Estuarine, Coastal and Shelf Science (1985) **20**, 559–568

Seasonal Changes in the Feeding Ecology of Guillemots (*Uria aalge*) off North and East Scotland

B. F. Blake, T. J. Dixon, P. H. Jones and M. L. Tasker
Nature Conservancy Council, 17 Rubislaw Terrace, Aberdeen, U.K.

Received 3 January 1984 and in revised form 21 June 1984

Keywords: diet, birds, fisheries, North Sea

Stomach contents were examined from 750 guillemots collected at several sites in the northern North Sea. The dietary composition was compared between months and between localities in order to assess seasonal and geographical trends in feeding strategy.

From March to August sandeels dominated the diet, but in September a changeover period occurred when clupeid and gadoid remains became increasingly frequent in the stomach contents. This situation persisted over the winter period, but the importance of the two fish families varied with area, clupeids being more important in more southerly samples and gadoids in the north. Dietary data were considered in relation to available fisheries information and to known guillemot distribution patterns.

Introduction

The spatial distribution of guillemots in the North Sea was described by Blake *et al.* (1984), but there is no published account of the diet of auks through the course of the year in the North Sea. Pearson (1968), Harris & Hislop (1978) and Hislop & Harris (1985) have described the food brought to chicks, and Langslow *et al.* (1985) examined the diet of guillemots around Fair Isle during the breeding season. Winter studies were made by Madsen (1957) in the Kattegat, Hedgren (1976) in the Baltic, and Blake (1983) in the Skagerrak; the only North Sea data are those of Blake (1984) for February 1983.

Methods

Sample collection

Guillemots were either shot at sea under licence ($N = 246$) or collected from beaches after oil spills or other incidents ($N = 504$).

When birds were shot the stomachs were removed as soon as possible and stored in industrial methylated spirits (IMS). Bird samples collected from the beaches were often frozen prior to the removal of the stomachs. Corpses from this source may have been on the shoreline for periods varying from hours to days prior to collection.

Stomach content analysis

The oesophagus/proventriculus and gizzard were opened longitudinally and the contents handled according to type:

0272–7714/85/050559 + 10 $03.00/0

(a) *Soft vertebrate tissues:* Whole or partly digested prey items were removed and stored in 10% formalin. These were later identified, measured and weighed. Unidentifiable soft tissue masses were also weighed and examined for skeletal remains.

(b) *Hard vertebrate remains:* After the removal of soft tissue, remaining debris was flushed into a gridded petri dish with IMS. Microscopic examination was essential to detect bones lodged in the convolutions of the gizzard wall. Fish otoliths were separated and stored dry for identification and measurement. Identification was made by use of Scott (1905) and by comparison with a reference collection. Calculation of fish lengths and weights were made from otolith measurements in accordance with Blake (1984). Sandeel otoliths in good condition were aged by the method described by Reay (1972). The prootic and pterotic bones of clupeids (Svetovidov, 1952) were counted and stored with otoliths from the same stomach. Other bones were classified as far as possible and recorded on an arbitrary three-point scale (few, moderate, many).

(c) *Invertebrate remains:* Whole organisms were stored in 4% formalin, and identifiable partial remains such as polychaete jaws or cephalopod beaks were counted and retained.

Analysis of data

Stomachs containing no identifiable food material were excluded from the analysis. Fish remains were first described in terms of the frequency with which a given species or family occurred in a sample (Table 1). Selected prey items were then considered in terms of the percentage contribution they made to the total identifiable remains in each stomach. These values were used as the basis for Mann Whitney tests between samples to test the significance of apparent differences (Bradstreet, 1982; Blake, 1984).

Problems associated with the methods employed

Bradstreet (1977) and Blake (1983) discussed some of the general problems associated with the analysis of auk stomach contents. The present work involved three main considerations:

(a) *Sample collection:* All data used in a dietary study should ideally be collected from shot birds, preferably observed to have been feeding, but in practice this was rarely possible. The stomach contents of shot birds may reflect natural diet to a greater extent than those from beached birds, and the utilization of corpses from both sources is therefore a possible source of bias. Also, small samples necessitated the combination of data from different years (1981/1982) for some months, which generated a further source of inaccuracy.

