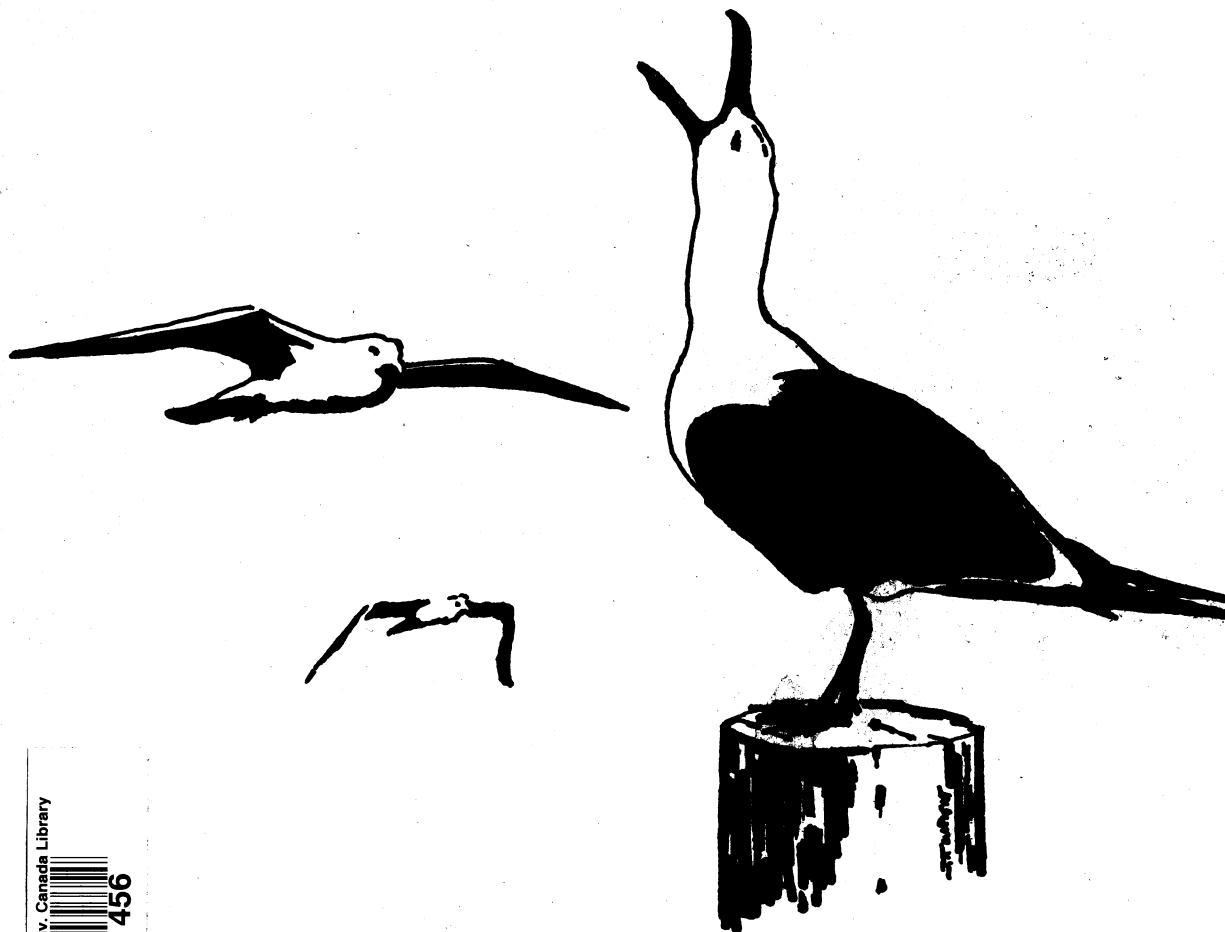


STUDIES OF ALCIDS BREEDING AT THE
GANNET CLUSTERS, LABRADOR, 1982

T.R. Birkhead & David N. Nettleship

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¹ An investigation associated with the program "Studies on northern seabirds", Seabird Research Unit, Canadian Wildlife Service, Environment Canada (Report No. 149).

TABLE OF CONTENTS	<u>Page</u>
List of Figures	vi
List of Tables	iii
INTRODUCTION	1
STUDY AREA, METHODS, FIELD PARTY AND ENVIRONMENTAL CONDITIONS . .	2
ADULT BIOMETRICS	8
TIMING OF BREEDING	11
BREEDING SUCCESS	21
EGG SIZE AND COMPOSITION	34
<u>Egg Volume</u>	34
<u>Seasonal Changes in Egg Size</u>	42
<u>Replacement Eggs</u>	46
<u>Composition of Eggs</u>	49
FEEDING ECOLOGY	49
<u>Feeding Rates</u>	53
<u>Species and Size of Prey</u>	66
<u>Food Intake of Chicks</u>	77
CHICK GROWTH	77
DISCUSSION AND CONCLUSIONS	92
<u>Adult Biometrics</u>	92
<u>Timing of Breeding</u>	93
<u>Egg Size and Composition</u>	97
<u>Breeding Success</u>	99
<u>Feeding Ecology</u>	100

TABLE OF CONTENTS (CONT'D)

	<u>Page</u>
<u>Chick Growth</u>	100
<u>Recommendations</u>	101
ACKNOWLEDGEMENTS	103
LITERATURE CITED	104

Appendix

1. Scientific names of fish prey mentioned in the text.

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Comparison of mean temperatures in 1981 and 1982 in Battle Harbour, Labrador, taken from ice maps (Anon. 1981/1982)	3
2. Body weights of alcids at the Gannet Clusters 1982	9
3. Summary of the major features of the breeding cycle of alcids at the Gannet Clusters in 1982	12
4. Median hatching dates for alcids at the Gannet Clusters 1981 and 1982	13
5. Pattern of egg-laying in Razorbills in four study areas at the Gannet Clusters in 1982	14
6. Breeding success in Razorbills at the Gannet Clusters 1982 on two undisturbed control plots and one disturbed plot	23
7. Breeding success at regularly disturbed Razorbill plots in 1981 and 1982	25
8. Breeding success in Common Murres at the Gannet Clusters in 1982	26
9. Breeding success in Thick-billed Murres at the Gannet Clusters in 1982	28
10. Comparison of breeding success of Common Murres and Thick-billed Murres at the Gannet Clusters in 1982	29
11. Success of first and replacement eggs in Common Murres and Thick-billed Murres	31
12. Breeding success at the same sites in 1981 and 1982 at Common Murre plot A	32
13. Comparison of mean egg volume indices of alcid eggs in 1982 and 1981 at the Gannet Clusters	35
14. Comparison of mean volume indices for eggs laid at the same sites in 1981 and 1982 for Razorbills and Atlantic Puffin	36

LIST OF TABLES (CONT'D)

<u>Table</u>	<u>Page</u>
15. Volume indices of first and replacement eggs for Razorbill and Common Murre	47
16. Composition of first eggs of Atlantic Puffin	50
17. Comparison of the composition of Atlantic Puffin eggs from the Gannet Clusters, Labrador and Isle of May, Scotland	51
18. Comparison of the composition of eggs in 1981 and 1982 for Razorbills and Common Murre at the Gannet Clusters . .	52
19. Feeding rates of alcids at the Gannet Clusters in 1981 and 1982	54
20. Mean length and weight (+ S.D.) of fish specimens collected from ledges and burrows	67
21. Mean (+ S.D.) weight of loads for Atlantic Puffins	68
22. Meal size for Atlantic Puffins at the Gannet Clusters and at two colonies in Great Britain	69
23. Seasonal changes in prey composition for Atlantic Puffin	70
24. Composition of Atlantic Puffin chick diet, comparison between 1981 and 1982	75
25. Comparison of chick diets (percent by number) for Razorbill, Common Murre and Thick-billed Murre at the Gannet Clusters in 1981 and 1982	76
26. Food intake of alcid chicks at the Gannet Clusters in 1982	78
27. Relationship between hatching date and growth parameters in Razorbills	80
28. Razorbill chick growth in 1981 and 1982 - comparison . . .	81
29. Comparison of weight in relation to wing-length for Razorbill chicks visited only once and those visited regularly	85

LIST OF TABLES (CONT'D)

<u>Table</u>		<u>Page</u>
30.	Comparison of fledging weights of Atlantic Puffin at the Gannet Clusters and other colonies	88
31.	Relationship between chick weight and wing-length for Atlantic Puffin in 1981 and 1982	89

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Gannet Clusters 1-4 showing main working areas	4
2. Sea-ice conditions during early May - early June 1982 in the vicinity of the Gannet Clusters. Key: Black = solid (land fast) ice, hatched = 1/10 - 9/10 ice cover, and stippled = open water	5
3. Sea ice conditions during early May - early June 1981: (see Fig. 2 for key)	6
4. Mean air temperature during the 1982 field season at the Gannet Clusters. The line shows 7-day running-mean values . .	7
5. Seasonal changes in adult body weights of alcids breeding at the Gannet Clusters 1982. Values are means \pm S.D.	10
6. Frequency distribution of laying dates for alcids at the Gannet Clusters in 1982	15
7. Frequency distribution for hatching dates in murrelets at the Gannet Clusters in 1982	16
8. Frequency distribution for fledging dates for alcids at the Gannet Clusters in 1982	17
9. Pattern of fledging in alcids at the Gannet Clusters in 1982	18
10. Frequency distribution of incubation and chick- rearing periods for Common Murre	19
11. Frequency distribution of incubation and chick-rearing periods for Thick-billed Murre	20
12. Frequency distribution of egg volume indices for alcids at the Gannet Clusters in 1982	37
13. Relationship between egg volume index in 1981 and 1982 for Razorbill eggs at the same sites	35
14. Relationship between egg volume index in 1981 and 1982 for Atlantic Puffin eggs in the same burrows	39
15. Seasonal changes in egg volume indices of Atlantic Puffin eggs at the Gannet Clusters in 1982	40

LIST OF FIGURES (CONT'D)

<u>Figure</u>		<u>Page</u>
16.	Seasonal changes in egg volume indices of Atlantic Puffin eggs. Values are means \pm S.D.	43
17.	Seasonal changes in egg volume indices of Common Murre eggs	44
18.	Seasonal changes in egg volume indices of Thick-billed Murre eggs	45
19.	Relationship between the volume indices of first and replacement eggs for Razorbill, Atlantic Puffin and Common Murre	48
20.	Seasonal pattern of feeding rate in Common Murre chicks . . .	55
21.	Seasonal pattern of feeding rate in Thick-billed murre chicks	56
22.	Seasonal pattern of feeding rate in Razorbill chicks	57
23.	Seasonal pattern of feeding rate in Atlantic Puffin chicks	58
24.	Changes in feeding rate in relation to chick age in Common Murre	60
25.	Changes in feeding rate in relation to chick age in Thick-billed Murre	61
26.	Changes in feeding rate in relation to chick age in Atlantic Puffin	62
27.	Diurnal pattern of chick-feeding rates for Common Murre and Thick-billed Murre	63
28.	Diurnal pattern of feeding rates for Atlantic Puffin chicks	67
29.	Trip duration for Common Murre, Thick-billed Murre and Razorbill at the Gannet Clusters in 1982	68
30.	Percentage by number composition of fish in alcid chick diets at the Gannet Clusters in 1982	71
31.	Percentage by weight composition of fish in alcid chick diets at the Gannet Clusters in 1982	73

LIST OF FIGURES (CONT'D)

<u>Figure</u>		<u>Page</u>
32.	Growth of Razorbill chicks at the Gannet Clusters in 1982	82
33.	Weight increments in two day periods for Razorbill chicks at the Gannet Clusters in 1982	83
34.	Growth of Atlantic Puffin chicks at the Gannet Clusters in 1982	90
35.	Growth (wing length) of Atlantic Puffin chicks at the Gannet Clusters in 1982	91

STUDIES OF ALCIDS BREEDING AT THE GANNET CLUSTERS, LABRADOR 1983

INTRODUCTION

This report documents findings from the second season of alcid studies at the Gannet Clusters, Labrador. The main objectives of the overall study, a description of the environment, population size for different seabird species breeding on the Gannet Clusters are presented in the 1981 report (Birkhead & Nettleship 1982a).

The aims of the 1982 season were similar to those for 1981 and constituted the following (a) to examine the timing of breeding of the four most abundant alcids, i.e. the Common Murre, Uria aalge, Thick-billed Murre, U. lomvia, Razorbill, Alca torda, and Puffin, Fratercula arctica. (b) To conduct daily counts throughout the season in order to examine seasonal patterns of colony attendance, and to derive k values for study plots so that we can interpret census counts and determine whether the alcid populations on the Gannet Clusters are increasing, decreasing or stable. (c) To measure reproductive success of the four most abundant alcids and relate this to any change in population status. (d) To examine the size of eggs, chick growth and fledging weights of alcid chicks and to relate these measures to the timing of breeding and to reproductive success. We also made records of the food and feeding rates at which alcid chicks were provisioned. (e) The incubation and brooding patterns of Common Murres were examined using pairs where one bird was of the bridled form.

In addition to these objectives a number of others, specific to the 1982 season were identified. This was possible largely because of the earlier

opening of the camp in 1982. This allowed us to record the precise timing of arrival of the different alcid species and to record their behaviour and attendance prior to egg laying. It also enabled us, in contrast to the 1981 season, to examine the temporal pattern of egg laying and to record the duration of the incubation periods and the rate of replacement of lost eggs. In addition, the 1982 season allowed us to make the following comparisons. (1) Several aspects of the breeding biology of alcids (a) - (e) (above) can be compared between 1981 and 1982, and together with data for 1983 should provide a reasonable measure of inter-year variation in these parameters. (2) To continue our observations of incubation and brooding patterns of Common Murres using mixed bridled-normal pairs, but for 1982 with all such pairs sexed by observing copulations prior to egg laying. Common Murres like most other seabirds are sexually indistinguishable in the field and the roles of each sex in the incubation of eggs and care of the chick are only poorly known. The use of sexed, mixed bridled-normal (BN) pairs at a colony like Gannet Clusters where 18% of the birds are bridled and hence about 30% of all pairs are mixed provides an opportunity to examine the roles of the sexes. This technique was pioneered by H.N. Southern (see Southern et. al. 1965), but they had only a low percentage of bridled birds at their colony and their observations were of unsexed birds over only a few days each year.

STUDY AREA, METHODS, FIELD PARTY

AND ENVIRONMENTAL CONDITIONS

Descriptions of the islands comprising Gannet Clusters and our working areas are given in Birkhead & Nettleship (1982a); and only a few additions will be made here. The location of study areas used during the 1982 field season are shown in Fig. 1.

The field party in 1982 comprised the following (in alphabetical order) T.R. Birkhead, J. Gibson, S. Johnson, W. Lidster, M. Malone, R. Milton,

TABLE 1. Comparison of mean temperatures in 1981 and 1982 in Battle Harbour, Labrador. Taken from Ice Maps (Anon. 1981/1982). Data for May and early June.

	Temperature this year			Normal Temperature			Paired t-test		
	\bar{x}	S.D.	n	\bar{x}	S.D.	n	t	df	p
1981	3.57	1.90	7	5.29	4.54	7	1.55	7	N.S.
1982	1.68	1.70	19	3.26	1.59	19	6.37	17	<0.001

NOTE: n = number of days on which air temperatures recorded.

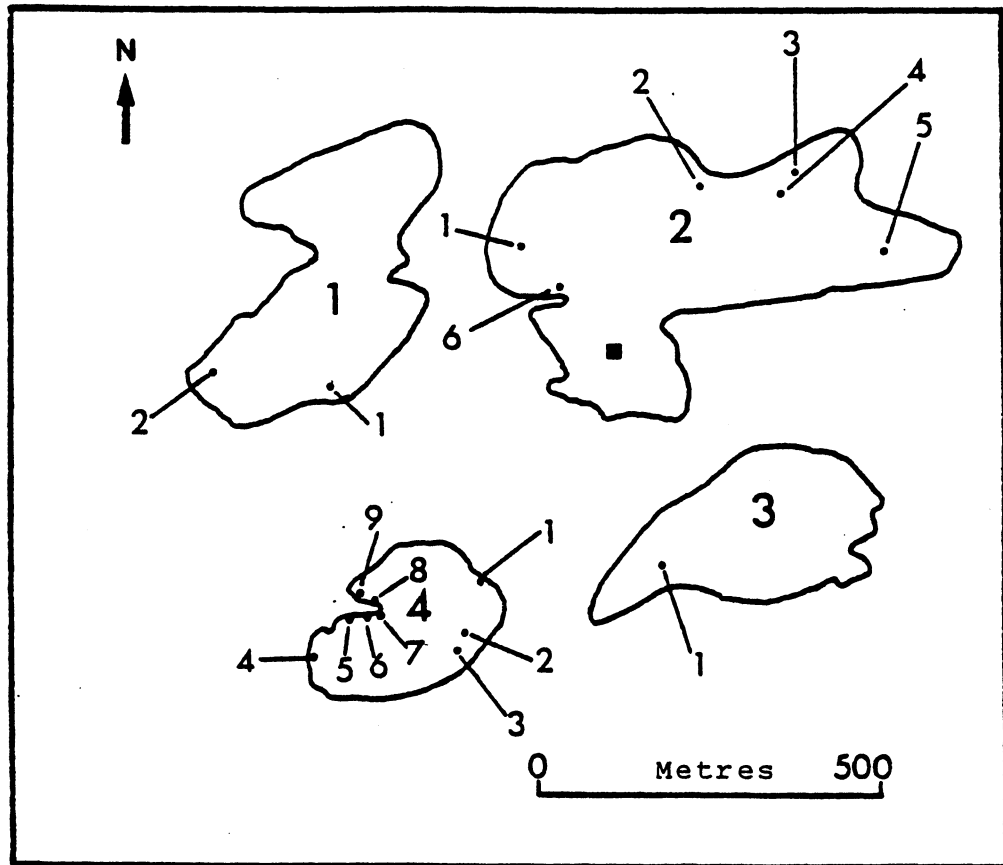


Figure 1. Working areas on the Gannet Clusters, 1982. Large numbers refer to islands; small numbers to specific working areas. GC1: 1, Thick-billed Murre breeding sites where we measured eggs and adults. 2, site where Common Murre chicks were caught at fledging. GC2: 1, Razorbill plot A; 2, Razorbill plot B; 3, Razorbill replacement plot; 4, Atlantic Puffin plot; 5, Razorbill plot C; 6, Atlantic Puffin plot. GC3: 1, Razorbill control plot. GC4: 1, Razorbill plot B (see 4 below); 2, Atlantic Puffin feeding watch area; 3, Common Murre chick growth area; 4, Razorbill plot A (N.B. the position of plot A and B were reversed in the 1981 report); 5, study plot TBM-C; 6, study plot TBM-B and CM-B (in 1981 report this plot = CM-4C); 7, Razorbill incubation plot; 8, study plot TBM-A; 9, study plot CM-A.

