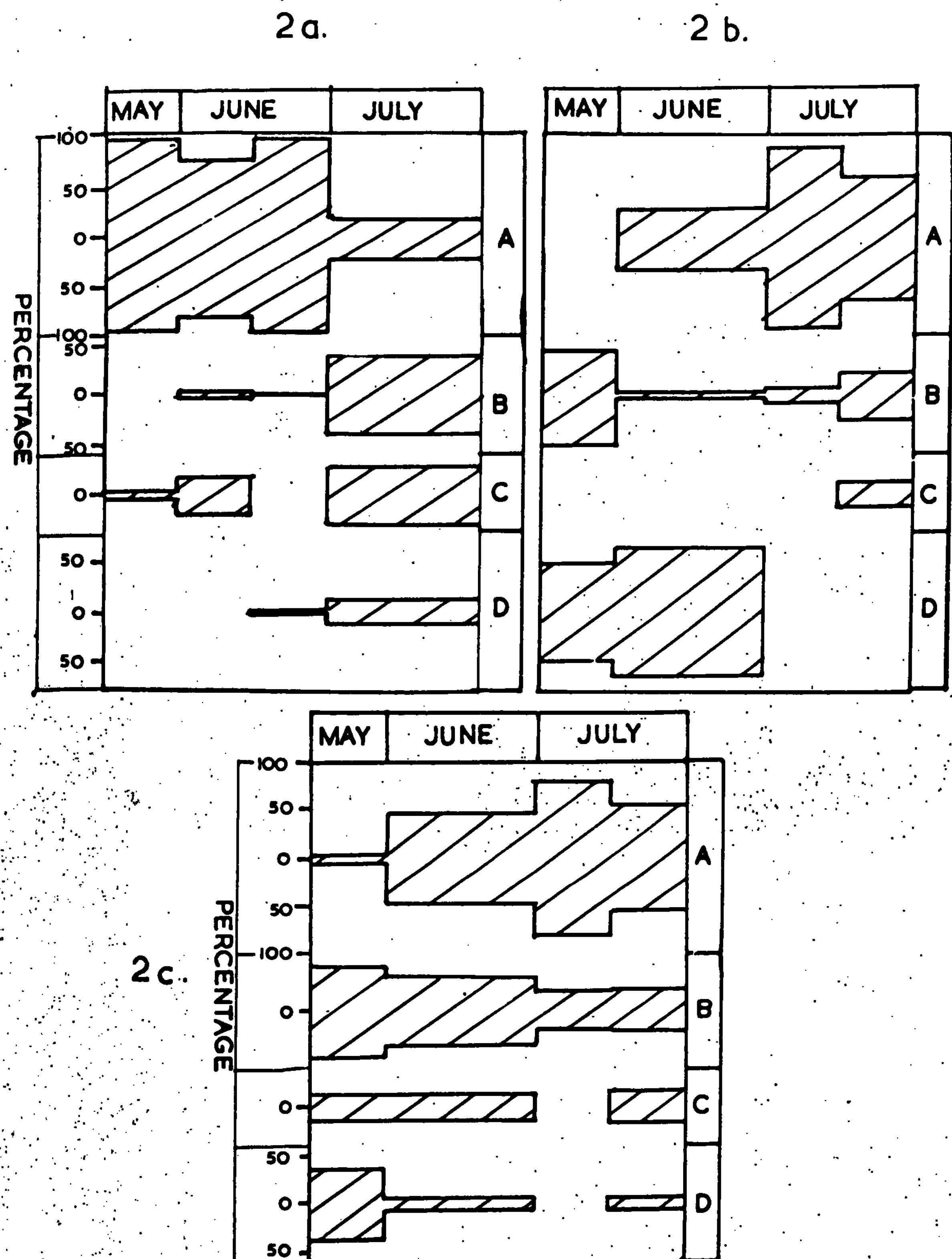
c = Based on counts from observations of birds carrying fish, 1962.

A = Ammodytidae

B = Clupeidae

C = Other fish species

D = Non-fish groups.



2a.
2 b.
MAY
JUNE
JULY
100
50
0
50
100
PERCENTAGE
A
B
C
D
2 c.

greatest when the proportion of sand-eels was lowest i.e. in the early part of the season, and lowest in late June and July when the proportion of sand-eels was highest. The non-fish food groups (Crustacea, Cephalopoda, Insecta) were most prominent in the early part of the season when few sand-eels were taken. The reverse situation occurred in 1961 when the percentage of sand-eels was greatest early on in the year, falling off only slightly in early June, and then reaching a peak towards the end of June. In July there was a considerable diminution in the proportion of sand-eels, and a corresponding increase in the proportion of other fish species. At no time in 1961 did the non-fish groups form more than 15% of the diet.

These differences in the results of the two years indicate that the birds have no rigid dietic preferences but amend their diet in favour of what is most available at the time of fishing. Thus it seems evident that in 1961 sand-eels were abundant until mid-June and were taken in preference to any other type of food. Whether this reflected a super-abundance of sand-eels in the waters around the Farne Islands at this time, or was brought about by a definate searching preference for these fish on the part of the birds is debatable. The former hypothesis would seem to be the most likely however as the differences in shape of the various species of planktonic fish taken by those birds would be alike when viewed from the air. Assuming all species were present in the fishing grounds in similar numbers, the searching and differentiating ability of the terns would have to be considerable in order that sand-eels could be taken to the virtual exclusion of all other fish species. Also their preference for sand-eels would have to follow the fluctuations shown in Figures 2 a, b, and c, being exactly the reverse in 1962 of their monthly preference in 1961. This would be most unlikely, and the fluctuations are much more rationally explained by assuming that a predominance of sand-eels in the diet reflects an abundance of these in the waters fished, and that the birds take the most abundant food supply. Should this be so then it would appear that the diet of the terns would be dependent to a large extent on the movements and interactions of the various prey species. There may, however, be a definite selection on the part of the birds for fish of a certain size. As Figure 1 shows the fish taken varied in size from under 30 to over 100mm. in length, but the great majority taken were between 40 and 80mm., long. It is notable however that in 1961 the most frequently taken size group was 40-60 mm., whereas in 1962 it was 60-80 mm. This again points to the birds taking the most readily available type of fish, rather than searching for those of a specific size.

The prominence of non-fish groups in the diet, at the beginning of the season, when there is a low proportion of Ammodytidae, but not in late July when the sand-eels are replaced by other fish species, probably indicates a definite preference by the terns for fish as opposed to other types of food, and may be a reflection of the relative availability of these food groups throughout the season. Thus it is probable that although Crustacea and Cephalopoda are still present in July, a decrease in the numbers of Ammodytidae would lead to the birds feeding on the other types of young fish available, rather than on the non-fish groups. In the early spring such secondary fish species are not present.

Diurnal variation in diet.

The variation in the percentage of the various prey species taken throughout the day is shown in Figure 3. As described previously, the numbers of Ammodytidae taken in the late morning was significantly greater than at any other time of day. During this period fewer Clupeidae were taken as can be seen from the diagram, but the difference was not significant except when compared with the afternoon and early evening. More Clupeidae were taken in the afternoon but fewer of the non-fish groups. These variations probably

FIGURE 3.

Diurnal variation in the diet of the Arctic Tern and Common Tern, as the average percentage of each prey group taken throughout the day.

a = Arctic Tern 1961

b = Arctic Tern 1962

c = Common Tern 1962

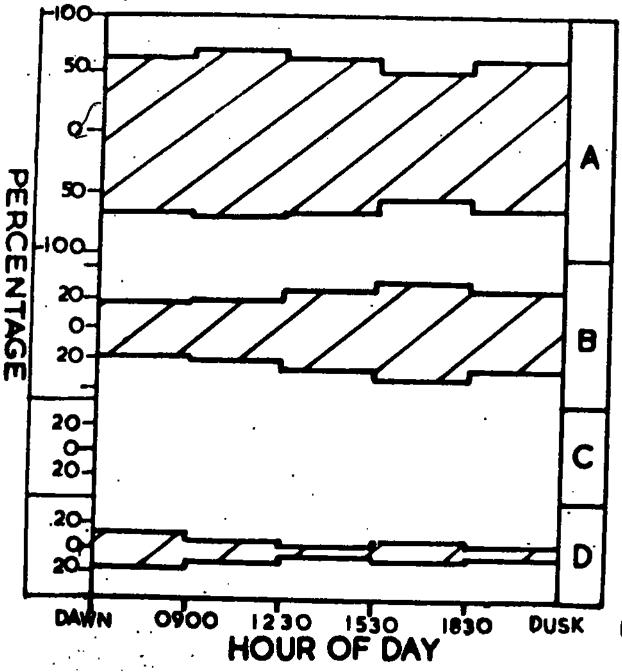
A = Ammodytidae

B = Clupeidae

C = Other fish species

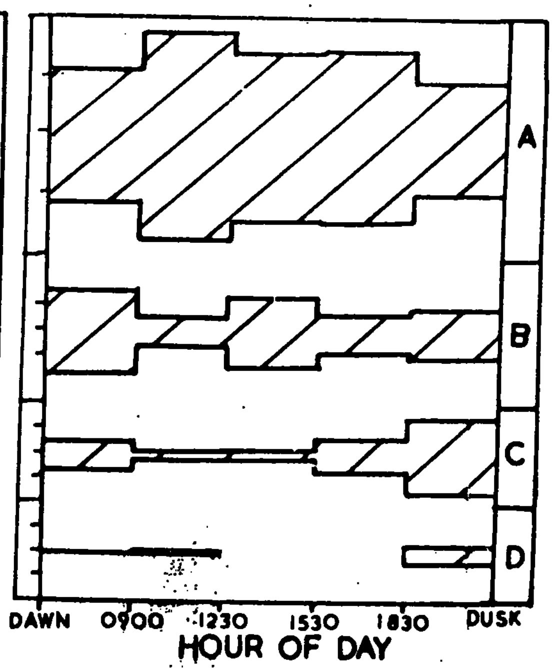
D = Non-fish groups

3a.



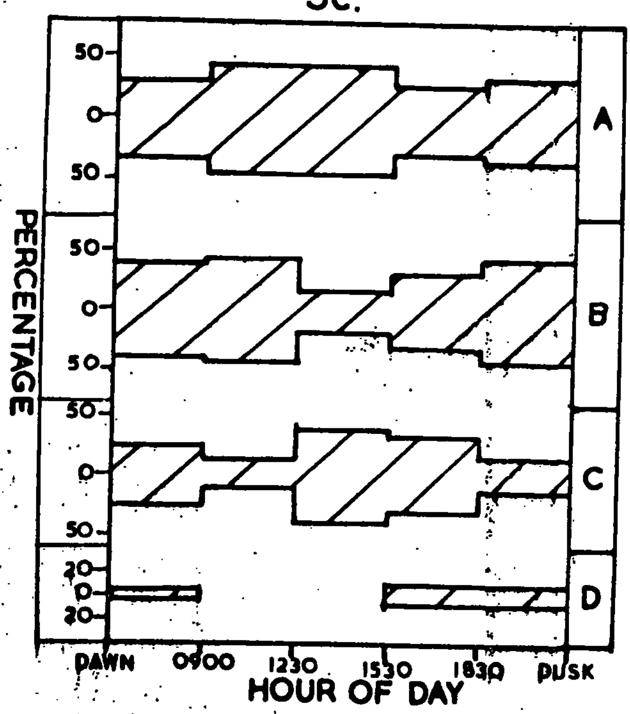
PERCENTAGE
100
50
0
50
100
20
0
20
20
0
20
20
0
20
A
B
C
D
DAWN
0900
1230
1530
1830
DUSK
HOUR OF DAY

3b.



A
B
C
D
DAWN
0900
1230
1530
1830
DUSK
HOUR OF DAY

3c.



PERCENTAGE
50
0
50
50
0
50
50
0
50
20
0
20
A
B
C
D
DAWN
0900
1230
1530
1830
DUSK
HOUR OF DAY

reflect the relative availability of the various prey species throughout the day. Thus the Ammodytidae may be closer to the surface in the late morning than at other times of day, whereas the Clupeidae may be commoner at the surface in the afternoon. It would seem that the Crustacea and Cephalopoda are unavailable in the afternoon period, it being probable that they leave the surface during the period of greatest light intensity. Smitt (1892) notes that sand-eels only move about near the surface in the morning and evening and on dull days. Thus the drop in the numbers of Ammodytidae taken in the afternoons may be due to this migration from the surface during the period of high light intensity. In the present study it was impracticable to investigate further the possibility of such diurnal migration in the prey species. The evidence seems to indicate however that such migrations may have a considerable influence on the fishing activities of the terns.

Average diet over both years.

The diet of the Arctic Tern, obtained by averaging all of the results for both years, emphasizes the predominance of fish in the diet of this bird on the Farne Islands, the non-fish items in the diet comprising only 5.6% of the total (see Table 6).

Of the fish taken it can be seen that although Ammody-

		Morris(1898)	Collinge(1925)	Present work	Palmer(1941)	Hawksley(1957)	Parmelee(1960) and McDonald	Drury(1960)	Gudmundsson(1956)	[illegible](1959)	Bird & Bird(1941)	Salomonsen(1950)	Dolopolskii(1957)	Hartley & Fisher (1936)	Burton & Thurston (1959)
AREA		BRITAIN	BRITAIN	BRITAIN	NEW ENGLAND	NEW ENGLAND	CANADA	CANADA	ICELAND	ICELAND	GREENLAND	GREENLAND	BARENTS SEA	SPITZBERGEN	SPITZBERGEN
PLANTS	Berries												•	•	
CRUSTACEA FRESH WATER	Lepidurus														
CRUSTACEA LITTORAL	Gammaridae						•	•			•			•	•
CRUSTACEA PELAGIC	Mysidaceae													•	
	Euphausiidaceae								•					•	•
	Crangonidae			•	•			•							
	Unspecified	•			•	•					•	•	•		•
PYCNOGONIDA															•
ANNELIDA	Oligochaeta								•						
	Polychaeta											•	•		•
PELAGIC MOLLUSCA	Pteropoda					•									
	Cephalopoda			•		•	•					•			
INSECTA	Larvae & ground living types	•	•		•				•	•					
	Flying insects	•	•	•		•			•	•					
	Unspecified								•				•		
FISH FRESH WATER	Gasterosteidae														
	Mallotus villosus								•			•			
	Salmonidae									•					
FISH MARINE	Blenniidae					•									
	Gasterosteidae			•		•									
	Gadidae	•		•		•			•						
	Clupeidae		•	•	•	•			•						
	Ammodytidae	•		•	•	•			•						
	Unspecified	•		•	•		•	•					•	•	

tidae make up two-thirds of the total diet by number, when estimated by weight they are less important, being 22% as opposed to 63% by weight of the Clupeidae.

COMPARISON WITH PREVIOUS WORK ON THE DIET OF THE ARCTIC TERN.

These present findings compare fairly closely with those of Cullen (pers.comm.) who also studied the Farne Islands Arctic Terns. Whilst studying the behaviour he made observations of the types of fish carried by the birds, finding that on average the diet was made up of 76% Ammodytidae, 18% Clupeidae and 6% other species including Crustacea. Another reference to the food of the Arctic tern on the Farne Islands is found in Bolam (1912), who mentions them taking sand-eels and herring-sile, but gives no proportions. Numerous other workers have commented on the diet of the Arctic Tern at some of its Northern breeding stations. Table 9 analyses the findings of these workers as to the composition of the diet of the Arctic Tern, in relation to geographical area. Most of the authorities listed, although giving species or groups taken by the terns, give no indication of their relative importance as items in the diet. The exceptions to this are Hawksley, Gudmundsson, and Solomonsen, who indicate that some items are more important than others, and Belopoloskii, Hartley and Fisher, and Burton and Thurston, who detail the comparative importance of each food group, either as a percentage, or by relative occurrence. The other workers quoted merely indicate that certain general food types are taken. Only those reports giving a detailed description of the diet, in any particular area, are included.

It can be seen that in the higher latitudes the main emphasis in the diet changes from species of small fish to various types of pelagic and littoral Crustacea. Insects appear to be a common item in the diet except in the extreme north. On the Farne Islands however, they were only taken in any numbers during an apparent scarcity of fish.

This summary makes it increasingly apparent that the Arctic Tern will take the food most commonly available in the surface waters of the sea. If however, such food is scarce then it is capable of exploiting insects, both flying and terrestrial (both Morris (1898) and Gudmundsson (1956) record it following the plough) and of hunting over fresh water and littoral areas. Such secondary food sources are more commonly used in its more northerly breeding areas, reflecting the relative paucity of surface living fish in these areas.

COMMON TERN.

The Common Tern breeds in much smaller numbers on the Farne Islands than the Arctic Terns, and prefers breeding

TABLE 10.

Composition of diet of Common Tern by observation.

SPECIES.	(NO.)	(% by NO.)	(WT.)	(% by WT.)
Ammodytidae	226	44	189	10
Clupeidae	192	38	1344	68
Gasterosteidae	10	2	33	2
Gadidae	55	11	385	19
'Fry'(inc. Trachinidae)	16	3	10	<1
Crustacea	4	1	6	<1
Cephalopoda	5	1	17	1
Totals	508		1984	

sites amongst the longer grass on the tops of the islands, rather than nearer the shore-line where the greatest concentration of Arctic Terns are found.

Information on the feeding biology of the Common Tern was collected only in 1962, and due to the small numbers present, it is less comprehensive than that obtained for the Arctic Tern. The study colonies under observation contained a mixed group of Arctic and Common Tern nests, and the same techniques of observation as described for the Arctic Terns were used for both species. The size of fish taken by the Common Terns, as shown in Figure 1c, were similar to those taken by Arctic Terns, and the small differences were not significant ($P > 0.3$).

Both observations on the feeding of individual chicks and periodic counts of birds carrying fish into the study area were undertaken for Common Terns. Table 10 gives a

TABLE 11. Composition of diet of Common Tern by periodic counts on different days. 1962.

DATE	Time of Day	AMMODYTIDAE No.	AMMODYTIDAE % by No.	CLUPEIDAE No.	CLUPEIDAE % by No.	GADIDAE No.	GADIDAE % by No.	'FRY' No.	'FRY' % by No.	CRUSTACEA No.	CRUSTACEA % by No.	CEPHALOPODA No.	CEPHALOPODA % by No.
22/7/62	1415-1445	19	50	8	21	10	26	1	3				
	1545-1615	7	30	7	30	9	39						
	1815-1845	5	26	6	32	3	16	2	11	3	16		
23/7/62	0600-0630	12	29	16	38	8	19	5	12	1	2		
	0800-0830	17	35	19	40	8	17	1	2			3	6
25/7/62	1130-1200	7	44	7	44	1	6	1	6				
	1300-1330	3	37	1	13	4	50						
	1830-1900	9	41	12	55	1	4						

summary of the results from all observations. As very few samples of fish taken by Common Terns were obtained the numbers are here converted into weights using the average weights of fish taken by the Arctic Terns. Such weights should be reasonably accurate for comparative purposes since, as was shown above, the sizes of fish taken by both species are similar. These results represent the diet of the chicks. The lack of an adequate number of regurgitated food samples from the adults has prevented a reasonable analysis of their diet from being made.

As all the observations were made during July no analysis has been made of seasonal changes in the diet. It seems probable however, that any such changes would be similar to those in the diet of the Arctic Tern, due to the close similarity in both feeding behaviour, and feeding areas of the two species (see Section 2). Thus any changes in the availability of different types of prey in the surface waters during the season would affect the diets of these species similarly.

DIURNAL VARIATION IN DIET.

Table 11 shows the composition of the diet by periodic counts on different days, and Figure 3 compares these figures diagrammatically. These results are too few to permit reasonable statistical analysis, but the trends shown are similar to those seen in the Arctic Tern. Thus there is a rise in the percentage of Ammodytidae taken during the mid-morning period, and a corresponding fall in the late afternoon.

COMPARISON WITH PREVIOUS WORK ON THE DIET OF THE COMMON TERN.

Nearly all the records published on the food of the Common Tern have been made in Britain or North America. Its breeding distribution, although world-wide, is by no means as northerly as that of the Arctic Tern, being almost entirely south of the Arctic circle, and there is thus not as much geographical variation in the food items of the diet as one finds with the Arctic Tern.

Table 12 gives an analysis of published records of the diet of the Common Tern, only the more detailed works being included. It can be seen that the records for North America are very similar to those for this country in terms of the types of food taken (although the individual species are, of course, different). The North American birds do, however, seem to take more fresh water fish and insects than the birds of this country. This is no doubt due to the fact that the Common Tern very rarely breeds inland in this country, and its colonies tend to be on islands off the coast, rather than in the vicinity of estuaries and inland lakes, as are some of the North American colonies. The record from the

TABLE 12. Analysis of published records of the diet of the Common Tern.

AREA	PLACE	AUTHORITY	FISH Marine	FISH Fresh water	CRUSTACEA Pelagic	CRUSTACEA Littoral	ANNELIDA	MOLLUSCA Pelagic	MOLLUSCA Littoral	ECHINODERMATA	INSECTA	VEGETATION
	Farne Islands	Present work	****		*							
GREAT BRITAIN	E. and N.E. coasts of Scotland	Collinge 1925	****		**		**	**				
	Blakeney Pt. Norfolk	Collinge 1925	***		**		**	**			**	
	General	Collinge 1925	***		**		**	**				
GERMANY	Lower Elbe	Peters 1933	****									
	General	McAtee & Beal 1912	***	**	*		*	*			*	
NORTH AMERICA	New England	Palmer 1941	***	***		*					*	
	Maine	Mendall 1935	***		***	*			*	*	**	*
	New England	Floyd 1930	****									

**** = Very important (over 50%)
*** = Important (30-50%)
** = Occurring commonly (10-30%)
* = Recorded occasionally (under 10%)

Elbe, in Germany, gives the Smelt (*Osmerus eperlanus*) as the most common prey, which indicates that the birds, as would be expected, take the most readily available food supply, for the Smelt is known to occur in large numbers in that area (Jenkins, 1936, p.247). The records of Collinge (1925), on the diet in various parts of Great Britain, suggest that the preponderance of fish in the diet of the birds in the Farne Islands area may be exceptional, and that in other areas Crustacea and Pelagic Mollusca assume a greater importance. In this connection it is interesting to note that Seebohm (1896) records the Common terns on the Farne Islands as taking herring-fry, sand-eels, and Crustaceans, but gives no indication of the relative proportions.

. SANDWICH TERN.

In 1961 the Sandwich Terns did not breed on the Inner Farne, the island where nearly all the present investigations were carried out, but bred in a large colony on the Brownsman, one of the outer islands inaccessible for regular research visits. In 1962 however, a group of about 400 pairs of Sandwich Terns bred on the Inner Farne, enabling information about their feeding habits to be collected.

TABLE 13. Sandwich Tern. Composition of diet by analysis of samples and by observations. 1962.

GROUP	Analysis of samples regurgitated					Obs. of fish carried by birds	
	No.	% by No.	Wt.	% by Wt.	Av. wt. of Indiv. taken	No.	% by No.
Ammodytidae	89	77	176	63	2.1	569	74
Clupeidae	10	9	42	15	4.3	120	16
Gadidae	10	9	32	11	3.2	46	6
Gasterosteus aculeatus	3	3	6	2	2.1	) 12	) 2
Gasterosteus spinachia	4	3	24	8	6.0	)	)
Pholis gunnellus						6	1
Trachinus vipera						3	<1
Liparis liparis						1	<1
Crustacea						6	1
Cephalopoda						6	1
Total number of fish in samples.	116					769	
Total number of samples.	61						

ANALYSIS OF REGURGITATION SAMPLES.

Due to the comparative timidity of the Sandwich Tern, and its habit of deserting a colony 'en masse' if unduly disturbed, no attempt was made to trap adults during the early part of the season. It was found however, that the Sandwich Tern chicks would sometimes regurgitate on handling. In addition a number of samples of fish were collected after having been dropped in the colony during the feeding of chicks. Thus the samples obtained were all of the food of chicks, and no estimate of the food of adults has been made. Table 13 gives an analysis of the samples obtained.

ANALYSIS OF DIRECT OBSERVATION RESULTS.

Similar methods were used in observing the Sandwich Terns as those described for Arctic Terns. The feeding of individual chicks was, however, difficult to observe due to the height of the vegetation, but the type of prey could generally be noted as the birds flew past. The Sandwich Terns tended to take larger fish than the other two tern species breeding on the island. Figure 1f, g, shows the size frequencies of sand-eels taken by Sandwich Terns, based both on specimens obtained and measured, and on estimated sizes from observation. The two methods show similar results, except that more small fish appear in the estimated sizes than among the measured specimens. These records are not statistically comparable due to the relative inaccuracy of the size ranges estimated from observations.

TABLE 14.

Composition of diet of Sandwich Tern. All results.

	NO.	% by No.	Wt.(gm.)	% by Wt.	Est.Av.Wt.of Indiv. taken
Ammodytidae	658	74	1409	61	2.1
Clupeidae	130	15	560	24	4.3
Gadidae	56	6	181	8	3.2
Gasterosteidae	19	2	76	3	4.0
Pholidae	6	1	30	<1	5.0
Trachinidae	3	<1	21	1	7.0
Liparidae	1	<1	15	1	15.0
Crustacea	6	1	10	1	1.7
Cephalopoda	6	1	20	1	3.3
Total	885		2322		

Table 13 also gives the results of all observations taken. It can be seen that some types of fish appear here which were not seen when observing the other terns. These, the Butterfish (Pholis gunnellus), the Lesser Weaver, (Trachinus vipera), and the Sea Snail (Liparis liparis) were all readily distinguishable at fairly close range. Only one specimen of the latter was seen however, and it did not appear in the diet of any other of the birds studied. Thus the observer was not familiar with the species for the purposes of sight identification, and the record is dubious.

OVERALL DIET.

The average diet of the Sandwich Tern, being a combination of the results obtained from sampling and from observation, is given in Table 14. The weights are here based on the average weights of specimens obtained. In those cases where no specimen was obtained, the weights are an estimate based on the apparent size of the prey taken.

As has been pointed out previously these results are based only on food fed to the chicks, and no information has been obtained concerning the food of adult birds. There is no reason to believe that this would differ greatly however. As was seen with the Arctic Terns, the relative percentages of the various food groups may fluctuate slightly, but it is probable that the adults, like the chicks, feed to a very large extent on fish, predominantly Ammodytidae and Clupeidae.

Observations and counts of Sandwich Terns were made only in July, between the hatching and the fledging of the chicks. No estimate can therefore be made of seasonal changes in the diet.

As with the other two species of tern discussed it can be seen that the Sandwich Tern depends to a very large extent on fish as its main food, the non-fish items in the diet comprising only 1.4% of the total number of food items.

COMPARISON WITH PREVIOUS WORK ON THE DIET OF THE SANDWICH TERN.

Very little data of any sort havebeen published as to the diet of the Sandwich Tern. Morris (1898) records the diet as fish, mainly Sand-launce and Garfish. Lowe (1914) states that in Lancashire the chief food of young Sandwich Terns is young Whiting and postulates that the early arrival of Sandwich Terns at the breeding grounds may be prompted by the early appearance of young Whiting, as compared with other fry sought by terns. This would seem unlikely as, as has been seen, Whiting are also taken by Common and Arctic Terns. Walker (1956) states that Sandwich Terns take sand-eels, molluscs, and the fry of Herring and Whiting. The only quantitative work published on the diet is in Collinge (1926), who examined the stomachs of 9 birds shot at Blakeney Point in Norfolk. He found the following percentages by volume of various food items.

Ammodytidae	34.8	
'Food Fish'	31.5	(probably herring and Gadidae).
Annelida	32.5	
Marine Molluscs	1.3	

The major difference between these results and the present ones is the large percentage of Annelida found in the birds from Blakeney Point. No worms of any kind were found in the diet of the Sandwich Terns on the Farne Islands, which probably indicates their absence from the waters round the island rather than the birds selectively omitting them.

KITTIWAKE.

This small, cliff-nesting gull breeds in large numbers on the Farne Islands. Between 450 and 550 pairs nest round the cliffs of the Inner Farne, the nests of perhaps half of these being accessible for study purposes. The Kittiwake, like the tern, is a surface feeder, generally plunge-diving for prey from a height of a few feet. Kittiwakes are rarely seen fishing within sight of the islands, other than when large surface shoals of fish occur near the islands. They are, however, occasionally seen fishing over the tide rips around the islands, and it seems likely that they would prefer such roughened waters for fishing, for the same reasons as postulated for the terns.

ANALYSIS OF REGURGITATION SAMPLES.

The only practicable method for investigating the diet of Kittiwakes on the Farne Islands was by the collection and analysis of regurgitation samples. The chicks are fed by regurgitation from the parent, thus direct observation methods cannot be used.

At the start of the present investigation it had been hoped that the regular collection of regurgitation samples from Kittiwake chicks throughout the pre-fledging period, would yield enough material to obtain a comprehensive idea of the diet of the Kittiwakes throughout the breeding season.

Unfortunately difficulties arose in obtaining an adequate number of regurgitation samples, as only about 10% of the chicks regurgitated on being handled. An analysis of the samples obtained is given in Table 15.

TABLE 15.

Kittiwake. Analysis of diet from regurgitation samples.

YEAR	PREY	No. of Samples	Analysis by No.		Analysis by Wt.		Av. Wt. of Indiv. prey
			No.	%	Wt.	%	(g.)
1961	Ammodytidae	146	194	66	686	46	3.5
	Gadidae		45	15	412	27	9.1
	Clupeidae		41	14	379	25	9.2
	Crustacea		8	3	5	0	0.6
	Offal		4	1	15	1	
1962	Ammodytidae	72	435	89	747	69	1.7
	Gadidae		12	2	132	12	11.0
	Clupeidae		40	8	199	18	4.9
	Crustacea		0	0	0	0	
	Offal		0	0	0	0	

Each sample, being the regurgitation from a single individual at any one time, generally contained the remains of a number of food items. These were nearly always partly digested and battered however, and often only part, usually the tail, of a specimen was present. Thus identification to species level was often impossible, and for the purpose of analysis specimens were merely assigned to one of the major groups shown in the table. The damaged condition of most of the specimens made it necessary for the weights to

TABLE 16. Monthly analysis of diet from regurgitation samples. (Weights in g.).

1961.

	Period	No. of Samples	Analysis by no. No.	Analysis by no. %	Analysis by wt. Wt.	Analysis by wt. %	Period	No. of Samples	Analysis by no. No.	Analysis by no. %	Analysis by wt. Wt.	Analysis by wt. %
Ammodytidae			4	40	46	42						
Gadidae	June	10	6	60	62	58						
~~Clupeidae~~												
Ammodytidae			54	57	208	46			190	68	646	46
Gadidae			20	21	187	42	Average		38	14	350	25
Clupeidae	July 1st-10th	54	8	9	34	8	for	135	41	15	379	27
Crustacea			8	9	5	1	July		8	3	5	<1
Offal			3	4	15	3			3	1	15	1
Ammodytidae			88	77	315	58						
Gadidae	July 11th-20th	53	16	14	155	28						
Clupeidae			10	9	74	14						
Ammodytidae			48	65	123	31						
Gadidae	July 21st-31st	28	2	3	8	2						
Clupeidae			23	32	271	67						

1962

	Period	No. of Samples	Analysis by no. No.	Analysis by no. %	Analysis by wt. Wt.	Analysis by wt. %	Period	No. of Samples	Analysis by no. No.	Analysis by no. %	Analysis by wt. Wt.	Analysis by wt. %
Ammodytidae			125	94	226	81	Average		151	94	338	85
Gadidae	June 10th-20th	24	6	5	42	15	for	40	6	4	42	11
Clupeidae			2	1	8	4	June		4	2	12	3
Ammodytidae			26	93	112	97						
Gadidae	June 21st-30th	16	0	0	0	0						
Clupeidae			2	7	4	3						
Ammodytidae			173	88	269	59	Average		284	87	409	60
Gadidae	July 1st-10th	21	6	3	90	20	for	32	6	2	90	13
Clupeidae			16	8	98	21	July		36	11	187	27
Ammodytidae			111	85	140	61						
Gadidae	July 11th-20th	11	0	0	0	0						
Clupeidae			20	15	89	39						

be estimated in many cases.

All samples were collected in June and July, i.e. whilst the chicks were at the nest. Table 16 shows the results for successive 10 day periods, and also for each month as a whole.

There was considerable variation in the size of fish taken. Figure 4a shows the length frequencies of the Ammodytidae taken by the Kittiwakes. Too few Gadoids and Crustacea were taken to give an accurate picture of the relative variation in size. The Clupeidae taken were generally in a much poorer condition than the other species, their flesh being, apparently, more readily digestible. It was rarely possible to accurately measure the length of specimens, but the weights could be estimated even from fragmented specimens. Thus a frequency histogram of the weights of Clupeidae taken has been drawn up (Figure 4c).

There was a significant difference in the sizes of Ammodytes taken in the two years ($P<0.001$). In 1961 there were more of the smallest (41-50mm.) and largest (over 120mm.) groups but fewer of the mid-range fish (80-100). The smallest fish taken was 42mm. long, weighing about 0.3g. and the largest specimen recorded was over 300mm. long and weighed over 40g. The size of Clupeidae taken in each year did not differ significantly ($P>0.05$).

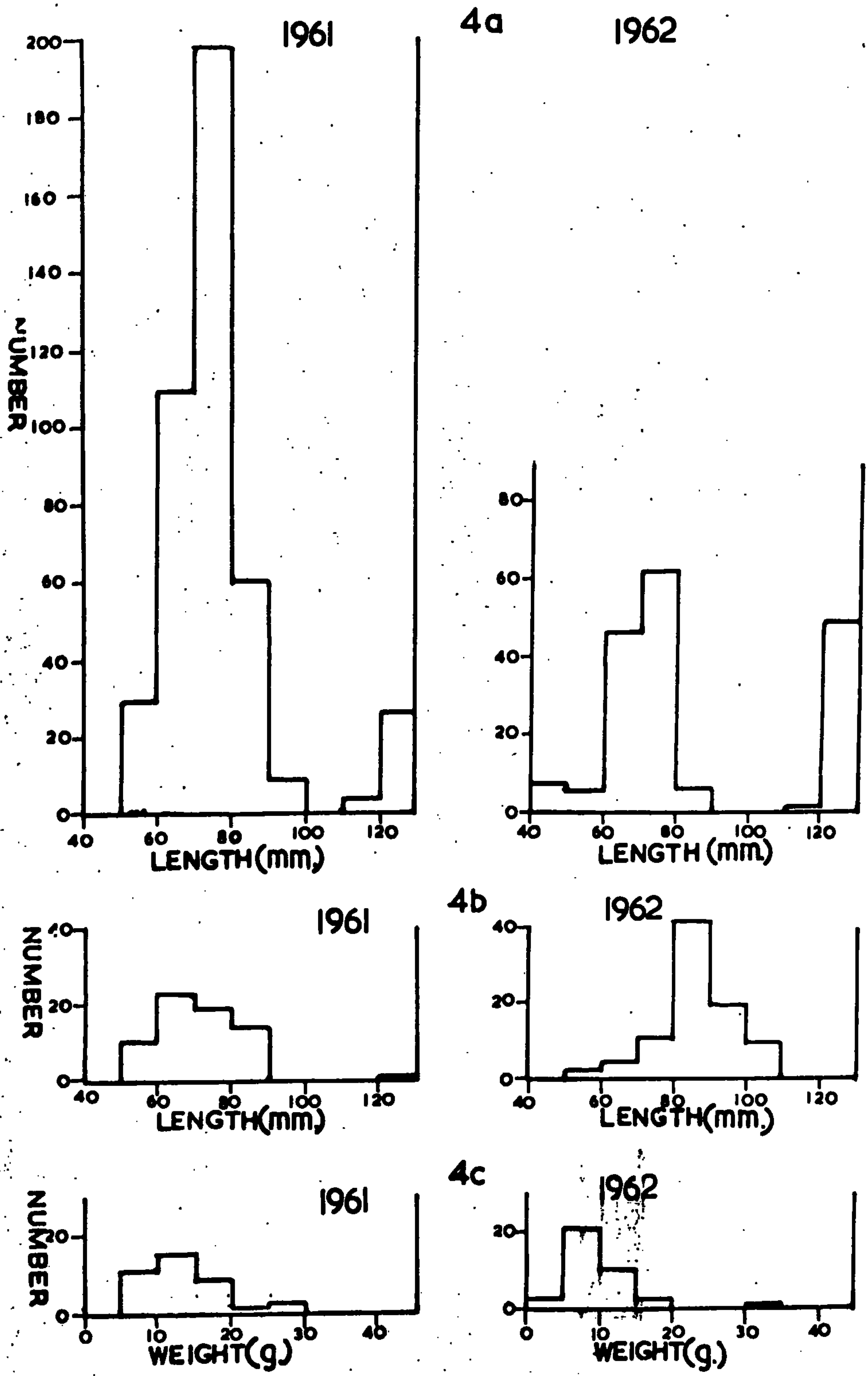
FIGURE 4.

Size frequencies of fish taken by Kittiwakes and Lesser Black-back Gulls.

a = Lengths of Ammodytidae taken by Kittiwakes in 1961 and 1962.

b = Lengths of Ammodytidae taken by Lesser Black-back Gulls in 1961 and 1962.

c = Weights of Clupeidae taken by Kittiwakes in 1961 and 1962.



4a
1961
1962
NUMBER
LENGTH (mm.)
LENGTH (mm.)
4b
1961
1962
NUMBER
LENGTH (mm.)
LENGTH (mm.)
4c
1961
1962
NUMBER
WEIGHT (g.)
WEIGHT (g.)

The largest Clupeoid taken weighed 36.8g. (1961) and the smallest 2.8g. (1961).

TABLE 17.

Kittiwake. Average diet over two seasons (1961-62).

PERIOD	PREY	Analysis by No. No.	Analysis by No. %	Analysis by Wt. Wt.	Analysis by Wt. %	Av. Wt. of Indiv. prey (g.)
Overall	Ammodytidae	629	81	1433	56	2.3
	Gadidae	57	7	544	21	9.5
	Clupeidae	81	10	578	22	7.1
	Crustacea	8	1	5	<1	0.6
	Offal	4	<1	15	<1	
June	Ammodytidae	155	9	384	77	2.5
	Gadidae	12	7	104	21	8.7
	Clupeidae	4	2	12	2	3.0
	Crustacea	0	0	0	0	
	Offal	0	0	0	0	
July	Ammodytidae	474	78	1054	51	2.2
	Gadidae	45	7	439	22	9.7
	Clupeidae	77	13	566	26	7.3
	Crustacea	8	1	5	<1	
	Offal	4	<1	15	1	

AVERAGE DIET.

Table 17 shows the total figures for the diet of the Kittiwake, being an average of the results for both years. The average monthly totals of both years are also given.

As has been stated these results are based almost entirely on samples obtained from the chicks. Belopolskii (1957) found that on the East Murman Coast the diet of young and adult Kittiwake did not differ markedly, although the adults were found to take slightly more molluscs and crustacea than the young. It is possible that on the Farne Islands, the young are fed a higher percentage of fish than that taken by the adults, but unlikely in view of the apparent abundance of fish in the Farne Islands area (see general discussion below).

As can be seen from Table 17 fish form a preponderant part of the diet of the Kittiwake on the Farne Islands, non-fish food comprising only 1.8% by number of the overall diet. Of the types of fish taken Ammodytidae are by far the most important with Clupeidae and Gadidae, in that order, being secondarily important. When the actual weight of food taken is considered the Ammodytidae are less important, but still comprise 55% of the total food taken. The Gadidae and Clupeidae each form just over 20% by weight, whilst crustacea and offal taken are almost negligible as part, by weight, of the diet. The occurrence of offal in the diet, although only three specimens were noted, is interesting in that the Kittiwake is not generally a scavenger. There are, however, numerous records of it following fishing boats and regularly frequenting fishing grounds, (c.f. Boswall, 1960, and Gudmundsson, 1955) and it is probable that it regularly feeds on offal at such times.

SEASONAL CHANGES IN THE DIET.

As all the samples were taken in June and July a comparison of the dietic variation in those two months only can be made. Table 17 shows that on average more Clupeidae and fewer Ammodytidae were taken in July than in June, these differences being highly significant ($P<0.001$). No specimens of crustacea and offal were taken in June.

If each year is considered separately then significantly more Ammodytidae were taken in July 1962 than in July 1961 ($P<0.001$) and conversely significantly fewer Gadidae were taken in July 1962 than in the corresponding month in 1961. The number of Clupeidae taken in July did not differ significantly from one year to the next ($P>0.2$). The yearly figures for June cannot be compared adequately due to the small number of samples obtained in June 1961. It thus seems probable that the number of Ammodytidae available to the birds declines in July, and that these fish are to a certain extent replaced by Clupeidae, together with minor dietic items such as crustacea and offal. The fewer sand-eels taken in July 1961 as opposed to 1962 could indicate either a relative paucity of these fish in the former year, or a correspondingly larger number of Gadoids being available. The fact that crustacea and offal were also taken in July 1961, whilst not appearing at all in 1962 would indicate, however, that there was a scarcity of the more usual food items at that time.

In order to ascertain whether there were any significant fluctuations in the composition of the diet within the monthly periods so far examined comparison was made of two successive 10 day periods in July. In 1961 over 30 samples were taken in each period and in the corresponding periods the following year between 10 and 20 samples were taken. It was found that there was a significant difference between the number of Ammodytidae taken in the first 10 day period in 1961 as opposed to the second ($P<0.01$), but otherwise the numbers of each type of prey taken in each period did not differ significantly. Thus it may be assumed that whilst short term fluctuations (i.e. from week to week) in the composition of the Kittiwake's diet may occur occasionally, dietic composition is normally more stable, changing only gradually from month to month.

COMPARISON WITH PREVIOUS WORK ON THE DIET OF THE KITTIWAKE.

Early writers on the Kittiwake mention its' dependence on small fish and crustaceans as the major items of the diet, but also stress the habit of the taking of offal (Seebohm (1896) and Morris (1898)). Gudmundsson (1956), in describing the diet of these birds in Iceland, also men-

TABLE 18. Geographical variation in the diet of the Kittiwake.

FOOD GROUP	GREAT BRITAIN Farne Islands (Present work)	GREAT BRITAIN General (Collinge) 1925	ICELAND (Gudmundsson) 1956.	GREENLAND (Salomonsen) 1950.	JAN MAYEN (Soligman & Willcox 1940)	EAST MURMAN (Belopolskii) 1957.	NOVAYA ZEMLYA (Belopolskii) 1957.	SPITZBERGEN (Hatley & Fisher 1936)
FISH	***	**	***	***	**	***	**	*
Ammodytidae	***		*			*	*	
Clupeidae	*		*			**		
Gadidae	*		*			*	*	
Boreogadus saida				*			**	
Mallotus villosus			*	***		*	*	
Others						*		
POLYCHAETA		**		*		*		*
ECHINODERMATA						*		
MOLLUSCA		**		*	**	*	*	
INSECTA		*				*		
OFFAL	*		**	*				
CRUSTACEA	*	**	**	*	*	*	**	***

*** = Very important
** = Important
* = Recorded

tions offal as being an important item in the diet, in addition to various small fish and crustaceans. Both Uspenski (1956 trans. 1960) and Salomonsen (1970) note the scavenging habits of Kittiwakes, the former recording their dependence on the fish remains from Guillemot ledges in Novaya Zemlya, and the latter noting their taking of whale faeces in Greenland.

A number of authors have published comprehensive surveys of the diet of the Kittiwake in various parts of its range. These records are summarized in Table 18, in terms of the relative importance of the major food groups in each area.

It can be seen that there is considerable geographical variation in the diet of the Kittiwake, it being evident that the emphasis changes from fish to crustacea as the major item of diet, from the more southerly, warmer latitudes to the northerly, colder areas, although no major food group is entirely excluded even in the most northerly area. The two extremes are found in the Farne Island area of Great Britain, where there is an almost complete dependence on fish as a food source, and Spitzbergen, where crustacea are taken almost exclusively. The areas lying between these geographical points show a gradation of diet, and include a much wider range of food groups. It would seem highly probable that, in any one area, there is no rigid dependence on a particular food group but rather the exploitation of the type of food most readily available. Thus on the Farne Islands the birds normally take a very high percentage of Ammodytidae, but when this falls off a number of other food groups or fish species occur, notably the Clupeidae. In Greenland the birds depend largely on _Mallotus villosus_, but can exploit a number of other types of prey, both crustaceans and fish, should these prove scarce. In Novaya Zemlya, Iceland, and recently in England on the River Tyne, the Kittiwake would appear to feed to a fairly large extent as a scavenger. In the last mentioned areas the birds also take living fresh-water organisms. (Coulson and Macdonald, 1962) All these instances would suggest that the Kittiwake is by no means a ridgidly specialized feeder, but possesses a marked capability for exploiting any readily available food source, within its limits as a surface feeder. Only in favourable feeding areas, in which category the Farne Islands area undoubtedly falls, do we find a narrow food spectrum composed of surface living fish and crustacea.

• LESSER BLACK-BACK GULL.

It is estimated that approximately a thousand pairs of Lesser Black-back Gulls (_Larus fuscus_) breed on the Farne

TABLE 19. Lesser Black-back Gull. Analysis of diet from regurgitation samples.

YEAR	NUMBER OF SAMPLES	PREY	ANALYSIS BY NUMBER		ANALYSIS BY WEIGHT		AVERAGE WEIGHT OF INDIVIDUAL PREY
			NUMBER	PERCENTAGE	WEIGHT	PERCENTAGE	
1961	35	Ammodytidae	73	65	120	23	1.6
		Clupeidae	10	9	104	20	10.4
		Gadidae	8	7	80	15	10.0
		Anguillidae	0	0		0	
		Offal	9	8	197	38	
		Insecta	2	2	<1	<1	0.1
		Annelida	9	8	10	2	1.1
		Vegetation	2	2	4	1	
1962	33	Ammodytidae	104	49	145	11	1.4
		Clupeidae	8	4	89	6	11.1
		Gadidae	35	17	857	67	24.4
		Anguillidae	1	<1	13	1	13.0
		Offal	3	4	142	11	
		Insecta	2	1	1	<1	0.5
		Annelida	53	25	40	3	0.7
		Vegetation	0	0	0	0	

Islands, in contrast to the much smaller numbers of Herring Gulls, of which there are not more than 150 pairs.

ANALYSIS OF REGURGITATION SAMPLES.

The chicks of the Lesser Black-back Gull are fed by regurgitation from the parent, and it is thus impossible to obtain any idea of the food being fed by observing the feeding process. Thus the only method used to investigate the diet was analysis of regurgitation samples. This, of necessity, confined the investigation to the diet of the chicks as the parents were extremely difficult to trap successfully being the most timid of any of the sea-birds breeding on the islands.

Unfortunately the eggs of these gulls are collected regularly by the local fishermen during May and June, and only in mid-June are the birds allowed to lay and incubate unmolested. Thus the first chicks are not hatched until mid-July and no samples were collected until after this time. An analysis of the samples obtained is given in Table 19.

Each sample, being the regurgitation from a single individual at any one time, generally contained the remains of a number of food items. As with the Kittiwake, these were generally partly digested, and thus identification to species level was not often possible, the specimens being put only into one of the groups listed.

TABLE 20. Lesser Black-back Gull. Monthly analysis of diet from regurgitation samples. (weights in g.)

Year	Month & No. of samples.	PREY	Analysis by No.		Analysis by Wt.	
			No.	%	Wt.	%
1961	JULY (17)	Ammodytidae	47	71	63	33
		Clupeidae	2	3	17	9
		Gadidae	4	6	24	13
		Anguillidae				
		Annelida	9	14	10	5
		Insecta				
		Offal	4	6	78	41
		Vegetation				
	AUGUST (18)	Ammodytidae	26	55	57	18
		Clupeidae	8	17	87	27
		Gadidae	4	8	56	17
		Anguillidae				
		Annelida				
		Insecta	2	4	0.2	<1
		Offal	5	11	119	37
		Vegetation	2	4	4	1
1962	JULY (10)	Ammodytidae	88	61	138	65
		Clupeidae	2	1	33	15
		Gadidae				
		Anguillidae				
		Annelida	53	36	40	19
		Insecta	2	1	0.6	<1
		Offal				
		Vegetation				
	AUGUST (23)	Ammodytidae	16	26	7	1
		Clupeidae	8	13	89	8
		Gadidae	31	50	834	78
		Anguillidae	1	2	13	1
		Annelida				
		Insecta				
		Offal	6	10	122	11
		Vegetation				

Table 20 shows an analysis of the samples taken in each month.

There was considerable variation in the size of fish taken in the two years. Figure 4b shows the length frequencies of Ammodytidae taken in each year. It can be seen that in 1961 the fish taken were generally smaller, lying mainly in the range 50-90mm., whilst in 1962 the birds took fish generally in the range 80-110mm. long. These differences are highly significant ($P<0.001$). The smallest Ammodytes taken were 54mm. long, weighing 0.6g., and the largest over 300mm. long, weighing approximately 40g. Too few Clupeidae and Gadidae were taken to enable a size frequency comparison to be made, and the specimens obtained tended to be much more damaged than the smaller Ammodytidae thus rendering the estimation of actual size difficult. However estimates of approximate size were made where possible, and the average weight of 10 Clupeidae in 1961 was found to be 10.4g., and of 8 in 1962 to be 11.1g. The average weight of 8 Gadidae in 1961 was 10.0g. and of 35 in 1962 was 24.4g. Thus in 1962 the Clupeidae and Gadidae taken were larger than those taken in 1961.

AVERAGE DIET.

The total figures for the diet of the Lesser Black-

TABLE 21. Lesser Black-back Gull.

Average diet over two seasons. (1961-62)

PERIOD	No. of Samples	PREY	Analysis by No. No.	Analysis by No. %	Analysis by Wt. Wt.	Analysis by Wt. %	Av. Wt. of Indiv. prey
Overall	68	Ammodytidae	177	57	265	14	1.5
		Clupeidae	18	6	194	11	10.8
		Gadidae	43	13	955	53	22.2
		Anguillidae	1	<1	13	1	13.0
		Offal	17	5	339	19	
		Insecta	4	1	1	<1	0.2
		Annelida	62	19	50	3	0.8
		Vegetation	2	1	4	<1	
July	27	Ammodytidae	135	64	201	50	
		Clupeidae	2	1	17	4	
		Gadidae	6	3	57	14	
		Anguillidae	0	0	0	0	
		Offal	4	2	78	19	
		Insecta	2	3	1	1	
		Annelida	62	29	50	12	
		Vegetation	0	0	0	0	
August	41	Ammodytidae	42	38	64	5	
		Clupeidae	16	15	177	13	
		Gadidae	35	32	890	64	
		Anguillidae	1	1	13	1	
		Offal	11	10	241	17	
		Insecta	2	2	<1	<1	
		Annelida	0	0	0	0	
		Vegetation	2	2	4	1	

back Gull, being an average of the results for both years are given in Table 21 together with the average monthly totals for both years.

The most important item of the diet is seen to be live fish, comprising 74% by number and 78% by weight of the total diet. The most numerous fish taken are the Ammodytidae, forming 55% by number, but the Gadidae are more important when considering the weight of food taken, comprising 52% of the total diet by weight. Apart from fish, the other important types of food taken are offal, and earthworms. The former was almost exclusively fish offal, probably obtained by following the local seine-net fishing boats. Seventeen samples of this were taken, each sample counting as a single unit in the total of food items taken, as opposed to samples of fish taken which might contain up to 15 individual specimens. Thus the offal formed only a small part of the diet by number, but over 18% by weight. Conversely the earthworms were numerous individually, forming 21% of the diet by number, but weighed very little and formed only 3% of the diet by weight. The few specimens of insects taken were beetles of the family Carabidae.

SEASONAL CHANGES IN THE DIET.

Table 21 gives the average diet for July and August, all samples being collected in these two months. A significantly higher percentage of Ammodytidae were taken in July as opposed to August ($P<0.001$), and significantly lower percentages of Clupeidae, Gadidae and offal ($P<0.001$) (in each case). It is thus probable that in July the Ammodytidae are more readily available to the gulls than in August, and thus form a major part of the diet, whilst during the latter months the birds turn to the secondary food sources. The other notable difference in the diet during the two months is the large number of earthworms taken in July, whereas none were found in the diet in the following month.

If dietetic differences between the two years are compared it is found that there is no significant difference in the numbers of Ammodytidae and Clupeidae taken in July 1961 as opposed to July 1962 ($P>0.02$ and >0.7 respectively). Small numbers of Gadidae and offal were taken in July 1961 but none were found in the samples during July 1962. Significantly more Ammodytidae were taken in August in 1961 than in 1962 ($P<0.01$) but fewer Gadidae were taken ($P<0.01$). There was no significant difference in the numbers of Clupeidae, or the amounts of offal taken ($P>0.8$ and >0.9 respectively).

COMPARISON WITH PREVIOUS WORK ON THE DIET OF THE LESSER BLACK-BACK GULL.

Little comprehensive work has been published on the food of this species. Early writers (Morris (189[illegible]) and Seebohm (1896) mention fish, offal, insects and earthworms as being the most important food item. Nordberg (1950), in one of the few detailed works on the food of the Lesser Black-back Gull, analysed the pellets produced by chicks from 12 different nests on the Åland Archipeligo in Finland. In all he examined 481 pellets collected during late July and early August. His findings are given in Table 22.

TABLE 22.

Analysis of 481 pellets of Lesser Black-back Gull from Åland Archipeligo, Finland : from Nordberg. (1950).

FOOD GROUP	TOTAL NO. FOUND	PERCENTAGE BY NO.
Fish	436	58
Crustacea	134	18
Insects	51	7
Molluscs	20	3
Bird chicks	69	9
Mammals	35	5
Vegetation	6	<1

It can be seen that although fish form over half the total diet (58.0%) they are not as important a group as are fish to the birds in the present investigation. The Finnish birds also took Crustacea, Mollusca, Bird chicks and Mammals, which were not found in the diet of the Farne Island birds. It must be noted however that although the remains of bird chicks were not found in any of the samples examined in the present investigation, on two occasions on the Farne Islands Lesser Black-back Gulls were seen to snatch day old chicks of the Eider, (Somateria mollissima) as they left for the sea.

Condor (1952) in an account of the feeding habits of Lesser Black-back Gulls breeding on Skokholm Island off the Pembrokeshire coast, states the main food source to be offal from the fish docks at Milford Haven. Other foods taken were mussels and limpets from the shore, eggs, young rabbits and insects. Unlike the birds of the Farne Islands these gulls took little live fish.

Such differences indicate that the Farne Island area provides exceptionally good feeding grounds for surface feeders, precluding any great diversification of feeding habit, even in those species, such as the Lesser Black-back Gull which are capable of exploiting a wide range of feeding habitats. Condor also stresses the great variation in feeding habits of individual birds, some concentrating on hunting for mussels in littoral areas, some exclusively depending on offal, others on the eggs and chicks of other birds. Nordberg also mentions such individual variation.

Variable feeding behaviour in individuals is also mentioned by Barnes (1952 and 1961) who, in a survey of the status of the Lesser Black-back Gull in Britain, found that the most commonly used food sources were all man-made i.e. rubbish tips, ploughed fields, drain effluents and sewage farms .

Gudmundsson (1955) in describing the food of these birds in Iceland notes their dependence on human settlements where they obtain offal, etc., and also that they take large numbers of insects, insect larvae, and earthworms.

Davis (1956) examined the pellets from a number of Lesser Black-back Gulls roosting in a field in Pembrokeshire and found them to be composed largely of corn husks. He also cites a number of other reports of gulls taking corn.

This brief survey of the literature on the feeding habits of the Lesser Black-back Gull suggests that those breeding on the Farne Islands are by no means typical in their feeding habits, utilizing live fish to an unusually large extent and having a comparatively restricted range of food sources. Thus in July and August, 1960 and 1961, there were apparently sufficient numbers of small fish available in the Farne Islands area to provide the major part of the diet of these birds, perhaps thus inhibiting them from utilizing the no doubt slightly less readily available food sources provided by the other nesting species and the activities of man.

COMPARISON OF THE OVERALL DIET OF THE DIFFERENT SPECIES OF SURFACE FEEDERS INVESTIGATED.

The five sea-bird species so far considered are all surface feeders as opposed to the groups of birds which dive and swim underwater in pursuit of prey.

Comparison of type of food taken.

Table 23 gives a comparative summary of the various types of food taken by the five species, the figures being given as percentage by number. Thus, in all five species, fish form an overwhelming proportion of the total diet, being 98% in the diet of the Kittiwake and the Common and Sandwich Terns. The only species in which other types of food assume any degree of importance is the Lesser Black-back Gull which has 19% earthworms and 5% offal in its diet.

The most important type of fish taken are the sand-eels, (Ammodytidae) forming from 44% of the diet of the Common tern to 81% of the diet of the Kittiwake. Stat-

TABLE 23. Comparative summary of types of food taken by five surface-feeding sea-bird species breeding on the Farne Islands. (as percentages of total numbers taken).

FOOD GROUP	ARCTIC TERN	COMMON TERN	SANDWICH TERN	KITTIWAKE	LESSER BLACK-BACK GULL
FISH (total)	95	98	98	98	74
Ammodytidae	65	44	74	81	55
Clupeidae	22	38	15	10	6
Gadidae	2	1	6	7	13
Gasterosteidae	2	2	2		
Pleuronectidae	<1				
Trachinidae	4	3	<1		
Pholidae			1		
Liparidae			<1		
Anguillidae					<1
CRUSTACEA	2	1	1	1	
CEPHALOPODA	2	1	1		
ANNELIDA					19
INSECTA	1				1
OFFAL				<1	5
VEGETATION					1

istical comparison of the proportion of Ammodytidae taken by each species shows that each species differs significantly ($P<0.01$) from the others in the numbers of the fish taken, the only exception to this being Sandwich Tern and Kittiwake which take 74% and 81% respectively, which is not a significant difference ($P>0.3$). Similarly comparison of the proportions of Clupeidae taken shows significant differences between each species ($P<0.01$) with the exception of the Kittiwake and Lesser Black-back Gull ($P>0.02$). The numbers of Gadidae taken by each species are significantly different ($P<0.01$) except between the Common Tern and Kittiwake ($P>0.05$), Common Tern and Lesser Black-back Gull ($P>0.3$) and Sandwich Tern and Kittiwake ($P>0.5$) which take similar proportions of these fish. An analysis of the comparative importance of the non-fish groups in the diet shows that the Lesser Black-back Gull took significantly more of this type of food than any of the other species ($P<0.001$ in each case), and the Arctic Tern took significantly more than all but the Lesser Black-back Gull ($P<0.001$ in each case). It must be noted however that earthworms predominated in the non-fish items taken by the gulls, whereas the Arctic Terns took crustaceans and cephalopods, thus remaining strictly marine in diet.

It must be stressed that these dietic analyses are based predominantly on data concerning the food of the chicks, the Arctic tern being the only species for which adequate data on the food of the adults was obtained. However, there is no reason to believe that the food of the adults would differ greatly from that of the chicks in the Farne Islands area. The apparent abundance of the small fish taken predominantly by these surface feeding species is such that it is unlikely that the birds would seek alternative food sources for themselves. A possible exception to this would be when these fish are in short supply viz. in May 1962 when it was apparent that many more crustaceans and cephalopods were being taken by the Arctic Terns. Unfortunately no comparative data were obtained for the other species, but it seems probable that they would follow the same trend.

The differences in the proportions of each fish species taken by the various birds may be attributable to their fishing over different areas. As will be described in a later section, each species tended to favour a different feeding area, and it would be expected that the proportions of the various fish species may well differ from place to place. It was impossible to obtain any data on this problem however. It may be, of course, that the different species have specific preferences for a certain species of fish, and take this type, when available, to the exclusion of others. This problem has been discussed previously, with reference to the Arctic Tern, and it seems probable that no specific discrimination of prey in the water is possible, assuming that the fish of the various species are of similar size.

Comparison of size of prey taken.

When the different prey species differ markedly in size there may well be a definite selection on the part of the birds for fish of a certain size range. Table 24 compares the average weights of prey taken by surface feeding species. In some cases, where prey species were observed being taken by birds in the field but no further specimens were obtained for examination i.e. in the case of the Pholidae, and Liparidae taken by the Sandwich Terns, an estimate of weight was made based on the apparent size in the field. Due to the obvious inaccuracy of this procedure, these figures have been omitted from the averages given. The figures demonstrate that there is a progressive increase in the size of fish taken from the Arctic Tern to the Sandwich Tern to the Kittiwake, culminating in the Lesser Black-back Gull which takes on average

TABLE 24. Average weights of prey taken by surface feeding species (in g.).

TYPES OF PREY	AVERAGE WEIGHT OF PREY. Arctic Tern	Sandwich Tern	Kittiwake	Lesser Black-backed Gull
Ammodytidae	0.8	2.1	2.3	2.4
Clupeidae	7.0	4.3	7.1	16.9
Gadidae	6.1	3.2	9.5	38.1
Gasterosteidae	3.2	4.0		
Pleuronectidae	1.8			
Trachinidae	0.6	7.0		
Pholidae		(5.0)*		
Liparidae		(15.0)*		
Anguillidae				12.7
Crustacea	1.6	1.7	0.6	
Cephalopoda	3.3	3.3		
Average weight of all marine organisms taken, taking account of their relative proportions in diets.	2.4	2.6	3.3	6.0

* Estimate of weight based on apparent size.

TABLE 25. Surface-feeding sea-birds. Correlation between average weight of individual marine organism taken, (y), and average weight of bird (x).

SPECIES	Average weight of marine organism taken (g.)	Average weight of bird (g.)
Arctic Tern	2.4	104
Sandwich Tern	2.6	237
Kittiwake	3.3	350
Lesser Black-backed Gull	6.0	854

Regression coefficient (r) = 0.997
Standard error of estimate = 0.102g. prey
Regression equation y = 0.0051x + 1.61

slightly larger fish than the Kittiwake. There is very little difference in the size of crustaceans and cephalopods taken by any of the birds. The overall averages take into account the percentage weight of each species in the diet, thus many more of the small Ammodytidae are taken than of the large Gadidae, hence lowering the overall average size. Very little data was obtained on the size of fish taken by Common Terns, but as has been stated previously there was no significant difference in the apparent size of Ammodytidae taken by Arctic and Common Terns as estimated from observations of fish fed to chicks, and it is probable that there is little difference in the size of the other species taken. Sufficient data was obtained on the Ammodytidae taken by each species to enable a detailed comparison of the size frequencies taken to be made. Figure 5 compares the size frequencies of Ammodytidae taken by the five species, based on totals of all information obtained from measuring specimens and from estimating size ranges in the field. This shows that the Arctic Tern took mostly fish of the 25-50mm. and 50-75mm. ranges, only about 12% of the fish taken being larger. The Common Tern took slightly fewer of the 25-50mm. range and more of the 50-75mm. range than the Arctic Tern, but similarly took few above these ranges. The Sandwich Terns

FIGURE 5.