(b) *Diet interpretation from otoliths:* Whole fish occurred infrequently, even in shot birds, presumably due to rapid digestion. Assessment of fish numbers, lengths and weights was, therefore, normally made from otoliths. The most accurate estimates of fish numbers and weights were possible from shot samples; otoliths were grouped by total length and the number in each size group was divided by two.

No data are available for the retention time of otoliths. Uspenski (1958) suggested that 50% of otoliths were voided 12 h after feeding, but his experiments took no account of otolith type, and lacked a 'control' sample of starved birds. Therefore it is difficult to

TABLE 1. The frequency of occurrence of fish remains in guillemot stomachs. Figures are the percentage of stomachs with identifiable fish remains in which each prey group occurred

Locality	Date	Frequency of occurrence				No. of stomachs	No. with identifiable fish remains
		Clupeid	Sandeel	Gadoid	Goby		
Shetland	June	0	93	11	1	109	83
Buchan coast	Aug	20	90	10	0	18	14
Buchan/Aberdeen coast	Sep	58	77	42	0	55	32
Buchan coast	Oct	72	38	10	7	54	29
Aberdeen coast	Nov/Dec	35	24	35	24	37	17
Shetland	Jan	2	24	83	2	51	41
Shetland	Feb	43	68	48	18	199	130
Firth of Forth	Feb	81	29	39	2	54	31
Firth of Forth	Mar	0	98	18	20	44	44
Buchan coast	Mar	2	96	19	0	108	49
Aberdeen coast	Apr	0	94	0	6	21	17
Total						750	487

relate otolith numbers to meal size or to assess the relative importance of different prey species.

(c) *Invertebrates:* The efficiency of digestion inferred by the scarcity of intact fish in guillemot stomachs could lead to the under assessment of the invertebrate component of the diet. While the hard parts of polychaete worms are obviously retained for some time it is likely that more delicate animals such as euphausiids will be digested more rapidly, and their importance may be underestimated.

The problems described undoubtedly impose quantitative limits on the accuracy of the sampling methods available to us, but the methods employed do provide a comparative guide to seasonal and geographic variability in the fish component of guillemot diet.

Results

The frequency of occurrence of items in the stomach contents suggested a seasonal pattern in guillemot diet (Tables 1 and 2) although interpretation was complicated by variation between sampling sites.

Invertebrates

The only vertebrate remains found regularly were polychaete jaws (Table 2). These were not identified to species, but the size of the jaws indicated that most were from large nereid worms (P. E. Gibbs, pers. comm.). Polychaetes appeared to be of importance only

TABLE 2. Frequency of occurrence of invertebrates in guillemot stomachs. Figures are percentages of total stomach numbers

	Frequency of occurrence for locality and month							
	Shetland June	Buchan/Aberdeen Sep	Aberdeen coast Nov/Dec	Shetland Jan	Shetland Feb	Firth of Forth Mar	Buchan coast Mar	Aberdeen coast Apr
Polychaete jaws	2			27	32	54	4	10
Polychaete setae				18	4	14		5
Polychaete tissue				4		2		
Crustacean parts				2	0·5		1	
Cephalopod beaks			5					
Cephalopod eyes			3					
Crab chelae/carapace		4						
No. of stomachs	109	55	37	51	199	44	108	21

in winter, particularly in Shetland waters. From a total of 102 stomachs (Shetland and Firth of Forth) containing jaw parts, 17% occurred in the absence of fish remains and a further 43% were found in stomachs containing only planktivorous sandeel or clupeid remains. It seems likely therefore that polychaetes are a primary prey item of guillemots in some areas during the winter.

Fish

Otoliths in the guillemot stomachs were identified with some certainty to four main families and tentatively to eighteen species of fish (Table 3).

Ammodytes marinus was undoubtedly the commonest sandeel found, although other species, particularly *A. lancea,* probably comprised an unknown proportion of the otoliths too small to identify positively.

Gadoid otoliths were often broken or eroded beyond identification, and the relative species numbers in Table 3 are assumed to be representative of the proportions of this family in guillemot diet. The occurrence of Norway pout (*Trisopterus esmarkii*) in the stomach probably reflects the bias of samples towards northern waters where this fish is commonest, and the abundance of saithe (*Pollachius virens*) as the commonest gadoid probably reflects the inshore and semi-pelagic distribution of this fish in the first year of life (DAFS data; J. R. G. Hislop, pers. comm.).