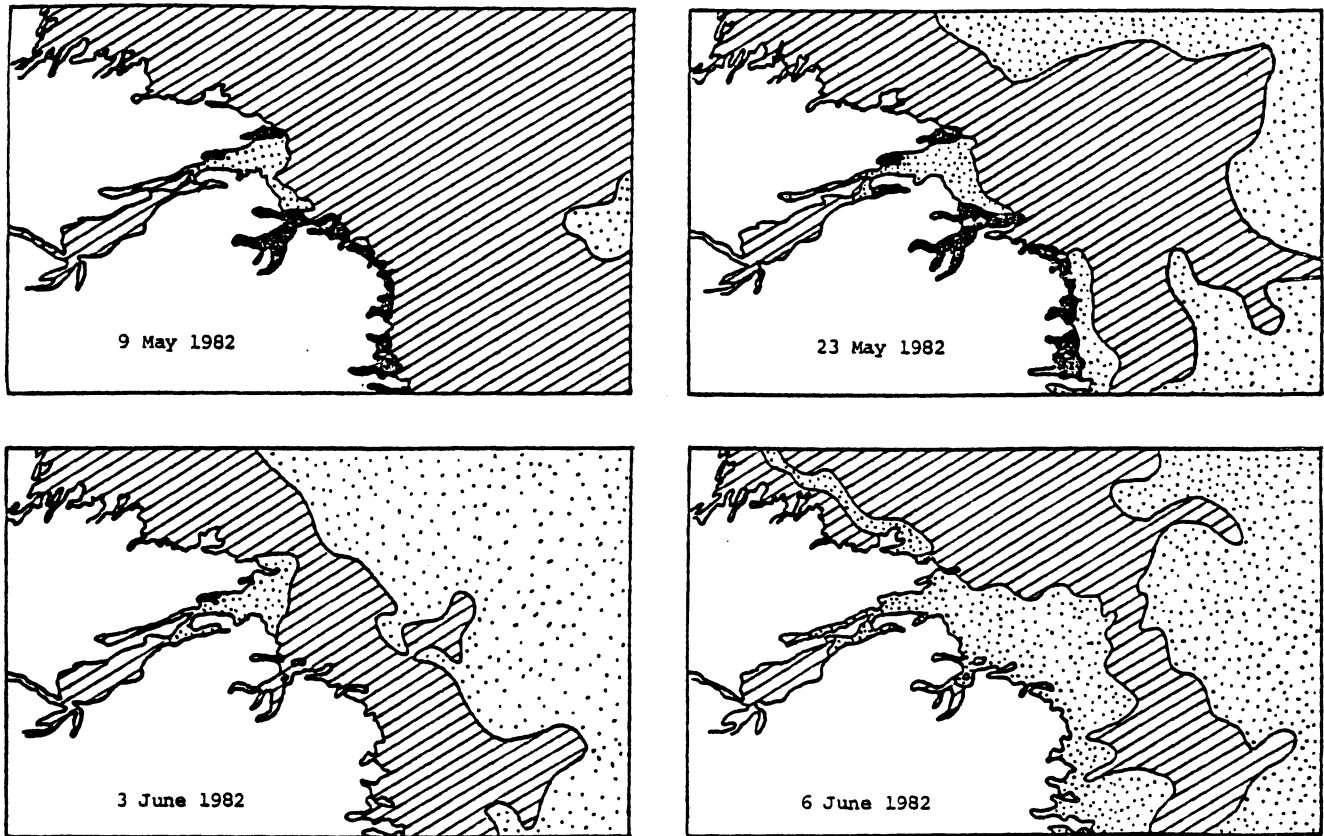


Figure 2. Sea ice conditions during early May - early June, 1982, in the vicinity of the Gannet Clusters. Key: Black = solid (landfast) ice, hatched = 1/10 - 9/10 ice cover, and stippled = open water.

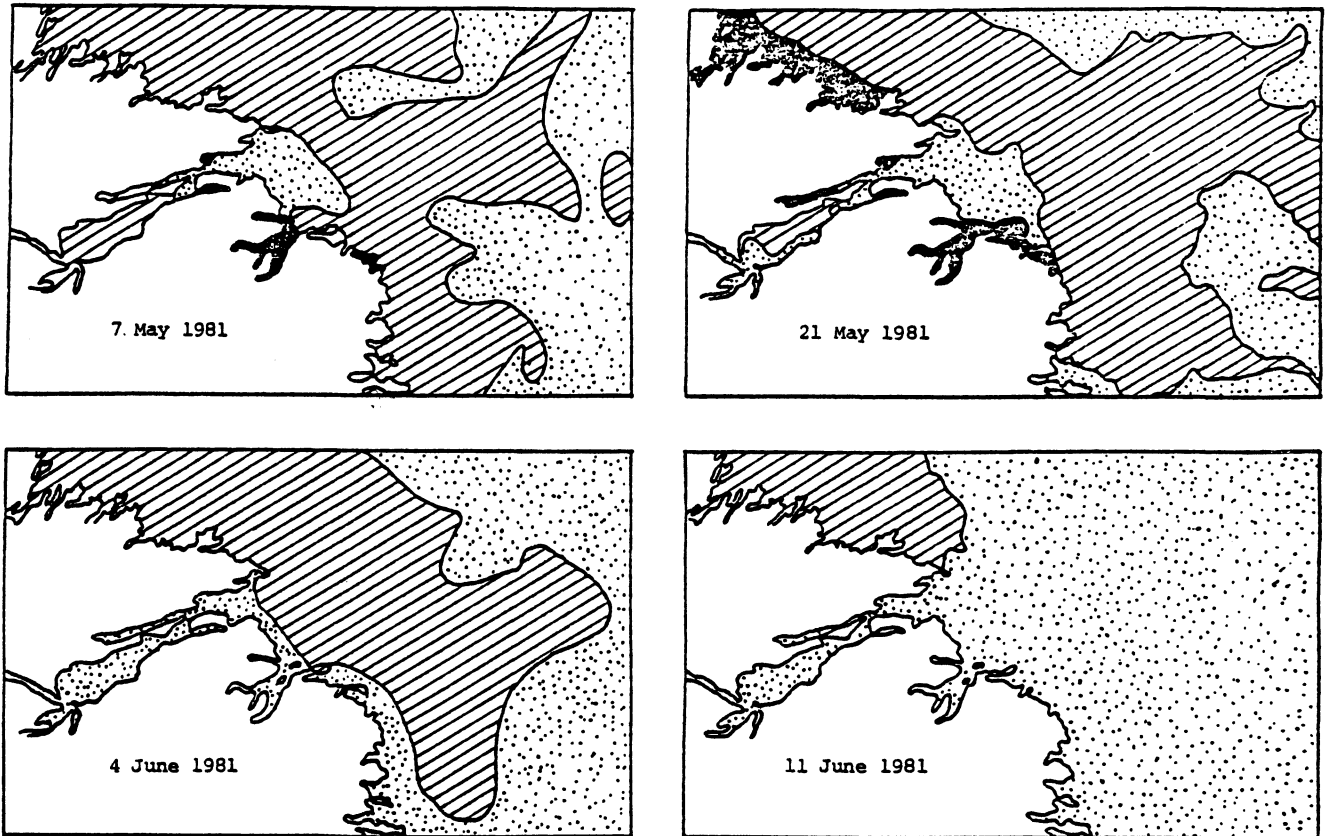


Figure 3. Sea ice conditions during early May - early June, 1981 (see Fig. 2, for key). Note that there was more open water earlier in the season in 1981 compared to 1982 (Fig. 2).

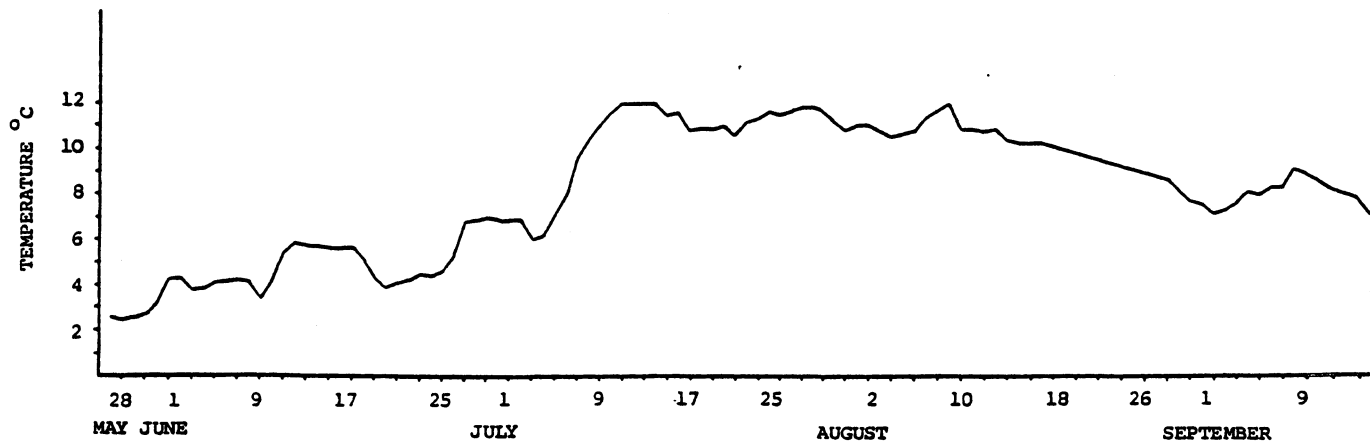


Figure 4. Mean air temperatures during the 1982 field season at the Gannet Clusters. The line shows 7-day running mean values. Intervals are 2 days.

D.N. Nettleship, J. Piatt and E. Verspoor: a maximum of five individuals was present on the islands at any one time. The main camp was located as in 1981, on the southern part of GC2, but in contrast to 1981 we also had a small cabin on GC4. Observations commenced on 24 May and continued until 24 September by which time all Murres and Razorbills and most Puffins had left the vicinity of the islands.

The 1982 spring was relatively late compared to 1981, and when the camp opened air temperatures were significantly lower than normal and 1981. In addition ice-cover was more extensive and persisted until later in the season in 1982 (Table 1, Figs. 2 & 3). The sea around the Gannet Clusters became ice-free about 6 June 1982, whereas it was largely ice-free by 7 May in 1981. Fig. 4 shows the mean air temperatures recorded at the Gannet Clusters through the 1982 season.

RESULTS

ADULT BIOMETRICS

Details of adult biometrics are presented in Table 2 and Fig. 5. In contrast to 1981 we were able, for Common Murres and Razorbills to obtain body weights during the pre-laying period and therefore were able to examine changes in body weight throughout the season (Fig. 5). Mean body weights were similar to those obtained in 1981, and as in that year all species showed a decline in weight between the incubation period and the chick-rearing period. Some authors (e.g. Croxall 1982) have suggested that such weight changes may occur as a consequence of reproduction and may reflect the energetic cost of breeding. Others (e.g. Norberg 1981) have proposed that such loss is an adaptation (and not a consequence of breeding) to reduce the energetic cost of flight during the time when adults make numerous trips between feeding areas and their breeding site, while provisioning their young.

TABLE 2. Body weights of alcids at the Gannet Clusters 1982.

Species	Prelaying			Incubation			Chick-rearing		
	\bar{x}	S.D.	(n)	\bar{x}	S.D.	(n)	\bar{x}	S.D.	(n)
Common Murre ¹	972.85	73.73	(34)	993.06	61.45	(31)	944.33	56.35	(30)
Thick-billed Murre ²	-	-	-	971.40	60.23	(30)	903.00	47.09	(20)
Razorbill ³	781.80	61.90	(30)	751.30	52.19	(30)	720.00	40.53	(30)
Atlantic Puffin ⁴	-	-	-	498.29	31.16	(44)	458.38	30.02	(77)

NOTES: ¹ANOVA $F_{2,92} = 4.36$, $P < 0.05$

² $t = 4.49$, 48 df, $P < 0.001$

³ANOVA $F_{2,87} = 10.75$ $P < 0.001$

⁴ $t = 6.87$, 119 df, $P < 0.001$

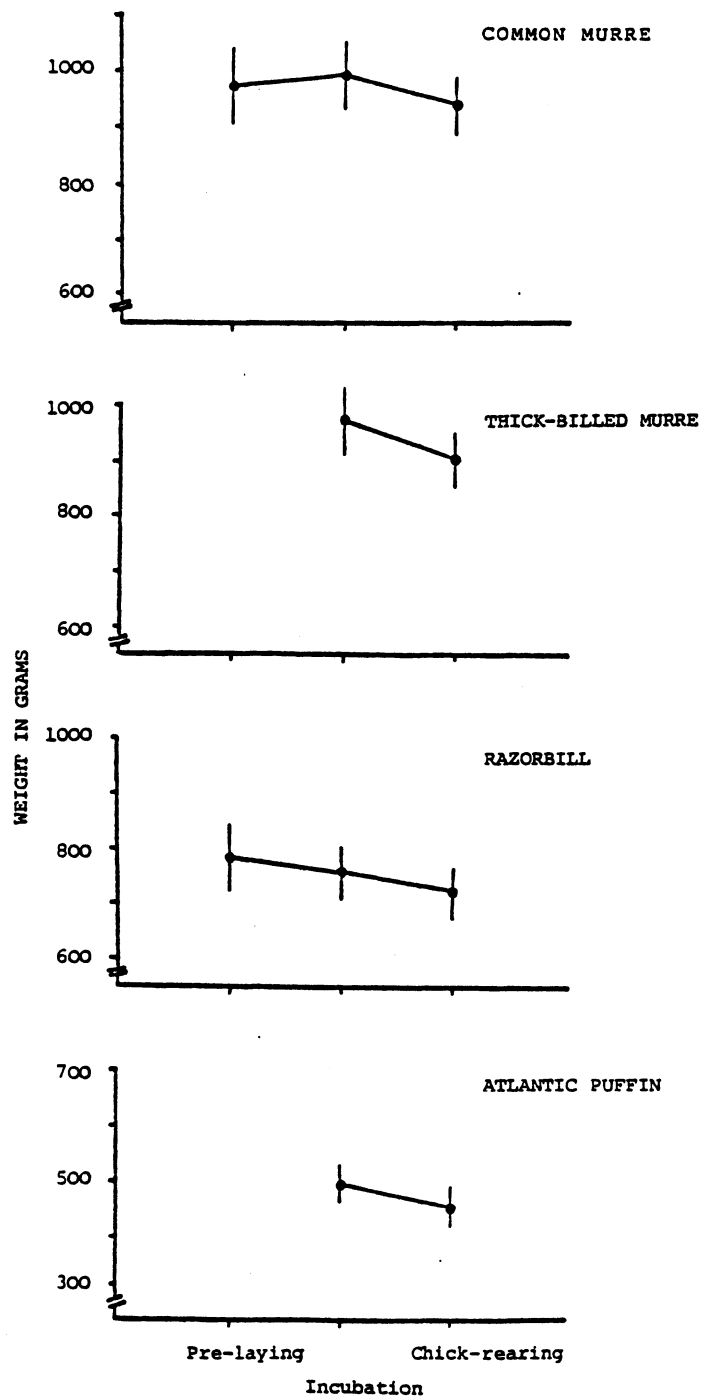


Figure 5. Seasonal changes in adult body weights of alcids breeding at the Gannet Clusters 1982. Values are means \pm S.D..

The percentage weight loss between incubation and chick-rearing differed between species and between years. In 1981 Common Murres lost 7.6% whereas in 1982 the loss was 4.9%. In 1981 Thick-billed Murres lost 4.6% but 7% in 1982. Razorbills lost 8.7% in 1981 but 4.2% in 1982. Atlantic Puffins lost 8% in 1982.

Throughout this report where values such as egg weight or chick hatching weights are expressed as a percentage of adult weight we have used values obtained during the incubation period of 1981 (see Birkhead & Nettleship 1982a). These values did not differ significantly from those obtained during the incubation period of 1982, and using the 1981 values allowed us to make comparisons between 1981 and 1982 more readily.

TIMING OF BREEDING

In contrast to 1981 the 1982 season was relatively late, presumably because of low temperatures and extensive ice-cover at the beginning of the season (see above). Snow cover on breeding areas on the islands may also have contributed to the delay in breeding. A summary of the timing of breeding for all alcid species is given in Table 3. The order of laying (median laying dates) in 1982 was, Common Murre, Thick-billed Murre, Razorbill and Atlantic Puffin. In 1981 when laying was earlier for all species (Table 4) the rank order was Common Murre, Razorbill, Thick-billed Murre and Atlantic Puffin. However, as we pointed out in the 1981 report (Birkhead & Nettleship 1982a) the situation for Thick-billed Murre in 1981 was difficult to interpret because of the high rate of egg-loss in this species and the time when observations began. Therefore the apparent reversal of laying order between Razorbill and Thick-billed Murre may be an artefact.