Size frequencies of Ammodytidae taken by the various surface feeding species investigated.

a. Total of all measured specimens and estimated sizes from observations, in both 1961 and 1962.

b. Measured specimens only.

x = Percentage taken by each species.

y = Length of Ammodytidae taken (mm.).

A = Arctic Tern

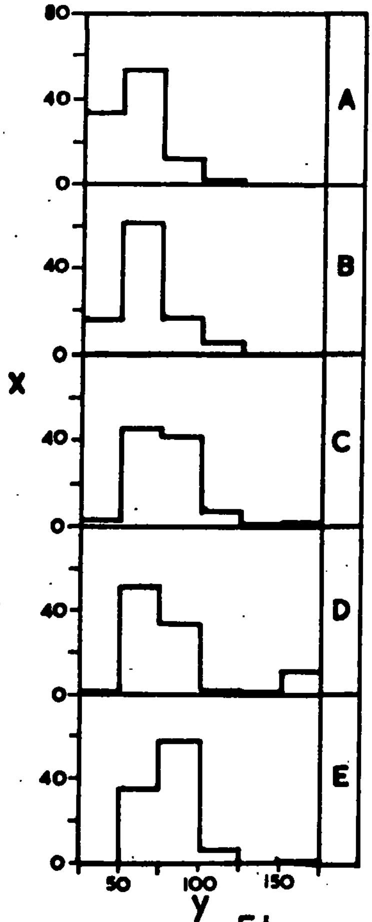
B = Common Tern

C = Sandwich Tern

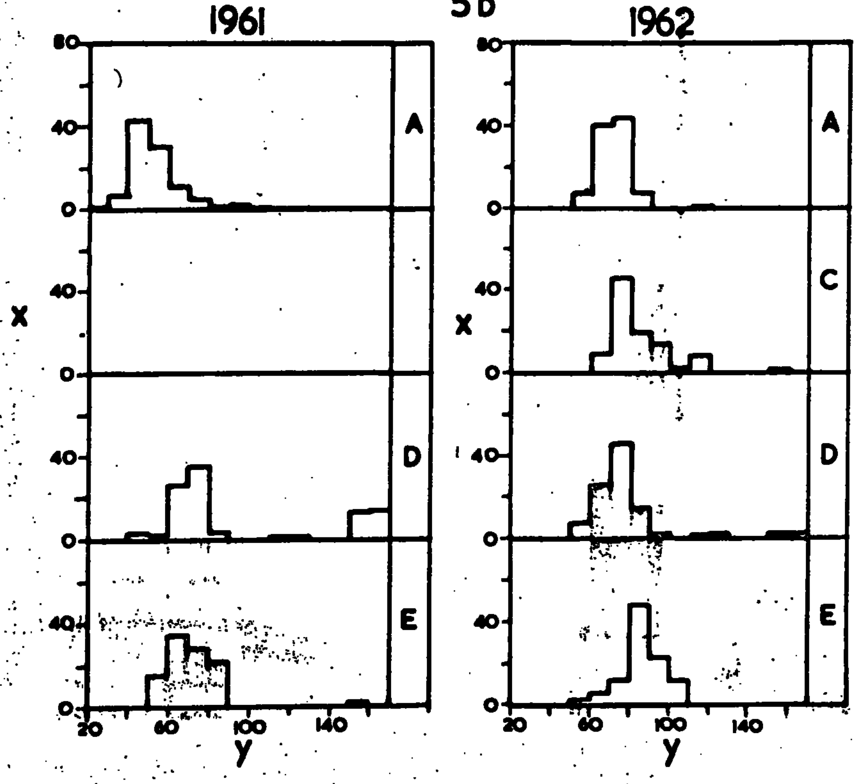
D = Kittiwake

E = Lesser Black-back Gull

5a



5b



took approximately similar proportions of the 50-75mm. range and the 75-100mm. range, but few greater than 100mm. The Kittiwake like the Sandwich tern took mostly fish between 50 and 100mm. in length, but had a number of the larger specimens, over 10% being in the 150-175mm. group. The Lesser Black-back Gull took similar groups to the Kittiwake, but fewer of the large size ranges. The data on which these comparisons are based is given in Appendix B. If an account is taken of directly measured specimens only a more detailed examination of size frequencies can be made. No specimens of prey from Common Terns or from Sandwich Terns in 1961 were obtained for measurement, but comparisons of the size of fish taken by Arctic Terns, Kittiwakes and Lesser Black-back Gulls in 1961 and 1962, and of Sandwich Terns in 1962 can be made. The information is given in Appendix B and diagramatically expressed in Figure 5b. This again shows the tendency for an increase in size of prey taken to occur with an increase in size of the bird. In addition a comparison of the data for 1961 with that of 1962 shows that in the former year all three species for which data was available took smaller Ammodytidae than in the subsequent year. This is almost certainly the results of the Ammodytes available during July, when most samples were taken, being larger in 1962 than in 1961, rather than being caused by a change in selectivity on the part of the bird.

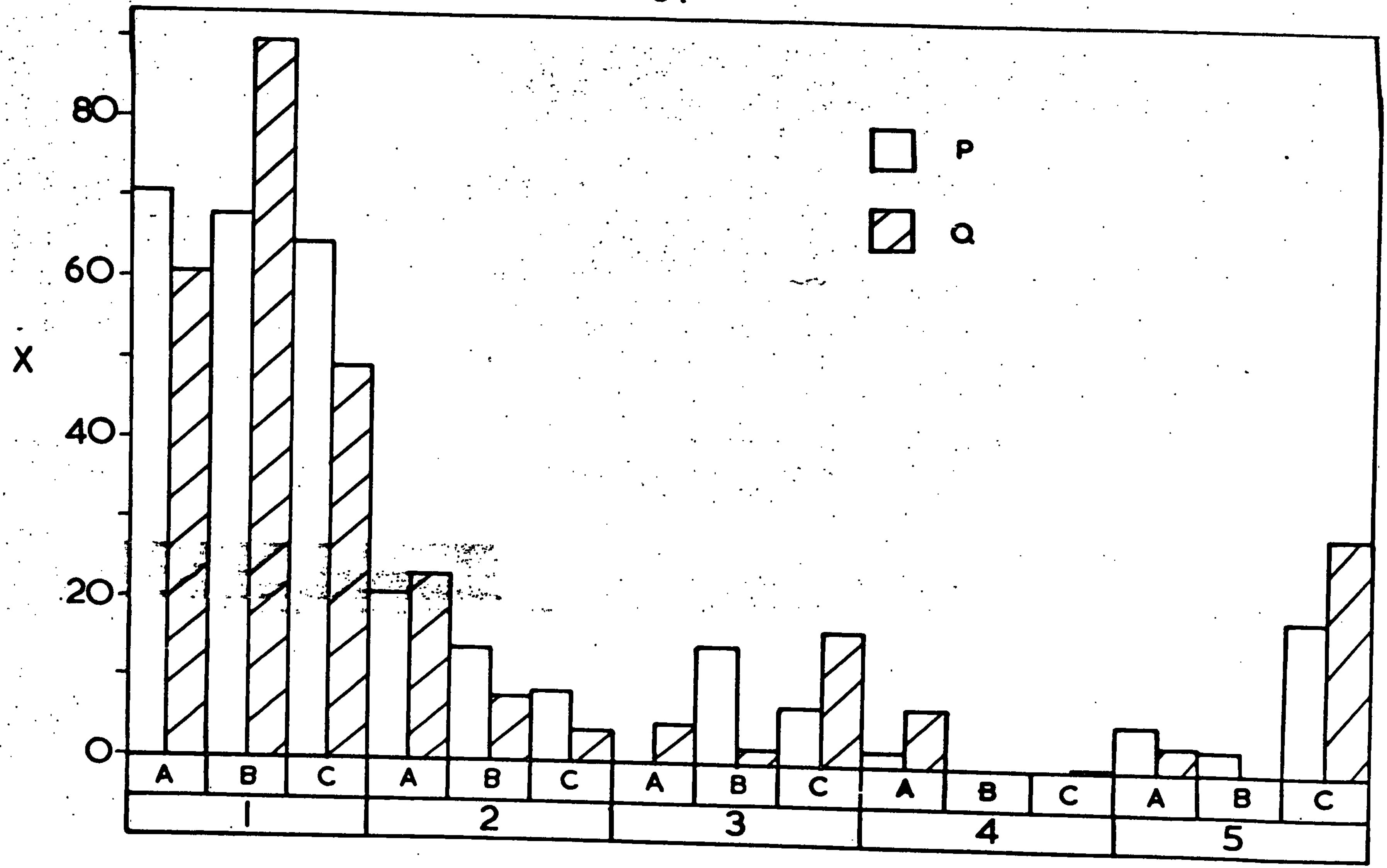
The possibility that there is a direct relationship between the size of bird and the size of its prey appears to arise from the examination of this data. Assuming that the effort involved in obtaining prey is independent of its size, then it would be advantageous for the larger species, having greater food requirements, to take bigger fish than the smaller species. Thus some sort of relationship between size of bird and size of prey would be expected. Table 25 gives the values of these two factors for the four surface-feeding species for which the data was obtained, together with the regression coefficient and the corresponding regression equation relating the factors. A t-test based on the regression coefficient reveals that the correlation is significant at the one percent level (P 0.01 with 2 degrees of freedom). The slope of the regression line (x/y) is 0.0051. It appears therefore that there is a direct relationship between the average weight of the birds and the average weight of prey taken, such that for every hundred grams increase in the weight of the bird the weight of prey taken increased by 0.5g.

Comparison of annual changes in diet.

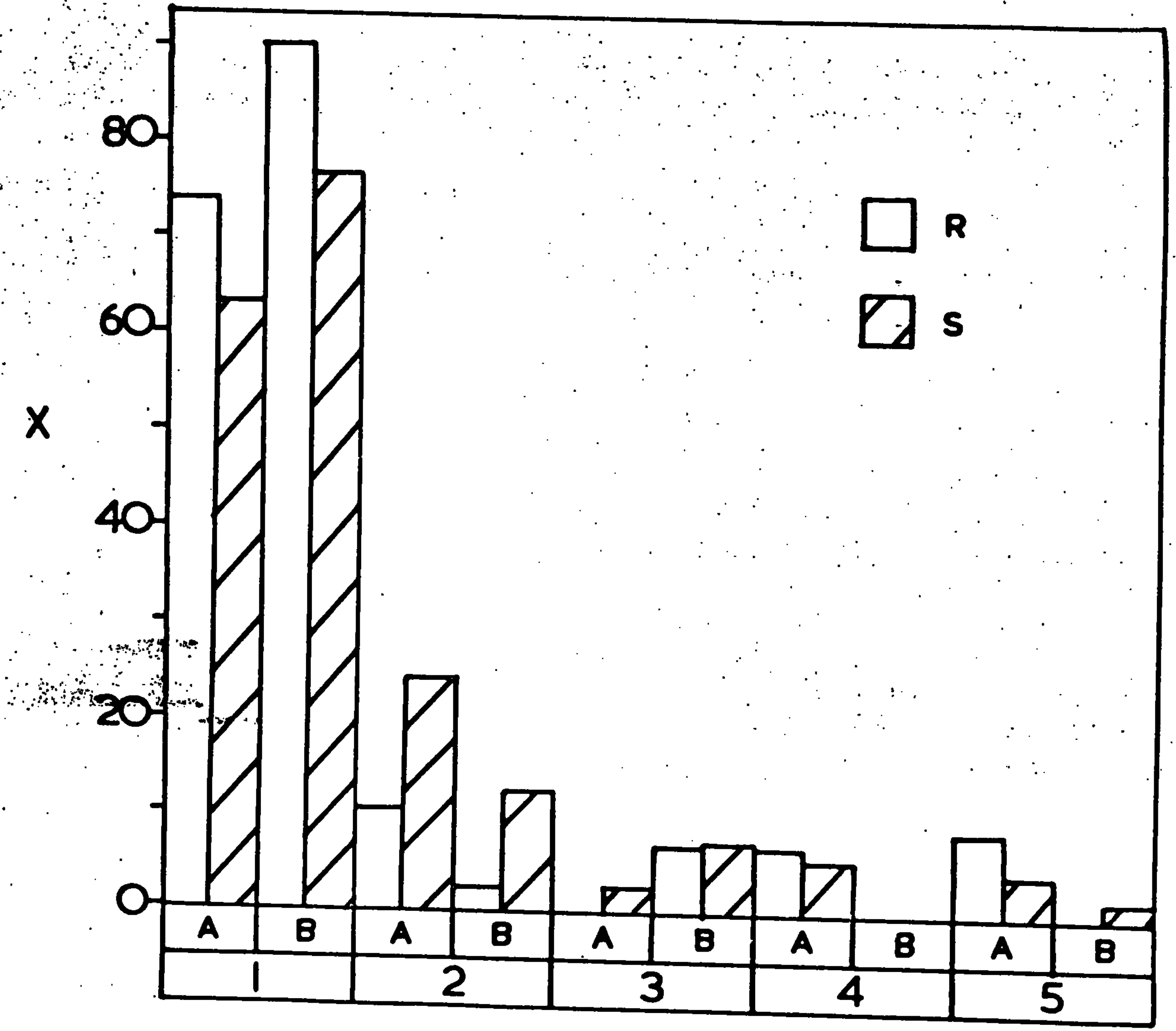
Information concerning the diet in both 1961 and 1962 was obtained for only three of the five species, namely the Arctic Tern, Kittiwake, and Lesser Black-back Gull. Figure 6 compares the diet of these three species over both years.

The differences shown can possibly be explained with reference to the different feeding areas exploited by these species (see subsequent section on Feeding Range). The Kittiwake feeds generally much further out to sea than either the Arctic Tern or the Lesser Black-back Gull, and it may be that there was a relative shortage of sand-eels in the inshore zone in 1962 as compared with 1961, but an abundant supply further out, thus increasing the number available to the Kittiwake, and reducing their availability to the other two species. Certainly in the May and June of 1962 the Arctic Terns were bringing in far greater proportions of fish other than sand-eels, than they were at any time the previous year, and later in the season the gulls were relying to a great extent on earthworms and offal. This would seem to point to a comparative lack of sand-eels in the area over which they normally fished, as compared with the previous year. It is probable that Ammodytes were more abundant, in the off-

6.



7.



shore waters fished by the Kittiwake, in 1962 than in 1961, and that the Gadidae were taken in 1961 only when the Ammodytidae were absent. Such movements of fish must have a very important effect on the breeding success of the birds, although it is probable that in the Farne Islands area marine food organisms are in such abundance that the presence or absence of one particular prey species, even though it is normally the most important, will have no disastrous effect. In areas where a particular prey species is superabundant to the exclusion of other species e.g. certain parts of the Low Arctic where the Capelin (Mallotus villosus), or the High Arctic where the Euphausiacea, are predominant, the failure of that species to arrive in the feeding grounds of the birds may have an injurious effect on the breeding success of the birds (c.f. Belopolskii (1957) page 371).

Seasonal changes in diet.

Insufficient data was obtained for months other than July on the diet of the Sandwich and Common Terns to provide any comparison of dietic variation. Information on the diet of the Arctic Tern covered the months of May, June, and July, on the diet of the Kittiwake the months of June and July, and on the diet of the Lesser Black-back Gull the months of July and August. Thus direct comparison of seasonal variation in diet can only be made between the months of June and July for the Arctic Tern and Kittiwake. Figure 7 shows this comparison, being based on the figures for percentage occurrence by number given in Tables 7 and 17. Both the Arctic Tern and Kittiwake took some 10% fewer Ammodytidae in July than they did in June, and correspondingly more Clupeidae in July. No great difference is shown in the other food-groups taken, except that the Arctic Terns took a slightly smaller percentage of non-fish food in July, and the Kittiwakes a greater percentage. Thus it would seem that there is a decrease in the proportion of Ammodytidae available to surface-feeding birds as the season progresses, and an increase in the relative proportion of Clupeoids available.

2. Diving Sea-Birds.

The diving sea-birds which breed on the Farne Islands fall into two major groups, the Auks, and the Cormorants. The Auks are primarily mid-water feeders, generally hunting fish from the surface down to 10 or 15 fathoms, whereas the Cormorants tend to exploit the bottom-living fish as is seen from the type of prey taken. A further major difference, as is shown below, is found in the size of fish taken, the Cormorants taking, on the whole, far larger prey than the Auks. For convenience, these two groups of birds will be dealt with separately.

THE AUKS.

Three species of Auk breed on the Farne Islands viz. the Puffin, the Guillemot and the Razorbill. Of these the first two species are numerous, there being thousands of breeding pairs on the islands, whereas there are only a few pairs of Razorbills.

<u>The Puffin.</u> <u>Fratercula arctica.</u>

The Puffins breed in burrows dug into the soft peat which covers the tops of the islands. Numbering at least 15,000 pairs they are the most numerous of the sea-birds breeding on the Farne Islands. Puffins may dive to considerable depths, but it is probable that the major part of their hunting activities take place between the surface and a depth of from 15 to 20 metres. Meinertzhagen (1959) states that the Puffin fishes in shallow water when feeding young, but in winter they will fish in water over 100 fathoms deep. He gives the usual time spent submerged as between 24 and 31 seconds, with occasional dives lasting as long as 58 seconds. The Farne Islands' Puffins frequent fishing grounds well out to sea, and are infrequently observed fishing within sight of the islands. In mid-July however, during the time of greatest abundance of the sand-eels, when these fish form huge shoals close to the surface in the immediate vicinity of the islands, Puffins, together with many other species of fish-eating birds, may be observed in large numbers diving into the shoals and taking fish from just below the surface. As many as a dozen fish at a time have been observed in the bill of a Farne Islands' Puffin. Myrberget (1962) when studying Puffins at Lovunden, North Norway, found individuals carrying loads of 10 or 11 fish, but states the average load to be 5 fish. This agrees well with the results obtained from the present observations. Lockley and Burton however record that the Puffins on Skomer bring in as many as 20 fish at a time. The fish are held crosswise in the bill between the tongue and the upper mandible. Gibson-Hill (1947) and Seebohm (1896) state that young chicks are fed regurgitated food at first. Myrberget (1962) states however that he found no evidence of this, and concludes that fish are placed on the floor of the burrow for the young to pick up. Meintzerhagen describes the process of feeding the fish to the young as follows:- "The fish were presented to the chick who took the one nearest the tip of the mandible first, then the second, then the third until the whole of one side was exhausted. A similar act of acceptance was then performed on the other side of the mandible commencing at the tip and working to the gape". It was never possible to observe such feeding behaviour during the present study. Attempts to prepare burrows for observational purposes invariably resulted in the desertion of the adults.

Accurate assessment of the diet of Puffins proved to be difficult. Neither the young nor the adults regurgitated on handling, and it was difficult to observe and identify with any accuracy fish carried in the beak, due to the rapid flight of the birds and their habit of rapidly entering the nesting burrow when bringing in food. Only rarely did a bird with a load of fish hesitate at the burrow entrance or walk about in the vicinity. The only reliable method of collecting food samples was by scaring the adult birds as they approached the burrow, thus causing them to drop the fish, or by erecting nets across the colony in order to trap incoming birds. The latter method was most frequently used as it proved more productive in terms of fish obtained, in addition to allowing the trapped birds to be measured and examined. In addition fish were occasionally found lying uneaten in burrows containing the chicks which were being regularly weighed.

TABLE 26. Analysis of complete loads of fish taken from individual birds in July, 1962. (Weights in g.)

No. of fish in load.	No. of loads observed	Av. total wt. of fish/load	Av. wt. of indiv. fish	Extremes
1	2	4.5	4.5	4.0-5.0
2	3	4.0	1.9	1.7-2.5
3	7	4.5	1.4	1.1-2.2
4	1	9.3	2.3	1.9-3.2
5	10	10.6	2.1	0.4-9.6
6	2	3.5	0.6	0.3-0.7
7	4	18.0	2.8	0.8-17.1
8	3	10.5	1.3	0.5-2.2
9	1	5.0	0.5	0.4-0.7
10	0			
11	0			
12	1	16.6	1.4	0.7-2.2
Totals Overall Average	34	8.6	1.9	0.3-17.1

Overall average no. of fish/load = 5.

TABLE 27. Analysis of diet of Puffins, 1962.

No. of Samples	SPECIES	No.	% by No.	Wt.	% by Wt.
42	Ammodytidae	168	82	295	83
	Clupeidae	4	2	42	12
	Trachinidae	31	16	18	5
	Totals	203		355	

TABLE 27A. Analysis of diet of Puffins, 1961.

No. of Samples	SPECIES	No.	% by No.	Wt.	% by Wt.
10	Ammodytidae	14	87	26	64
	Gasterosteus spinachia	2	13	14	36
	Totals	16		40	

ANALYSIS OF FISH SAMPLES COLLECTED.

No attempts were made in 1961 to obtain fish from adult birds but a number of samples were obtained of uneaten fish from burrows. In 1962 thirty four full loads of fish were obtained from adult birds either by scaring the birds or by catching them in nets as explained above. Table 26 analyses the number and size of fish per load. This shows that the average number of fish per load was 5, the average weight of fish per load 8.6g., and the average weight of individual fish 1.9g. As might be expected there is a tendency for the larger loads of fish to be composed of smaller individuals. However in some cases, notably in the loads of 7 fish recorded, numerous large individuals were carried. These were usually Clupeoids, whereas most of the fish taken were the smaller Ammodytes. In the very large loads of 8, 9, and 12 fish, the fish were small Trachinidae, approximating to half a gram weight each, leavened by a few small Ammodytidae. In each case where a bird was caught carrying a single fish it was always a large sand-eel.

Table 27 analyses the fish taken during the above investigation in terms of the different species. These figures include a further sample of fish obtained from burrows, but not included in the above analysis. These numbered thirty-eight specimens obtained from eight different burrows.

In 1961 sixteen fish were collected from ten different burrows. Data on these is given in Table 27A. All samples were collected in July, thus no estimate of seasonal differences in diet can be made.

As has been described previously, it was found impossible to distinguish the Ammodytidae as to species. A few of the larger specimens were positively identified as Ammodytes lanceolatus, and a few more tentatively as Ammodytes lancea (=tobianus). The majority however were young juvenile specimens which were impossible to place specifically with any confidence. The Clupeidae taken were all Clupea sprattus, and the Trachinidae were young post-larval stages of Trachinus vipera.

DIRECT OBSERVATION RESULTS.

Although it proved difficult to observe and identify accurately fish being carried in the bills of Puffins before they vanished into their burrows, there were always a few birds which wandered about the colony with loads of fish without going to a particular burrow. However during watches from a hide at the colony site some information was obtained by noting the loads carried by such birds. This is given in Table 28.

TABLE 28. Direct observation on fish carried by Puffins. 1962.

No. of loads observed	Fish Species	No.	% by No.	Wt.*	% by Wt.
7	Ammodytidae	37	95	65	75
	Clupeidae	2	5	21	25

* Weights here are estimates based on the average weight of individuals collected.

SIZE OF FISH TAKEN BY PUFFINS.

Figure 8 shows the length range frequencies of Ammodytidae taken by the Puffins. Most fish taken were between 60 and 90mm. in length with a few as large as 150mm. in length being taken, but none unde r 50mm. long. The Clupeidae taken ranged from 80 to 134mm. in length (weight 4.0 to 17.1g.) and the Gasterosteidae from 129-148mm. (5.6 to 9.2g.). The young <u>Trachinus vipera</u> taken were very small, being from 25 to 43mm. in length (0.3 to 0.7 g. weight). The data on which Figure 18 is based is given in Appendix B.

The information obtained from all sources is combined in Table 29 to give an analysis of average diet of the Puffins.

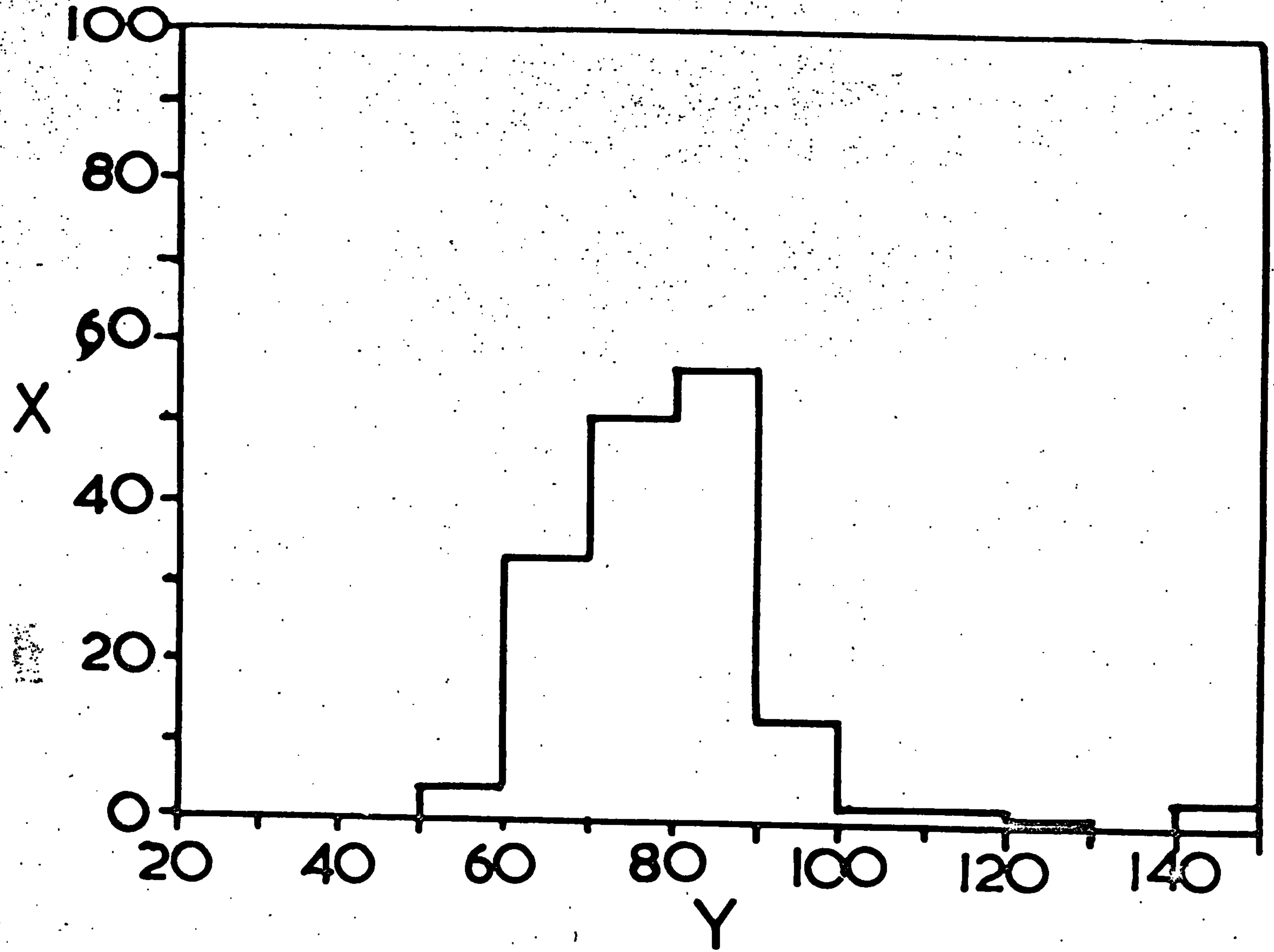
As all the specimens obtained were of fish about to be offered to the chicks or obtained from chick-occupied burrows the information so obtained relates only to the

FIGURE 8.

Length frequencies of Ammodytidae taken by Puffins.

x = Number of each length group taken.

y = Length (mm.).


100
80
60
40
20
0
X
20
40
60
80
100
120
140
Y

diet of the chicks. The adults feed as they catch their prey, and thus no information can be obtained as to their diet, without shooting them, a procedure which was impossible during the present study.

It would appear that the Puffins on the Farne Islands feed exclusively on fish, no other type of organism having been found to be taken. This agrees with the observation of Myrbergot (1962) who found the Puffins in North Norway to be feeding their young exclusively on fish. Over eighty percent of the fish taken were Ammodytidae, with only small numbers of Clupeidae, Gasterosteidae and Trachinidae being taken in addition.

The size of fish taken is probably also dependent to a large extent on the type of fish available at the time of hunting, although it is more probable that there is some selectivity on the part of the bird in this case. The limits to the size of fish the Puffin is able to take are probably represented at one end of the scale by the young Trachinidae of less than half a gram weight, and at the other by the large Sprats of nearly 20g. It is possible that birds which hunt their prey under water do not maintain as rigid a selectivity over size of prey as do the surface feeding birds. Thus any fish which comes within the fairly wide limits set by the capacity of the

TABLE 29. Average diet of the Puffin. (Wt. in g. Based on average wt. of specimens taken if no direct figures available.)

No. of Samples	SPECIES TAKEN	ANALYSIS BY NO. No.	ANALYSIS BY NO. %	ANALYSIS BY WT. Wt.	ANALYSIS BY WT. %
59	Ammodytidae	219	85	386	80
	Clupeidae	6	2	63	13
	Gasterosteidae	2	1	14	3
	Trachinidae	31	12	18	4
	Totals	258		481	

TABLE 30. Analysis of published records of the diet of the Puffin, in terms of the major food groups taken.

AUTHORITY	FOOD GROUP: FISH	MOLLUSCA (mainly Cephalopoda)	CRUSTACEA	ANNELIDA
Present work Farne Islands	****			
Collinge (1925) Great Britain	**	*	***	
Myrbergot (1962) North Norway	****			
Gudmundsson (1953) Iceland	****			
Salomonsen (1950) Greenland	***			*
Upenski (1950) Novaya Zemlya Barents' Sea	***			***
Bolopolskii (1957) Barents' Sea General	***	*	*	*
Seligman & Willcox (1940) Jan Mayen	***	*	*	

**** Taken exclusively
*** Very important
** Moderately important
* Occasional

back may be taken by the Puffin, whereas the terns or Kittiwake may be more selective in diving for a particular size of prey. The size of fish taken by the slightly larger Puffins in North Norway was found by Myrberget to be similar to those taken by Puffins on the Farne Islands. Thus in Norway the Ammodytidae taken ranged in length from 44 to 129mm., and had an average weight of 1.50g., whereas on the Farnes the limits were 50 to 150mm., and the average weight was 1.9g.

COMPARISON WITH PREVIOUS WORK ON THE DIET OF THE PUFFIN.

It was found that the young Puffins were fed exclusively on a fish diet, and there are a number of references in the literature which support this observation. Both Lockley (1934) for the Puffins on Skomer, and Perry (1940) for those on Lundy, found the young to be fed on small fish, chiefly sand-eels. Myrberget (1962) found young Puffins at Lovunden North Norway to be fed exclusively on fish, and Belopolskii (1957) notes that in the Barents' Sea area the young are fed on fish alone, whereas the adult Puffins take only 87% fish in their diet. Other references to the food of adult Puffins indicate that they are by no means restricted to fish in their diet. Table 30 summarizes the published records on the diet of the Puffin in various parts of it's range. The records from the present work, and of Myrberget and

Gudmundsson are from chicks, and the others from adult birds. It would appear that in the more northerly areas a greater range of food groups are exploited, probably due to fish being less readily available in such areas. The type of fish taken varied from area to area. Table 31 shows the figures given by Belopolskii for different regions of the Barents' Sea, together with the figures given by Myrberget for the fish taken by Puffins at Lovundon, North Norway, and the data from the present study. This indicates that the role of sand-eels in the diet of the Puffin decreases in importance progressively to the north and west, the lowest numbers being taken in the Western Barents' Sea, whereas the proportions of Clupeoids and Capelin taken increase. The small proportions of Trachinidae and Gasterosteidae taken on the Farne Islands do not occur elsewhere, and the Capelin is not taken outside the Barents' Sea area. These differences reflect to some extent the relative occurrence of these types of fish in the areas investigated. Thus the Capelin is not found outside the Arctic Seas, whereas the Trachinidae and Gasterosteidae are confined to temperate areas. The Ammodytidae extend to some parts of the low Arctic but are not as numerous in these areas as in the temperate parts of the North Sea. Herring, however, are numerous throughout the low Arctic area.

Both Belopolskii and Myrberget comment on the seasonal variation in the diet of the Puffin. Belopolskii states that "During the spring the Puffin adds a number of secondary foods to its basic fish diet, consisting primarily of pelagic crustaceans and Polychaetes. Toward the end of summer, the Puffin turns entirely to fish. At the same time, it varies its consumption of certain fish species". He shows that in June the sand-eels account for over 50% of the fish taken, but fall off to under 40% in August. The percentage of Capelin taken also falls from 35% in June to about 20% in July, with none being taken in August. The Clupeoids increase from 10% in June to over 45% in August, and a small number of Gadidae are taken in August, but none previously.

Myrberget also comments on seasonal variation in the fish taken, the results being similar to those of Belopolskii. The sand-eels taken fell from 77.3% in early July to 44.9% in late August. Whereas the Clupeoids taken increased during the same period from 8.0% to 52.8%. In Norway however 12% Gadoids were taken in early July, but only 1% in late August, the reverse of the situation in the Barents' Sea.

Such changes in the diet of the Puffin over the summer months must reflect the changes taking place in the waters fished. Thus some surface living fish species are prominent in the early summer, only to be superceded later by different species. Thus the Ammodytidae appear to reach their peak abundance a month earlier than the Clupeiods in the areas investigated.

Guillemot. Uria aalge

The Guillemots breed mostly on the outer islands of the Farne Island group. Approximately 1100 pairs breed on the tops of "the pinnacles," a group of high, rock stacks isolated from the main islands. In addition a further 100-150 pairs are scattered on the main islands. On the Inner Farne, where the major part of this study was carried out, little more than half a dozen pairs breed, and as there were few opportunities to visit the outer islands, the information obtained concerning the feeding biology of this species was restricted.

Guillemots swim, and hunt their prey, in the same manner as do the Puffins. Meintzerhagen (1959) timed a number of birds diving and gives the time submerged as being between 20 and 62 seconds, the average being about 40 seconds, but when scared he noted birds staying down as long as 92 seconds. Madsen (1957) notes the general

TABLE 31. Comparison of diet of Puffin (fish only) in the Barents' Sea, North Norway and on the Farne Islands.

PERCENTAGE OCCURRENCE (of total no. of fish taken)

SPECIES TAKEN	Seven Islands (East Murman) Barents' Sea 100 stomachs.	Ainovy Islands (West Murman) Barents' Sea 39 stomachs.	Lovunden North Norway (89 loads)	Farne Islands (59 loads)
Ammodytidae	56.8	6.3	73.3	84.9
Clupeidae	19.7	50.0	22.1	2.3
Gadidae	2.5	-	4.6	-
Capelin (*Mallotus villosus*)	21.0	43.7	-	-
Trachinidae	-	-	-	12.0
Gasterosteidae	-	-	-	0.8

Barents' Sea. Information from Belopolskii (1957)
Lovunden. Information from Myrbergot (1962)
Barents' Sea. Information based on analysis of stomachs.
Lovunden and Farne Island. Information based on counting loads of fish brought to young.

TABLE 32. Average diet of the Guillemot. (Wt. in g. Based on average wt. of specimens taken if no direct figures obtained).

	Analysis by No. No.	%	Av.Wt.of Indiv.	Analysis by Wt. Wt.	%
Ammodytidae	41	49	10.5	367	57
Clupeidae	35	42	5.9	196	30
Pholidae	4	5	5.0*	20	3
Gadidae	3	4	20.0*	60	9
Totals	83			643	

* No specimens obtained - weight estimated from apparent size.

TABLE 33. Guillemot. Size frequency of Ammodytidae taken. (Length in mm.)

SIZE RANGE(mm.)	NO.	SIZE RANGE(mm.)	NO.
71-80	1	131-140	2
81-90	1	141-150	3
91-100	0	151-160	0
101-110	0	161-170	0
111-120	1	171-180	2
121-130	6	181-190	1

depth of fishing to be 4 to 5 metres, and states that they reach the bottom at least to 8 metres. Like the puffins, the Guillemots utilize feeding areas well out to sea away from the breeding colonies. During the times when sand-eels are shoaling about the islands however, they can be seen preying on these shoals, as do most of the other species, though under those conditions relatively few fish within sight of the islands.

ANALYSIS OF DIET.

In 1962, 27 fish were picked up from breeding ledges in fresh condition. All were obtained in July, and were Ammodytidae or Clupea sprattus and Clupea harengus. In addition during the count, made in 1962, of the fish being brought to the chicks, Gadidae and Pholis gunnellus were identified, together with the Ammodtyidae and Clupeidae. Table 32 gives an analysis of the diet based on both the count and the specimens obtained.

Table 33 shows the length range frequency of Ammodytidae taken. The majority of these fish were between 120 and 150mm. in length, the average being 143mm. Most of the Clupeidae taken were between 85 and 95mm. long, the average being 94mm. On average the Ammodytidae taken weighed twice as much as the Clupeidae (10.5g. as opposed to 5.9g.)

As all the specimens recorded were either dropped by, or fed to, the chicks, this dietic analysis refers only to the food of the young, and not to that of the adults. Both Upenski (1950) and Belopolskii (1957), when investigating the food of the Common Guillemot in the Barents' Sea, found little difference between the food.

TABLE 34. Analysis of the major prey groups in the diet of the Guillemot according to various authors.

		MAJOR PREY GROUPS			
AUTHORITY	AREA	FISH	MOLLUSCA	CRUSTACEA	ANNELIDA
Collinge (1925)	Gt.Britain	***	*	**	**
Perry (1940)	Gt.Britain	****		*	*
Gibson - Hill (1945)	Gt.Britain	**	*		
Buxton & Lockley (1950)	Gt.Britain	****			
Madsen (1957)	Denmark	****			
Dent (1919)	Eastern North America	***		*	
Storer (1952)	California	****			
Salomonsen (1935)	Faeroes	****			
Tunig (1935)	Iceland	****			
Salomonsen (1935)	Iceland	****			
Belopolskii (1957)	Barents' Sea	***	*	*	*
Upenski (1950)	Barents'Sea	***	*		
Heath (1915)	South Alaska	***		*	
Preble & McAtee (1923)	Pribiloff Islands	*		***	
Sergeant (1950)	Bear Island N.Atlantic				***

**** Only item in diet.
*** Over half of diet.
** Frequently taken.
* Occasional.

COMPARISON WITH PREVIOUS WORK ON THE DIET OF THE GUILLEMOT.

Table 34 presents a summary of previously published accounts of the diet of the Guillemot, in terms of the major food groups taken. It would seem that in nearly all areas fish form an overwhelming proportion of the diet. The exceptions appear to be in the Pribiloff Islands, where crustaceans are of major importance, and Bear Island, where Annelids (Polychaeta) are the most important item. In general the small nektonic types of fish are taken exclusively, particularly Ammodytidae and young Clupeoids, but Mackerel and Capelin are also said to assume importance in those areas where they are available. In Northern areas (Iceland, the Faeroes, and the Barents' Sea) Cod species (Gadidae) are also taken fairly widely.

THE CORMORANTS.

Two species of Cormorant breed on the Farne Islands. These are the Shag, or Green Cormorant, and the Common Cormorant.

<u>The Shag.</u> <u>*Phalacrocorax aristotelis*</u>.

The Shags breed on wide cliff ledges around the islands, generally in colonial groups. Approximately 440 pairs breed on the Farne Islands, mostly in large colonies on the outer islands. When swimming underwater the Cormorants differ from the Auks in that they do not use their wings, but swim by simultaneous strokes of both feet. Lumsden and Haddow (1946) give a detailed description of the feeding habits and fishing methods of the Shag.

In timing a series of dives they found the average time submerged when hunting to be 1[illegible] seconds. During the present study the average time submerged was found to be 30 seconds, and Buxton and Harkness (1937) in timing 54 dives found the average duration to be 54 seconds.

The Shags tend to feed close inshore, within site of the islands on many occasions. Communal feeding behaviour is a common feature of their fishing activities. The birds tend to leave the colonies in long lines in the early morning and proceed to the fishing areas where they form large rafts of actively fishing birds. The formation of such fishing groups seems to be generally proceded by single birds, or small groups widely scattered, fishing in such areas, and it is probable that signs of successful fishing are immediately seen and followed up by the main group. On the other hand it seems apparent that there are regular feeding grounds round the islands, which are constantly frequented. These areas change with the state of the tide, and also with the prevailing weather conditions. Generally patches of roughened water, such as the tide rips, are much favoured. As with the Arctic Terns, this is probably because such areas provide both a greater chance of catching fish, and a greater number of fish. It is also probable that in such turbulent areas the shoaling behaviour of small fish is inhibited, which would increase the chances of the individual fish being caught. The young are fed by regurgitation. The head of the young Shag is inserted well into the mouth of the parent, and the regurgitated food taken from the upper part of the gullet. It is thus impossible to observe what type of fish is being fed to the young. The collection of regurgitation samples was thus the only available means of investigating the diet of the living birds. It was found however that neither the adult birds, nor the young, would regurgitate readily on capture, and only rarely was it possible to obtain samples. A number of shot birds were obtained from the estuary of the River Tweed at Berwick, and stomach analyses were carried out on these specimens.

ANALYSIS OF REGURGITATION SAMPLES.

In all 12 samples were collected in 1961 and 12 in 1962. The composition of these samples is detailed in Table 35. All samples were collected in July other than one taken in August in 1961, and one in June in 1962.

TABLE 35. Analysis of regurgitation samples from Shag.

a) 1961.

SPECIES	No.	% by No.	Wt.	% by Wt.	Av.Wt.of Indiv.taken
Ammodytidae	68	94	195	77	5.47
Gadidae	4	6	60	23	44.25
Totals	72		255		

b) 1962.

SPECIES	No.	% by No.	Wt.	% by Wt.	Av.Wt.of indiv.taken
Ammodytidae	131	100	452	100	5.22

Each sample invariably contained a number of fish, most of which were both battered and partly digested. This did not facilitate identification to species level, but it proved relatively simple to identify the specimens as to family, as shown in the table.

STOMACH ANALYSES OF DEAD SPECIMENS.

In all 28 dead birds were obtained, all of which were shot during mid-morning in the estuary of the Tweed on various dates during the Autumn and Winter of 1960 and 1961. Table 36A shows the data obtained by analysis of the stomach contents, in relation to the dates on which the birds were shot. It can be seen that there was considerable variation in the type of food taken on the different days. Table 36B gives a total of all the in-

TABLE 36. Stomach analysis of Shags.

a) According to date shot.

SPECIES	18/10/60 21 Birds		15/1/61 5 Birds		26/10/61 2 Birds	
	No.	%	No.	%	No.	%
Ammodytidae sp. indet.	2	4	81	99		
Pholis gunnellus	28	53			1	8
Gadidae sp. indet.	10	19				
Pleuronectes flesus					6	50
Zoarces viviparous	1	2			5	42
Cottus bubalis	5	9				
Blennius pholis	2	4				
Serranidae sp. indet.	1	2				
Clupeidae sp. indet.			1	1		
Salmonidae sp. indet.	1	2				
Crustacea	3	6				
Totals.	53		82		12	

b) Total stomach analysis. 1961.

SPECIES	No.	% by No.	Wt.	% by Wt.
Ammodytidae sp. indet.	83	57	671	30
Pholis gunnellus	29	20	231	10
Gadidae sp. indet.	10	7	839	37
Pleuronectes flesus	6	4	62	3
Zoarces viviparous	6	4	121	5
Cottus bubalis	5	3	105	5
Blennius pholis	2	1	20	1
Serranidae sp. indet.	1	1	50	2
Clupeidae sp. indet.	1	1	10	<1
Salmonidae sp. indet.	1	1	150	7
Crustacea	3	2	5	<1
Totals.	147		2264	

formation as to total numbers and weight of prey. The sizes of the various species taken are given in Table 37. In some cases when very few individuals of a species were present there were no specimens in a complete enough state to permit accurate estimation of their original size.

TABLE 37. Size ranges of prey species taken. Stomach analysis of Shags.

SPECIES	No. of Specimens	LENGTH (mm.) Average	LENGTH (mm.) Extremes	WEIGHT (grams) Average	WEIGHT (grams) Extremes
Ammodytidae sp.indet.	62	102.5	43-190	8.1	0.6-21.5
Pholis gunnellus	27	140.4	85-210	7.9(estimated)	
Gadidae sp.indet.	5	210.4	180-262	158.3	150.5-170.0
Pleuronectes flesus	6	93.7	25-125	9.2	7.5-18.0
Zoarces viviparous	5	172.0	130-210	24.2	11.0-45.0
Cottus bubalis	5	82.0	50-105	21.0	10.0-30.0
Blennius pholis	2	150.0	105-195	10.0(estimated)	
Serranidae sp.indet.	1			50.0(estimated)	
Clupeidae sp.indet.	1			10.0(estimated)	
Salmonidae sp.indet.	1			150.0(estimated)	
Crustacea	3			1.6(estimated)	
Overall Average Weight				40.9	

* Only complete specimens, or those complete enough for a reasonable estimate of their original length and weight to be made, were taken into account in the table.

When this was the case rough estimates were made of the probable weight of the original specimen(s), these estimates being noted in the table. It can be seen that the largest fish taken were the Gadidae, being on average 210 mm. long and 158 g. in weight. Specimens of both Gadus merlangus and Gadus morrhua were taken, but in most cases, the specimens were identifiable only as to family, being too battered to distinguish the species. This was also true of the single specimens of Percidae, Clupeidae, and Salmonidae which were taken, which were present only as fragments. The smallest fish taken were Flounders, *Pleuronectes flesus*, being on average 94mm. long and 9g. in weight. The crustacea taken were all small, and badly damaged. It is possible that these were not taken directly by the birds, but were from the stomachs of the fish.

SIZE RANGES OF AMMODYTIDAE TAKEN BY THE SHAGS.

Table 38 shows the frequency of occurrence of the various length groups among the Ammodytidae taken by Shags. Only those specimens which could be accurately measured, or for which a reasonable estimate of original length could be made, were grouped. The data shows that in the summer of 1961 few small sand-eels were taken, the majority of fish caught being between 90 and 120mm. long. In the summer of 1962 however a number of fish ranging between 50 and 90mm. in length were taken, together with a number of larger size, between 100 and 140mm. During the winter months of 1960-61 no fish of a particular size group were taken predominantly, small numbers of every group from the smallest to the largest being present.

TABLE 38. Length frequencies of Ammodytidae taken by Shags.

Length (mm.)	SPECIMENS FROM REGURGITATION SAMPLES Summer 1961	SPECIMENS FROM REGURGITATION SAMPLES Summer 1962	SPECIMENS FROM STOMACH ANALYSIS Winter 1960-61
41-50	0	1	1
51-60	0	6	7
61-70	0	6	3
71-80	1	26	11
81-90	9	11	7
91-100	8	1	6
101-110	24	20	5
111-120	13	13	8
121-130	5	11	7
131-140	1	12	6
141-150	1	4	6
151-160	2	1	5
over 160	3	5	4

AVERAGE DIET OF THE SHAG.

All the information obtained, both from stomach analysis (winter months) and from regurgitation samples (summer months) is combined to give the average data reproduced in Table 39. As stated before the weights are based on estimations where the specimens obtained were too fragmentary to permit adequate measurement. Where possible the average weights of individuals of each species are based on whole specimens only, but in those cases where few specimens were available, and those damaged, the weights are necessarily estimated.

The information obtained indicates that, in the Farne Island and Berwick areas, the Shags feed almost exclusively on fish, taking 99.1% by number or 99.8% by weight of this

TABLE 39. Average diet of the Shag. (Weight in g.)

	No.	% by No.	Wt.	% by Wt.	Av. wt. of indiv. taken
Ammodytidae	282	81	1318	44	6.7
Pholis gunnellus	29	8	231	8	7.9
Gadidae	14	4	899	30	128.9
Pleuronectes flesus	6	2	62	2	9.2
Zoarces viviparous	5	1	121	4	24.2
Cottus bubalis	5	1	105	3	21.0
Blennius pholis	2	1	20	1	10.0
Serranidae	1	<1	50	2	50.0
Clupeidae	1	<1	10	<1	10.0
Salmonidae	1	<1	150	5	150.0
Crustacea	3	1	5	<1	1.6
TOTALS	349		2951		

Overall average weight 37.9

type of food. The only other food group appearing were crustacea, but these were a dubious record being probably derived from the stomachs of fish taken by the Shags. Both Collinge (1925) and Steven (1933) also found the diet of the Shag to consist almost entirely of fish. Lumsden and Haddow however, found that the Shags in the Clyde sea area took 7.2% (by number) crustaceans and a small number of worms and molluscs in addition. Table 40 compares the amount of fish taken by the Shag, as found by these workers. For the purposes of comparison each regurgitation sample taken during the present work is taken as representing the stomach contents of one bird. It would seem that the Shags are almost entirely dependent on fish in all areas. It is notable, however, that Lumsden and

Haddow found a higher percentage of crustaceans (up to 16%) being taken by birds feeding over rocky bottoms than by those feeding over sandy or muddy bottoms.

SIZE OF FISH TAKEN.

The great variation in size of fish taken by the Shag emphasizes the flexibility of its diet, fish varying in length from 0.6mm. to 170mm. being taken. It would seem that any fish present in the hunting area is taken by these birds, and that there is little selection of individuals of a particular size.

The variation in the sizes of Ammodytidae taken during the summers of 1961 and 1962 are interesting. It would seem that fish of two distinct age groups, or of two different species, were being taken in 1962, whereas only one group was taken in the previous year. It is possible that the specimens were all _Ammodytes lancea_, which has two races, one spawning in the spring and the other in the autumn. (Cameron unpublished thesis). This data given by Cameron indicates that _Ammodytes lancea_ spawning in autumn would have reached a length of between 105 to 115mm. by the following July, whereas those spawning in the spring of the year would have reached a length of between 58 and 75mm. These size ranges correspond fairly closely with the two groups of sizes of Ammodytidae

TABLE 40. Diet of Shag. Major food groups taken according to different workers.

FOOD GROUP	Collinge (1925) (see Britain)	Steven (1933) (Cornish coasts)	Lumsden & Haddow (1946) (Clyde Sea)	Present work (Farne Islands)
Fish	96.4	98.3	92.1	99.1
Crustacea	-	1.7	7.2	0.9
Annelida	-	-	0.6	-
Mollusca	-	-	0.1	-
Others	3.6	-	-	-
TOTALS	100.0	100.0	100.0	100.0
No. of birds on which investigation based.	?	188	81	52

taken by the Shags in 1962. On this basis the fish taken in 1961 represent only the autumn spawning race of _A. lancea_.

The fish taken by the Shags are nearly all bottom-living types, other than the Ammodytidae. The sand-eels taken were generally of the medium-sized range (100-150mm.) which are usually found at depths between three and ten metres (Meek, 1916). It would seem, therefore, that the Shags generally hunt from the mid-waters to the bottom.

TABLE 41. Comparison of the diet of the Shags.

SPECIES TAKEN	PERCENTAGE OF TOTAL NUMBERS FOUND. STEVEN (1933) (Cornish coast) 188 birds	LUMSDEN & HADDOW (1946) Clyde Sea 81 birds	PRESENT WORK Farne Isles & Berwick 52 birds
Ammodytidae	32.9	54.1	80.8
Pholidae		)	8.3
Zoarcidae		) 8.3	1.4
Blenniidae	0.1	)	0.6
Gadidae	1.2	4.1	4.0
Pleuronectidae	0.6		1.7
Cottidae	0.2	1.8	1.4
Serranidae	0.1		0.3
Clupeidae	48.8	11.4	0.3
Salmonidae			0.3
Callionymidae	2.7	3.4	
Gobiidae	3.7	2.7	
Labridae	7.3	2.7	
Gasterosteidae	0.1	2.2	
Syngnathidae	0.1	1.1	
Agonidae		0.3	
Congridae	0.1		
Trachinidae	0.1		
Crustacea	1.7	7.2	0.9
Mollusca		0.1	
Annelida		0.6	

COMPARISON WITH PREVIOUS WORK ON THE DIET OF THE SHAG.

The work of Steven, and of Lumsden and Haddow has already been mentioned. Table 41 summarizes the findings of these workers in comparison with the present work. It can be seen that there is considerable variation, in the type of fish taken, between the various areas. The Ammodytidae are the most numerous fish taken in both the Farne

Island area and the Clyde Sea area. In the Cornish area Clupeidae were taken in greater numbers than Ammodytidae. Clupeidae were also important in the Clyde Sea area, but not off the north east coast. Their omission from the diet of Shags on the Farne Islands is puzzling in that they were being taken by other species feeding in the area at the same time. It is possible that the Clupeidae were to be found farther offshore than the Ammodytidae, and were thus not hunted for by the Shags, which apparently utilize the fish in most abundant supply near the islands. The variations in the other species taken between the various areas probably reflects the relative abundance and availability of these bottom-living types in the respective areas where the birds were fishing.

Other than the works mentioned, very little has been published concerning the diet of the Shag. Collinge (1925) looked at the stomach contents of some Shags, but merely divided the contents into the categories; Food fish, and Miscellaneous animal matter, the percentages of which were given in Table 40. Snow (1960) states that the Shags on Lundy feed in the main on Ammodytes species.

<u>The Common Cormorant.</u> <u>Phalacrocorax carbo.</u>

The Cormorants on the Farne Islands breed in closely associated colonies on rocky outcrops on the tops of islands. During the breeding seasons of 1961 and 1962 there were two such colonies, each on a separate small island, and the total number of breeding pairs was approximately 100. In some seasons however either one or other of the colonies may fail, usually due to heavy seas washing out the nests, in which case the disturbed birds may go to swell the numbers of the other group, or may even fail to breed that season. Their methods of swimming and of hunting their prey are similar to those of the Shag. Like the Shags, Cormorants tend to fish close inshore and round the islands. As will be more fully described later, however, they tend to prefer fishing in estuaries, and over fresh water, at least in the winter months. Communal feeding behaviour is also common in this species, the fishing activities of one bird often attracting numbers of others. They do not tend to congregate in very large rafts of fishing birds as do the Shags however. Bartholomew (1942) describes the communal fishing activities of Double-crested Cormorants (<u>Phalacrocorax auritus</u>) on San Francisco Bay. These birds congregate in flocks of 50 or more birds and form a long narrow line at right angles to the direction of movement. The forward movement of the flock is divisible into three components viz. swimming on the surface, swimming beneath the water, and flying from front to rear of the flock. Large fishing flocks of Double-crested Cormorants pursue entire schools of fish in this manner, constantly driving them before them. Such complex fishing behaviour has not been directly observed during the present work, but Van Dobben (1952) records seeing a large raft of Cormorants in Holland. There is no doubt that the habit, of both Shags and Cormorants, of fishing in large groups, will decrease the chances of escape for any fish in the area, and hence increase the fishing efficiency of the birds as a whole.

Cormorant chicks are fed by regurgitation, in the same manner as are the young of the Shag. A characteristic of the Cormorants, however, is that, unlike the Shags, they will regurgitate very readily on being disturbed. Thus by merely walking into a colony it was possible to obtain the stomach contents of nearly all the chicks present, and occasionally of some adults also, which would sometimes regurgitate before leaving the nest at the approach of the intruder.

ANALYSIS OF REGURGITATION SAMPLES.

As the Cormorant colonies were situated on small islands, isolated from the main groups, it was not found possible to visit them with any frequency. In 1961 3 visits were made, and in 1962 5 visits. At each visit

TABLE 42. Analysis of regurgitation samples from Farne Islands. Monthly diet of the Cormorant. Numbers of different species collected.

SPECIES	MAY (1961) No.	MAY (1961) %	JUNE (1961) No.	JUNE (1961) %	JULY (1962) No.	JULY (1962) %	AUGUST (1962) No.	AUGUST (1962) %
PISCES								
Pleuronectes platessa	1	2			5	5	15	23
Pleuronectes flesus	21	43	6	5	49	45	31	47
Pleuronectes limanda					5	5		
Salmonidae sp. indet.	2	4			6	6	2	3
Anguilla vulgaris			3	3	9	8	3	4
Cottus bubalis	6	12	3	3	3	3	2	3
Cottus scorpionis			1	1				
Trachinus vipera					5	5		
Pholis gunnellus	6	12	4	4	16	15		
Triglidae sp. indet.					1	1		
Labrus mixtus					2	2		
Zoarces viviparous	4	8	5	4	2	2		
Cyprinidae sp. indet.			3	3				
Percidae sp. indet.			3	3				
Cyclopterus lumpus			1	1				
Motella sp. indet.					1	1		
Scyllium sp. indet.	1	2						
Gadidae sp. indet.	7	14	2	2	4	4	4	6
Ammodytes sp. indet.			77	70			9	14
MOLLUSCA								
Trivia arctica			1	1				
CRUSTACEA								
Eurynome aspersa	1	2						
Carcinus maenas			1	1				
Cancer pagurus			1	1				
TOTALS	49		111		108		66	

however a large amount of regurgitated food was collected. Unfortunately it was not possible to count with any accuracy the number of birds which had regurgitated. The young chicks would scramble from nest to nest ahead of the intruder as he progressed through the colony and would often regurgitate a little at a time as they became progressively more alarmed. Often a number of chicks would regurgitate in the same place, which also confused any attempt to count the number of birds contributing. The samples obtained did, however, enable the range of species taken by the Cormorant to be assessed. In 1962 the visits were made in July and August. Table 42 analyses the diet according to the month in which the samples were collected. Table 43 gives the overall analysis of the regurgitation samples obtained. Many of the specimens were partly digested, and nearly all were damaged in some way. It was possible in most cases to both identify and weigh and measure the specimens however. In some cases it was possible only to identify specimens as to family, due to the damaged condition. Such cases are noted in the tables where necessary. In addition to the samples obtained from the Farne Islands a small sample of regurgitated fish was obtained from Cormorant chicks on Anglesey in June 1963. Information obtained from the analysis of

TABLE 43. Diet of the Cormorant. Analysis of all regurgitation samples from Farne Islands.

PHYLA	SPECIES	NO.	% by NO.	WT.	% by WT.
PISCES	Pleuronectes platessa	21	6.3	417	3.2
	Pleuronectes flesus	107	32.0	3192	24.5
	Pleuronectes limanda	5	1.5	425	3.3
	Salmonidae sp.indet.	10	3.0	1253	9.6
	Anguilla vulgaris	15	4.5	1686	12.9
	Cottus bubalis	14	4.2	1077	8.3
	Cottus scorpius	1	0.3	287	2.2
	Trachinus vipera	5	1.5	135	1.0
	Pholis gunnellus	26	7.8	243	1.9
	Triglidae sp.indet.	1	0.3	30	0.2
	Labrus mixtus	2	0.6	131	1.0
	Zoarces viviparus	11	3.3	443	3.4
	Motella sp.indet.	1	0.3	84	0.6
	Cyprinidae sp.indet.	3	0.9	390	3.0
	Percidae sp.indet.	3	0.9	389	3.0
	Cyclopterus lumpus	1	0.3	154	1.2
	Scyllium sp.indet.	1	0.3	33	0.3
	Gadidae sp.indet.	17	5.1	2474	19.0
	Ammodytidae sp.indet.	86	25.7	192	1.5
MOLLUSCA	Trivia arctica	1	0.3		
CRUSTACEA	Eurynome aspera	1	0.3		
	Carcinus maenas	1	0.3		
	Cancer pagurus	1	0.3		
	TOTALS	334		13034.	

this sample is given in Table 44. Two further species of fish occur here viz. Rhamphistoma belone, the Garpike, and a species of Goby. The former is restricted, in its distribution, to the south and west, and does not occur in the North Sea.

TABLE 44. Diet of Cormorant. Analysis of regurgitation samples from Anglesey, June 1963. (Weight in g.)

	No.	% by No.	Wt.	% by Wt.
Pleuronectes flesus	3	43	400	30
Rhamphistoma belone	2	29	750	56
Anguilla vulgaris	1	14	120	9
Gobiidae sp. indet.	1	14	75	6
TOTALS	7		1345	

STOMACH ANALYSIS OF DEAD SPECIMENS.

In all the stomachs of 13 birds were examined, Of these three were shot in the estuary of the Tweed at Berwick, seven were shot on the estuary of the Lune in Lancashire, one was shot inland at Skerton Weir in Lancashire, and two were shot on Lake Windermere. Due to the greatly differing areas from which these birds were taken the analysis of diet from these stomach analysis, shown in Table 45, is presented with relation to where the birds were taken, rather than as a whole. The weights are given, where possible, as the weight of the whole fish. In many cases the specimens were badly digested and broken,

TABLE 45. Stomach analysis of Cormorants.

AREA AND DATE SHOT.	NO. of BIRDS	SPECIES TAKEN.	NO.	WT. (g.)
Estuary of Tweed (North-east coast) 18/10/60 and 26/10/61	1 2	Salmonidae sp. indet. *Zoarces viviparus* *Pleuronectes flesus* Gadidae sp. indet.	5 2 3 2	707 58 113 56
Estuary of Lune (North-west coast) 16/2/63 and 4/3/63	3 4	*Pleuronectes flesus* *Anguilla vulgaris* *Pholis gunnellus* Clupeidae sp. indet. Blenniidae sp. indet. *Petromyzon fluviatilis* Crustacea	7 6 1 1 1 1 many small	420 703 5 12 3
Sperton Weir (Lancs.) Inland (23/2/63)	1	*Gobius gobius*	1	138
Lake Windermere 17/3/63.	2	*Anguilla vulgaris* Salvelinus sp.	1 1	56 300
TOTALS	13		32	2565.

in which case the weight was estimated as far as possible from the weight of a whole fish of similar size. In some cases where no comparable fish was available the weights have been omitted (e.g. Clupeidae and Blenniidae) or given as the actual weight of the damaged specimens (e.g. *Petromyzon fluviatilis*). The crustaceans from the stomachs of birds shot on the estuary of the Lune were all very small, being mainly Gammarids, and were probably secondarily derived from the stomach of some fish eaten, rather than being taken by the birds.

SIZE OF FISH TAKEN.

The size ranges of the species of prey taken by Cormorants are given in Table 46. Only those specimens which were complete enough to be accurately measured, or for which an approximately true measurement could be estimated by comparison with a specimen of similar size, are included in this data. Some species were too fragmented to obtain a measurement of length, in which case the total weight of all fragments is given (e.g. Cyclopterus lumpus). In other cases the vertebral column and cranium were present, but much of the flesh digested, enabling a measurement of length to be obtained, but not of weight (e.g. Petromyzon fluviatilis). Whenever there were a number of specimens it was possible to obtain an approximate length and weight by comparison with whole specimens, if fragmentation was not too great. The smallest fish taken were young Pleuronectids, some being less than half a gram in weight and only 8mm. long. The largest species taken were the Salmonidae, Gadidae, and Rhombistoma belone, the Garpike, all of which were represented by specimens of up to 400g. weight. Anguilla

TABLE 46. Size ranges of prey species taken by Cormorants.

