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Offshore Wind Farm



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THE FEEDING BIOLOGY OF SEA-BIRD SPECIES BREEDING ON THE FARNE ISLANDS, NORTHUMBERLAND

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INTRODUCTION

Very little comprehensive work has been published concerning the feeding biology of sea-birds in Britain. Collinge (1925) made a detailed study of the stomach contents of a number of species and Lumsden & Haddow (1946) and Steven (1933) described comprehensively the diets of the shag and the cormorant. Moreover, the interspecific feeding relationships of the colonial associations of species breeding in this country have received little attention. Such relationships were investigated by Hartley & Fisher (1936) for a specific and specialized feeding area in Spitzbergen, and more recently Belopolskii (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, however, of the synecology of North Atlantic sea-birds have been published and the present study is designed to go some way towards filling this gap.

The study was made between 1961 and 1963 on the Farne Islands, Northumberland (Nat. Grid Ref. NU220360) which lie between 1 and 4½ miles (1.6–7 km) off the north Northumberland coast. The islands are small (largest 16 ac, 6.5 ha) and eight of them support large colonies of sea-birds during the breeding season. The food and the feeding biology of the following species were investigated: Arctic tern (*Sterna paradisaea* Pont.), common tern (*S. hirundo* L.), sandwich tern (*S. sandvicensis* Latham), kittiwake (*Rissa tridactyla* (L.)), lesser black-backed gull (*Larus fuscus* (L.)), puffin (*Fratercula arctica* (L.)), guillemot (*Uria aalge* (Pont.)), shag (*Phalacrocorax aristotelis* (L.)), cormorant (*P. carbo* (L.)).

FOOD OF THE BIRDS

Methods

The traditional method of obtaining information about the food of birds is by shooting them and examining the stomach contents (e.g. Collinge 1925; Hartley & Fisher 1936). This indicates the food taken during the hours preceding shooting but there is a problem of differential digestion which may produce biased results (Hartley 1948). In the present investigation, carried out on a nature reserve, this method could not be used, except in the case of shags and cormorants which were shot nearby at Berwick-on-Tweed. Instead the food of the birds was studied by examination of food regurgitated by the young and adults when captured or by the observation of food carried in the bill in those species which do not ingest the food intended for their young. The former method is subject to some of the disadvantages of the examination of the stomach contents of dead birds, but because the diet of most of the species studied consists almost entirely of fish (see below) the problem of differential digestion in regurgitated food intended for the chicks is not great. Moreover as the parent birds normally tend to feed the young soon after returning to the nest from a fishing trip, during which period most of the regurgitation samples were

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collected, digestion was not greatly advanced in the majority of the samples. It was, however, difficult in many cases to make specific identifications amongst groups of closely related fish species (see below). In addition, a second group of data was obtained by examining food which was unintentionally dropped by birds, and while this latter information may be biased, it forms only a small proportion of the total records for any species. Table 1 lists the methods which were used for each species. In those species where extensive samples were obtained by both methods, no significant differences were found between the two groups of information so obtained.

Observation blinds (hides) were used for direct observation of food carried to the young. The food could be inspected at close range and no difficulties were encountered in either identifying or counting the prey; and no cases of error were recorded when periodic checks were made on the identification and count by subsequently capturing the bird before it could feed its young. Such checks were undertaken at least once for each species of prey noted, during each observational period. As will be seen later, relatively few prey species were taken by most birds and this facilitated their identification in the field.

In the majority of species studied, the diet consisted almost entirely of fish of which the majority of samples collected by regurgitation were partly decomposed. Nevertheless, the species could usually be identified and good estimates obtained of the number and weight of individuals concerned. When digestion had resulted in loss of part of the body, the maximum breadth of the fish was measured and related to weight using a graph of weight/maximum breadth produced from intact specimens of the same species.

The descriptions of Day (1884) and Jenkins (1936) have been used to identify fish. The nomenclature used by Jenkins is followed in this paper. In the case of *Ammodytes* identification to species often provided difficulties as many of the specimens were juvenile stages and lacked the characters which make specific identification possible from published work. Corbin (personal communication) states that it is possible to identify immature *Ammodytes* on the basis of scale pattern on the abdomen and tail but the great majority of specimens were sufficiently damaged to make this procedure unreliable or even impossible. Three species of Ammodytidae are found off the north-east coast. These are *A. lanceolatus* Lesauvage, a large species possessing vomerine teeth, *A. tobianus* L. (= *A. lancea* Cuvier) and *A. marinus* (Raitt). The last two do not possess vomerine teeth and are distinguished on meristic characters. There has been considerable confusion in the literature over the identity of these two species (see Richards, Perlmutter & McAneny 1963). Prior to the description of *A. marinus* as a separate species by Raitt (1934) *A. tobianus* was thought to have schools which spawned offshore in winter and inshore in spring and summer. It now seems probable that the former are in fact *A. marinus* and the latter *A. tobianus* (Richards *et al.* 1963). Undoubtedly these three species have different migration patterns inshore and offshore, which will be of importance to the feeding ecology of the sea-birds. At present, however, little is known about such migrations (a summary of the available information appears below in the discussion of food availability) and, in the absence of any detailed knowledge, bearing in mind the difficulty of identifying damaged specimens accurately, it was decided to treat Ammodytidae as a single group within the scope of this paper.

Composition of the diet

The number of food samples collected and examined and the number of prey identified for each species is given in Table 1. The detailed breakdown of this examination is shown

Table 1. *The number of food samples collected, and the number of identified prey observed, Farne Islands, 1961-63*

Species	Analysis of food samples		No. of identified prey fed to chicks	Total no. of prey identified
	No. of samples collected	No. of individual prey in samples		
Arctic tern	166	468	1624	2092
Common tern	11	11	508	519
Sandwich tern	61	116	769	885
Kittiwake	218	779	0	779
Lesser black-backed gull	68	324	0	324
Puffin	52	219	39	258
Guillemot	27	83	56	139
Shag	24	349	0	349
Cormorant	100*	346	0	346

* Exact number of chicks contributing to the regurgitation samples unknown. In addition complete stomach contents were examined from twenty-eight shags and three cormorants.

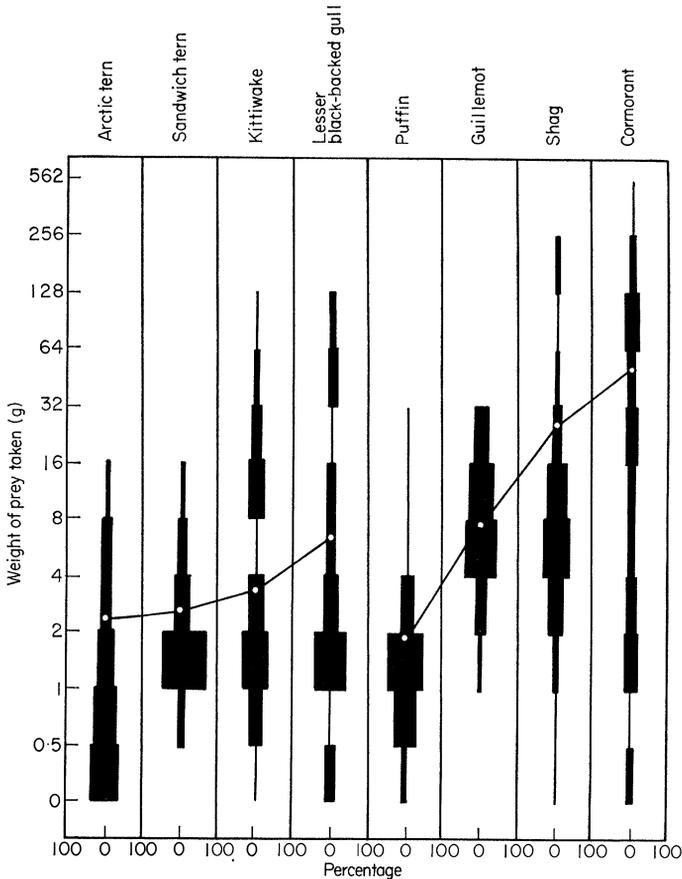


FIG. 1. Comparison of the weights of prey taken by various sea-bird species. Blocks represent the percentage of each weight group taken. The points represent the average weight of prey taken by each species. Terrestrial food items are omitted.