In 1981 Common Murres laid both earlier and more synchronously than Thick-billed Murres (Birkhead & Nettleship 1982a), and our more detailed observations in 1982 show the same effect (Fig. 6). As in 1981 egg-laying among Razorbills was less synchronous than in Murres and Atlantic Puffins

TABLE 3. Summary of the major features of the breeding cycle of alcids at the Gannet Clusters in 1982

Species	Birds first seen on land	First eggs	Median laying	First Chicks	Median hatching	First fledging	Median fledging
Common Murre	3 June	20 June	24 June	23 July	26 July	14 Aug	19 August
Thick-billed Murre	1 June	20 June	26 June	23 July	28 July	12 Aug	20 August
Razorbill	3 June	23 June	1 July	26 July	4 Aug	17 Aug	24 August
Atlantic Puffin	3 June	24 June	1 July	7 Aug	10 Aug	13 Sept	18 September

TABLE 4. Median hatching dates for alcids at the Gannet Clusters in 1981 and 1982.

Species	Median hatching dates		
	1981	1982	Days difference
Razorbill	23 July	4 August	11
Common Murre	16 July	26 July	10
Thick-billed Murre	26 July	28 July	2 ¹
Atlantic Puffin	-	10 August	-

NOTE: ¹ May be an underestimate - see text.

TABLE 5. Pattern of egg-laying in Razorbills in four study areas at the Gannet Clusters 1982. Values are percentages.

Date	Study Area			
	GC2 A	GC4 A	GC4 B	GC4 inc.
22-25 June	5.3	10.9	2.3	31.8
26-29 June	25.0	47.8	27.2	27.3
30-3 July	23.2	17.4	29.5	13.6
4-7 July	26.8	6.5	18.2	13.6
8 July	19.6	17.4	22.7	13.6
n	56	46	44	22

NOTE: χ^2 for heterogeneity = 29.16, 12 df, $P < 0.01$

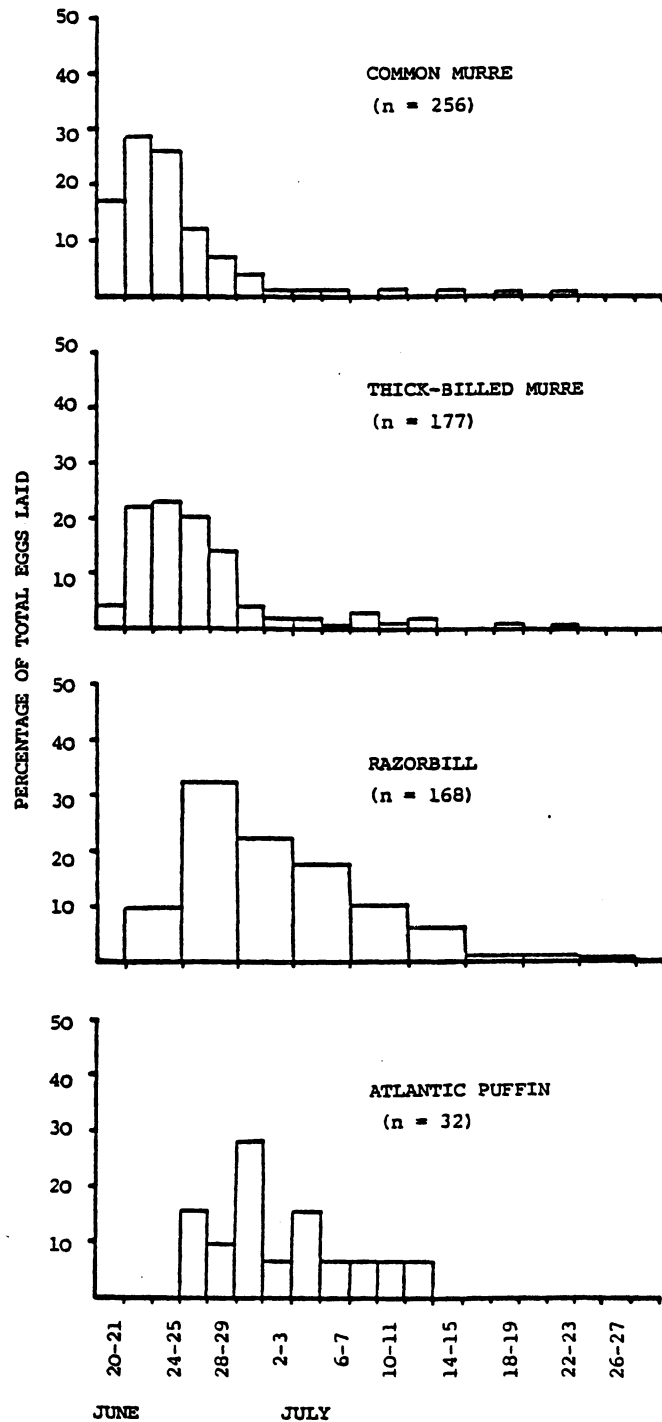


Figure 6. Frequency distribution of laying dates for alcids at the Gannet Clusters in 1982. Note that Razorbill sites were checked at 4-day intervals (hence wider bars) whereas data for other species are calculated for 2-day intervals.

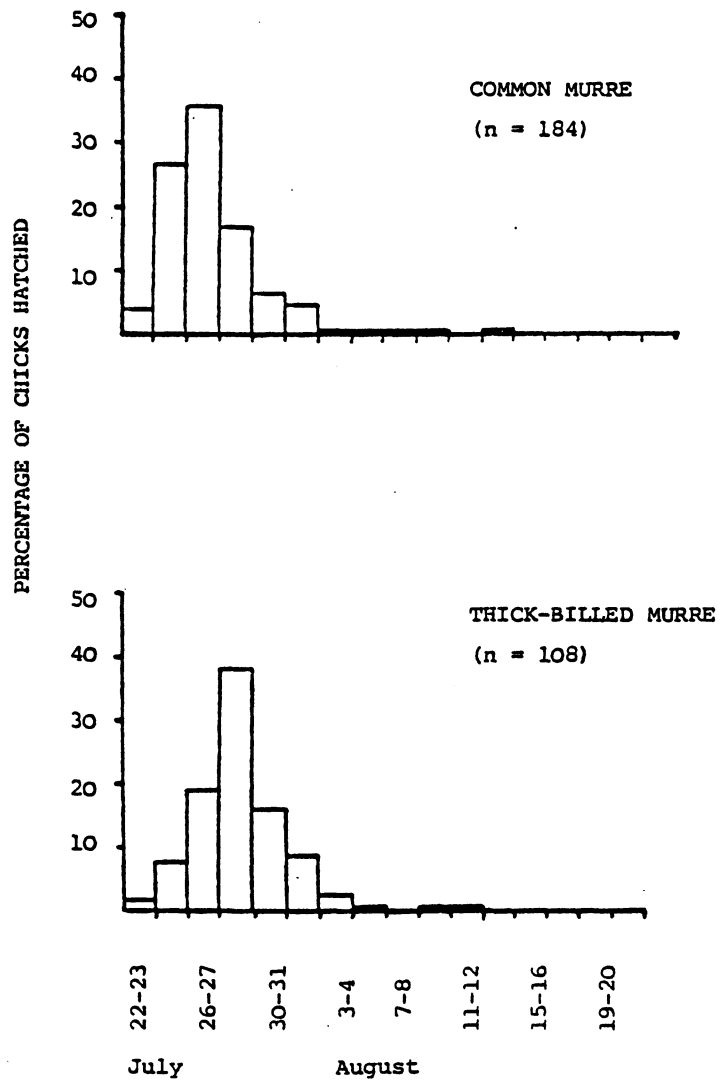


Figure 7. Frequency distribution for hatching dates in murres at the Gannet Clusters in 1982.

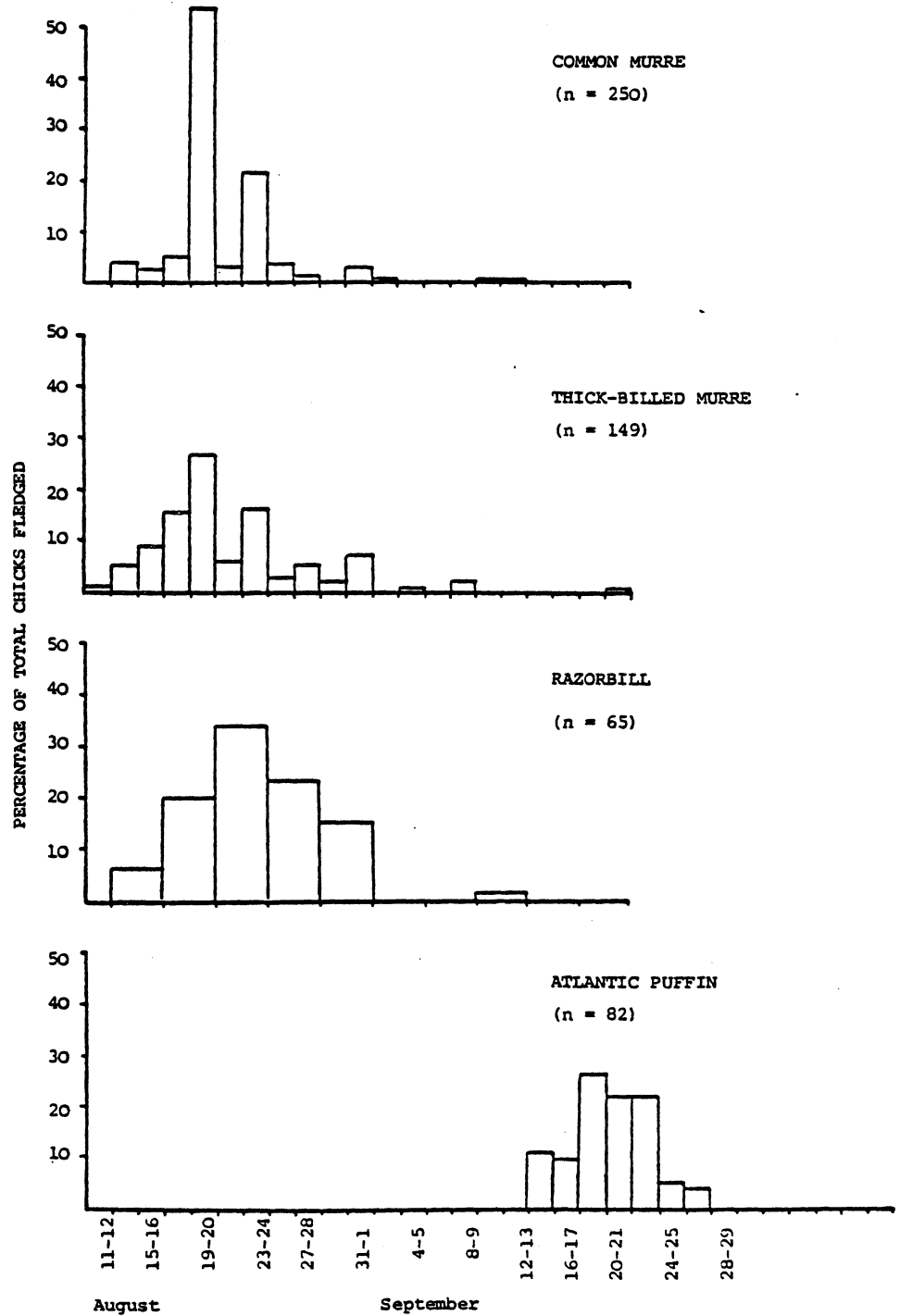


Figure 8. Frequency distribution for fledging dates for alcids at the Gannet Clusters in 1982 (see also legend to Fig. 6).

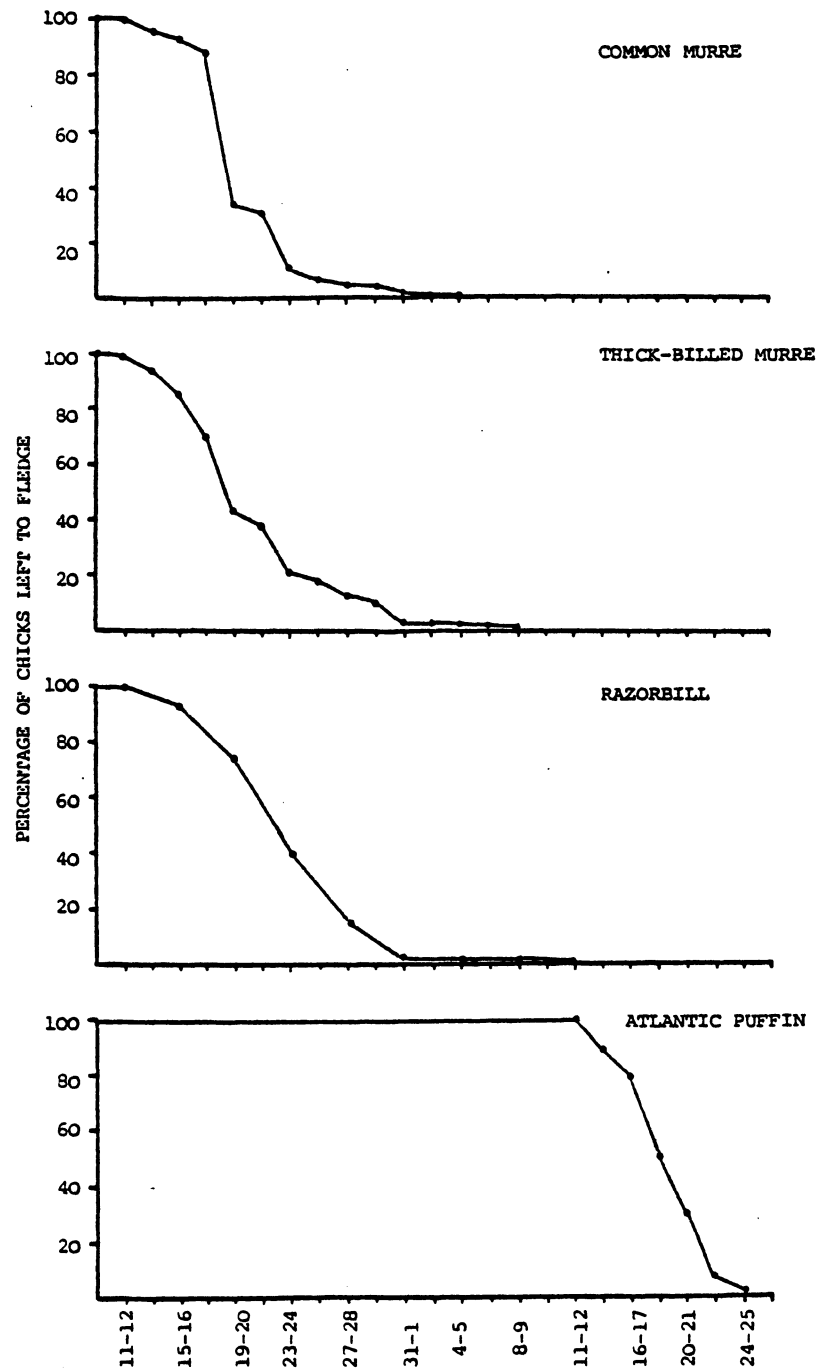


Figure 9. Pattern of fledging in alcids at the Gannet Clusters 1982.

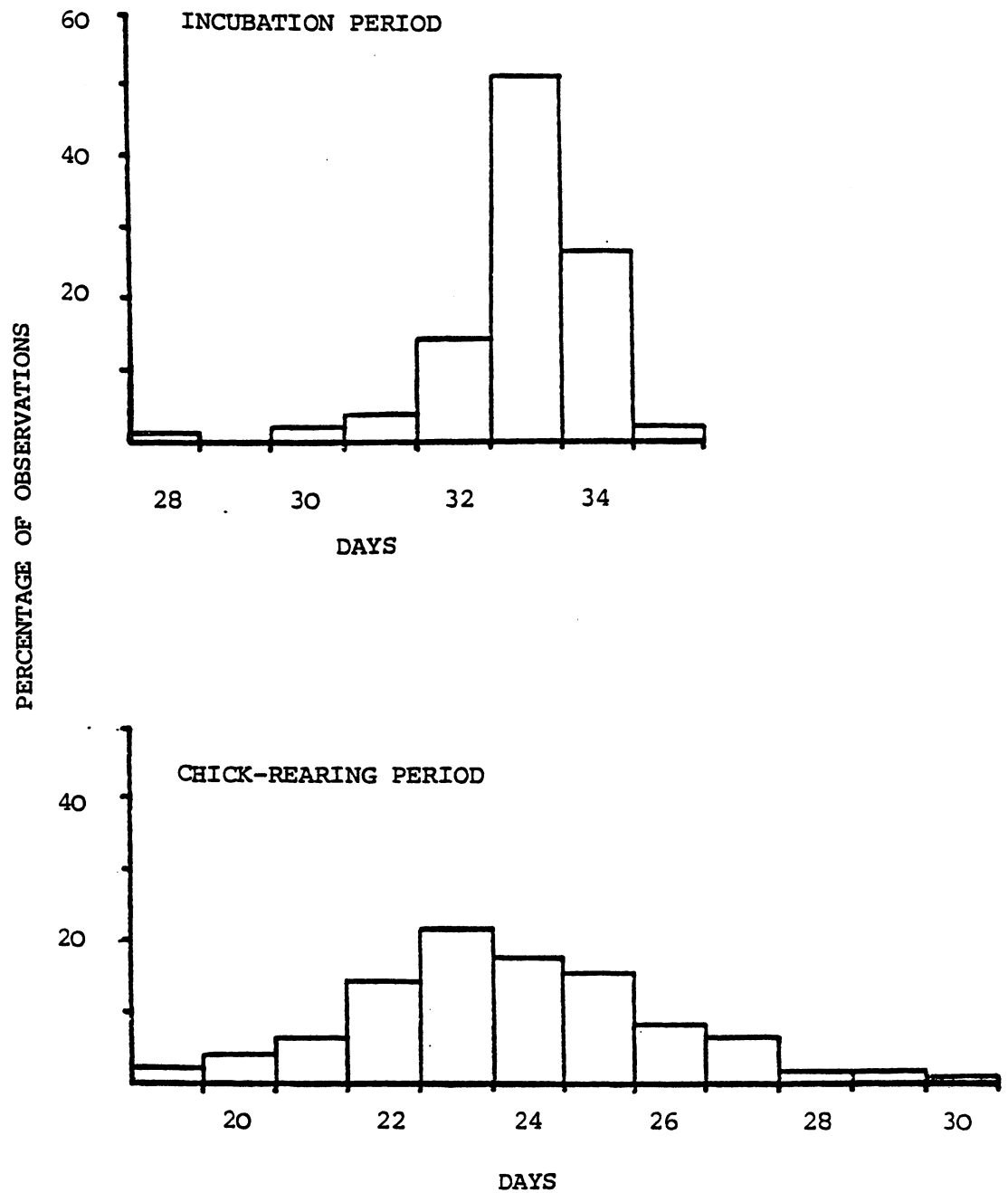


Figure 10. Frequency distribution of incubation and chick-rearing period for Common Murre.