		LENGTH (mm.)		WEIGHT (g.)	
		Average	Extremes	Average	Extremes
Pleuronectes flesus	83	117.2	11-325	36.0	0.5-200
Pleuronectes platessa	20	39.3	8-202	18.7	0.4-105
Pleuronectes limanda	6	145.0	90-210	105.0	60-160
Salmonidae sp.indet.	11	232.6	65-380	127.4	10-400
Salvelinus	1	250.0		300.0	
Anguilla vulgaris	21	345.7	194-620	102.6	16-281
Cottus bubalis	11	137.0	85-230	92.5	20-300
Cottus scorpioides	1	255.0		300.0	
Trachinus vipera	4	134.5	115-144	32.3	25-41
Pholis gunnellus	17	139.1	70-167	9.0	6-15
Triglidae sp.indet.	1			30.0	
Labrus mixtus	2	147.0	145-150	66.7	63-70
Zoarces viviparous	11	192.4	90-300	42.8	27-80
Gadidae sp.indet.	10	221.0	145-300	165.0	25-400
Ammodytidae sp.indet.	88	95.3	75-130	3.0	1-9
Motella sp.indet.	1	180.0		83.7	
Cyprinidae sp.indet.	2			130.0	122-138
Percidae sp.indet.	3			163.0	36-303
Cyclopterus lumpus	1			154.0	
Scyllium sp.indet.	1			60.0	
Belone belone	2	425.0	400-450	380.0	360-400
Gobio gobio	1	270.0		138.0	
Petromyzon fluviatilis	1	160.0			

Overall average weight 115.9

vulgaris, the eel, was the longest type taken, one specimen exceeding 600mm., but were by no means as bulky as the above species.

The size frequencies of the two fish taken in the greatest numbers, viz. Ammodytidae, and _Pleuronectes flesus_, are given in Table 47. Nearly all the Ammodytidae taken were between 70 and 100mm. in length (1.2-2.5g. weight). The Flounders taken were not predominantly of any particular size group, but there were slightly more of the range 100-160mm. in length (12-60g.).

TABLE 47. Size frequencies of fish taken by Cormorants.

AMMODYTIDAE

LENGTH (mm.)	NO.
51-60	
61-70	2
71-80	16
81-90	28
91-100	25
101-110	3
111-120	7
121-130	7
131-140	
141-150	

Mean length 95.3mm.

PLEURONECTES FLESUS

LENGTH (mm.)	NO.
0-20	5
21-40	4
41-60	16
61-80	5
81-100	3
101-120	15
121-140	10
141-160	9
161-180	5
181-200	4
201-220	2
221-240	2
241-260	1
261-280	0
281-300	0
Over 300	2

Mean length 117.2mm.

The diet of the Cormorant appears to consist almost entirely of fish in all the areas examined. The only other groups occurring were crustacea and mollusca, the latter being represented by one small shell, probably an accidental inclusion. Parts of three decapod crustaceans of moderate size were included in one of the regurgitation samples and may have been taken deliberately, but the small Gammarids from the stomachs of the birds from Lancashire were almost certainly secondarily derived from fish stomachs. Other authors concurr that the Cormorant is almost exclusively a fish eater. Madson and Spark (1950) state that the southern Cormorant in Denmark takes no crustaceans. Collinge (1925) found the number of crustaceans taken to be less than 1%. Salomonsen (1950) notes that the Cormorant in Greenland is exclusively marine and takes fish, mainly Sea Scorpions and Codlings. Bolam (1912) however states that the remains of Carcinus maenas were found in a Cormorant shot off the Northumberland Coast, and Stevens (1933) found Cormorants shot off the Cornish Coast to contain 24.6% (by total number) of crustaceans. These latter are recorded as shrimps and prawns.

DIFFERENCES IN THE DIET OF CHICKS AND ADULT.

Any differences observed in the composition of the diet as obtained by analysis of regurgitation samples obtained from the chicks, and by analysis of the stomach contents of adults, are more likely to be due to the geographical variation in feeding areas where the specimens were obtained, than to a difference in the diet of chick and adult. Table 48 compares the average weights of fish as obtained from analysis of regurgitation results (chicks) and from stomach analysis (adults). In nearly all cases where the same species of fish were found in both the regurgitation samples and the stomach analyses the fish regurgitated were on average larger than those from the stomachs of adults. This is the reverse of what would be expected should the chicks be fed a special diet. Moreover the overall average weights of fish from adults and of fish from chicks are relatively similar, viz. 99g. and 121g., in comparison with the large range of average sizes of fish taken, an individual of the smallest species being on average 30g. weight, and of the largest species 380g. weight. There would thus appear to be no real difference between the diets of larger young and adult birds, the species and prey-weight variation between them being more probably attributable to their being collected in widely differing areas. It is notable however that very small chicks are not fed whole fish, but are given a type of predigested pap from the parents stomach. Madsen and Spark describe

TABLE 48. Size ranges of prey species taken by young and adult Cormorants.

SPECIES	NO. OF SPECIMENS MEASURED Adult	Young	ADULT BIRDS (from stomach analysis) Av. Wt. (g.)	Av. Lgth. (mm.)	YOUNG BIRDS (from regurgitation samples) Av. Wt. (g.)	Av. Lgth. (mm.)
Pleuronectes flesus	11	72	76.0	176.0	30.0	108.0
Pleuronectes platessa		20			18.7	39.3
Pleuronectes limanda		6			105.0	145.0
Salmonidae sp. indet.	5	6	25.8	138.0	212.0	322.0
Salvelinus	1		300.0	250.0		
Anguilla vulgaris	7	14	100.6	330.6	103.6	353.0
Cottus bubalis		11			92.5	137.0
Cottus scorpioides		1			300.0	255.0
Trachinus vipera		4			32.3	134.5
Pholis gunnellus		17			9.0	139.1
Triglidae sp. indet		1			30.0	
Labrus mixtus		2			66.7	147.0
Zoarces viviparous	2	9	26.5	198.5	49.4	213.3
Gadidae sp. indet.	2	8	25.0	145.0	200.0	240.0
Motella sp. indet.		1			83.7	180.0
Cyprinidae sp. indet.		2			130.0	
Percidae sp. indet.		3			163.0	
Cyclopterus lumpus		1			154.0	
Scyllium sp. indet.		1			60.0	
Belone belone		2			300.0	425.0
Gobio gobio	1		138.0	270.0		
Ammodytidae sp. indet.		88			3.0	95.3
Overall average weight			98.8		120.6	

this as follows:- "The nestlings in the first time after hatching are fed by their parents with regurgitated fluid of an already much digested stomach content, the parents carefully taking the head of the young by the lower beak and then pouring fluid into them. In this investigation the stomach of a single small naked nestling, weighing only 86g. was opened. It was found to be full of a fine porridge-like substance in which were found chitinous fragments of an isopod, a prawn, and a few vertebrae of an eel". During the pres nt investigation no observations were made of the feeding of very young chicks, but regurgitation samples were obtained from two naked chicks, both of about 120g. weight. In one case pulped fragments of Pleuronectes flesus were recorded, and in the other small pieces of flesh, probably from a gadoid fish.

SEASONAL VARIATION IN DIET.

The analysis of regurgitation samples according to month, as shown in Table 42, indicates that there may be considerable variation in the type of species taken from month to month. These results are not strictly comparable however, as the information for May and June was obtained in 1961 and that for July and August in 1962, and there may well be annual variation in the type of fish available to the birds, in addition to seasonal variation. Such a possibility will necessarily have to be ignored in the present discussion due to lack of sufficient data. Assuming annual differences to be negligible, the results show that Pleuronectes flesus was taken predominantly in all months but June, when the most numerous fish taken were Ammodytidae. This suggests that in times of abundance of Ammodytidae they will be taken in preference to the more usual bottom-living forms. Indeed it is probable that when dense shoals of these fish occur round the islands they will present a much easier catch to the Cormorants, than will the bottom-dwellers. Another feature of note is the absence of the small bottom-living fish, such as Pholis gunnellus and Zoarces viviparous, in August. There is no immediately discernible reason for this, although it is noticeable that Ammodytidae were again taken in this month, in addition to numerous small Plaice and Flounders; it may be that the latter three species were all relatively abundant, and provided adequate food sources without the necessity of hunting for the less gregarious, and hence more difficult, bottom-living fish.

SIZE OF FISH TAKEN.

The most remarkable fact indicated by the data in

Table 48 is the great range in size of the fish taken by Cormorants. Young Pleuronectids of less than half a gram weight, and large Garpike and Salmonidae of over 400g. weight were relatively frequent.

Madsen and Spark state that the Southern Cormorant generally takes fish of over 150mm. in length, and doubt that it takes sand-eels due to their small size. It is apparent from the present work however, that the lower limit to the size of fish taken is much smaller than that imagined by these authors, although there is, no doubt, a definite preference for the larger type of fish.

COMPARISON WITH THE WORK OF PREVIOUS AUTHORS ON THE DIET OF THE CORMORANT.

Comparative analyses of the diet of the Cormorant are given by Collinge (1925), Steven (1933), Madsen and Spark (1950) and Van Dobben (1952). The latter two were studies on the Southern Cormorant, Phalacrocorax carbo sinensis, in Denmark and the Netherlands respectively. The work of Van Dobben is particularly comprehensive. He studied a large colony of Cormorants near the Ijsselmeer in Holland, and working mainly from regurgitation samples, recorded in detail the variation in their diet over the year. The majority of the fish taken were of fresh-water origin, and he concluded that the Cormorants would take

TABLE 49. Diet of Cormorant. Comparison of work of various authors. Figures given as a percentage of total numbers taken.

GROUP	FAMILY	COLLINGE (1925) 34 Birds	STEVEN (1933) 27 Birds	MADSEN & SPARE (1950) 258 Birds	PRESENT WORK ESTUARY OF TWEED 3 Birds	PRESENT WORK ESTUARY OF LUNE 7 Birds	PRESENT WORK ANGLESEY Regurgitation	FAROE ISLANDS Regurgitation
MARINE FISH	Pleuronectidae		26.2	6.3	25.0	41.2	42.8	39.8
	Cottidae		2.8	2.8				4.5
	Trachinidae							1.5
	Pholidae			0.1		5.9		7.8
	Zoarcidae			18.9	16.7			3.3
	Blenniidae					5.9		
	Callionymidae		2.2					
	Triglidae		0.6					0.3
	Gobiidae		17.3					
	Labridae		5.0					0.6
	Gadidae	95.8 "food-fish" mainly Gadidae		8.3	16.7			5.1
	Ammodytidae							25.7
	Cyclopteridae							0.3
	Mugilidae		0.6					
	Agonidae		5.0					
	Clupeidae		5.6	36.8		5.9		
	Scombridae			2.2				
	Gasterosteidae			4.3				
	Belonidae						28.6	
	Scyliorhinidae							0.3
	Congridae		0.6					
	Anguillidae		1.1	18.5		35.3	14.3	4.5
FRESH-WATER FISH	Salmonidae				41.7			3.0
	Percidae			0.5				0.9
	Cyprinidae			1.0			14.3	0.9
	Petromyzontidae					5.9		
NON-FISH GROUPS	Crustacea	0.75	33.0					0.9
	Molluscs							0.3
	Others	2.31						

the most available fish in the grounds over which they were fishing, qualified by their preference for larger fish. He found that specimens under 6g. weight were rarely taken, and the average weight of individual fish taken was between 280 and 340g. Thus it would seem that in that area the Cormorants were taking larger fish than in the Farne Island area, or in the other British areas investigated. This is probably due to there being more larger fish available in the IJsselmeer, a protected inland water, than in the open sea. Van Dobben notes both annual and seasonal fluctuations in the type of fish taken, and attributes them to annual changes in the fish population, and to seasonal changes in the size and behaviour of fish. In less detailed surveys Collinge, Madsen and Spark, and Stevens examined the stomach contents of dead birds. Table 49 compares their various findings with those of the present work. For the sake of completeness the figures obtained from data on birds shot on the Tweed and Lune, and from regurgitation samples from Anglesey, are included, but it must be stressed that these are derived from very small samples. If we consider those investigations in which reasonably comprehensive analyses have been made, i.e. those of Stevens, Madsen and Spark, and the present work, we find that flat-fish, the Pleuronectids were common to all three, and the most numerous fish taken in two out of the three areas. Anguillidae were also common to all three, but only taken commonly (over 19%) in one. Cottidae were also common to all three, but in small numbers only. Fish occurring in two of the three areas, and numerous in at least one, were Zoarcidae and Clupeidae, whilst those occurring in two of the three areas, but not commonly were Pholidae, Triglidae, Labridae, Gadidae, Percidae and Cyprinidae. Crustacea were numerous in the birds shot off the Cornish coast, and occurred in the Farne Island birds, but not in those of Denmark. These differences must reflect the distribution of the various fish species and their relative availability in the different areas. A less detailed account of the diet of the Cormorant on the Northumberland coast is given by Bolam (1912) who states that in the Tweed estuary Flounders are the most important fish taken, in addition to Eels, Trout and the 15 Spined Stickle-back. This puts into better perspective the data obtained from the three birds shot on the Tweed, indicating that the three Salmonidae found out of seven fish may represent too high a proportion due to the small sample.

TABLE 50. Comparison of the diet of four species of diving sea-birds in the Farne Island area.

GROUP	PREY TAKEN FAMILY	PUFFIN % by No.	PUFFIN % by Wt.	GUILLEMOT % by No.	GUILLEMOT % by Wt.	SHAG % by No.	SHAG % by Wt.	CORMORANT % by No.	CORMORANT % by Wt.
MARINE NEKTONIC FISH	Ammodytidae	84.9	80.1	49.4	57.1	80.8	44.5	25.7	1.5
	Clupeidae	2.3	13.2	42.2	30.5	0.3	0.3		
	Trachinidae(fry)	12.0	3.7						
	Gasterosteidae	0.8	3.0						
MARINE BENTHONIC FISH	Gadidae			3.6	9.3	4.0	30.2	5.4	19.6
	Pholidae			4.8	3.1	8.3	7.7	7.8	1.9
	Trachinidae(adult)							1.5	1.0
	Pleuronectidae					1.7	2.1	39.8	31.0
	Zoarcidae					1.4	4.1	3.3	3.4
	Cottidae					1.4	3.5	4.5	10.5
	Blenniidae					0.6	0.7		
	Serranidae					0.3	1.7		
	Scyliorhinidae							0.3	0.3
	Triglidae							0.3	0.2
	Labridae							0.6	1.0
	Cyclopteridae							0.3	1.2
MARINE & FRESH WATER FISH	Salmonidae					0.3	5.0	3.0	9.6
	Anguillidae							4.5	12.9
FRESH WATER FISH	Percidae							0.9	3.0
	Cyprinidae							0.9	3.0
	CRUSTACEA					0.9	0.2	0.9	-
	MOLLUSCA							0.3	-

COMPARISON OF THE DIET OF THE DIVING SEA-BIRDS INVESTIGATED.

The four species of diving sea-birds on which information was obtained prey almost exclusively on fish. No other type of organism was found to be taken by the Puffins and Guillemots, and crustacea taken by Shags and Cormorants amounted to less than one percent of the total diet. Table 50 compares the composition of the diet of those four species in the Farne Island area. Ammodytidae are the most important fish taken by the Puffins, Guillemots and Shags, but are less numerous than the Pleuronectidae in the diet of the Cormorants. The true importance of Ammodytidae in the diet of the Cormorants, is much less than these figures would suggest when the relative weights of the fish are taken into account. Thus they amount to only 1.5% of the diet by weight as opposed to 25.7% by number (See Table 50), the relative importance of Gadidae and Anguillidae increasing when the weights are considered. Similarly the Ammodytidae taken by Shags, although constituting over 80% of the diet by number taken, make up only 44.5% of the diet by weight, the Gadidae being much more important when weights are considered. The percentage by number and the percentage by weight of the Ammodytidae taken do not differ much with the Puffin, and in the Guillemots the Ammodytidae are more important when their weight is considered, due to their being heavier than other species taken. Secondarily important prey differ in each species. The Puffin would appear to take wholly nektonic, or mid-water fish, the most important being Trachinidae (fry) and Clupeidae. The Guillemot, whilst taking Clupeidae and young Gadidae in addition to Ammodytidae all of which are wholly nektonic, takes some Pholidae, specifically _Pholis gunnellus_, which is an exclusively benthonic form spending most of its time under rocks. This seems to indicate that in some places, no doubt shallower areas, the Guillemot must occasionally hunt on the bottom. In addition to the Ammodytidae and Clupeidae, which are nektonic, the Shag takes a wide range of bottom-living forms. The most important of these are the Gadidae, almost all of which were adult, presumably bottom-living forms, and the Pholidae. The only nektonic fish taken by the Cormorant were the Ammodytidae, all the rest being bottom-living forms. The most important of these were Pleuronectidae, Gadidae, Cottidae, Salmonidae and Anguillidae. In addition the Cormorant was the only one of the four species to take freshwater forms, although not in any great number in the Farne Island area. The Salmonidae taken by Shags were almost certainly marine in origin.

TABLE 51. Average weights of prey taken by diving sea-birds. (Weights in g.)

PREY	PUFFIN		GUILLEMOT		SHAG		CORMORANT	
	% BY WT.	AV. WT.	% BY WT.	AV. WT.	% BY WT.	AV. WT.	% BY WT.	AV. WT.
Ammodytidae sp. indet.	80.1	1.9	52.2	10.5	44.5	6.7	1.1	3.0
Clupeidae sp. indet.	13.2	10.5	31.0	5.9	0.3	10.0*		
Gadidae sp. indet.			12.6	10.0*	30.2	125.9	15.6	165.0
<u>Gasterosteus spinachia</u>	3.0	7.2						
Trachinidae (fry) sp. indet.	3.7	0.6						
<u>Pholis gunnellus</u>			4.2	5.0*	7.7	7.9*	1.4	9.0
<u>Pleuronectes flesus</u>					2.1	9.2	25.4	36.0
<u>Pleuronectes platessa</u>							24.3	18.7
<u>Pleuronectes limanda</u>							12.5	105.0
<u>Zoarces viviparous</u>					4.1	24.2	2.9	42.8
<u>Cottus bubalis</u>					3.5	21.0	6.3	92.5
<u>Cottus scorpioris</u>							1.7	300.0
<u>Blennius pholis</u>					0.7	10.0*		
Serranidae sp. indet.					1.7	50.0*		
<u>Trachinus vipera</u>							0.8	32.3
Triglidae sp. indet.							0.2	30.0
<u>Labrus mixtus</u>							0.8	66.7
Motella sp. indet.							0.5	83.7
<u>Cyclopterus lumpus</u>							0.9	154.0
Scyllium sp. indet.							0.2	60.0
<u>Rhamphistoma belone</u>							4.4	380.0
<u>Gobio gobio</u>							0.8	133.0
<u>Anguilla vulgaris</u>							14.4	102.6
Salmonidae sp. indet.					5.0	150.0*	12.0	111.8
<u>Petromyzon fluviatilis</u>							0.5	87.0
Percidae sp. indet.							2.3	163.0
Cyprinidae sp. indet.							2.3	130.0
Crustacea					0.2	1.6*		
Average weight of all prey taken.		1.9		7.7		8.5		48.1

The differences in the types of marine benthonic fish taken by the Shags and Cormorants is probably due to their fishing over different areas. The Shags tended to exploit feeding grounds within sight of the islands, whereas the Cormorants, on the whole, dispersed along the coasts. The Cormorants would seem to have a definite preference for Pleuronectidae, however, which does not seem to be explicable in terms of variation in feeding areas. It may be that the Shag hunts more in mid-water than does the Cormorant, a conclusion which would seem to be valid when the preference of Shags for fishing in deeper waters, as opposed to the coastal fishing of the Cormorant, is considered. Thus in deep water it would be considerably more time consuming to hunt bottom-living fish, than nektonic types.

SIZE OF FISH TAKEN.

The great differences in the relative importance of some species in the diet when assessed as percentage of total numbers or of total weight, emphasizes the great range in size of the various species taken. Table 51 compares the average sizes of the prey species taken by each of the four diving species of sea-birds. The Puffin takes fish of an average size ranging from 0.6g. to 10.5g. whilst the Guillemot takes them of an average size of from

5.9g. to 10.5g. Thus the Guillemot takes fish of a larger average size on the whole, with the exception of the Clupeidae, of which the Puffin takes the larger. The Shag takes fish ranging in weight from 7.9g. to 150g. on average, and the Cormorant takes species of an average weight of 3.0g. to 380g. In those species of fish taken by both the Shag and the Cormorant, the latter takes specimens of a greater average weight than the former, except for the Ammodytidae, where those taken by the Shag were larger, and the Salmonidae, which were similar in size. The average weights of all prey, taking into account the relative proportions of each species in the diet, are also given in Table 51. There is a progressive incr ase in the average size, the Puffin taking much smaller fish than the Guillemot and the Shag and the Cormorant much larger fish. Thus, as with the surface-feeding sea-birds, there is an increase in the size of fish taken with increasing size of bird. Table 52 gives the average size of fish taken, and the regression coefficient and corresponding regression equation relating these factors. A t-test based on the regression coefficient reveals that the correlation is significant at the one percent level (P 0.01 with 2 degrees of freedom). The slope of the regression line is 0.018. Thus for every 100g. increase in the average weight of the

TABLE 52. Diving sea-birds. Correlation between average weight of prey taken and average weight of bird. (g.)

SPECIES	Av. wt. of prey taken	Av. wt. of bird
Puffin	1.9	380
Guillemot	7.7	925
Shag	8.5	1738
Shag (Ammodytidae excluded from diet)	24.8	
Cormorant	48.1	2967

Regression coefficient (r) = 0.9972
Standard error of estimate = 1.33g. prey
Regression equation $y = 0.0184x - 7.01$

bird the average weight of prey increases by 1.8g. In deriving this regression coefficient the average weight of prey taken by the Shag has been estimated from all prey with the exception of Ammodytidae. If the Ammodytidae are included then the average weight falls to 8.5g. and the correlation ceases to be significant. It thus seems probable that the high percentage of Ammodytidae taken by the Shags in the present investigation does not present a true picture of the diet of this bird, and is produced by the abnormal conditions of a superabundance of sand-eels at the time when samples were taken. Thus the link between the average size of prey and the average size of bird must be imposed by the exigencies of hunting efficiency. Storer (1952) in his discussion of the evolution of Auks notes that they all pursue their prey in a similar manner, and that the primary size categories seem to be based on adaptations to preying on organisms of different sizes. The diving sea-birds all hunt in a similar manner and hence probably expend similar amounts of energy in hunting, in proportion to their size. The observed increase in size of prey with increase in size of bird is therefore to be expected. This would be modified if small prey were so numerous that a number of individuals could be taken simultaneously, or with no greater expenditure of energy than would usually be spent in hunting a single individual. In such a case large numbers of small fish could be taken almost as efficiently as a few large fish, and this may well be the case with the Shags round the Farne Islands when sand-eels are present in large, dense shoals. The fact that sand-eels were not taken to any great extent by the Cormorants may indicate that even with dense shoals of small fish present it is more economical for such large birds to hunt larger species individually. It may be, however, that the sand-eels were not as abundant in the estuarine, littoral and sub-littoral areas where the Cormorants tended to concentrate their fishing. This would seem unlikely however, as during the summer months the Ammodytidae migrate into the littoral areas in vast shoals and bury themselves in the sands.

COMPARISON OF THE RELATIONSHIP BETWEEN SIZE OF PREY AND SIZE OF BIRD IN SURFACE-FEEDERS AND IN DIVING-FEEDERS.

It was found that with the surface-feeding sea-birds, for every 100g. increase in the weight of the birds the average weight of prey taken increased by 0.5g., whereas in diving feeders for every 100g. increase in body weight, the average weight of prey taken increased by 1.8g. It would thus seem that the relative energy expenditure per g. weight in obtaining food is greater in diving-feeders than in surface-feeders. This is to be expected due to the greater resistance encountered in moving through water as compared with air, thus exacting a correspondingly greater energy expenditure in moving a body through the medium.

SIZE OF AMMODYTIDAE TAKEN.

Comparison of the length frequencies of Ammodytidae taken by Puffins and by Shags in 1962 (Figure 9) show that whilst the Shags were taking fish of two distinct sizes, the Puffins were taking fish only of the smaller

FIGURE 9.

Length frequencies of Ammodytidae taken by diving sea-birds, in 1961 and 1962.

x = Percentage

y = Length (mm.)

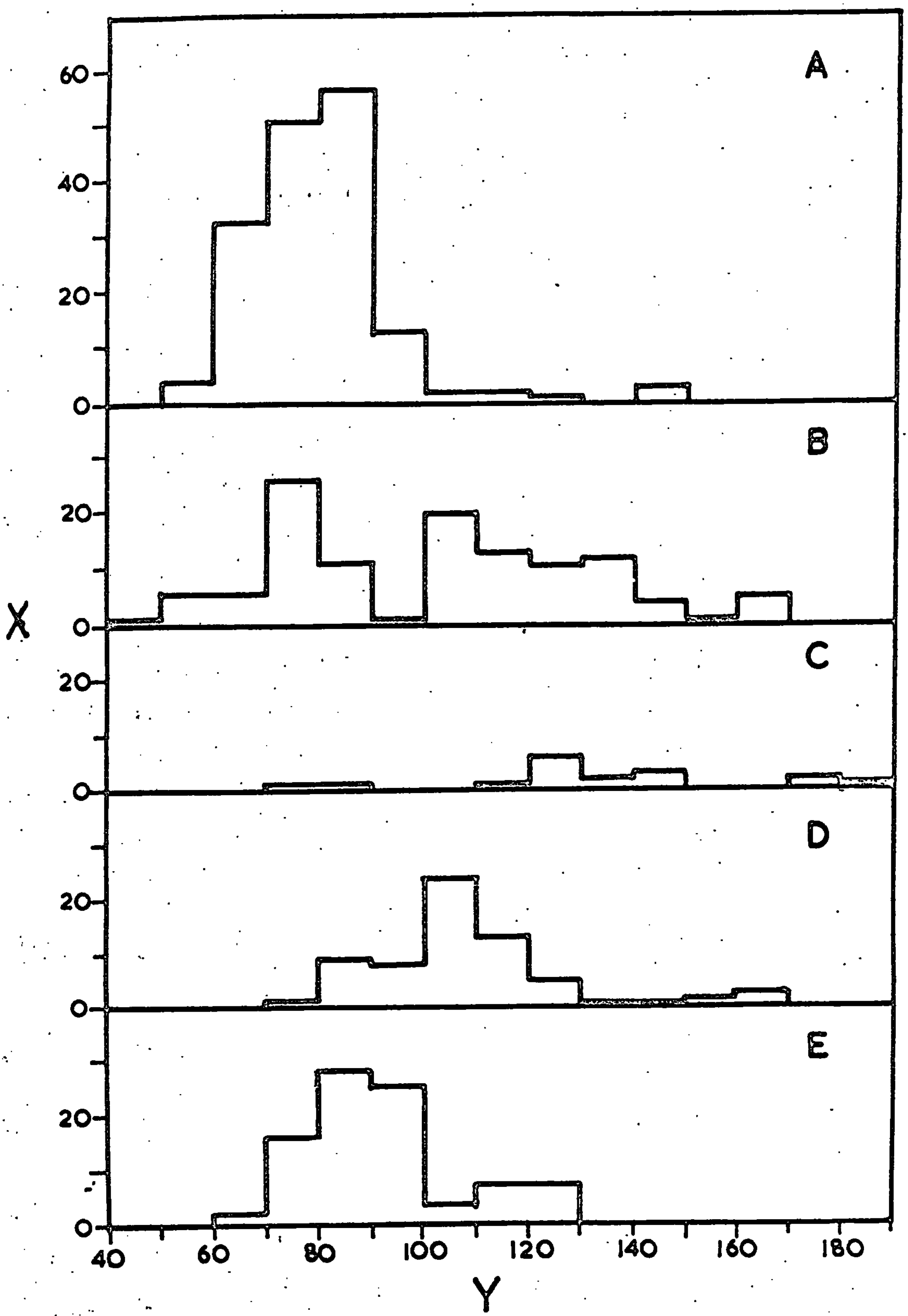
A = Puffin 1962.

B = Shag 1962.

C = Guillemot 1962.

D = Shag 1961.

E = Cormorant 1961.



A
B
C
D
E
X
Y
0
20
40
60
40
60
80
100
120
140
160
180

size. This probably indicates that in the off-coast fishing grounds of the Puffins the larger size group was not present, the difference between the two general size groups being too small to give credence to the possibility of deliberate selection by the Puffin for the smaller fish. The Guillemots tended to take larger sand-eels than both the Puffin and the Shag, which might indicate that it is either exploiting different hunting grounds, from the Puffin, or is taking these fish from greater depths beyond the reach of the Puffins' diving abilities. The Ammodytidae taken by the Cormorants in 1961 (see Figure 9) tended to be slightly smaller than those taken by the Shags in the same year. Thus the most frequent size group taken by the Cormorants was 81-90mm. and by the Shags 101-110mm. The sizes taken by both species overlap extensively, and probably do not represent two different population groups of fish.

GENERAL DISCUSSION ON THE DIET OF FARNE ISLANDS SEA-BIRDS.

It must be stressed that nearly all the information obtained was on the diet of the birds during the summer breeding season, the only data on food taken at other times of year being obtained from stomach analysis of a number of Shags and Cormorants.

The most important point to arise from this invest-

TABLE 53. Comparison of major items in the diet of Farne Island sea-birds.

BIRD	FISH				Crustacea	Cephalopoda	Annelida	Others	Totals
	PERCENTAGE OF TOTAL NUMBERS OF PREY TAKEN								
	All	Ammod-ytidae	Clup-eidae	Others					
Arctic Tern	95	64.6	21.9	8.0	2.2	2.5		0.9	100.1
Common Tern	98	44.5	37.8	15.9	0.8	1.0			100.0
Sandwich Tern	99	74.3	14.7	9.5	0.7	0.7			99.9
Kittiwake	98	80.7	10.4	7.3	1.0			0.5	99.9
Lesser Black-back Gull	74	54.6	5.6	13.6			19.1	7.0	99.9
Puffin	100	84.9	2.3	12.8					100.0
Guillemot	100	49.4	42.2	8.4					100.0
Shag	99	80.8	0.3	18.0					100.0
Cormorant	99	25.7		73.1					100.0

igation has been the heavy dependance, of nearly all the species investigated, on fish, and on the Ammodytidae in particular. Table 53 summarizes the data obtained for all species in terms of major items and groups taken. The Clupeidae were also taken extensively by most species, but they were generally of secondary importance to the Ammodytidae. It is possible that the breeding cycle of these sea-birds is timed to coincide with the period of greatest abundance of the Ammodytidae and Clupeidae in the area. Several authors have discussed the numerous occurrences in bird species of the peak food availability coinciding with hatching of the young. Marshall (1951) states that "there is accumulating specific evidence that a genetically determined response to widely varying factors has evolved in some species in a way that ultimately gears the sexual cycle so that the young will hatch at times when the environment contains abundant food on which they are traditionally fed". Salomonsen (1955) noted that the breeding, and in particular the hatching, of Icelandic sea-birds was linked with the annual upsurge of phytoplanktonic productivity in the spring and summer. McIntosh and Masterman (1897) describe the migrations of Ammodytidae, both A. lanceolatus and A. tobianus from the bottom to the surface layers in the waters off the N.E. coast. They show that young Ammodytidae spawned between January and April reach the surface waters in May and June, when they are between 30 and 40mm. long. Autumn spawned fish of the previous year reach the surface waters at the same time, but have a length of between 40 and 50mm. All age groups of developing Ammodytidae tend to spend the winter and early spring in mid-water offshore, according to these authors, but migrate to the surface and move inshore in late April and May. Most of the sea-birds breeding on the Farne Islands arrive in April, or even earlier in the case of the Kittiwakes, Shags, and Cormorants, but the tern species may sometimes be as late as early May. The first chicks are hatched in late May, and early June, with the majority occurring in the last 3 weeks of June and early July. Thus the hatching coincides with the arrival at the surface, and inshore around the islands, of the shoals of juvenile Ammodytidae. Snow (1960) notes that the hatching and period of most rapid growth of young Shag chicks on Lundy coincides with the seasonal movements of Ammodytidae into the area. Cameron (unpublished thesis) studied the movements of Ammodytes species off the Isle of Man, and found that both Ammodytes lancea, and Ammodytes lanceolatus migrated from the inshore waters into which they moved in the early summer to offshore areas during the late summer. She found that by the end of July nearly all fish in the first and second year groups had left the inshore grounds. Coinciding with this offshore migration of Ammodytidae, there is an influx of Clupeidae however. Jenkins (1927) states that the Herring spawn in the spring and autumn on the bottom, offshore. Hatched young take a few days to absorb the yolk-sac and when about 10mm. long they move to mid-water levels. There they remain until between 12 and 16mm. long, when they move to the surface.

On attaining a length of 26 to 83mm. the young herring then comes in shoals to the coast. The period of growth before this inshore migration is about 3 months for spring spawned fish, and 7-8 months for autumn spawned fish. Thus spring spawned fish would start appearing inshore in July, and the autumn spawned fish a little earlier. Meek (1916) observes that the Northumberland coast is visited each year by immense numbers of young Herring, which he thinks from their size, to be products of the Firth of Forth winter spawning school. Thus the birds on the Farne Islands are ensured of an abundant source of food throughout the summer, for when the young sand-eels begin to leave the area they are replaced by the vast schools of young Clupeiods. This is reflected in the seasonal fluctuations in the diets, the numbers of Ammodytidae being taken by the Kittiwakes and Arctic Terns decreasing in July, and the numbers of Clupeidae taken increasing correspondingly. It is possible that an influx of Clupeidae into the area would alone account for the increased percentage of these fish in the diet of the birds during the late summer, and that there may be no corresponding offshore movement of the Ammodytidae. The inshore migrations of young Ammodytidae and Clupeiods may have differential effects on the various sea-bird species. As will be described more fully later, the feeding ranges of the various species differ considerably. In general the Kittiwakes, and Auks tend to feed much further offshore than the terns and the Cormorants. Thus, whilst the latter may be suffering from a scarcity of Ammodytidae and Clupeidae, should the shoals of these fish fail to move into the inshore surface waters for some reason, the Kittiwakes and Auks may well be able to exploit populations in the offshore areas which are beyond the range of the other species. On the other hand these offshore-feeding birds are well able to exploit the inshore areas about the islands should fish be present there in abundance. The failure of either the Ammodytidae or the Clupeidae to appear round the islands at the usual time may well have serious consequences for the terns. As has been stated previously this probably occurred in May and early June 1962 when there appeared to be a lack of sand-eels, and the terns in particular appeared to be depending to a large extent on crustaceans and cephalopods. In that year the breeding season of the terns appeared to be delayed, the major part of the chicks were not hatched until early July, as opposed to the more usual time of mid-June. Such a delay can not be ascribed specifically to the failure of normal food supply however, for there may well have been other factors operating, in particular adverse weather conditions for fishing. It is notable that the summer of 1962 was particularly wet and dull with a greater number of gales than usual. Pettingill (1939) states that lack of sufficient food, for the Arctic Terns breeding on Machias Seal Island, in ~~northern~~ MAINE ~~Jarred~~, was suspected as being an indirect cause of both "marauding" (i.e. intra-specific predation of eggs and chicks) in the colony, and a failure of nesting drive. Thus the adult birds were forced to take the eggs and young for food purposes, and to stop incubation and young rearing through lack of food for themselves and the young. A similar increase in the number of clutches broken or deserted by adults was noted in May and early June 1962 on the Farne Islands, during the apparent dearth of Ammodytidae in the area. Rooth and Morzer Briujns (1959) note the periods of low temperatures and high winds have an adverse effect on the fishing activities of Sandwich Terns, often leading to starvation of the chicks should such conditions occur in the period immediately after hatching. However, it is possible that death of chicks under such conditions is due directly to adverse weather rather than to starvation as these authors suggest.

INTRASPECIFIC VARIATION IN DIET.

The possibility that individuals within a species may develop characteristic specialisations in the type of food taken has been discussed by many authors. Bel-opolskii (1957) gives a number of examples of individuals or groups of the same bird species taking consistently different types of food in the same area. Thus the Arctic Skuas on the Litskie Islands in the Barents' Sea took birds eggs extensively, whereas on Kharlov Island, 20 kilometres to the west they took almost entirely fish and berries. It is possible that the dependence of certain groups of birds, within a species, on a particular type of food, may lead to evolutionary selection of morphological and behavioural patterns differing from those of the main group, and hence lead eventually to speciation. Both Cushing (1944) and Thorpe (1945) discuss this possibility, and the latter reviews probable mechanisms whereby such habits could be assimilated into the genotype. On the Farne Islands little evidence was gathered concerning food preferences of individuals of most of the species studied, but observations made of the fish fed to individual common and Arctic Tern chicks provide a basis for comparing variation in the diet of individual birds of those species.

TABLE 54. Arctic and Common Terns. Variation in the type of prey taken by individual birds.

TYPE OF PREY TAKEN

	No. of bird.	AMMODYTIDAE	CLUPEIDAE	GASTEROSTEIDAE	GADIDAE	'FRY'
ARCTIC TERN	1.	20	3		2	2
	2.	43	4		1	5
	3.	18	3		0	3
	4.	23	3		1	20
	5.	34	4		0	2
	6.	15	5		0	3
	Totals	153	22		3	35
	Means	25.5	3.7		0.5	5.8
COMMON TERN	1.	17	11	3	3	0
	2.	18	16	0	1	2
	3.	54	11	1	2	3
	4.	17	15	1	1	0
	5.	21	9	1	2	1
	6.	9	7	0	2	0
	Totals	134	69	6	11	6
	Means	22.3	11.5	1.0	1.8	1.0

Table 54 shows the numbers of each prey species taken by individual Common and Arctic Terns. The observations were made over five different days and concerned all times of day, but all birds were under observation for the same length of time. It is obvious however that the numbers of birds observed, the number of observations made, and the range of species taken are all too small to provide a reasonable basis for the statistical estimation of individual variation in the diet. Nevertheless the data does give some indication of the degree of variability between individuals. Thus Arctic Tern 4 took four times as many 'Fry' as any of the other birds, and Arctic Tern 2 took nearly twice as many Ammodytidae as any of the others. Similarly bird number 3 among the Common Terns took many more Ammodytidae than the average. Similar comparisons were carried out on the numbers of the different size groups of Ammodytidae taken by the Common and Arctic Terns during the same periods of observations. This was to investigate the possibility that certain individuals might be selecting fish of a specific size range. The size ranges of fish were judged subjectively by the observer, as described on Page . Table 55 lists the numbers of each size group taken by the individual birds. It would seem that of the 12 birds of both species observed only Arctic Tern 2 took a greater proportion of one particular size group, i.e. the smallest (1-2") size group, as compared with the other birds, and it is thus possible that particular bird was selecting for fish of that size.

It is apparent however, that the minor differences shown in the diet of individuals emphasizes the uniformity rather than the diversity of the diet of these birds

TABLE 55. Arctic and Common Tern. Variation in the size of Ammodytidae taken by individual birds.

	No. of bird.	Size of Ammodytidae taken. (Approximations by eye.) 1-2"	2-3"	3-4"	over 4"
ARCTIC TERN	1.	3	15	2	0
	2.	15	21	4	1
	3.	4	10	1	0
	4.	3	9	1	0
	5.	3	19	6	0
	6.	1	8	3	2
	Total	29	82	17	3
	Mean	4.8	13.7	2.8	0.5
COMMON TERN	1.	4	7	3	3
	2.	3	12	3	0
	3.	5	36	7	2
	4.	4	11	2	0
	5.	3	10	5	2
	6.	0	3	3	0
	Total	19	79	23	7
	Mean	3.2	13.2	3.8	1.2

on the Farne Islands. It is probable that in such areas, where one or two food sources are particularly abundant, in this case the Ammodytidae and Clupoidae, there is little reason for the birds to develop individually varying patterns of diet. This is the conclusion of Ticehurst (1940), who surveyed the individual feeding habits of a number of bird species, finding some evidence for individual preferences. He concluded however, that the superabundance of one particular type of food would override such preferences. In this context L.

Tinbergens' hypothesis of the role of specific search images, as described by Gibb (1962), is perhaps relevant. Tinbergen suggested that birds only find and accept prey after acquiring the appropriate specific search image, which only happened when the prey exceeded a certain threshold density. If this is true then when one prey is superabundant in a particular area all the birds will form an image of that prey, probably to the virtual exclusion of other prey which will not reach the appropriate threshold level. If, however, a number of different types of prey occur in the same area, none of which are much more or less numerous than the others, then individual birds will tend to form search images for different prey, depending on the particular type they encounter, and thus individual variation in the type of prey hunted will occur. That the diet of the Arctic and Common Tern can differ widely in different geographical areas was shown previously. That feeding habits may change also, in addition to the type of food taken, is shown by the account given by Norrevang (1960) of the Arctic Terns on Mykines in the Faroes. There they have apparently taken to obtaining their food almost entirely by parasitisation of the Puffins. By swooping down on fish-carrying Puffins they can cause them to drop their lords, which the attacking bird then snatches up. Such ...ar-like behaviour was never observed in the Farne Islands terns, but has been occasionally reported in other ...rers. Many other examples of differentiation of feeding habits in the same species can be found in the literature, and it seems probable that it is the rule, rather than the exception for such individual variation to occur. It would be particularly important for those species which exploit a wide range of scattered food sources, i.e. the Gulls and the Skuas, when it would tend to both reduce the possibility of intraspecific competition occurring and increase the chances of survival of at least some of the group, for it is unlikely that all sources of food would be unavailable, even should some fail from time to time. For those species and populations exploiting abundant food supplies, which no doubt includes the Farne Islands groups, the importance of such variation would be minimal.

SECTION 2.

INVESTIGATIONS INTO THE FEEDING ACTIVITIES OF CERTAIN SEA-BIRDS.

Observations made both of the feeding activities at the nest, and of the fishing activities at sea, enabled the diurnal feeding ranges of the adults to be estimated. In addition, information was obtained concerning the variation in feeding areas favoured by the different species. No information could be obtained with regard to the feeding frequency of adults, because of the difficulty of observing them on their feeding grounds. It seems probable however, that they would satisfy their own needs prior to feeding the chicks, and observations of the feeding times, also includes the time taken to find food for themselves. This possibility is discussed more fully below.

THE DIURNAL FEEDING RHYTHMS OF FARNE-ISLAND SEA-BIRDS.

In the investigation of feeding rhythms direct observations were made of the birds at their nesting sites, and counts made at regular intervals of the numbers of birds both at the nest and in the immediate vicinity of the nesting area, including those birds occupying 'club' areas near the nesting sites. From such counts the number of birds away feeding at any one time could be estimated. In the case of the terns, counts of birds flying into a specific colony area carrying fish gave similar information whilst being less open to the errors inherent in the first method. With the indirect method the assumption has to be made that all birds not at the nest site, or occupying 'club' areas, are away fishing, but there may well be some birds which use areas away from the vicinity of the nest site for rest and preening, and would thus not figure in general counts.

In order to establish the presence or absence of diurnal fluctuations in feeding activity, it is necessary to observe a specific group of nests, or a colonial area, over the full daylight period. The repetition of such day-long counts at intervals throughout the season is necessary in order to assess the extent of seasonal fluctuations in the pattern of activity. Unfortunately it was impossible to obtain a comprehensive series of day-long counts for many of the species under study. Adequate data were obtained for the Arctic Tern and Kittiwake, less comprehensive information on the Common Tern, Puffin, and Shag, and some knowledge was gained concerning the activities of Guillemots. The information obtained on each species will be discussed separately and is followed by a general discussion of the patterns of feeding activity among the Farne Islands sea-birds.

Arctic Tern. *Sterna paradisaea*.

Two methods were used to assess the feeding activity of the Arctic Terns. First, counts were taken of birds flying into the colony with fish on a number of dates, at various times of day, and secondly more detailed counts were taken of the number of fish brought and the times they were fed to specific chicks under investigation. Both these methods were used after the hatching of the chicks, when birds were carrying fish into the colony. No counts were made of general activities within the colony prior to this time, because of the practical difficulty of counting fluctuations in numbers of terns amongst the fairly dense vegetation on the breeding sites.

COUNTS ON THE NUMBERS OF FISH CARRIED INTO THE COLONY.

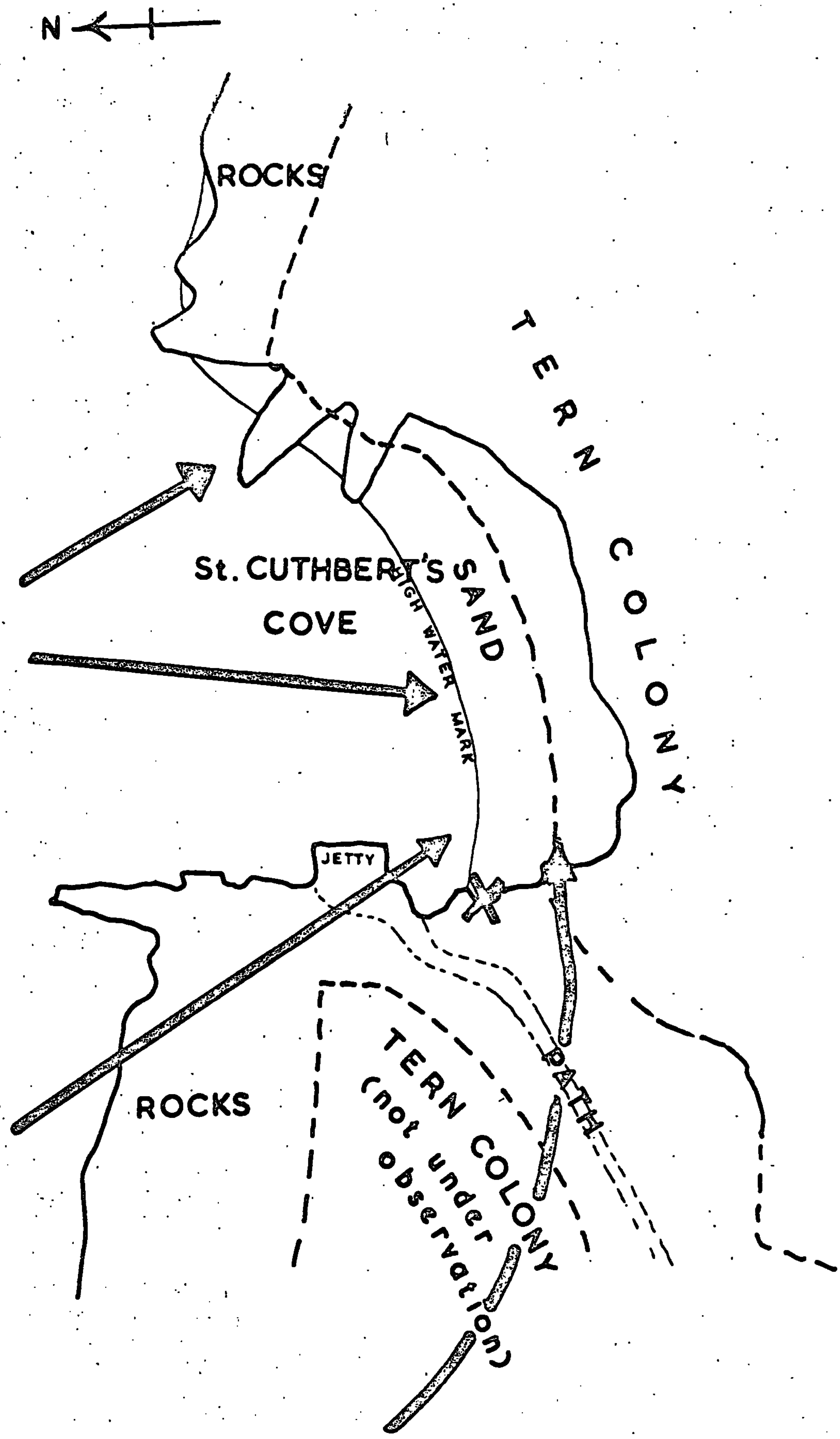
After hatching of the chicks, counts were made of the numbers of birds returning to the colony carrying prey. Figure 10 shows the position of the observer in relation to the colony when making these counts, and the general paths of the birds as they entered the colony. The majority of Arctic Terns on the Inner Farne nested in the area surrounding St. Cuthbert's Cove, and when returning to the colony from the sea tended to fly in over the Cove. To a large extent this applied also to birds com-

FIGURE 10.

Plan of the Tern colony in St. Cuthberts' Cove, showing the position from which counts were made of the number of birds entering the colony with fish.

Broken lines represent approximate limits of Tern colonies. Arrows represent the direction of flight of birds arriving at the colony with fish.

Cross marks the position of the observer.


N
ROCKS
TERN COLONY
St. CUTHBERT'S COVE
SAND
HIGH WATER MARK
JETTY
PATH
ROCKS
TERN COLONY (not under observation)

ing from the south, i.e. the other side of the island, as well as from the north, the tendency being to detour round the island rather than fly over it; thus an observer, positioned as shown in the diagram, could record the majority of birds entering the colony. There were a few (less than 3%) Common Terns nesting in the study area but no attempt was made to separate these from Arctic Terns during the observations.

The numbers of birds entering the colony per minute were recorded, in some cases for a continuous period of hours, and in others for 10 minutes in every hour. Figure 11 shows the results of counts taken throughout the daylight hours on two separate days. The weather was similar on both days, being sunny and warm. The count taken in June 1961 was based on continuous observations over the day, except for a short period in the early morning, whereas the count undertaken in July the following year is based on counts taken for ten minutes in every hour. The pattern of activity was similar on both days. Fishing commences soon after dawn, and is most intensive during the early morning, and late evening, when there are pronounced peaks in fishing activity. In June 1961 the morning activity peak was less pronounced but still apparent. There was a considerable diminution in fishing

FIGURE 11.

Arctic Tern. Counts of the number of birds carrying fish into St. Cuthbert's Cove throughout the day.

Solid line - Count on 27/7/62.

Weather a.m. Wind N-NW Force 0-1

Hot and Sunny.

p.m. Wind S Force 0-2

Hot and Sunny.

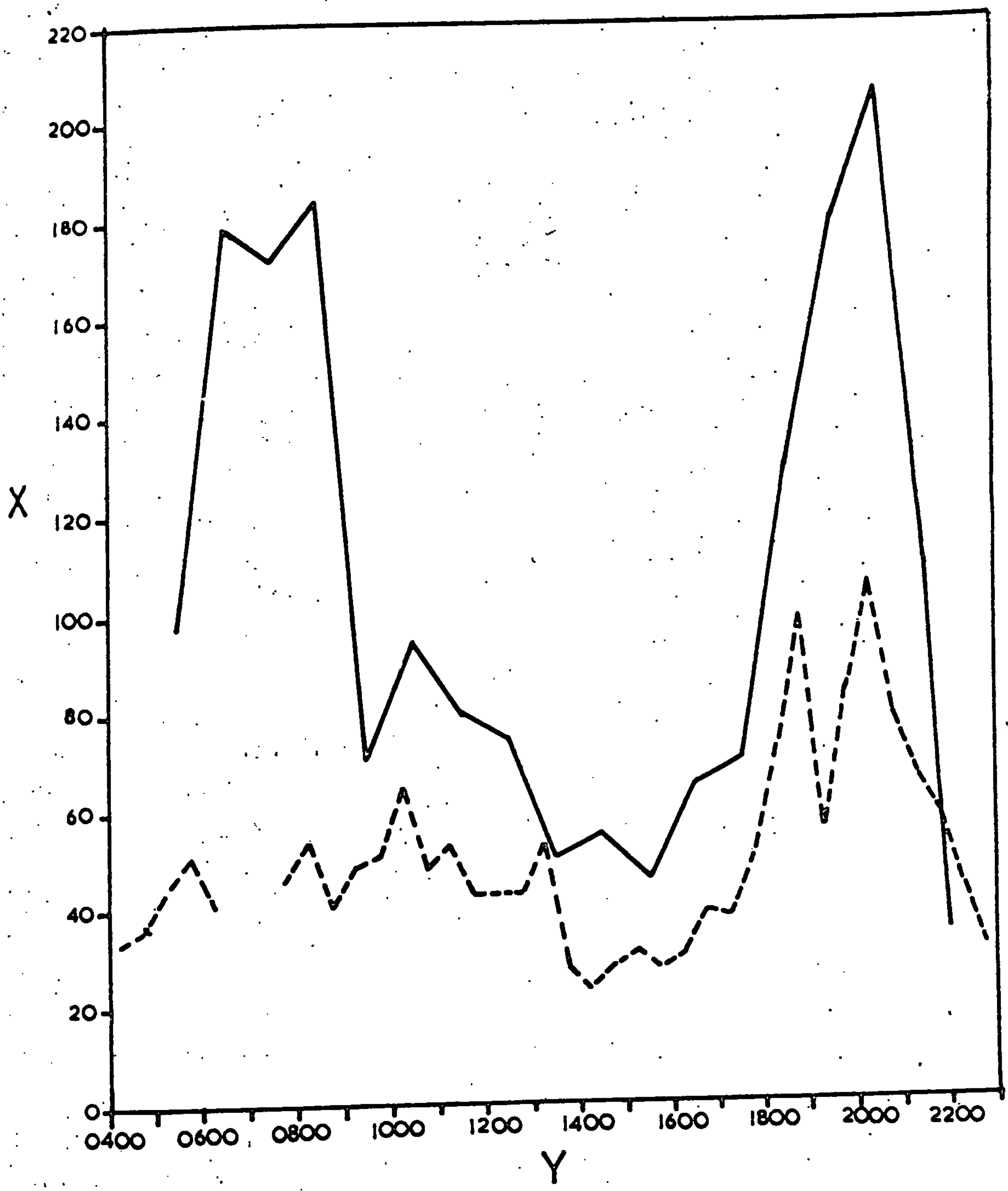
Broken line = Count on 24/6/61.

Weather All day. Wind W Force 2-4

Hot and Sunny.

x = Number of birds carrying fish into the cove per 10 minutes.

y = Hour of day. (B.S.T.)



220
200
180
160
140
120
100
80
60
40
20
0
X
0400
0600
0800
1000
1200
1400
1600
1800
2000
2200
Y

activity during the early afternoon, lasting till about 1600 hours. The numbers of birds carrying fish into the colony on the two days are not strictly comparable, because of the variation in nesting numbers between the two years, and the different phase of the breeding cycle at which the counts were made. Thus the 1961 count was made in June before the majority of the chicks were hatched, whereas the 1962 count was taken in late July at a time when most of the eggs had hatched.

OBSERVATIONS ON THE FEEDING OF INDIVIDUAL CHICKS.

In both 1961 and 1962 observations were made, from a hide, on a group of nests. The feeding of individual chicks could be closely followed, and the number of feeds over specific periods of time noted. On some occasions watches were undertaken throughout the daylight hours, but at other times it was only possible to watch for shorter periods. The number of times each chick under observation was fed during each hour of the day was recorded. The averages of all observations made in both years, in terms of the number of feeds per chick, and per brood, are given in Appendix C. Since nearly all the broods under observation contained only one chick, these averages do not differ greatly. Certain chicks were watched during the same period of the day on a number of different days, in which case each watch during the particular hour of each day was counted seperately. Figure 12a gives a histogram of the average number of feeds per hour taken by the individual chicks. It can be seen that the same pattern of feeding activity as was noted in the direct counts is also apparent here. Thus there are peaks of feeding activity in the morning and evening, and a period of relative quiescence during the afternoon. All the watches on which these figures are based were undertaken during July, in both 1961 and 1962.

Common tern. *Sterna hirundo.*

As has been stated no distinction was made between Arctic and Common Terns during the counts of birds bringing fish into the Cove, and the latter were discounted due to their relatively small numbers. Thus the only data on the fishing activities of Common Terns obtained, was deduced from watches on individual chicks at the nest site. The number of feeds given to each chick under observation during each hour of the day were recorded, and the totals summed to give the average number of feeds per chick for each hour of the day. This information is shown in Figure 12b and the data on which it is based are given in Appendix C. It can be seen that the pattern of activity is similar to that of the Arctic Terns, there

FIGURE 12.

Average number of feeds per hour taken throughout the day by Tern chicks, during observations in 1961 and 1962.

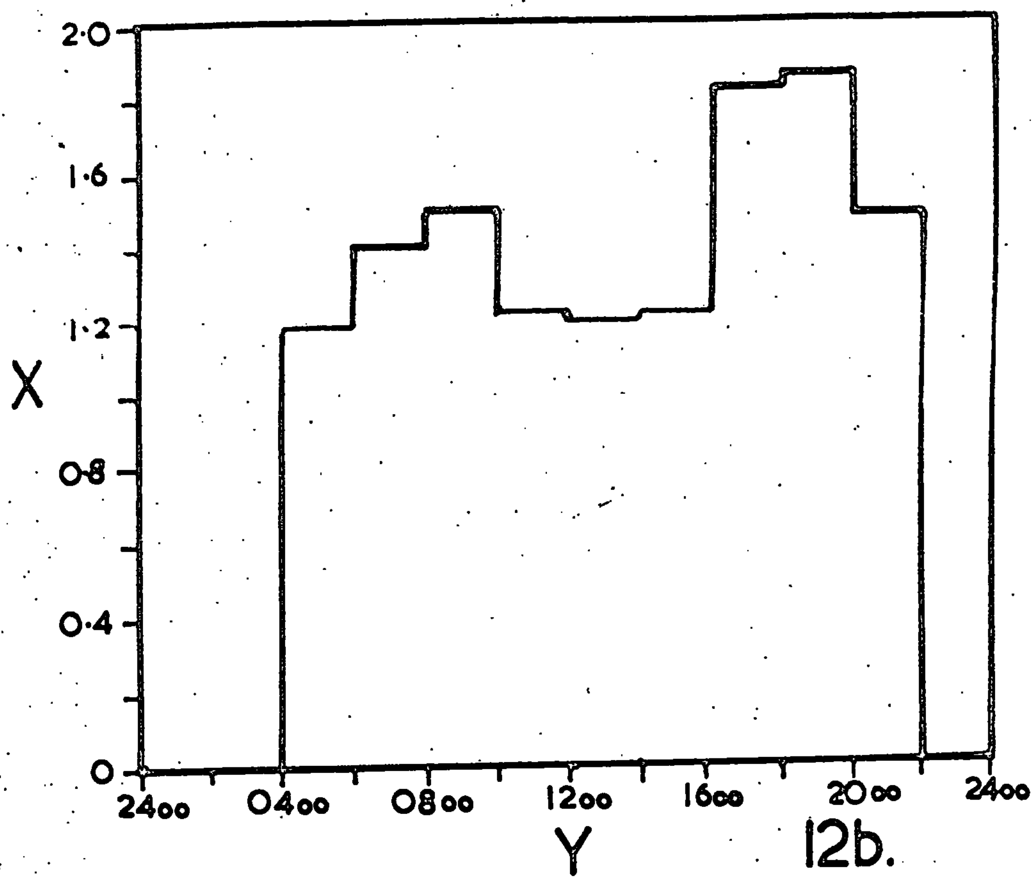
a = Arctic Tern.

b = Common Tern.

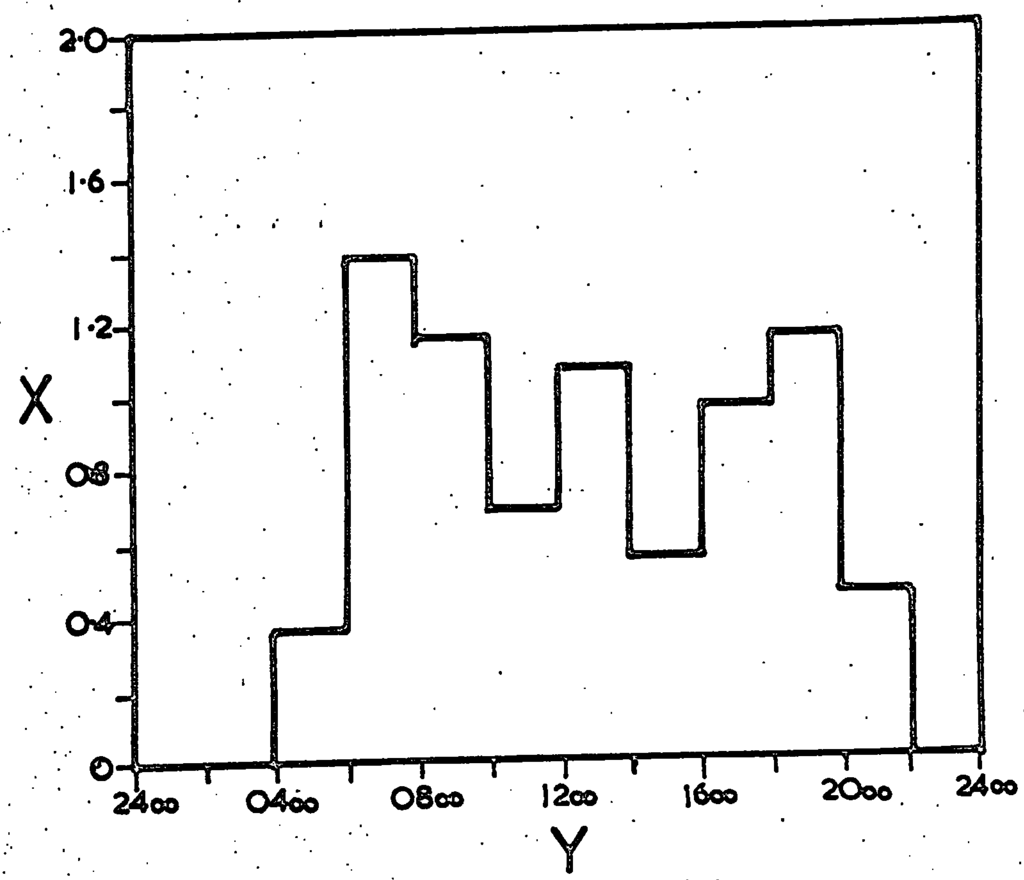
x = Average number of feeds taken per hour.

y = Hour of day.

12a.


2·0
1·6
1·2
0·8
0·4
0
X
2400
0400
0800
1200
1600
2000
2400
Y

12b.


2·0
1·6
1·2
0·8
0·4
0
X
2400
0400
0800
1200
1600
2000
2400
Y

being peaks of activity in the early morning, and the evening. In addition there is a possibility of a third active period about midday, but further observations are required to establish this point.

Kittiwake. *Rissa tridactyla.*

Two methods were used to assess the variation in the feeding activities of Kittiwakes throughout the day. Firstly, direct counts of the number of birds at, or about, a particular group of nests throughout the day, were made on a number of different dates, and secondly observations were made after the chicks had hatched of the times individual chicks were fed.

COUNTS OF THE VARIATION IN THE NUMBERS OF BIRDS ATTENDING THE COLONY.

Two study areas were chosen for these observations. Nearly all the counts were carried out at the 'Stack' colony where 127 pairs of birds could be kept under observation, but in addition a few counts were made at the 'East' colony, which was an isolated group of 18 pairs of birds some way from the main group.