Table 2. Analyses of the diet of Farne Islands sea-birds (presented as percentages of total number of prey taken, and of total weight of prey taken)

	Arctic tern		Common tern		Sandwich tern		Kittiwake		Lesser black-backed gull		Puffin		Guillemot		Shag		Cormorant		
	% no.	% wt	% no.	% wt	% no.	% wt	% no.	% wt	% no.	% wt	% no.	% wt	% no.	% wt	% no.	% wt	% no.	% wt	
FISH	95	94	98	99	98	98	98	99	74	77	100	100	100	100	99	99	99	99	99
Ammodytidae	65	22	44	10	74	61	81	56	55	14	85	80	49	57	81	44	26	1	1
Clupeidae	22	63	38	68	15	24	10	22	6	11	2	13	42	30	*	*	5	19	5
Gadidae	2	6	11	19	6	8	7	21	13	52	1	3	4	9	4	30	5	19	5
Gasterosteidae	2	2	2	2	2	3													
Pleuronectidae	*	*																	
<i>Pholis gunnellus</i>																			
Trachinidae	4	1	3	*	1	*					12	4	5	3	2	2	40	31	8
Anguillidae									*	1					8	8	1	1	1
Cottidae																	4	13	4
Salmonidae																	4	10	4
<i>Zoarces viviparus</i>																	3	10	3
Others																	3	3	3
Others					*	1											4	9	4
MARINE	4	5	2	1	2	2	1	*									1	*	1
INVERTEBRATES	2	2	1	*	1	1	1	*									1	*	1
Crustacea	2	3	1	1	1	1													
Cephalopoda	2	3	1	1	1	1													
TERRESTRIAL	1	*																	
INVERTEBRATES	1	*							20	3									
Insecta									1	1									
Annelida									19	3									
Offal								*	5	19									
VEGETATION									1	*									

* Denotes present but less than 1%.

in Table 2. In all of the species studied fish formed the greatest part of the diet, being well over 90% by both weight and number in all species except the lesser black-backed gull where three-quarters of the food consisted of fish. It is clear that expressing the food composition either by number or weight gives comparable results, but this does not apply when the fish food is broken down into families and species when there is considerable difference in the figures. The discrepancies arise because certain species of fish were consistently larger than others and this should be borne in mind when assessing which are the important food species.

A detailed list of species of fish taken is given in Appendix A. It must be stressed that all the information obtained was on the diet of the birds during the summer breeding season, except that on food obtained from stomach content analysis of a number of shags and cormorants, shot during November and December.

Size of prey taken

The distribution in weight of prey taken by each species of sea-bird is shown in Fig. 1. The majority of the prey taken by all species except the cormorant were smaller than 16 g and all species took a proportion of small items weighing less than 1 g with the exception of the guillemot.

Table 3. *Average weights of adult birds*

Species	No. of specimens in sample	Average weight (g)	Area in which sample was taken	Authority
Arctic tern	90	104 ± 0.93	Farne Islands	Present work
Common tern	11	125 ± 3.98	Farne Islands	Present work
Sandwich tern	8	237 ± 3.34	Farne Islands	Present work
Kittiwake	23	350 ± 9.22	Farne Islands	Present work
Lesser black-backed gull	41	854	Switzerland	Borg (1959)
Puffin	107	380 ± 2.82	Farne Islands	Present work
Guillemot	6	925 ± 31.95	Farne Islands	Present work
Shag	26	1785 ± 43.66	Estuary of Tweed	Present work

The birds may be divided into two groups according to their feeding habits; those which feed from the surface or near the surface, e.g. terns, kittiwake, lesser black-backed gull, and those which regularly dive well below the surface in search of food, e.g. cormorant, shag, guillemot and puffin. In both of these groups the mean weight of prey taken increases progressively with the mean weight of the birds. In the case of surface feeders, the linear regression is

$$\text{prey weight} = 0.0051 \text{ adult weight} + 1.61$$

and for diving species

$$\text{prey weight} = 0.0184 \text{ adult weight} - 7.01$$

Table 3 gives the mean weights of the adult birds on which these regressions are based. These regressions imply that, within the size range studied, the prey of a diving species increases by 1.8 g for every 100 g increase in weight of the adult birds while the equivalent value is 0.5 for a surface feeder.

Despite this relationship between size of the bird and the size of prey, there is considerable overlap in both the size and the species taken by all of the species studied. This is emphasized by the size of *Ammodytes* taken by the birds. This group of prey constitutes

by far the greatest proportion of items used as food weighing less than 4 g and Fig. 2 shows the size distribution of these fish taken by each species. Again there is a tendency for the larger species to take larger individuals, but all species took sand-eels between 50 and 100 mm in length, and the majority took them up to 150 mm.

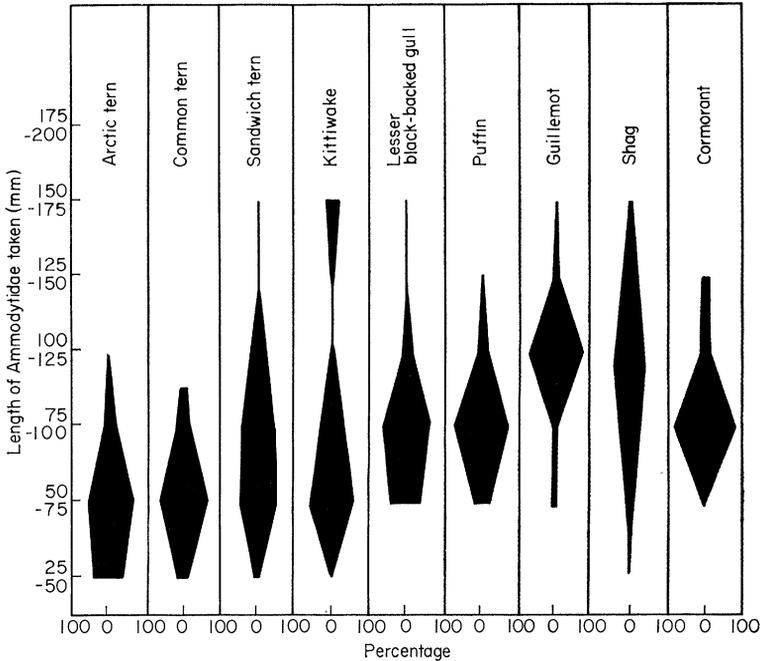


FIG. 2. The length (mm) of the Ammodytidae taken by each species.

Origin of fish taken

A considerable amount of information is available concerning the habitat and distribution of marine fish. The species of fish taken as food can be used to give an indication of the region from which the food was collected. This is presented diagrammatically in Table 4. It is immediately evident that the cormorant and shag feed almost exclusively on mid-water and bottom-living fish while the guillemot takes predominantly mid-water species and the puffin mid-water and surface-living stages. The remaining sea-birds do not dive beyond the surface metre and are predominantly surface feeders taking a very similar diet. The lesser black-backed gull and the cormorant both take food of non-marine origin. The former takes an appreciable proportion of earthworms and offal of terrestrial origin, (e.g. meat scraps, bread, etc. obtained near houses and tips) while the latter takes some freshwater fish. The offal taken by kittiwakes is of marine origin, and is probably obtained whilst following fishing boats. Insects (particularly Lepidoptera) were taken occasionally by the Arctic terns, which obtained them on the wing over the nesting area.

Breeding season and availability of food

This investigation has shown that the Ammodytidae are predominant in the diet of most of the species studied, the exceptions being the common and Arctic terns and the cormorant. The Clupeidae were also taken extensively by most species, but they were

generally of secondary importance to the Ammodytidae. The breeding of these sea-birds coincides with the period of greatest abundance of the Ammodytidae and Clupeidae in the area. Several authors have discussed the numerous occurrences of the peak food availability for bird species coinciding with the 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

Table 4. *Analysis of diet in terms of the habitat distribution of prey*

Prey taken		Cormorant	Shag	Guillemot	Puffin	Kittiwake	Lesser black-backed gull	Sandwich tern	Common tern	Arctic tern
Habitat	Group									
Terrestrial	Insecta						*			*
	Annelida						*			
	Offal						**			
Littoral	Cottidae							*		
	Liparidae							*		
Surface-living	Offal					*	*			
	Gasterosteidae				*			*	*	*
	Cephalopoda							*	*	*
	Crustacea					*		*	*	*
	P.-L. & J. Blenniidae				*			*	*	*
	P.-L. & J. Gadidae					**	****	**	*	**
	P.-L. & J. Ammodytidae				*	****	**	****	**	**
P.-L. & J. Clupeidae				**	**	**	**	****	****	
Mid-water	Im. & Ad. Ammodytidae	*	***	****	*****					
	Im. (sm.) Clupeidae		*	***						
	Im. (sm.) Gadidae			**						
	Serranidae		**							
	Salmonidae	**	*							
Bottom-living	Ad. Gadidae	**	***							
	Pholidae	*	**	*				*		
	Blenniidae		*							
	Cottidae	**	*							
	Zoarcidae	*	*							
	Pleuronectidae	***	*							*
	Others	**	*							
	Crustacea	*	*							
Fresh-water	Anguillidae	**					*			
	Cyprinidae	*								
	Petromyzontidae	*								

P.-L., Post-larval; J., juvenile; Im., immature; sm., small; Ad., adult.