The proportion of sprat to herring otoliths varied with area, although the overall ratio was 7 : 3 ($N = 254$) in favour of sprat. The only area where herring otoliths predominated was in the Firth of Forth (7 : 3, $N = 36$). In the majority of cases clupeid otoliths were too damaged to permit identification, and the presence of clupeid remains was determined from the otic bullae.

Seasonal trends in prey composition

(a) *Adjacent sites in the same month:* To provide grounds for general statements on seasonal trends the contributions by the three main prey families were compared for samples collected from Noss and Fair Isle in June, and from the Firth of Forth and the

TABLE 3. Fish species found in guillemot stomachs. Figures are the numbers of otoliths positively identified for each species

Family	Common name	Scientific name	*N*
Clupeidae	Herring	*Clupea harengus* L.	73
	Sprat	*Sprattus sprattus* (L.)	181
Gadidae	Cod	*Gadus morhua* L.	9
	Haddock	*Melanogrammus aeglefinus* (L.)	2
	Whiting	*Merlangius merlangius* (L.)	26
	Saithe	*Pollachius virens* (L.)	132
	Pollock	*P. pollachius* (L.)	8
	Blue Whiting	*Micromesistius poutassou* (Risso)	6
	Norway pout	*Trisopterus esmarkii* (Nilsson)	40
	Bib	*T. luscus* (L.)	11
	Poor cod	*T. minutus* (L.)	18
	Trisopterus sp.		102
Ammodytidae	Sandeel	*Ammodytes marinus* Raitt	8638
	Sandeel	*A. lancea* Cuvier	13
	Greater Sandeel	*Hyperoplus lanceolatus* (Lesauvage)	10
	Smooth Sandeel	*Gymnammodytes semisquamatus* (Jourdain)	8
Gobiidae	Goby[a]		697
	Pearlsides	*Maurolicus muelleri* (Gmelin)	108

[a]Only two species of goby were positively identified: *Gobiusculus flavescens* (Fabricius), *Crystallogobius linearis* (Düben).

TABLE 4. Results of statistical tests (Mann–Whitney z)

Locality	Month	*N*	Clupeid remains	Gadoid remains	Sandeel remains
Noss	June	47	Few	$z=0.540$	$z=0.374$
Fair Isle	June	36	Few	$P>0.2$	$P>0.3$
Firth of Forth	Mar	44	None	$z=0.725$	$z=0.620$
Buchan coast	Mar	49	None	$P>0.2$	$P>0.2$
Shetland	Jan	39	Very few	$z=5.228$	$z=4.640$
Shetland	Feb	130	Many	$P<0.001$	$P<0.001$
Shetland	Feb	130	Many	$z=4.068$	$z=7.004$
Shetland	June	83	None	$P<0.001$	$P<0.001$
Buchan/Aberdeen coast	Sep	32	Many	$z=1.405$	$z=4.764$
Buchan coast	Mar	49	None	$P>0.05$	$P>0.001$
Buchan coast	Oct	29	$z=2.584$	$z=2.157$	$z=2.330$
Buchan coast	Sept	32	$P<0.01$	$P>0.01$	$P<0.01$
Firth of Forth	Feb	31	Many	$z=2.245$	$z=7.708$
Firth of Forth	Mar	44	None	$P<0.01$	$P<0.001$
Shetland	Feb	130	$z=7.726$	$z=1.289$	$z=5.002$
Firth of Forth	Feb	31	$P<0.001$	$P>0.05$	$P<0.001$

Buchan coast in March. In neither case were there significant differences between sites (Table 4). Sandeels dominated all samples in which there were few gadoids or clupeids.

(b) *Selected sites in different months:* To assess seasonal changes, data were compared for Shetland in January, February and June, the Buchan/Aberdeen coasts in March, September and October, and the Firth of Forth in February and March (Table 4).