The numbers of birds at the nest sites, the numbers standing out on the rocks and the cliff-tops surrounding the colony, the numbers resting on the sea within approximately 200 yards of the cliffs, and the numbers flying about the colony at the time of the count, were all recorded, counts being taken every 15 or 30 minutes. The number of birds away at any one time were estimated from the difference between the number of birds in the vicinity of the colony and the total numbers of birds occupying nest sites in the colony. Figure13 shows the average number of birds away throughout the day during April and May. The figures are based on at least five separate counts on different days in each month. Although not all the records were maintained for the full period of daylight each hour was covered on at least four occasions. It can be seen that following the return of the birds to the colony in the early morning, there is a further outward migration later in the morning, followed by a period of maximum attendance around midday. From 1500 hours the number of birds away increases steadily until all have left by 2200 hours. In April (Figure 13A) it is probable that an afternoon increase of birds leaving and returning to the colony on feeding flights is masked by the early start to the evening migration. Such an afternoon peak of activity is shown in Figures 13B, representing activity in May. Only the afternoon was covered adequately in these counts, but they show a definite increase in returns between

FIGURE 13.

Kittiwake feeding activity. Average number of birds away from the colony throughout the day (as a percentage of the total numbers in the colony.)

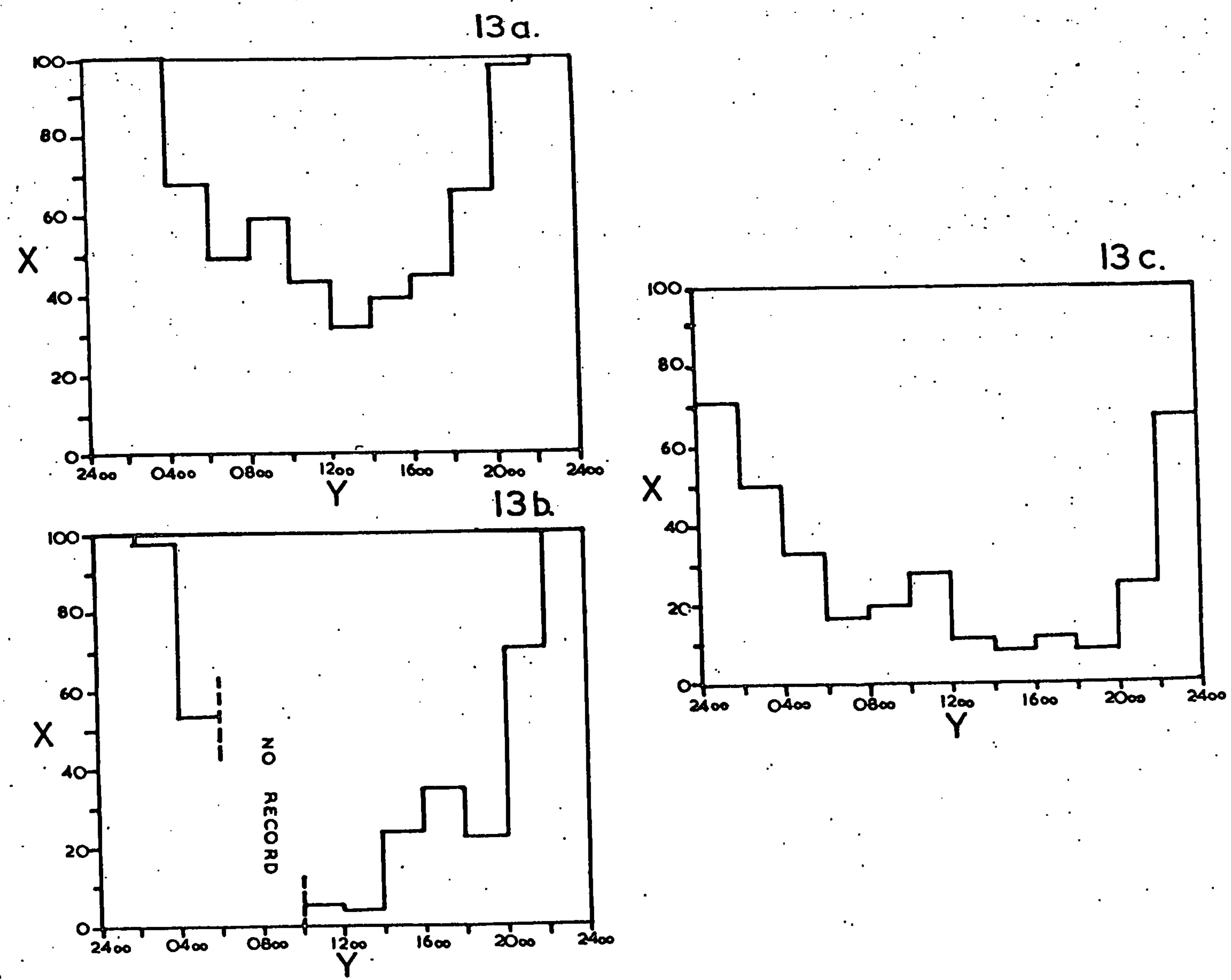
a = April

b = May

c = July

x = Percentage of birds away.

y = Hour of day.


13a.
13b.
13c.
X
Y
100
80
60
40
20
0
2400
0400
0800
1200
1600
2000
NO RECORD

1300 and 1800 hours, followed by a period of high attendance at the colony before the evening emigration commences. During this month, and in June, the number of birds present at the colony at any hour of the day is in general higher than in April, when the nesting activities had only just commenced. Figure 13C is the average of two counts taken at the 'East' colony during July. The birds were counted only every second hour at this time, thus the data was less comprehensive than that previously obtained. Nevertheless the morning peak of activity is clearly indicated, but there is little more than a suggestion of an afternoon increase in the number of birds away from the colony.

If it is assumed that the birds away from the colony are away feeding, it appears from these data that there are two main feeding periods during the day, one in the mid-morning, and one in the late afternoon. These are, however, only indicated by the general trends in the movement of the birds. Only on two occasions were all the birds in the vicinity of the colony (May 1200 hours). Generally at least 30% of the birds were absent at all times. The fact that only about 60% of the birds return in the early morning indicates that the rest may be fishing at that time, and that their return later may be reduced to some extent by the movement of the first-returning birds out to feed later in the morning.

OBSERVATIONS BASED ON THE FEEDING OF INDIVIDUAL CHICKS.

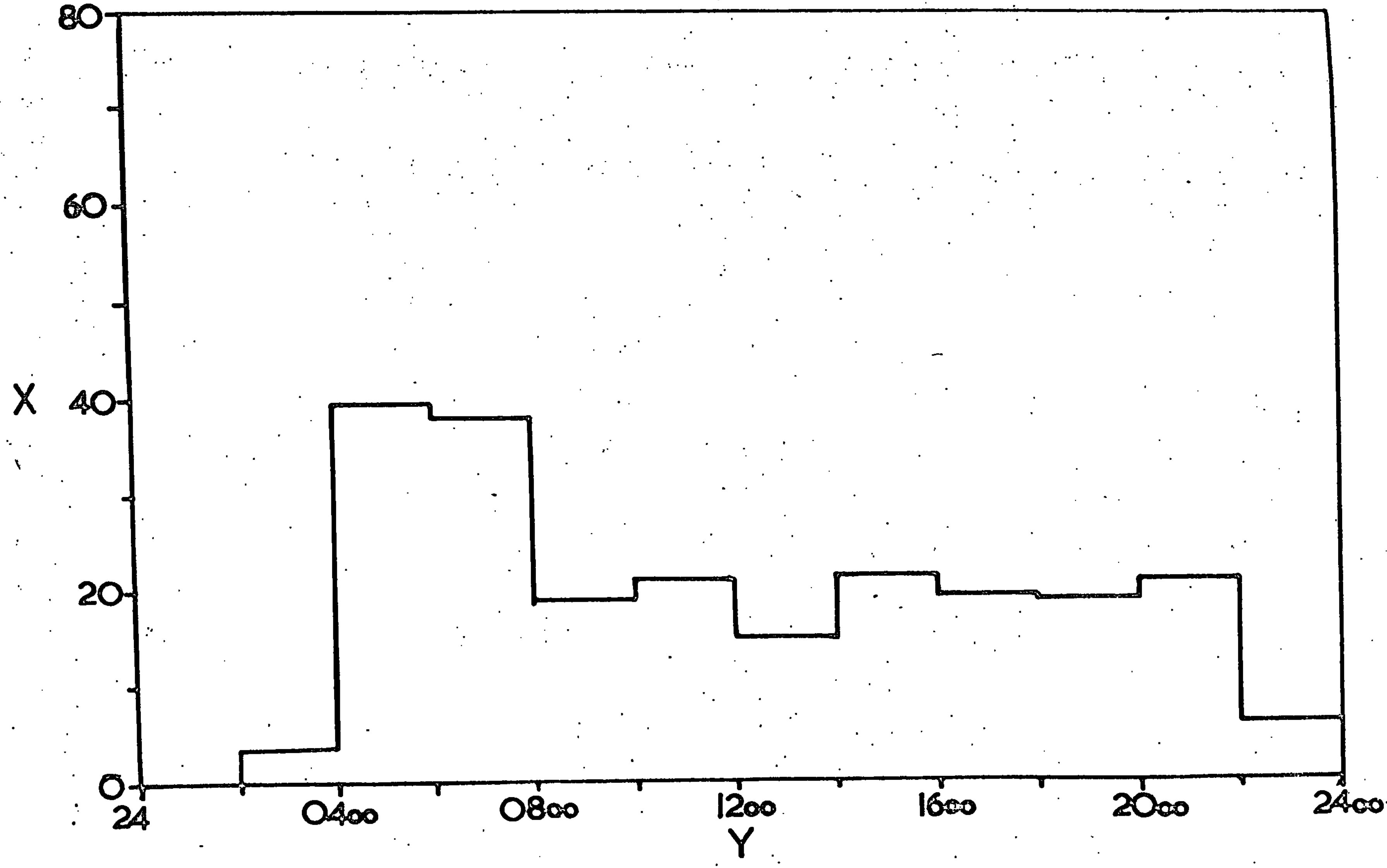
After the chicks were hatched, counts were taken at a selected number of nests over a number of hours, and the time of feeding of the chicks was noted. As well as yielding data on feeding rates of chicks, this information gave a good indication of the time of day the parents' fishing activities took place. The times of return to the nest of the parent birds were noted in these counts, in addition to the times of feeding of the chicks. Figure 14 shows the average number of birds returning to the nest over two-hourly periods as a percentage of the total number of breeding birds under observation. For this purpose only those returning birds which subsequently fed the chicks have been included, thus ensuring that the birds were in fact returning from foraging, rather than at the conclusion of other activities. The data for each period is the average of at least four counts over the appropriate hours of the day, and the hours from 1300 to 1800 are the average of seven counts. The results show a good measure of agreement with those obtained from counting the total numbers attending the colony, and tend to emphasize the general trends indicated previously. It

FIGURE 14.

Kittiwake feeding activity. Proportion of birds returning to the colony from feeding trips throughout the day.

x = Proportion of birds returning, as a percentage of the total numbers under observation (average over 2-hourly periods).

y = Hour of day.



80
60
X
40
20
0
24
04oo
08oo
12oo
16oo
20oo
24oo
Y

appears that the early morning is the time when the greatest degree of fishing activity takes place, the numbers out fishing falling off about 0900 hours, rising again to a slight peak in mid-morning, and then dropping to a low level of activity about midday. Throughout the afternoon there is a slight rise in activity up to 1800 hours, thereafter remaining at the general level of about 20% of the birds engaged in fishing activity until dusk (2230-2330 hours). The counts were all taken within a 25 day period from the 5th July.

This would appear to be a much more accurate method of assessing fishing activity than that of conducting general activity counts, but it has the limitation of being applicable only when the chicks are at the nest, since the only way of being certain that the adult has been fishing is to see it feed the chick on return.

The Puffin. *Fratercula arctica*.

In order to assess the feeding activity of Puffins, counts were made of the numbers of birds attending a relatively small colony. The study area was on the north-west corner of the Inner Farne Island, where there was an isolated group of approximately 220 occupied burrows. The entire colony could be kept in view from the top of a stone tower some 150 yards away; from this systematic counts were taken without in any way disturbing the birds. The birds standing about the burrows, and on the 'club' area, flying, and resting on the water below the cliffs, were all counted at regular intervals throughout the day. The 'club' area was a point of rock on the cliff tops in the centre of the colony, and was frequented regularly by most of the resting birds throughout the day. The nature of the diurnal fluctuations in the numbers of birds attending the colony was independant of the actual numbers of birds in the colony (which it was found difficult to estimate), and gave a good indication of when most of the birds were away from the colony and presumably feeding. Figure 15, showing the fluctuations in the number of birds attending the colony on the 9th May 1961, indicates the typical diurnal rhythm in the numbers attending. There are very few birds visibly present during the early morning, although no doubt there were large numbers of incubating birds present but uncounted, but the numbers gradually build up until 0900 hours. Thereafter there is a decrease in the numbers present until 1300 hours, followed by a slight increase during the subsequent hour, and a further decrease into the late afternoon. From 1700 hours onwards there is a rapid increase in the numbers of birds present, which reaches a peak at 2000 hours. This is

FIGURE 15.

Fluctuations in the numbers of Puffins attending the colony throughout the day.

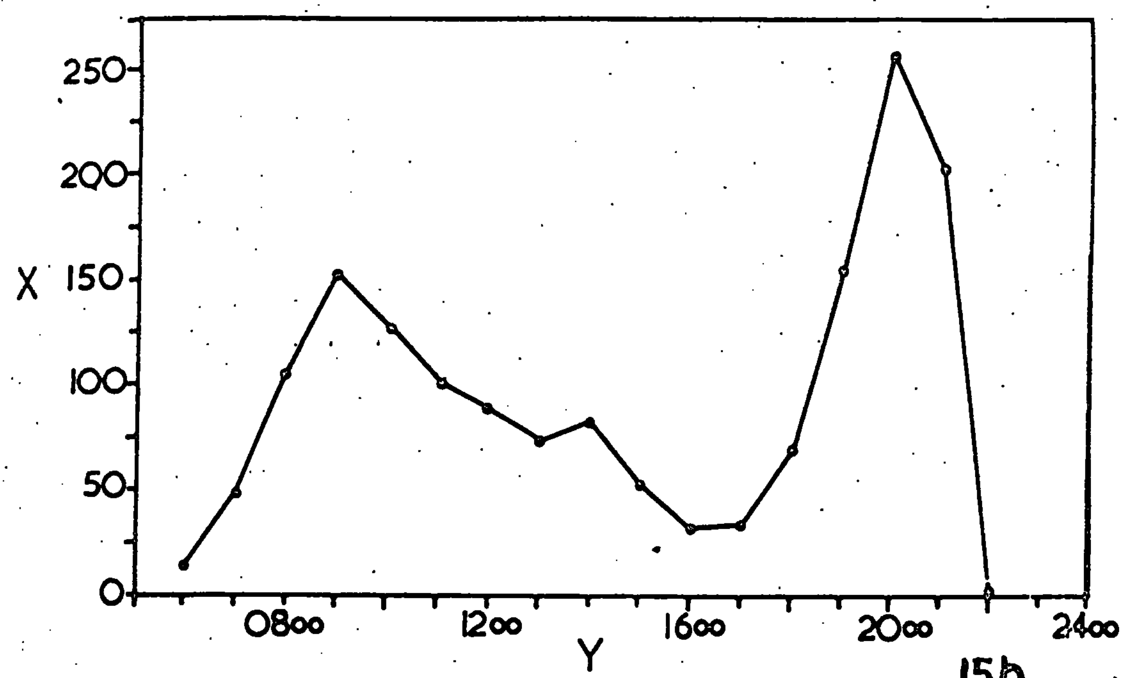
a = Counts made on 9/5/62.

b = Counts made on 17/5/62.

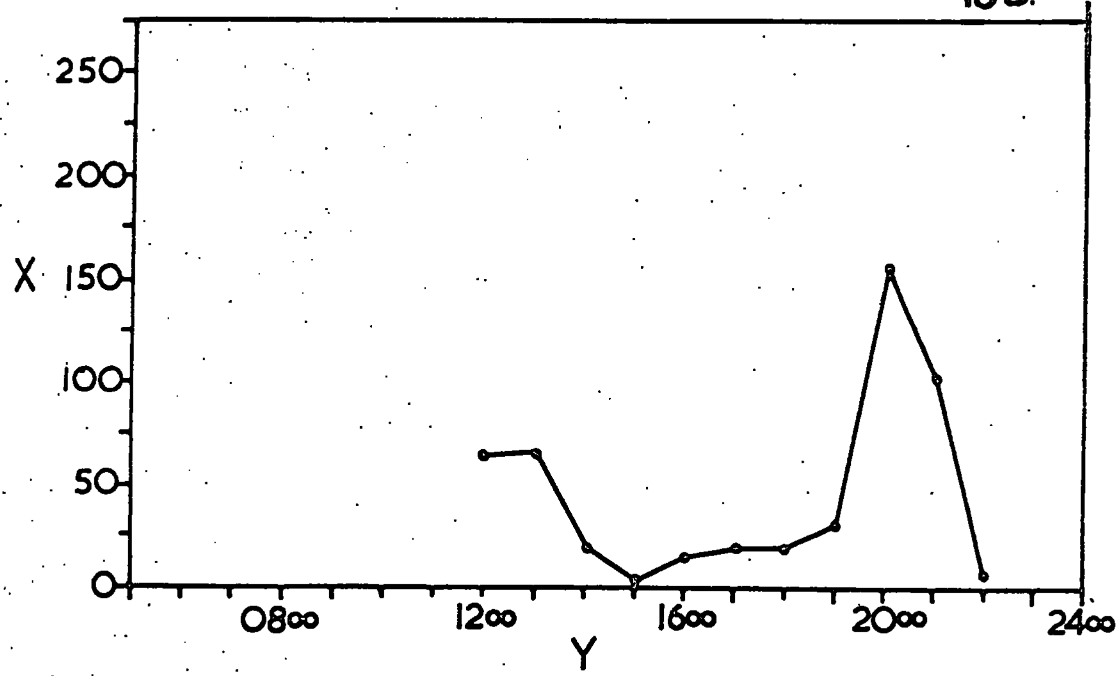
x = Number of birds attending the colony.

y = Hour of day.

15a.


250
200
X 150
100
50
0
0800
1200
1600
2000
2400
Y

15b.


250
200
X 150
100
50
0
0800
1200
1600
2000
2400
Y

followed by an equally rapid decrease in numbers until by 2200 hours the colony is deserted, except of course, for those birds incubating in the burrows. Since dawn at that time of year is at approximately 0300 hours it would seem that the birds may well spend one or two hours feeding before coming into the colony. There would appear to be a rest period around 0900 hours, when very few of the birds are away, followed by a period of gradually increasing activity. This is interrupted to some extent around midday, and then resumed throughout the afternoon. Very little fishing appears to be done in the evening.

OBSERVATIONS ON THE FEEDING OF INDIVIDUAL CHICKS.

On two occasions watches were made, from a hide, on a group of burrows in a Puffin colony, the first covering 12 hours, from 0500 to 1700 hours, and the second covering the full daylight period from dawn to dusk. Both watches were undertaken in late June when most chicks were between two and three weeks of age. In all, the entrances of four burrows containing chicks were in view from the hide, and the times the adult birds entered the burrows with fish were noted. The results of these watches are given in Figure 16, and the information on which this is based is given in Appendix J. Despite the small number of observations on which these figures are

FIGURE 16.

Puffin. Average number of feeds per hour brought to burrows throughout the day. June 1962.

x = Average number of feeds per hour.

y = Hour of day.

FIGURE 17.

Guillemot. Fluctuations in the numbers of Guillemots attending a small colony on Brownsman Island throughout the day 30/4/63.

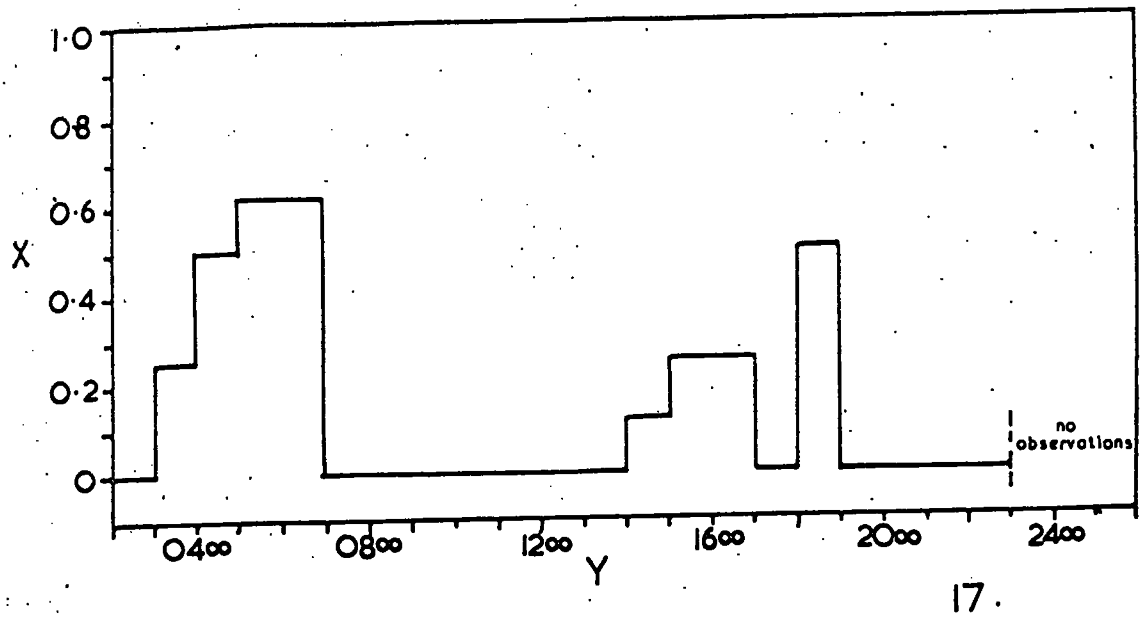
Weather Wind NW Force 3-4.

Fine and Sunny.

x = Number of birds present at the colony.

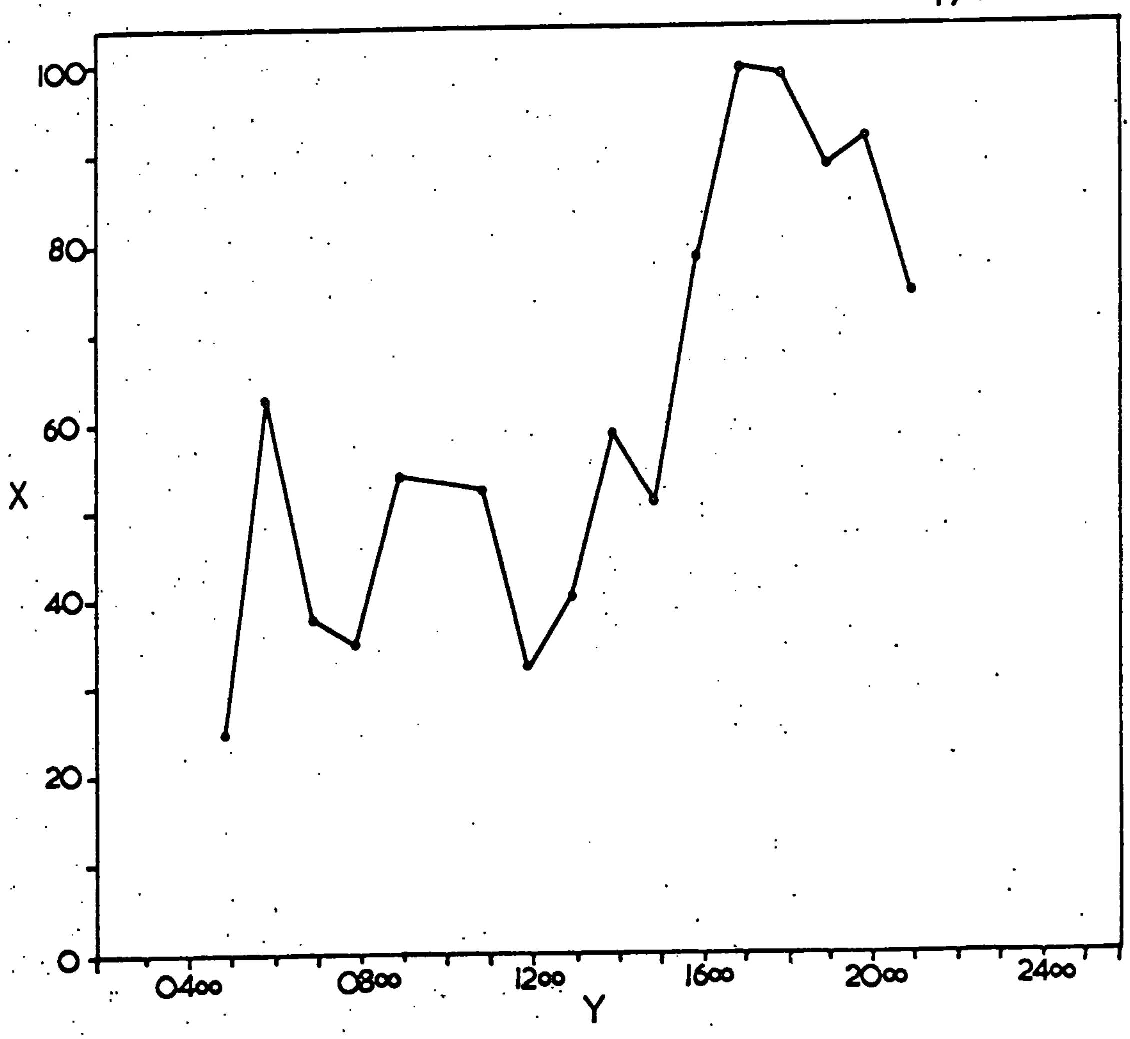
y = Hour of day.

16.



1·0
0·8
0·6
0·4
0·2
0
X
no observations
0400
0800
1200
1600
2000
2400
Y

17.



100
80
60
40
20
0
X
0400
0800
1200
1600
2000
2400
Y

brood it can be seen that the pattern of early morning, and afternoon, feeding is again indicated, with little feeding activity taking place in the late morning, and evening.

These results are comparable to those given by Myrberget (1962) who found the feeding activity of the Puffins to be most intense early in the morning, followed by a period of quiescence around 0900 hours, and thereafter maintained at a fairly steady, relatively low, level, until late afternoon. He found however little evidence of any diminution in activity about midday.

<u>The Guillemot. *Uria aalge*.</u>

Only on very few occasions was it possible to undertake the protracted observations necessary to assess the diurnal rhythms in the activity of Guillemots. The outer islands, where nearly all the Guillemots bred, were generally only visited for short periods. However during April 1963 a longer visit was made which enabled counts of the numbers of Guillemots, present on the nesting ledges, to be made at intervals throughout the hours of daylight. At this time of year the birds were occupying the breeding ledges, but no eggs had yet been laid. An isolated group of approximately 50 pairs of birds was selected for observation, but the exact number of birds could not be assessed due to the rapid changes of position, arising by territorial squabbles, amongst the birds on the favoured ledges. Figure 17 shows the results of a count, taken every hour, of the number of birds on the ledges. The weather was fine, with a fairly strong north-west breeze.

The general pattern of considerable morning activity, followed by a gradual falling off towards evening is again demonstrated. As the Guillemots generally hunt over feeding grounds at some considerable distance from the islands, and are only rarely seen fishing within sight of the colony (see description of feeding ranges, below) than it seems reasonable to assume that during the morning hours many of the birds are away fishing, and that the build up in numbers during the afternoon marks the return of these birds and a general diminution in feeding activity.

The Shag. *Phalacrocorax aristotelis*.

Since no large colonies of these birds nested on the Inner Farne, where most observations were made, the information obtained on the diurnal rhythms in feeding activity was limited. Counts were made of the number of Shags sitting out on the rocks below the cliffs on the Inner Farne, and on the water in the immediate vicinity. This area was used as 'club' ground by a number of both breeding and non-breeding birds, thus the counts gave reasonable information on the periods of rest taken by the Shags during the day. Additional information was obtained from observations made at individual nests of the attendance of the parent birds throughout the day, and on one occasion a watch was kept of the number of birds leaving, and returning to, a large colony of Shags on the outer islands.

COUNTS OF BIRDS RESTING ON 'CLUB' AREA THROUGHOUT THE DAY.

Figure 18 showing the number of birds resting on the 'club' area, gives indication of resting periods throughout the day. Thus it is apparent that in the early afternoon many of the birds are resting, whereas in the early morning, late afternoon, and evening few of the birds are on the 'club' area. There is no indication however, whether or not the birds are away fishing during these periods. The information is based on the average of 6 counts made during April in 1961 and 1962.

COUNTS OF THE NUMBER OF BIRDS ATTENDING A LARGE COLONY ON THE OUTER ISLANDS.

In April 1963 a stay on the outer islands made it possible to conduct extended watches on a large colony of Shags. A group of 47 pairs of birds was kept under observation throughout the hours of daylight on two separate

FIGURE 18.

Shag feeding activity. Average number of birds resting on the 'club' area throughout the day.

x = Number of birds.

y = Hour of day.

FIGURE 19.

Shag feeding activity. Average number of birds away from the colony throughout the day (as a percentage of the total numbers in the colony).

x = Percentage of birds away.

y = Hour of day.

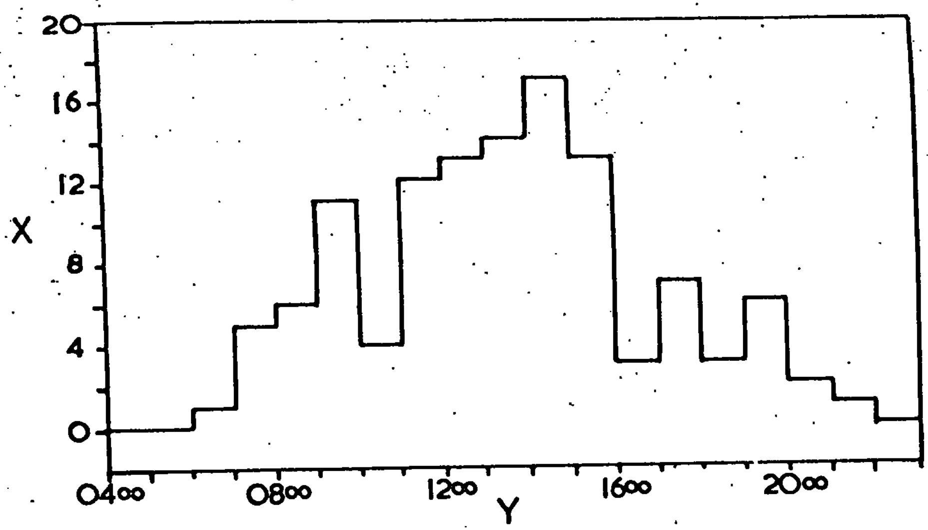
FIGURE 20.

Shag feeding activity. Average number of birds returning to the nest per hour throughout the day. (based on observations at two Shag nests on numerous occasions during 1961 and 1962.

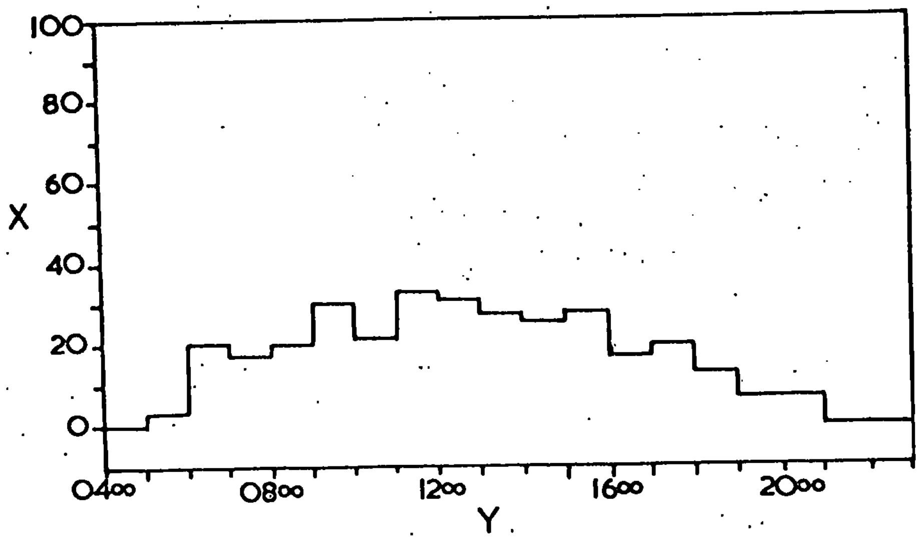
x = Average number of birds returning to the nest per hour.

y = Hour of day.

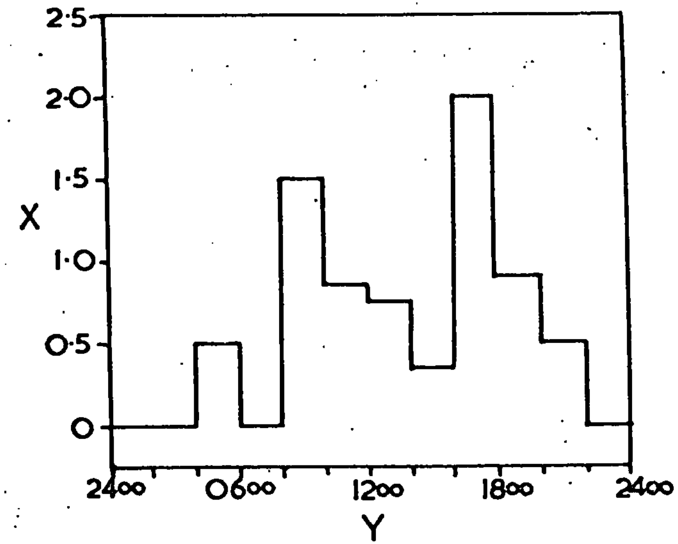
18.


20
16
12
8
4
0
X
0400
0800
1200
1600
2000
Y

19.


100
80
60
40
20
0
X
0400
0800
1200
1600
2000
Y

20.


2·5
2·0
1·5
1·0
0·5
0
X
2400
0600
1200
1800
2400
Y

days, and the numbers of birds at the nest, and resting on 'club' areas in the vicinity of the colony were counted. As the number of pairs nesting in the area under observation was accurately known, it was possible to estimate the number of birds away at any one time with reasonable accuracy, and Figure 19 gives the average of the two days observation in terms of the number of birds away at any one time. Counts of the numbers of birds at the nest, on the 'club' areas, and on the water in the vicinity of the colony were taken every hour from dawn till dusk. From the information it would appear that there is no one period of the day when most of the birds are away feeding. The greatest numbers are away around midday, when over 30% are absent from the colony, but it is possible that the birds may then be sitting out on some area out of the view of the observer, rather than fishing. There is evidence of a small exodus in the early morning, about 20% of the birds leaving in the hour after first light, but the number absent built up gradually to the midday peak, thereafter falling off gradually until by 2115 hours all the birds were present at the colony. The absence of any large fluctuations in the numbers of birds away suggests that the numbers leaving may be approximately balanced by the numbers returning to the colony throughout the day.

OBSERVATIONS AT THE ATTENDANCE OF BIRDS AT INDIVIDUAL NESTS.

More accurate information as to the times of absence of individual birds from the nest site was obtained by making day-long watches of the activity at specific nests. During 1961 and 1962 a number of watches were undertaken on two nests situated close together, and the times of departure and arrival of the adult birds noted. Figure 20 shows the average number of birds returning to the nest per hour throughout the day. Each hourly figure is the average obtained from at least five watches made through that period. The figures are necessarily low due to their being only four adult birds under observation. If it is assumed that the birds returning have been away feeding, then these results suggest that there are three main feeding periods throughout the day:- viz. in the early morning, between 0600 and 0900 hours, in the late morning between 1100 and 1300 hours, and in the early afternoon between 1400 hours and 1600 hours. In view of the information given in Figures 18 and 19 however, concerning the fluctuations in the number of birds at rest on the 'club' areas, it is probable that during the latter two periods the birds are frequenting these 'club' areas, as well as fishing.

COUNTS OF THE NUMBER OF BIRDS LEAVING, AND RETURNING TO, A LARGE COLONY.

During April 1963 observations were made on the fluctuations in the numbers of birds leaving, and returning to, the large colony of Shags on Staple Island in the outer group. The vast majority of the birds from the colony fished over grounds to the north of the islands, and, to reach these fishing grounds, invariably took a route to the west of Staple Island, which carried them past the north end of the nearby Brownsman Island. Thus an observer, positioned on Brownsman could easily count the number of birds leaving the colony. Counts of the numbers of birds leaving, and returning to, the colony were taken for five minutes in every half hour, on the 30th April 1963. Figure 21 gives the results obtained in terms of the average over each hour. The main exodus of birds started just after 0600 hours. Thereafter much lower numbers were counted, between 5 and 15 leaving per 5 minutes, until 1230 hours, followed by a period when very few birds were observed flying until by 1600 hours about 10 birds were observed leaving per five minute period. This level was maintained until 1830 hours, after which there was a decrease with the onset of dusk. The number of birds returning followed a similar pattern, but total numbers seen

FIGURE 21.

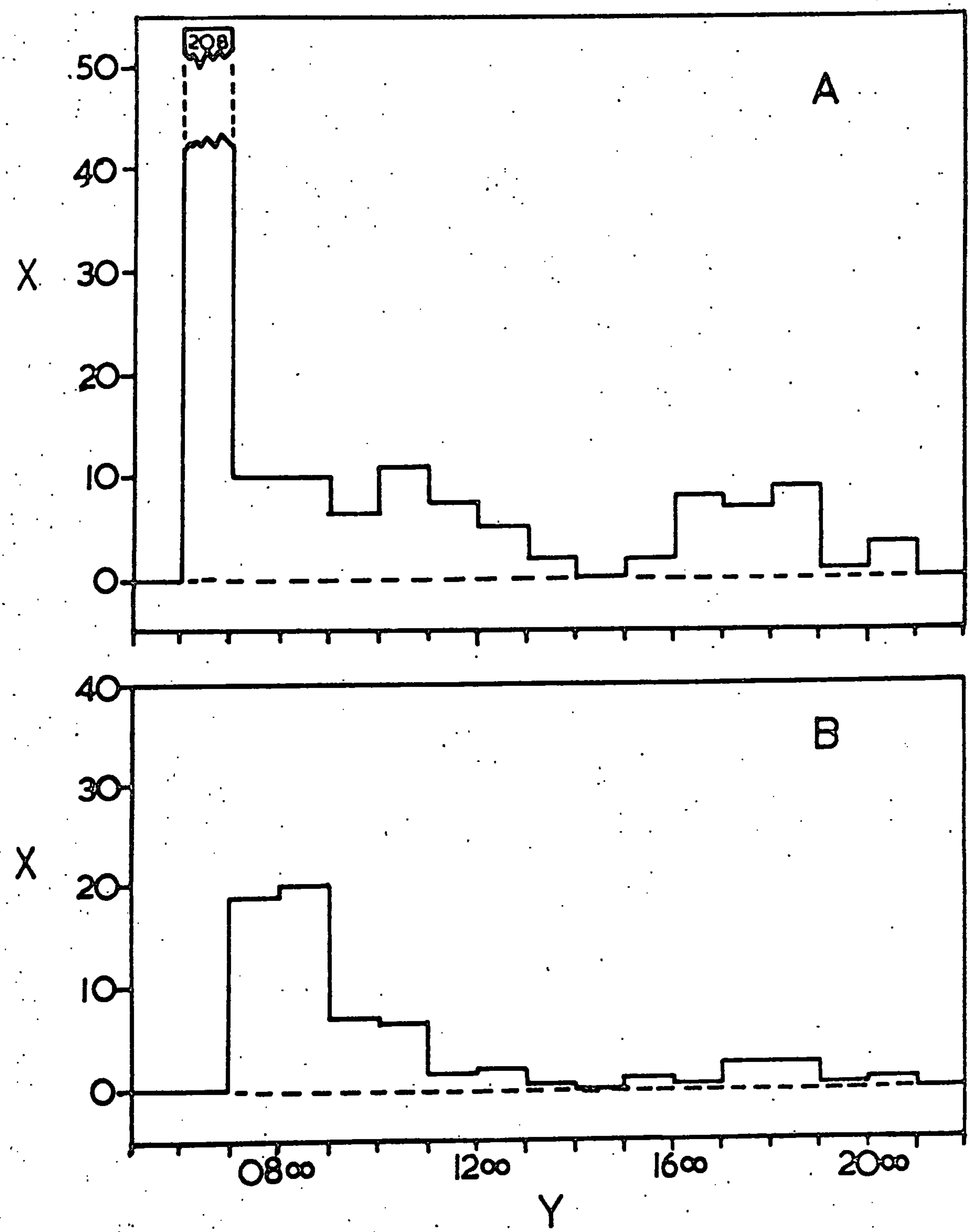
Counts of the number of birds leaving, and returning to, a large colony throughout the day.

x = the number of birds leaving or returning to the colony per five minutes.

y = hour of day.

A = records of the numbers leaving the colony.

B = records of the numbers returning to the colony.


208
A
B
X
50
40
30
20
10
0
08⁰⁰
12⁰⁰
16⁰⁰
20⁰⁰
Y

were much fewer, suggesting that the birds may return to the colony by other routes. The greatest numbers returning were seen about one hour after the large outward flight in the early morning, suggesting that little more than an hour had been spent in fishing.

The information obtained, although somewhat limited, suggests that the major feeding activity of the Shags takes place in the early morning, that it may continue for most of the morning and in the late afternoon and early evening to a lesser extent, but that there is a period of inactivity in the early afternoon, extending approximately from 1200 hours to 1500 hours.

DISCUSSION OF THE COMPARATIVE DIURNAL FEEDING RHYTHMS OF FARNE ISLANDS SEA-BIRDS.

In all the species studied there is strong evidence of diphasic activity with periods of activity in the morning and evening separated by a period of rest in the early afternoon. The species studied therefore conform to the typical rhythmic pattern of diurnal activity exhibited by most avian species. Palmgren (1949) in a study of the rhythms of activity and rest in birds found evidence of the diphasic pattern in many species of widely differing families, and states that " a tendency towards diphasic sleep is inherent in most birds, indicated by their afternoon period of inactivity". In addition he found that in higher latitudes periods of activity were extended to conform with increasing day-length, a phenomenon which was observed during the present study. Thus the Kittiwakes and Shags commenced their morning's activities half an hour earlier in May than they did in April, and correspondingly ceased their evening activities earlier in April than in May.

Interspecific differences are, however, present within this general diphasic activity pattern. Thus the terns have marked morning and evening activity peaks, but the evening peak is more pronounced. The Kittiwake, on the other hand, has the greatest peak of activity in the morning, although maintaining a fairly pronounced evening peak. The evidence for the activity patterns of Puffins and Guillemots was less reliable, but pointed to a pronounced activity level in the morning, with only a small concentration of activity in the evening. Similarly the Shags appeared to do nearly all their feeding in the early morning, and had only a low level of activity in the evening. These differences may be explained with reference to the different feeding methods of the various species. The terns, bringing a single fish at a time to their young, need to exploit a large part of the daylight hours for fishing purposes. In contrast the Shags, which take a large number of fish at each feed, appear to be capable of satisfying their needs, and those of their young, by feeding only once, or at the most, twice per day. In between these lie the Kittiwakes, and the Auks, which make several trips per day. Thus the majority of Shags can feed in the morning, and remain comparatively inactive for the rest of the day, whereas the terns, after a mornings fishing, followed by the afternoon rest, resume their fishing activities with increased intensity in order to obtain sufficient food to maintain them through the prolonged period of inactivity during the hours of darkness. In some small passerines the search for food may be so intense as to preclude altogether the possibility of an afternoon rest period, and the diphasic rhythm may never appear, as was demonstrated by Kussimoto (1941) in a study of the Willow Warbler.

It is more probable that the feeding rhythms investigated are derived from the general biological rhythm of activity in the birds than that they are brought about by similar diurnal fluctuations in the availability of prey. Thus Cloudsley-Thompson (1961) states that many of the activities of birds show a morning peak, afternoon trough and minor evening peak, and quotes examples of such fluctuations in the song intensity of Passerines. Rollin (1958) made observations on the levels of vocal activity in the Arctic Tern colonies on the Farne Islands, and found that these were correlated with the varying levels of physical activity among the birds, there being a marked diminution in vocal activity in the early afternoon, and between 2300 hours and 0900 hours. Cullen (1954), in describing the diphasic rhythm patterns in feeding activity of sea-birds on Jan Mayen Island in the Arctic, found that marked rhythms persisted even in the absence of extreme changes in light intensity. He thought however, that light was probably the most important factor in causing a bird to roost, and that the other parts of the daily rhythm are probably prompted by internal physiological drives i.e. hunger.

THE FEEDING FREQUENCIES AND DAILY FOOD INTAKE OF THE YOUNG.

The variation in feeding methods of the different species studied must result in differing feeding frequencies, i.e. the number of feeds taken by the chicks over a specific period. Obviously the species which take only a single fish at a time, must hunt more frequently than those species which take many fish during one hunting period. Estimation of the feeding rates of each species had to be based entirely on evidence obtained concerning the feeding of the chicks, due to the impossibility of observing the adults at their feeding grounds. However the number of feeds per day taken by the chicks of each species provides data for interspecific comparisons of feeding frequencies, which probably bears a direct relation to the comparative feeding frequencies of the adults. Feeding frequencies were estimated by direct observations on individual nests, note being taken of the times each chick was fed. In addition some information was obtained by weighing selected individual chicks at regular intervals throughout the day, and noting any increase in weight as evidence of the chick having been fed in the period preceding weighing. This latter method was unreliable, due to the great disturbance caused to the birds by the weighing process and was only used where the method of direct observation was inapplicable.

1. ESTIMATES OF FEEDING FREQUENCY AND DAILY FOOD INTAKE BY DIRECT OBSERVATION, AND THE COLLECTION OF FOOD SAMPLES.

Results.

Table 56 gives the information obtained, for all species examined, on the average number of feeds per day, and the daily food intake. The amount of food consumed

TABLE 56. Estimation of the number of feeds taken per day, and the daily food intake, of chicks of various Farne Islands sea-birds, based on direct observations, and the collection of food samples.

SPECIES	AVERAGE NUMBER OF FEEDS TAKEN PER INDIVIDUAL CHICK PER DAY.	NUMBER OF CHICKS PER BROOD.	AVERAGE NUMBER OF FEEDS PER BROOD PER DAY	AVERAGE WEIGHT OF PREY TAKEN PER FEED (g.)	AVERAGE DAILY FOOD INTAKE PER INDIVIDUAL (g.)
Arctic Tern	26	1 or 2	29	2.4	63.4
Common Tern	16	2 or 3	24	3.9	62.4
Sandwich Tern	14*	-	-	2.6	36.4
Kittiwake	4	-	-	26.3**	105.2
Lesser Black-Back Gull	2	-	-	17.8**	36.6
Puffin	3	-	-	9.5	28.5
Shag	3	-	-	54.5**	163.5
Guillemot	2x	-	-	7.7	15.4
Cormorant	2xx	-	-	197.0	394.0

* 1. estimated from observations made over 7 hours of the day only.

** 2. estimated from regurgitation samples (see text).

x 3. based on data from Belopolskii (1957)

xx 4. based on data from Van Dobben (1952) and du Plessis (1957).

per day by the young can be estimated from a knowledge of the feeding frequencies, and the average weight of prey taken. Thus in the tern species, which are generally fed a single fish at a time, the daily food intake can be estimated directly from the average number of feeds taken per day, and the average weight of individual prey, as detailed in Section 1. Similarly with the Auks, where the average number, and weight of fish per meal has been assessed, the daily food intake can be estimated from the feeding frequencies. With those species which are fed by regurgitation however, e.g. Kittiwakes, Lesser Black-back Gulls, and Shags, the average weight of each meal taken is more difficult to assess, as there is no means of knowing whether the regurgitation samples collected represent a full meal, or not. Estimates of the weight of the average meal have been made however by taking the average weight of the regurgitation samples collected from these species. The frequency distributions of the weights of the samples collected both as found, and estimated true weight, on which these averages are based, are given in Appendix D. The products of these averages, and the number of feeds per day, have been taken as the daily food intakes for these species. The average number of feeds per day are based in most cases on at least 6 watches covering the full daylight period, during which time all feeds taken by the chicks were noted. In the case of the Sandwich Tern however only two watches were undertaken, covering the early morning and late afternoon in each case, and the number of feeds taken per day was extrapolated from the average number of feeds per hour taken over those periods. The feeding frequencies of the Guillemot and Cormorant were not assessed during the present study, and the figures given are based on information from previously published work.

The average number of feeds per brood is given for the Arctic Tern and Common Tern, i.e. those species where an increase in the number of chicks entails a corresponding increase in the number of feeding journeys. The average figures include both single and multiple broods. With those species fed by regurgitation the parent will generally regurgitate food to each chick, of a multiple brood, in turn without further fishing, thus no extra journeys need be made.

Discussion.

A point of interest is that the number of feeds taken by individual Common and Arctic Tern chicks differed quite markedly, the former taking an average of 16 feeds per day, and the latter 26. When the number of feeds per brood are considered however, there is very little difference, the feeding frequencies then being 24 and 29 per day respectively. Thus the adult Common Terns did not undertake many more feeding journeys than the Arctic Terns, although they raise more chicks per brood. The smaller number of fish given to the individual Common Terns might indicate that the individual prey taken are larger since the growth rates of the two species are very similar (see Section 3). However no information was obtained concerning the size of prey taken by Common Terns.

The figures estimated for the average daily food intake do not seem particularly reliable. Thus the figures of over 60g. obtained for the Common and Arctic Terns seem very high for chicks which reach only 100-120g. weight before fledging. Similarly the figures for the Lesser Black-back Gull, Puffin and Guillemot appear to be very low, even for very young chicks.

Estimation of the variation of food intake of the chicks with age, based on direct observation.

Table 57 gives the average number of feeds per day, and corresponding daily food intake of chicks of known age of the Arctic Tern, Common Tern and Kittiwake. Only the latter part of the growth period was covered for the Common Tern, but it illustrates the probability of a

TABLE 57 A. Arctic Tern. Number of feeds taken per day by individual chicks of known age.

AGE OF CHICK (DAYS)	NUMBER OBSERVED	AVERAGE NO. OF FEEDS TAKEN OVER 24 HOURS	DAILY FOOD INTAKE (g.)
1-2	3	13.7	33.4
9	2	53.5	130.5
10	1	31	74.6
12	1	31	74.6
22	1	12	29.3
23	1	14	34.2

TABLE 57 B. Common Tern. Number of feeds taken per day by chicks of known age.

AGE OF CHICK (DAYS)	NUMBER OBSERVED	AVERAGE NO. OF FEEDS TAKEN OVER 24 HOURS	DAILY FOOD INTAKE (g.)
21	2	14	54.6
22	1	7	27.3
23	5	12.2	47.6
24	3	12.7	49.5
25	2	20.5	80.8
26	2	20.5	80.8

TABLE 57 C. Kittiwake. Average number of feeds per day of chicks of known age.

AGE OF CHICK (DAYS)	NUMBER OBSERVED	AVERAGE NO. OF FEEDS TAKEN OVER 24 HOURS	DAILY FOOD INTAKE (g.)
0-4	10	4.3	113.1
5-8	2	4.0	105.2
9-12	3	5.7	140.9
13-16	2	4.5	118.3
16-20	4	5.2	136.8
20-28	3	3.3	86.8
28-36	9	3.2	84.2

diminution in the feeding rate at the time of fledging. Thus at 22 days, when most of the chicks first began to fly any distance, the number of feeds recorded fell off considerably. The Arctic Tern and Kittiwake both show the pattern of increasing feeding frequency over the first third of the growth period, followed by a gradual reduction in the number of feeds over the middle and latter parts of the period.

2. ESTIMATION OF FEEDING FREQUENCY AND DAILY FOOD INTAKE FROM VARIATIONS IN THE WEIGHT OF CHICKS OVER CONSECUTIVE LIMITED PERIODS.

In view of the unsatisfactory nature of much of the information obtained from direct observation an attempt was made to assess the food intake of chicks of various species by weighing selected individuals at intervals throughout the day. Increases in weight between one record and the next indicated that the chick had been fed during the interval. This method was used most frequently and successfully with chicks of the Lesser Black-back Gull, thus a full description of the method and the results obtained will be given for this species, followed by a summary of the results obtained by using the method for other species.

Estimation of daily food intake and feeding frequency of Lesser Black-back Gull chicks from variations in weight.

No direct observations were made of chicks at the nest in estimating the feeding frequencies of Lesser Black-back Gulls. A number of chicks were, however, weighed periodically over a 36 hour period, and the changes in weight recorded as shown in Table 58. As with the other species which were weighed in this manner, the birds lost weight generally over the recording period. This was possibly due to their regurgitating on being handled for weighing, rather than to lack of attention on the part of the parents, due to the disturbance caused in the colony. This second factor was apparently having some effect however, judging by the small amount of food fed to the two chicks in nest 28 over the full period. The amount of food taken by the chicks was estimated as the increase in weight recorded over a two-hourly period plus a figure for the average weight loss over such a period. The average weight loss was taken as the mean of the weight losses over those periods, both during the day and overnight, when no food was taken, and when the weight loss did not exceed 10g. During those periods when the weight loss exceeded 10g. it was assumed that the chicks had regurgitated a part of their stomach contents. As there was a long interval between the last weighing in the evening and the first the following morning (10 hours) the chicks had in some cases been fed prior to the morning weighing, thus the loss of weight overnight could not be taken as the standard for the periodic weight loss. The number of feeds, and weight of food taken, over the first 24 hour period from 0845 hours on the 18th August 1962 to 0845 hours on the 19th August, and over the second 24 hour period from 2045 hours on the 18th August to 2045 hours on the 19th August have been assessed separately although the periods overlap. Chick Number 63 could not be found on the second day, and thus the records for this cover only the first 24 hours. In all, then, 9 such 24 hour periods were recorded, during which 17 feeds were taken, giving an average number of feeds per 24 hours of 2. The average weight of food taken per meal was unsufficient to maintain the body weight of the chicks, even considering the losses due to regurgitation. Chick 90 did however gain weight over the full 36 hour period, despite a large regurgitation at the onset of the weighing, and it is probable that the amount of food taken by this bird most nearly represents the true daily food intake of an actively growing chick. During the first and last 24 hours of the period it took 93 and 105g. of food from three feeds, an average of 99g. per 24 hours. The daily food intake can be estimated more reliably from a plot of the food intake (x) against the weight change (y) over 24 hours. Figure 22 shows the plot, together with the regression line drawn to the data. The data used have been corrected to exclude losses due to regurgitation from the total food intake over the period. Any weight loss over 4g. higher than the average weight loss over the 2-hourly period between weighings, has been assumed to be due to regurgitation, and thus discounted. Table 59 shows the corrected values. The amount of food required for maintenance, when no weight gains or losses are made, i.e. the intercept of the regression line on the x axis, was 110g. The amount of food required to bring about a weight gain of 1g., after maintenance needs have been met, i.e. the slope of the regression line, was 2.5g. Thus, assuming an average daily weight increase of 23.6g. (see Section 3), the average daily food intake to meet all needs, would be 110 + (2.5 x 23.6)g. = 169g.

<u>Estimation of daily food intake and feeding frequency</u>

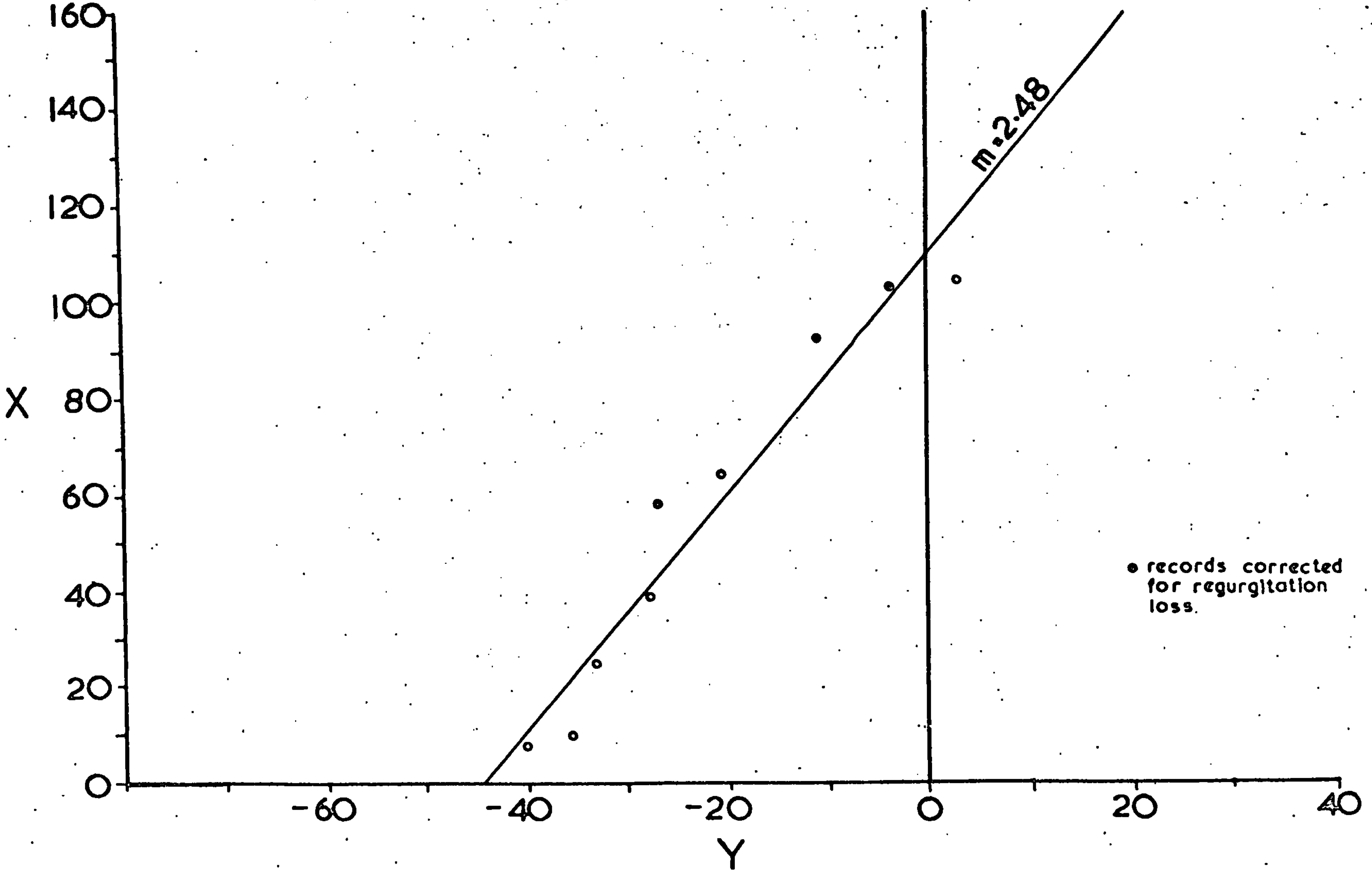
FIGURE 22.

Lesser Black-back Gull chicks. Periodic weighing of chicks in the field.

Correlation of food intake with weight change over 24 hours.

x = Food intake over 24 hours (g.).

y = Weight change over 24 hours (g.).



160
140
120
100
80
60
40
20
0
X
-60
-40
-20
0
20
40
Y
m=2.48
records corrected
for regurgitation
loss.

TABLE 59. Values for the food intake and weight change over 24 hours of Lesser Black-back Gull chicks in the field, corrected for losses due to regurgitation. (Weight in g.).

CHICK NUMBER.	FOOD INTAKE.	WEIGHT CHANGE.
64 (1st. 24 hours)	58.5	-27
90 (1st. 24 hours)	93	-11
63	102	-3.5
28A(1st. 24 hours)	39.5	-28
28B(1st. 24 hours)	25	-33
64 (2nd. 24 hours)	64.5	-20.5
90 (2nd. 24 hours)	105	+3
28A(2nd. 24 hours)	8	-40
28B(2nd. 24 hours)	10	-39.5

<u>of other sea-bird species by variations in weight over consecutive limited periods.</u>

Measurements of the variations in weight at intervals over 24 hours were made on a number of chicks of other species, in the same manner as that described above for the chicks of the Lesser Black-back Gull. Table 60 presents a summary of the results obtained. Full details of the actual weights on which these figures are based are given in Appendix E. Regression lines were derived, of food intake on weight change, for those species where three or more individuals were examined. The daily food intake has been estimated from the data given by the regression line, using the average daily weight increases of the various species as detailed in Section 3. The daily food intake of the Herring Gull and the Shag has been estimated as the average of the observed data, since too few results were obtained to plot a regression line for these species.

Discussions of the results obtained from measuring weight variations.

Both the Fulmar and the Sandwich Terns had values for m, the slope of the regression line, which represents the amount of food required to bring about a weight increase of 1g. after maintenance needs have been met, which were less than unity. These are obviously aberrent, since, even assuming the birds were 100% efficient in converting food into flesh, the lowest possible value of m would be 1.0. The values obtained for both the Kittiwake and the Puffin were also suspiciously low, being less than 1.1. Only the Lesser Black-back Gull chicks produced a result which is credible, the value of m for those being 2.48. But this result suffers the reverse defect of being too high, implying, as it does that these chicks were only 40% efficient in converting food into flesh after maintenance needs had been met. There is no way of checking the accuracy of the values obtained for the amounts of food required for maintenance.

but it is probable that they would be as inaccurate as the conversion values obtained.