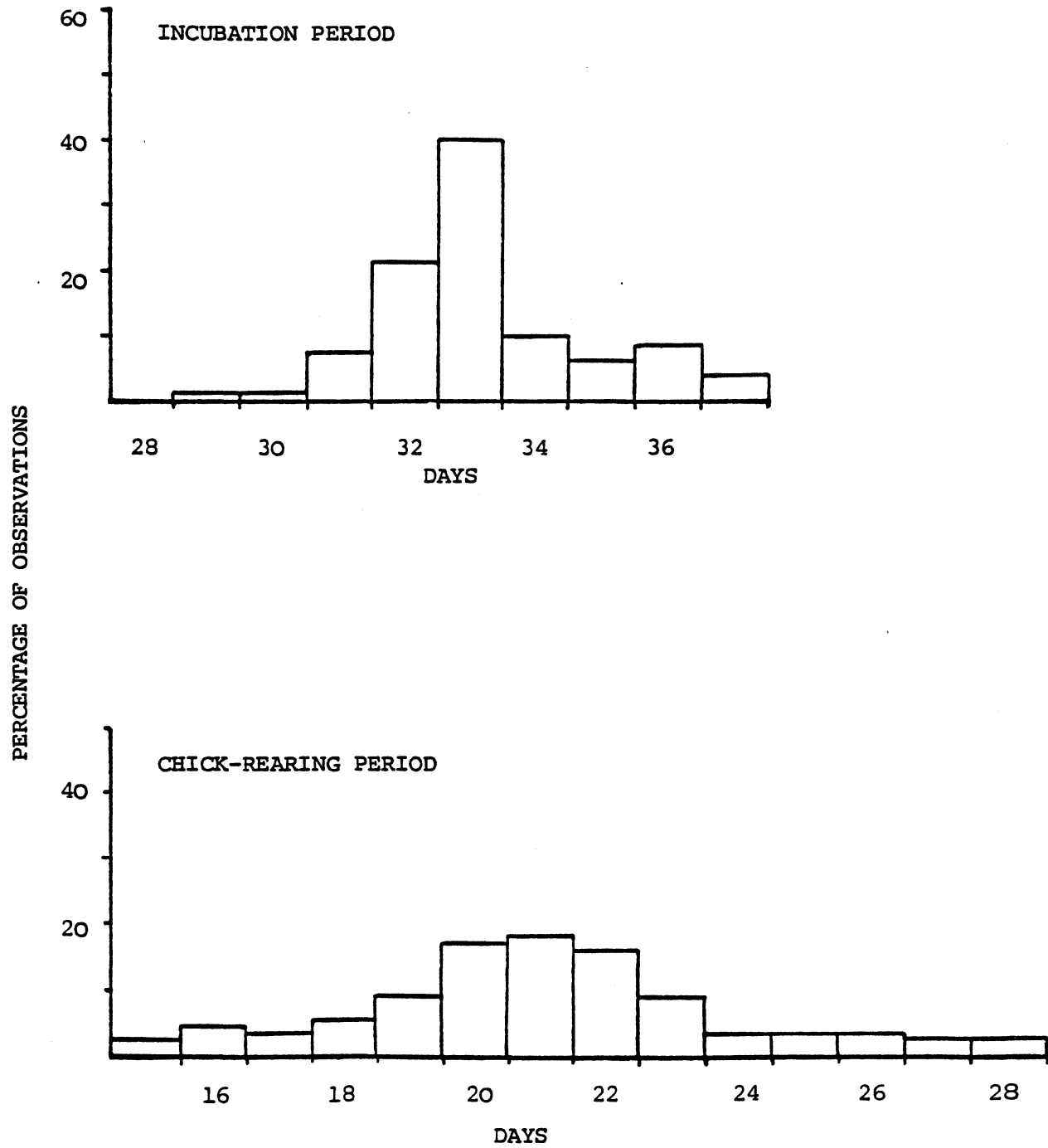


Figure 11. Frequency distribution of incubation and chick-rearing period for Thick-billed Murre.

(Fig. 6). There were significant differences in the temporal pattern of egg laying in Razorbills between study plots (Table 5).

The temporal pattern of laying, hatching and fledging for different species are shown in Figs. 6,7,8 & 9.

The mean incubation periods of Common Murre and Thick-billed Murre did not differ significantly, but, as in 1981, Thick-billed Murre chicks left the colony at significantly younger ages than Common Murre chicks (Figs. 10 & 11).

BREEDING SUCCESS

The methods used to determine breeding success differed between Razorbills, murres and Atlantic Puffin, so these will be considered separately.

(a) Razorbill. Most Razorbills breed in crevices or under boulders so that the presence of an egg or chick can be detected only by actually visiting the breeding site. However, the regular visiting of Razorbill breeding areas to check for the presence or absence of eggs or chicks undoubtedly increases egg and/or chick losses, and therefore clearly does not provide a reliable estimate of Razorbill breeding success. In some areas Razorbills breed on open ledges like murres, and it is possible to use the same observational technique as for murres, which does not involve any disturbance. However, even this may not provide a good measure of breeding success because such open sites are not typical of Razorbill breeding habitat on the Gannet Clusters. Moreover, data from other studies provide conflicting evidence concerning the relative success of Razorbills in enclosed and open breeding sites (Lloyd 1979, Hudson 1982).

Most studies of Razorbills have shown that the greatest mortality occurs during the incubation period and that usually 90-95% of all chicks which hatch survive to fledge (Lloyd 1979, Hudson 1982, Bédard 1969, Ingold 1974). In other words the major component of Razorbill breeding success is the proportion of eggs which hatch. We therefore used the following technique

22

to estimate hatching success causing a minimum of disturbance for birds breeding in a mixture of open and enclosed sites.

Four control study plots were used (Fig. 1); three were on islands other than those which we regularly worked and one, plot B, was on Gannet Cluster 2. These control plots were visited after 90% of Razorbills on our other study plots (visited every 4 days) had laid. All breeding sites with eggs within a defined area were located and identified by a number painted on the rock. The egg was also numbered and measured (length and breadth). These control study plots were then visited after an interval of 40 days, when approximately 90% of the Razorbill chicks on our other study plots had hatched. On the second visit we checked each site in turn and recorded the presence of an egg or chick, or evidence of a chick having hatched, or an empty site. Results are presented in Table 6, and suggest a relatively high hatching success. However, there are two opposing biases inherent in these estimates of hatching success. First, by leaving our first visit until after 90% of Razorbills had laid increases the chance of some eggs having already been lost, leaving only those in 'safe' sites. If this occurred, this would tend to inflate our estimate of hatching success. The other bias, operating in the opposite direction, is concerned with the presence of eggs on our second visit. Some eggs which were present on the second visit were clearly abandoned and were not being incubated, but others were still being incubated. Excluding these eggs from our calculations we would obtain a reduced estimate of hatching success, and we did not make additional visits to check for the hatching of these eggs since this would have decreased their chances of hatching still further.

On our first visit we did not find many potential Razorbill sites without eggs, so the first bias is probably relatively unimportant. Our final estimate of hatching success assumes that half the eggs still being incubated on our second visit would hatch successfully. We subjectively

TABLE 6. Breeding success in Razorbills at the Gannet Clusters
1982 on two undisturbed control plots and one
disturbed plot.

plot	No. eggs	No. eggs hatched ¹	% eggs hatched		
Control	169	135	79.9)	$x^2 = 3.98$ 1 df, $P < 0.05$
)	
Disturbed	144	101	70.1)	
)	$x^2 = 4.06$ 1 df, $P < 0.05$
GC4 Inc.	27	24	88.9)	

NOTE: GC4 Inc. vs Control $x^2 = 1.23$, 1df, N.S.

made this decision in the hope that it would counter the two opposing biases outlined above. There is some evidence that this is reasonable since our single Razorbill study plot, monitored in the manner used for murres had a similar hatching success (88.9%) to our control Razorbill plots (79%), ($\chi^2 = 1.23$, 1 df, $P > 0.1$). Hatching success for control plots compared with those visited regularly (i.e. disturbed) is summarised in Table 6.

We have also compared the breeding success of Razorbills for plots between 1981 and 1982 visited at the same rate in both years (Table 7). These data suggest that unlike murres, breeding success of Razorbills in 1982 was significantly higher than in 1981. Part of this difference may be due to the fact that some Razorbills on the study plots apparently became accustomed to our presence and remained longer at their breeding site while an observer was on the plot. Razorbills also appeared to return to their sites sooner after a disturbance in 1982 than they had done in 1981. Another factor which may have been important was that environmental conditions were better in 1982 than in 1981, with fewer cool, foggy days, higher mean daily temperatures during the chick rearing period (see Fig. 4, and Birkhead & Nettleship 1982a).

(b) Murres. The methods used to determine breeding success for Common Murre and Thick-billed Murre are the same as those outlined in Birkhead & Nettleship(1980). We observed the same two Common Murre plots as in 1981, CM-A and CM-B. The former contained 248 sites in 1982, and the latter contained 72 sites. Breeding success for these two plots is summarized in Table 8. In contrast to 1981 breeding success was not significantly higher on CM-A than CM-B, and breeding success on CM-A was significantly lower in 1982 than it had been in 1981. This difference may have been related to the later season in 1982. However, breeding success on CM-B was similar in both 1981 and 1982. For CM-A the difference in

TABLE 7. Breeding success at regularly disturbed Razorbill plots in 1981 and 1982.

Plot	Year	No. Eggs	No. Hatch (%)	No. Fledge (%)	Breeding Success
GC2 (all)	1981	346	190 (54.9)	140 (73.7)	40%
GC4 + GC2	1982	144	101 (70.1)	80 (79.2)	55%
Breeding Success $\chi^2 = 9.36$, 1 df, $P < 0.01$					

TABLE 8. Breeding Success in Common Murres at the Gannet Clusters 1982.

Plot	First Eggs			Replacement Eggs			Totals	
	No. laid	No. hatch	No. fledge	No. laid	No. hatch	No. fledge	Hatch	Fledge
CM-A	248	203	193	9	4	2	207	196
CM-B	72	61	58	7	4	3	64	61
Total	320	264	251	16	8	5	271	257
%		82.5%	95.1%		50%	62.5%	84.7%	94.8%

breeding success between 1981 and 1982 is small, and comparing all data for 1981 and 1982 the overall difference between years was not significant ($\chi^2 = 2.84$, 1df, NS).

Breeding success for Thick-billed Murre was lower than for Common Murre (Table 9) as we found in 1981. This difference was due mainly to a higher rate of egg-loss among Thick-billed Murre than Common Murre, and this in turn may have been due to a difference in habitat between the two species (see Birkhead & Nettleship 1982a). Breeding success of Thick-billed Murre on different plots were very similar (Table 9), and overall breeding success for Thick-billed Murres and Common Murres is presented in Table 10.

In 1981 observations started after egg laying had commenced and as a result we were unable in that year to determine the precise number of murre sites at which eggs were laid. In an attempt to allow for the possibility of underestimating the number of sites we calculated two measures of breeding success: a maximum value which ignored any sites regularly occupied but at which we did not see an egg; and a minimum value which assumed that all regularly occupied sites had had an egg at some stage. In reality, the true value for breeding success for both murre species would fall somewhere between these two estimates. In 1982 we were able to collect data which allowed us to re-evaluate our 1981 estimates.

To determine whether our maximum or minimum estimate of breeding success in murres for 1981 was more accurate we compared the proportion of regularly occupied sites at which no egg was laid in 1982 with the 1981 data. If these proportions were not significantly different between years this would suggest that our maximum values for breeding success in 1981 were more accurate than the minimum estimates. In fact there were no significant differences in these proportions between 1981 and 1982. Therefore in making comparisons between 1981 and 1982 we have assumed that the maximum value for 1981 is correct.

TABLE 9. Breeding success in Thick-billed Murre at the Gannet Clusters in 1982.

Plot	First Eggs			Replacement Eggs			Totals	
	No. laid	No. hatch	No. fledge	No. laid	No. hatch	No. fledge	Hatch	Fledge
TBM-A	66	49	43	5	1	1	50	44
TBM-B	87	59	52	10	6	4	65	56
TBM-C	101	76	67	9	2	2	78	69
Total	254	184	162	24	9	7	193	169
%		72.4	88.0		37.5	77.8	76.0	87.6

TABLE 10. Comparison of breeding success of Common Murre and Thick-billed Murre at the Gannet Clusters in 1982.
Data include first and replacement eggs.

Species	No. laid	No. hatch (%)	No. fledge (%)	Breeding Success (%)
Common Murre	320	271 (84.7%)	257 (94.8%)	80.3
Thick- billed Murre	254	193 (76.0%)	169 (87.6%)	66.5

NOTE: Breeding success $\chi^2 = 14.05$, 1 df, $P < 0.001$.

30

A number of factors are important in influencing breeding success. First, the timing of breeding, as in 1981, birds which laid late (replacement eggs) had a lower success rate than early breeders (Table 11). The lateness of the 1982 season compared with 1981 may also explain the overall reduction in breeding success on CM-A. In 1982 for Common Murre sites which were successful in 1981 also tended to be successful in 1982 (Table 12), which suggests that certain characteristics of either breeding sites or the birds occupying the sites had an important effect on reproductive success (see Birkhead & Nettleship 1982a).

Predation by Great Black-backed Gulls Larus marinus was probably more important in 1982 than we thought in 1981. Great Black-backed Gulls were particularly active in taking murre eggs during the early part of the season, especially during the egg-laying period, and taking chicks later on. We may have underestimated this effect in 1981 for two reasons. First, we were not present during egg-laying in 1981, and second no observers lived on GC4 in 1981 and were therefore unable to observe study plots early and late in the day: Great Black-backed Gulls seemed to be most active during these times. It is also possible that the gulls were most often seen on the murre breeding areas early and late in the day because our activity around the blinds was least at these times. However, although Great Black-backed Gulls were seen at the periphery of CM-A and CM-B, they were never seen to take either eggs or chicks from incubating or brooding birds from these plots. They did take abandoned eggs on several occasions, however.

For Thick-billed Murres the situation was slightly different. Observations made towards dusk showed that in the first few days after egg-laying some Thick-billed Murres left their egg unattended overnight. Such eggs were left alone from dusk one evening until first light the

TABLE 11. Success of first and replacement eggs in Common Murre
and Thick-billed Murre at the Gannet Clusters in 1982.

Species	No. 1st eggs	Success (%)	No. replace- ment eggs	Success (%)	χ^2	df	P
Common Murre	320	251 (78.4)	16	5 (31.2)	18.70	1df	<0.001
Thick- billed Murre	254	162 (63.8)	24	7 (29.2)	11.02	1df	<0.001

TABLE 12. Breeding success at the same sites in 1981 and 1982 at Common Murre plot A.

		1981	
		Succeed	Fail
1982	Succeed	172	16
	Fail	24	15

$$\chi^2 = 24.57, 1df, P < 0.001$$

following morning when one of the pair would return to continue incubation. We sometimes saw gulls take such unattended eggs at dusk. Although our dusk observations were not made on a regular basis, this type of egg predation probably accounted for a relatively small proportion of the Thick-billed Murre eggs which were lost. Most eggs were lost through rolling off ledges into inaccessible places or off the ledge on to areas below. Nevertheless, the fact that some Thick-billed Murres left their eggs unattended, making them vulnerable to predation contributed to this species' relatively low breeding success. Common Murres were not observed to leave their eggs unattended; the reason for this difference between species is not clear.

An additional factor, for which we have only qualitative observations concerns the loss of chicks during fledging. All Thick-billed Murre breeding areas were on cliff habitat and relatively little of the cliff habitat on the Gannet Clusters is directly adjacent to the sea. As a consequence, at fledging most Thick-billed Murre chicks alighted among boulders or on flat rock, rather than in the sea. On several occasions we saw Great Black-backed Gulls take apparently stunned Thick-billed Murre chicks which alighted on rocks. Great Black-backed Gulls also took chicks of both murre species directly from the sea and although we were unable to quantify this, the synchronous fledging by murres probably meant that only a small proportion of chicks were taken at this time.

It was very noticeable that as murre fledging started increased numbers of Great Black-backed Gulls started to remain on GC4 in the vicinity of the murre breeding areas. They occasionally scavenged chicks which had died during or soon after fledging, but appeared to be most active in hunting chicks during fledging.

(c) Atlantic Puffin. Breeding success in Atlantic Puffins was recorded in the following way. All burrows in which an egg was laid, but which

observers did not later reject, were used to measure success. Some burrows were rejected if they were subsequently found to be incomplete or if the egg or chick were inaccessible. Of 88 eggs, 58 (65.9%) hatched and 31 chicks fledged (53.5% of eggs hatched). Overall breeding success was therefore 31/88 or 35.2%. This value is almost certainly too low, probably because disturbances by observers increased egg and chick-loss.