For Shetland, significant differences were found between the contribution by the three major families for all months. In January, gadoid remains were most numerous, there were few sandeel otoliths and clupeid bones were found in only one stomach. In February, sandeels and clupeids contributed more, and gadoids less than in January. In June, only sandeel remains were important, and gadoids and clupeids contributed less than in February.

For Buchan, there were some differences between all months. In March, stomach contents were dominated by sandeel, with lesser contribution by gadoids and there were no clupeids. Small samples from April and August (Table 1) indicated that this situation persisted throughout the summer in this area. In September, sandeels contributed less than in March, and there was no significant difference in the contribution by gadoids, but clupeids increased in importance. In October, sandeels contributed less than in September, and clupeids increased in importance. Sample numbers were low for this area in November/December (Table 1) but the data suggest that clupeids and gadoids were still more important in the diet than sandeels.

For Firth of Forth in February, sandeels contributed the least; gadoids were common, but the diet was dominated by clupeids. In March, sandeels dominated the diet with a smaller gadoid contribution than in February, and no clupeid remains.

(c) *Widely separated areas in the same month:* Data from the same month were available only for Shetland and the Firth of Forth in February. The contribution by sandeels was significantly greater, and that of clupeids less, in the Shetland sample. There was no difference in the relative proportions contributed by gadoids.

In summary, sandeels were generally dominant in the diet from March to August, with clupeids and gadoids being taken more often in September and October, particularly off the Buchan coast. In winter clupeids predominated in the diet in the south and gadoids in the north, with sandeels still taken, but less frequently. A change back towards sandeel dominance occurred in February/March according to area.

Prey size

The lengths and weights of some fish species were calculated from otoliths found in selected samples of shot birds.

(a) *Sandeels:* The size frequency distribution of *Ammodytes marinus* from guillemot stomachs showed a clear seasonal pattern (Figure 1). In February/March birds were feeding mainly on the 1-group fish spawned in January of the previous year, with few older age classes represented. In April a wider range of sizes was found in birds from Fowlsheugh, and this situation was also recorded at Fair Isle in June 1981. In contrast, a sample from Noss in June 1980 contained mainly 0-group fish, suggesting that there was a change from reliance on older fish when the young of the year became abundant. This suggestion is supported by samples from the Buchan coast in September and October where the sandeels were also mainly 0-group. The only winter sample comprising mainly fish older than 0/1-group was taken at Noss in January.