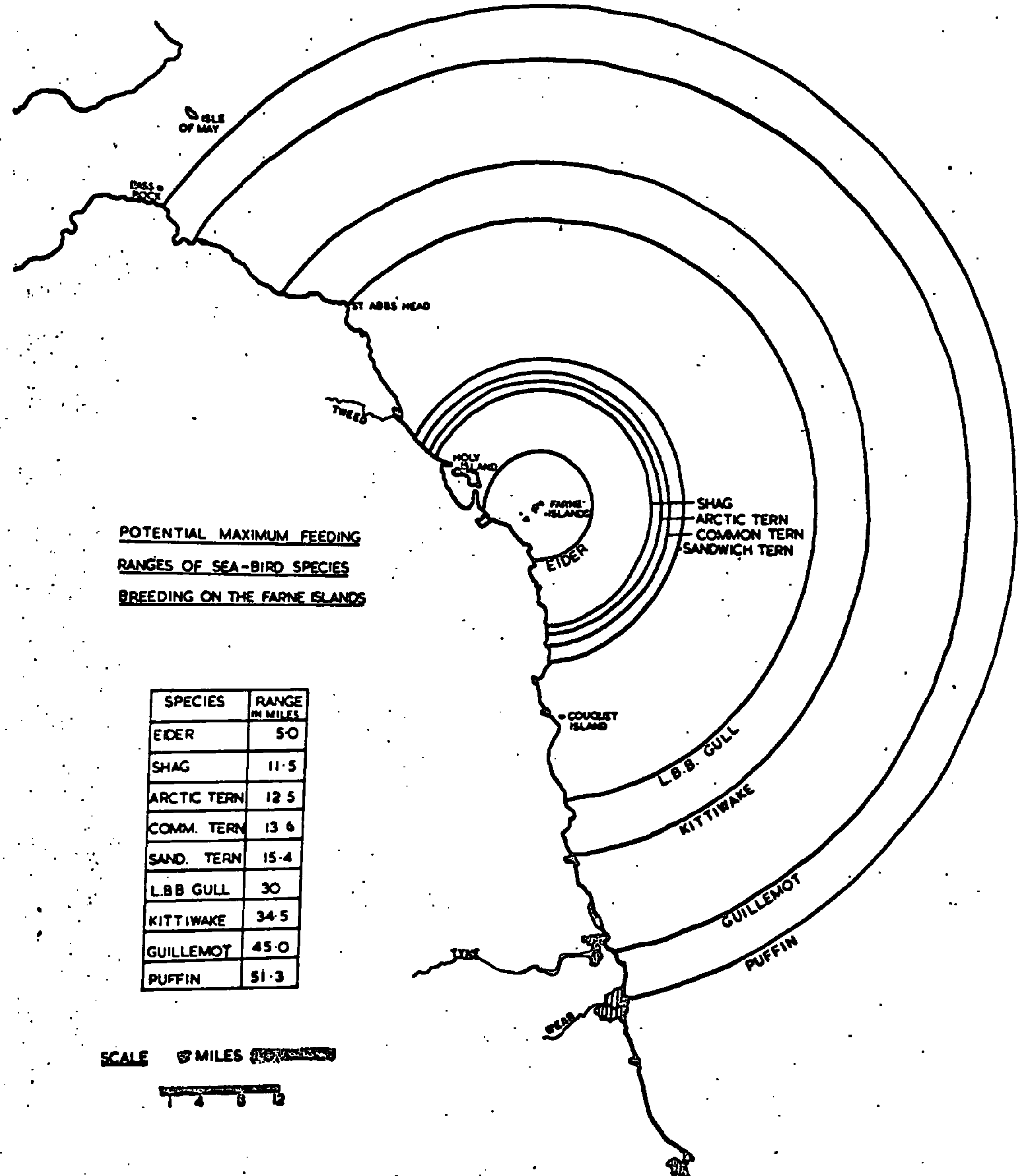
No doubt the fact, that nearly all the chicks involved in these experiments lost weight over the period of investigation, has some bearing on the apparent unreliability of the results. It would appear that the disturbances caused by the frequent weighing of the chicks had a very deleterious effect on their normal growth, and probably interfered with both their normal feeding rhythm and their physiological balance. In view of this the results obtained must be treated sceptically. An attempt has been made to improve on these field results by rearing chicks under controlled conditions in the laboratory, where they could be conditioned to accept the interference of weighing as part of the normal feeding process. These experiments are described in Section 4.

3. THE FEEDING RANGES OF FARNE ISLANDS SEA-BIRDS.

The distances flown in search of food by the various species under study would obviously vary considerably, both between individuals on the same day, and the same individual on different days, according to the prevailing conditions of food availability, feeding pressure of the chicks, etc. It is reasonable to assume however, that in general any interspecific differences in feeding range would be reflected in the time spent away from the nest on feeding flights by the parent birds. Thus in watches made on the chicks of each species the time of feeding of the chicks were noted, as were the times of return of the parent birds to the nest, when these differed from actual feeding times, i.e. with the Kittiwakes and Shags. Considering only those journeys from which the birds returned to subsequently feed the chicks, the average time taken on such trips can give a measure of the maximum possible distance flown. Since no measure can be taken of the actual time spent fishing, it was assumed that all the time away was spent in flying to and from the fishing grounds, and the distance flown, deduced from this, was taken as the potential maximum feeding range of the bird. It was further assumed that the approximate average speed of flight is 30 miles per hour for all the species. This figure is an approximation from the speeds of flight of various species of sea-birds as given by Meinertzhagen, (1955). Using this figure for the speed of flight, the average potential maximum feeding ranges of the various species can be estimated, as given in Table 61A and Figure 23. With the tern species a slightly different method of estimating time away on feeding flights was used. Since in most cases the two parent birds

FIGURE 23.

Diagram showing the potential maximum feeding areas of sea-bird species breeding on the Farne Islands.



POTENTIAL MAXIMUM FEEDING RANGES OF SEA-BIRD SPECIES BREEDING ON THE FARNE ISLANDS

SPECIES	RANGE IN MILES
EIDER	5.0
SHAG	11·5
ARCTIC TERN	12·5
COMM. TERN	13·6
SAND. TERN	15·4
L.B.B GULL	30
KITTIWAKE	34·5
GUILLEMOT	45·0
PUFFIN	51·3

TABLE 61A. Estimates of the average, maximum feeding range of Farne Islands sea-birds. (assuming flight speed of 30m.p.h.)

	(minutes) AVERAGE TIME AWAY ON FEEDING FLIGHTS	(miles) POTENTIAL MAXIMUM DISTANCE FLOWN	(miles) RADIAL DISTANCE FROM [illegible]
Arctic Tern	50.2	25.1	12.5
Common Tern	54.5	27.3	13.6
Sandwich Tern	61.8	30.9	15.4
Kittiwake	158.0	79.0	34.5
Lesser Black-back Gull			) 30*
Herring Gull			)
Fulmar	720*	360*	180*
Puffin	207.3	103.7	51.3
Guillemot			45*
Shag	46.0	23.0	11.5
Elder Duck			5*

Those figures marked with an asterisk are estimates only. (see text).

could not be identified separately, and as they were generally both away from the nest at the same time, the average time between feeds given to the chick was recorded, and the maximum time away for a single bird was taken to be twice this figure. With the other species observed, only one parent was generally away from the nest at any one time, the other remaining at the nest or in the vicinity, thus the time spent away by individual birds could be estimated. Table 61B shows the frequency distribution

TABLE 61B. Frequency distribution of times spent away on feeding flights by various species.

FREQUENCY OF FEEDING FLIGHTS IN EACH TIME-GROUP.

Length of time away on feeding flight. (minutes).	ARCTIC TERN		COMMON TERN		SANDWICH TERN		KITTIWAKE		PUFFIN		SHAG	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
0-20	69	36.9	38	26.9	8	29.6	0	0	0	0	3	11.1
20-40	44	23.5	24	17.0	5	18.5	4	4.6	0	0	11	40.7
40-60	24	12.8	26	18.4	4	14.8	8	9.3	0	0	5	18.5
60-80	10	5.3	14	9.9	3	11.1	6	7.0	0	0	5	18.5
80-100	13	6.9	12	8.5	1	3.7	6	7.0	0	0	2	7.4
100-120	4	2.1	7	5.0	2	7.4	11	12.8	1	11.1	0	0
120-140	5	2.7	5	3.5	1	3.7	7	8.1	1	11.1	1	3.7
140-160	1	0.5	4	2.8	0	0	7	8.1	0	0	0	0
160-180	0	0	3	2.1	1	3.7	9	10.5	0	0	0	0
180-200	4	2.1	3	2.1	0	0	7	8.1	3	33.3	0	0
200-220	3	1.6	2	1.4	0	0	6	7.0	0	0	0	0
Over 220	10	5.3	3	2.1	2	7.4	15	17.4	4	44.4	0	0
Total no. of feeding flights observed.	187		141		27		86		9		27	
Average time away on feeding flights (mins.)	56.2		54.5		61.8		158		207		46	

of the times spent away on feeding flights by the various species.

The figures given in Table 61A for the Lesser Black-back and Herring Gulls, and for the Fulmar, Guillemot and Eider are estimates only, because little data was available for the average time away from the nest for these birds. The Lesser Black-back and Herring Gulls were known to feed largely either along the shore, within a few miles of the islands particularly in the harbours and mud flats at Sea houses, Holy Island and Berwick-on-Tweed, or off the fishing banks which lie approximately 15 miles south-east of the islands. These fishing grounds were also often frequented by the Fulmars. The figure of 100 miles range for these birds is based on the approximate 12 hourly interval between feeds taken by the young Fulmar which was weighed regularly. It is probable however that the Fulmars do not spend much of this time in flying in search of food, as they were often seen in the immediate vicinity of the islands feeding on sand-eels and other small fish which were shoaling within sight. The figure of 45 miles quoted for the Guillemot is based partly on information given by fishermen in the Farne Islands area, who state that these birds are met with up to 40 or 50 miles from the coast, and partly on data given by Tuck

(1960), who states that the Common Guillemots of the New-foundland colonies fly up to 45 miles in search of food. The Eider Duck, appears to remain in the immediate vicinity of the islands throughout the breeding season, and is rarely met with outside a radius of five miles from the islands.

It is probable that in normal conditions, most of the species feed within a few miles of the islands during the summer months. Indeed, during late June and July when vast shoals of sand-eels appear in the inshore water, some individuals of nearly all the species mentioned can be seen preying on these fish within a few hundred yards of the islands. However under conditions of relative food scarcity the birds no doubt exploit the full extent of their range, and it is notable that on many occasions, even at the height of the summer, very few birds other than Shags and Eiders are seen fishing within sight of the islands. This is presumable connected with a lack of small fish in the inshore waters at these times, although no specific data wasaobtained to confirm this.

4. VARIATION IN FEEDING AREAS UTILIZED BY THE DIFFERENT SPECIES OF SEA-BIRDS.

Partially linked with the feeding ranges of the birds are the feeding areas favoured by the various species.

Each species tended to favour different fishing grounds, and variations were assessed both by observations of the directions taken by birds leaving and returning to the island, and where possible by direct observation of fishing activities. The various fishing areas exploited by the birds were assessed as follows:-

a) THE OPEN SEA. This included all hunting areas over 15 miles from the shore.

b) OFFSHORE WATERS. Marine areas between half a mile, and 15 miles from the shore. This included the fishing banks 15 miles from the islands.

c) WATERS ROUND THE ISLANDS. The marine area within sight of the islands i.e. approximately 1.5 miles radius from the islands.

d) INSHORE WATERS. The shore and tidal areas to half a mile offshore.

e) FENHAM FLATS. This area is included separately as it is apparently a rich ground for sand-eels, and was much favoured by the tern species, Shags, and Cormorants. It consists of a wide area of tidal mud flats behind Holy Island, approximately 5 miles from the Farne Islands.

f) HARBOURS AND ESTUARIES. Principally, the Harbours at Sea-houses and Holy Island, and the harbour and estuary at Berwick-on-Tweed.

g) INLAND. Terrestrial and fresh-water feeding areas.

Figure 24 shows the position of these areas in relation to the islands, and Figure 25 shows how these various feeding areas are utilized by the different species. The commonest feeding grounds of the Fulmar, Guillemot and Puffin was the open sea, but they were sometimes seen in the offshore zone on occasions. The Kittiwake appeared to feed most commonly in the offshore zone, but was probably a regular frequenter of the open sea. It was also seen fishing round the islands. The Sandwich Tern was most commonly seen fishing in the inshore zone along the shore-line, but was noted occasionally round the islands and over Fenham Flats, and rather more frequently in the offshore zone. The Common and Arctic Terns mostly favoured the fishing areas round the islands and over Fenham Flats, but were also seen irregularly in the inshore zone and offshore. Shags most commonly utilized the inshore areas, both along the mainland shore-line and round the islands. They were also seen in the Fenham Flats area, and in harbours. The Eider Ducks fed almost exclusively round the islands and in the sub-littoral zone of the shore-line, and were occasionally seen feeding in harbours. The Lesser Black-back Gulls were found in all the feeding areas, other than the open sea, but tended to favour the

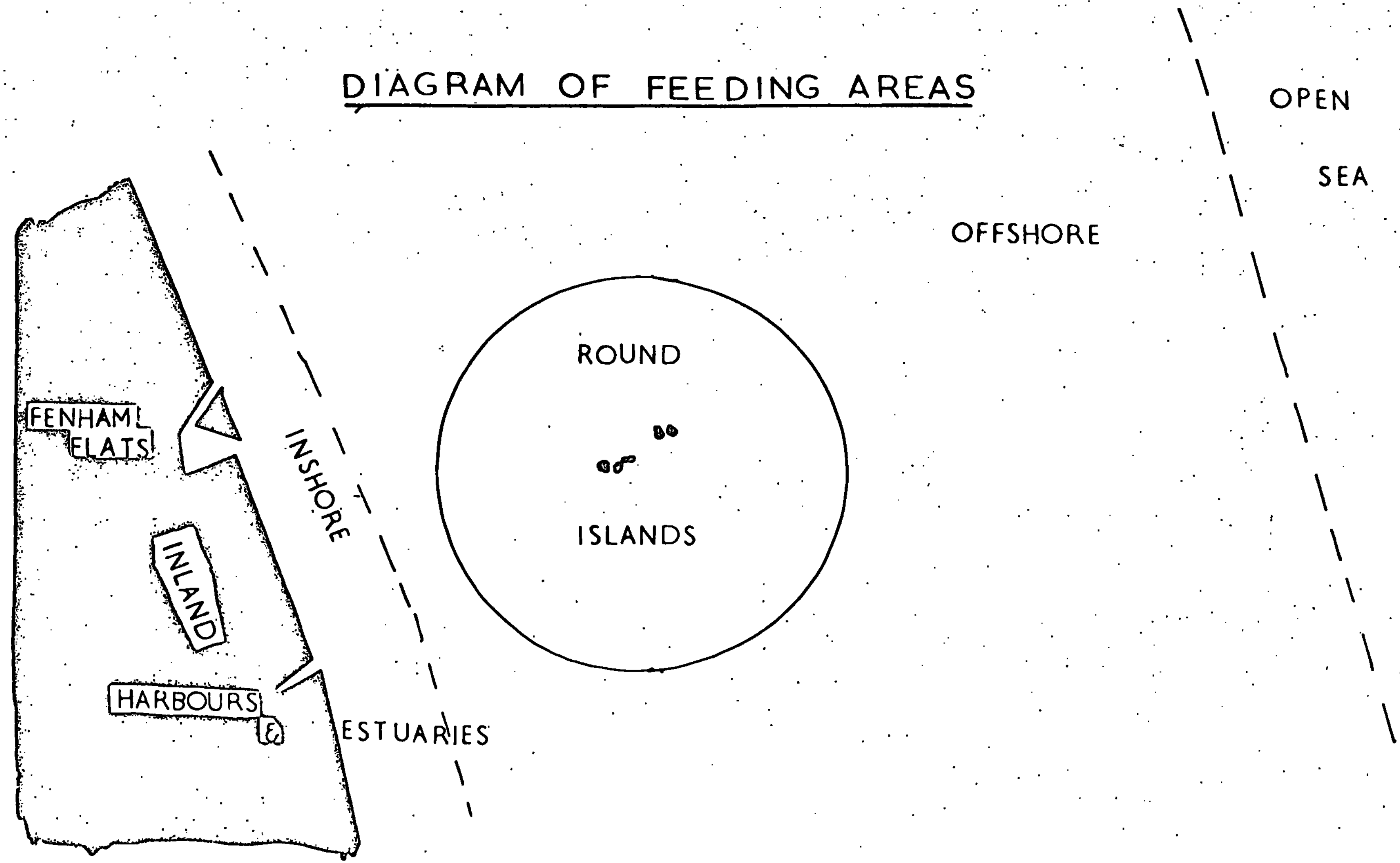
FIGURE 24.

Diagram showing the spatial relationship of the various feeding areas utilized by the sea-birds breeding on the Farne Islands.

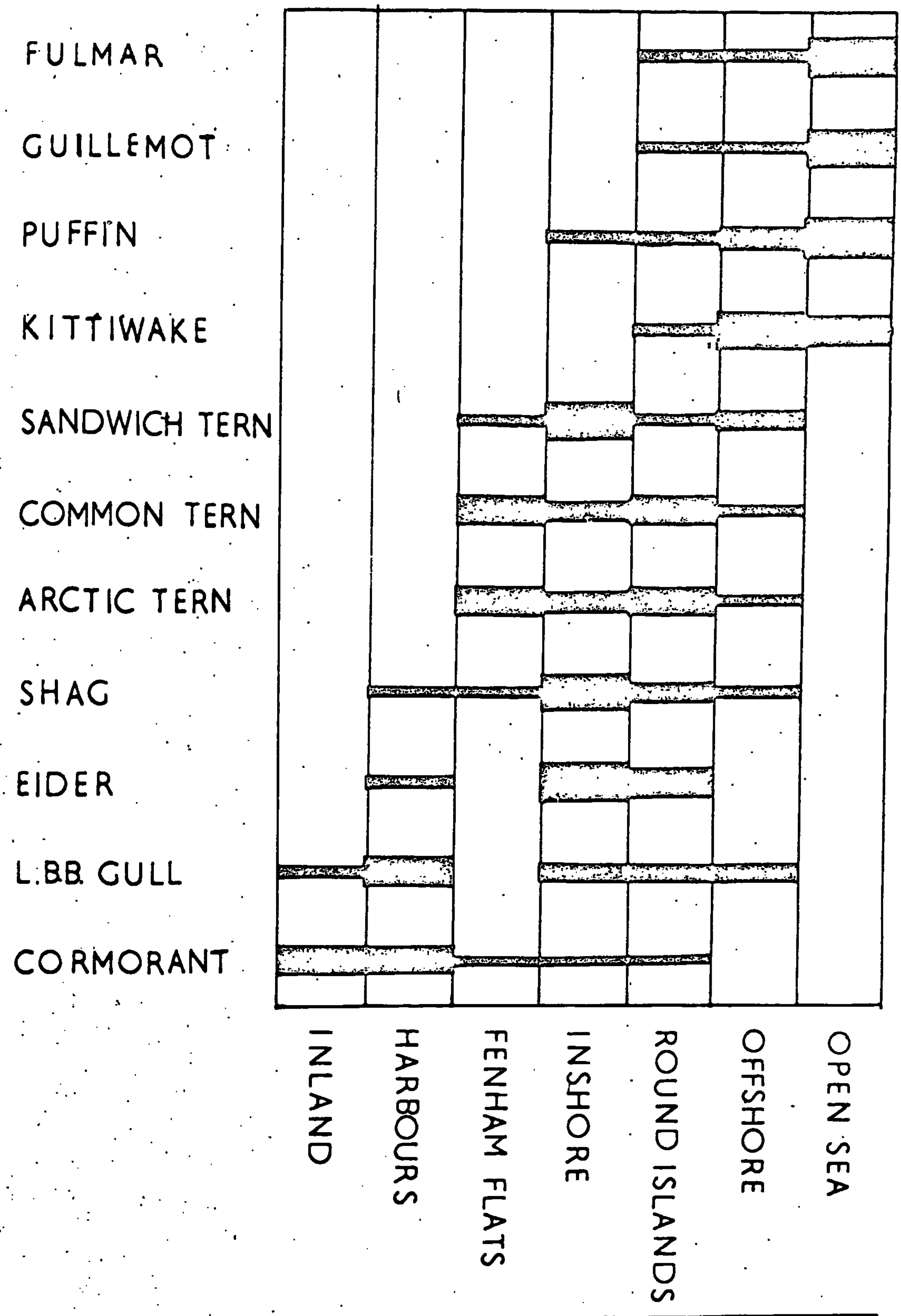
FIGURE 25.

The variation in the feeding areas utilized by the different sea-bird species in the Farne Island area.

DIAGRAM OF FEEDING AREAS



VARIATION IN FEEDING AREA



harbours more than other areas. The Cormorants favoured fresh-water, harbour areas in the inshore zone, but were occasionally seen round the islands and over Fenham Flats.

These variations in feeding areas tend to emphasize the interspecific differences demonstrated in the analysis of feeding ranges as would be expected. Thus those species which tend to favour the shore-line and inter-island areas are generally those with the shortest feeding ranges, whereas those with the greatest feeding ranges i.e. the auks, were generally found to feed in the offshore or open sea areas.

5. CONCLUSIONS.

The information obtained on the feeding frequencies, rhythms, and ranges, of the sea-birds studied enables a general comparison to be made of their relative effectiveness in feeding their young. Table 62 shows a comparison of the number of fishing journeys made by the birds in relation to the average time spent fishing. The number of fishing journeys is estimated by assuming that both parents share equally in feeding the young, and that each meal given to the young represents one feeding journey. The number of meals brought per day to each brood of chicks was estimated by direct observation in the case of the Arctic Tern and Common Tern, but for the other species the product of the number of chicks in a brood, and the

TABLE 62. Comparison of the percentage of the day spent in fishing activities by various sea-bird species.

	ARCTIC TERN	COMMON TERN	SANDWICH TERN	KITTIWAKE	LESSER BLACK-BACK GULL	PUFFIN	GUILLEMOT	SHAG
Average no. of meals brought per day to each brood of chicks	24	28	14-28	4-8	3-6	3	2-3	3
Average no. of fishing trips made by each parent.	12	14	7-14	2-4	1-3	1-2	1-2	1-2
Average time away on each fishing trip (hours).	0.83	0.92	1.03	0.44	0.25	0.67	3.0	0.38
Total time spent away on fishing trips (hours).	10.00	12.83	7.23-14.46	5.27-10.53	2.0-6.0	3.45-6.90	3.0-6.0	0.77-1.53
Percentage of daylight hours spent in fishing activities.	55.5	71.3	40.2-80.3	29.3-58.5	11.1-33.3	19.2-38.3	16.7-33.3	4.28-8.50

number of feeds brought to individual chicks has been used. The Sandwich Tern, Kittiwake, and Lesser Black-back Gull had either one or two chicks per brood, the Puffin and the Guillemot one, and the Shags generally three. The Shag chicks were however generally all fed by the same parent after a feeding trip, and thus three trips only were necessary for the whole brood per day. For the purpose of estimating the percentage of the day spent in fishing activities, the daylight hours when the bird could be fishing have been taken as from 0400 hours to 2200 hours, i.e. a total of 18 hours. The Arctic Terns each made an average of 12 fishing trips a day, and spent 55% of their time, during the hours of daylight, in fishing, whereas the Common Terns made 14 trips per day, and spent 71% of their time in fishing. The Sandwich Terns spent between 40 and 80% of the day in fishing in making 7 or 14 trips a day, depending on whether they fed one or two chicks, and the Kittiwakes between 29% and 58% according to brood size, in making 2-4 trips a day. The Lesser Black-back Gulls made between 1 and 3 trips a day, spending between 11 and 33% of their time fishing, whereas the Puffins and the Guillemots made either one or two trips a day, the former spending between 19 and 38%, and the latter between 17 and 33% of their time in fishing. The Shag, in making 1-2 trips per day, spent only 4 to 8% of its time in fishing. Thus in terms of the amount of time spent in fishing activities on behalf of the young the tern species are the least effective, spending between 40 and 80% of the day in obtaining, and returning with food, and the Shag is the most effective having to spend at the most only 8% of the daylight hours on these activities. These data reflect to a certain extent the relative distances that the birds fly in search of food. If however, an estimate is made of the percentage of the day spent in fishing per individual prey caught, some indication is obtained of the comparative competence in hunting of the birds concerned. Table 63 shows the number of prey taken per day by each bird for the young, and the percentage of the daylight hours spent in fishing for every individual caught. With those birds fed by regurgitation the average number of fish per meal has been obtained by dividing the average weight of a regurgitation sample by the average weight of individual prey taken. The percentage of the day spent in fishing per individual caught is based only on the numbers of fish taken to feed the young, there being no information on the numbers of fish taken for their own needs by the birds. It may thus be assumed that the percentages given are too high if all the fish caught are taken into account. However the numbers of fish taken by the adults should be in the same interspecific proportions as the numbers taken for the young, and thus the proportional relationships between the percentages given should be valid.

TABLE 63. Comparison of the percentage of the day spent in fishing per individual caught by various sea-bird species.

	ARCTIC TERN	COMMON TERN	SANDWICH TERN	KITTIWAKE	LESSER BLACK-BACK GULL	PUFFIN	GUILLEMOT	SHAG
Average no. of prey taken per fishing trip.	1	1	1	6	8	5	1	2
Average no. of prey taken per day by each parent for young.	12	14	7-14	12-24	8-24	5-10	1-2	2-4
Percentage of day spent in fishing per individual caught.	4.6	5.1	5.7	2.4	1.4	3.7	16.7	2.1

The Lesser Black-back Gull spends only 1.4% of its time in hunting for every fish caught, the Shag 2.1% of its time, and the Kittiwake 2.4% of its time. At the other end of the scale the Guillemot spends 16.7% of its time in obtaining one fish, but it flies very long distances and takes only a single fish. The Puffin, which travels similar distances, takes five fish per trip, and thus spends only 3.7% of its time fishing for every fish taken. Amongst the terns it would seem that the Arctic Tern is slightly more efficient than the Common Tern, taking only 4.6% of the day per fish taken to the 5.1% taken by the Common Tern. This could possibly be a reason for the Arctic Tern being the more numerous species in the Farne Island area. The Sandwich Tern, at 5.7% of the day spent per fish caught, is the least efficient of the three species of terns.

RELATIONSHIP BETWEEN THE SIZE OF BIRD, AND THE AMOUNT OF TIME SPENT FISHING.

In order to investigate the possibility of there being a relationship between the size of bird and the length of time spent fishing, these two factors were plotted together, as shown in Figure 26.

In order to make all the data strictly comparable the values of the time spent fishing by birds with the maximum brood size have been used. In the case of the Arctic and Common Terns, where the values given in Table 42 were for

FIGURE 26.

Relationship between the average weight of the bird and the potential maximum number of hours spent fishing.

x = Potential maximum number of hours spent fishing.

y = Average weight of bird (g.).

at = Arctic Tern

st = Sandwich Tern

lbb = Lesser Black-back Gull

p = Puffin

ct = Common Tern

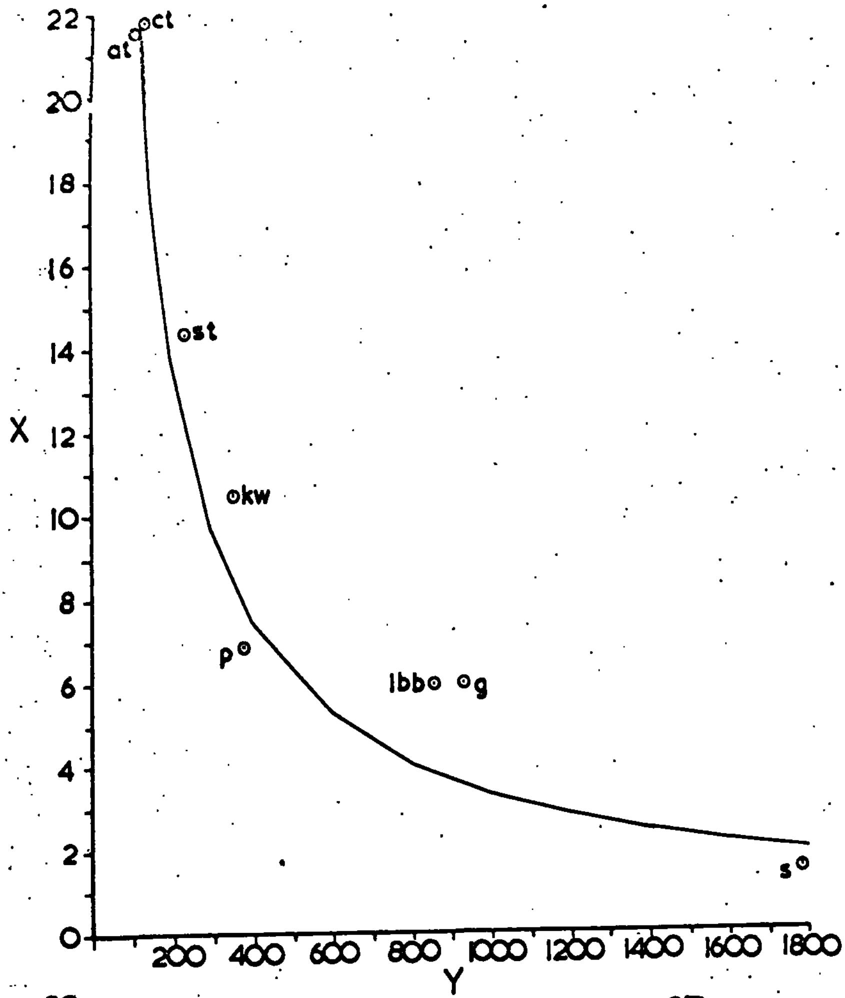
kw = Kittiwake

g = Guillemot

s = Shag

FIGURE 27.

Correlation of the logarithm of the average weight of bird (x) with the logarithm of the potential maximum number of hours spent in feeding (y).



at
ct
st
kw
p
lbb
g
s
X
Y
0
2
4
6
8
10
12
14
16
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22
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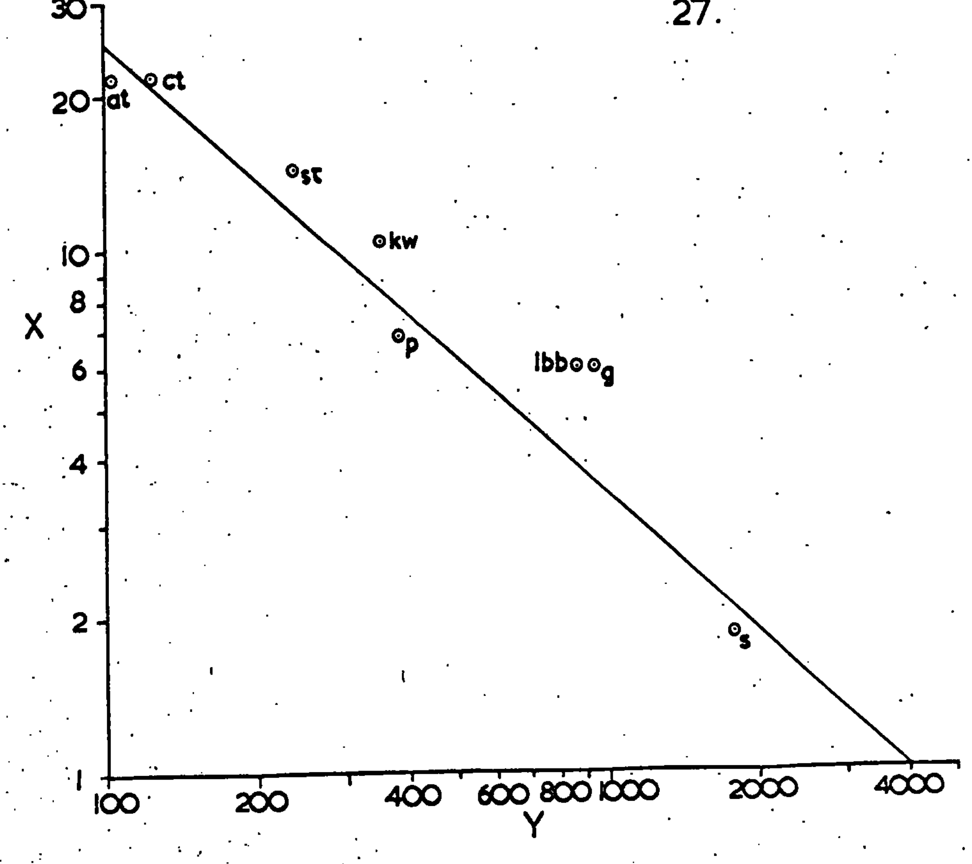
1000
1200
1400
1600
1800



at
ct
st
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lbb
g
s
X
Y
1
2
4
6
8
10
20
30
100
200
400
600
800
1000
2000
4000

the average brood size as estimated by direct observation, the values have been re-estimated using the average number of feeds per chick (given on page 173) for broods of 1 or 2 chicks in the case of the Arctic Tern, and 1 to 3 chicks in the case of the Common Tern. Thus the number of hours spent in fishing in each case would be between 10.8 and 21.7 for the Arctic Tern and 7.3 and 21.8 for the Common Tern. The fact that with the larger brood size for each species the birds would be spending more daylight time than is available in fishing suggests that those birds with two or three chicks must reduce the number of feeds per chick. No evidence concerning this was obtained, but it seems possible that if this occurs then the birds may be taking larger fish in order that the total food intake of the chicks might not be reduced. However the high values for fishing time given for these two species does not impare the general relationship between size of bird and time spent fishing, shown in Figure 26. Since the plot of these factors appears to demonstrate a curvilinear relationship, the data was replotted on a log-log basis as shown in Figure 27. The regression coefficient for these values was 0.9485, which is highly significant ($P<0.001$ with 6 degrees of freedom). The slope of the regression line which is drawn to the values in Figure 27 is -0.87 and the point of intersection on the log x axis is log 3.613. Thus the equation of the curve relating the original values is

$$y = 4102x^{-0.87}$$

i.e. the average weight of the bird is a power function of the time spent feeding such that with decreasing weight of bird the time spent feeding increases logarithmically. The above curve has been drawn to the data in Figure 26. The form of the curve suggests that birds of smaller weight than 173g. must spend all their time in fishing, whereas birds greater in weight than 1400g. will spend less than 15% of their time fishing. The fact that Arctic and Common Terns can rear broods of 2 and 3 chicks respectively, and that no difference was found in the growth rates of such large broods as compared with smaller broods (see Section 3) suggests that this relationship in practice does not hold true for the smaller birds with large broods. It has been mentioned above that increasing the size of fish taken would increase the food intake without a concomitant increase in the fishing time, and this may be one mechanism whereby the smaller birds manage to feed larger broods.

The reasons underlying the curvilinear relationship shown are not immediately apparent. The disparate factors of brood size, distance flown in search of food, and the number of feeds per chick per day all contribute to the relationship in differing degrees for each species, such that the larger species would appear to enjoy a disproportionate advantage in hunting efficiency, as compared with the smaller species.

SECTION 3.

THE GROWTH OF CHICKS UNDER FIELD CONDITIONS.

INTRODUCTION.

During the summers of 1961 and 1962 studies were made in the field of the growth of the chicks of several species of sea-birds breeding on the Farne Islands. In 1961 three species, the Arctic Tern, the Kittiwake, and the Shag, were studied, whereas in 1962 a further six species were included in the survey. These were the Common tern, Sandwich Tern, Lesser Black-back Gull, Fulmar, Puffin and Guillemot. In all cases records of the growth of the chicks were taken at the nest sites, causing as little disturbance as possible to the normal activities of the birds.

METHODS.

With those species which nest on the tops of the islands i.e. the terns, and the gulls, it proved difficult to locate individual chicks of over approximately 3 days age for weighing, since after this age they tend to wander about the colony, and, when alarmed, hide in the thick undergrowth. In order to overcome this problem a selected series of nests of each of these species were surrounded by low wire-mesh barriers during the period whilst the eggs were being incubated. These barriers were approximately one foot high by four feet in diameter for the tern species, and 1.5 feet high by six feet in diameter for the gulls. They apparently caused very little inconvenience to the adult birds, for in no case where a nest was thus surrounded were the eggs deserted. Such enclosures confined the chicks to the nest site throughout the pre-fledging period, and therefore enabled a series of weight records to be taken of the same individual. The chicks of the Arctic Terns and Common Terns which were confined in this manner did not appear to suffer in any way in comparison with those outside the barriers. They reached fledging at the same time, i.e. between 22 and 23 days, and were fed in the normal manner by the parents throughout their period within the enclosures. This was shown by undertaking watches from a hide, as described in Section 2, on chicks both outside and inside the enclosures. The chicks of the Sandwich Tern proved to be less amenable to this type of study however, and a different method of enclosure was devised for this species. Because of the dense aggregation of the nest sites of Sandwich Terns, it was found to be impossible to surround a single nest with a sufficiently large enclosure without disturbing the adjacent nests. Larger enclosures were thus erected around groups of between five and seven nests. These proved to be successful in that they did not disturb the incubating birds unduly, and the majority of the enclosed clutches hatched successfully. Difficulties arose, however, during the development of the chicks, due to aspects of the behaviour of the birds. Young Sandwich Tern Chicks normally leave the nest site soon after the third day and, after a short period spent wandering in the immediate vicinity, tend to gather in 'creches' on or near the shore line of the islands. The enclosing of the chicks prevented this from taking place, and in addition appeared to strengthen the territorial behaviour of both chicks and parents. Thus one particular chick, together with its parents when they were present, would dominate the area within the enclosure to the detriment of other chicks. This was overcome by placing the chicks in separate enclosures soon after hatching, but a number of young chicks were lost through the attacks of their neighbours, before they could be removed. The chicks within the pens also appeared to be growing at a slower rate than the chicks which were free, but no comparative data could be obtained because of the difficulty of repeatedly capturing specific chicks outside the enclosure. It is probable however that the parents of those chicks within the pens would spend a considerable time attending the 'creches' and that their own chicks would thus be neglected.

For these reasons the data obtained on growth of the Sandwich Tern chicks within the pens must be treated with caution, since it is probably unrepresentative of growth under natural conditions.

The barriers used to enclose the Lesser Black-back Gull chicks proved useful up to about the 30th day after the hatching of the chicks. By that time the chicks were large enough to climb over the barrier, although they were not yet fledged. The records obtained for this species thus appertain only to the first 30 days after hatching.

The primary object of the investigations was to establish, as far as possible, the relationship between the food intake and the growth rates of the birds concerned. Thus the records taken were predominantly measurements of weight made at frequent intervals throughout the period when the chicks were present at the breeding site. From this information estimates could be made of the daily weight increase of the chicks in relation to the amount of food consumed. Weights were taken by means of spring balances, accurate to within one gram, or, in the case of the larger birds, with a pan balance which was also accurate to within one gram. In some cases measurements were also taken of the increase in wing length, measured from the 'elbow' to the tip of the longest primary feather, for comparison with growth as measured from weight increase. This latter method provides a more accurate general estimate of the relative growth of individual chicks, for it is subject to fewer inconsistencies than is the measurement of weight. Thus many authors have pointed out that intermittent records of the weight of chicks will be greatly affected by the time when the chick was last fed in relation to the time of weighing. If a weight record on one day is taken just prior to the chick being fed, and on the following day taken after the chick has been fed, then the apparent weight increase over the period would be much greater than that due to normal growth (c.f. Richdale (1943), Young (1963) and Dorward (1963)). Such inconsistencies can be minimised however, by grouping records over a specific period, or by averaging data from a number of chicks of similar ages. Both these methods have been used in the present work in deriving mean growth curves of weight against age and wing length against age for each of the species under study. In most cases it was found to be impracticable to weigh and measure the individual chicks daily, and in general records were taken every three days. On occasions, however, records were made at much longer intervals. In addition, as the chicks being examined were of differing ages, there was thus no regularity in the relationship between the age of the chicks and the periods when records were taken. In order to assess the weights and wing lengths of chicks at specific regular intervals the data obtained from each individual were plotted separately to give a curve of weight or wing length against age. The weights and wing lengths of the chicks at intervals of two days were read off from these curves, and these values were then used to deduce the mean growth curve of the species. This method minimises the inconsistencies in the individual weight records taken, by tending to smooth out minor fluctuations in weight increase, and in addition provides comparable weight-age records for each chick. The mean growth curves so obtained have been used as standards on which analyses of the comparative deviations in the growth rates of groups of chicks under different conditions can be assessed, in addition to providing data on the average daily weight increase and wing length increase of each species over the full growth period.

SIZE OF SAMPLES.

Table 64 lists the number of chicks of each species which were weighed regularly in each year of the investigation.

TABLE 64. Size of samples of chicks weighed regularly in each year.

SPECIES	NO. OF CHICKS WEIGHED. 1961	1962	SPECIES	NO. OF CHICKS WEIGHED. 1961	1962
Arctic Tern	6	22	Lesser Black-Back Gull	0	14
Common Tern	0	10	Herring Gull	0	1
Sandwich Tern	0	16	Puffin	0	13
Kittiwake	31*	25	Guillemot	0	10
Fulmar	0	4	Shag	7	20*

* a number of chicks weighed less regularly have been omitted.

It can be seen that only 1 Herring Gull chick, and 4 Fulmar chicks were weighed, and thus the growth of these species was not adequately assessed. In 1961 many more Kittiwake chicks were weighed during the initial stages of growth, up to about the 10th day over 50 chicks being weighed, but only 31 of these were weighed regularly until fledging. The Shags weighed in 1962 consisted of 6 chicks from two nests on the Inner Farne, which were weighed regularly every 3-4 days, and 14 chicks from a large colony on Staple Island which were weighed at intervals of 8-10 days.

RESULTS.

<u>Increase in weight with age.</u>

The mean growth curves of weight with age, together with the range of the values, of the species investigated, are given in Figures 28 A to K. The data includes all

FIGURE 28.

Growth of chicks. Increase of weight with age.

Open circles represent the mean values of the weight of chicks at two-day intervals. Vertical lines represent the range of weight values at each age.

x = Weight in grams.

y = Age in days.

N = Number of weight records, in each sample.

A = Arctic Tern.

B = Common Tern.

C = Sandwich Tern.

D = Kittiwake.

E = Lesser Black-back Gull

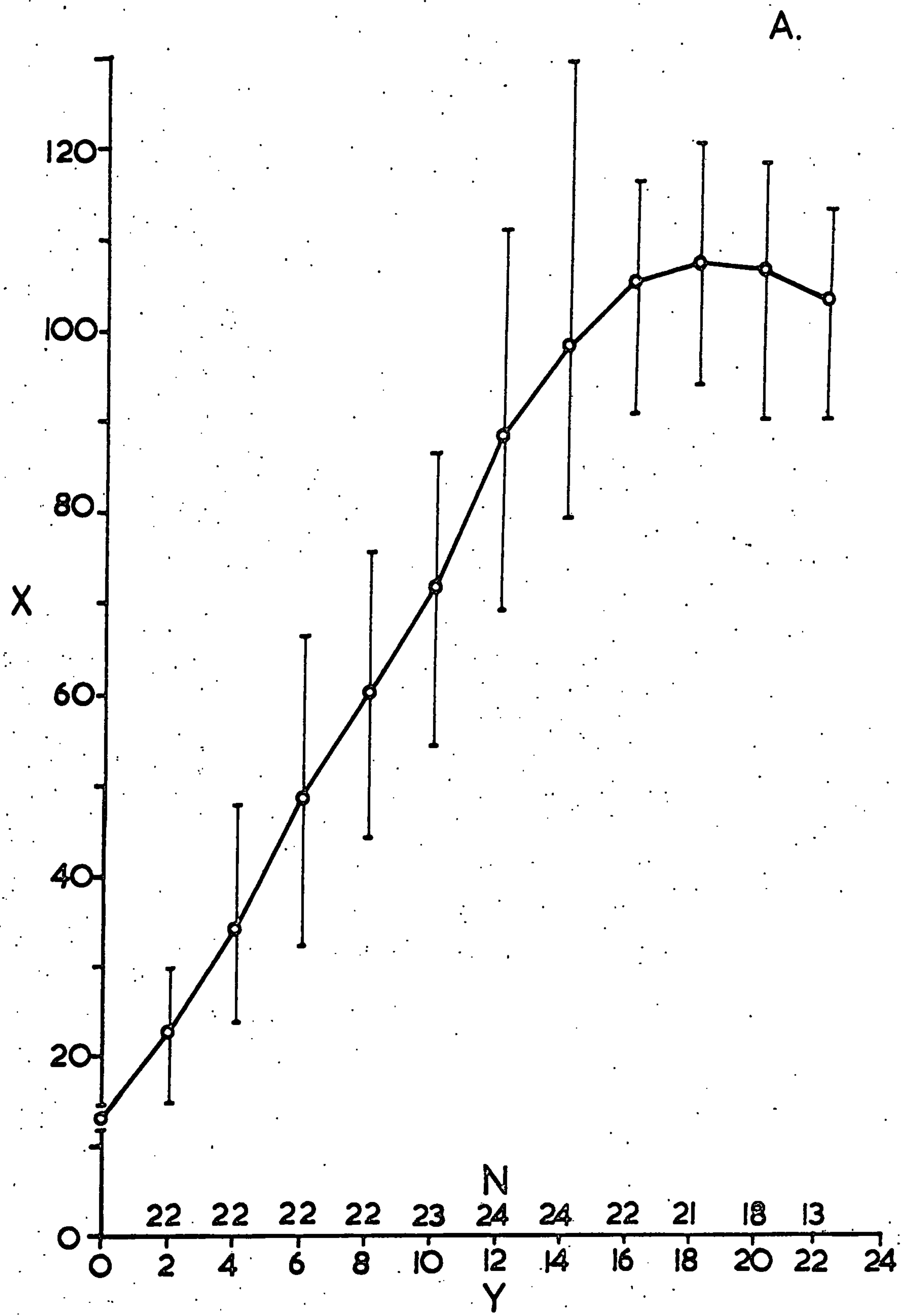
F = Herring Gull.

G = Fulmar.

H = Puffin.

J = Guillemot.

K = Shag.


A.
X
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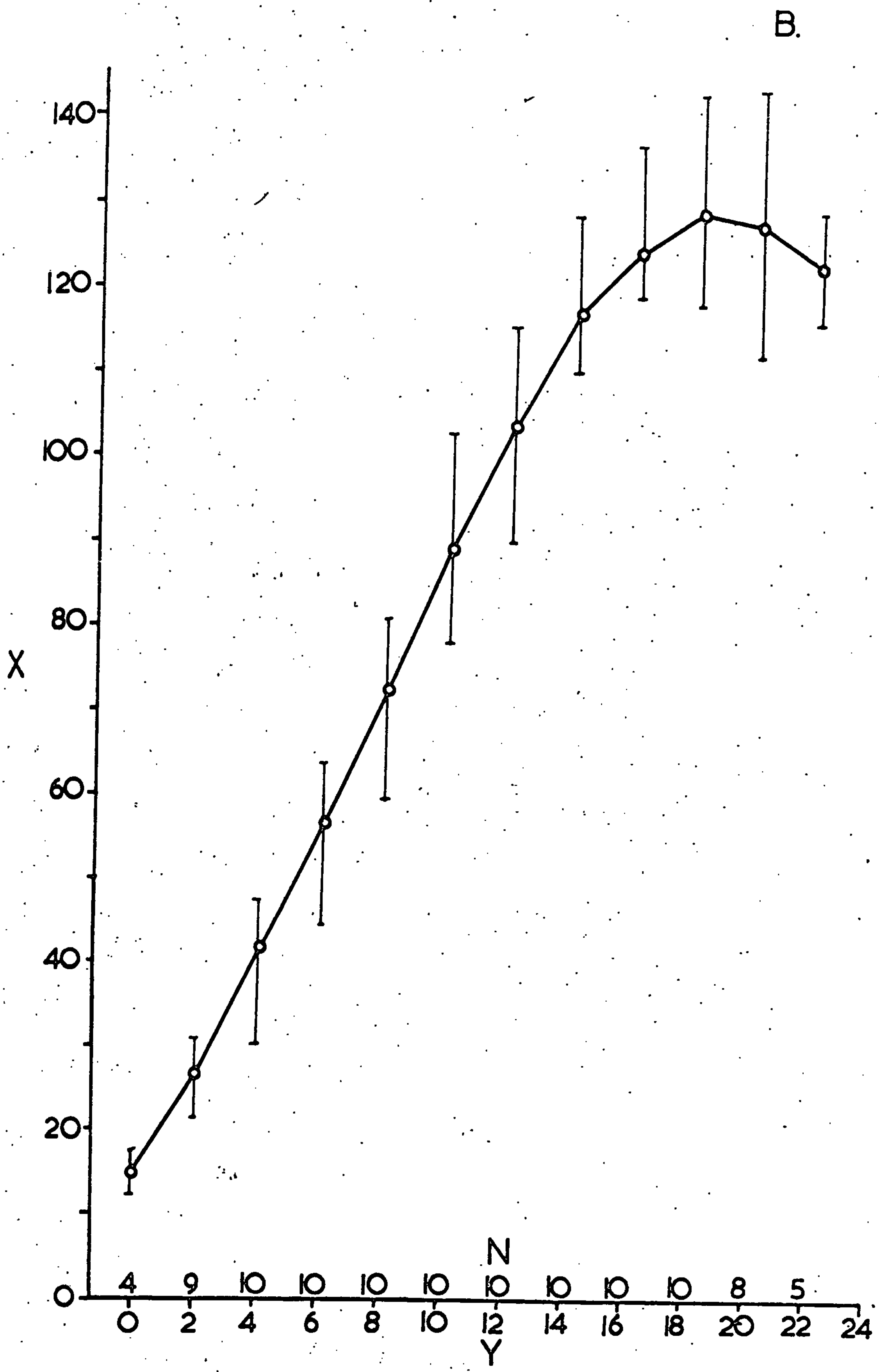
22 22 22 22 23 24 24 22 21 18 13
0 2 4 6 8 10 12 14 16 18 20 22 24
Y



B.
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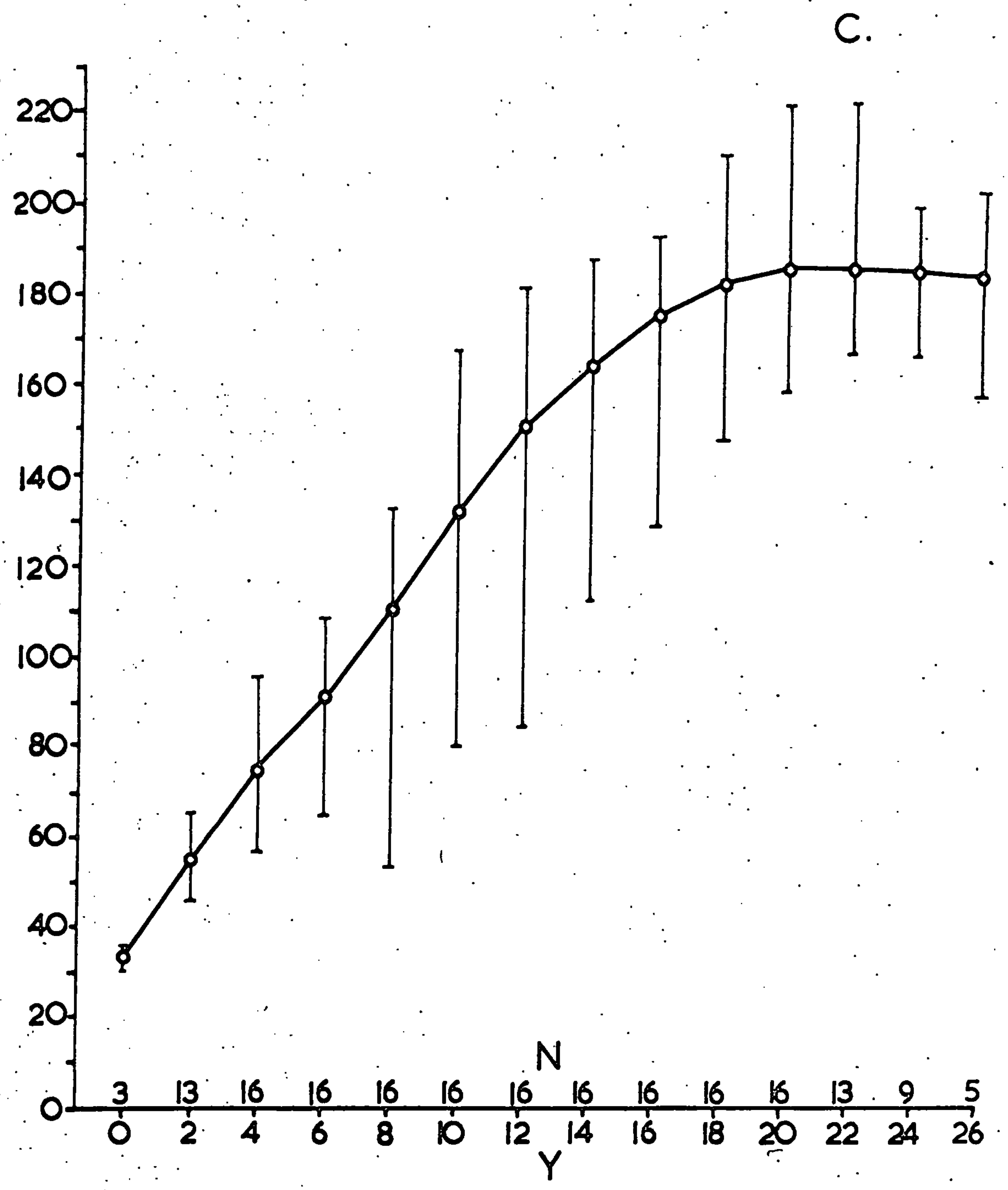
0 2 4 6 8 10 12 14 16 18 20 22 24
Y



C.
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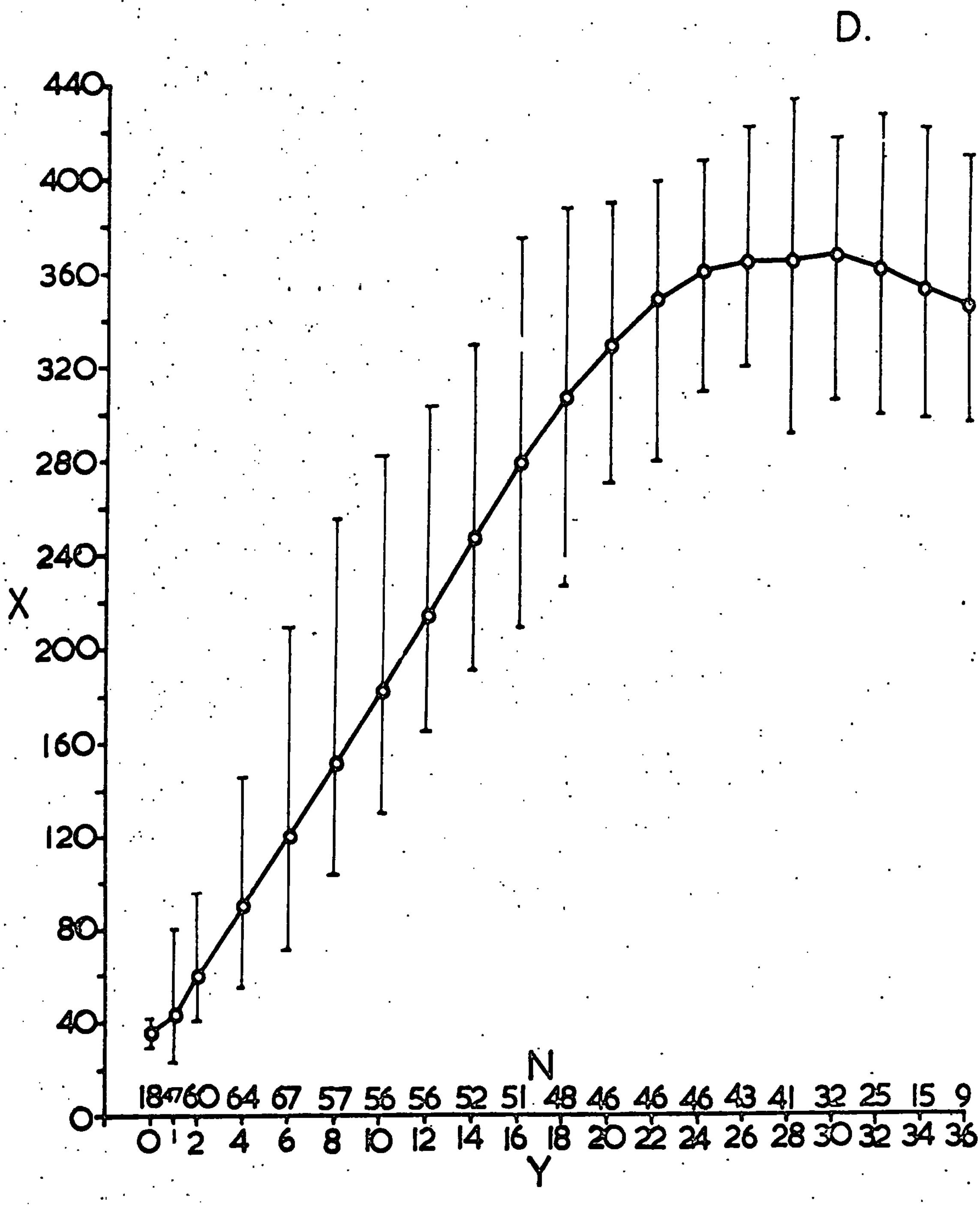
Y



D.
X
440
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320
280
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120
80
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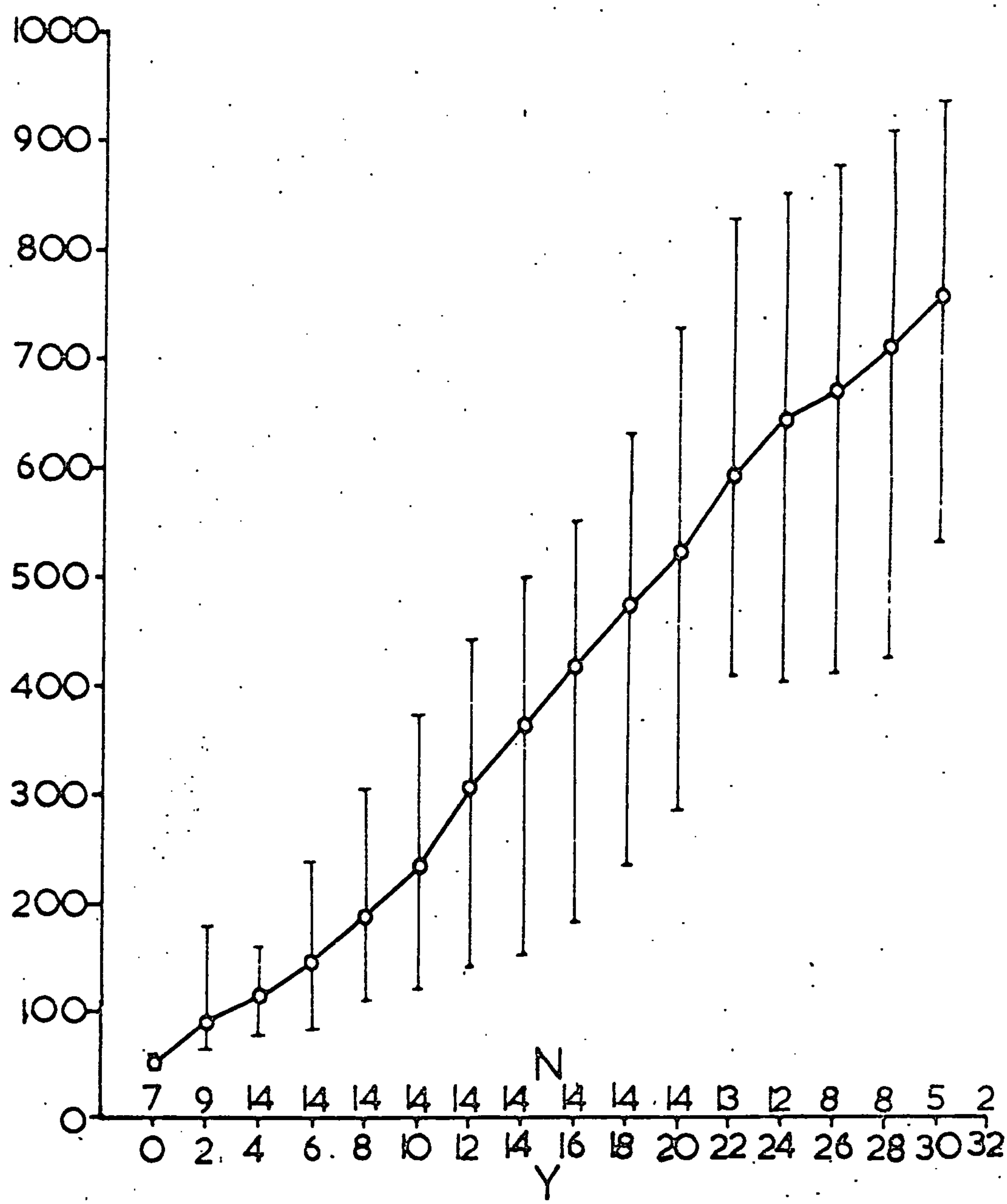
N
18 47 60 64 67 57 56 56 52 51 48 46 46 46 43 41 32 25 15 9
0 1 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36
Y

E.