EGG SIZE AND COMPOSITION

Egg Volumes

The mean volumes indices ($1 \times b^2$) for first eggs of Razorbill, Common Murre, Thick-billed Murre and Atlantic Puffin are presented in Table 13. Frequency distributions of egg volume indices are shown in Fig. 12 and all appeared to be symmetrically distributed. The mean volume indices of eggs for 1981 and 1982 are compared in Table 13. Only the difference between 1981 and 1982 for Razorbills was significant.

Other studies (e.g. Gaston & Nettleship 1981) have shown that egg size decreases with laying date, within a season, and also between seasons, and since the 1982 season was relatively late, we expected egg volume indices to be lower than in 1981 (when breeding was earlier), but in all species the size of eggs were very similar between years.

For Razorbills and Atlantic Puffins we were able to compare the volume indices of eggs laid at the same sites in 1981 and 1982. Since adult survival rates for these species are at least 90% per annum, then a very high proportion of sites will have been occupied by the same female in both years. Consequently eggs measured at the same sites in 1981 and 1982 are likely to have been produced by the same female. Comparing 165 Razorbill eggs using a matched pairs t test indicated no significant difference in egg volume indices between years (Table 14). The same was true for 54 Atlantic Puffin eggs (Table 14). However in Razorbills this lack of significance

TABLE 13. Comparison of mean egg volume indices of alcid eggs
in 1982 and 1981 at the Gannet Clusters.

	1982			1981			t	df	P
	\bar{x}	S.D.	(n)	\bar{x}	S.D.	(n)			
Razorbill	177.44	13.39	(255)	179.80	14.92	(333)	2.01	585	<0.05
Common Murre	218.29	19.53	(217)	218.60	18.75	(197)	0.18	412	N.S.
Thick- billed Murre	204.99	19.66	(92)	204.25	18.22	(72)	0.25	162	N.S.
Atlantic Puffin	127.67	10.61	(127)	126.97	9.69	(150)	0.57	275	N.S.

TABLE 14. Comparison of mean volume indices for eggs laid at the same sites in 1981 and 1982 for Razorbill and Atlantic Puffin.

	1981		1982		n	t^1	df	P
	\bar{x}	S.D.	\bar{x}	S.D.				
Razorbill	180.56	12.68	179.84	13.06	165	0.84	163	N.S.
Atlantic Puffin	128.00	9.38	126.05	11.66	54	1.48	52	N.S.

NOTE: 1t = matched pairs t test.

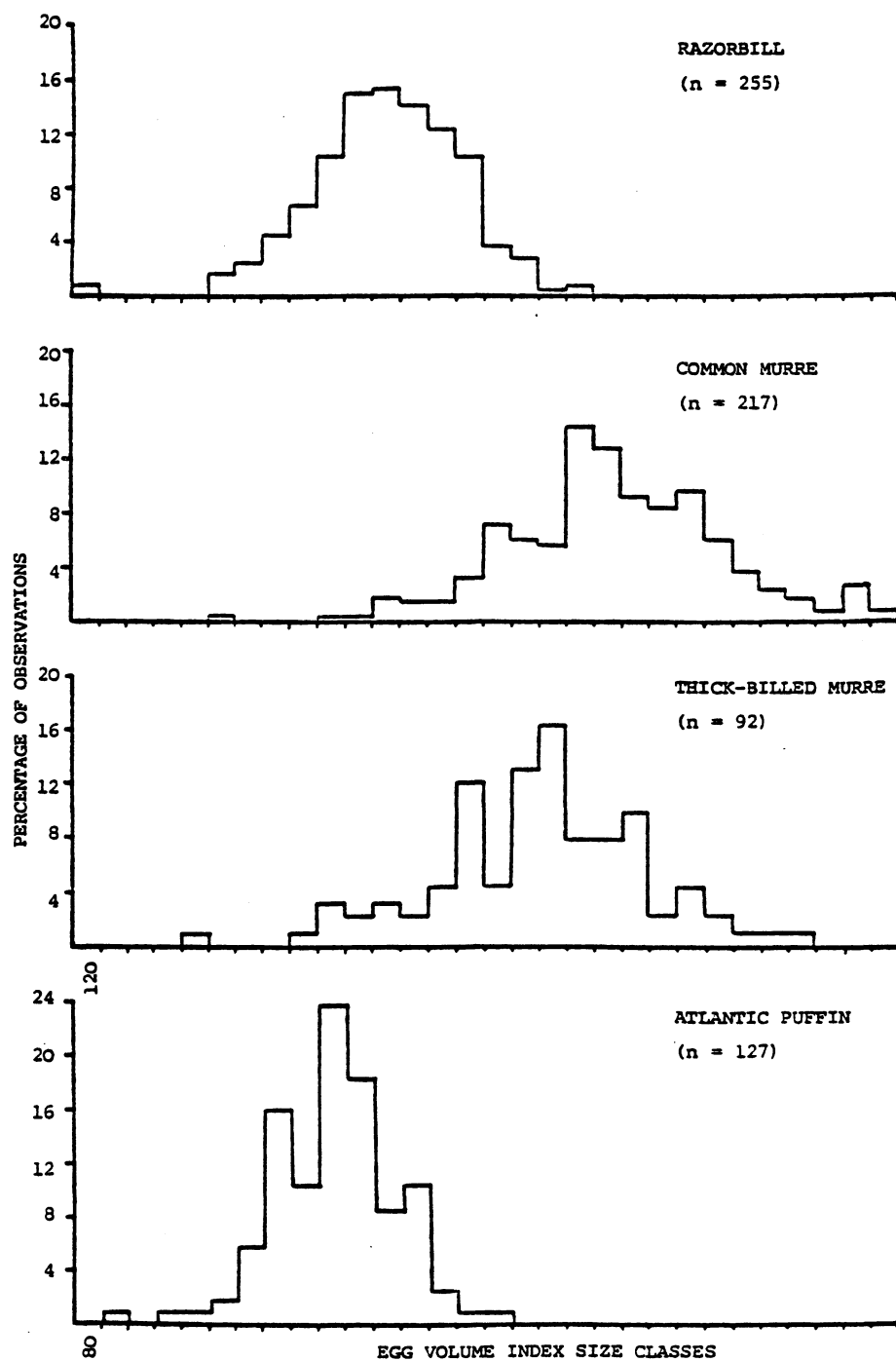


Figure 12. Frequency distribution of egg volume indices for alcids at the Gannet Clusters in 1982. For murres and the Razorbill, the x axis starts at 120- 124.9, Atlantic Puffin starts at 80- 84.9; in all species intervals are 4.9 units.

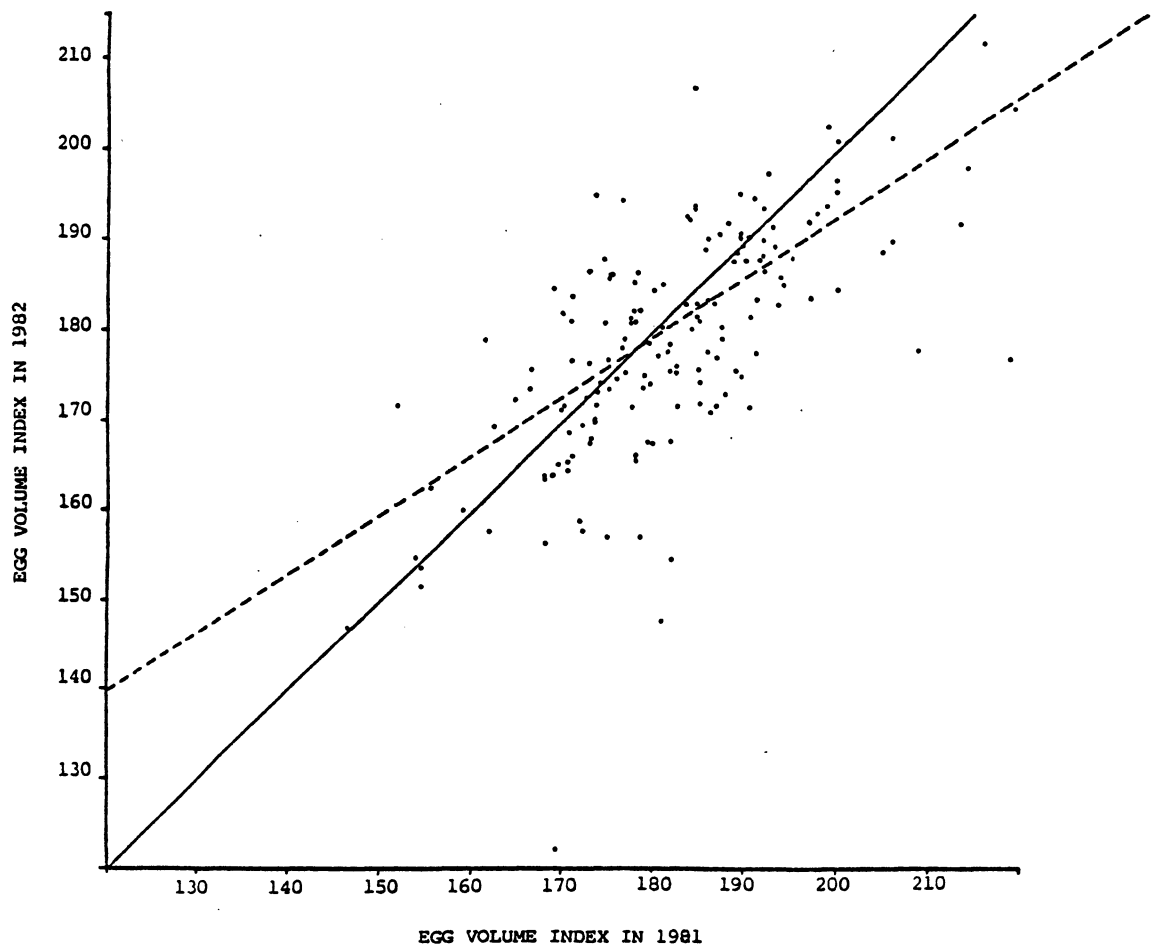


Figure 13. Relationship between egg volume index in 1981 and 1982 for Razorbill eggs at the same sites (see text for further details).

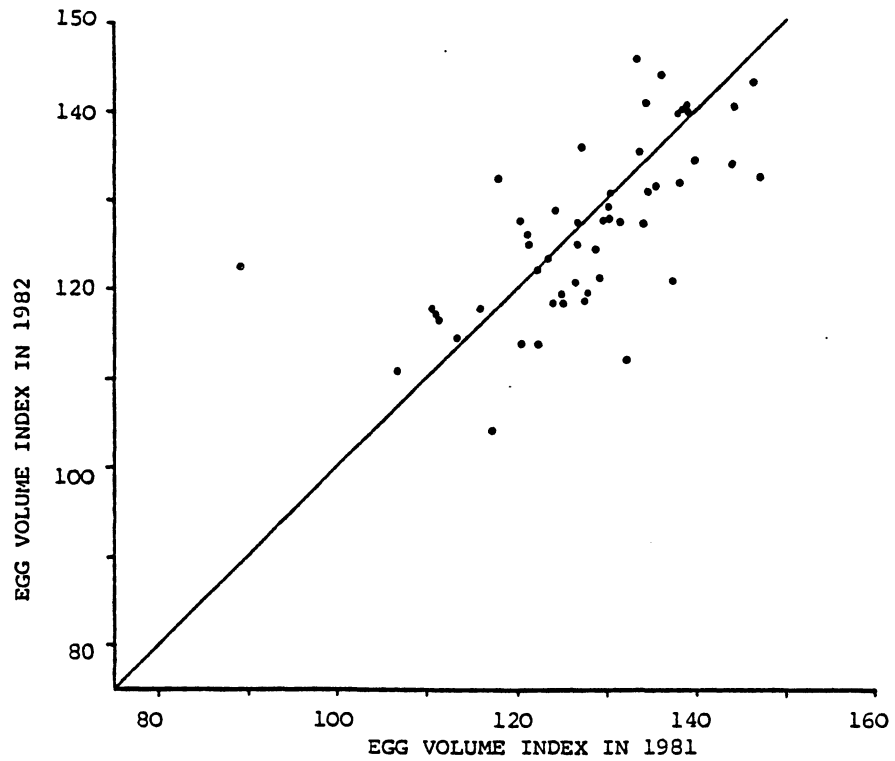


Figure 14. Relationship between egg volume index in 1981 and 1982 for Atlantic Puffin eggs in the same burrows (see text for further details).

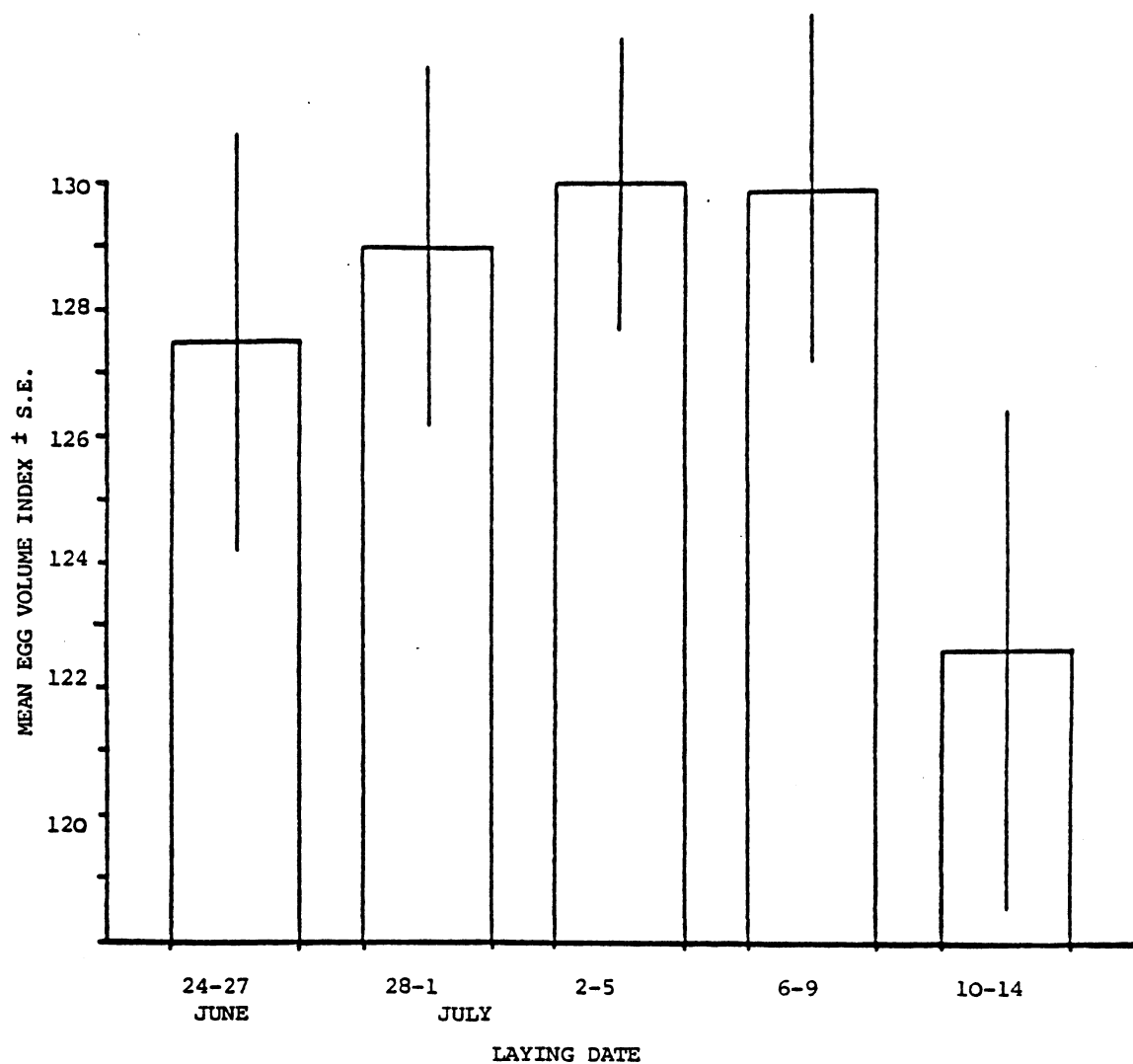


Figure 15. Seasonal changes in egg volume indices of Atlantic Puffin eggs at the Gannet Clusters in 1982.

(and the very small significant difference in means between years (Table 13)) masks a more subtle difference between years. First, as expected, there was a significant positive correlation between egg volumes in 1981 and 1982 ($r = 0.641$, 131 df, $P < 0.001$) and $r^2 \times 100 = 41.4\%$, suggesting that at least 40% of the variance in egg volume is accounted for by a female effect. Most of the residual variation is probably accounted for by a between-year effect, and the fact that some sites would be occupied by different females in the two years. Where this occurred there may be a large discrepancy in egg size between years with a corresponding decrease in the correlation coefficient and the coefficient of determination. For this reason inter-year comparisons involving cases where female identity is unknown will tend to underestimate the proportion of variance in egg size accounted for by female effects. In fact a more sensitive method is to examine the correlation between the first and second (i.e. replacement) eggs laid by the same female in a single year. Data for 1981 showed a correlation coefficient of $r = 0.815$, $P < 0.001$, $r^2 \times 100 = 66.4\%$, indicating that closer to 66% of the variation in egg size is accounted for by a female effect (Birkhead & Nettleship 1982a). A more detailed ANOVA showed that over 70% of the variance in egg size could be explained by female effects (T.R. Birkhead, unpublished).

Second, since there was little difference in mean egg volumes between years, but a strong positive correlation for eggs laid at the same site, we predicted that the slope of the relationship for egg volumes in 1981 and 1982 would be close to 1. Fig. 13 shows that contrary to our expectation the slope was 0.66, significantly less than 1 ($t = 5.46$, 161 df, $P < 0.001$). This means that females laying different sized eggs responded to the late 1982 season in different ways. Females which laid relatively small eggs in 1981 produced larger eggs, while those which produced large eggs in 1981 laid smaller eggs in 1982.