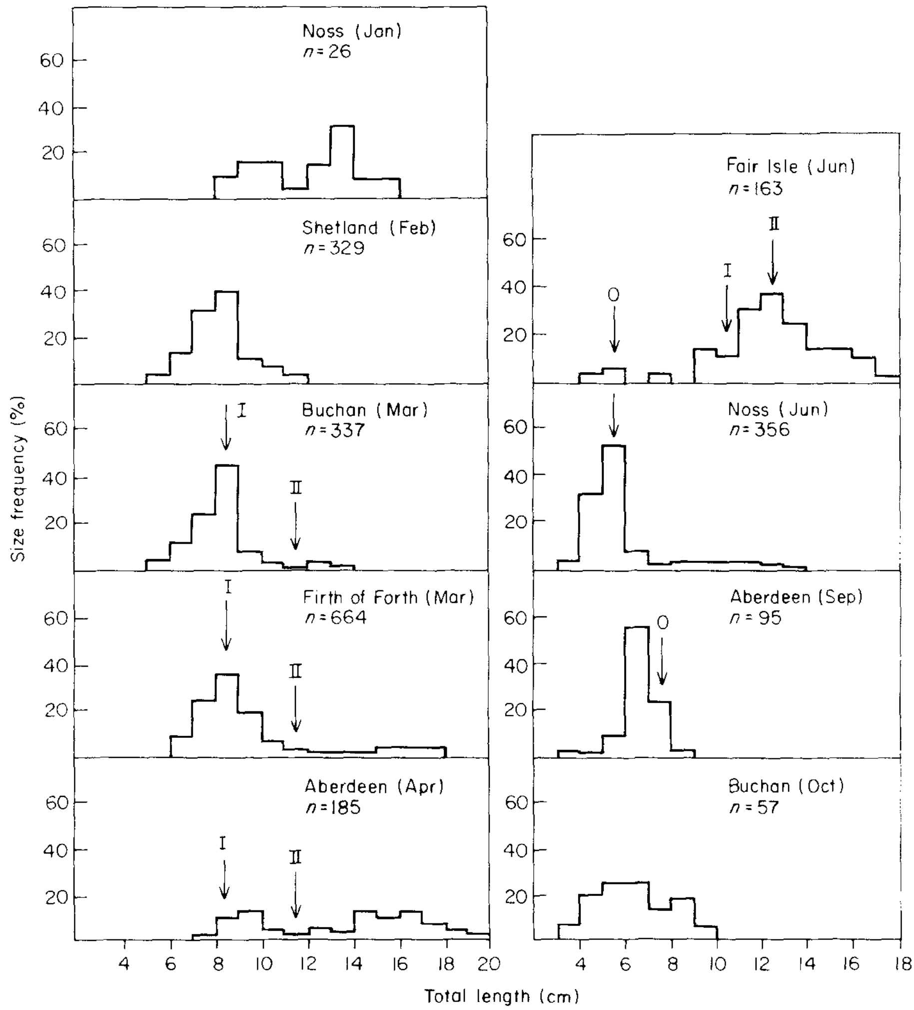

Figure 1. Sandeel lengths calculated from otoliths in guillemot stomachs. Arrows indicate the mean length of age classes derived from the closest available fisheries date: March, commercial sample, Shetland, April 1981; April, as March; June, commercial sample, Fair Isle, June 1981; September, commercial sample, Shetland, September 1981.

(b) *Gadoids:* Relatively few otoliths were recovered in suitable condition for measurement, and data are presented for only saithe, Norway pout and poor cod (Figure 2). In all cases the samples were collected from the winter (January/February) and comprised 1-group fish (spawned the previous year). This presumably reflects the rapid growth of gadoids which (with the exception of *Trisopterus* spp.) probably precludes their consumption by guillemots beyond the first year of life (Blake, 1983). The largest gadoid otolith recorded was from a cod calculated to be 21 cm in length (still 1-group).

There was little evidence that guillemots utilized small 0-group gadoids in the summer when these fish are in their pelagic phase (Daan *et al.,* 1975), perhaps because of the abundance of sandeels close to colonies.

(c) *Sprat/herring:* Sprat otoliths were collected from the January/February period. Fish of 1-group size predominated in the samples, although older fish up to 12 cm in length

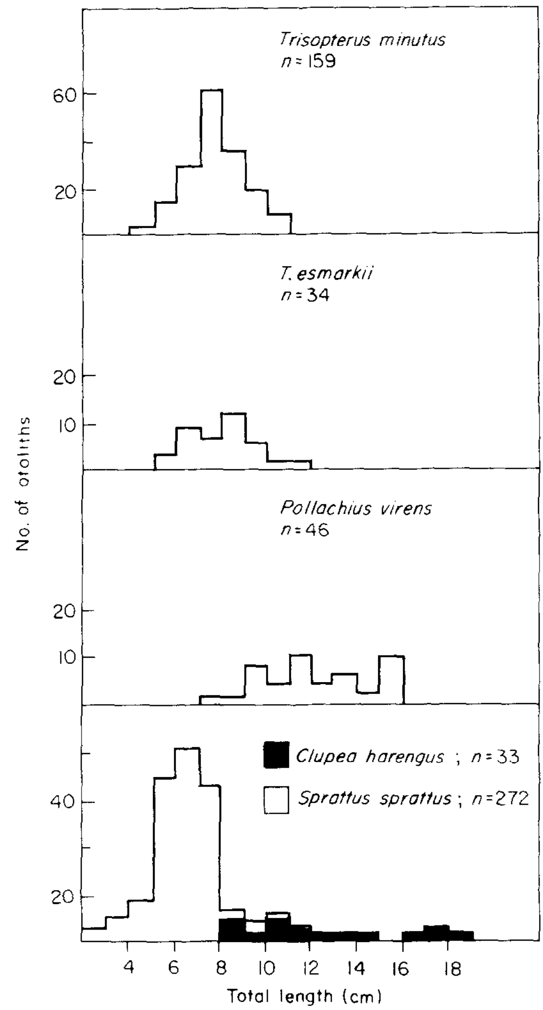

Figure 2. Fish lengths calculated from otoliths in guillemot stomachs.

were also recorded (Figure 2). Relatively few herring otoliths were measured; the indicated size range was from 9–19 cm total length, the majority in the range 9–13 cm.