Percentage (by weight of diet); *, 1-5; **, 5-25; ***, 25-50; ****, 50-75; *****, 75-100.

sexual cycle so that the young will hatch at times when the environment contains abundant food on which they are traditionally fed'. Lack (1954) gives many examples of the close correlation between breeding season and the seasonal abundance of food. Salomonsen (1955) noted that the breeding, and in particular the hatching, of Icelandic sea-birds was linked with the annual upsurge of phytoplankton productivity in the spring and summer which is followed by the corresponding increase in zooplankton and macroplankton predators.

Recent work on photoperiodism and circadian rhythms in birds (see Farner 1965;

Wolfson 1965) has shown that in many avian species in mid and high latitudes the gonadal cycle is controlled photoperiodically. Although such evidence has not been obtained for the species under study it seems reasonable to assume that such controls are common among birds at these latitudes. Thus the correlation between this and the annual upsurge of marine productivity in the spring which is also triggered by increasing light intensity, would appear quite feasible. McIntosh & 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 north-east 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 40 mm long. Autumn-spawned fish of the previous year reach the surface waters at the same time, but have a length of between 40 and 50 mm. All age groups of developing Ammodytidae tend to spend the winter and early spring in mid-water offshore, 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 or early July. Thus the hatching coincides with the arrival at the surface, and inshore around the islands, of the shoals of juvenile Ammodytidae. The appearance of the shoals of juvenile Ammodytidae round the islands was noted both directly, by observation from the cliffs, and by inference from the number of sand-eels being carried back to the breeding colonies in relation to the time spent feeding. On many occasions throughout the summer, but particularly on calm days, it was possible to observe mixed flocks of birds fishing in dense aggregations over shoals of sand-eels at the surface. Subsequent checks made on fish brought in to the island by terns returning from these fishing flocks showed them to be Ammodytidae (*A. tobianus* or *A. marinus*). The larger *A. lanceolatus* were only rarely positively identified in the diet of the tern and gull species, but were frequently recorded in that of the auks. This suggests that this species did not shoal inshore at the surface within fishing range of the surface-feeding birds. 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 (1959, unpublished thesis) studied the movements of *Ammodytes* species off the Isle of Man, and found that both *A. tobianus* and *A. lanceolatus* migrate 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, but 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 10 mm long they move to mid-water levels. There they remain until between 12 and 16 mm long, when they move to the surface. On attaining a length of 26–88 mm the young herring then come 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 increased 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, the Ammodytidae present during the early summer being supplemented by an influx of clupeoids in July. This is reflected in monthly

variation in the diets; Table 5 records the variation in the diet of the kittiwake and Arctic tern in June and July, showing that in the latter month the proportion of clupeoids taken increases at the expense of the Ammodytidae taken.

Table 5. *Monthly variation in the diet of two surface-feeding sea-birds*

		June		July	
		No.	%	No.	%
Arctic tern	Ammodytidae	236	74	1250	63
	Clupeidae	33	10	477	24
	Gadidae			51	3
	Other fish	22	7	70	6
	Crustacea			55	3
	Other items	28	9	31	1
Kittiwake	Ammodytidae	155	91	474	78
	Clupeidae	4	2	77	13
	Gadidae	12	7	45	7
	Other fish				
	Crustacea			8	1
	Other items			4	<1

THE FEEDING RANGE

During preliminary observations it became obvious that there were considerable differences in the areas from which each species would usually obtain its food.

In order to obtain some measure of the potential feeding range of each species when they are feeding young, records were made of the period of time spent by individuals away on fishing trips. If a series of fishing trips are timed, then it is possible to calculate the maximum distance the birds could have flown knowing the average flight speed. This value, divided by two, gives the maximum distance the birds could have flown to obtain their food, and so indicates the area which is potentially available for each species. For this purpose only those trips were timed from which the bird subsequently returned to feed the chick. Fishing trips by birds of those species which carry food for their young in the beak could easily be recorded, but the duration was more difficult to calculate in the kittiwake and shag since the young are fed by regurgitation. In these last two species only the periods of absence have been used when the returning bird subsequently fed at least one of the chicks.

The flight speed of the various species on which the present calculations are based are taken from the data summarized by Meinertzhagen (1955). Table 6 gives the data presented for the species under study. During the present work no comprehensive attempt to record flight speed was made, but there seems no reason to suspect that this would differ substantially from the speeds recorded above. Thus an average ground speed of 30 miles/h for the gulls, terns, fulmar and cormorants, and of 50 miles/h for the auks, has been assumed. Using this speed and the mean time of feeding trips, a distance can be calculated for each species which represents the potential feeding range for that species under the conditions existing on the Farne Islands (Table 7 and Fig. 3). It is immediately obvious from these values that all of the tern species have a very limited feeding area. This is partly because these species take small fish and do not normally carry more than one fish at a time. The shag has a feeding range comparable to that of the terns but is capable of carrying a much greater amount of fish than the latter group. The kittiwake and puffin have a feeding range three to four times greater than that of the terns and it is clear that

Table 6. *Flight speeds of various species from Meinertzhagen (1955)*

Reference	Species	Ground speed (miles/h)	Method of measurement and remarks
Roberts	Common tern	15, 29	Speedometer
Harrisson	Common tern	25, 27	Speedometer, 'easy, effortless flight'
Meinertzhagen (1955)*	'Gulls' (herring and lesser black-backed gull)	31-34	Stop-watch, 'migrating, flapping'
Meinertzhagen; Roberts	Herring gull	18, 20	Speedometer
Joy	Herring gull	21-36	Seven counts, flapping flight
Harrisson	Herring gull	17-20	Speedometer, three counts, easy flight, flapping
Harrisson	Lesser black-backed gull	31	Instrument, migrating, flapping
Roberts	Herring gull	21, 36, 30, 27	Speedometer
Meinertzhagen	Fulmar	26-39	Stop-watch, fifteen counts. Birds on straight course over short distance
Meinertzhagen	Puffin	25-29	Stop-watch, five counts. Normal flight when disturbed
Meinertzhagen	Puffin	48-51	Stop-watch, seven counts, of birds bringing food to young
Meinertzhagen	Razorbill	49-54	Stop-watch, eight counts. Migrating
Portal	Guillemot	50-55	Estimated from speed of ship
Roberts	Cormorant	27, 35	Speedometer
Powell	Cormorant	45	Speedometer. Tailwind
Cooke	Cormorant	20	Speedometer. Headwind

* All other references are cited in Meinertzhagen (1955).

Table 7. *Frequency distribution of times spent away on feeding flights of various species*

Length of time away on feeding flight (min)	Frequency of feeding flights in each time-group											
	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 (min)	50.2		54.5		61.8		158		207		46	
Maximum distance which could be flown from nest (miles)	12.5		13.6		15.4		34.5		85.7		11.5	

these species are potentially able to feed over an area about ten times greater than that utilized by terns breeding in the same locality.

It should be emphasized that the values for the potential feeding ranges do not indicate the maximum range for the species. It is reasonable to assume that individuals can exceed this distance, but, on the other hand, it is unlikely that the flight to and from the fishing

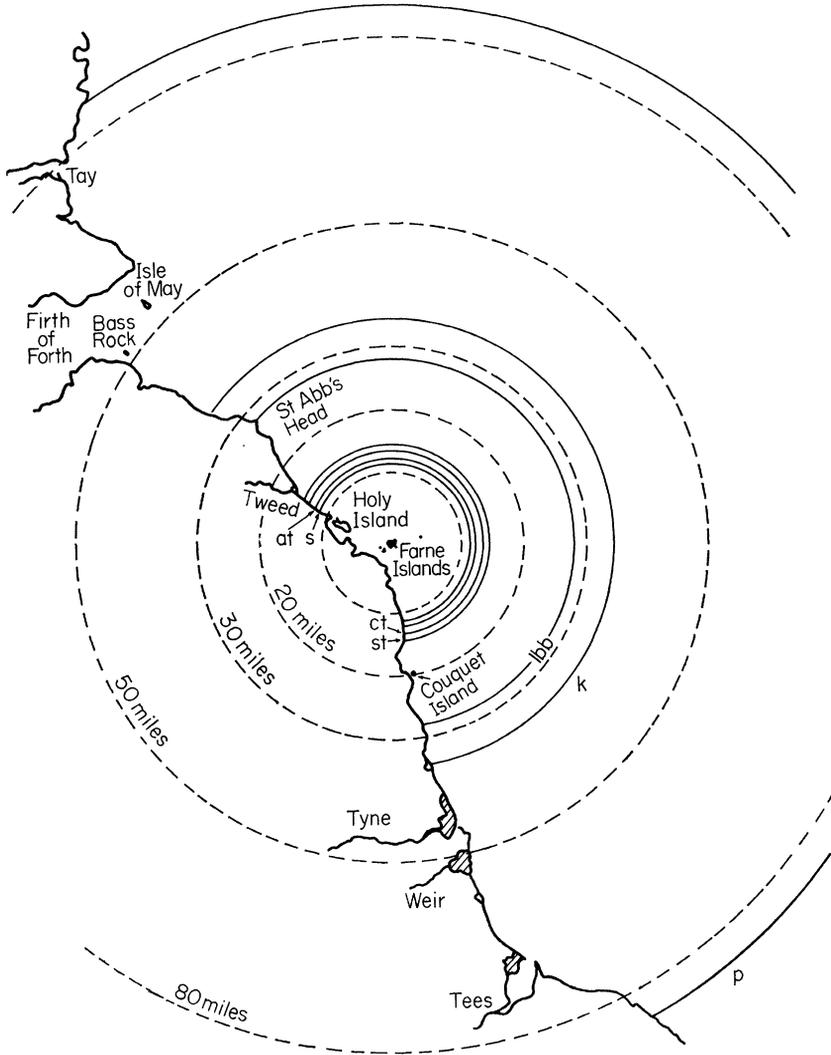


FIG. 3. The average potential feeding ranges of sea-bird species breeding on the Farne Islands: at, Arctic tern; st, sandwich tern; ct, common tern; lbb, lesser black-backed gull; k, kittiwake; p, puffin; s, shag.

area is strictly linear, and time must be allowed for fishing (particularly in the diving species), so that only a few individuals will exceed this distance.