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X
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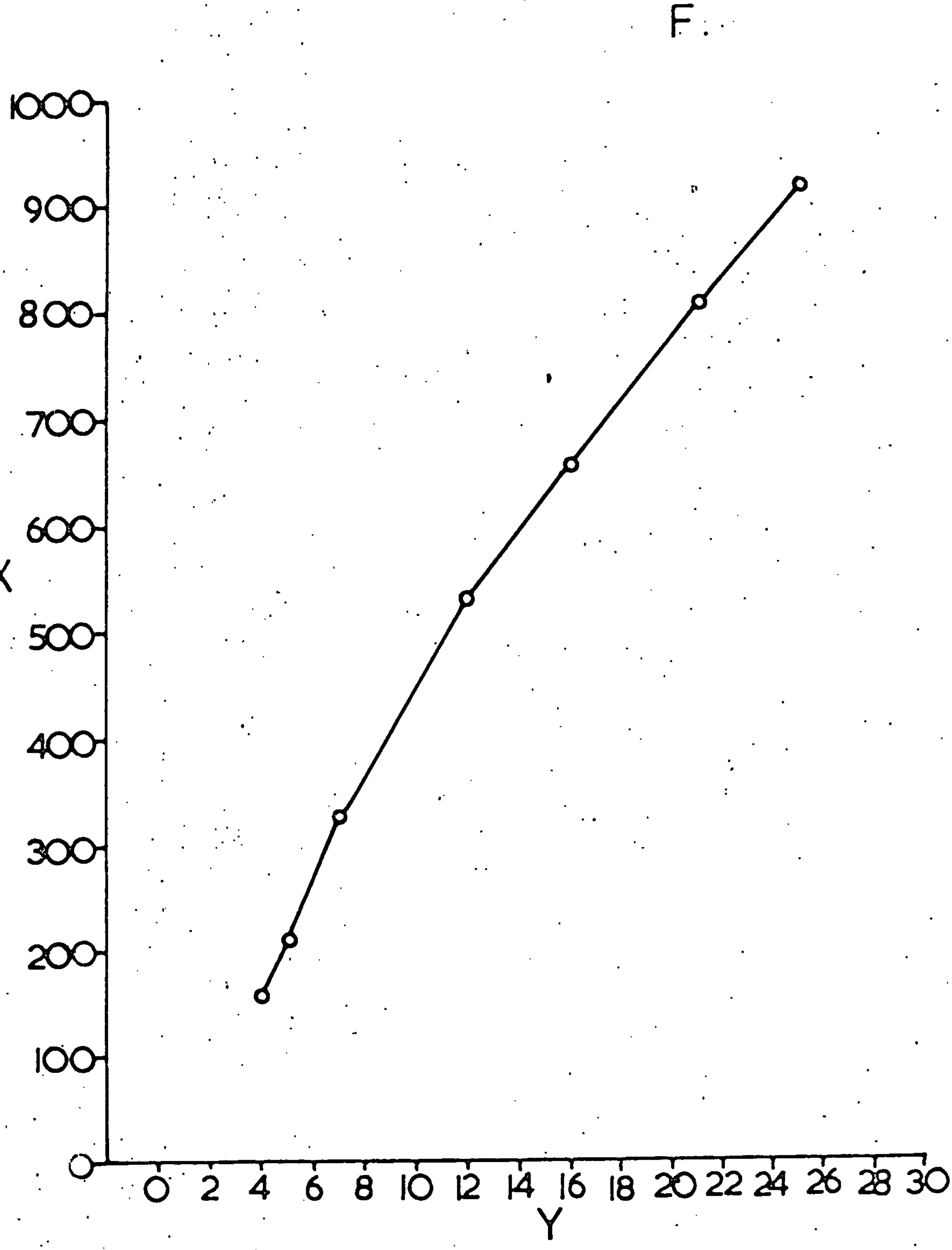
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32
Y


F.
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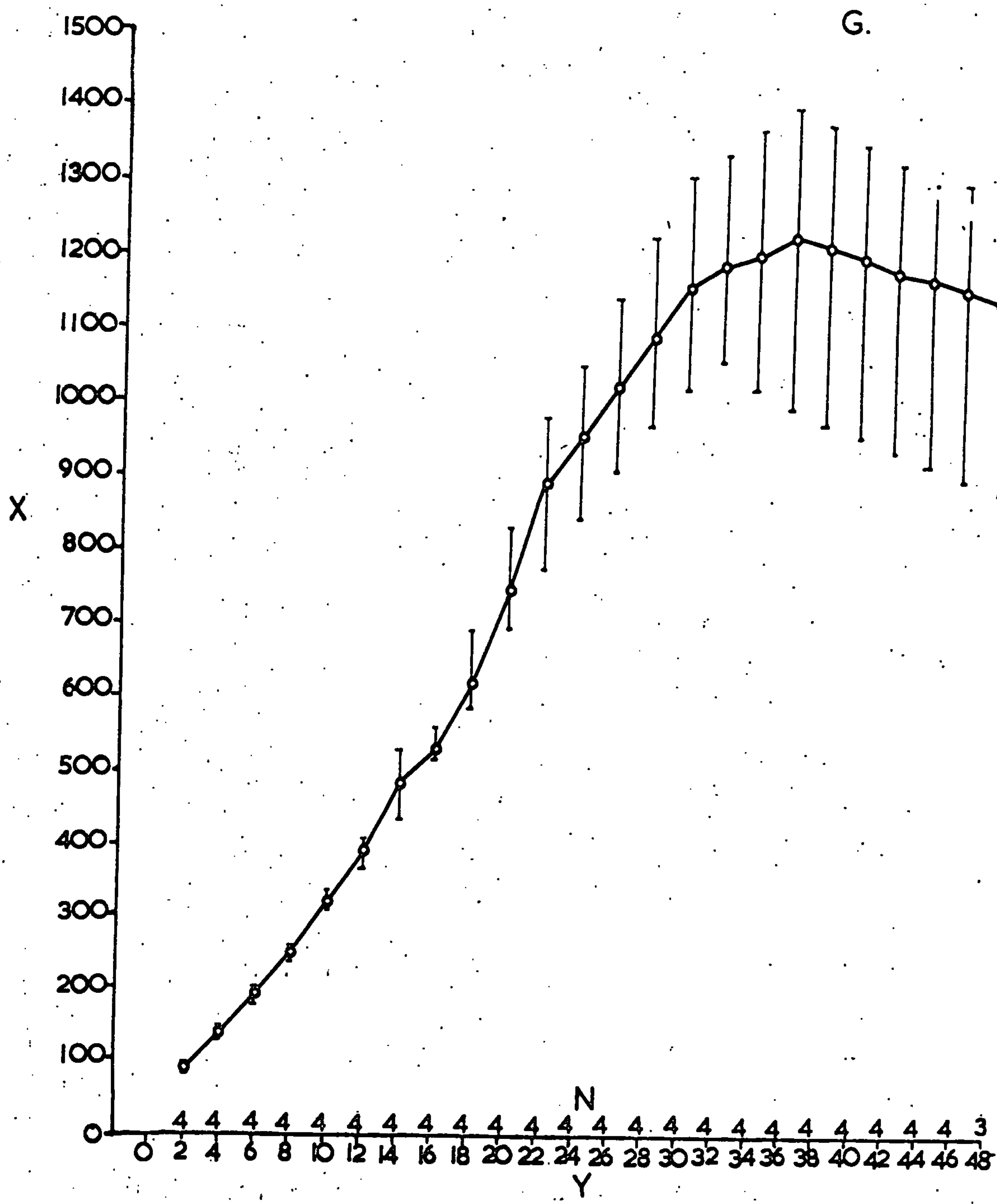
Y


G.
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Y
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100
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700
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1000
1100
1200
1300
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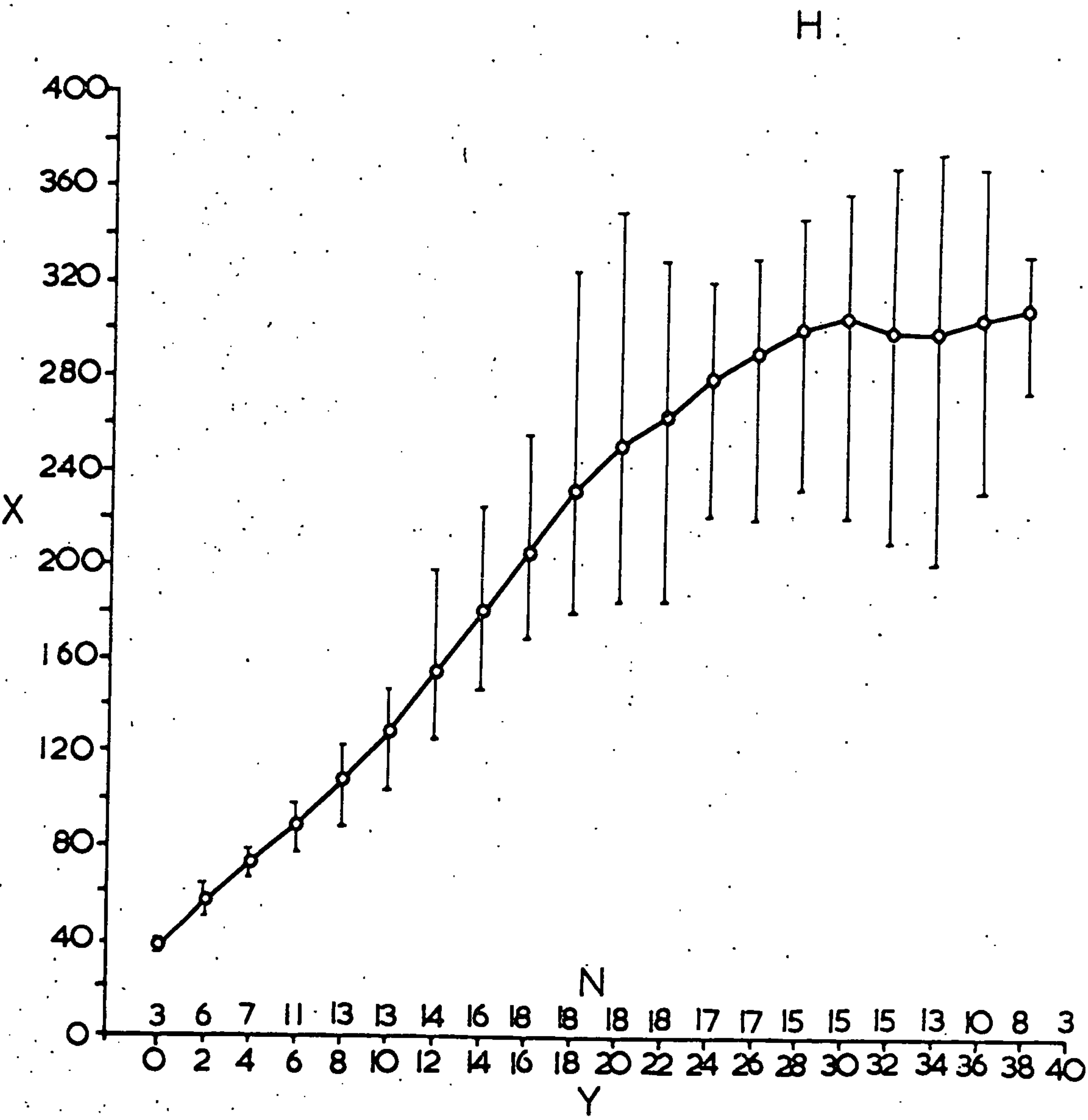
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42 44 46 48


H
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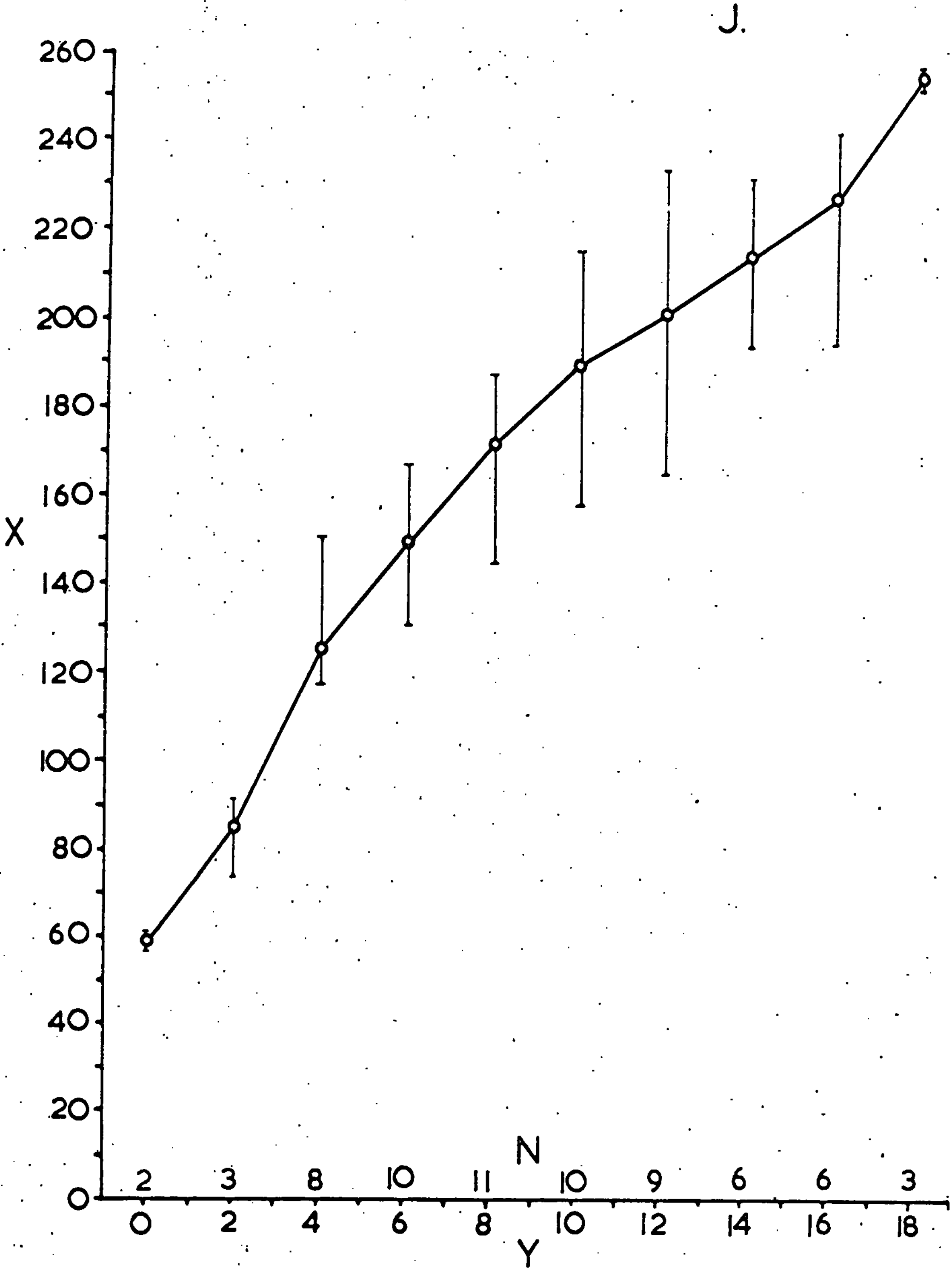
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40
Y


J.
X
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220
200
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N
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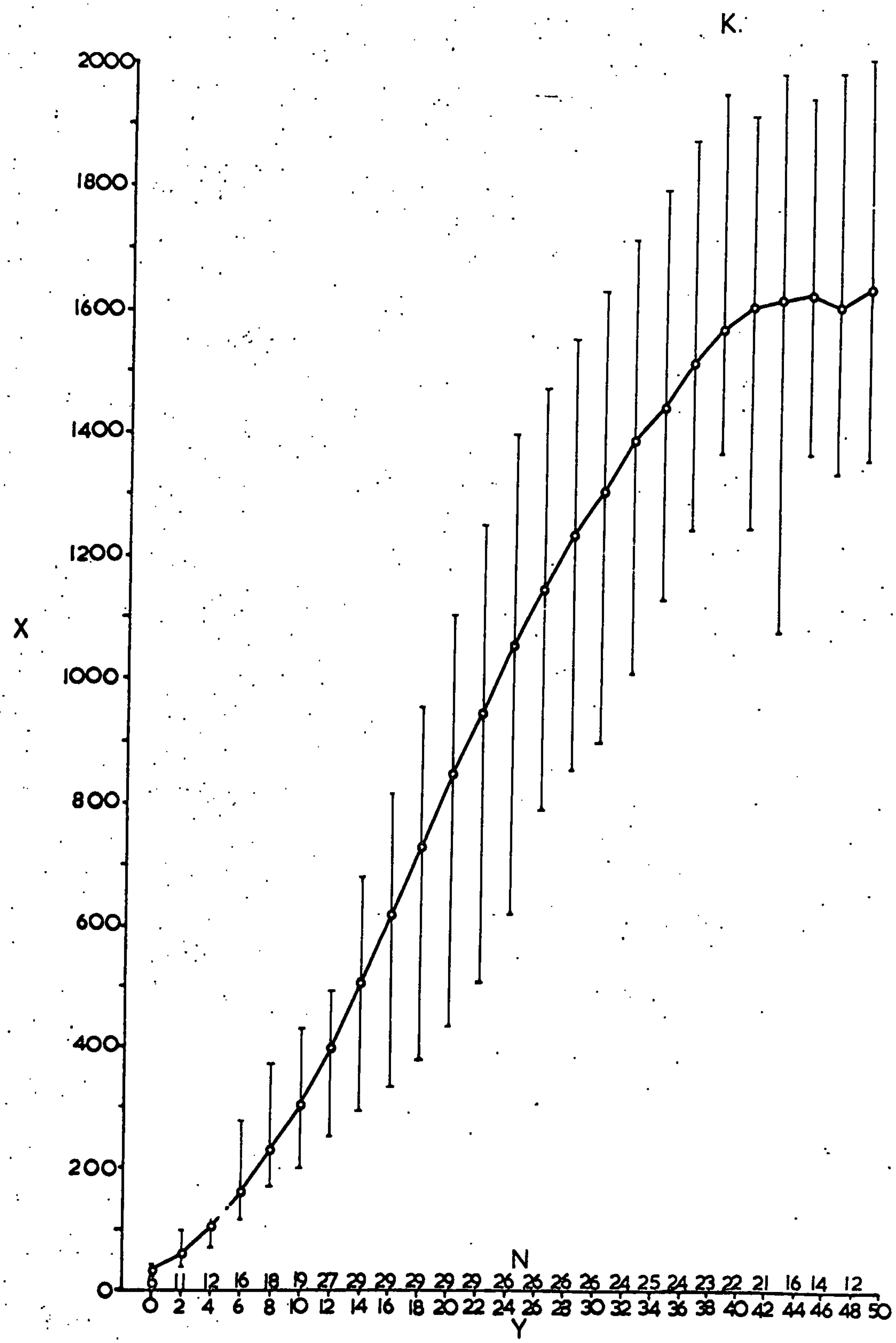
0 2 4 6 8 10 12 14 16 18
Y


K.
X
2000
1800
1600
1400
1200
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600
400
200
0
N
6 11 12 16 18 19 27 29 29 29 29 29 26 26 26 26 24 25 24 23 22 21 16 14 12
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42 44 46 48 50
Y

TABLE 65. Average daily weight increases throughout the period of growth of various sea-birds breeding on the Farne Islands.

AVERAGE INCREASE IN WEIGHT PER DAY OVER EACH TWO-DAY PERIOD (g.)

AGE PERIOD (days)	ARCTIC TERN	COMMON TERN	SANDWICH TERN	KITTIWAKE	LESSER BLACK-BACK GULL	HERRING GULL	FULMAR	PUFFIN	GUILLEMOT	SHAG
0-2	4.8	6.0	10.8	11.8	19.2	-	-	9.9	13.1	13.0
2-4	6.3	7.6	10.4	14.7	11.1	-	25.6	8.2	20.2	21.3
4-6	6.7	7.6	7.8	15.6	17.0	53.0	26.6	7.8	11.7	29.0
6-8	5.8	7.9	9.8	14.9	21.6	58.0	29.6	9.7	11.1	34.0
8-10	5.9	8.4	10.8	15.7	22.2	41.2	36.0	9.8	9.2	30.2
10-12	8.2	7.2	9.1	15.8	36.6		34.6	13.0	5.4	56.4
12-14	5.0	6.6	6.8	16.8	26.4	30.7	47.9	12.3	6.4	56.5
14-16	3.5	3.6	5.6	15.8	26.9		22.8	12.7	6.4	57.3
16-18	1.1	2.3	3.4	14.3	27.8	30.4	43.7	13.3	13.7	55.5
18-20	-0.4	-0.7	1.7	11.1	24.9		62.1	9.6		52.7
20-22	-1.6	-2.3	-0.1	9.6	34.1	27.5	74.6	5.7		56.8
22-24			-0.3	6.3	27.0		32.1	8.0		53.7
24-26			-0.5	2.5	12.4		33.7	5.4		45.7
26-28				0.2	20.2		34.2	4.8		44.1
28-30				1.3	24.5		33.5	2.7		37.4
30-32				-2.6			14.8	-3.0		41.3
32-34				-4.6			8.7	-0.2		27.1
34-36				-3.6			16.9	2.8		35.4
36-38							-7.1	1.[illegible]		28.8
38-40							-6.7			17.7
40-42							-10.1			5.3
42-44							-3.2			3.7
44-46							-7.0			-[illegible]
46-48							-34.0			14.0
Period of most rapid growth (days).	4-12	2-10	0-10	2-10	-	-	8-28	0-20	-	10-24
Average daily weight increase over period of most rapid growth (g.)	6.[illegible]	7.8	9.8	15.5	-	-	41.4	10.6	-	55.5
Average daily weight increase over the whole period of positive weight increases (g.).	5.2	6.4	7.6	11.1	23.6	40.1	33.9	6.9	10.5	33.7

observations made, and the number of measurements in each age-sample are given in the figures.

Daily weight increase.

The average daily weight increases throughout the period of growth, for the various species investigated, are given in Table 65. The period of growth from hatching to fledging is covered in all the species but the two gull species and the Guillemot. The former were lost from their pens when between 22 and 30 days old, and the latter leave the ledges for the open sea at about 18 days, at which time they are only about one third of their final weight. A measure of the average daily weight increase over the most rapid period of growth is given for each species, excepting the three mentioned above where the weight increase over the whole period of positive weight increases is also given for each species.

Increase in wing length with age.

The mean growth curves of increase in wing length, measured from the 'elbow' to the tip of the longest primary feather, with age, together with range of values, of the species investigated on which these measurements were made, are given in Figure 29 A to C. The data includes all observations made, and the number of measurements in each age sample are given in the figures.

FIGURE 29.

Growth of chicks. Increase in wing length with age.

Open circles represent the mean values of the wing length of chicks at two day intervals. Vertical lines represent the range of wing length values at each age.

x = wing length in mm.

y = Age in days.

N = Number of wing length records in each sample.

A = Arctic Tern.

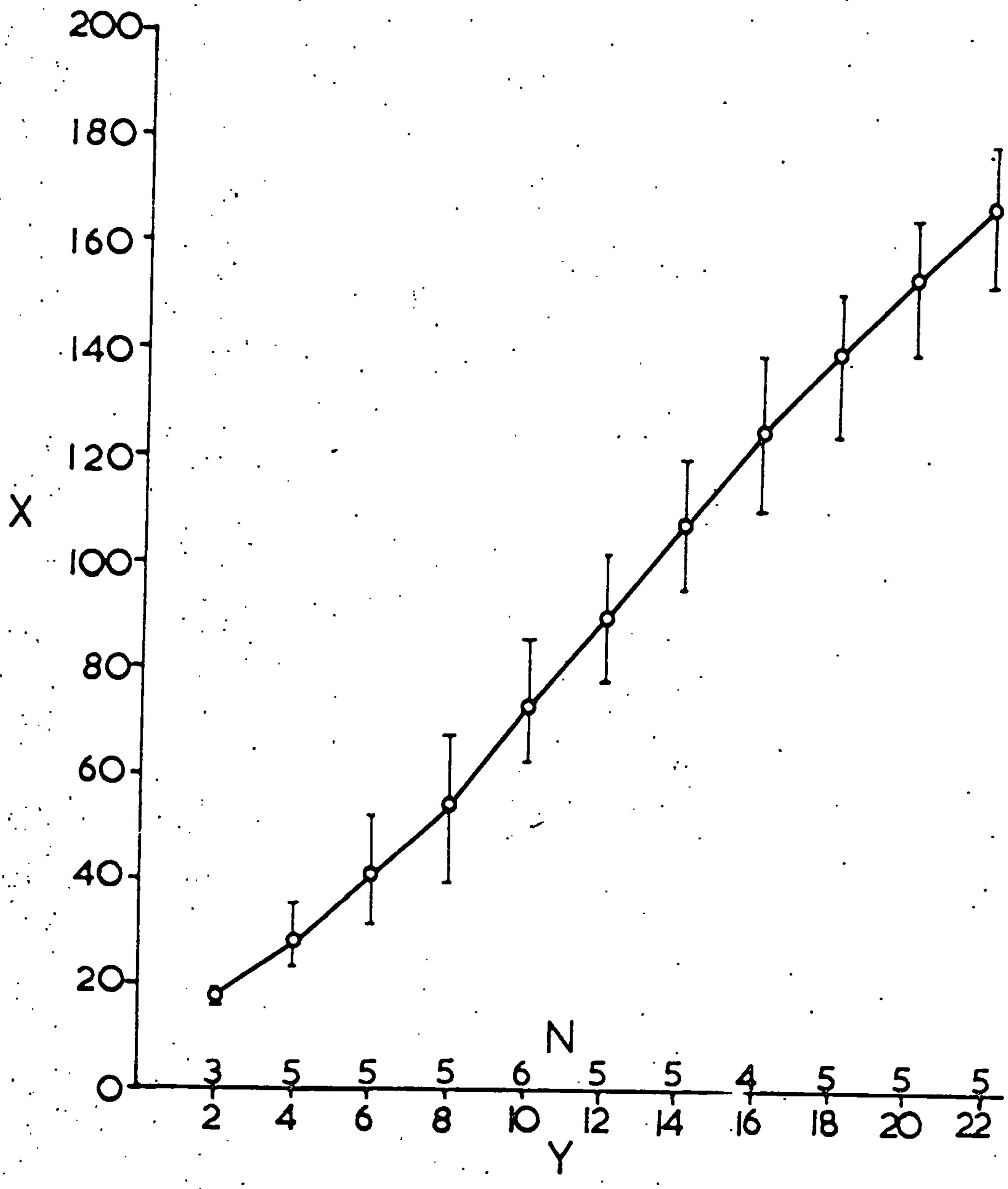
B = Kittiwake.

C = Lesser Black-back Gull.

D.= Fulmar.

E = Shag.

A.


200
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X
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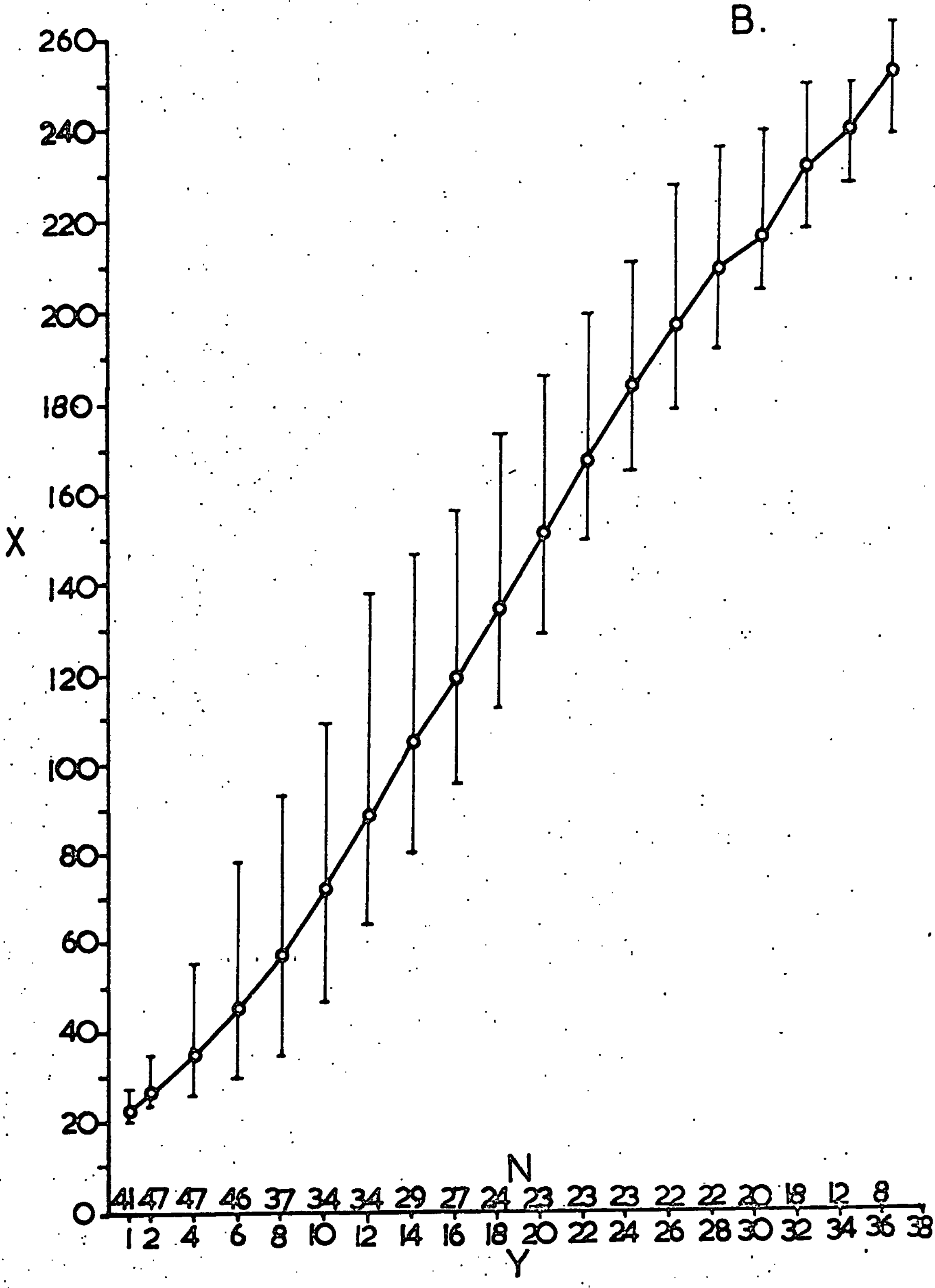
2 4 6 8 10 12 14 16 18 20 22
Y



B.
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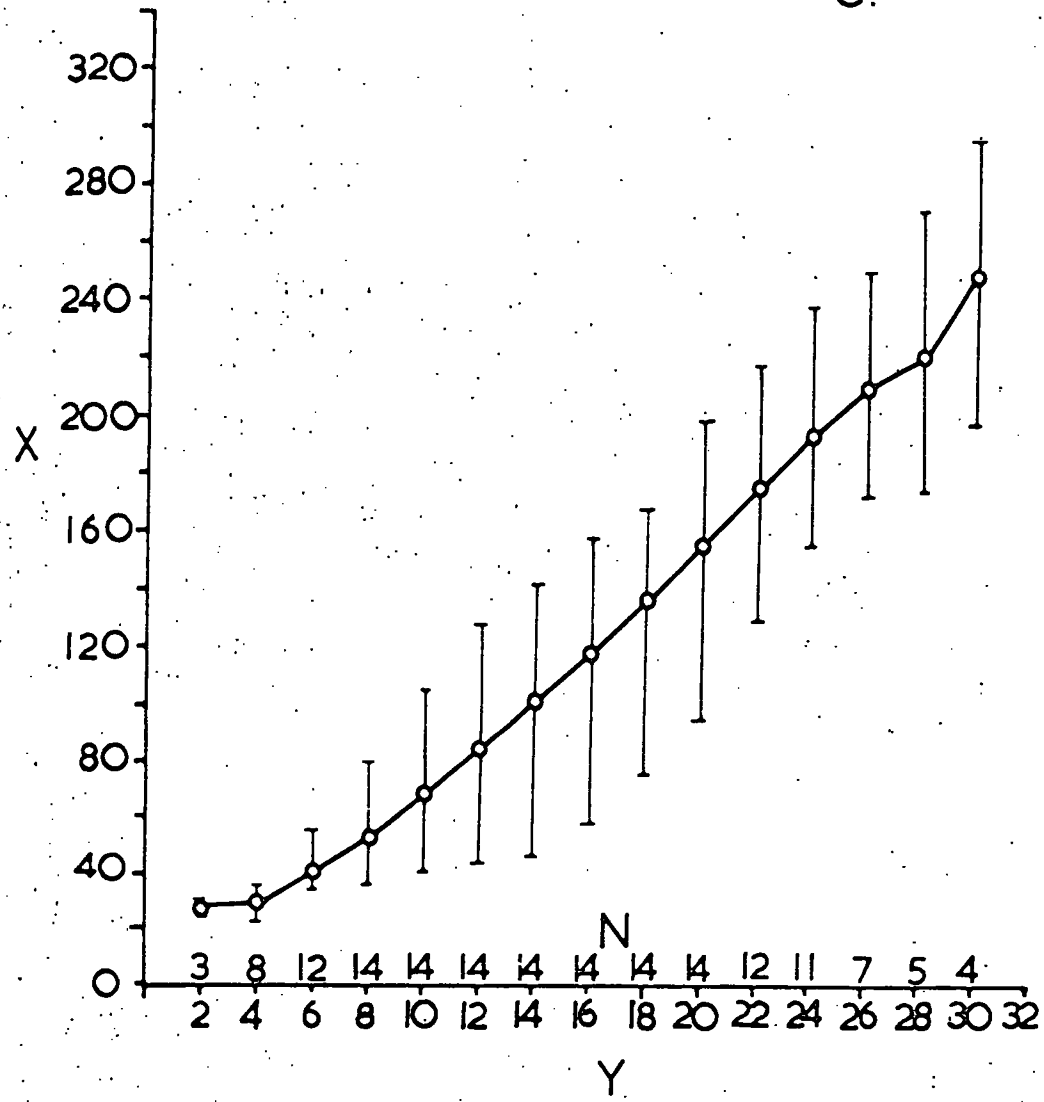
41 47 47 46 37 34 34 29 27 24 23 23 23 22 22 20 18 12 8
1 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38

C.



X
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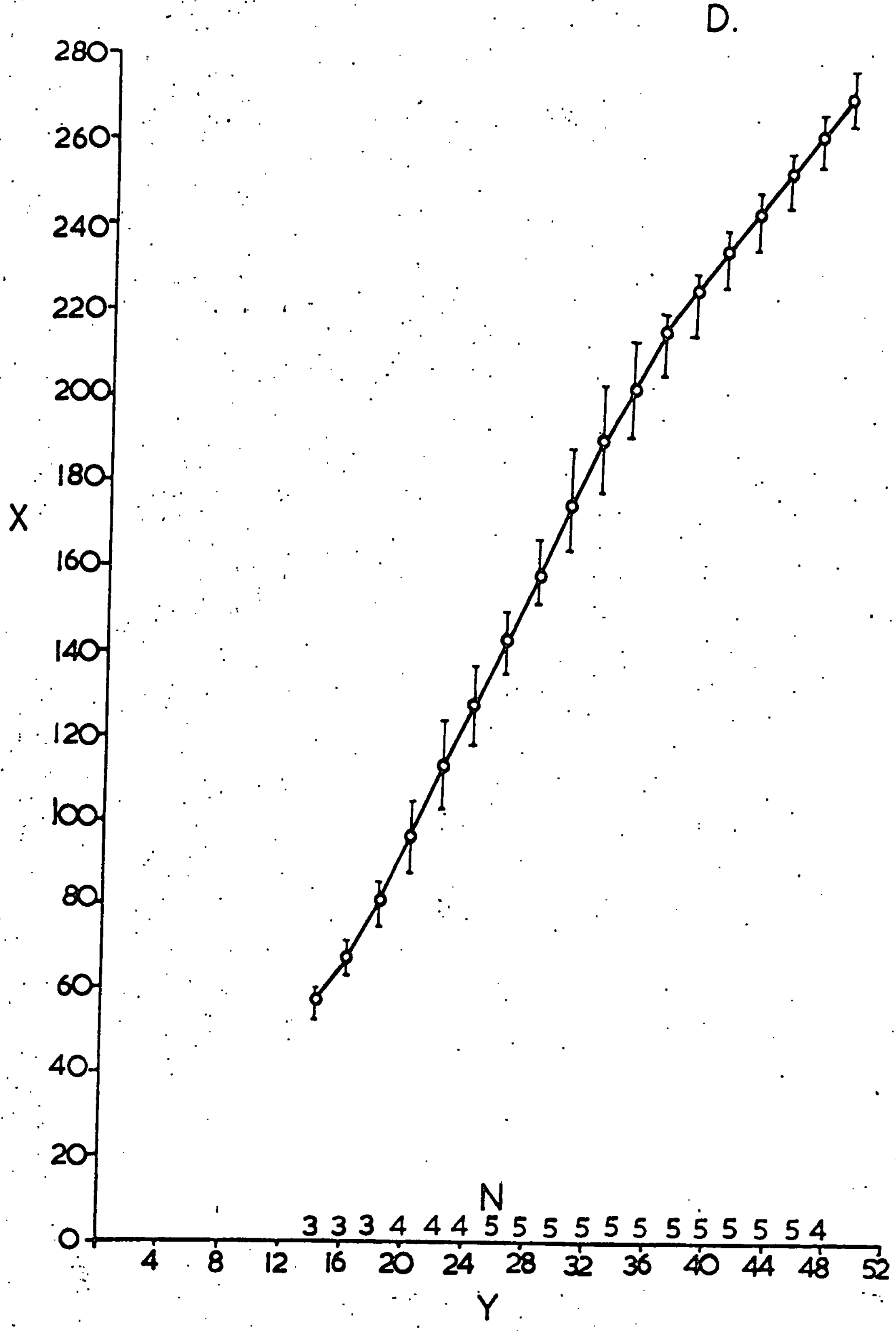
2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32
Y


D.
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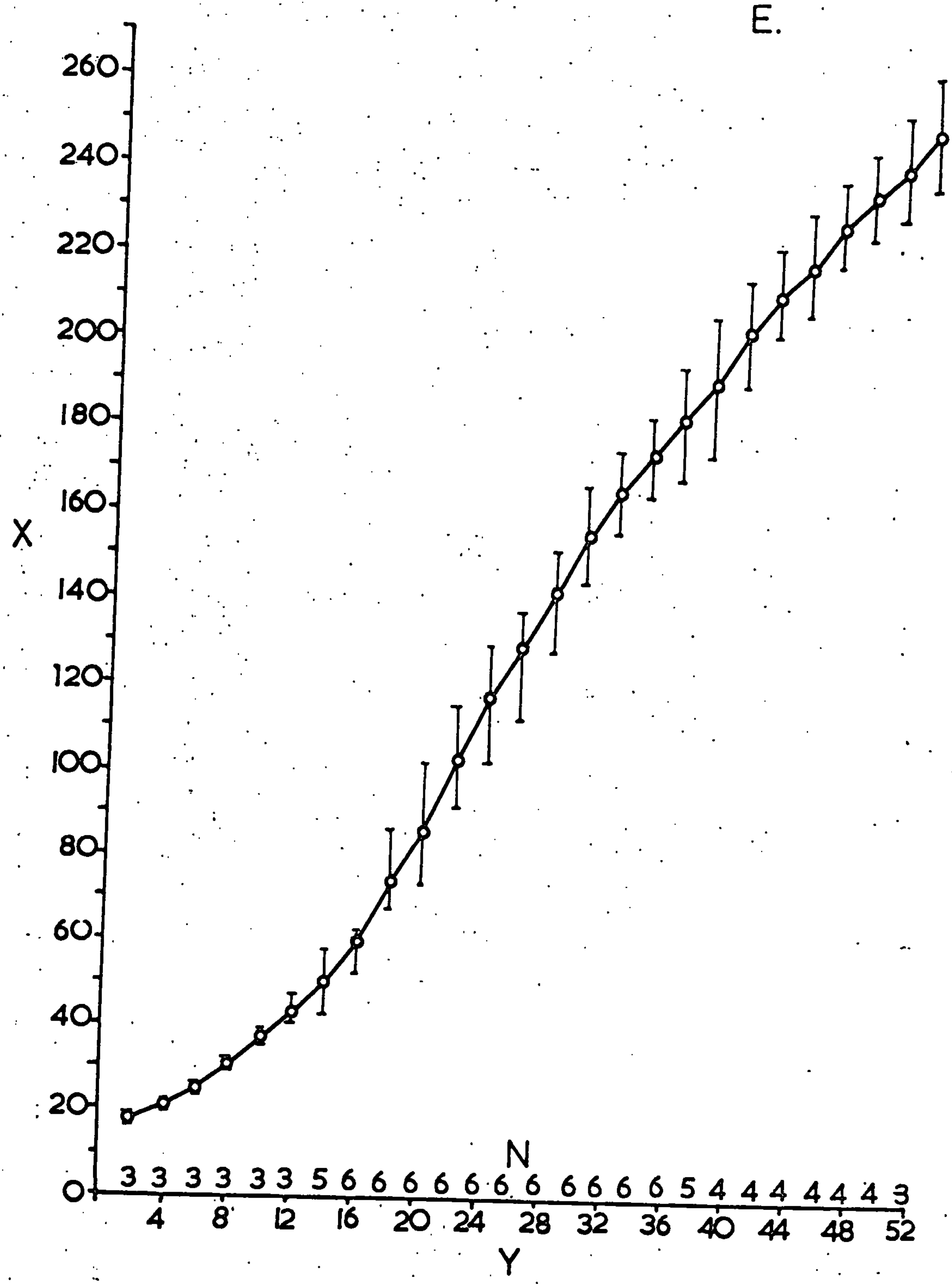
4 8 12 16 20 24 28 32 36 40 44 48 52
Y



E.
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4 8 12 16 20 24 28 32 36 40 44 48 52
Y

ily wing length increase.

The average daily wing length increases, throughout the eriod of growth, are given in Table 66. Of the five spec-es on which measurements were made, only the Lesser Black-ck Gull did not reach fledging age before the measure-nts were discontinued. The average daily increases in ng length over the whole period for which measurements re made are also given in the table.

mparison of increase in wing length and increase in weight indices of growth in sea-bird chicks.

Under adverse feeding conditions chicks both lost ight and the growth of the wing was retarded. The de-ease in the growth rate of the wing was, however, of aller relative value than the decrease in the growth of tal weight i.e. under adverse conditions the chicks uld tend to lose weight fairly rapidly, and the range weights from good feeding conditions, to bad conditions, uld be large. The wing length, however, does not decrease, y the rate of increase is slowed, thus there is a much aller range of variation in wing length under fluctuating eding conditions. For this reason it was thought that asurements of weight increase would give the most posi-ve indication of fluctuations in the growth rate caused external factors, in particular the availability of food.

[illegible] Average daily wing length increases, throughout the period of growth, of various sea-bird species breeding on the Farne Islands.

AGE PERIOD (days)	AVERAGE INCREASE IN WING LENGTH/DAY OVER EACH TWO-DAY PERIOD (mm.) ARCTIC TERN	KITTIWAKE	LESSER BLACK-BACK GULL	FULMAR	SHAG
0-2	-	3.5	-	-	-
2-4	5.1	4.6	0	-	1.5
4-6	6.4	5.2	6.2	-	2.0
6-8	6.6	5.8	6.1	-	2.6
8-10	9.3	7.6	7.6	-	3.3
10-12	8.4	8.4	8.3	-	3.0
12-14	8.8	8.2	8.3	-	3.4
14-16	8.7	7.0	7.9	5.0	4.9
16-18	7.3	7.6	9.1	7.0	7.4
18-20	7.1	8.1	9.7	7.7	6.0
20-22	6.6	8.5	9.5	8.4	7.9
22-24		8.0	0.6	7.7	7.4
24-26		6.8	9.8	7.4	5.9
26-28		6.1	12.2	7.5	6.1
28-30		3.1	14.7	8.3	7.1
30-32		7.8		7.6	6.9
32-34		3.9		6.6	8.2
34-36		6.5		6.5	4.1
36-38				4.5	9.1
38-40				4.8	6.1
40-42				4.4	4.3
42-44				4.5	3.2
44-46				4.6	4.9
46-48				4.5	3.7
48-50					3.0
50-52					4.5
Average over whole period.	7.4	6.5	7.9	6.3	4.8

therefore comparisons of the growth rates of different groups of chicks were based on weight records rather than on wing lengths.

COMPARISON OF THE GROWTH OF GROUPS OF CHICKS UNDER DIFFERENT CONDITIONS.

Because of the variation in the ages of chicks weighed at any one particular time it was found to be impossible to compare directly the weight gains of individual chicks over a particular period. Thus in order to obtain an accurate comparative analysis of the growth of individuals, the growth curve of each individual was used to estimate the amount of time taken for the weight of the chick to rise from weight A to weight B. This period was adjusted for each species to cover the part of the growth curves when weight gains were greatest, and most regular (see Figure 26), and was thus considered to be the most useful indicator of the general growth of the chick. The data, presented in terms of the average daily weight increases during the stated periods, are given in Table 67 A-C. Significance tests were made on the variation between the average daily weight increases of the various groups of chicks within each species. The results of these tests are summarized in Table 68. It can be seen that in no case was there found to be a significant difference in

TABLE 67. Comparison of the average daily weight increases of individual chicks over a standard period of growth. (All data in g.)

A. Tern species.

SPECIES / PERIOD OF GROWTH CURVE COMPARED.		ARCTIC TERN 20-90g. Average daily wt. increase 1961	ARCTIC TERN Average daily wt. increase 1962	ARCTIC TERN Average daily wt. increase for each group.	COMMON TERN 30-110g. Average daily wt. increase 1962	COMMON TERN Average daily wt. increase for each group.	SANDWICH TERN 50-170g. Average daily wt. increase 1962 June 15-19	SANDWICH TERN Average daily wt. increase 1962 June 20-23	SANDWICH TERN Average daily wt. increase for each group.
BROODS OF ONE CHICK.		7.65	5.90				5.43	13.19	
		5.51	6.60				9.16	14.37	
		5.71	7.25				9.80	12.06	
		5.88	7.91	7.02			9.06	11.37	
		6.33	6.31				9.56	11.37	9.99
			7.53				9.60	5.45	
			7.65				8.70		
							10.08		
							12.56		
							8.11		
BROODS OF TWO CHICKS.	First Hatched		6.86		6.75				
			6.63		8.25				
			6.17	6.61	9.04	7.77			
			6.86		6.96				
			6.54		7.84				
	Second-Hatched		6.45		6.67				
			6.25		8.38				
			6.03	6.29	7.24	7.45			
			6.45		7.51				
Average daily wt. increase for each group.		6.22	6.71		7.63		9.21	11.30	

[illegible] over a standard period of growth. (All data in g.) [illegible]
B. Gull species.

SPECIES		LESSER BLACK-BACK GULL		KITTIWAKE (All chicks)			KITTIWAKE (Early & late chicks only).			
PERIOD OF GROWTH COMPARED		100-650g. Average D.W.I. 1962	Average D.W.I. for each group.	100-300g. Average D.W.I. 1961	1962	Average D.W.I. for each group.	100-300g. Average D.W.I. 1961 Before June 21	1961 After July 1	1962 June 9-12	1962 June 15-17
BROODS OF ONE CHICK		32.45	26.73	16.19		17.16	16.19	12.70	13.65	13.70
		27.93		12.70			17.24	22.73	16.74	20.30
		30.05		18.18			17.39	15.50	18.35	15.75
		26.57		17.32			17.32	14.49	18.69	14.71
		19.71		19.80			19.80	11.59	19.80	15.56
		23.71		18.78			18.52	20.62	17.09	17.09
				16.39			14.98	14.60	14.49	16.81
				17.09				17.09	15.33	
				18.02				18.02	14.68	
BROODS OF TWO CHICKS	First-Hatched	36.67	32.51	17.24	16.74	16.34 (1961)				
		28.35		14.98	18.35	16.41 (1962)				
				14.81	19.42					
				12.82	19.80					
				19.05	14.49					
				22.73	15.75					
				14.49	14.68					
				14.60	13.70					
					15.33					
	Second-Hatched	28.28	29.99	17.39	13.65	15.64 (1961)				
		31.70		15.27	17.62	16.22 (1962)				
				18.52	20.03					
				14.08	15.09					
				13.07	16.95					
				15.56	14.71					
				11.59	17.09					
				20.62	16.81					
				14.71	14.68					
Average D.W.I. for each group		28.54		16.38	16.28		17.35	16.37	16.25	16.27

TABLE 67. Comparison of the average daily weight increases (D.W.I.) of individual chicks over a standard period of growth (All data in g.).
C. Puffin and Shag.

SPECIES Period of growth compared		SHAG 400-1400g. AVERAGE D.W.I. 1961	SHAG 400-1400g. AVERAGE D.W.I. 1962	SHAG AVERAGE D.W.I. FOR EACH GROUP	PUFFIN 100-250g. AVERAGE D.W.I. Before June 9	PUFFIN 100-250g. AVERAGE D.W.I. After June 10
Broods of one chick		42.55	63.69 61.35	55.86	13.64 10.20 10.99 12.82 11.49 12.60 14.02	11.07 15.96 11.36 10.34 14.71
Broods of two chicks.	First-Hatched		60.42 38.17 60.06 55.87	53.63		
Broods of two chicks.	Second-Hatched		66.67 52.08 49.75	56.17		
Broods of three chicks.	First-Hatched	51.15 47.73	43.48 50.00 45.04	47.48		
Broods of three chicks.	Second-Hatched	50.89 47.17	58.48 50.76 47.06	50.87		
Broods of three chicks.	Third-Hatched	41.67 46.94	39.37 44.74 38.46	42.24		
Average D.W.I. for each group.		46.07	51.17		12.25	12.69

GROUPS OF CHICKS COMPARED	PROBABILITY (P.) ARCTIC TERN	COMMON TERN	SANDWICH TERN	KITTIWAKE 1961	KITTIWAKE 1962	LESSER BLACK-BACK GULL	PUFFIN	SHAG
1962 chicks with 1961 chicks	<0.05 >0.01	-	-	>0.1		-	-	>0.1
Chicks hatched in early part of season with chicks hatched towards end of season.	-	-	<0.1 >0.05 *1.	>0.1 *2	>0.1 *3	-	>0.1 *4	-
First hatched chicks from broods of 2 or 3 with second hatched chicks.	<0.1 >0.05	>0.1	-	>0.1	>0.1	>0.1	-	>0.1
First hatched chicks from broods of 2 or 3 with single chicks.	<0.1 >0.05	-	-	>0.1	-	>0.1	-	>0.1
Second hatched chicks from broods of 2 or 3 with single chicks.	>0.1	-	-	>0.1	-	>0.1	-	>0.1
First hatched chicks from broods of 3 with third hatched chicks.	-	-	-	-	-	-	-	<0.05 >0.02
Second hatched chicks from broods of 3 with third hatched chicks.	-	-	-	-	-	-	-	<0.05 >0.01
Third hatched chicks from broods of 3 with single chicks.	-	-	-	-	-	-	-	<0.05 >0.02
First hatched chicks from broods of 2 with first hatched chicks from broods of 3.	-	-	-	-	-	-	-	>0.1
Second hatched chicks from broods of 2 with second hatched chicks from broods of 3.	-	-	-	-	-	-	-	>0.1

the growth rates of the various groups compared, in any of the species examined. Groups of Sandwich Tern, Puffin, and Kittiwake chicks were compared, to assess whether there was any difference in the growth rates of chicks hatched early in the season, and chicks hatched later in the season. Since no difference was shown in any of these species it would seem that there is sufficient food available throughout the summer in the Farne Islands area to allow for the successful rearing of chicks. Similarly it would seem that those birds which hatch two or three chicks had no difficulty in raising that number as efficiently as those which had only a single chick, no differences being shown in the growth rates of any of these groups, which were examined in the Arctic Tern, Common Tern, Kittiwake, Lesser Black-back Gull, and Shag. Thus it can be assumed that food was readily available to supply the demand of birds with larger brood sizes. A further support for this assumption is that in no case was there found to be any death of chicks which could be attributed to starvation, although deaths due to exposure during excessively wet and windy weather occurred on at least two occasions, particularly amongst the terns, and Kittiwake chicks. Differences in growth rates in 1961 and 1962 were examined in the Arctic Tern, Kittiwake, and Shag, but were not found to be significant. It would thus seem that available food was equally abundant in both years.

The results for the Kittiwake are similar to those found by Coulson and White (1958), who examined the growth rates of groups of Kittiwake chicks at North Shields, but found no evidence of a distinction between the growth rates of first and second hatched chicks in any of the four years during which data was collected.

Because of the difficulty of sexing chicks correctly, no distinction was made between male and female chicks. It is probable, however, that there would be discernible differences in the growth rates of the two sexes, as the females of all the species studied have a somewhat lower average weight than the males.

INCREASE IN WEIGHT AS A PERCENTAGE OF THE AVERAGE WEIGHT OF THE ADULT BIRDS OF THE SPECIES STUDIED.

For the purpose of discussing comparatively the growth curves of the various species the mean weights of the growing chicks can be represented as a percentage of the average adult weight, thus reducing all the values of the abscissae of the different curves to the same scale. In most cases adult birds of the species under study were weighed during the investigation, although in some cases only small numbers were weighed. Average weights for the Shags and Cormorants are based on the weights of birds shot

TABLE 69. Average weights of adult birds of 11 species of sea-birds.

SPECIES	NO. OF SPECIMENS ON WHICH SAMPLE IS BASED	AVERAGE WEIGHT (grams)	AREA IN WHICH SAMPLE WAS TAKEN	AUTHORITY
Arctic Tern	74	103.6	Farne Islands	Present work
Common Tern	11	125.0	Farne Islands	Present work
Sandwich Tern	8	236.6	Farne Islands	Present work
Kittiwake	23	349.9	Farne Islands	Present work
Lesser Black-back Gull	41	854.0	Switzerland	Borg (1959)
Herring Gull	206	1154.0	Switzerland	Borg (1959)
Fulmar	13	768.0	Scotland	Dunnet & Anderson(1961)
Puffin	107	380.4	Farne Islands	Present work
Guillemot	6	925	Farne Islands	Present work
Shag	26	1785	Berwick-on Tweed	Present work
Cormorant	11	3034	Estuaries of Tweed & Lune Lake Windermere.	Present work

off the mouth of the Tweed, and on the North-West coast, during the winter months. The weights for Herring and Lesser Black-back Gulls and for the Fulmar, are taken from previously published work. Table 69 shows the average weights of the adult birds, the number of specimens weighed, the area where the birds were weighed, and the authority, for each of the species under investigation.

COMPARISON OF THE GROWTH RATES OF SEA-BIRDS ON THE FARNE ISLANDS, AND IN THE BARENT'S SEA AREA.

Belopolskii (1957) gives details of the growth, taken as the increase in weight with age, of the chicks of the following species, which are in common with the present study, in the East Murman area of the Barents' Sea :- Arctic Tern, Kittiwake, Puffin, Guillemot, and Shag. A comparison of the weight/age curves of these species in the two areas is given in figure 30. The weights are given as percentages of the mean adult weights in the two areas.

TABLE 70. Mean adult weights of sea-bird species in the Farne Island area and in the Barents' Sea (East Murman coast).

SPECIES	MEAN ADULT WEIGHT FARNE ISLAND AREA	EAST MURMAN COAST
Arctic Tern	103.6	107.0
Kittiwake	349.9	408.4
Puffin	380.8	490.5
Guillemot	925.0	1054.9
Shag	1785	-

On the Murman coast the average adult weights are higher than in the Farne Islands area, as would be expected according to Bergman's rule which states that the average weight of the individuals of a species of warm blooded animal increases with increasing latitude. The respective mean adult weights are given in Table 70. It can be seen that in all the 5 species compared, the Farne Island birds

FIGURE 30.

Comparison of the growth of five sea-bird species breeding on the Farne Islands and on the east Murman Coast of the Barents' Sea.

x = Percentage of adult weight.

y = Age in days.

A (unbroken line)	= Arctic Tern	)	
B (dashed line)	= Kittiwake	)	1 = Farne Island birds
C (dashes & dots)	= Puffin	)	
D (unbroken line)	= Guillemot	)	2 = East Murman birds
E (dotted line)	= Shag	)	

Data on birds in Barents' Sea area from Belopolskii (1957)

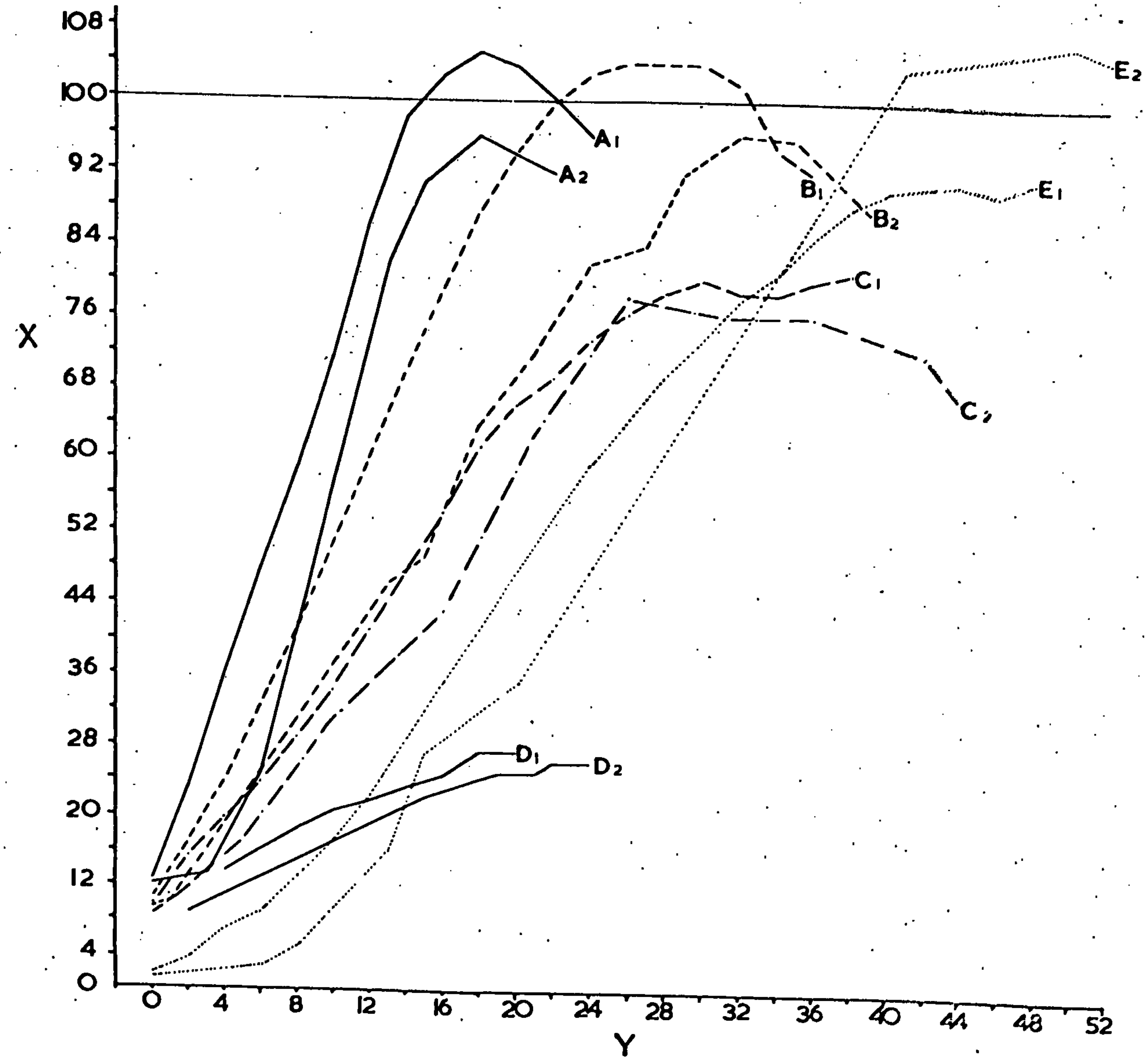

X
108
100
92
84
76
68
60
52
44
36
28
20
12
4
0
Y
0
4
8
12
16
20
24
28
32
36
40
44
48
52
A₁
A₂
B₁
B₂
C₁
C₂
D₁
D₂
E₁
E₂

TABLE 71. Comparison of the daily weight increases (as a percentage of adult weight) of chicks in the Farne Islands and in the Eastern Murman.

AVERAGE WEIGHT INCREASE PER DAY (as percentage of adult weight)

PERIOD OF GROWTH (days after hatching)	ARCTIC TERN Farne Islands	ARCTIC TERN Eastern Murman	KITTIWAKE Farne Islands	KITTIWAKE Eastern Murman	PUFFIN Farne Islands	PUFFIN Eastern Murman	GUILLEMOT Farne Islands	GUILLEMOT Eastern Murman	SHAG Farne Islands	SHAG Eastern Murman
1-3	6.3	0.4	11.6	1.9	2.7	1.1	1.7	0.3	1.4	0.05
4-10	6.9	5.7	6.4	3.1	2.8	2.3	1.6	1.3	1.8	0.8
11-15	5.6	7.3	5.2	2.5	4.5	2.7	2.6	1.0	3.2	2.9
16-20	1.1	0.7	2.7	3.7	6.3	5.0	0.6	0.4	2.9	2.7
21-30	-3.4	-0.7	-0.5	2.3	-1.4	0.8		0.3	2.9	3.1
31-40			-0.6	-0.5	2.6	-0.2			1.5	3.0
41-50						-2.5			-0.1	0.8
51-60									0.6	-0.5
Mean fledging period. (days)	22	22	34	39	40	42	22*	21	51	60

East Murman data after Belopolskii (1957)

* Mean length of period on breeding ledges.

grew at a faster rate than did the birds of the Murman coast, and in all species but the Arctic Tern the Farne birds left the nest site earlier than did the Barents' Sea birds. Table 71 gives the average weight increases per day, as a percentage of adult weight, in the two areas, together with the average fledging times. The figures quoted indicate the fastest growth increase of a given species, not the mean daily weight increases, as the Russian data is presented in this way. In all five species the Farne Islands birds have a much more rapid growth rate over the first 3 days after hatching, and reach a maximum growth increase, followed by a fall off culminating in a decrease in weight, sooner than the East Murman birds. Also the maximum growth increases achieved are higher than in the Russian birds. The time spent at the nest site is similar in both areas for the Arctic Tern, but shorter in the Farne Island area for the Kittiwakes, Puffins and Shags. Accurate data on the time the Guillemot chicks left the ledges were not obtained in the Farne Island area, but was thought to be about the 21st-23rd day, a similar period to that observed in the East Murman area.

These differences reflect the more favourable conditions, both of temperature, and possibly also of food availability, in the Farne Islands area. Because of the generally lower temperatures in the Barents' Sea area, chicks reared there have to expend a proportionally greater amount of energy in maintaining their body temperatures, than do chicks in the Farne Islands area, and thus a smaller percentage of the total food intake will be utilised for growth purposes. A further factor which will tend to lower the percentage daily weight increases of the West Murman birds, is the fact that they attain a higher final weight than do the birds on the Farne Islands. This may also account, in part, for the longer period of development exhibited by those birds.

A COMMENT ON THE FORM OF THE GROWTH CURVES OF INCREASE IN WEIGHT WITH AGE.

A feature of the growth curves of nearly all the species was a period of weight loss immediately prior to fledging. In the majority of organisms the final weight achieved during the growth process is the mature weight, which will be maintained at a more or less constant level in the future. However, loss of weight immediately following the attainment of a maximum weight level by the normal growth processes appears to be a feature of avian species, and has been reported in most birds whose growth curves have been investigated. In some cases the maximum weight achieved by the growing chick is higher than that of the adult bird, and there follows a gradual loss of weight up to and after fledging, until the bird achieves its final mature weight level. This is the case with the Arctic Tern and the Kittiwake in the present investigation (see Figure 30). On the other hand some species reach a maximum pre-fledging weight which is lower than the final mature weight, (c.f. Sandwich Tern and Puffin in the present investigation) but a loss of weight still occurs prior to fledging. A post-fledging growth period must occur in these species, when the mature weight will finally be reached. It is probable that the observations on the Sandwich Tern made during the present work are aberrant, and that under natural conditions the chicks would conform to the pattern of the other tern species, achieving a higher prefledging weight followed by a drop to mature weight. Bertram (1938) has described the prefledging peak in weight as being due to the very rapid development of the liver and the intestines which reach a maximum size and then decrease. The possibility of any large weight losses during the prefledging period being due to diminution in organ size is remote however, although small weight fluctuations may be due to such causes. It is more likely that considerable fat reserves are built up, under favourable growth conditions, during the later periods of growth, and that these are utilized during the prefledging period when energy demands are very high as the chicks greatly increase their activity. Thus Fulmar chicks of 30-40 days are very fat and inactive, being as much as twice the final mature weight, but undergo very severe weight losses during the immediate prefledging period.

A number of writers (e.g. Sumner (1933) Poyntery (1954)) suggest that the inflection in the growth curve, when the growth rate starts declining coincides with the period of maximum feather growth, and that the two factors are correlated. It has been pointed out however that the sigmoid form of growth is basic to nearly all organisms, and that the point of inflection is inherent in the growth pattern. As such it is unlikely that any one factor, such as increase in feather growth, would be the only inhibiting force acting on the growth rate. It is more probably one of a complex series of interrelated developmental factors, all of which will affect the timing of the inflection in the growth curve.

SECTION 4.

THE GROWTH AND FOOD INTAKE OF CHICKS IN THE LABORATORY.

Due to the difficulty of accurately estimating the food intake of chicks in the field (see Section 2), a number of chicks were reared in the laboratory in order to assess the relationship between food intake and weight gain. Young chicks, or hatching eggs, of the following species were obtained - Kittiwake, Guillemot, Herring Gull, Sandwich Tern, Arctic Tern and Puffin - but of these only the first three named were reared successfully.