(d) *Prey weights:* The calculation of the weights of prey represented by fish remains in guillemot stomachs was difficult, due to the scarcity of whole fish and the occurrence of fresh material with otoliths or other older remains. The fresh weights recorded from shot birds (Table 5) showed that guillemots are capable of consuming at least 114 g of fish in one feeding period. Otoliths and fresh sandeels from the stomach of one bird from the Firth of Forth in March gave a total fish weight estimate of 500 g. Accurate estimates are, however, impossible in the absence of data on otolith erosion/retention times.

Discussion

On the basis of the distribution data collected by Blake *et al.* (1984) an attempt can be made to relate the observed trends in diet to seasonal patterns of occurrence in guillemots.

TABLE 5. Prey weights from guillemot stomachs

Locality	Month	*N*	Tissue weights (g) Max	Tissue weights (g) Mean (SD)	Maximum possible weight (g)[a]
Shot birds					
Noss	Jan	2	40	26·5 (19·1)	61
Firth of forth	Mar	25	114	41·6 (29·2)	477
Fowlsheugh	Apr	3	15	10·0 (4·4)	230
Noss	Jun	7	19	10·9 (5·0)	66
Fair Isle	Jun	8	22	11·5 (4·7)	68
Birds oiled and either beached or shot[b]					
Hvaler (Norway)	Jan	34	84	26·5 (5·9)	
Aust-Agder (Norway)	Jan	29	63	18·1 (5·8)	
Bohüslan (Sweden)	Jan	16	83	24·3 (11·6)	

[a]Maximum possible weight in one bird if actual tissue weight and otolith-based estimates are combined.
[b]From data presented in Blake (1983).

During the breeding season the location of nest sites is probably the main factor determining the distribution of adult guillemots in the North Sea. Work in the Shetland area in June has shown that at this time bird density on the water is negatively correlated with distance from land (Blake *et al.*, 1984); and around Fair Isle guillemots were found mainly within 6 kilometres of the island (Langslow *et al.*, 1985). The main prey group at this time is sandeels, and although the 0-group age class are distributed across the whole of the northern and north central North Sea during the summer the highest concentrations are found inshore (DAFS data; J. G. R. Hislop, pers. comm.). These fish thus provide an easily accessible food source for breeding guillemots. Adult fish are widespread but patchy in distribution.

From late June, adult guillemots and their chicks begin to disperse from the colonies, at a time when sandeels are still the main food item. By September the largest concentrations of adult and juvenile guillemots were recorded off the east coast of Scotland and north-east England. Stomach samples from the Aberdeen and Buchan coasts at this time indicated a decreased reliance on sandeels with more 0-group clupeids and gadoids in the diet. In the winter, guillemots remain less attached to the vicinity of colonies, paying only brief visits to the breeding ledges (Harris & Wanless, 1985), and the availability of food is probably a major factor in determining the bird distribution at that time. Data presented here and in Blake (1984), suggest, moreover, that there are marked differences in diet with area in the winter, with sprats more important in the south and gadoids (and possibly polychaetes) in the north. Bird surveys also suggest that there is a southward shift in guillemot distribution in winter (Blake *et al.*, 1984), a time when the largest concentrations of sprats in the North Sea occur south of the Humber (P. Johnson, pers. comm.).

At colonies where winter monitoring studies are carried out it has been found that by February, guillemots begin to spend more time in the vicinity of the breeding ledges (M. Harris, pers. comm.). Clupeids were still important in the diet at this time although sandeels were more common than in January, particularly in Shetland. By March, at the start of the breeding season, sandeels were again the main food item.

In conclusion it is apparent that while the numerical approach applied to dietary study of North Sea guillemots permits comparison between area and season, it may not always reflect the energetic value contributed by the various prey items at different times of year. Further work would benefit greatly from contemporary studies of the digestive rates and calorific values of various food items, and field study should rely entirely on shot birds. It may then be possible to provide more accurate inputs to the kind of energetic models proposed by Furness (1978).