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 (*Somateria mollissima* (L.)) are seen fishing within sight of the islands. This is presumably connected with a lack of small fish in the inshore waters at these times, although no specific data were obtained to confirm this. The inshore migrations of young Ammodytidae and clupeoids may have differential effects on the various sea-bird species. Since the feeding ranges of the various species differ considerably, those species with the shorter range, i.e. the terns, 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, when the kittiwakes and auks are 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. Thus in times of scarcity, it might be expected that the terns would be less successful in rearing young than the kittiwakes and auks.

FEEDING FREQUENCIES

Observations on the feeding of individual chicks

In both 1961 and 1962 observations were made, from a hide, on groups of nests of the following species, Arctic tern, common tern, sandwich tern, kittiwake and shag. The feeding of individual chicks could thus be followed closely, and the number of feeds over specific periods of time noted. On a number of occasions watches were undertaken throughout the daylight hours, but at other times it was possible to watch only for shorter periods. The number of times each chick under observation was fed during each hour of the day was recorded.

The Arctic terns under observation were in broods of one or two, the common terns in broods of one, two or three, the sandwich terns in broods of one only, the kittiwake in broods of one or two and the shags in broods of three only. The number of feeds taken per day by the broods of differing sizes is recorded in Table 8. The mean number of feeds per day is recorded as the total of the number of feeds/h throughout the daylight hours.

All the sandwich tern chicks observed were single, thus no direct evidence of the influence of brood size on the feeding frequency of this species was obtained. The kittiwake and shag feed their chicks by regurgitation, and each chick in the brood was generally fed in turn by the parent bird on return to the nest. Thus one feeding journey usually suffices for the whole brood, and if more than one chick was fed on the return of the parent bird this was recorded as a single feed for the purposes of estimating the feeding frequency.

As would be expected the mean number of feeds per day increased with increasing brood size but in all the species the number of feeds per chick decreased with increasing brood size. Thus with broods of more than one, either each individual chick was given less food, or the total weight of each feed given increased. Assuming the former, it might be expected that the growth rates of chicks in multiple broods would be lower. Since this was not the case (see below) then it might be postulated that the total weight of each feed given to the larger broods increased.

Table 8. Feeding frequencies (number of feeds taken per hour and per day in relation to brood size)

Species	Brood size	1	Hours																								Mean no. of feeds per brood/day
			04.00-05.00	05.00-06.00	06.00-07.00	07.00-08.00	08.00-09.00	09.00-10.00	10.00-11.00	11.00-12.00	12.00-13.00	13.00-14.00	14.00-15.00	15.00-16.00	16.00-17.00	17.00-18.00	18.00-19.00	19.00-20.00	20.00-21.00	21.00-22.00	22.00-23.00	23.00-24.00	24.00-25.00				
Arctic tern	No. of broods observed	24	36	36	31	31	22	22	18	18	18	29	29	19	19	11	33	33	11	11	11	0	0	0	0		
	Total no. of feeds to all chicks	14	59	39	50	30	49	25	14	22	21	42	24	33	45	16	75	34	17	0	0	0	0	0	0		
	Mean no. of feeds per brood	0.6	1.6	1.1	1.6	1.0	2.2	1.1	0.8	1.2	1.2	1.4	0.8	1.7	2.3	1.4	2.5	1.0	1.5	0	0	0	0	0	0	0	
2	No. of broods observed	6	10	10	9	4	3	3	3	3	3	7	7	4	4	3	3	6	6	6	6	6	6	6	6	46	
	Total no. of feeds to all chicks	5	33	62	24	27	12	10	11	12	5	10	12	5	8	9	4	5	19	0	0	0	0	0	0	0	
	Mean no. of feeds per brood	0.8	3.3	6.2	2.7	3.0	3.0	3.0	3.7	4.0	1.7	1.4	1.7	1.2	2.0	3.0	1.3	0.8	3.1	0	0	0	0	0	0	0	
Common tern	No. of broods observed	2	3	3	3	3	3	3	2	2	2	5	5	5	5	3	3	7	7	7	7	7	7	7	7	15	
	Total no. of feeds to all chicks	0	5	3	3	7	0	2	2	1	1	6	6	6	6	1	2	2	9	2	0	0	0	0	0	0	
	Mean no. of feeds per brood	0	1.0	1.7	1.0	2.3	0	1.0	0.5	0.2	1.2	1.2	1.2	0.2	0.7	0.7	1.3	3.0	0	0	0	0	0	0	0	0	
2	No. of broods observed	5	7	7	7	7	7	7	6	6	6	12	12	9	9	6	6	12	12	9	9	6	6	6	6	23	
	Total no. of feeds to all chicks	2	7	12	22	6	13	7	5	6	10	12	14	11	18	8	14	5	7	0	0	0	0	0	0	0	
	Mean no. of feeds per brood	0.4	1.0	1.7	3.1	0.9	1.9	1.0	0.8	1.0	1.3	1.0	1.2	1.2	2.0	1.3	2.3	0.4	0.6	0	0	0	0	0	0	0	
3	No. of broods observed	2	2	2	2	2	2	2	2	2	2	5	5	2	2	2	2	2	5	5	5	5	5	5	5	38	
	Total no. of feeds to all chicks	0	0	15	2	5	4	3	5	7	1	4	7	5	5	8	5	9	6	0	0	0	0	0	0	0	
	Mean no. of feeds per brood	0	0	7.5	1.0	2.5	2.0	1.5	2.5	3.5	0.5	0.8	1.4	2.5	2.5	4.0	2.5	1.8	1.2	0	0	0	0	0	0	0	
Sandwich tern	No. of broods observed	9	9	9	9	9	9	12	12	12	9	9	9	9	11	11	11	11	11	11	11	11	11	11	11	14	
	Total no. of feeds to all chicks	0	6	10	6	4	2	3	2	3	2	5	6	11	21	19	23	11	9	0	0	0	0	0	0	0	
	Mean no. of feeds per brood	0	0.7	1.1	0.7	0.3	0.2	0.2	0.2	0.2	0.2	0.5	0.7	1.2	1.9	1.7	2.1	1.0	0.8	0	0	0	0	0	0	0	
Kittiwake	No. of broods observed	10	10	10	4	4	4	4	10	17	22	22	24	16	16	16	11	11	11	11	11	11	11	11	11	5	
	Total no. of feeds to all chicks	5	2	1	1	0	0	1	3	2	5	6	6	6	3	3	3	3	3	3	3	3	3	3	3	8	
	Mean no. of feeds per brood	0.5	0.2	0.1	0.2	0	0	0.2	0.3	0.1	0.2	0.3	0.2	0.4	0.2	0.2	0.3	0.3	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	
2	No. of broods observed	11	11	11	5	5	5	5	11	15	18	18	22	14	14	14	11	11	11	11	11	11	11	11	11	8	
	Total no. of feeds to all chicks	5	5	2	0	3	1	2	1	6	13	6	12	4	10	1	3	12	10	5	5	5	5	5	5		
	Mean no. of feeds per brood	0.4	0.4	0.2	0.0	0.6	0.2	0.4	0.1	0.4	0.7	0.3	0.5	0.3	0.7	0.1	0.3	1.1	0.9	0.4	0.4	0.4	0.4	0.4	0.4		
Shag	No. of broods observed	5	5	5	3	3	3	3	5	9	11	11	11	9	9	9	9	9	9	9	9	9	9	9	9	3	
	Total no. of feeds to all chicks	0	0	0	0	1	2	1	0	2	1	2	0	2	2	2	2	5	3	0	0	0	0	0	0		
	Mean no. of feeds per brood	0	0	0	0	0.3	0.7	0.3	0	0.2	0.1	0.2	0	0.2	0.2	0.2	0.5	0.4	0.3	0	0	0	0	0	0		

Estimation of feeding frequency from variations in the weight of chicks over consecutive limited periods