METHODS.

Eggs at the hatching stage, or young chicks of not more than two days of age were obtained from the colonies on the Farne Islands, and carried to the laboratory in insulated containers. They were transferred to an incubator, where they remained for the first 2-4 days after hatching, following which they were placed in seperate cages in the laboratory. Both the incubator compartments and the cages were lined with absorbent paper, which was changed daily, being weighed both before and after being placed in the cages. Thus a weight record was obtained of all faeces excreted during the experimental period. The chicks were fed on a mixture of herring and cod to which was added a few drops of cod liver oil, and a vitamin concentrate. It was impossible to obtain live or whole fresh fish, and throughout the experiments the fish used was obtained through a local retailer. This undoubtedly was a major contributing factor in the failure to rear the tern chicks successfully, and in the comparatively poor rate of growth shown by the other species. Nearly all the chicks had to be force fed on a mixture of chopped fish, although the Herring Gull chicks would occasionally take food unassisted. The chicks were either weighed before and after each feed, or were fed a known weight of food, and weighed less frequently. All weights were taken on a pan balance which was accurate to 0.1 grams.

RESULTS.

The most successful of the species of chicks reared were Guillemots. Thus the results obtained for this species will be described fully to demonstrate the experimental details, followed by a summary of the results obtained for the other species.

1. GUILLEMOT.

Two Guillemot chicks were obtained, aged 2 and 5 days, together with two chipping eggs which were hatched

TABLE 72. [illegible] chicks. Values for the number of grams of food required for maintenance (c) and the number of grams of food required to bring about weight increase of 1 gram (m_1) for chicks of different ages.

AGE PERIOD (DAYS)	m_1	c
0-4	1.61	12.63
5-9	2.04	23.90
10-14	2.11	44.37
15-19	1.56	74.56
20-30	2.14	99.26

in the incubator. These latter survived for only 2 and 14 days respectively after hatching, but the two obtained as chicks adapted very well to laboratory conditions and grew normally throughout the period of the experiment. They were released on the Farne Islands when aged 29 and 25 days respectively. At the time of release they were thus some five days older than the average age at which naturally reared chicks leave the nesting ledges for the open sea.

A. RELATIONSHIP BETWEEN FOOD INTAKE AND WEIGHT CHANGE OVER 24 HOURS.

The amounts of food taken by individual chicks over 24 hours, (F), and the resulting weight changes, (W), over the same period, are plotted in Figures 31 A-E for the periods of growth from 0-4 days, 5-9 days, 10-14 days, 15-19 days and 20-30 days. The regression line $F=mW + c$, where m is the slope of the line, and c the point of interception on the F axis, calculated on the method of least squares, is fitted to the data on each of the graphs. Table 72 gives the values of c, the intercept on the F axis, being the amount of food required for maintenance, and of m_1, the slope of the line, being the number of grams of food required to bring about a weight change

FIGURE 31.

Artificial rearing of Guillemot chicks. The relationship between food intake and weight change over 24 hours.

x = Food intake over 24 hours (g.).

y = Weight change over 24 hours (g.).

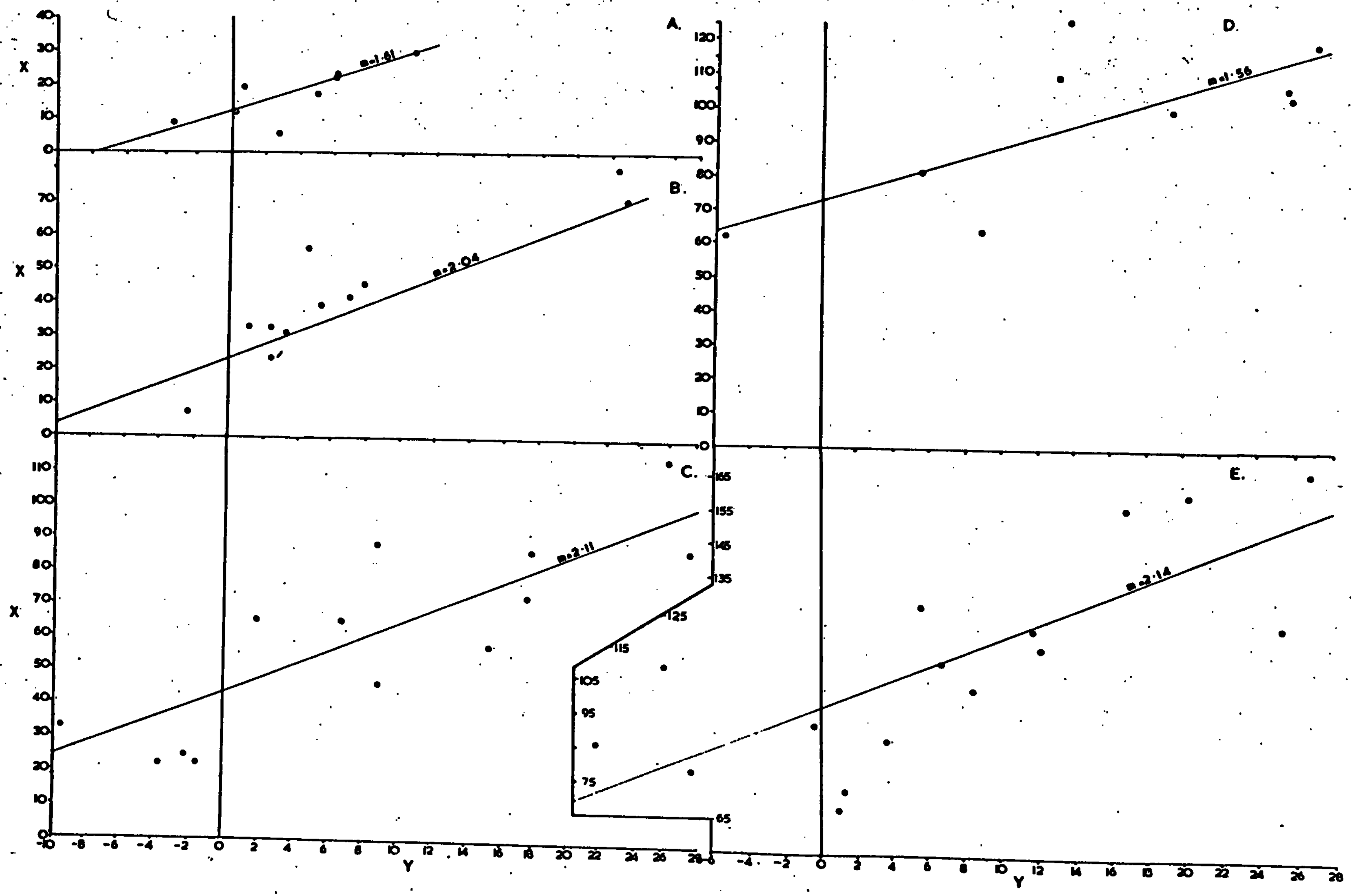
A = 0-4 days.

B = 5-9 days.

C = 10-14 days.

D = 15-19 days.

E = 20-30 days.


A.
B.
C.
D.
E.
m=1·61
m=2·04
m=2·11
m=1·56
m=2·14
X
Y

of 1 gram after maintenance needs have been met, for each of the age periods. The average value of m_1, for the whole experimental period of growth, was 1.89.

B. RELATIONSHIP BETWEEN THE FOOD INTAKE AND THE WEIGHT OF FAECES EXCRETED

The faeces were collected on absorbent paper and dried in an oven for 24 hours at 70°C. The difference in the weight of the paper before being placed in the cages, and after drying in the oven, was taken to be the dry weight of the faeces. The weight of food taken has been reduced to equivalent dry weights using the ratio 1: 0.49 for wet: dry weight of herring, and 1: 0.24 for wet: dry weight of cod, as found experimentally by drying varying weights of each type of fish in the oven for 60 hours at 70°C.

There was a margin of error in the method of recording the amount of faeces excreted, due to the impossibility of collecting all the excreta. Inevitably some was lost through the bars of the cages due to displacement of the lining of absorbent paper. The chicks also tended to defaecate on being handled for weighing, which caused further losses. However corrections were made to the total weight of faeces by finding the average weight of a number of defaecations, and counting the number of defaecations outside the cages. The product of these values was added to the weight of faeces contained on the absorbent cage lining. Due to the considerable variation in faeces weights from day to day due in part to variation in the degree of loss incurred in their collection, the weight of faeces collected over 2-day periods has been equated with the weight of food taken over the same periods. Figure 32 shows a plot of those values for the whole growth period. The regression line drawn to the data has a slope, m_2, of 2.21, thus for every 2.2 grams of food ingested 1 gram of faeces was excreted on average over the whole growth period.

2. OTHER SPECIES INVESTIGATED.

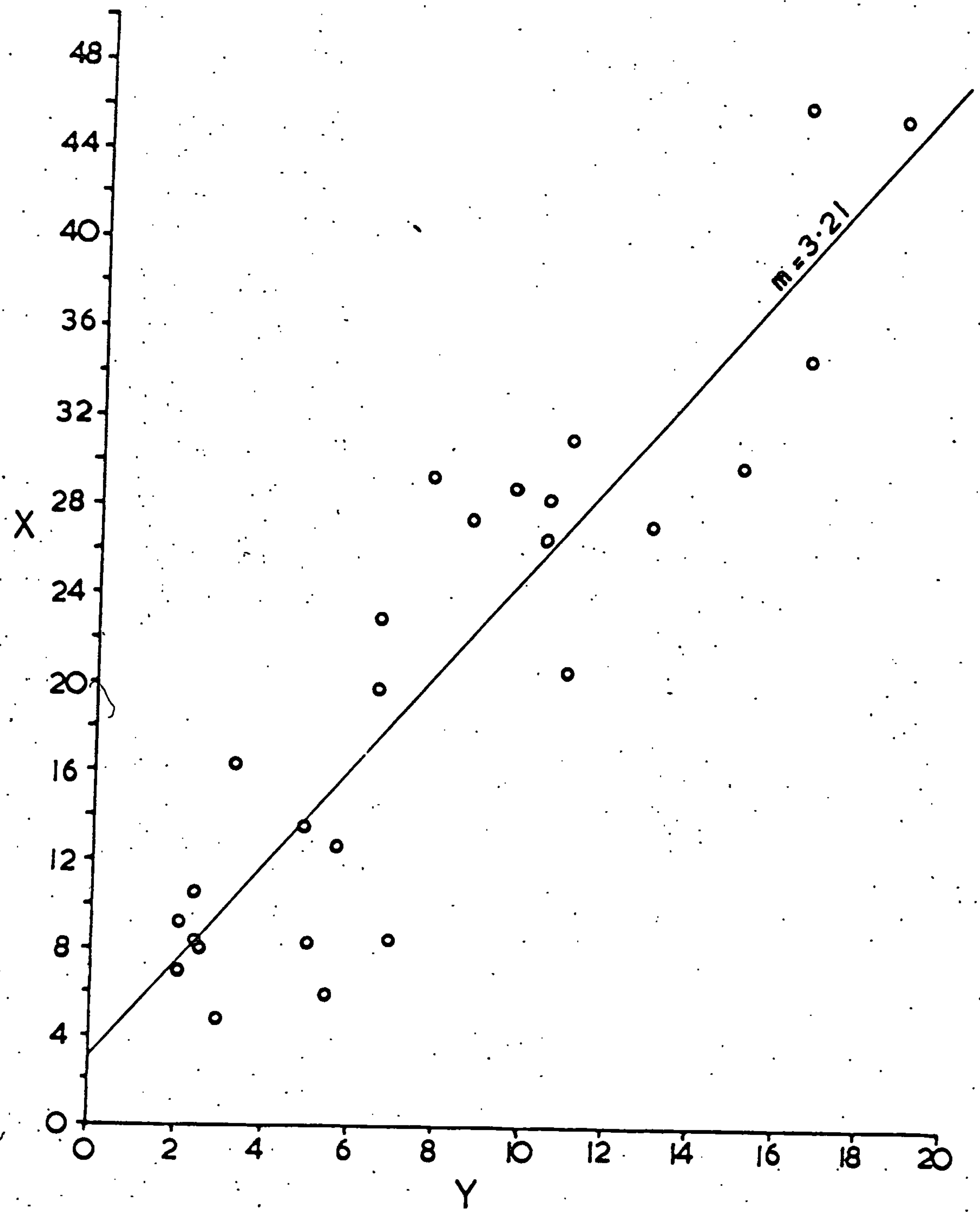
Data were obtained in a similar manner for chicks of the Herring Gull, Kittiwake, Arctic Tern and Sandwich Tern. Attempts at rearing the latter two species failed however, information being obtained only on the first 5 days after hatching, and this was unreliable due to the poor physical condition of the chicks. Table 73 lists the results obtained for all the species investigated. The number of chicks of each species on which the results are based, and the average total

FIGURE 32.

Artificial rearing of Guillemot chicks. The relationship between the food intake and the weight of faeces excreted over 48 hours for chicks aged 0-30 days.

x = Food intake over 48 hours (grams dry weight).

y = Weight of faeces excreted over 48 hours (grams dry weight).



X
48
44
40
36
32
28
24
20
16
12
8
4
0
m = 3·21
Y
0
2
4
6
8
10
12
14
16
18
20

TABLE 73 All species.
Summary of the values of m_1, m_2, and c, together with the number of chicks of each species investigated, and the total body weight over each age period.

SPECIES	NUMBER OF CHICKS INVESTIGATED	AGE PERIOD (DAYS)	FOOD/WEIGHT CHANGE RELATIONSHIP m_1	AVERAGE VALUE OF m_1	c	FOOD FAECES RELATIONSHIP m_2	AVERAGE TOTAL BODY WEIGHT
KITTIWAKE	6	0-5	2.88	1.69	6.9	2.46	36.9
		6-10	1.59		25.9		72.4
		11-15	1.92		35.9		105.2
		16-20	1.72		45.2		142.7
		over 20	1.54		51.7		172.7
HERRING GULL	4	0-4	1.03	1.46	21.3	3.16	63.1
		5-9	1.89		27.1		106.0
		10-14	1.42		46.3		170.0
		15-19	1.16		59.9		217.4
		20-24	1.78		61.3		270.9
GUILLEMOT	3	0-4	1.61	1.89	12.6	2.21	66.4
		5-9	2.04		23.9		104.1
		10-14	2.11		44.1		161.7
		15-19	1.56		74.6		253.4
		20-30	2.14		99.3		335.8
ARCTIC TERN	4	0-5	1.32		5.1	1.28	15.3
SANDWICH TERN	4	0-5	1.56		10.6	1.21	29.0

body weight over each age period are also given. For the Kittiwake chicks the percentage of weight gain for unit amount of food is based on the average values of m_1 from the fifth day onwards. The values for the earliest age period have been omitted , as during this period the chicks were kept in the incubator, and the collection of faeces was not undertaken daily. In addition the chicks were not maintained in seperate compartments in the incubator, and thus the amount of faeces produced could only be assessed for the chicks as a whole, and not for individuals, as was done later when the chicks were kept in seperate cages. For these reasons the values for the food/faeces relationship obtained over the period were inaccurate and have been omitted in the derivation of the average valuo for the food/faeces ratio. Thus in comparing the values of the food/weight gain, and the food/faeces ratio, the earliest period has been omitted for both values. The Herring Gull and Guillemot chicks were not kept together in the incubator for any length of time, but were transferred to seperate cages almost immediately. The collection of faeces during the initial period was thus undertaken regularly, and for this reason the values for the initial period both for m_1, and for m_2 have been included in deriving the average values.

Graphs of the relationships between the food intake and weight change over 24 hours for the various age periods, and of food intake and the amount of faeces excreted over a specific period for the whole time of the experiment, for the various species investigated, are given in Figures 33 to 38.

DISCUSSION.

All the species reared experimentally, other than the Guillemot, had abnormally low growth rates as compared with naturally reared chicks. This should not affect, however, the values obtained for the amount of food required for maintenance, and the amount of food required to bring about a particular increase in body weight, as the method of analysis used, i.e. the grouping of the data into 5 day periods. allowed these values to be derived over periods of net weight increase, the actual size of the weight increase being irrelevant. No attempt has been made to interpret the results obtained in terms of energy levels, although average calorific values could be used to derive comparative metabolic data. The relevance of the experiments is, however, to comparative food-intake values and thus

FIGURE 33.

Artificial rearing of Kittiwake chicks. The relationship between food intake and weight change over 24 hours.

x = Food intake over 24 hours (g.).

y = Weight change over 24 hours (g.).

A = 0-4 days.

B = 5-9 days.

C = 10-14 days.

D = 15-20 days.

E = over 20 days.

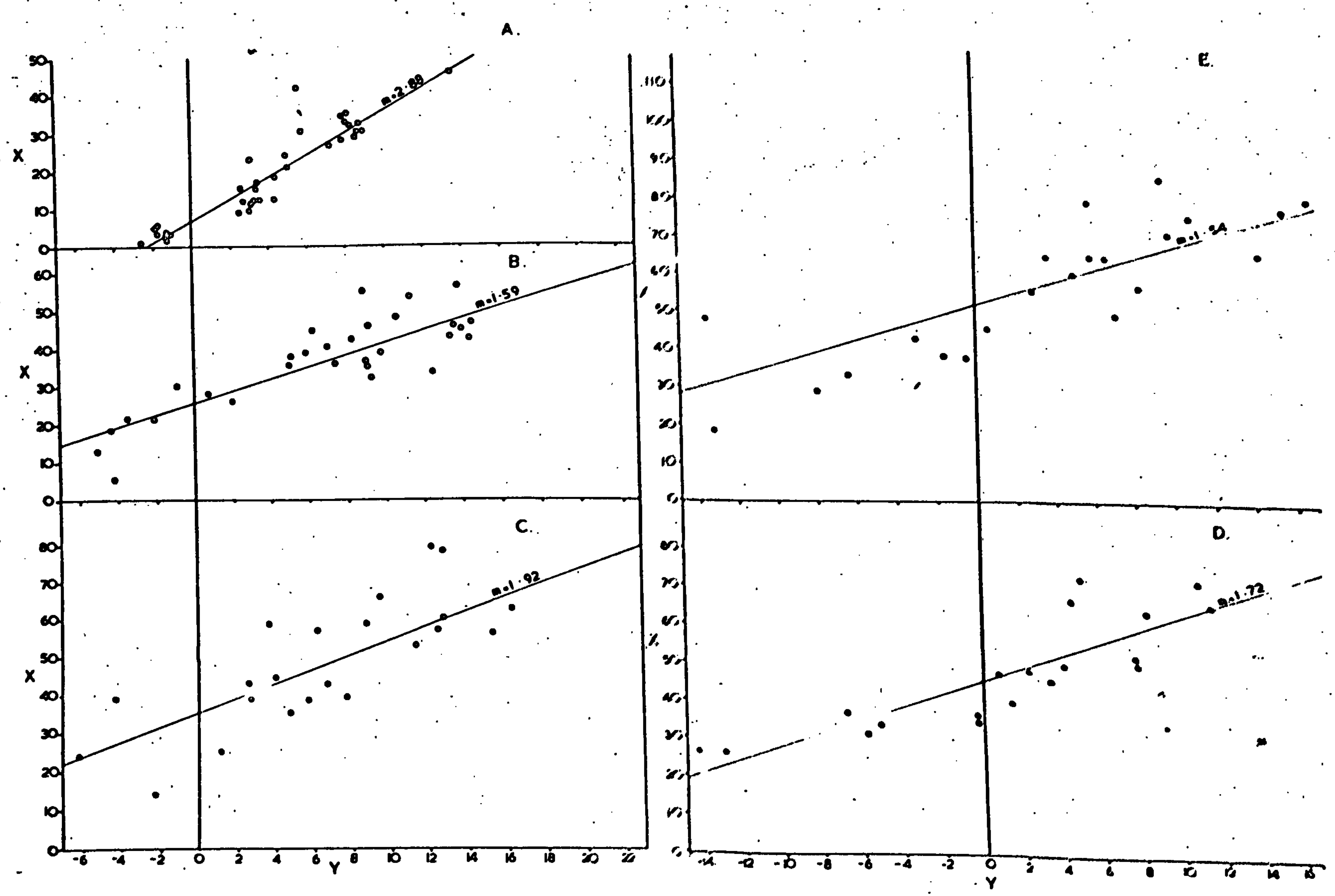
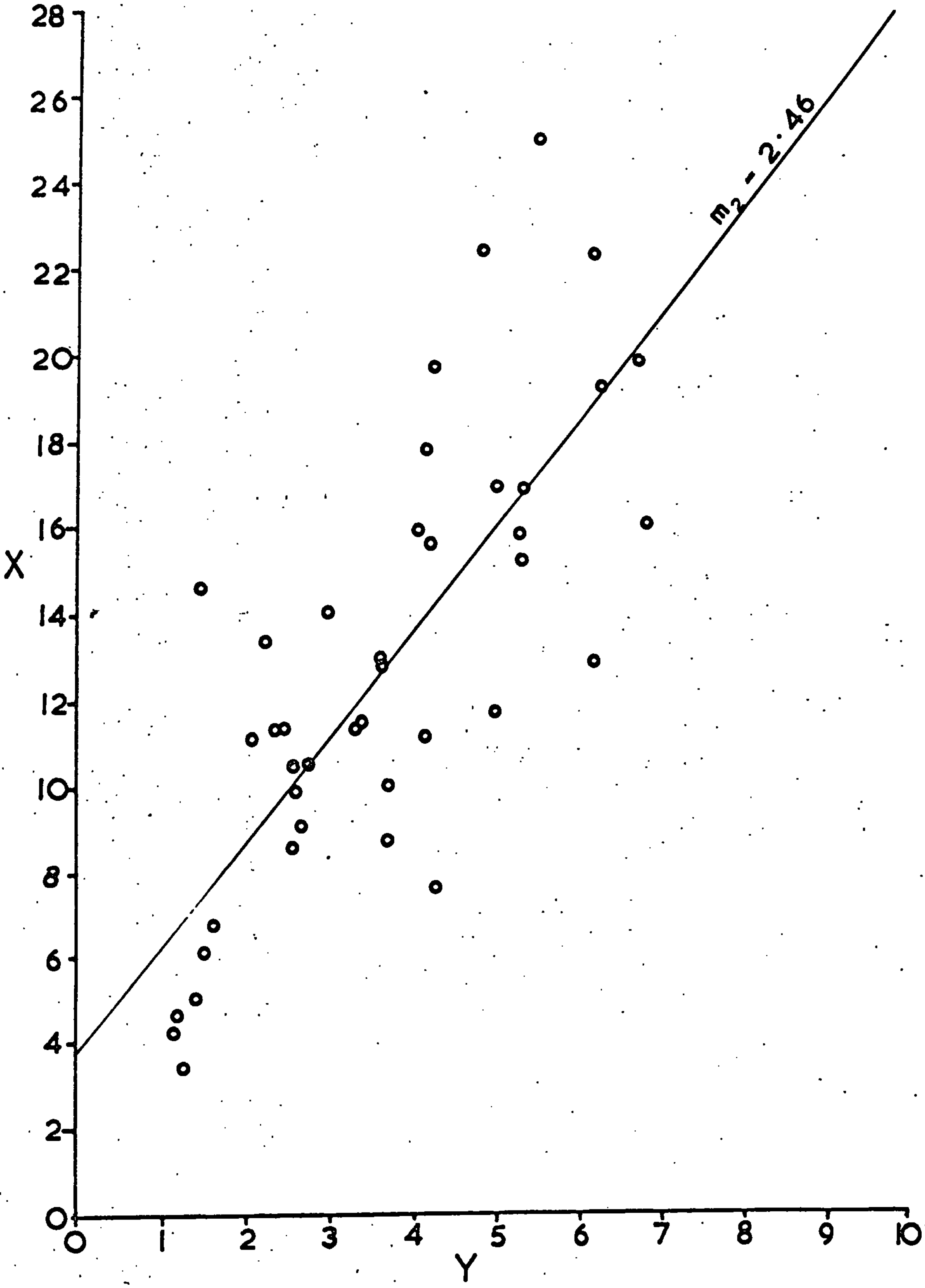

A.
m=2.89
B.
m=1.59
C.
m=1.92
D.
m=1.72
E.
X
Y

FIGURE 34.

Artificial rearing of Kittiwake chicks. The relationship between the food intake and the weight of faeces excreted, over 3-day periods for chicks aged 0-28 days.

x = Food intake over 3-day period. (grams dry weight).

y = Weight of faeces excreted over 3-day period (grams dry weight).



m₂ - 2·46
X
Y
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
1
3
5
7
9

FIGURE 35.

Artificial rearing of Herring Gull chicks. The relationship between food intake and weight change over 24 hours.

x = Food intake over 24 hours (g.).

y = Weight change over 24 hours (g.).

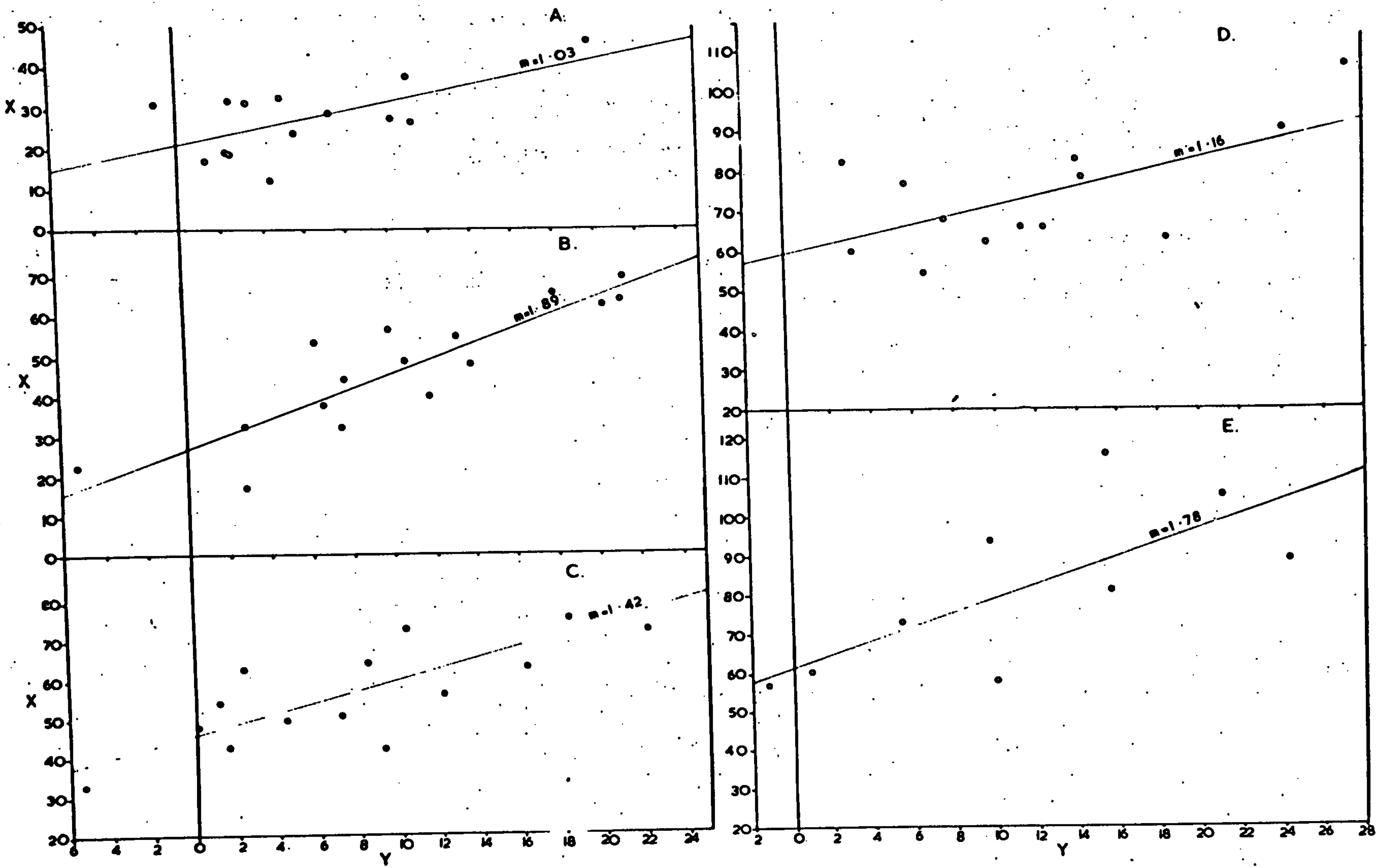
A = 0-4 days.

B = 5-9 days.

C = 10-14 days.

D = 15-19 days.

E = Over 20 days.



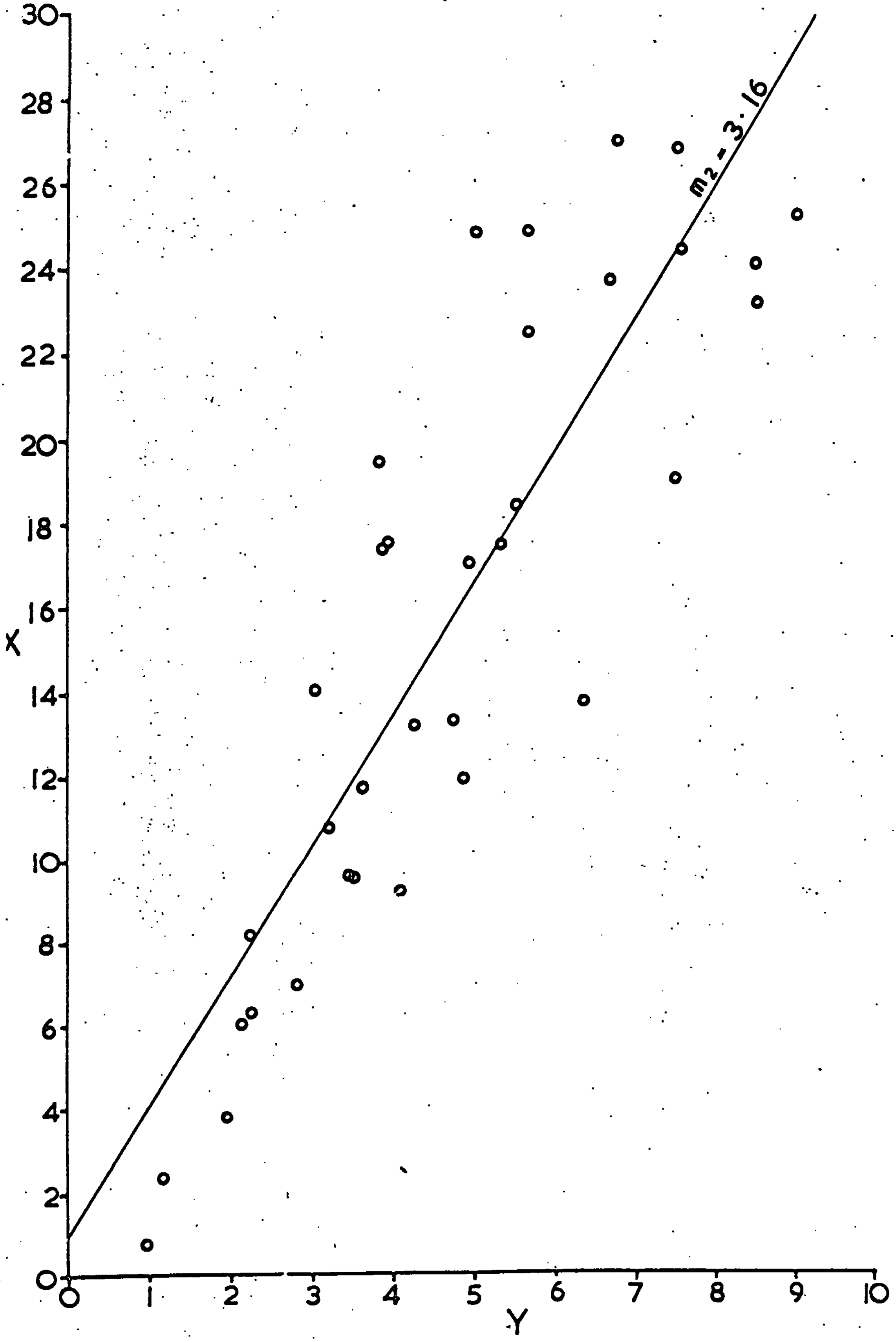
A.
m=1·03
B.
m=1·89
C.
m=1·42
D.
m=1·16
E.
m=1·78
X
Y

FIGURE 36.

Artificial rearing of Herring Gull chicks. The relationship between the food intake and the weight of faeces excreted over 48 hour periods for chicks aged 0-24 days.

x = Food intake over 48 hours. (grams dry weight).

y = Weight of faeces excreted over 48 hours. (grams dry weight).



X
Y
$m_2 - 3 \cdot 16$
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
0
1
2
3
4
5
6
7
8
9
10

FIGURE 37.

Artificial rearing of Arctic Tern chicks.

A. The relationship between food intake and weight change over 24 hours for chicks aged 0-5 days.

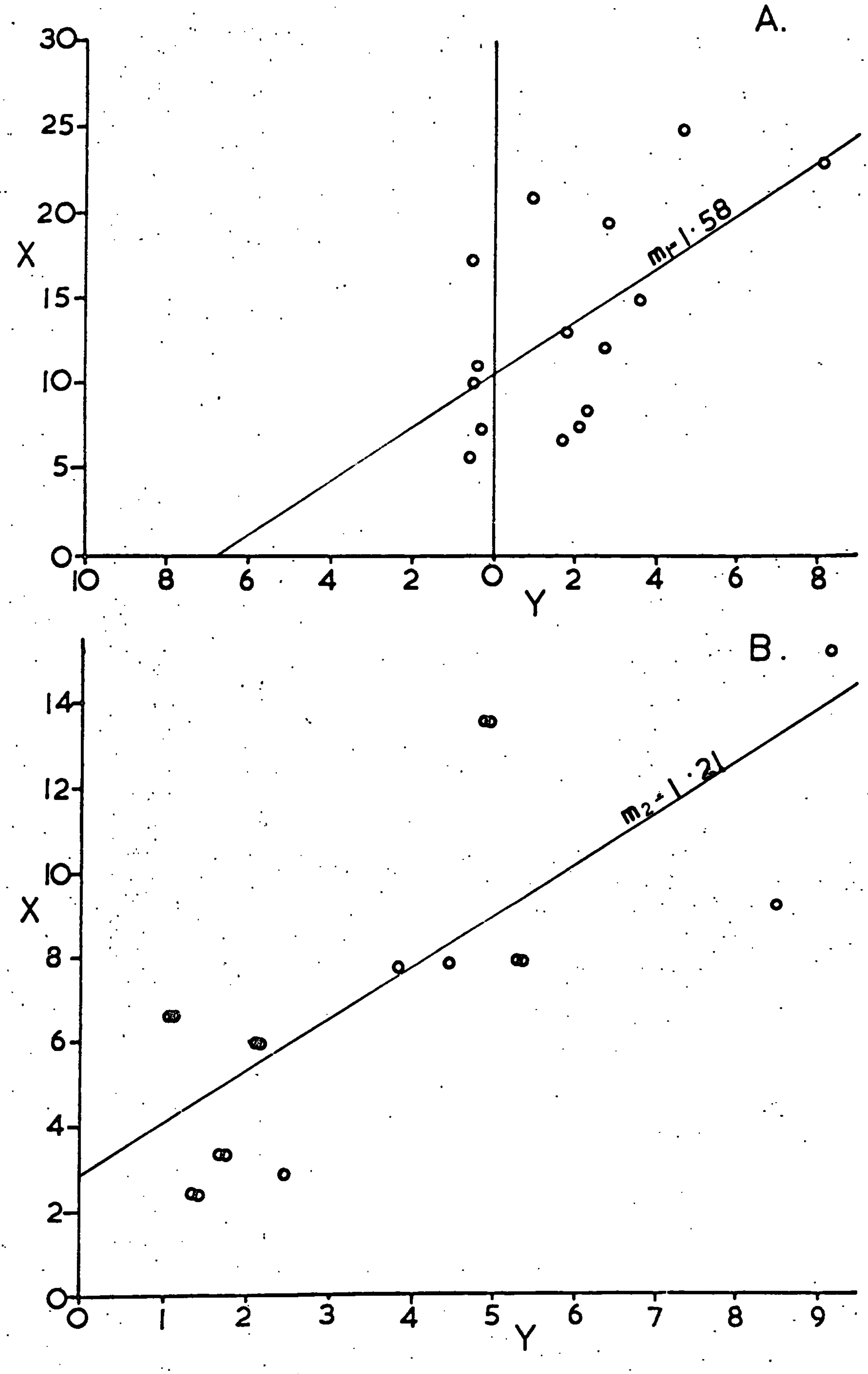
x = Food intake over 24 hours. (grams).

y = Weight change over 24 hours. (grams).

B. The relationship between the food intake and the weight of faeces excreted over 24 hours for chicks aged 0-5 days.

x = Food intake over 24 hours. (grams dry weight).

y = Weight change over 24 hours. (grams dry weight).



A.
X
Y
m1 = 1·58
B.
m2 = 1·21

a closer analysis of the energetics of the feeding process is omitted.

EFFICIENCIES OF CONVERSION OF FOOD INTO FLESH, AND FOOD INTO FAECES.

Table 74 gives the percentages of food converted into flesh, and into faeces, for the various species investigated, based on the values of m_1 and m_2.

For the Kittiwake, of unit amount of food taken after maintenance needs had been met, 59.2% was converted into flesh (weight gain) and 40.6% was converted into faeces and excreted, a total of 99.8%. Similarly for the Herring Gull 68.5% was converted into flesh and 31.6% into faeces, a total of 100.1%, and for the Guillemot 52.9% was converted into flesh and 45.2% into faeces, a total of 98.1%. The fact that these values complement each other so closely, the largest error being 2.9% in the case of the Guillemot, indicates that the methods of measuring food intake, and particularly faeces production, were accurate. Loss of energy by respiration, and other associated metabolic losses, is accounted for in the amount of food taken for maintenance (c). Thus the percentage values relate only to that part of the food which was utilized for growth, and it would be expected that the amount not

LE 74 The percentage of food converted into flesh, and into faeces, for the various species investigated, based on values of m_1 and m_2.

SPECIES	PERCENTAGE OF FOOD CONVERTED INTO FLESH	PERCENTAGE OF FOOD CONVERTED INTO FAECES	TOTAL
TIWAKE	59.2	40.6	99.8
RING GULL	68.5	31.6	100.1
LEMOT	52.9	45.2	98.1
IC TERN	75.7	78.1	153.2*
WICH TERN	64.1	82.3	146.4*

*Erroneous values due to poor experimental success (see text) actually incorporated in the body of the chick would be lost through excretion. The close agreement of the conversion values obtained by measuring the food/faeces and the food/weight gain relationships emphasize the validity of the experimental record and justified the extrapolation of these values to birds in the field.

The values obtained for the Arctic Tern and Sandwich Tern, covering only the first five days after hatching, show no such measure of agreement. For the Arctic Tern 75.7% of food taken was converted into weight gain, and 78.1% into faeces, and for the Sandwich Tern 64.1% was converted into weight, and 82.3% into faeces. It is probable that in these cases the values obtained for the food/faeces conversion are aberrant, as for much of the time the chicks were kept in the incubator, and accurate records of the faeces production of individual birds could not be kept. The efficiencies of conversion of food into weight gain described correspond generally to the 'Net efficiency' value given by Brody (1945) for animal production as

$$\frac{\text{energy output}}{\text{energy input less maintenance energy}}$$

nd to the 'Partial efficiency' value given by Kleiber
1961) as

$$\frac{\text{Heat equivalent of work performed}}{\text{ifference between metabolic rate working, and standing at rest}}$$

lthough, as has been stated, no attempt has been made
relate the present data to the calorific units used
these workers.

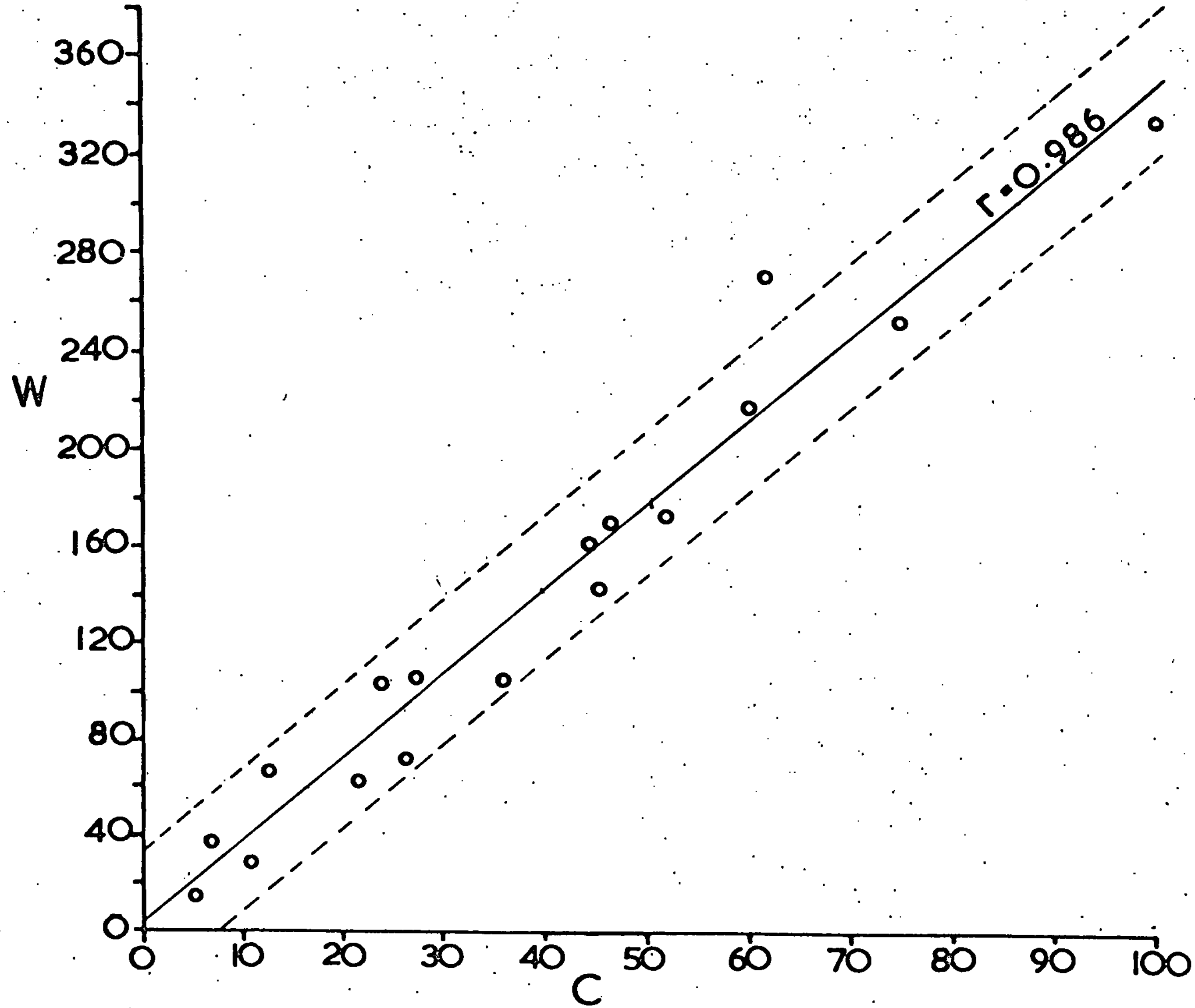
THE RELATIONSHIP BETWEEN THE FOOD REQUIRED FOR MAINTENANCE AND THE BODY SIZE

The values of c, the amount of food required for
intenance, for the different age groups of the various
ecies of chicks, together with the average body weight
each age group, were summarized in Table 73. Figure 39
ows a plot of the average body weight with the
rresponding values of c. There appears to be a close
rect relationship between these two factors, the
rrelation coefficient (r) being 0.986. A t-test
ed on the coefficient reveals that the correlation
highly significant ($P<0.001$ with 15 degrees of
edom). The regression line of W on C is plotted
Figure 39 with control limits placed at two standard
ors of estimate. All but one of the points fall
hin these narrow limits, emphasizing the very close
ect relationship between the two factors. Such a

FIGURE 39.

orrelation of the total body weight (w) with the amount f food required for maintenance (c) for all species of hicks.

= regression coefficient.



W
360
320
280
240
200
160
120
80
40
0
0
10
20
30
40
50
60
70
80
90
100
C
r = 0.986

relationship is however at variance with previous observations on the variation of maintenance needs with body weight, and indeed appears to contradict most accepted metabolic data. (e.g. Brody 1945 chapters 13 and 15 and Kleiber 1961 pp. 200 214). It would be expected that maintenance needs are directly related to the basal metabolic rate, being an expression of the amount of energy intake necessary to maintain a steady metabolic state. In all animal groups investigated however metabolic rate varies as a power function of body size, the two factors being related by the equation

$M = a + W^b$ where M = metabolic rate

W = body size and

a and b are constants.

The value of b appears to be between 0.7 and 0.75 for all animal groups investigated (Brody). In view of this it would be expected that the food required for maintenance in the present experiments would vary with such a power function of the body weight, and not directly as was found. A possible explanation of the direct relationship observed is that the range of body weights over which the feeding experiments were conducted was too small to show the probable curvilinear relationship. Thus the Guillemot chicks reached the greatest weights of about 370 grams, but this is only just over a third of the final adult weight. It is perhaps significant that the value of c for the final stage of growth of the Guillemots in the laboratory was the only value to lie outside the standard errors of estimate of the regression line being, smaller than would be expected from the straight line relationship. Similarly both the Kittiwakes and Herring Gulls were only reared to about one third of the usual adult weight. It is possible therefore that if the experiments could have been carried further, and food intake over a much greater weight range measured, that a relationship between food intake and 3/4 power of the weight would have been apparent. This is however pure conjecture, and lacking any further information it would seem that between the weights of 5 and 340 grams, for those sea-bird species investigated, there is a direct relationship between the amount of food required for maintenance, and the body weight. The slope of the regression line in Figure 39 is 3.49, thus for every 3.49 grams of body weight 1.0 gram of food was required for maintenance i.e. for maintenance needs alone the chicks took 29% of their own weight in food per day.

c. THE RELATIONSHIP BETWEEN THE AMOUNT OF FOOD REQUIRED FOR GROWTH, AND BODY SIZE.

Figure 40 shows a plot of the values of m, the amount of food required to bring about a weight increase of 1 gram after maintenance needs have been met, with the average total body weight of the different age groups of the various species of chicks. There appears to be no correlation between the two factors, the values of m varying between 1.04 and 2.88 irregularly with body weight. By averaging values of m where two or more values were obtained over a range in body weight of 25 grams or less, an apparent pattern emerges however, as shown by the broken line on the graph. It would seem that the value of m varies on average between 1.4 and 1.9 irrespective of body weight. The mean of all values of m was 1.72.

d. ESTIMATION OF TOTAL FOOD INTAKE OF CHICKS IN THE FIELD.

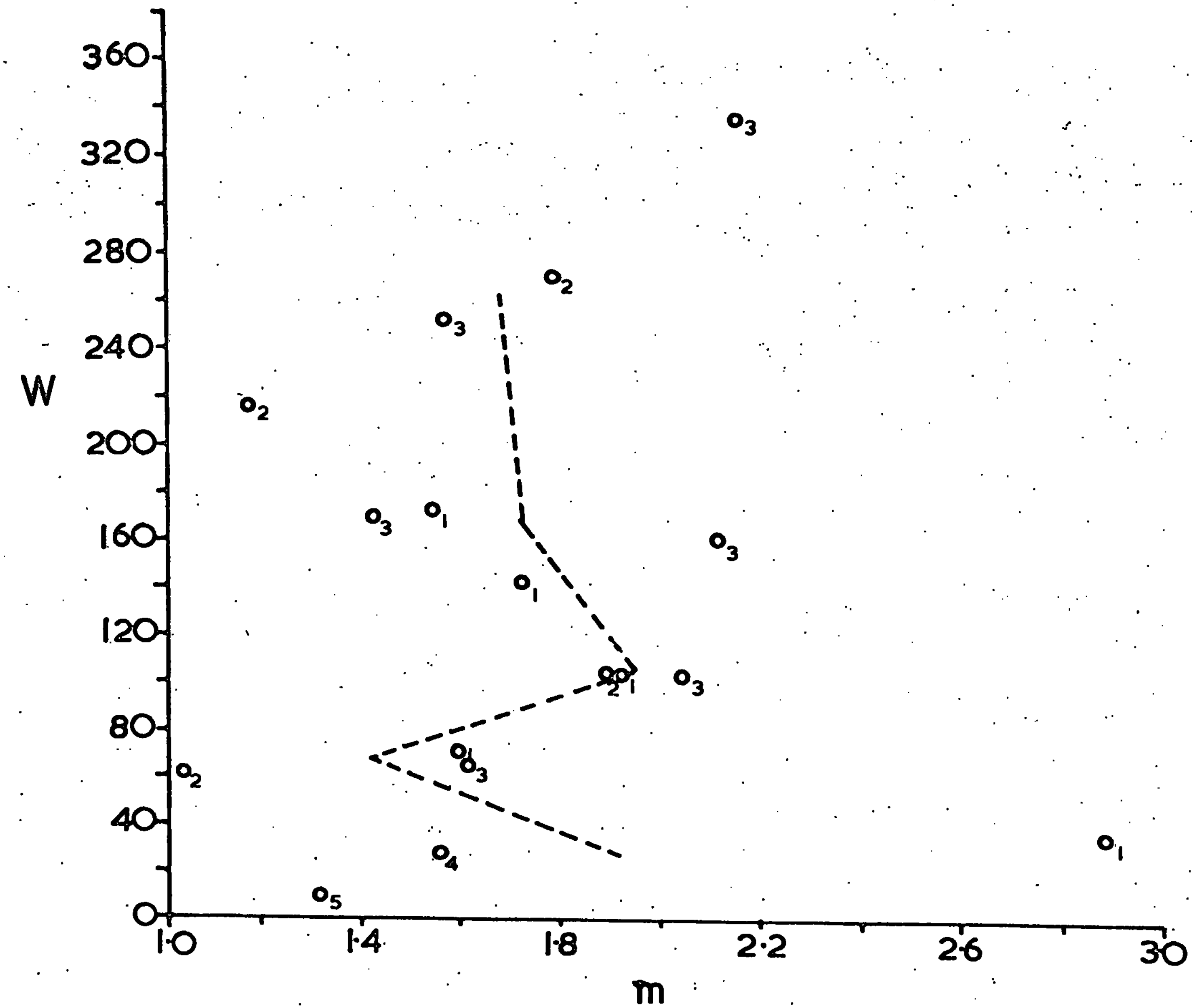
The purpose of the experiments in laboratory rearing of the chicks, described above, was to obtain relaiable data on the food intake of chicks which could be used to estimate the food intake necessary to produce the average daily weight increase observed in the different species of chicks in the field. As has been

FIGURE 40.

Plot of the total body weight (w) with the amount of food required to bring about a weight increase of one gram after maintenance needs have been met (m), for all species of chicks.

1. = Kittiwake.
2. = Herring Gull.
3. = Guillemot.
4. = Sandwich Tern.
5. = Arctic Tern.

The dotted line represents the mean of groups of two or more values (see text).


W
360
320
280
240
200
160
120
80
40
0
1·0
1·4
1·8
2·2
2·6
3·0
m

pointed out however the data obtained on the maintenance needs of the chicks in the laboratory showed a direct rather than a curvilinear relationship between food intake and body weight. It is thus probable that extrapolation of the straight line relationship found, to chicks of greater body weight than those used in the experiments, would lead to erroneous results, in that the food intake would be estimated as too large in relation to the body weight. However, for comparative purposes the experimental data obtained have been used to estimate the food intake of chicks in the field sufficient to bring about the observed daily weight increases. The ratio of 1 gram of food for every 3.5 grams body weight has been used to estimate maintenance needs, and the amount of food required for growth has been estimated from the values of m, the amount of food required to produce a weight gain of 1 gram, obtained. As the value of m differed slightly in the species studied experimentally the observed values have been used for those species where it was ascertained, but for those species not studied experimentally the average value of 1.72 has been used. Table 75 gives the average daily food intake over the whole hatching to fledgling period, as estimated by the above method,

TABLE 75 Average daily food intake over the fledging period of the chicks of Farne Islands sea-birds as estimated from field data (direct observations and periodic weighing) and from data obtained in laboratory rearing experiments.

	FLEDGING PERIOD (DAYS)	AVERAGE DAILY FOOD INTAKE ESTIMATED FROM FIELD DATA (g.) FROM DIRECT OBSERVATIONS	FROM PERIODIC WEIGHING	AVERAGE DAILY FOOD INTAKE ESTIMATED FROM EXPERIMENTAL DATA. (g.)
Arctic Tern	24	63.4	-	27.4
Common Tern	22	62.4	-	32.5
Sandwich Tern	27	36.4	52.8	48.5
Kittiwake	36	105.4	61.1	89.5
Lesser Black-back Gull*	0-30	36.6	169.0	146.1
Herring Gull*	4-24	-	148.2	219.5
Fulmar*	2-48	-	88.9	272.3
Puffin	38	28.5	50.4	70.4
Guillemot*	0-18	15.4	-	67.1
Shag	48	163.5	170.5	322.4

*Field growth records for these species were obtained only for the part of the fledging period given.

and from field data. (See section 2). It can be seen that for all species there is a considerable discrepancy between the various figures. With the Arctic Tern and Common Tern the daily food intake as estimated from direct observation is much greater than that estimated from the data obtained from the laboratory rearing experiments, whereas with the Herring Gull, Fulmar, Puffin, Guillemot and Shag, the daily food intake estimated from experimental data is much greater than that derived from both methods used in the field. With Kittiwake and Lesser Black-back Gull the figures estimated from experimental data fall between the estimates made by the two methods used in the field. It is probable that the estimates made from the experimental data obtained in the laboratory are the most accurate, being based on detailed information concerning the maintenance and growth requirements of the chicks. It was pointed out in Section 2 that both the methods used for estimating food intake in the field, were subject to considerable inaccuracy and could not be considered as truly assessing the normal daily food intake of the chicks concerned. Thus, whilst it is recognised the experimental data obtained in the laboratory was not as comprehensive as might have been desired, in that the smaller and larger species were not adequately represented in the experiments, it would seem justifiable to base further estimates of the food intake of the colonies as a whole on this data, rather than that obtained in the field.

SECTION 5.

ESTIMATION OF THE TOTAL FOOD RESOURCES NECESSARY TO SUPPORT THE SEA-BIRD COLONIES ON THE FARNE ISLANDS DURING THE BREEDING SEASON.

The figures derived for the daily food intake of the chicks of sea-bird species breeding on the Farne Islands may be used to provide an estimate of the overall food requirements of the colonies during the breeding season. The figures obtained however relate only to the food intake of chicks during the hatching-fledging period, no information having been obtained on the food requirements of adults. The extrapolation of the values obtained, for the relationship between maintenance needs and body weight of the chicks, to the adult birds is suspect, for the reasons explained in Section 4, page 242, nor is the food intake in relation to the work done known for adult birds. Thus in order to assess the daily food intake of the adults it is necessary to postulate, and to define, the relationship between the food intake of the chicks and that of the adults.

THE RELATIONSHIP BETWEEN THE FOOD INTAKE OF YOUNG AND OF ADULTS.

Detailed information on the nutrition and metabolism of a wide range of laboratory and domestic animals is given by Albritton (1954). This information includes values for the food intake and body weight of the young and of the adult members of each species. Table 76 lists the total food intake derived from this information and gives the food intake of the young, half grown, animals as a percentage of the adult food intake. In all species the food intake of the young was between 65 and 80 percent that of the adults, the average for the nine species listed being 74.5 percent. The average for the three domesticated avian types included in the list was 73.7%. It thus seems reasonable to assume that for the sea-bird species under investigation the food intake of the young would be about 75% that of the adults, and this figure will be used in estimating the total resources necessary to support the Farne Islands colonies.

THE DAILY FOOD INTAKE OF THE YOUNG.

In Section 4 a comparison was made between the average daily food intake of the young birds as estimated from observations in the field, and from experimental data, and it was concluded that the information obtained from experimental data was more accurate. Thus the estimates of daily food intake based on experimental data will be used to assess the total needs of the colonies. In the case of the Cormorant no field or laboratory data on food intake was obtained during the present study, and the estimate of

TABLE 76. Values for the total daily food intake of half-grown and of mature animals of different species. (from Albritton 1954).

SPECIES	AGE CATEGORY	BODY WT. (Kg.)	TOTAL DAILY FOOD INTAKE (g.)	FOOD INTAKE OF YOUNG AS A PERCENTAGE OF FOOD INTAKE OF ADULTS.
CHICKEN Rhone Island Red.	Half grown	1.25	84	75.0
	Mature	2.50	112	
CHICKEN White Leghorn.	Half grown	0.91	71	65.0
	Mature	1.82	109	
TURKEY Broad Breasted Bronze.	Half grown	4.0	208	81.2
	Mature	8.0	256	
DOG	Half grown	4.5	238	78.4
	Mature	13.6	304	
SHEEP	Half grown	36.0	1548	82.0
	Mature	59.0	1888	
BEEF CATTLE	Calf	227.0	6356	76.1
	Steer	363.0	8349	
DAIRY CATTLE	Calf	45.0	5440	73.2
	Heifer	272.0	7432	
HORSE	Half grown	363.0	7986	66.2
	Mature	635.0	12065	
MINK	Half grown	0.45	50.0	73.5
	Mature	0.68	68.0	

300g./day for the young has been taken from Van Dobben (1952).

NUMBERS OF SEA-BIRDS ATTENDING THE BREEDING COLONIES.

As far as has been practical direct counts have been made of the numbers of sea-birds attending the breeding colonies. With the more numerous species, e.g. the Puffin, Guillemot, Lesser Black-back Gull etc., these counts are of necessity approximations. The numbers of non-breeding birds attending the colonies is the most difficult element of the population to assess, and as accurate data on this element are lacking for most of the species a maximum approximate percentage of non-breeders has been added in most cases, in order to assess the total resources needed by the colonies. Table 77 shows the populations of the various species. In the case of the Puffins the population was assessed by counting the total number of burrows on the islands, and estimating that 70% would be occupied by breeding birds. The population counts on all the species listed have been carried out by members of the Zoology Department of the University of Durham, between 1959 and 1963.

Table 77 also gives estimates of the overall breeding success of each species, in terms of the number of chicks reared per pair, and the resulting total number of chicks

TABLE 77. Population census of sea-birds breeding on the Farne Islands. 1961-1962.

SPECIES	NO. OF BREEDING PAIRS.	MAXIMUM PERCENTAGE OF NON-BREEDING BIRDS PRESENT	OVERALL BREEDING SUCCESS (No. of chicks per pair)	NO. OF YOUNG REARED	NO. OF BIRDS AT BEGINNING OF SEASON	NO. OF BIRDS AT END OF SEASON
Arctic Tern	3900	25	1.2	1800	9750	10550
Common Tern	200	25	1.5	150	500	650
Sandwich Tern	1200	25	0.5	600	3000	3600
Kittiwake	1800	50	1.1	1880	5400	7280
Lesser Black-Back Gull	1000	50	1.0	1000	3000	4000
Herring Gull	100	50	1.0	100	300	400
Fulmar	30	200	0.2	6	180	186
Puffin	22000	50	0.8	17600	66000	83600
Guillemot	1200	50	0.6	720	3600	4320
Shag	424	50	1.8	760	1288	2044
Cormorant	100	50	2.4	240	300	540

TABLE 78. Duration of period spent in the Farne Island area for the breeding season.

SPECIES	LENGTH OF TIME ADULTS PRESENT MONTHS	DAYS	LENGTH OF TIME CHICKS PRESENT MONTHS	DAYS
Arctic Tern	May-July	84	Late June-July	42
Common Tern	May-July	84	Late June-July	42
Sandwich Tern	May-July	84	June-Early July	42
Kittiwake	March-August	154	June-Early August	70
Lesser Black-Back Gull	Late March-August	140	July-August	56
Herring Gull	Late March-August	140	July-August	56
Fulmar	Late March-August	140	July-August	56
Puffin	Late March-August	140	June-August	90
Guillemot	Late March-August	140	June-August	90
Shag	March-August	154	June-Early August	70
Cormorant	March-August	154	June-Early August	70

reared in the colonies. The breeding success of most of the species has been roughly estimated from data obtained during the present investigations, but that of the Kittiwakes is taken from data given by Coulson and White (1958), and of the Guillemots from data given by Tuck (1960).

DURATION OF THE BREEDING SEASON.

Table 78 lists the approximate length of time that the various species spend in the Farne Islands area for the breeding season, together with the time during which the chicks are present. In the case of the Gulls and Shags, many of which probably spend most of the year in the Farne Islands area, the period has been defined as the maximum time during which other species are present in the breeding area.

THE DAILY AND SEASONAL FOOD INTAKE OF THE VARIOUS COLONIES.

Table 79 shows the daily and seasonal food intakes of all adult, and all young birds of each species, together with the total seasonal food intake, as estimated using the data given in Tables 77 and 78. Thus the total seasonal food intake for all birds was estimated to be 1429 metric tonnes (1406 tons). The daily food intake at the beginning of the season, when only the adults were present, was estimated as 9.2 metric tonnes (9.0 tons). At the end of the season, when both adults and young were present the

TABLE 79. Estimation of the daily and seasonal food intakes of the various colonies of sea-birds breeding on the Farne Islands.

SPECIES.	DAILY FOOD INTAKE OF MATURE BIRDS (g.) *	TOTAL DAILY FOOD INTAKE OF ALL MATURE BIRDS (kg.)	SEASONAL FOOD INTAKE OF ALL MATURE BIRDS (kg.)	DAILY FOOD INTAKE OF YOUNG (g.)	TOTAL DAILY FOOD INTAKE OF ALL YOUNG (kg.)	SEASONAL FOOD INTAKE OF ALL YOUNG (kg.)	TOTAL DAILY FOOD INTAKE OF YOUNG AND ADULTS (kg.)	TOTAL SEASONAL FOOD INTAKE OF YOUNG AND ADULTS (kg.)
Arctic Tern	40	390	32760	30	54	2269	444	35028
Common Tern	40	20	1680	30	4	189	24	1869
Sandwich Tern	67	201	16884	50	30	1260	231	18144
Kittiwake	120	648	99792	90	169	11830	817	111622
Lesser Black-back Gull	200	600	84000	150	150	8400	750	92400
Herring Gull	290	87	12180	220	22	1232	169	13412
Fulmar	360	65	9100	270	2	90	67	9190
Puffin	93	6138	859320	70	1232	110880	7370	970200
Guillemot	93	335	46900	70	50	4500	385	51400
Shag	430	554	85316	320	243	17010	797	102326
Cormorant	400	120	18480	300	72	5040	192	23520
Totals all species.		9158	1266412		2028	162700	11186	1429111

* Taken as 125% that of the young birds.

daily food intake was 11.2 metric tonnes (11.0 tons).