Acknowledgements

We would like to thank Drs J. Hislop, D. Langslow and R. Mitchell for constructive criticism of this manuscript. The work was made possible by the cooperation of a variety of organizations and individuals, and we are particularly grateful to all those who assisted in the collection of corpses from North Sea beaches. Dr R. Bailey and Mr P. Johnson of DAFS and MAFF, respectively, kindly provided much fisheries data, and Mr B. Edelston and Dr J. Hislop of DAFS gave expert advice on otolith identification.

We also acknowledge the tremendous general support given to the research programme in Shetland by Dr M. Richardson.

References

Blake, B. F. 1983 A comparative study of the diet of auks killed during an oil incident in the Skagerrak in January 1981. *Journal of Zoology, London* **201**, 1–12.

Blake, B. F. 1984 Diet and fish stock availability as possible factors in the mass death of auks in the North Sea. *Journal of Experiment Marine Biology and Ecology* **76**, 89–103.

Blake, B. F., Tasker, M. L., Jones, P. H., Dixon, T. J., Mitchell, R. & Langslow, D. 1984 Distribution of seabirds in the North Sea. Nature Conservancy Council publication.

Bradstreet, M. S. W. 1977 Feeding ecology of seabirds along fast-ice edges in Wellington Channel and Resolute Passage, N.W.T. Report to the Polar Gas Project by LGL Ltd, Environmental Research Associates, Toronto, Ontario. 36 pp.

Bradstreet, M. S. W. 1982 Pelagic feeding ecology of dovekies, *Alle alle*, in Lancaster Sound and Western Baffin Bay. *Arctic* **35**, 126–140.

Daan, N., Hislop, J. R. G., Holden, M. J. & Lahn-Johanesson, J. 1975 Report of the pelagic 0-group gadoid survey in the North Sea in 1975. *International Council for Exploration of the Sea* CM 1975/F: 33, Copenhagen.

Furness, R. W. 1978 Energy requirements of seabird communities: a bioenergetics model. *Journal of Animal Ecology* **47**, 39–53.

Harris, M. P. & Hislop, J. G. R. 1978 The food of young puffins *Fratercula arctica*. *Journal of Zoology, London* **185**, 213–236.

Harris, M. P. & Wanless, S. 1985 The effect of the wreck of seabirds in February 1983 on auk populations in the Isle of May. *Bird Study* (in press).

Hedgren, S. 1976 On the food of the Guillemot *Uria aalge* at the island of Stora Karlsö, the Baltic Sea. *Vär Fägelvärld* **35**, 287–290.

Hislop, J. G. R. & Harris, M. P. 1985 Recent changes in the food of young puffins *Fratercula arctica* on the Isle of May in relation to fish stocks. *Ibis* **127** (in press).

Langslow, D. R., Blake, B. F., Dixon, T. J., Jones, P. H. & Tasker, M. L. 1985 The distribution and feeding of Guillemots *Uria aalge* at sea around Fair Isle, Shetland, during the breeding season (in preparation).

Madsen, F. J. 1957 On the food habits of some fish-eating birds in Denmark. *Danish Review of Game Biology* **3**, 19–83.

Pearson, T. H. 1968 The feeding biology of seabird species breeding on the Farne Islands, Northumberland. *Journal of Animal Ecology* **37**, 521–522.

Reay, P. J. 1972 The seasonal pattern of otolith growth and its application to back-calculation studies in *Ammodytes tobianus* L. *Journal du Consiel permanent international pour l'exploration de la mer* **34**(3), 485–504.

Scott, T. 1905 II–Observations on the otoliths of some teleostean fishes. *Annual Report of the Fishery Board for Scotland* **24**, 48–82.

Svetovidov, A. N. 1952 Clupeidae. In: *Fishes*, vol. II, no. 1. *Fauna of USSR, New Series* no. 48. Israel Program for Scientific Translations, Jerusalem, 1963.

Uspenski, S. M. 1958 The bird bazaars of Novaya Zemlaya. Department of Northern Affairs and National Resources, Canada. *Translation of Russian Game Reports*, No. 4.