For Atlantic Puffins the predicted positive correlation between eggs laid in the same burrows in 1981 and 1982 was present ($r = 0.597$, 52 df, $P < 0.001$, $r^2 \times 100 = 35.68\%$), but the slope of the relationship did not differ significantly from 1 (regression equation $y = 0.742x + 31.02$, $t = 1.86$, 52 df, NS). In other words females produced eggs of similar relative size in both years (Fig. 14).

Seasonal Changes in Egg Size

In contrast to 1981 we obtained data to examine the seasonal changes in egg size for all species, although different techniques were used for different species. In Razorbills and Atlantic Puffins both egg volume and laying date were recorded and measured directly. Because of disturbance problems it was not possible to collect this information for the two murre species. For murre we used the same technique as Gaston (1981) which involved estimating the laying date from the density of the egg. Gaston (1981) showed that this technique is reliable, and our own independent check, with more detailed information, confirmed that the technique is adequate for examining seasonal changes in egg volumes.

Among Atlantic Puffins there was no evidence for a seasonal change in egg size, except that the latest laid eggs appeared to be relatively small. However, a one-way ANOVA did not reveal any significant difference between time periods ($F_{4,66} = 1.05$, $P > 0.01$) (Fig. 15).

For Razorbills we calculated the mean volume of eggs for 4 day periods from the start of laying (Fig. 16): this showed that a decrease in mean egg volumes occurred around 7 July, with reduced values thereafter. Overall there was a decline in mean egg size although it was not quite statistically significant ($r = -0.699$, 6 df, $P < 0.1 > 0.05$).

In Common Murres the seasonal decrease in egg volumes was most pronounced, $r = -0.895$, 5 df, $P < 0.01$ (Fig. 17). The situation was less clear in Thick-billed Murres ($r = -0.809$, 3 df, $P > 0.05$) (Fig. 18).

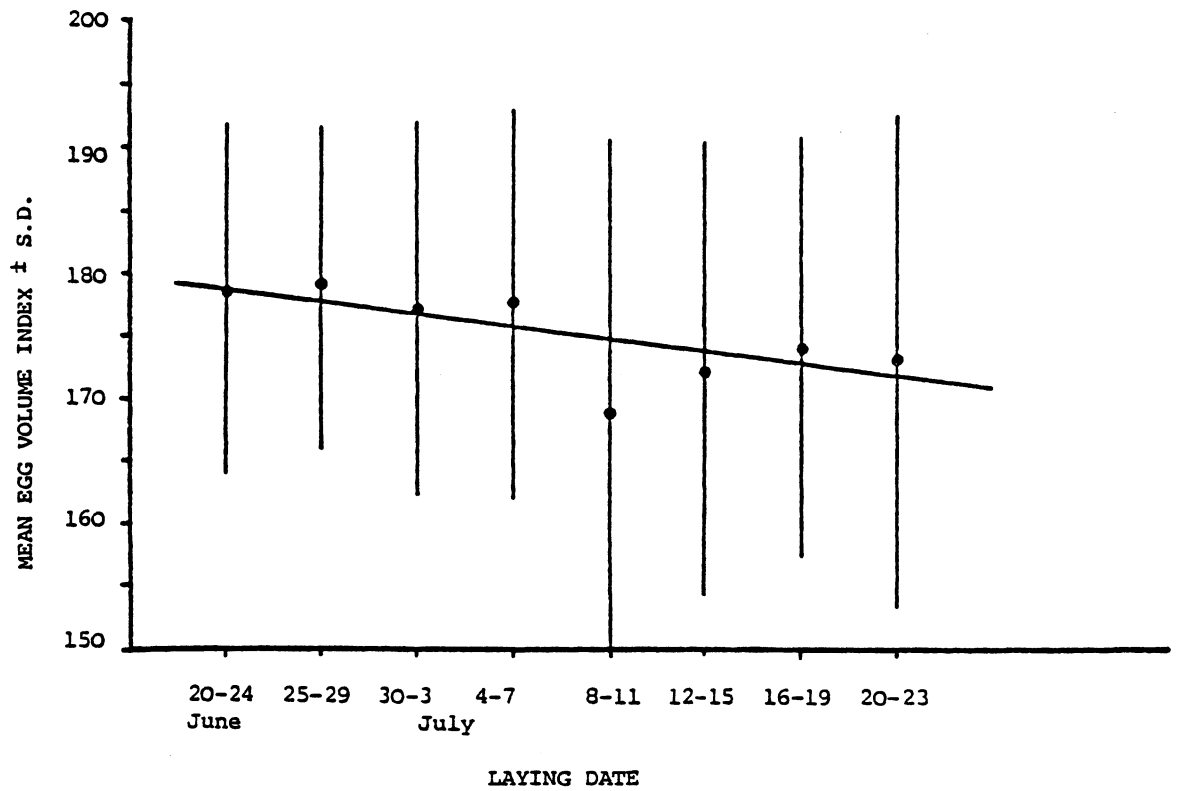


Figure 16. Seasonal changes in egg volume indices of Razorbill eggs.
Values are means \pm S.D.

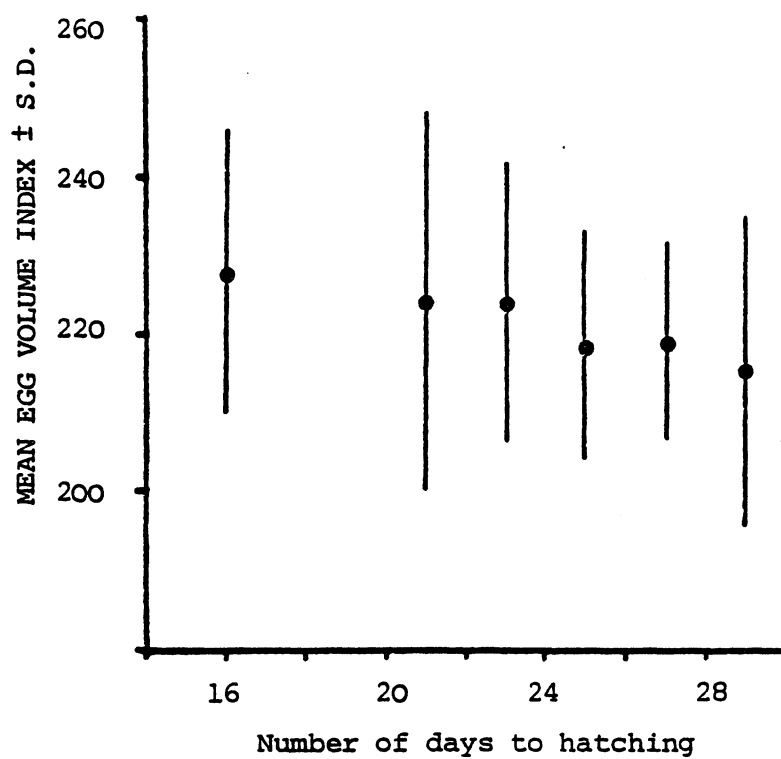


Figure 17. Seasonal changes in egg volume indices of Common Murre eggs. The number of days to hatch was determined from the density of eggs (see text).

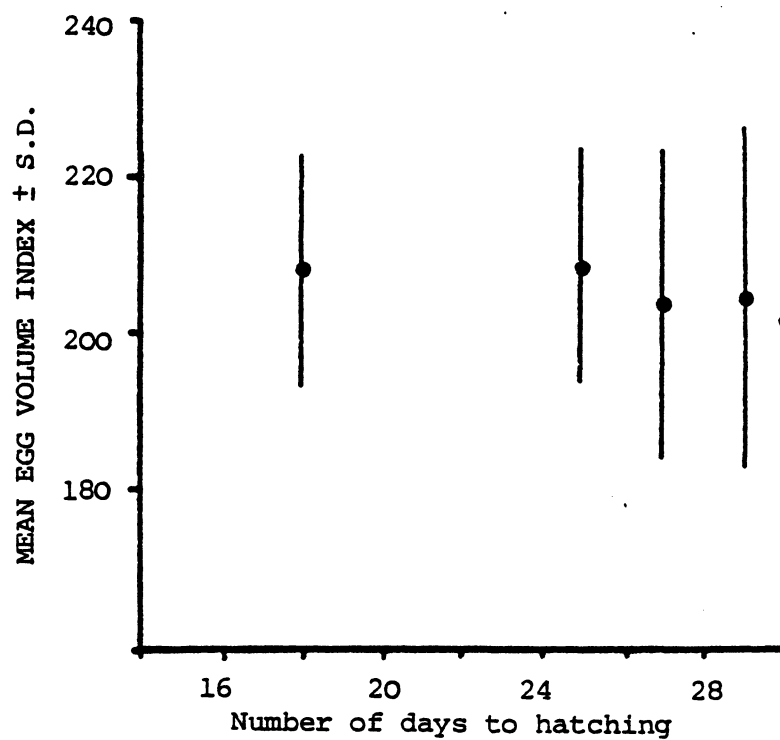


Figure 18. Seasonal changes in egg volume indices of Thick-billed Murre eggs. The number of days to hatch was determined from the density of eggs (see text).

Replacement Eggs

As our previous studies (Birkhead & Nettleship 1982a) have shown, replacement eggs in 1982 for Razorbills and Common Murres were significantly smaller than first eggs laid by the same female (Table 15). There were also significant positive correlations between the size of first and replacement eggs (Fig. 19). The difference in volume index between first and replacement eggs was $5.57\% \pm 3.38$ S.D. ($n = 7$) for Common Murres and $9.01\% \pm 6.13$ S.D. ($n = 8$) for Razorbills. This difference was not significant ($t = 1.78$, 25 df, NS), nor were the values for 1981 and 1982 between the same two species.

The interval between loss and replacement was 14.86 days ± 2.19 S.D. ($n = 7$) in Common Murres and 15.33 days ± 3.84 S.D. ($n = 9$) for Razorbills. In 1981 this interval was significantly longer among Razorbills than it was for Common Murres, but in 1982 the difference was not significant ($t = 0.31$, 15 df, NS). The above data on replacement egg size and the interval between loss and replacement were obtained by visiting sites at daily intervals. We were able to compare the interval between loss and replacement on these sites with undisturbed sites for Common Murres on study plots CM-A and CM-B: here the interval was 13.80 days ± 1.40 S.D. ($n = 10$), which was not significantly less ($t = 1.13$, 15 df, NS) than the value obtained from disturbed plots.

Among Atlantic Puffins there was a significant positive correlation between first and replacement eggs ($r = 0.756$, 5 df, $P < 0.05$) (Fig. 19). Although first eggs were larger than replacements, the difference was not statistically significant ($t = 1.25$, 5 df, NS). The interval between loss and replacement was similar to Common Murres and Razorbills, mean: 14.71 days ± 2.81 S.D. ($n = 7$).

TABLE 15. Volume indices of first and replacement eggs
for Razorbill and Common Murre.

	First Egg		Replacement Egg		t	df	P
	\bar{x}	S.D.	\bar{x}	S.D.			
Razorbill	182.04	10.84	165.37	13.12	5.90	18	<0.001
Common Murre	215.97	12.70	203.84	12.49	4.15	7	<0.01

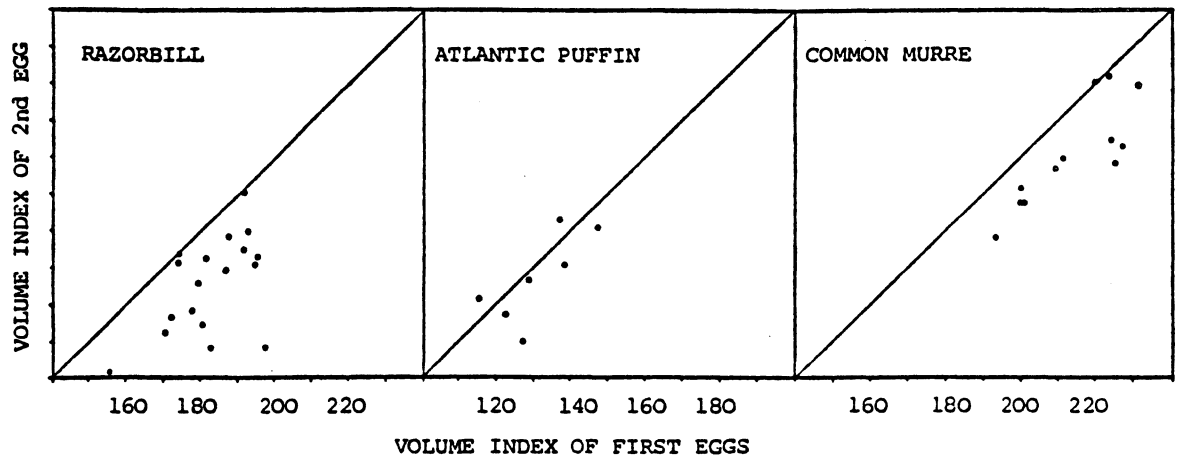


Figure 19. Relationship between the volume indices of first and replacement eggs for (a) Razorbill, (b) Atlantic Puffin and (c) Common Murre. The lines in each case represent a slope of 1; in all species most points fall below the line.

Composition of Eggs

Detailed information on the composition of eggs was obtained for all species except Atlantic Puffins in 1981 (Birkhead & Nettleship 1982 a). In 1982 we obtained details of the composition of fresh Atlantic Puffin eggs, together with small samples of Common Murre and Razorbill eggs to make inter-year comparisons of the relative amounts of yolk and albumin. Table 16 presents details of the size and composition of fresh Atlantic Puffin eggs. These data are compared with those for other alcids elsewhere (Birkhead & Nettleship, in prep.). Table 17 compares the composition of Atlantic Puffin eggs with a sample of Atlantic Puffin eggs from the Isle of May, Scotland (see Birkhead & Nettleship 1982a), and this shows that, first, egg weights at the Gannet Clusters were greater than those from Scotland. Second, among Atlantic Puffin eggs from the Isle of May, relative yolk weight was significantly greater than for eggs at the Gannet Clusters ($t = 2.29$, 26 df, $P < 0.02$), and that there were (inevitably) correspondingly smaller amounts of albumin ($t = 2.51$, 26 df, $P < 0.01$).

Among Common Murres at the Gannet Clusters, the relative size of yolks in 1982 was 2% larger in 1982 than in 1981 ($t = 2.58$, 34 df, $P < 0.02$) (Table 20). The converse was true for Razorbills: in 1981 yolk constituted 34.9% of mean fresh egg weight, whereas in 1982 the value was 32.86%, a difference of 2.07% ($t = 2.17$, 33 df, $P < 0.05$) (Table 18).

FEEDING ECOLOGY

In this section we present information on the following aspects of alcid feeding ecology during the chick-rearing period, (a) rates at

TABLE 16. Composition of fresh eggs (n = 20) of Atlantic Puffin.

Component	Mean	S.D.	C.V.
Fresh wt.	70.43	5.57	7.91
Shell wet wt.	5.65	0.63	11.15
As % fresh wt.	8.04	0.84	10.45
Shell dry wt.	4.70	0.43	9.15
As % fresh wt.	6.68	0.50	7.48
Yolk wet wt.	23.48	1.80	7.77
As % fresh wt.	33.41	2.26	6.76
Yolk dry wt.	12.30	1.01	8.21
As % fresh wt.	17.49	1.09	6.22
Albumin wet wt.	41.14	9.38	22.80
As % fresh wt.	56.66	4.07	7.18
Albumin dry wt.	6.32	1.13	17.88
As % fresh wt.	8.94	1.29	14.42
Yolk: % water	47.62	0.82	17.22
% lipid	33.79	1.20	3.55
% non-lipid dry	18.58	1.10	5.91
Albumin % water	84.08	2.10	2.50
Whole egg:			
% water	64.70	2.91	4.50
lipid % dry	34.12	2.66	7.80
Yolk : albumin ratio	0.57		

TABLE 17. Comparison of the composition of Atlantic Puffin eggs from Gannet Clusters, Labrador and Isle of May, Scotland.

Gannet Clusters (n = 20)			Isle of May (n = 8) ¹						
Component	\bar{x}	S.D.	\bar{x}	S.D.	t	df	P	F ratio	P
Fresh egg wt.	70.43	5.57	58.83	5.90	4.77	26	<0.001	1.12	N.S.
Yolk wet wt.	23.48	1.80	20.67	2.56	2.84	26	<0.01	2.02	N.S.
Yolk as % of egg	33.41	2.26	35.78	2.29	2.48	26	=0.02	1.20	N.S.
Albumin wet wt.	41.14	9.38	30.49	3.67	4.43	26	<0.001	6.53	<0.00
Albumin as % egg	56.66	4.07	52.59	2.51	3.20	26	<0.01	2.63	<0.05

NOTE: ¹ see Birkhead & Nettleship (1982a)

TABLE 18. Comparison of the composition of eggs in 1981 and 1982
for Razorbills and Common Murres at the Gannet Clusters.

1. RAZORBILL

Component	1981		1982		t	df	P	F ratio	P
	\bar{x}	S.D.	\bar{x}	S.D.					
Fresh egg wt.	96.30	9.02	94.77	7.49	0.52	33	NS	1.45	>0.1
Yolk wet wt.	33.65	4.21	31.17	3.69	1.76	33	NS	1.30	>0.1
Yolk as % wt.	34.93	2.17	32.86	2.82	2.17	33	<0.05	1.11	>0.1
Albumin wet wt.	50.96	5.02	51.18	5.26	0.12	33	NS	1.10	>0.1
Albumin % wt.	52.99	3.25	53.99	3.16	0.98	33	NS	1.06	>0.1

NOTE: n values, 1981 n = 13, 1982 n = 22

2. COMMON MURRE

Component	1981		1982		t	df	P	F ratio	P
	\bar{x}	S.D.	\bar{x}	S.D.					
Fresh egg wt.	108.83	13.50	109.05	5.84	0.06	34	NS	5.34	<0.001
Yolk wet wt.	34.53	5.46	36.53	2.25	1.34	34	NS	5.90	<0.001
Yolk as % wt.	31.56	2.46	33.53	1.95	2.58	34	<0.02	1.59	>0.05
Albumin wet wt.	58.28	6.04	58.00	4.37	0.15	34	NS	1.91	>0.05
Albumin % wt.	53.79	3.19	53.19	2.99	0.57	34	NS	1.14	>0.05

NOTE: n values, 1981 n = 15, 1982 n = 21.

which chicks were provisioned, (i) overall, (ii) in relation to calendar date, (iii) in relation to the age of chick, (iv) diurnally, and (iv) in relation to the duration of foraging trips. (b) The species* and size of prey taken by different alcid species, and (c) the daily food intake of chicks.