THE WEIGHT AND NUMBERS OF THE VARIOUS TYPES OF PREY TAKEN BY THE SEA-BIRDS BREEDING ON THE FARNE ISLANDS.

Using the analysis of diet described in Section 1 the weight and numbers of the various prey species taken per day, and over the whole season, were estimated. The numbers were estimated from the average weight of individual prey taken by the various species. Table 80 gives the estimates in terms of Kilograms weight and numbers to the nearest thousand.

Table 81 shows the total numbers and weight of prey of each type taken by all bird species. Thus over 450 million sand-eels are taken in the course of the season, having a weight of 943 metric tonnes (928 tons). The other major prey types are the Clupeidae, young herring and sprats, of which over 21 million are taken in the season; the Gasterosteidae or Sticklebacks of which over 4 million are taken, and the Gadidae, mainly young cod and whiting of which nearly 4 million are taken. The only potentially important commercial fish which are taken are the flat-fish, and the Salmonidae, of which over 450 thousand and 55 thousand respectively are taken during the season, almost entirely by the Cormorants and Shags.

TABLE 80. Number and weight of different types of prey taken by each species of sea-bird breeding on the Farne Islands.

BIRD SPECIES / PREY	PERCENTAGE TAKEN (By weight).	WT. TAKEN PER DAY BY ALL BIRDS (kg.)	WT. TAKEN OVER WHOLE SEASON (kg.)	AVERAGE WT. OF INDIVIDUAL PREY	NO. TAKEN PER DAY (000's)	NO. TAKEN PER SEASON (000's).
Ammodytidae	22.4	94.9	7846.2	0.8	118	9808
Clupeidae	63.0	279.7	22067.6	7.0	40	3152
Gadidae	6.0	26.6	2101.8	6.1	4	344
Gasterosteidae	2.5	11.1	875.7	3.2	3	273
Pleuronectidae	0.1	0.4	35.0	1.8	<1	19
Other fish	0.9	4.0	315.2	0.6	6	525
Crustacea	1.5	6.6	525.4	1.6	4	328
Cephalopoda	3.4	15.1	1109.9	3.3	5	361
Ammodytidae	9.6	2.3	179.4	0.8	3	224
Clupeidae	67.7	16.6	1265.3	7.0	2	180
Gadidae	19.4	4.7	362.6	6.1	1	59
Gasterosteidae	1.6	0.4	29.9	3.2	<1	9
Other fish	0.5	0.1	9.3	0.6	<1	15
Crustacea	0.3	<0.1	5.6	1.6	<1	3
Cephalopoda	0.8	0.2	14.9	3.3	<1	4
Ammodytidae	60.7	140.2	11013.4	2.1	67	5244
Clupeidae	24.1	55.7	4372.7	4.3	13	1017
Gadidae	7.[illegible]	18.0	1415.2	3.2	6	442
Gasterosteidae	3.3	7.6	598.7	4.0	2	150
Pholidae	0.4	0.9	72.6	5.0	<1	14
Trachinidae	0.8	1.8	145.1	7.0	<1	21
Liparidae	1.3	3.0	237.9	15.0	<1	16
Crustacea	0.9	2.1	163.3	1.7	1	96
Cephalopoda	0.6	1.4	108.9	3.3	<1	33
Ammodytidae	5[illegible].0	449.3	61392.1	5.0	90	12278
Clupeidae	22.0	179.7	24556.8	13.6	13	1806
Gadidae	22.5	183.8	25114.9	29.8	6	843
Crustacea	0.1	0.8	111.6	2.4	<1	46
Offal	0.5	4.1	558.1			
Ammodytidae	14.5	108.7	13398.0	2.4	45	5582
Clupeidae	10.6	79.5	9794.4	16.9	5	579
Gadidae	52.5	393.7	48510.0	38.1	10	1273
Anguillidae	0.7	5.2	646.8	12.7	<1	51
Insecta	0.1	0.7	92.4	0.6	1	154
Annelida	2.8	21.0	2587.2	1.0	21	2587
Offal	18.6	139.5	17186.4			
Ammodytidae	80.1	5903.4	777130.2	1.9	3107	409016
Clupeidae	13.2	972.8	128066.4	10.5	93	12197
Gasterosteidae	3.0	221.1	29106.0	7.2	31	4042
Other fish	3.7	272.7	35897.4	0.6	454	59829
Ammodytidae	52.2	201.0	26830.8	10.5	19	2555
Clupeidae	31.0	119.3	15934.0	5.9	20	2701
Gadidae	12.6	48.5	6476.4	10.0	5	648
Pholidae	4.2	16.2	2158.8	5.0	3	432
Ammodytidae	44.5	354.7	45536.1	6.7	53	6796
Clupeidae	0.3	2.4	307.0	10.0	<1	31
Gadidae	30.2	240.7	30902.4	125.9	2	245
Pholidae	7.7	61.4	7879.1	7.9	8	997
Pleuronectidae	2.1	16.8	2148.8	9.2	2	234
Scorcidae	4.1	32.7	4195.4	24.2	1	173
Cottidae	3.5	27.9	3581.4	21.0	1	170
Blenniidae	0.7	5.6	716.3	10.0	1	72
Sorranidae	1.7	13.5	1739.5	50.0	<1	35
Salmonidae	5.0	39.8	5116.3	150.0	<1	34
Crustacea	0.2	1.6	204.6	1.6	1	128
Ammodytidae	1.1	2.1	258.7	3.0	<1	86
Gadidae	15.6	29.9	3669.1	165.0	<1	22
Pleuronectidae	30.3	58.2	7126.6	32.0	1	202
Anguillidae	14.4	27.6	3386.9	102.6	<1	33
Salmonidae	12.8	24.6	3010.6	141.8	<1	21
Pholidae	1.9	3.6	446.9	9.0	<1	50
Other fish	[illegible]	[illegible]	[illegible]			

ABLE 81. Total number and weight of all prey types taken by all birds of all species per day, and per season.

	NUMBER AND WEIGHT TAKEN PER DAY BY ALL BIRDS OF ALL SPECIES		NO. & WT. TAKEN OVER WHOLE SEASON BY ALL BIRDS OF ALL SPECIES	
	Wt. (Kg.)	No. (000's)	Wt. (Kg.)	No. (000's)
mmodytidae	7257	3562	943585	451589
lupeidae	1706	186	206364	21663
adidae	946	34	118552	3876
asterosteidae	240	36	30610	4474
leuronectidae	75	3	9310	455
nguillidae	33	<1	4034	84
holidae	82	11	10557	1493
almonidae	64	<1	8127	55
ther fish	135		52506	
rustacea	11	6	1010	601
ephalopoda	17	5	1234	398
nnelids	21	21	2587	2587
nsecta	1	1	92	154

OMPARISON OF THE TOTAL FEEDING AREAS UTILIZED BY THE SPECIES ITH THE NUMBERS OF FISH TAKEN.

The maximum total area of sea over which each species an hunt has been estimated from the feeding ranges of he species given in Section 2. It can be seen from figure 23, Section 2 that a third of the possible feeding ranges re over the land, and this area is excluded in calculating he total feeding areas available to the birds. Table 82 hows the maxim total feeding areas of each species, calulated in square miles, together with the total number of rey taken per day by all birds of each species. The number

TABLE 82. Comparison of the maximum total feeding areas utilized by the various species, and the total number of prey taken per day, to assess the number of prey taken per square mile of sea per day.

	MAXIMUM TOTAL FEEDING AREA (sq.miles)	TOTAL NO. OF PREY TAKEN PER DAY	NUMBER OF PREY TAKEN PER SQUARE MILE OF SEA PER DAY. From Maximum Total Feeding area	From Smallest Observed * Feeding area
Arctic Tern	331	180000	544	647
Common Tern	390	8000	20	29
Sandwich Tern	502	91000	181	327
Kittiwake	2504	110000	44	396
Lesser Black-Back Gull	1893	82000	43	295
Puffin	5543	3685000	665	13255
Guillemot	4260	47000	11	169
Shag	278	70000	252	252

Total prey taken per square mile when all birds feeding over minimum area. 15370

* See text for explanation.

of prey taken per square mile of sea per day, derived from those figures, are also given in the table. The numbers taken per square mile assuming that each species is utilizing all the potential feeding area available to it are given, together with the numbers taken per square mile assuming that all the birds are feeding within the smallest feeding area observed for any of the species, i.e. that of the Shag, having a radius of 11.5 miles from the islands, and a corresponding sea area of 278 square miles. The object of this latter set of figures is to assess the possible predation rate should all the birds be feeding intensively within the same area. It can be seen that should this occur the number of prey taken by all the birds per square mile per day would be about 15400, which, although high, does not seem excessive in view of the vast numbers of young fish which are present in the area during the summer. The figures estimating the numbers taken per square mile when the maximum feeding area is used, show that only the Arctic Tern and Puffin, taking 544 and 660 fish per square mile respectively, have predation rates of any magnitude, and again even these are very low considering the probable abundance of prey.

It must be emphasized that these figures apply to the Farne Islands area only, and that the same species breeding in different areas will have different feeding ranges, in accordance with the abundance, and distribution of the local prey species. It is probable however that the interspecific variation in predation rates shown here will occur in similar ratios in other areas.

SECTION 6.

GENERAL DISCUSSION.

Whilst many points arising from this work have been discussed at the ends of each section, there remain some fundamental problems about which little has yet been said. An attempt is made below to approach such problems of more general interest.

ECOLOGICAL SEPARATION AND THE PROBLEM OF COMPETITION.

Introduction.

In recent years there has been considerable discussion and controversy concerning the general hypothesis known as 'Gause's theorem' which states that "two species with similar ecology cannot live in the same region", (Lack 1946). There are many other variants of this hypothesis (see e.g. Gilbert, Reynoldson and Hobart (1952) Allee Emerson, Park, Park and Schmidt (1949) Sperber(1947) Udvardy (1951) which was not, in point of fact, originated by Gause, but was implied by his theoretical and experimental analysis of competition in insects (Gause 1934). In fact, as has been pointed out (Crombie (1947) Elton (1946) Park (1959)), the idea was propounded by Darwin (1859) (p. 93) who said "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera". The results of the present work present an opportunity for examining this thesis in the light of competition for food amongst a number of species, some of which are congeneric. It is necessary, however, to examine first the precise meaning and implications of the stated thesis, since imprecise usage in the past has led to a confusion which is reflected in much of the recent literature. Thus there has been considerable disagreement over the correct interpretation of the concept of competition, and over the possible meanings of the terms 'similar ecology' (e.g. Lack (1946)) or 'identical ecology' (e.g. Allee et al (1949)) etc. A discussion of these terms will therefore precede an examination of the main thesis.

THE CONCEPT OF 'COMPETITION'.

This term has been used extensively by ecologists over the last 50 years in commenting on both the inter and intraspecific interactions of organisms. Only rarely has its exact meaning been defined however, as a result of which 'its' interpretation has tended to vary from author to author. Recently, however, there have been attempts to restrict its meaning to a specific concept (Odum (1959) Milne (1961) Klomp (1961) Birch(1957)) but unfortunately no general agreement has emerged as to what such a definition should be. Thus there are two general interpretations i) what might be termed the broad interpretation, as exemplified by Odum (1959), and ii) what might be called the narrow definition, supported most recently by Milne (1961).

i) Odum (1959) states "Competition refers to the interaction of two organisms striving for the same thing. In ecology, interspecific competition is any interaction between two or more species populations which adversely affects their growth and survival" (p. 330). He later goes on to state that the interaction can involve common space, food or nutrients, light, waste material action, mutual predation, susceptibility to carnivores, disease, and many other types of interaction. Thus by this definition 'competition' becomes a blanket term to describe the interactions of two contiguous species. Elton (1946) interprets the term n a very similar manner, when he stressed that "'competition' s . . . . used not merely for direct antagonism . . . . but s an objective description . . . . of the interplay of ongevity and fertility factors of all kinds (known and nknown) favouring one species at the expense of another". hen interpreted in this way competition can be described s consisting of two components a) the exploitation component, and b) the interference component (Park 1954) (Crombie 1947). Brian (1956) described 'exploitation' as "the ability of a species to find, occupy, and retain vacant vital resources", and 'interference' as "the ability of a species to damage another . . . . either directly by attacking its individuals or indirectly by harming its resources or blocking its access to them". Such components have also been variously described as 'direct' and 'indirect' competition (Knight-Jones and Moyse 1961), and 'active' and 'passive' competition (Birch 1957). Competition has been used in this broad sense, although the duality of the meaning described above has not always been recognised, by such authorities as Haldane (1934), Huxley (1942), Mather (1961) and Carter (1956). It is also widely used in this context by botanists (e.g. Harper (1961) and Sakai (1961)).

A more refined, but still general, interpretation is given by Klomp (1961), who defines competition as "the process occurring between animals living in the same habitat or medium and the numbers of which are limited by the same mechanism of (natural) control". Williamson (1957) gives substantially the same definition. Thus under this interpretation the controlling factor need not be a specific resource, such as food, or space, but may be a parasite, predator or any other limiting factor of the environment.

ii) The most recent proponent of a narrow definition, Milne (1961), defines competition as "the endeavour of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing when that supply is not sufficient for both (or all)". This is very similar to the definition of Clements and Shelford (1939), and is tantamount to restricting the use of the term 'competition' to the 'exploitation' concept of the broad definitions described above. This meaning of the term has been used in most of the more recent investigations into competition in field and laboratory population (c.f. Ullyett 1950, Sokoloff 1955, Bakker 1961). It was used by Elton and Miller (1954) in contrast to the earlier, broader, interpretation used by Elton, and this meaning of the term is favoured by Andrewartha and Birch (1954) although these authors dispute its general applicability as a controlling factor in population dynamics.

Of the various interpretations of the term 'competition' referred to that of Milne (1961) appears to be the most acceptable, in that it embraces the strict definitions of striving for a common resource in short supply. The definition of Klomp (1961) is considered to be unacceptable as it involves the acceptance of predator (or other environmental) interactions as part of the competitive process. Thus although predation pressure may decrease the number of 'places' available in the environment to the competing organisms, as Klomp points out, and thus be the controlling factor, the predation is merely the causative factor of the resulting competition for space not that competition itself. The same objection can be made to all the broad definitions, in that they involve factors controlling the populations, other than the factor of competition for an environmental resource in short supply. In any discussion of the implications and meaning of interspecific competition it is thought essential that strict and definitive usage of the term competition be made, and that the use of a broader interpretation would merely complicate the arguments unnecessarily.

INTERSPECIFIC COMPETITION, AND INTRASPECIFIC COMPETITION.

These terms, used to describe competition between species, and competition within a species are useful disjunctions of the original term, in that they describe processes which, whilst using the same mechanism of population control i.e. competition, produce different ecological results. Thus Svardson (1949) showed that dominant interspecific competition may cause a species to retreat to the most optimal habitats, while dominant intraspecific competition may cause a much greater variety of habitats to be occupied. In the present work consideration is given more to the possibility of interspecific competition occurring among the Farne Islands populations than intra-specific competition, although the latter can not be ignored in considering factors likely to affect the regulation of the numbers of sea-birds in the colonies. (see below).

THE CONCEPT OF 'SIMILAR ECOLOGY'.

The possible meanings of this phrase, and equivalent phrases, in the various formulations of Gauses' Hypothesis, have been the subject of even more controversy than has the competition concept. As has been pointed out by many authors (notably in the arguments of Gilbert, Reynoldson and Hobart (1952), Ross (1957 and 1958), and Savage 1958) the relevance of the hypothesis hinges on the interpretation of this phrase. Thus how similar do the ecologies of two species have to be before competition precludes their coexistance? The difficulty is the result of loose definition, and may be overcome by use of the 'niche' concept. Thus Savage (1958) defines Gauses' Law as "no two species with identical niches (identical environmental relations) can occur together without one form being eliminated within a few generations through competition". The meaning of 'niche' requires explicit clarification before this definition can be accepted. Udvardy (1959) states that the word was first coined by Grinnell (1917) and used to denote "the concept of the ultimate distributional unit within which each species is held by its structural and instinctive limitations". Elton (1927) used the word in a similar context when he says "the niche of an animal means its place in the biotic environment, its relation to food and enemies". Other authors have however used the term to in a much broader sense, often making it synonymous with 'habitat' or 'biotope' (see discussion in Udvardy (1959) Ross (1957 and 1958) and Savage (1958)). More recently however the earlier and strict meaning has been used extensively, (Odum 1959), particularly with reference to Gauses' Hypothesis (Parker and Turner (1961) Crowell (1962)). The clearest definition of 'niche' (in the strict sense), and the one which will be implied in the following discussion of 'Gauses Hypothesis', is that given by Parker and Turner (1961) who state that "the 'operational niche' of any organism represents the complement of the activities (active, reactive, and interactive) of that organism in a given habitat and biotope at a given time".

INTERSPECIFIC COMPETITION BETWEEN CLOSELY RELATED SPECIES.

Bearing in mind the meaning implied by the various terms used, the problem of competition between closely related (congeneric) species can now be examined. There has been some argument as to the validity of the Gause Hypothesis. Williams (1947) carried out a mathematical analysis of the frequency of occurrence of genera among a large number of species from a series of animal and plant communities and found that they contained fewer genera than would be expected in a sample of the same number of species taken at random, thus apparently contradicting Gauses' Hypothesis.

The communities analysed were the same as those used by Elton (1946) to demonstrate the opposite point of view i.e. in support of Gauses' theorem, namely that the number of species was less than might be expected. Bagenal (1951) pointed out, however, that the term 'habitat' had been interpreted differently by the two workers. Thus Elton's analysis holds true if the term 'niche' (in the context defined above) is used in defining the ecological limits of each species whereas the mathematical approach of Williams precludes any such narrow definition. Thus as Bagenal states "when Williams communities were large enough to contain more than one example of the same niche there were more species per genus than would be expected, and when the communities were small . . . . he found that each species was in its own genus". Williams (1951) later provided further evidence that similar species will tend to exist in similar areas, by an analysis of the ratio of genera to species in East African bird communities. He recognised however that such a tendency would be balanced by the tendency for closely related species to compete. Thus the apparent paradox brought forward by Williams's work resolves itself about the recognition that competition takes place within the niche, but that species with similar requirements coexist within the same habitat. That interspecific competition between closely related species can or does occur has been demonstrated with laboratory populations by Park (1954 and 1957) and Bakker (1961) among others. Evidence of its occurrence in the field is, as has been stressed by Orians and Collier (1963) mostly indirect, but such studies as that of Lack (1945 and 1946) MacArthur (1958) and Crowell (1962) on various congeneric species of birds, and of Carpenter (1952) and Hairston (1951) on reptiles, have been taken to indicate that it occurs widely. Orians and Collier themselves provide direct evidence of competition between the Red-winged Blackbird (Agelaius phoeniceus) and the Tricolour Blackbird (A. tricolor) in California, and Pitelka (1951) showed that interspecific competition occurred between species of humming birds in Woolsey Canyon, California.

A completely contrasting view of the validity and importance of Gauses' theorem is given by Andrewartha and Birch (1954), who reject it entirely as having little relevance to the problems of population control. Thus they think that competition is rarely, if ever, a controlling factor either intra- or inter-specifically, and point out that most of the examples put forward as evidence for the reality of Gauses' theorem are based on the indirect evidence that closely related species occurring together differ in their ecological requirements. They see no need to postulate that this is the result of past competition, the theory of Lack (1945, '46 and '54) but take it merely as evidence that they are different species, and thus differ in their needs. Whilst this view has the virtues of simplicity it appears to treat the evidence of competition in laboratory populations too lightly, and to gloss over many of the implications of the studies of congeneric populations in the field.

To sum up, it would seem that there is a considerable amount of evidence tending to support the theory, known variously as Gauses' law (hypothesis) (theory) or Grinnell's Axiom, that no two species with identical niches can occur together without one form being eliminated within a few generations by competition. The information obtained in the present study will thus be used to see how far this theory applies to the various species of sea-birds breeding on the Farne Islands.

INTERSPECIFIC COMPETITION IN FARNE ISLAND SEA-BIRDS.

Before considering the special case of competition in congeneric species consideration will be given to the possibility of general competition taking place between species of sea-birds breeding on the Farne Islands.

Competition for food during the breeding season, and during the winter.

Most of the information obtained relates only to the time when the birds are resident on the Farne Islands during the breeding season. Nearly all the species studied disperse during the winter months. The Terns and Lesser Black-backed Gull migrate many thousands of miles to the south, the Puffins, Guillemots, Kittiwakes and Fulmars return to the open waters of the North Atlantic, and the Herring Gull, and to a lesser extent the Cormorants, disperse inland and along the coasts. Only the Shags tend to remain in any numbers in the immediate vicinity of the islands. It is probable therefore that the effect of competition between any of these species will be minimal or non-existent during the winter months, as the areas covered, and their potential food resources, are great in relation to the number of birds exploiting them. It is possible that this winter dispersal of sea-bird species is an adaptation to ameliorate competition for food, which would be severe if many species tended to congregate in the same area during the winter months. When all these species are concentrated in the one breeding area in the summer, and are all hunting over the same areas of sea, then the possibility of competition for food occurring, both inter- and intra-specifically, becomes much greater. It thus seems feasible to regard the breeding months as being the critical period when one might expect to find evidence of any mechanisms of ecological separation, which would tend to mitigate competition between the species. That such mechanisms exist has been shown in the information given in the preceeding sections, which is summarized below.

Differences in diet between the species.

It was shown in Section 1 that all the species feed almost exclusively on fish, only the Lesser Black-back Gull taking more than 10% of any other type of food. Moreover of the types of fish taken, Ammodytidae composed the greater part of the diet of all but the Cormorants, and to a lesser extent the Shags, and even in these species they were an important element in the diet. The other types of fish taken in any numbers, i.e. Clupeidae and Gadidae, were also common to nearly all the species, although the proportions taken differed significantly between the species. It would thus seem at first sight that all the species investigated are competing for the same resources. Examination of the feeding areas, and feeding ranges of the various species shows, however, that such a generalisation is by no means true, as is explained below. Nevertheless as has been described in Section 1, it is probable that the species of fish mentioned are extremely abundant in the Farne Islands area during the summer months, and that this alone would probably be sufficient to minimise competition between the species. Lack (1946) suggests that when available foods are temporarily much more abundant than the requirements of their consumers the latter will not effectively compete with each other when eating them, and that this would remain true even if the food in question temporarily provided the whole of the diet of the species involved. This conclusion seems to be equally valid for the situation found during the summer months round the Farne Islands, as long as the fish species in question appear in their usual numbers. However there remains the possibility that on occasions the usual prey species may not appear in the area. This question has been commented on earlier in connection with the records, (Belopolskii (1957)) of the Capelin off the Murmansk Coast, and the late appearance of the Ammodytidae around the Farne Islands in 1962. Under such conditions it is probable that there would be severe competition between the various species, were there no isolating mechanisms at work. Thus Lack (1946) goes on to state "While, it is argued, the consumer species do not effectively compete with each other when eating the super-abundant food, the situation is potentially quite different as soon as the food in question becomes scarce . . . . if Gauses' view holds one would expect that in any one region each predatory species would now turn to different prey". To this one might add that the same prey might be pursued in different areas under conditions of scarcity by the various species, which, under super-abundant conditions, all exploited food in the same area. This would appear to be the situation on the Farne Island, where the birds tend to disperse both vertically, in the depth at which they obtain food, and horizontally, in the distances flown in search of food, but may all be seen feeding in the same areas when shoals of sand-eels are particularly abundant.

Fishing depths.

It has been pointed out in Section 1 that the terns, Gulls, and the Fulmar were all Surface Feeders, obtaining their food from the top metre of the sea, whereas the Puffin, Guillemot, Shag and Cormorant were Diving Feeders. This latter group can be further sub-divided into the nektonic, or mid-water feeders, and the benthonic, or bottom feeders. These categories are illustrated in Figure 41, which shows the range of prey species taken by each predator and their vertical distribution in the marine environment. Thus the Puffin and the Guillemot feed primarily on mid-water fish, whereas the Shag and the Cormorant take bottom-living types. The latter is the only species to take fresh-water prey to any appreciable extent.

Feeding ranges and feeding areas.

It was shown in Section 2 that the species tended to exploit different feeding areas, and have greatly differing feeding ranges, the Puffins and the Guillemots feeding up to 50 miles from the islands whereas the Shags have a range of probably less than 11 miles.

These variations in feeding habitat may indicate that ecological separation plays an important part in the feeding biology of Farne Islands sea-birds, and is no doubt an essential mechanism in the amelioration of interspecific competition. It is evident however that such differences are by no means rigid, and that under the conditions of

FIGURE 41.

Analysis of the diet of the various sea-bird species breeding on the Farne Islands to show the range of prey species taken in relation to their vertical distribution in the marine environment.

ANALYSIS OF DIET

PREY TAKEN											
HABITAT		GROUP	CORMORANT	SHAG	GUILLEMOT	PUFFIN	KITTIWAKE	LESSER BLACK-BACK GULL	SANDWICH TERN	COMMON TERN	ARCTIC TERN
TERRESTRIAL		INSECTA						●			●
		ANNELIDA						●			
LITTORAL		COTTIDAE							●		
		LIPARIDAE							●		
SURFACE-LIVING		GASTEROSTEIDAE							●	●	●
		CEPHALOPODA							●	●	●
		CRUSTACEA							●	●	●
	P-L.&J.	BLENNIDAE				●				●	●
	P-L.&J.	GADIDAE					●●	●●●●	●●	●●	●●
	P-L.&J.	AMMODITIDAE				●	●●●●	●●	●●●●	●●	●●●●
	P-L.&J.	CLUPEIDAE				●●	●●	●●	●●●	●●●●	●●●
MID-WATER	IM.&AD.	AMMODITIDAE	●	●●	●●●●	●●●●●					
	IM.(SM)	CLUPEIDAE		●	●●●						
	IM.(SM)	GADIDAE			●						
		SERRANIDAE		●●							
		SALMONIDAE	●●								
BOTTOM-LIVING	AD.	GADIDAE	●●	●●							
		PHOLIDAE	●	●●	●						
		BLENNIDAE		●							
		COTTIDAE	●	●●							
		ZOARCIDAE		●●							
		PLEURONECTIDAE	●●●●	●●●							
FRESH-WATER		ANGUILLIDAE	●●					●			
		CYPRINIDAE	●								
		PETROMYZONTIDAE	●								

P-L = POST-LARVAL
J. = JUVENILE
IM. = IMMATURE
SM = SMALL
AD. = ADULT

PERCENTAGE (BY WEIGHT) OF DIET:

- 75-100 % ●●●●●
- 50-75 % ●●●●
- 25-50 % ●●●
- 5-25 % ●●
- 0-5 % ●

super-abundance that generally prevail during the summer months the birds of all species will exploit the same resources in the immediate vicinity of the islands. Only in those years when food is in short supply will competition be at all likely to be an important factor in the ecology of the birds.

Interspecific competition between closely related (congeneric) species.

Three congeneric groups were included in the various species of sea-birds investigated during the present work. These were the Arctic Tern (Sterna paradisaea) and Common Tern (S. hirundo), the Lesser Black-back Gull (Larus fuscus) and the Herring Gull (L. argentatus), and the Shag (Phalacrocorax aristotelis) and the Cormorant (P. carbo). Of these insufficient information was obtained about the Herring Gull to allow an adequate comparison to be made with the Lesser Black-back Gull. The feeding habits of the other two pairs can however be compared.

THE ARCTIC AND COMMON TERNS.

These two species both feed on very nearly the same type of food, and in areas which very largely overlap. Thus the two most important fish species taken by both species were Ammodytidae and Clupeidae, although the Common Tern tended to take slightly less of the former and more of the latter. The secondary prey species taken were also very largely complementary other than the very minor numbers of Pleuronectidae and insects taken by the Arctic Tern, which were not taken by the Common Tern. No great divergence could be discerned in the feeding areas utilized by these species, nor was there much distinction in the type of nest site utilized. The Arctic Terns tended to prefer to nest in areas near the shore where the vegetation was short, or absent altogether, and the Common Terns appeared to favour nesting in slightly longer vegetation, and were only rarely found in areas completely bare of vegetation, but such a distinction was very tenuous and there were many areas where the two species nested in close proximity under identical conditions.

THE SHAG AND CORMORANT.

Lack (1945) examined the problem of ecological relationships between the Shag and the Cormorant, and concluded that they were not competing either for food, or for other environmental resources. The present work supports this conclusion, for although both the Shag and Cormorant take bottom-living fish, they tend to feed in different areas, and only have a few of the more numerous fish species in common in the diet. Moreover in the Farne Islands area they do not compete for nest-sites; the other important environmental factor affecting the populations, for the Cormorants have two well defined colonies on the smaller out-lying islands in the group, whereas the Shags nest on the main islands, and prefer wide rock ledges on the cliffs, to the flat-rock platforms on the tops of the islands which are favoured by the Cormorants. Coulson (1961) showed that there were further ecological differences in the two species, in that their movements and dispersal during the winter months diverged markedly.

It has been shown that whilst the Shag and Cormorant differed considerably in their ecological requirements, the tern species differed very little. Lack (1945) concluded that the differences in the ecology of the Shag and Cormorant was evidence of past competition between the species as would be expected from Gauses' Hypothesis. Coulson (1961) points out that such a conclusion is debatable, and states that such differences could have arisen during a period of geographical isolation of the two species, when natural selection would cause the evolution of divergent habits. This is a similar argument to that of Andrewartha and Birch (1954) who rejected all such indirect evidence, for the validity of Gauses' Hypothesis, on just these grounds. The fact that the Tern species are coexisting on the Farne Islands, whilst occupying almost identical niches, is further evidence for this view. However it is possible that at present none of the resources utilized by these species is in short supply, and thus competition has not yet become a factor in their ecology. There is however little evidence that the numbers of the tern species on the Farne Islands are increasing, thus if competition between the species is not operative, then some other factor of population control must be postulated (see below). Coulson (1961) states that it is unlikely that two species could compete for more than one requisite at any one time, and thus only one character of the species would be actively selected for at any one time. That the Cormorant and Shag differ in a number of ways is cited as evidence of such differences having arisen from ecological isolation, rather than from competition. It seems, however, more probable that competition between closely related species would cause selection for a complex of factors, rather than a single factor, as initially the competing species would be utilizing many environmental resources in common i.e. the closer the relationship the more identical the 'operational niches'. Sperber (1947) postulates a method whereby speciation may take place by just such an ecological mechanism. If competition is accepted as a normal result of the co-habitation of closely related species then such ecological speciation would appear to be entirely feasible, despite the arguments of Mayr (1942) and others against this view. However the present study has shown no evidence for competition taking place between closely related species, even when some competitive components of their respective niches are apparently identical although the possibility cannot be ruled out that such competition may occur under adverse conditions. It thus seems reasonable to conclude that whilst Gauses' theorem may represent a true summary of the ecological implications of the association of certain congeneric systems, it would be misleading to apply it indiscriminately to all such associations before a detailed survey of the ecological situation is made.

THE REGULATION OF NUMBERS OF FARNE ISLAND SEA-BIRDS.

The various agencies which may theoretically have a regulatory effect on the populations of sea-bird species breeding on the Farne Islands may be listed as follows.

a) Competition for food.

b) Competition for nest-sites.

c) Predation or parasitism (including disease).

d) Effect of weather etc.

e) Homeostatic behavioural mechanisms.

The first four named work directly at the level of the individual in the population, whilst the latter postulates the existence of a group response to any or all of the direct factors such that behavioural mechanisms restrict the population to a level below that at which the direct regulatory factors would take effect. The possible impact of each of the above factors on the Farne Islands populations will be considered.

a) Competition for food.

i) During the breeding season.

The possibility that the populations of sea-birds breeding on the Farne Islands are in any way limited by the food supply during the breeding season would appear to be remote, judging by the evidence obtained from the present study. The super-abundance of the young Ammodytidae and Clupeidae in the area during the summer months appears to be a permanent ecological factor in the area, and in the event that their numbers are reduced to the level where interspecific competition might be important, it has been shown that the variation in feeding habits and areas of the various species is such that any competition would be minimised. The fact that many of the species investigated spent less than half the available time in fishing activities (see Section 2) supports the conclusion that there is little competition for food, either inter-, or intra-specifically, as does the fact that many of the birds could bear broods of 2 and 3 just as successfully as broods of 1. (Section 3).

ii) Outside the breeding season.

It has already been pointed out that competition for food in sea-bird species is unlikely outside the breeding season, due to the vast areas over which the birds can feed.

b) Competition for nest-sites.

It is possible that the Farne Islands colonies may be controlled largely by the availability of nest-sites. The islands are small, and for most of the species the number of suitable nest-sites is severely limited. However it is by no means certain that all available nest-sites are being used, and certain of the species, in particular the Shags and the Kittiwakes, appear to have been expanding rapidly in recent years (J.C. Coulson pers.comm.). With those species which are not obviously increasing in numbers there is no apparent competition for nest-sites, and the suitable areas are not all utilized. Should there have been intensive competition for nest-sites in these species it would be reasonable to assume that there would be a heavy incidence of broken and deserted clutches, but there was no evidence of this in any of the species studies. However, as no intensive studies were made of the breeding behaviour of the various species and no quantitative information on the intraspecific and interspecific pressures on available nest-sites was obtained, it is possible that competition was taking place which was not noted. This is considered unlikely however.

c) Predation or parasitism.

There is no evidence that parasitism or disease play any part in controlling the populations. Rowan (1962) records a number of Common Terns being picked up dead on the South African Coast, a mortality which may have been due to disease, but this is an isolated record. Neither is predation at present a decisive factor in mortality of species breeding on the Farne Islands. In the past the affect of human predation has had a considerable limiting effect on the populations, but the effect of the protection now afforded to the colonies is such that, except possibly in the case of the Shags and Cormorants which are occasionally shot in the rivers and estuaries of the north-east coast, there is little or no effective predation in the colonies.

d) Effect of weather.

Sea-birds are well adapted to resist the adverse effects of climatic conditions, and even in bad seasons when there is a certain amount of chick mortality due to storms, the numbers killed are small in relation to the size of the colony. Thus in July 1962 on the Farne Islands a large number of tern chicks were found dead after heavy overnight rain, but these were estimated at no more than ten percent of the chicks in the area. Similarly heavy seas and gale force winds washed off the ledges, or killed by exposure, a number of Kittiwake and Shag chicks on one occasion in June 1962. Such occurrences were unusual however, and affected only small numbers out of the whole population. There is some mortality of sea-birds, particularly first year juveniles, caused by 'wrecks' i.e. being blown inland by particularly strong winds during the winter months. It seems unlikely however, that the effect of weather, either during or outside the breeding season, could effectively limit the size of the populations breeding on the islands.

The four factors so far considered have all, at one time or another, been put forward as the ultimate controlling factor preventing the exponential increase in animal numbers. Discussions on the relative merits of each factor in particular the density dependence/density independance controversy, are given in Solomon (1949) Nicholson (1954) Milne (1957) and Andrewartha and Birch (1954) among others. However no attempt will be made here to assess the merits of the theories of these authors, as it would appear unlikely that any of these direct factors exert a significant amount of influence on the Farne Islands populations.

c) Homeostatic behavioural mechanisms.

Wynne-Edwards (1962) postulated that in many animal groups, including sea-birds, the populations are homeostatically controlled by the observance of behavioural conventions which limit the number of pairs breeding in any colony or area, and that such mechanisms are adjusted to conform with the available food supply, or any other resource that is limiting. Such mechanisms depend usually on the substitution of "conventional prizes", such as territory or social status, for the actual resource. By this means only a limited number of individuals or breeding pairs can occupy a given area, and any surplus, which has failed in the conventional contests for a place in the society, is driven away and inhibited from utilizing any of the available resources. The problem of the evolution of such behavioural mechanisms, and other altruistic (Haldane 1934) factors, which further the survival of the group or society at the expense of the individual, is the crucial point in accepting any such explanation of population regulation. Thus Ashmole (1963) Maynard-Smith (1964) and Amadon (1964) all reject Wynne-Edwards' thesis as unlikely, if not impossible, due to the fact that selection, acting as it does on the gene complexes at the individual level, would never favour the evolution of characteristics which benefitted the group, but resulted in the death or non-breeding of the individual. As Wynne-Edwards (1963) has pointed out however, there are a number of theoretical models which can explain the evolution of group selection for individually disadvantageous characters (Haldane 1934; Wright (1945) Williams & Williams (1957)), and that such characters, if of great use to the group, as they would be, in preventing the continual extinction of local populations through the exhaustion of resources, woucd have appeared very early in the evolution of species, and be well protected, or buffered, genetically, from being eliminated by later selection. Similar views have been advanced by Emerson (1960) who concludes "populations of different species with genetic control over relatively small population numbers can be selected in competitions with populations in the same habitat that have a larger reproductive potential". In birds Wynne-Edwards postualtes that low clutch-sizes, and long immature periods are group adaptations to lower the breeding rates and thus restrict the populations. This has been disputed by Ashmole (1963), and Amadon (1964) who maintain that bird populations are ultimately controlled directly by environmental factors, most importantly food, and that recruitment to the population will be such that the maximum possible use of the available resources will be made. Thus natural selection will favour those birds which rear the greatest number of successful chicks, i.e. those chicks which themselves survive to reproduce. In those birds which are highly specialized predators, e.g. fish-eating birds, the low reproductive rate is held to be due to the long period of apprenticeship which the young birds have to undergo to become skilled enough hunters to rear chicks for themselves. Similar views about the evolutionary pressure for maximum clutch sizes have been put forward by Lack (1954) and (1964) and Perrins (1964). However as Wynne-Edwards (1964) was stated, it is debatable whether even the species cited by these authors are actually producing the maximum number of young possible in the circumstances, and it seems equally likely that group selection for low clutch size could be operating. The present work has shown that most of the species studied spent only part of the day in fishing activities, whereas if the birds were rearing the maximum number of young which they could successfully support, it would be expected that they would spend nearly all the available time in hunting for food. Moreover the amount of time spent fishing was shown to bear a logarithmic relationship to the size of bird, and bears little relation to clutch size, as would be expected if the species were rearing the maximum number which the environment would support. It thus seems possible that the sea-bird populations on the Farne Islands may be regulated by behavioural mechanisms as postulated by Wynne-Edwards, for there is no evidence that any of the usual limiting factors on animal population increases are having any direct effect on the Farne Islands populations. However in the absence of any substantial direct evidence this explanation must remain a possibility rather than a probability.

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Summary.

An analysis is made of the diet of nine species of sea-birds breeding on the Farne Islands. In all the species fish formed an overwhelming proportion (85-98%) of the total diet, and in all but the Cormorant sand-eels (Ammodytidae) were the most important fish taken. The Cormorants depended on flat-fish (Pleuronectidae) for over 50% of their diet. Young Whiting and Codling (Gadidae) and young Herring and Sprats (Clupeidae) were also important in the diet of most of the species. Seasonal and annual fluctuations in the relative amounts of the types of prey taken were observed. It was found that there was a direct relationship between the average size of the bird species and the average size of prey taken, for both surface-feeders and for the diving birds.

The diurnal feeding rhythms of six sea-bird species were investigated, and strong evidence of diphasic activity was found, with periods of activity in the morning and evening separated by a period of rest in the early afternoon.

The maximum potential feeding ranges of various species are estimated, and the type of feeding areas utilized described.

Estimates are made of the proportion of the day spent in fishing and it is shown that the amount of time spent fishing increased logarithmically with decreasing average weight of the bird species. This relationship suggests that birds of less than 170g. weight must spend all their time fishing, whereas birds of greater weight than 1400g. will spend less than 15% of their time fishing.

The growth curves of increase in weight with age and increase in wing length with age are calculated and their form discussed. A comparison made of the growth of groups of chicks under different conditions and from broods of different sizes showed no significant difference in the growth rates of the various groups in any of the species examined.

The food intake and feeding frequencies of chicks in the field were studied by direct observation and by periodic weighings, and a comparison is made with the food intake of chicks reared under laboratory conditions. In the laboratory the efficiencies of conversion of food into flesh, and food into faeces were calculated, and estimates made of the amount of food required for maintenance and the amount of food required for growth. Estimates of the average daily and seasonal food intake of chicks and adults in the field are made based on the data obtained from studies on chicks in the laboratory. The total seasonal food intake for all birds is estimated to be 1409 tons, and the daily food intake to be 9 tons at the beginning of the season and 11 tons at the end of the season. It is calculated that in the course of a season the birds took over 450 million sand-eels and over 21 million Clupeidae. The relative predation rates by the birds under intensive and extensive fishing conditions are calculated.

The concepts of 'competition' and 'similar ecology' and the implications of 'Gauses Hypothesis' are discussed. It is thought to be unlikely that competition for food would be an important factor in the ecology of the birds on the Farne Islands; there was no evidence of competition for any resource occurring between any of the closely related (congeneric) species breeding on the islands. The various means by which the numbers of birds breeding on the Farne Islands might be regulated are discussed, and it is concluded that the populations might possibly be controlled by homeostatic behavioural mechanisms.

APPENDIX A.

Nomenclature.

1. List of bird species mentioned in the text.

Arctic Tern.	*Sterna paradisaea.* Pontoppidan.
Common Tern.	*Sterna hirundo.* Linnaeus.
Sandwich Tern.	*Thalasseus sandvicensis* (Latham).
Kittiwake.	*Rissa tridactyla* (Linnaeus).
Lesser Black-back Gull.	*Larus fuscus.* Linnaeus.
Herring Gull.	*Larus argentatus.* Pontoppidan.
Fulmar.	*Fulmarus glacialis* (Linnaeus).
Puffin.	*Fratercula arctica.* (Linnaeus).
Guillemot.	*Uria aalge.* (Pontoppidan.)
Razorbill.	*Alca torda.* Linnaeus.
Shag.	*Phalacrocorax aristotelis.* (Linnaeus).
Cormorant.	*Phalacrocorax carbo.* Linnaeus.
Eider Duck.	*Somateria mollissima* (Linnaeus.)

2. List of species, other than birds, mentioned in the text.

a) Fish.

Lamprey.	*Petromyzon fluviatilis*, Day.
Herring.	*Clupea harengus*, Linnaeus.
Sprat.	*Clupea sprattus*, Linnaeus.
Salmon.	*Salmo salar*, Linnaeus.
Char (Windermere).	*Salvelinus willughbii* (Günther).
Smelt.	*Osmerus eperlanus*, Linnaeus.
Gudgeon.	*Gobio gobio*. (Linnaeus).
Eel.	*Anguilla vulgaris*, Day.
Garfish.	*Belone belone*. (Linnaeus.)
Cod.	*Gadus morrhua*, Day.
Perch.	*Perca fluviatilis*, Linnaeus.
Greater Sand-eel.	*Ammodytes lanceolatus*, Lesauvage.
Lesser Sand-eel.	*Ammodytes tobianus*, Linnaeus.
Lesser Weever.	*Trachinus vipera*, Cuvier & Valenciennes
Butterfish.	*Pholis gunnellus*, Linnaeus.
Viviparous Blenny	*Zoarces viviparous*, (Linnaeus)
Father-lasher.	*Cottus scorpius*, Linnaeus.
Long-spined Sea Scorpion.	*Cottus bubalis*, Euphrasen.
Lump-sucker.	*Cyclopterus lumpus*, Linnaeus.
Sea snail.	*Liparis liparis* (Linnaeus).
Three-spined Stickleback.	*Gasterosteus aculeatus*, Linnaeus.
Fifteen-spined Stickleback.	*Gasterosteus spinachia*, Day.
Dab.	*Pleuronectes limanda*, Day.
Plaice.	*Pleuronectes platessa*, Linnaeus.
Flounder.	*Pleuronectes flesus*, Day.
Cuckoo Wrasse.	*Labrus mixtus*, Linnaeus.
Capelin.	*Mallotus villosus*, Müller.

b) Crustacea.

Common shrimp.	*Crangon vulgaris*. Linnaeus.

c) Cephalopoda.

Little Cuttle.	*Sepiola atlantica* (d'Orbigny).
Common Squid.	*Loligo forbesi*. Steenstrup.

d) Mollusca.

Edible Mussel.	*Mytilus edulis*. Linnaeus.

e) Insecta.	*Myrmica scabrinodis*.

3) Length frequencies of Ammodytidae taken by Puffins.
(lengths in mm.).

SIZE RANGE (mm.)	1961. No.	1961. %	1962. No.	1962. %
21-30	-	-	-	-
31-40	-	-	-	-
41-50	-	-	-	-
51-60	-	-	4	2.7
61-70	-	-	33	22.1
71-80	6	35.3	45	30.8
81-90	9	53.0	48	32.8
91-100	2	11.8	11	7.4
101-110	-		2	1.3
111-120	-		2	1.3
121-130	-		1	0.6
131-140	-		-	-
141-150	-		3	2.0

APPENDIX C. Observations of the number of feeds taken per hour throughout the day by chicks of various sea-bird species.

1) Arctic Tern. Observations on the feeding of individual chicks. Total of all observations during 1961 and 1962.

HOUR OF DAY.	NO. OF BROODS OBSERVED.	TOTAL NO. OF CHICKS OBSERVED.	TOTAL NO. OF FEEDS TO ALL CHICKS.	AVERAGE NO. OF FEEDS PER CHICK.	AVERAGE NO. OF FEEDS PER BROOD.
0400-0500	19	22	15	0.68	0.79
0500-0600	38	42	72	1.71	1.89
0600-0700	38	42	48	1.14	1.26
0700-0800	32	35	58	1.66	1.81
0800-0900	33	36	38	1.05	1.15
0900-1000	24	26	51	1.96	2.12
1000-1100	24	26	33	1.27	1.37
1100-1200	16	17	20	1.18	1.25
1200-1300	16	17	22	1.29	1.37
1300-1400	16	17	19	1.12	1.19
1400-1500	33	39	51	1.31	1.54
1500-1600	33	39	44	1.13	1.51
1600-1700	21	24	36	1.50	1.71
1700-1800	21	24	51	2.12	2.43
1800-1900	12	14	23	1.64	1.92
1900-2000	20	22	46	2.09	2.30
2000-2100	37	42	54	1.29	1.46
2100-2200	32	34	54	1.59	1.69

Average number of feeds per day per chick. 26.

Average number of feeds per day per brood. 29.

ii) Common Tern. Observations on the feeding of individual chicks. Totel of all observations during 1962.

HOUR OF DAY	NO. OF BROODS OBSERVED	TOTAL NO. OF CHICKS OBSERVED.	TOTAL NO. OF FEEDS TO ALL CHICKS.	AVERAGE NO. OF FEEDS PER CHICK.	AVERAGE NO. OF FEEDS PER BROOD.
0400-0500	7	11	2	0.18	0.29
0500-0600	11	18	10	0.55	0.91
0600-0700	11	18	24	1.33	2.18
0700-0800	11	18	26	1.44	2.36
0800-0900	11	18	12	0.66	1.09
0900-1000	11	18	21	1.67	1.91
1000-1100	11	18	9	0.50	0.82
1100-1200	5	7	6	0.86	1.20
1200-1300	5	7	7	1.00	1.40
1300-1400	5	7	8	1.14	1.60
1400-1500	22	42	17	0.40	0.77
1500-1600	22	40	27	0.67	1.23
1600-1700	15	24	22	0.92	1.47
1700-1800	15	24	24	1.00	1.60
1800-1900	10	15	15	1.00	1.50
1900-2000	10	15	20	1.33	1.80
2000-2100	23	42	23	0.55	1.00
2100-2200	24	43	15	0.35	0.62

Average number of feeds per day per chick. 16.

Average number of feeds per day per brood. 24.

iii) Sandwich Tern. Number of feeds per hour taken by chicks.

HOUR OF DAY	NO. OF CHICKS OBSERVED	TOTAL NO. OF FEEDS TO ALL CHICKS.	AVERAGE NO. OF FEEDS PER CHICK.	HOUR OF DAY	NO. OF CHICKS OBSERVED	TOTAL NO. OF FEEDS TO ALL CHICKS.	AVERAGE NO. OF FEEDS PER CHICK.
0400-0500	-	-	-	1300-1400	-	-	-
0500-0600	9	6	0.66	1400-1500	-	-	-
0600-0700	9	10	1.10	1500-1600	-	-	-
0700-0800	9	6	0.66	1600-1700	-	-	-
0800-0900	9	4	0.33	1700-1800	-	-	-
0900-1000	9	2	0.22	1800-1900	-	-	-
1000-1100	-	-	-	1900-2000 1930-2030	11	23	2.10
1100-1200	-	-	-	2000-2100 2030-2130	11	11	1.00
1200-1300	-	-	-	2100-2200			

Average number of feeds per day per chick. 14. (Assuming feeding frequencies over those hours when no observations were made are similar to the hourly frequencies detailed above).

iv) Kittiwake. Average number of feeds per hour taken by chicks.

HOUR OF DAY	NO. OF CHICKS OBSERVED	TOTAL NO. OF FEEDS TO ALL CHICKS.	AVERAGE NO. OF FEEDS PER CHICK.	HOUR OF DAY	NO. OF CHICKS OBSERVED	TOTAL NO. OF FEEDS TO ALL CHICKS.	AVERAGE NO. OF FEEDS PER CHICK.
0300-0400	18	3	0.16	1300-1400	57	16	0.28
0400-0500	32	7	0.22	1400-1500	57	11	0.19
0500-0600	32	8	0.25	1500-1600	67	19	0.30
0600-0700	32	3	0.09	1600-1700	43	10	0.23
0700-0800	14	1	0.07	1700-1800	43	13	0.30
0800-0900	14	3	0.21	1800-1900	43	4	0.09
0900-1000	14	1	0.07	1900-2000	43	6	0.14
1000-1100	14	3	0.21	2000-2100	43	15	0.35
1100-1200	32	4	0.12	2100-2200	43	18	0.42
1200-1300	47	8	0.17	2200-2300	43	13	0.30

Average number of feeds per day per chick. 4.

v) Puffin. Number of feeds per hour brought to burrow during observations in June 1962.

HOUR OF DAY	NO. OF BURROWS OBSERVED	TOTAL NO. OF FEEDS BROUGHT TO ALL BURROWS	AVERAGE NO. OF FEEDS PER CHICK.	HOUR OF DAY	NO. OF BURROWS OBSERVED	TOTAL NO. OF FEEDS BROUGHT TO ALL BURROWS	AVERAGE NO. OF FEEDS PER BURROW.
0300-0400	4	1	0.25	1300-1400	8	0	0
0400-0500	4	2	0.5	1400-1500	8	1	0.12
0500-0600	8	5	0.62	1500-1600	8	2	0.25
0600-0700	8	5	0.62	1600-1700	8	2	0.25
0700-0800	8	0	0	1700-1800	4	0	0
0800-0900	8	0	0	1800-1900	4	2	0.5
0900-1000	8	0	0	1900-2000	4	0	0
1000-1100	8	0	0	2000-2100	4	0	0
1100-1200	8	0	0	2100-2200	4	0	0
1200-1300	8	0	0	2200-2300	4	0	0

Average number of feeds per day per chick. 3.

vi) Shag feeding frequency. Number of feeds per two-hours taken by chicks throughout the day. Average of observations in 1961 and 1962.

HOUR OF DAY	NO. OF CHICKS OBSERVED	TOTAL NO. OF FEEDS TO ALL CHICKS.	AVERAGE NO. OF FEEDS PER CHICK.	HOUR OF DAY	NO. OF CHICKS OBSERVED	TOTAL NO. OF FEEDS TO ALL CHICKS.	AVERAGE NO. OF FEEDS PER CHICK.
0300-0500	20	0	0	1300-1500	48	7	0.15
0500-0700	26	0	0	1500-1700	52	6	0.11
0700-0900	14	1	0.07	1700-1900	50	10	0.20
0900-1100	14	3	0.21	1900-2100	44	21	0.48
1100-1300	31	4	0.13	2100-2300	32	6	0.19

Average number of feeds per day per chick. 3.

APPENDIX D.

Weight frequencies of samples of regurgitated food from Kittiwakes, Lesser Black-back Gulls, and Shags.

The frequencies of the actual weights of the samples collected is given, together with the frequencies of the estimated original weights of each sample before digestion took place. These estimates are based on the weights of undamaged prey specimens of similar apparent size to those found in the regurgitation samples.

WEIGHT RANGE. (g.)	KITTIWAKE.		LESSER BLACK-BACK GULL.		SHAG.	
	Actual weights	Estimated Original Weights.	Actual Weights	Estimated Original Weights.	Actual Weights	Estimated Original Weights.
0-10	53	33	20	10	1	0
11-20	32	20	16	15	3	0
21-30	12	29	8	20	5	2
31-40	4	5	2	2	2	1
41-50	1	7	2	1	0	6
Over 50	0	9	3	1	1	3

APPENDIX E. Records of measurements of the variation in weight over consecutive limited periods, of the chicks of various species of sea-birds.

TABLE E1. Weight records (in grams) of three Sandwich Tern Chicks over 24 hours.

HOUR OF DAY	LENGTH OF PERIOD BETWEEN WEIGHINGS (hours)	AGE OF CHICK (DAYS). 27 CHICK NO.77. W	C	E	24 CHICK NO. 76 W	C	E	28 CHICK NO.35 W	C	E
17th July										
1200	2	161	+3	7	192	-7		191	-5	
1400	4	164	+7	15	185	+3	11	186	-4	4
1800	2	171	-6		188	0	4	182	+2	6
2000	2	165	-4		188	-2	2	184	+4	8
2200		161			186			188		
18th July	8		-4	12		-3	13		-3	13
0600	2	157	+2	6	183	-3	1	185	+1	5
0800	2	159	-3		180	-3	1	186	+1	5
1000	2	156	-3		177	-2	2	187	-5	
1200		153			175			182		
Wt. change over 24 hour period.		-8			-17			-9		
Estimated wt. of food taken over 24 hour period. *				40			34			41
Estimated number of feeds taken over 24 hour period. *				14			13			11
Estimated weight loss over 2-hour period.				4			4			4

W = Weight recorded. C = Change in weight over the period between weighings.
E = Estimated weight of food taken over the period between weighings. *

* See text (Section 2) for explanation of derivation.

TABLE E2. Weight records (in grams) of four Kittiwake chicks over 24 hours, taken at 2-hourly intervals.

	CHICK NO.23			CHICK NO. 6			CHICK NO.40			CHICK NO. 2		
AGE OF CHICK (days)		30			15			29			10	
HOUR OF DAY.	W	C	E	W	C	E	W	C	E	W	C	E
12th July												
1300	371			264			433*			175		
1500	362	-9		275*	+11	16	379	-54		192*	+17	19
1700	359	-3		259	-16		398*	+19	23	173	-19	
1900	351	-8		261	+3	8	366	-32		182	+9	11
2100	348	-3		257	-4		362	-4		178	-4	
2300	345	-3		251	-6		359	-3		172	-6	
13th July		3×-4.3 =-13			3×-5 =-15			3×3.7 =-11			3×-2.3 =-7	
0500	332			236			348			165		
0700	337	+5	9	240	+4	9	364	+16	20	164	-1	1
0900	339	+2	6	281*	+41	46	406*	+42	46	166	+2	4
1100	333	-6		272	-9		368	-38		164	-2	
Estimated wt. loss over 2-hour period (see text)		4			5			4			2	
Initial wt.	371			264			433			175		
Final wt.	333			272			368			164		
Change in wt. over 24 hrs.	-38			+8			-65			-11		
Est. wt. of food taken.			15			79			89			35
No. of feeds.			2			4			3			4

W = Weights recorded.
C = Change in weight over two-hourly period.
E = Estimated weight of food taken over two-hourly period (see text).

* Whilst recording those weights marked by an asterisk the chicks regurgitated (Weight of regurgitated food included in that* weight, but not in subsequent weights, which are thus much lower).

TABLE E3. Weight records (in grams) of a Herring Gull chick over 36 hours, taken at 2-hourly intervals.

AGE OF CHICK (days)	25		
	CHICK NO.62.		
HOUR OF DAY	W	C	E
18th Aug.			
0845	930		45
1045	920	-10	
1245	954	+34	43
1445	937	-17	
1645	913.5	-23.5	
1845	973	+59.5	68.5
2045	949	-24	
19th Aug.		+2	47
0645	951		
0845	921	-30	
1045	900	-21	
1245	887	-13	
1445	876	-11	
1645	958	+82	91
1845	940	-18	
2045	933	-7	

Initial weight	930	
Wt. after 24 hours.	921	
Wt. after 36 hours.	933	
Wt. change over first 24 hours.	-7	
Wt. change over last 24 hours.	-16	
Estimated wt. of food taken over first 24 hours.		158.5
No. of feeds taken over first 24 hours.		3
Estimated wt. of food taken over second 24 hours.		138
No. of feeds taken over second 24 hours.		2
Average wt. taken per feed.		62.4

W = Weight recorded.
C = Change in weight over the two hourly period.
E = Estimated weight of food taken over the two hourly period. (see text).

TABLE E4. Weight records (in grams) of two Fulmar chicks over 48 hours and 36 hours.

AGE OF CHICK (days) 6

HOUR OF DAY	LENGTH OF PERIOD BETWEEN WEIGHINGS (hours)	CHICK NO. 1 W	CHICK NO. 1 C	CHICK NO. 1 E	CHICK NO. 3 W	CHICK NO. 3 C	CHICK NO. 3 E
17/7/62							
1230		192					
1830	6	207	+15	27			
2030	2	201	-6				
18/7/62	10.5		+1	21			
0700		202					
0900	2	206	+4	8			
1100	2	193	-13				
1300	2	186	-7				
1500	2	229	+43	47			
19/7/62	21		-7	35			
1200		222					

AGE OF CHICK (days)		14			11		
		CHICK NO. 1			CHICK NO. 3		
26/7/62							
0900		533			441		
1700	8	519	-14	14	368	-73	
27/7/62	12		+94	136		+48	90
0500		613			416		
0700	2	580	-33		404	-12	
1700	10	519	-61		368	-36	
1900	2	506	-13		360	-8	
2100	2	499	-7		351	-9	

AVERAGE WT. OF FOOD TAKEN PER DAY.	69
ESTIMATED WT. LOSS OVER 2-HOUR PERIOD	7
WT. CHANGE OVER FIRST 24 HOUR PERIOD	-6
WT. CHANGE OVER SECOND 24 HOUR PERIOD	+36
ESTIMATED WT. OF FOOD TAKEN OVER FIRST 24 HOURS	56
ESTIMATED WT. OF FOOD TAKEN OVER SECOND 24 HOURS	82
NO. OF FEEDS OVER FIRST 24 HOURS.	3
NO. OF FEEDS OVER SECOND 24 HOURS.	2

W = Weight recorded.
C = Change in weight over the 2-hourly period.
E = Estimated weight of food taken over the 2-hourly period (see text).

	CHICK No.1	CHICK No.3
WT. CHANGE OVER 24 HOUR PERIOD 1700-1700 HOURS	0	0
ESTIMATED WT. LOSS OVER 2-HOUR PERIOD	7	7
ESTIMATED WT. OF FOOD TAKEN OVER 24 HOUR PERIOD	136	90
NO. OF FEEDS OVER 24 HR PERIOD	1	1
AVERAGE WT. OF FOOD TAKEN PER DAY		113

TABLE E5. Weight records of six Puffin chicks over 24 hours. (in grams).

AGE OF CHICK (days)		33			26			32			39		
		CHICK NO.06			CHICK NO. 07			CHICK NO. 08			CHICK NO.09		
HOUR OF DAY	L	W	C	E	W	C	E	W	C	E	W	C	E
17th July													
1200	2	231	-8		329	-13.5		261	+5	+7	331	+11	+13
1400	4	223	-11.5		313.5	-2.5		266	-7		342	-16	
1800	2	211.5	+1.5	+3.5	311	-2		259	-1		326	-1	
2000	2	213	-6		309	-5		258	-1		325	-1	
2200		207			304			257			324		
18th July	8		-6	+2		+11	+17		-5.5	+2.5		-6	+2
0600	2	201	-2		315	-3		251.5	-0.5	+1.5	318	0	+2
0800	2	199	+2	+4	312	-11		251	0	+2	318	0	+2
1000	2	201	-2		301	+24	+26	251	-3		318	-2	
1200		199			325			248			316		
Wt.change over 24 hour period.		-32			-4			-13			-15		
Estimated wt. of food taken over 24 hours.				9.5			43			13			19
No. of feeds taken over 24 hours.				3			2			4			4

AGE OF CHICK (days)		28			21		
		CHICK NO.22			CHICK NO.23		
12th July							
1315	2	333	-6		248	-1	
1515	2	327	-5		247	+4	+6
1715	2	322	-5		251	-7.5	
1915	3	317	+11	+14	243.5	-5.5	
2215		328			238		
13th July	7		-16			-10	
0515	2	312	+20	+22	228	+4	+6
0715	2	332	-7		232	-5	
0915	2	325	-1		227	-5	
1115	2	324	-2		222	-1	
1315		322			221		

	CHICK No.22	CHICK No.23
WT.CHANGE OVER 24 HOUR PERIOD.	-11	-27
ESTIMATED WT.OF FOOD TAKEN OVER 24 HOURS.	36	12
NO.OF FEEDS TAKEN OVER 24 HOURS.	2	2

ALL CHICKS.

AVERAGE WT.OF FOOD TAKEN OVER 24 HOURS.	22.4
AVERAGE NO.OF FEEDS TAKEN OVER 24 HOURS.	2.8

W = Weight recorded.

C = Change in weight over the two hourly period.

E = Estimated weight of food taken over the two hourly period. (see text).

L = Length of period between weighings. (hours).

TABLE E6. Weight records (in grams) of two Shag chicks.

AGE OF CHICK (days) / HOUR OF DAY	LENGTH OF PERIOD BETWEEN WEIGHINGS	WEIGHT RECORDED	CHANGE IN WT. OVER PERIOD BETWEEN WEIGHINGS	ESTIMATED WT. OF FOOD TAKEN.
AGE OF CHICK (days)			40	
12th July				
1315	2	1387	-40	
1515	2	1347	-31	
1715	2	1316	-18	
1915	3	1298	+117	151
2215		1415		
13th July				
0515	2	1333	-26	
0715	2	1307	-13	
0915	2	1294	-15	
1115	2	1279	-22	
1315		1257		

Estimated average wt. loss over 2-hour period	23	
Weight change over 24 hour period.	-130	
Estimated wt. of food taken over 24 hours.		151
No. of feeds taken over 24 hours.		1

AGE OF CHICK (days) / HOUR OF DAY	LENGTH OF PERIOD BETWEEN WEIGHINGS	WEIGHT RECORDED	CHANGE IN WT. OVER PERIOD BETWEEN WEIGHINGS	ESTIMATED WT. OF FOOD TAKEN.
AGE OF CHICK (days)			29	
27th July				
0530	2	1289	-27	
0730	9.5	1262	+4	123
1700	2	1266	+42	67
1900	2	1308	-23	
2100		1285		

Estimated average wt. loss over 2-hour period.	25	
Wt. change over daylight period. (15.5 hr.)	-4	
Estimated wt. of food taken over daylight (15.5 hr) period.		190
No. of feeds taken over daylight (15.5 hr) period.		2