Further information concerning the feeding frequencies of several species was obtained by weighing selected individual chicks at intervals throughout the day. Increases in weight between one record and the next indicated that the chick had been fed during the interval. Table 9 summarizes the information obtained. This method suffers from the disadvantage of causing considerable disturbance to the birds during the periodic weighing, and it is possible that the number of feeds so recorded is lower than it would be should there have been no disturbance. This supposition is supported by the evidence

Table 9. *Number of feeds per day taken by chicks, deduced from repeated weighings*

Species	Length of interval between weighings (min)	No. of chicks weighed	Variation in age (days)	Mean number of feeds taken over 24 h
Sandwich tern	90	3	24-28	12.7 ± 1.5
Kittiwake	120	4	10-30	3.2 ± 1.0
Lesser black-backed gull	120	9	12-31	1.9 ± 0.8
Herring gull	120	2	25 and 26	2-3
Fulmar	120	4	6-14	1.7 ± 1.0
Puffin	120	6	21-39	2.8 ± 0.7
Shag	120	2	29 and 40	1-2

from those species where feeding frequency was estimated, both by direct observation and by weighing, i.e. the kittiwake and the sandwich tern. In both, the feeding frequency estimated by weighing was lower than that estimated from observations. In view of this the upper limits of the feeding frequencies obtained by this method have been used when comparing the numbers of feeding journeys made by those species on which no direct observations of feeding frequencies were made.

Time spent on fishing activities

The information on the number of feeding trips made each day and the duration of each journey has enabled estimates to be made of the amount of time spent by adult birds on fishing activities. For this purpose it has been assumed that the time spent away from the nest on feeding trips was exclusively devoted to fishing. It was impossible to check if in fact this was so. Some of the birds could have used a part of the time away in other activities, i.e. preening or resting. Such activities were however observed during those parts of the day when feeding activity was low, e.g. the mid-morning and mid-afternoon low periods of the normal diurnal rhythm of activity, and it seems reasonable to assume that a bird observed leaving the nest and later returning with food has not interrupted the primary behavioural pattern of hunting by secondary activities. It must be emphasized, however, that the following estimates will necessarily be maximum approximations of the time spent by the adult birds on fishing activities.

It has been shown that the number of feeding trips per pair is directly related to the number of young in the brood. The time and numbers of hours spent away on fishing trips for broods of maximum and minimum size has been calculated (Table 10). The feeding frequency of the guillemot is taken from information given by Tuck (1960). No reliable observations were made of the proportionate roles played by each parent in the feeding of the chicks, because of the difficulty of distinguishing the sexes in all the species studied.

Table 10. *Estimation of the number of fishing journeys made by each bird, and the percentage of the daylight hours spent in fishing activities*

	Arctic tern	Common tern	Sandwich tern	Kittiwake	Lesser black-backed gull	Puffin	Guillemot	Shag
Brood size	1-2	1-3	1-2	1-2	1-3	1	1	1-3
Mean no. of feeds/day (single chick)	25	15	14	5	2	3	2*	3
Mean no. of feeds/day (maximum brood size)	46	38	14	8	6	3	2	3
Estimated no. of trips made by each parent	12-23	8-19	7	3-4	1-3	2	1	1-2
Mean time away on each fishing trip (h)	0.83	0.92	1.03	2.63	2.0	3.45	3.0	0.77
Time spent away on fishing trips/day (h)	10.0-19.1	7.4-17.5	7.2-14.4	7.89-10.5	2.0-6.0	6.9	3.0	0.77-1.5
% of the daylight hours spent in fishing activities	54-103	40-94	39-76	43-57	11-32	37	16	4-8

* From Tuck (1960).

There is little in the published records to elucidate this point. Belopolskii maintains that among the tern and gull species breeding in the Arctic the female plays a dominant role in the feeding of the chicks, but produces no direct evidence of this. Fisher & Lockley (1954) are of the opinion that such species breeding in the British Isles share the duties of chick feeding equally. In the present study direct observations on kittiwakes and shags indicate that the parents of these species share equally in the feeding duties. Thus one parent is usually present at the nest site but leaves a short time after the return of its partner. The new arrival will then usually feed the chicks and remains at the site until the return of the second bird, which, in its turn, will subsequently feed the chicks.

Observations on the tern species were less conclusive, as both partners were often away from the nest site together. There seems no reason to doubt that both parents help in feeding the chicks however. Among the auk species both parents are thought to share equally in the feeding duties (Tuck 1960; Lockley 1934; Myrberget 1962; Belopolskii 1957). Therefore, in the absence of any evidence to the contrary, 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. Thus in the case of those species which make one fishing trip to feed each chick, i.e. the tern species, the number of fishing journeys made by a single parent is the product of the brood size and half the feeding frequency. The kittiwakes, lesser black-backed gulls and shags feed their young by regurgitation, and generally feed the whole of the brood after a feeding journey. Thus for these species the number of feeding trips made by each parent is estimated as being equivalent to half the chick-feeding frequency. Table 10 shows the average number of trips made by each parent according to brood size, and the consequent maximum and minimum percentage of the day spent in fishing activities. For the purpose of estimating the percentage of the day spent in fishing, the daylight hours when the birds could be fishing have been taken as from 03.30 to 22.00 hours, i.e. a total of 18.5 h, approximating to the average day length between mid-May and mid-July, the period when the majority of the chicks of all species are being reared.

These figures suggest that the care of a single chick for all species involved less than 10 h fishing per day and in several of the species was less than 6 h per day. When consideration is given to the maximum brood size typical of the species, much longer periods of time are involved reaching 19 and 17.5 h per day for the Arctic and common tern respectively, but only 1.5 h for a brood of three shags, as this species normally satisfies the whole brood from one feeding trip, except when the chicks are nearly full grown. This short period of time which shags need to fish to supply three young appears to be unexpectedly small, but it has been confirmed that this is a reasonable estimate by making observations on the amount of time that the parents spend at, or in the vicinity of, the nest site, e.g. during a 24-h watch in July 1961 on two shag nests each of which contained three chicks, nest A was attended by both parents for all but 7 h 10 min of the 24 and nest B for all but 3 h 33 min, and one parent was always present at the nest.

In general the amount of time required fishing to rear a single chick decreases with increase in size of the species. A log-log transformation of the plot of the mean weight of the adult birds of each species against time spent in fishing, using for comparability the values of fishing time for minimum brood size, is shown in Fig. 4, where a significant linear relationship exists ($r = 0.9236$, $P < 0.01$). The rapid increase in the amount of time required by small sea-birds to obtain food for their young suggests that species of about the size of the Arctic and common terns are almost the minimum size where it is possible, or at least economical, to feed on small marine fish. The little tern (*Sterna albifrons*

Pallas) is smaller than any of the terns studied and an investigation into its feeding biology, particularly when feeding young, would be rewarding. Neither the storm nor Leach's petrels (*Hydrobates pelagicus* (L.) and *Oceanodroma leucorhoa* Vieillot) breed in the North Sea area. These sea-birds are smaller than the terns but it is evident that their food and feeding biology are very different from those of the species studied and they are not strictly comparable. In the above study, no allowance has been made for the time adults hunt for food to satisfy their own needs as this usually takes place during the fishing trips which are made to obtain food for their young, and is therefore included in the estimates given above.

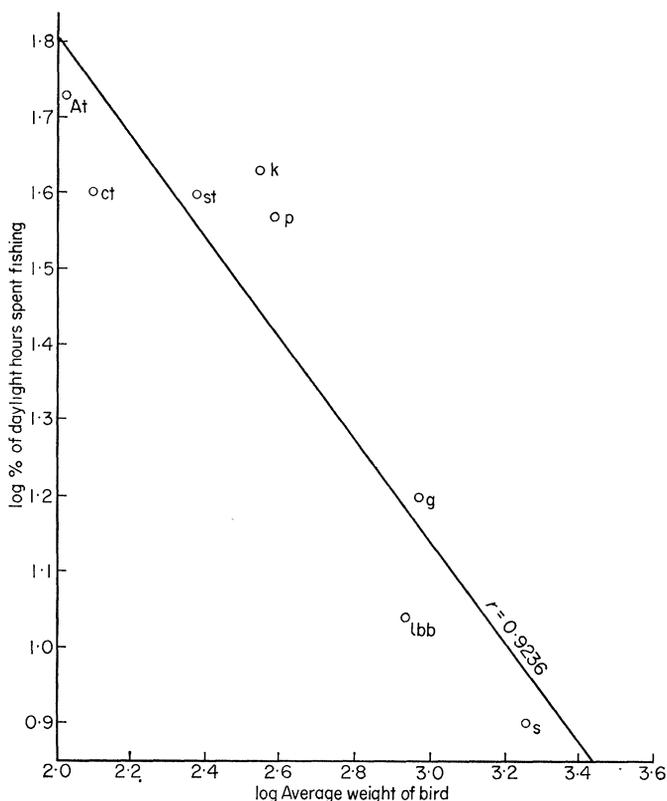


FIG. 4. The relationship between the average weight of the bird and the percentage of the day spent in fishing activities. Plot of transformation to log-values to show linear correlation. At, Arctic tern; st, sandwich tern; ct, common tern; lbb, lesser black-backed gull; g, guillemot; k, kittiwake; p, puffin; s, shag.