(a) Feeding Rates

(i) Overall Rates. Feeding rates were determined in different ways for Razorbills, murres and Atlantic Puffins. In the latter species the marked diurnal changes in feeding rate meant that to determine the rate at which chicks were fed, observations had to span the entire daylight period. For Razorbills and murres on the other hand, the lack of any marked diurnal changes in feeding rates (see below) allowed us to make observations on a number of days over a four hour period.

The highest feeding rates occurred among murres and the lowest among Razorbills and Atlantic Puffins (Table 19). The feeding rates in murres were about twice as high in 1982 as they had been in 1981, while among Razorbills rates were similar in 1981 and 1982. For Atlantic Puffins, feeding rates during the mid-chick-rearing period were slightly lower in 1982 compared with 1981 (Table 19).

(ii) Feeding rate and date. The seasonal changes in feeding rate for all alcid species are shown in Figures 20, 21, 22 and 23. In murres and the Atlantic Puffin feeding rates were highest during the mid-chick-rearing period, whereas in Razorbills the rate at which chicks were provisioned declined through the season ($r = 0.928$, $5df$, $p < 0.01$).

* Scientific names of fish species are given in Appendix 1

TABLE 19. Feeding rates of alcids at the Gannet Clusters in 1981 and 1982.

	1981			1982					
	Feeding rate			Feeding rate					
Species	\bar{x}	S.D.	n	\bar{x}	S.D.	n	t	df	P
Razorbill ¹	0.68	0.18	4	0.58	0.16	7	0.89	9	>0.05
Common Murre ¹	0.73	0.10	8	1.15	0.24	11	5.35	17	<0.001
Thick-billed Murre ¹	0.69	0.16	11	1.22	0.40	11	4.09	20	<0.001
Atlantic Puffin ²	4.50	-	-	3.05	2.15	2	-	-	

- NOTES: 1. Rates are feeds/4 hours: n values are 4h observation period.
2. Rates are feeds/day (15h): data collected in different manner from other species so no statistical comparison possible.
3. ANOVA comparing feeding rates for murres and for Razorbill in 1982, $F_{2,26} = 11.15$, $P < 0.01$.

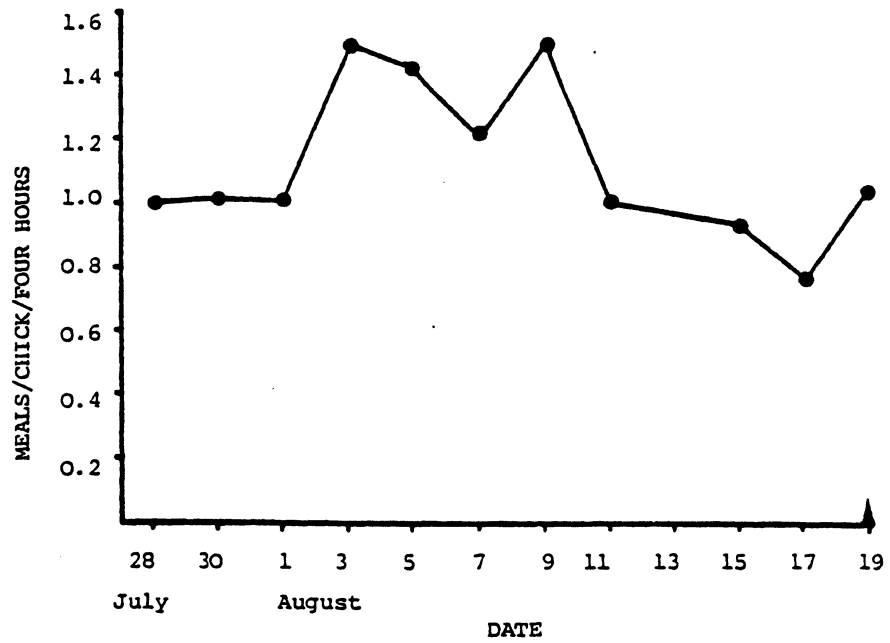


Figure 20. Seasonal pattern of feeding rate to Common Murre chicks. Arrow indicates median fledging date.

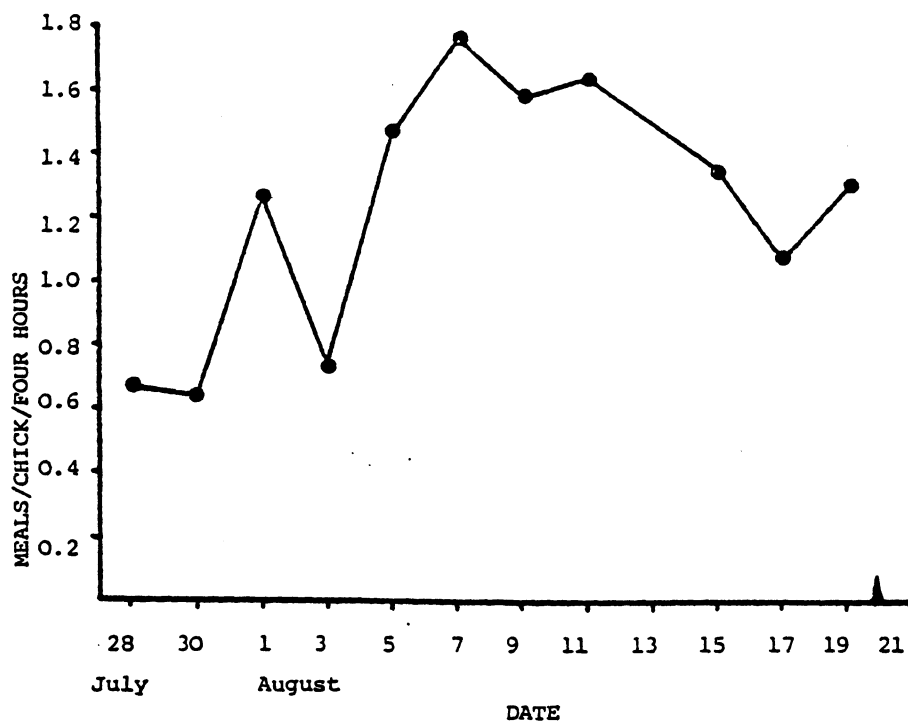


Figure 21. Seasonal pattern of feeding rate to Thick-billed Murre chick. Arrow indicates median fledging date.

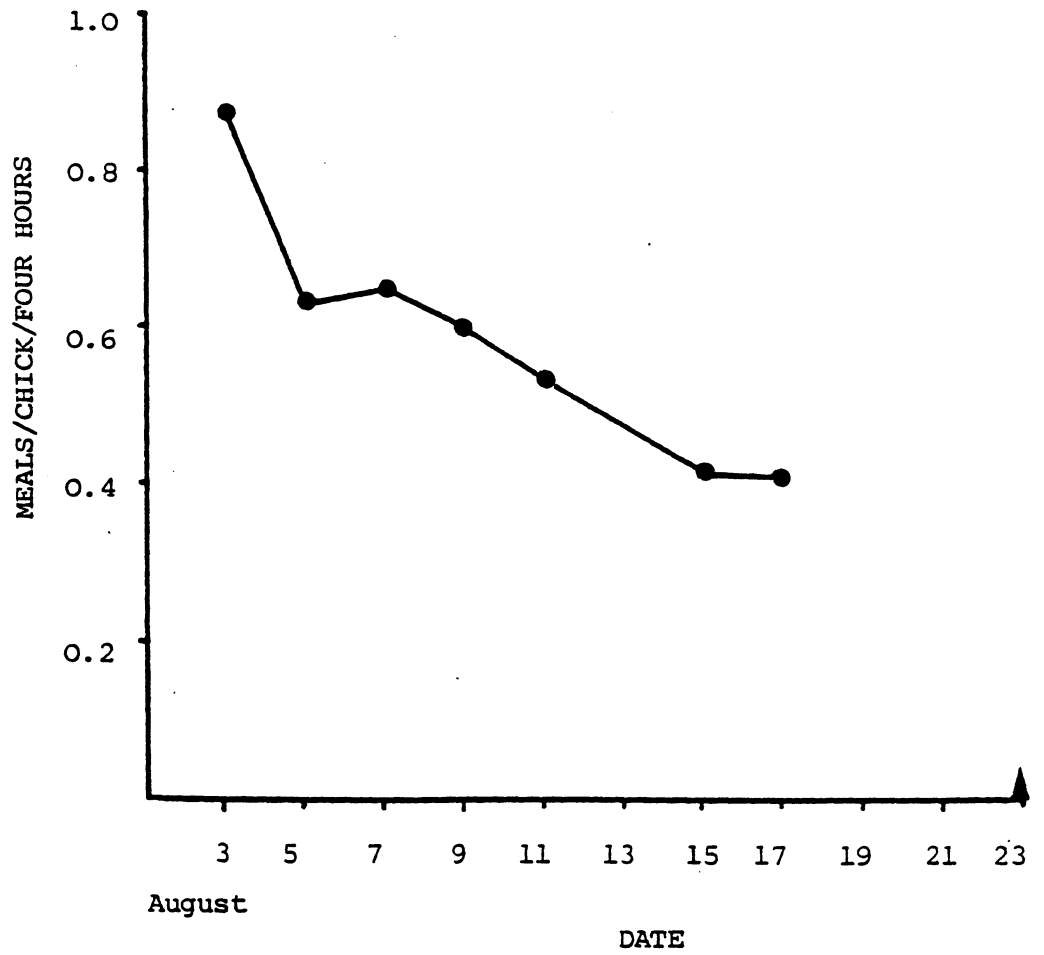


Figure 22. Seasonal pattern of feeding rate to Razorbill chicks. Arrow indicates median fledging date.

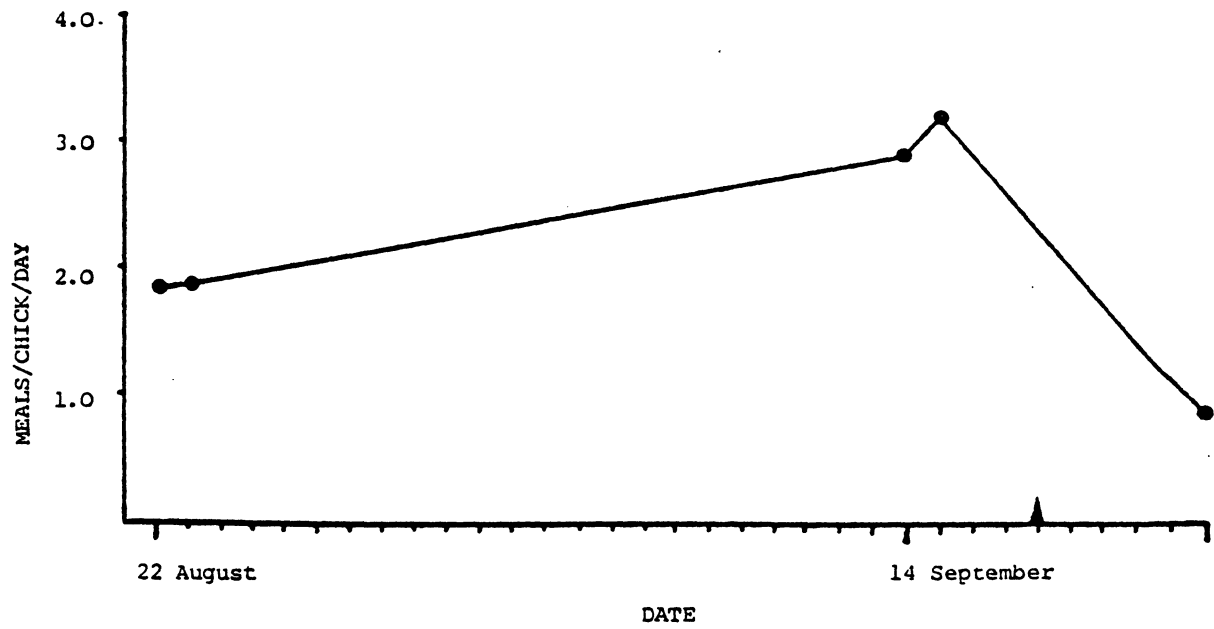


Figure 23. Seasonal pattern of feeding rate to Atlantic Puffin chicks. Arrow indicates median fledging date.

Because hatching in most species was fairly synchronous it is difficult to separate the effects of calendar date and chick age (see next section).

(iii) Feeding rate and chick age. We have insufficient information to examine this relationship for Razorbills, but in Common Murres there appeared to be a clear pattern of feeding rate in relation to chick age. Both older and younger chicks were fed at lower rates than middle-aged chicks (Fig. 24). The same type of effect was apparent in Thick-billed Murres, although there was less evidence for a decline in feeding rate to older chicks (Fig. 25). These results are unexpected since most workers have failed to record marked changes in feeding rate in relation to the age of murre chicks (Birkhead & Nettleship 1982a), which indicates that the effects shown in Figs 24 and 25 reflect seasonal changes rather than changes directly related to the age of chicks. For Atlantic Puffins the method of data collection precluded detailed analysis of chick-age effects, but the available information provides no indication of any marked change in feeding rate in relation to the age of chicks.

(iv) Diurnal patterns of chick feeding. Diurnal patterns of feeding rates are shown in Figs. 27 and 28 for murres and the Atlantic Puffins, respectively. No data were obtained for Razorbills in 1982, although detailed information was collected in 1981 (see Birkhead & Nettleship 1982a). The results shown in Figs. 27 and 28 are similar to those recorded by other workers: for Atlantic Puffins a peak of feeding in the early morning, and for murres, a similar pattern of feeding over the entire daylight period (see also Birkhead & Nettleship 1982a).

(v) Foraging trip duration. Values for foraging trip durations were obtained only for the Razorbill and murres because in these species one parent remains with the chick while the other forages. In

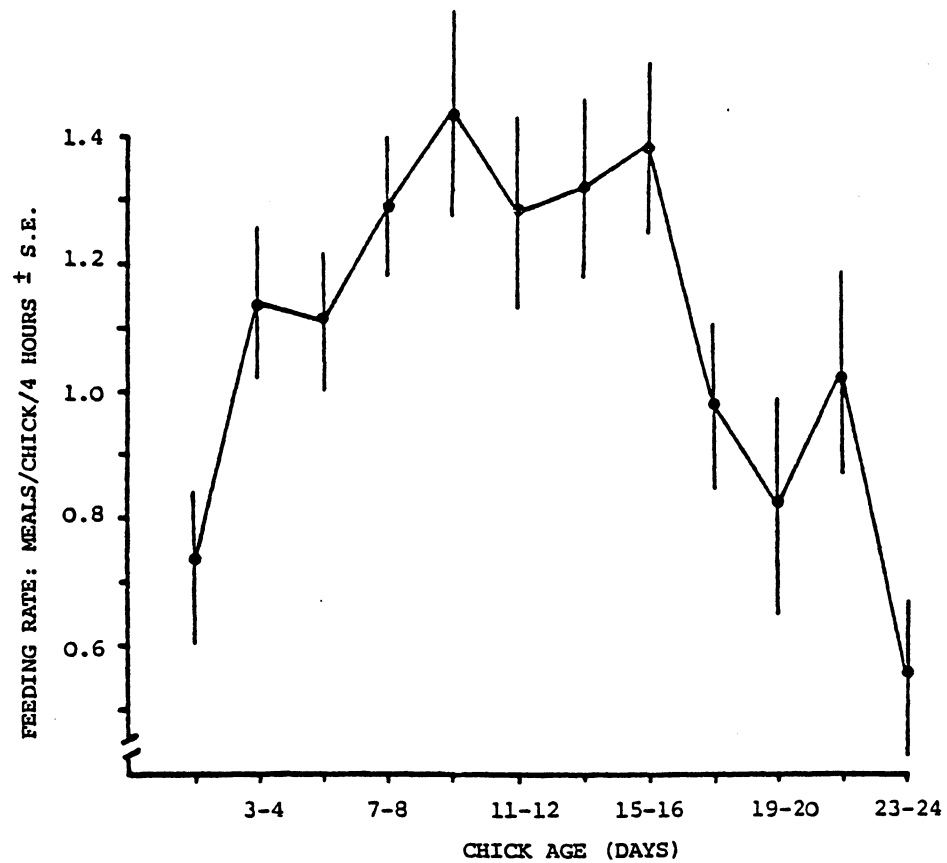


Figure 24. Changes in feeding rate in relation to chick age in Common Murre; values are means \pm S.D..