These results imply that the large sea-birds spend a small proportion of their time obtaining food for their young under the conditions existing when this study was made. Should the available food be less, the large sea-birds have a considerable time period which could be exploited to search for food whereas the terns are breeding near the physical limit of their capacity to hunt and find food and a decrease in the availability of fish must inevitably result in starvation amongst the larger broods, and also a reduction in the number of young which are reared. It is interesting to note that of the species studied only among the terns did both parents participate in food gathering simultaneously,

and these are the only species which tend to approach the upper limit of feeding time available. Among the gulls, auks and shag it was usual for one parent to be at the nest site at all times during the pre-fledging period. This evidence substantiates the suggestion of Nelson (1964), in discussing the gannet (*Sula bassana* (L.)), that a characteristic of species whose food-gathering abilities are not hard-pressed is that only one parent forages at any one time, the other remaining at the nest site.

GROWTH-RATES OF YOUNG

The ability of adult sea-birds to rear broods of different sizes also gives some indication of the ease with which adults can obtain food. The growth-rates of chicks are sensitive indicators of the ability of adults to supply sufficient food and studies were made of the growth rates of young from broods of different sizes. The average growth curve for most species of sea-birds (at least the species studied in this investigation) has a considerable period over which the daily growth increase is almost constant. This period can be used to obtain an average daily growth rate, and this average value used to compare the growth rates of broods of different sizes.

Methods

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. With those species which nest on the tops of islands, i.e. the terns and the gulls, it proved difficult to locate individual chicks of over approximately 3 days age for weighing. When older than this they tended to wander about the colony and, when alarmed, to hide in the undergrowth. In order to overcome this problem selected nests of each of the species studied were surrounded by low wire-mesh barriers during the incubation period. These barriers were approximately 1 ft high \times 4 ft in diameter for the tern species, and $1\frac{1}{2}$ ft high \times 6 ft in diameter for the gulls. They apparently did not unduly disturb the adult birds, for in no case where a nest was thus surrounded were the eggs deserted. Such enclosures confined the chick 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 21 and 23 days, and were fed in the normal manner by the parents throughout their period within the enclosures. This was seen in watches from a hide 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 type 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 were successful in that they did not disturb the incubating birds unduly, and the majority of the enclosed clutches hatched successfully. However difficulties arose during the development of the chicks because of 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 'crèches' on or near the shore line of the islands. Enclosure of the chicks prevented this movement 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 enclosures to the detriment of the 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 to confirm this because of the difficulty of repeatedly capturing specific chicks outside the enclosures. It is possible, however, that the parents of those chicks within the pens would spend a considerable time attending the 'crèches' and that their own chicks would thus be neglected. For these reasons the data obtained on growth of the sandwich tern chicks must be treated with caution for it is probably unrepresentative of growth under natural conditions.

The barriers used to enclose the lesser black-backed gull chicks proved useful up to about the thirtieth day after the hatching of the chicks. By that time the chicks were large enough to climb over the barrier although they were not then fledged. The records obtained for this species thus refer only to the first 30 days after hatching.

Table 11. *Number of chicks of each species which were weighed regularly in each year of the investigation into growth rates of the various species*

Species	No. of chicks weighed	
	1961	1962
Arctic tern	5	16
Common tern	0	9
Sandwich tern	0	16
Kittiwake	26	18
Lesser black-backed gull	0	10
Puffin	0	12
Guillemot	0	10
Shag	7	18

The records taken were predominantly measurements of weight made at frequent intervals throughout the period when the chicks were present at the breeding site. In most cases it was found to be impracticable to weigh the individual chicks daily, and in general records were taken every 3 days. Occasionally records were made at much longer intervals. From this information estimates could be made of the daily weight increase of the chicks. Weights were taken with spring balances, accurate to within 1 g, or, in the case of the larger birds, with a pan balance which was also accurate to within 1 g. 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, cf. Richdale (1943), Young (1963) and Dorward (1963). Such inconsistencies can be minimized 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 for each of the species under study. Since the chicks being examined were of different ages there was no regularity in the relationship between the age of the chicks and the periods when records were taken. In order to assess the weights of chicks at specific and regular intervals the data obtained from each individual were plotted separately to give a curve of weight against age. The weights of the chicks at intervals of

Table 12. Average daily weight increases throughout the period of growth of various sea-birds breeding on the Farne Islands

Age period (days)	Average increase in weight/day over each 2-day period (g)							
	Arctic tern	Common tern	Sandwich tern	Kittiwake	Lesser black-backed gull	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	8.2	20.2	21.3
4-6	6.7	7.6	7.8	15.6	17.0	7.8	11.7	29.0
6-8	5.8	7.9	9.8	14.9	21.6	9.7	11.1	34.0
8-10	5.9	8.4	10.8	15.7	22.2	9.8	9.2	36.2
10-12	8.2	7.2	9.1	15.8	36.6	13.0	5.4	56.4
12-14	5.0	6.6	6.8	16.8	28.4	12.3	6.4	56.5
14-16	3.5	3.6	5.6	15.8	26.9	12.7	6.4	57.3
16-18	1.1	2.3	3.4	14.3	27.8	13.3	13.7	55.5
18-20	-0.4	-0.7	1.7	11.1	24.9	9.6		52.7
20-22	-0.6	-2.3	-0.1	9.6	34.1	5.7		56.8
22-24			-0.3	6.3	27.0	8.0		53.7
24-26			-0.5	2.5	12.4	5.4		45.7
26-28				0.2	20.2	4.8		44.1
28-30				1.3	24.5	2.7		35.4
30-32				-2.6		-3.0		41.3
32-34				-4.6		-0.2		27.1
34-36				-3.6		2.8		35.4
36-38						1.8		28.8
38-40								17.7
40-42								5.3
42-44								3.7
44-46								-8.8
46-48								14.0
Period of most rapid growth (days)	4-12	2-10	0-10	2-10		0-20		10-24
Average daily weight increase over period of most rapid growth (g)	6.6	7.8	9.8	15.5		10.6		55.5
Average daily weight increase over the whole period of positive weight increase (g)	5.2	6.4	7.6	11.1	23.6	8.9	10.8	36.7
Fledging period (days)	24	22	27	36	0-30*	38	0-18*	48
Mean	18-26	21-26	22-23	27-42		34-51		39-59
Range								

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

2 days were read off from these curves, and these values were then used to deduce the mean growth curve of the species, throughout the pre-fledging period. This method minimizes 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 comparative deviation in the growth rates of groups of chicks under different conditions can be assessed.

Size of sample

Table 11 lists the number of chicks of each species which were weighed regularly in each year of the investigation. In 1961 many more kittiwake chicks were weighed during the initial stages of growth; up to about the tenth day over fifty chicks were weighed, but only twenty-six of these were weighed regularly until fledging. The shags weighed in 1962 consisted of six chicks from the Inner Farne, which were weighed regularly every 3–4 days, and twelve chicks from a large colony on Staple Island which were weighed at intervals of 8–10 days.

Comparison of the growth of groups of chicks under different conditions

It was impossible to compare the weight gains of individual chicks directly over any particular stage of growth because of the variation in the ages of chicks weighed at any

Table 13. Comparison of the average daily weight increases (DWI) of individual chicks over a standard period of growth (all data in g)

A. TERN SPECIES

Stage of growth curve compared	Arctic tern		Common tern		Sandwich tern		
	20–90 g		30–110 g		50–170 g		Average DWI for each group
	Average DWI	Average DWI	Average DWI	Average DWI	Average DWI		
	1961	1962	1962	for each group	1962	1962	
Broods of one chick	7.65	5.90	7.02		5.43	13.19	9.99
	5.51	6.60			9.16	14.37	
	5.71	7.25			9.80	12.06	
	5.88	7.91			9.06	11.37	
	6.33	6.31			9.56	11.37	
		7.53			9.60	5.45	
		7.65			8.70		
					10.08		
					12.56		
					8.11		
Broods of two chicks	6.86	6.61	6.75	7.77			
First-hatched	6.63		8.25				
	6.17		9.04				
	6.86		6.96				
	6.54		7.84				
Second-hatched	6.45	6.29	6.67	7.45			
	6.25		8.38				
	6.03		7.24				
	6.45		7.51				
Average daily weight increase for each column	6.22	6.71	7.63		9.21	11.30	

Table 13—*continued*

B. GULL SPECIES

Stage of growth curve compared	Lesser black-backed gull 100–650 g		Kittiwake (all chicks) 100–300 g		Kittiwake (early and late chicks) 100–300 g				
	Average DWI 1962	Average DWI for each group	Average DWI		Average DWI for each group	Average DWI			
			1961	1962		1961		1962	
						Before 21 June	After 1 July	9–12 June	15–18 June
Broods of one chick	32.45 27.95 30.05 26.57 19.71 23.71	26.73	16.19 12.70 18.18 17.32 19.80 18.78 16.39 17.09 18.02	16.74 18.35 19.42 19.80 14.49 15.75 14.08 13.70 15.33	17.16 (1961) 16.41 (1962)	16.19 17.24 17.39 17.32 19.80 18.52 14.98	12.70 22.73 15.50 14.49 11.59 20.62 14.60 17.09 18.02	13.65 16.74 18.35 18.69 19.80 15.09 14.49 15.33 14.08	13.70 20.30 15.75 14.70 15.56 17.09 16.81
Broods of one chick First-hatched	36.67 28.35	32.51	17.24 14.98 14.81 12.82 19.05 22.73 14.49 14.60	16.74 18.35 19.42 19.80 14.49 15.75 14.08 13.70 15.33	16.34 (1961) 16.41 (1962)				
Second-hatched	28.28 31.70	29.99	17.39 15.27 18.52 14.08 13.07 15.50 11.59 20.62 14.71	13.65 17.62 20.03 15.09 16.95 14.71 17.09 16.81 14.08	15.64 (1961) 16.22 (1962)				
Average DWI for each column	28.54		16.38	16.28		17.35	16.37	16.25	16.27

one time. 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 time was adjusted to cover the part of the growth over which weight gains were greatest and most regular. This stage was considered to be the most useful indicator of the general growth. Table 12 shows the mean increases in weight per day for the species studied, from which the stages of most rapid growth of the chick are assessed. The data, presented in terms of the average daily weight increases over the stated period, are given in Table 13 A–C. Significance tests were made on the variation between the average daily weight increases of the various groups of chicks within each species. In no case was there found to be a significant difference in the growth rates of the chicks reared in 1961 and those reared in 1962, and so the data for the two years have been combined in comparing the growth of different broods, and of early and late chicks. Groups of sandwich terns, puffin and kittiwake chicks were compared to assess any differences in the growth rates of chicks hatched early in the season

Table 13—*continued*

C. PUFFIN AND SHAG	Shag		Puffin		
	400-1400 g		100-250 g		
	Average DWI	Average DWI	Average DWI		
	1961	1962	for each group	1962	
Stage of growth curve compared			Before 9 June	After 10 June	
Broods of one chick	42.55	63.69	55.86	13.64	11.07
		61.35		10.20	15.96
				10.99	11.36
				12.82	10.34
				11.49	14.71
				12.60	
			14.02		
Broods of two chicks					
First-hatched		60.42	53.63		
		38.17			
		60.06			
		55.87			
Second-hatched		66.67	56.17		
		52.08			
		49.75			
Broods of three chicks					
First-hatched	51.15	43.48	47.48		
	47.73	50.00			
		45.09			
Second-hatched	50.89	58.48	50.87		
	47.17	50.76			
		47.06			
Third-hatched	41.67	39.37	42.24		
	46.94	44.74			
		38.46			
Average DWI for each column	46.87	51.17		12.25	12.69

and chicks hatched late 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 on the Farne Islands to allow for the successful rearing of all chicks irrespective of hatching date. Similarly there is no significant difference between the mean growth rates of the young from different brood sizes in the Arctic tern, kittiwake, lesser black-backed gull and shag, although in three of the four species the larger broods have a slightly lower mean growth rate. This is particularly so with broods of three young shags yet it has already been shown that the parents of such broods spend less than 10% of the daylight hours in fishing for food. It would therefore appear that, if this difference is real, it is difficult to explain it on the basis of food shortage. In the remaining species it is clear that the differences which exist between the growth rates of broods and one and two chicks are small and are unlikely to influence, appreciably, the survival of the young.

The results obtained for the kittiwake are similar to those found by Coulson & 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 were collected.

Comparison of the growth rates of sea-birds on the Farne Islands and in Arctic Russia

Belopolskii (1957) gives details of the growth, measured as the increase in weight with age, of the chicks of the Arctic tern, kittiwake, puffin, guillemot and shag in the East Murman area of the Barents Sea. Table 14 compares the growth rates of chicks of these species on the Farne Islands with the growth rates on the Murman coast. Figures are given only for that part of the growth period when positive weight increases occur. The daily weight increases are given as percentages of the mean adult weight (see Table 3)

Table 14. *Comparison of growth rates of sea-bird species on the Farne Islands (A) and on the East Murman coast, northern Russia (B)**

Age (days)	Weight as a percentage of adult weight									
	Arctic tern		Kittiwake		Puffin		Guillemot		Shag	
	A	B	A	B	A	B	A	B	A	B
0	17	12	12	9	10	8	6	9	2	1
2	23	12	17	13	15	11	9	11	3	2
4	36	17	25	19	20	15	14	13	6	2
6	48	25	34	26	24	18	16	15	9	3
8	59	41	43	32	30	25	18	17	13	5
10	72	57	52	38	34	31	20	19	17	9
12	87	73	61	44	41	34	22	21	22	11
14	98	86	71	49	47	39	23	22	28	21
16	103	93	80	55	54	43	24	24	35	28
18	105	96	88	64	61	51	27	25	41	32
20			94	69	66	59		26	48	35
22			100	75	69	66			53	41
24			103	82	73	72			59	48
26			104	83	76	78			65	54
28			105	87	79				69	61
30				93	80				73	67
32				96					78	74
34									81	80
36									85	85
38									88	93
40									90	100
42									91	104
44										105
46										105
48										106
50										107
Adult weights (g)	104	107	350	408	380	490	925	1054	1785	-†

* Russian data from Belopolskii (1957).

† Adult weight of shag not given.

in order to ensure comparability, as the mean weight of the same species in northern areas is often considerably greater than that of the birds on the Farne Islands. Moreover very few of the original figures are quoted by Belopolskii, the data being given only as percentages of the adult weight. The mean adult weight of shags on the East Murman coast, on which these figures are based, is not given. In each species the Farne Island birds had a much faster initial growth rate than the East Murman birds, and, with the exception of the puffin, reached their maximum weight at an earlier age. It is probable that the lower environmental temperature on the Murman coast breeding grounds is one factor contributing to the relatively slow growth of the Russian birds.

DISCUSSION

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 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. A similar view, suggesting that food resources outside the breeding season were not a limiting factor on the population growth of tropical sea-birds, was put forward by Ashmole (1963). However, the contrary opinion is expressed by Lack (1966), who suggests that many bird species, in particular the Procellariiformes amongst the sea-birds, are regulated in numbers by food supply outside the breeding season. It is possible that the winter dispersal of sea-birds breeding in temperate latitudes is an adaptation to alleviate competition for food, which might be severe if many species tended to congregate in the breeding area during the winter months. Between October and March there is evidence that the large shoals of juvenile Ammodytidae disappear offshore into deeper waters (Smitt 1895; McIntosh & Masterman 1897; Meek 1916; Cameron 1959); moreover the calanoid copepods which appear to form their main food supply (Macer 1966) migrate to deeper water from the surface levels they inhabit during the summer months (Marshall & Orr 1955). The juvenile herring (0 and 1 group), on which the birds have also been preying in the summer, approach close inshore during the winter months (Parrish & Saville 1965), but their level of feeding is much reduced from October to March, when they appear to take a greater proportion of bottom living Crustacea (Marshall, Nicholls & Orr 1939). This suggests that they do not inhabit the surface layers during the winter period. In view of such changes in the habits of the fish populations it is probable that the amount of food available to the surface-feeding birds in the area is much reduced during the winter months. There is at present no information on how successful a winter dispersal is in securing food resources for the total populations. However when all the species are concentrated in the one breeding area in the summer, and are all hunting over the same areas of sea, the possibility of competition for food occurring, both inter- and intra-specifically, would seem to be 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.

Comparison of diets of different species

All the species feed almost exclusively on fish, only the lesser black-backed 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. To what extent the different bird species may have been feeding on different *Ammodytes* species within the area is impossible to assess accurately because of the difficulty, mentioned above, found in differentiating the Ammodytidae species. It is probable however that the majority of the fish taken were *A. marinus* since this species appears to be the

predominant one both in the southern North Sea, where it forms over 97% of the total numbers of Ammodytidae taken in nets (Macer 1966), and in the northern areas of the North Sea (Raitt 1934). 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. The deduction of the feeding areas of the various species indicates, however, that such a generalization is by no means true (see below). Moreover, 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 minimize 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. In areas where a particular species is superabundant to the exclusion of other species, e.g. certain parts of the Low Arctic where the capelin (*Mallotus villosus* Muller) 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 their breeding success (cf. Belopol'skii 1957). 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 the most important, will have no disastrous effect, nevertheless, 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 superabundant food, the situation is potentially quite different as soon as the food in question becomes scarce . . . if Gause's 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 superabundant conditions, all exploited food in the same area. This would appear to be the situation on the Farne Islands, where the evidence suggests that 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 they may all be seen feeding in the same areas when shoals of sand-eels are particularly abundant.

Competition between congeneric species

Three congeneric groups are included in the various species of sea-birds investigated during the present work. These were the Arctic tern and common tern, the lesser black-backed gull and the herring gull, and the shag and the cormorant. Of these insufficient information was obtained about the herring gull to allow an adequate comparison to be made with the lesser black-backed gull. The feeding habits of the other two pairs can, however, be compared.

The Arctic and common terns

These two species 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 similar with the exception of the small numbers of Pleuronectidae and insects taken by the Arctic tern, but not by the common tern. Nor could much difference be found in the feeding areas or in the type of nest site utilized by these species. The Arctic tern 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.

Lack (1945) concluded that the differences in the ecology of the shag and cormorant were evidence of past competition between the species, as would be expected from 'Gause's Hypothesis', which he defines as the concept that 'two species with the same ecology cannot live in the same region'. (For a more rigorous examination of the theory embodied in Gause's Hypothesis see Ross (1958), Udvardy (1951), Parker & Turner (1961).) 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 & Birch (1954) who rejected all such indirect evidence for the validity of Gause's Hypothesis, on just these grounds. The fact that the tern species are co-existing on the Farne Islands, whilst occupying similar 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 between them has not yet become ecologically significant. There is however little evidence that the populations of the tern species on the Farne Islands are increasing, thus if competition between the species acting as a controlling mechanism on population growth is not operative, then some other factor of population control must be postulated. 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. That interspecific competition between closely related species can or does occur has been demonstrated with laboratory populations by Park (1954, 1957) and Bakkar (1961) among others. Evidence of its occurrence in the field is, as has been stressed by Orians & Collier (1963) mostly indirect, but such studies as those of Lack (1945, 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 & Collier themselves provide direct evidence of competition between the red-winged blackbird (*Agelaius phoeniceus* (L.)) and the tricolour blackbird (*A. tricolor* Audubon) in California, and Pitelka (1951) showed that interspecific competition occurred between species of humming birds in Woolsey Canyon, California. However the present study has shown no evidence for competition taking place between closely related species, even when their respective niches are similar although the possibility cannot be ruled out that such competition may occur under adverse conditions. It thus seems reasonable to conclude that whilst Gause's 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.

Relationship between feeding rates and brood size

The present work suggests that the majority of the species studied with the exception of the Arctic and common terns are not exploiting their full food-gathering potential when rearing chicks, and that among the various species studied brood size has a decreasing influence on the amount of time spent foraging as the size of the bird increases. It is also shown that there is little difference in the ability to rear one or two chicks among those species which have that potential. This corresponds with recent information obtained on the ability of some sea-bird species to rear artificially enlarged broods successfully. Harris & Plumb (1965) found that lesser black-backed gulls breeding on Skokholm Island, Pembrokeshire, were able to rear broods of five chicks adequately to fledging (normal broods one to three), and Nelson (1964) showed that the gannet on the Bass Rock was capable of rearing successfully two chicks, although only a single chick is raised under normal circumstances. Such results suggest that for these species, as for those in the present study, the brood size is not limited by shortage of food. This does not conform with the theory put forward by Lack (1954), further argued in the case of sea-bird species by Ashmole (1963), that clutch size is adapted to the largest number of young for which parents can provide food. However, it has also been shown by Harris (1966) that the Manx shearwater (*Puffinus puffinus* Brünnich) on Skokholm is incapable of rearing successfully a brood enlarged artificially from one to two, and a similar inability was demonstrated in the Laysan albatross (*Diomedea immutabilis* Rothschild) by Rice & Kenyon (1962). Moreover Lack (1966) quotes evidence that the Leach's petrel is also unable to rear artificially enlarged broods successfully. This implies that for these species the clutch size may well be limited by food supply in that those birds which might attempt to rear two chicks would fail to feed either successfully whereas single chicks can be fed and reared adequately. This would obviously result in selection for single egg clutches. All are pelagic feeders taking planktonic organisms, largely Crustacea and Mollusca, rather than

fish as do the species in the present study, which may go some way towards explaining their inability to rear enlarged broods. Gibb & Betts (1963) and Royama (1966) have shown that the great tit (*Parus major* L.) selects large items of food to be fed to the chicks rather than small items. Royama suggests that this is an adaptation to reduce the amount of work in rearing the brood, since the selection of large items reduces the number of feeding flights necessary. Similarly it can be argued that the petrels, feeding on small planktonic organisms, will have to spend considerably more time and effort per unit weight of food taken than the fish eating species, which take fewer, but larger, prey.

Apart from a small number of fulmars no petrels breed on the Farne Islands, thus no comparison can be made of their food-gathering abilities with those of fish-eating species in this area. A comparison of the feeding biology of these two types of predator in a joint breeding area would be useful in further elucidating the apparently conflicting evidence on their relative abilities to feed and rear young.

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SUMMARY

The results of a study of the feeding biology of nine sea-bird species breeding on the Farne Islands Northumberland, showed that:

1. Fish is the predominant food of all the species studied.
2. There is a considerable overlap between the size and species of fish taken by each of the sea-bird species.
3. The food obtained by each species is not necessarily taken from the same area, each species showing differences in the average distance travelled in search of food and the depth at which food is obtained.
4. The three species of terns which were studied were close to the limits of their physical ability to collect food whereas the larger sea-birds had considerable reserve of time which could be utilized for fishing should fish be less abundant.
5. During 1961 and 1962 there was little evidence to suggest that large broods were reared less successfully than those with only one chick.
6. Chicks on the Farne Islands grew more rapidly than did chicks of the same species in the Arctic, implying that available food was at least as abundant in this area as in the Arctic during the richly productive summer months.

These results suggest that during the study there was a superabundance of food and there was little or no starvation of the young; if food should at any time be less abundant,

then it is possible that the different feeding areas may well limit any interspecific competition.

No evidence was found of competition for any resource occurring between any of the congeneric species breeding on the island, even when there was no apparent ecological division between species.

It is concluded that in the fish-eating species of sea-birds breeding in the study area, brood size is not limited by food supply.

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APPENDIX

List of the identified prey species taken by the various birds (initials in brackets denote the bird species in the diet of which each type of prey was found).

FISH

Ammodytidae

- | | |
|---|--------------------|
| <i>Ammodytes lanceolatus</i> Lesauvage | (st, k, lbb, p, g) |
| { <i>A. tobianus</i> L. (= <i>A. lancea</i> Cuvier) | (All species) |
| { <i>A. marinus</i> Raitt | |

Clupeidae

- | | |
|---------------------------|--------------------|
| <i>Clupea harengus</i> L. | (At, ct, st, k, g) |
| <i>C. sprattus</i> L. | (At, k, p, g) |

Gadidae	
<i>Gadus merlangus</i> L.	(st, k, lbb, s)
<i>G. morrhua</i> Day	(k, lbb, s, c)
Gasterosteidae	
<i>Gasterosteus aculeatus</i> L.	(At, st, ct)
<i>G. spinachia</i> Day	(At, st, p)
Pleuronectidae	
<i>Pleuronectes flesus</i> Day	(At, s, c)
<i>P. platessa</i> L.	(c)
<i>P. limanda</i> Day	(c)
Pholidae	
<i>Pholis gunnellus</i> L.	(st, g, s, c)
Trachinidae	
<i>Trachinus vipera</i> Cuvier and Valenciennes	(c)
Anguillidae	
<i>Anguilla vulgaris</i> Day	(lbb, c)
Cottidae	
<i>Cottus bubalis</i> Euphrasen	(c, s)
<i>C. scorpius</i> L.	(c)
Zoarcidae	
<i>Zoarces viviparus</i> L.	(c, s)
Liparidae	
<i>Liparis liparis</i> L.	(st)
Blennidae	
<i>Blennius pholis</i> L.	(s)
Labridae	
<i>Labrus mixtus</i> L.	(c)
Cyclopteridae	
<i>Cyclopterus lumpus</i> L.	(c)
MOLLUSCA	
Cephalopoda	
<i>Sepiolo atlantica</i> (d'Orbigny)	(At, ct)
<i>Loligo forbesi</i> Steenstrup	(At, st)
CRUSTACEA	
<i>Crangon vulgaris</i> L.	(At, k)
<i>Eurynome aspersa</i> Pennant	(c)
<i>Carcinus maenas</i> Pennant	(c)
<i>C. pagurus</i> L.	(c)
INSECTA	
Diptera	
Cordyluridae	(At)
Tachinidae	(At)
Coleoptera	
Anobiidae	(At)
Carabidae	(lbb)

Key to initials:

At, Arctic tern; ct, common tern; st, sandwich tern; k, kittiwake;
lbb, lesser black-backed gull; p, puffin; g, guillemot; s, shag;
c, cormorant.