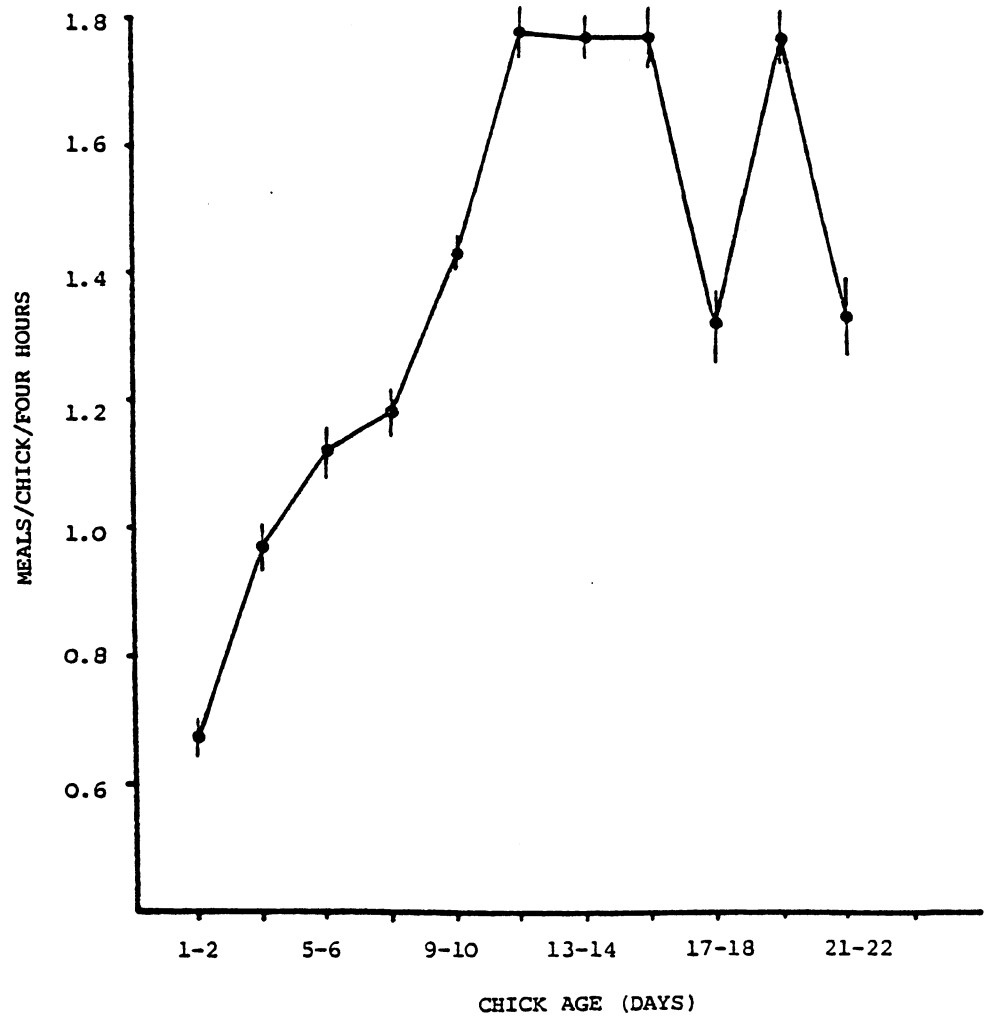


Figure 25. Changes in feeding rate in relation to chick age in Thick-billed Murre; values are means \pm S.D..

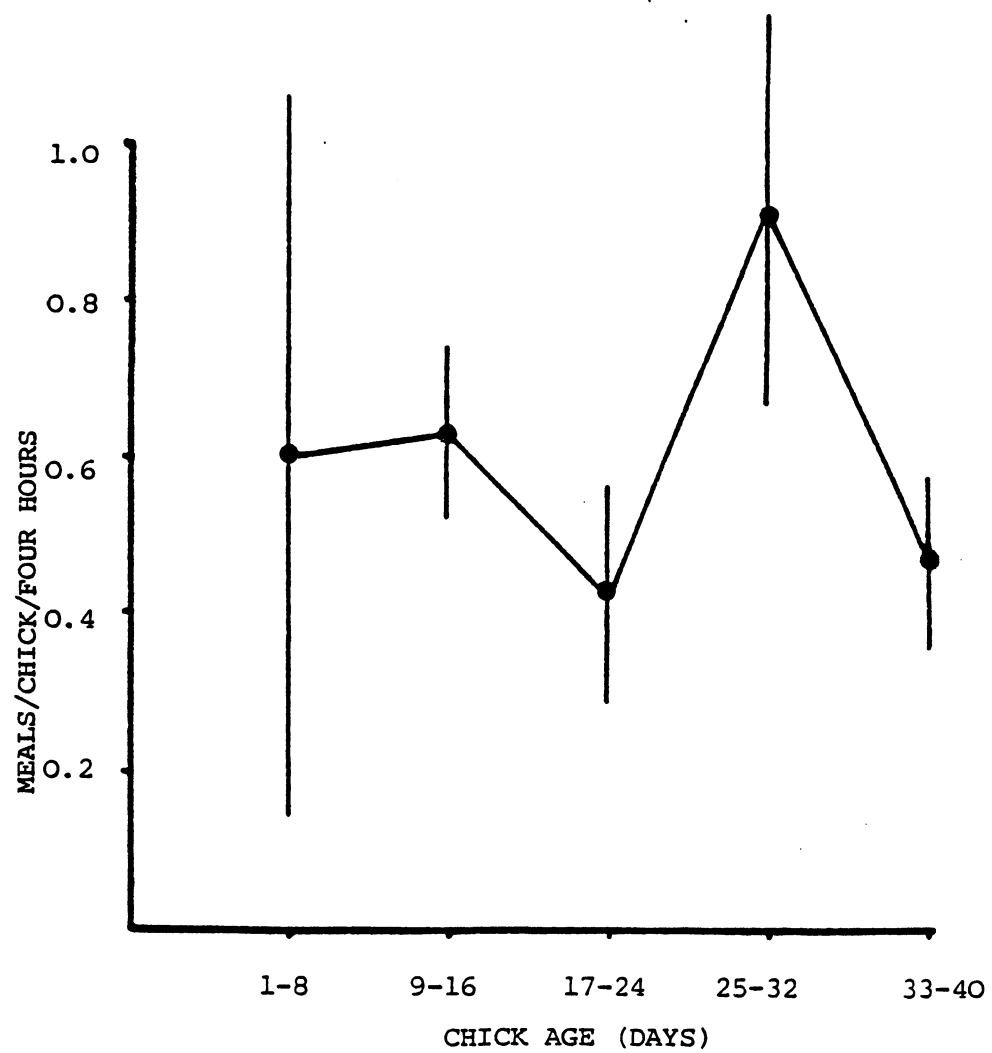


Figure 26. Changes in feeding rate in relation to chick age in Atlantic Puffin; values are means \pm S.D..

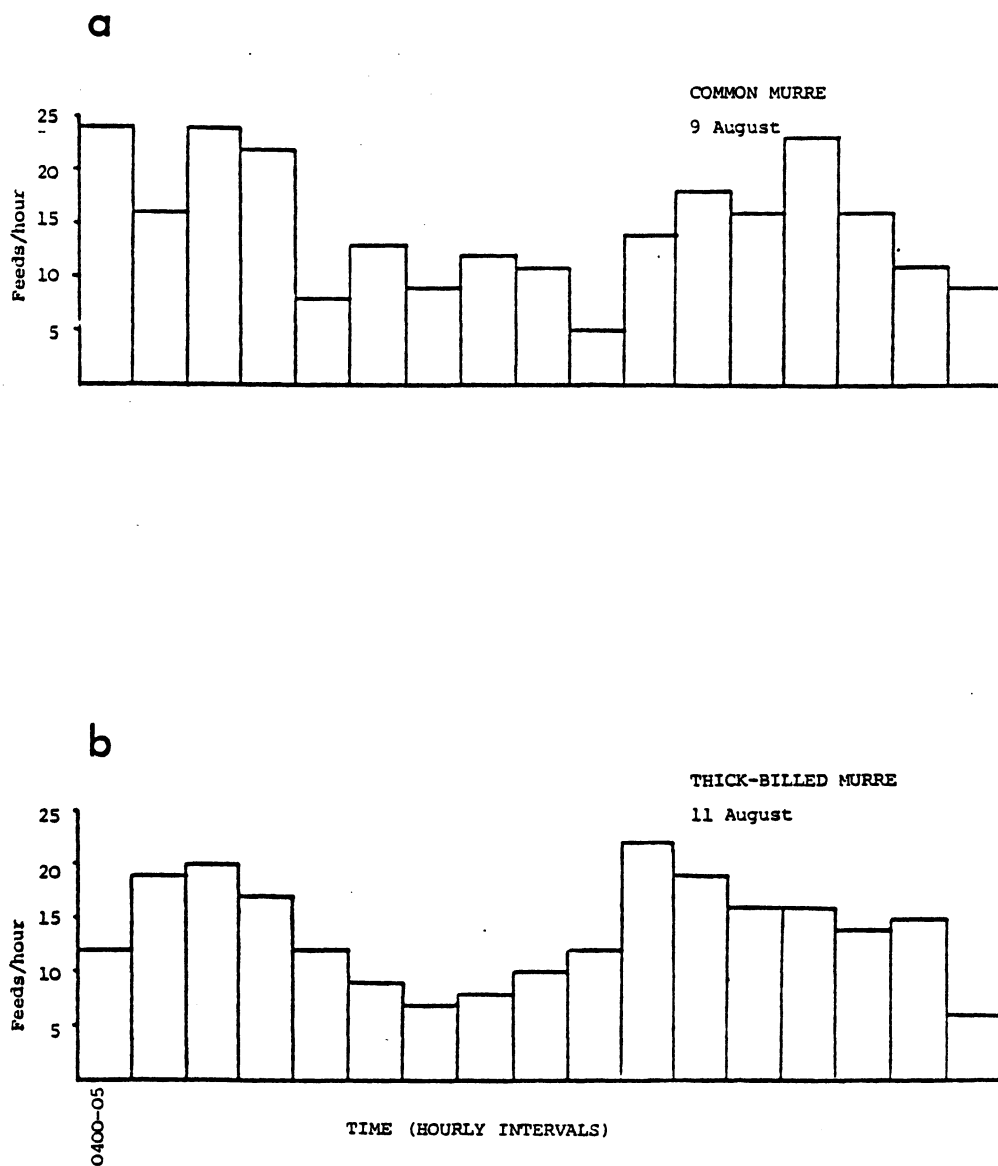


Figure 27. Diurnal pattern of feeding rates to (a) Common Murre and (b) Thick-billed Murre chicks.

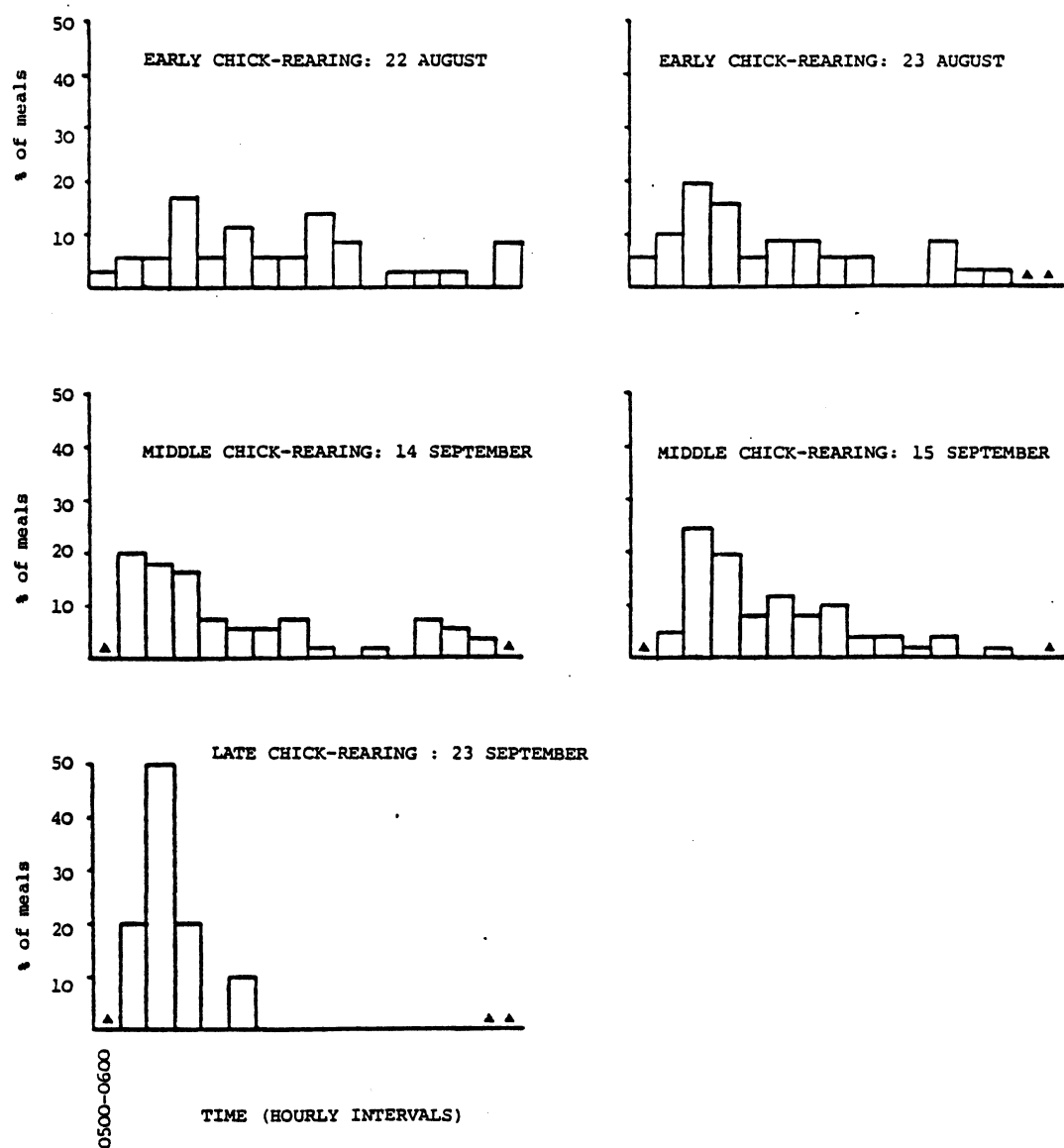


Figure 28. Diurnal pattern of feeding rates to Atlantic Puffin chicks on five days. Data for August represent the early part of the chick-rearing period, September 14 and 15, the middle and September 23 the late chick-rearing period. Triangles indicate hours in which no observations were made.



Figure 29. Trip duration for Common Murre, Thick-billed Murre and Razorbills at the Gannet Clusters 1982.

Atlantic Puffins both parents forage for the one chick, so it is not possible (without individually colour-marked birds) to distinguish members of the pair. The results are shown in Fig. 29. The median trip durations were the same for the two species of murre; 63 minutes, but were significantly longer (103 minutes) in the Razorbill ($p < 0.001$). This difference is as we would have predicted from the size of meals brought to chicks (see below).

Although feeding rates in the two murre species were higher in 1982 compared with 1981, trip durations were very similar. In Common Murre the median trip duration was 63 minutes in both years, in Thick-billed Murre it was 50 minutes in 1981 and 63 minutes in 1982.

(b) Species and size of prey

The species of fish fed to alcids were determined by two methods (1) visual; where we identified fish brought in to chicks without disturbing the birds and (2) from specimens collected from the vicinity of chicks. The first method was the main one used for Razorbills and murre, while method 2 was used for Atlantic Puffin. For Razorbills and murre, method 2 was used to verify visual records.

Fig. 30 presents information on the main prey species for four species of alcid. In terms of numbers, Common Murres and Atlantic Puffins fed their chicks mainly on Capelin, while Thick-billed Murres utilized blennies and Razorbills sandlance. The size of prey species differed: for example Capelin were usually the largest species, whereas sandlance were among the smallest. Table 20 presents the mean weight of fish species brought by different alcid species to their chicks. Because prey species differed in weight, Fig. 30 may not provide the most meaningful view of chick diet. We used the mean weight of fish species

TABLE 20. Mean lengths and weight (\pm S.D.) of fish species collected from ledges and burrows.

Alcid Species	Fish Species	Length (cm)			Weight (g)		
		\bar{x}	S.D.	n	\bar{x}	S.D.	n
Razorbill	Capelin	15.86	1.47	5	17.04	4.00	5
	Sandlance	13.17	1.60	4	6.10	2.5	4
Common Murre	Capelin	13.18	1.73	31	9.36	3.8	26
Thick-billed Murre	Capelin	13.58	1.71	10	10.40	1.64	3
	Daubed Shanny	14.78	0.67	12	9.82	1.17	4
Atlantic Puffin	Capelin	12.75	2.14	117	9.9	2.0	117
	Sandlance	11.00	3.54	63	4.6	3.6	63
	Arctic Cod	9.68	0.64	5	7.0	1.4	5

TABLE 21. Mean (\pm S.D.) weight of loads for Atlantic Puffin.

Period	\bar{x} (g)	S.D.	n
15-21.8.82	13.53	8.75	42
8-16.9.82	17.64	7.71	44
21-23.9.82	16.19	8.20	14

NOTE: ANOVA $F_{2,97} = 2.68$ $P > 0.05$

TABLE 22. Meal size for Atlantic Puffins at the Gannet Clusters
and at two colonies in Great Britain.

Area	\bar{x} meal size (g)	\bar{x} feeding rate (meals/day)	g/day intake
Gannet Clusters 1982			
early	13.5	1.87	25.24
middle	17.6	3.05	53.68
late	16.2	0.79	12.08
Isle of May ¹			
1975	8.18	7.0	57.26
1976	8.23	4.5	37.03
St Kilda ²			
1974	5.88	6.8	39.98
1975	5.83	9.6	55.97
1976	4.43	8.2	36.32

NOTES: ¹Isle of May = food rich area)

²St Kilda = food poor area) from Harris & Hislop (1978)

TABLE 23. Seasonal changes in prey composition for Atlantic Puffin.

Fish Species	15-21.8.82 Early		8-16.9.82 Middle		21-23.9.82 Late		Total	
	n	%	n	%	n	%	n	%
Capelin	38	(59.4)	54	(56.8)	22	(78.6)	114	(61.0)
Sandlance	21	(32.8)	28	(29.5)	5	(17.8)	54	(28.9)
Gadid	5	(7.9)	12	(12.6)	1	(3.6)	18	(9.6)
Other	0		1	(1.0)	0		1	(0.1)
Total	64		95		28		187	

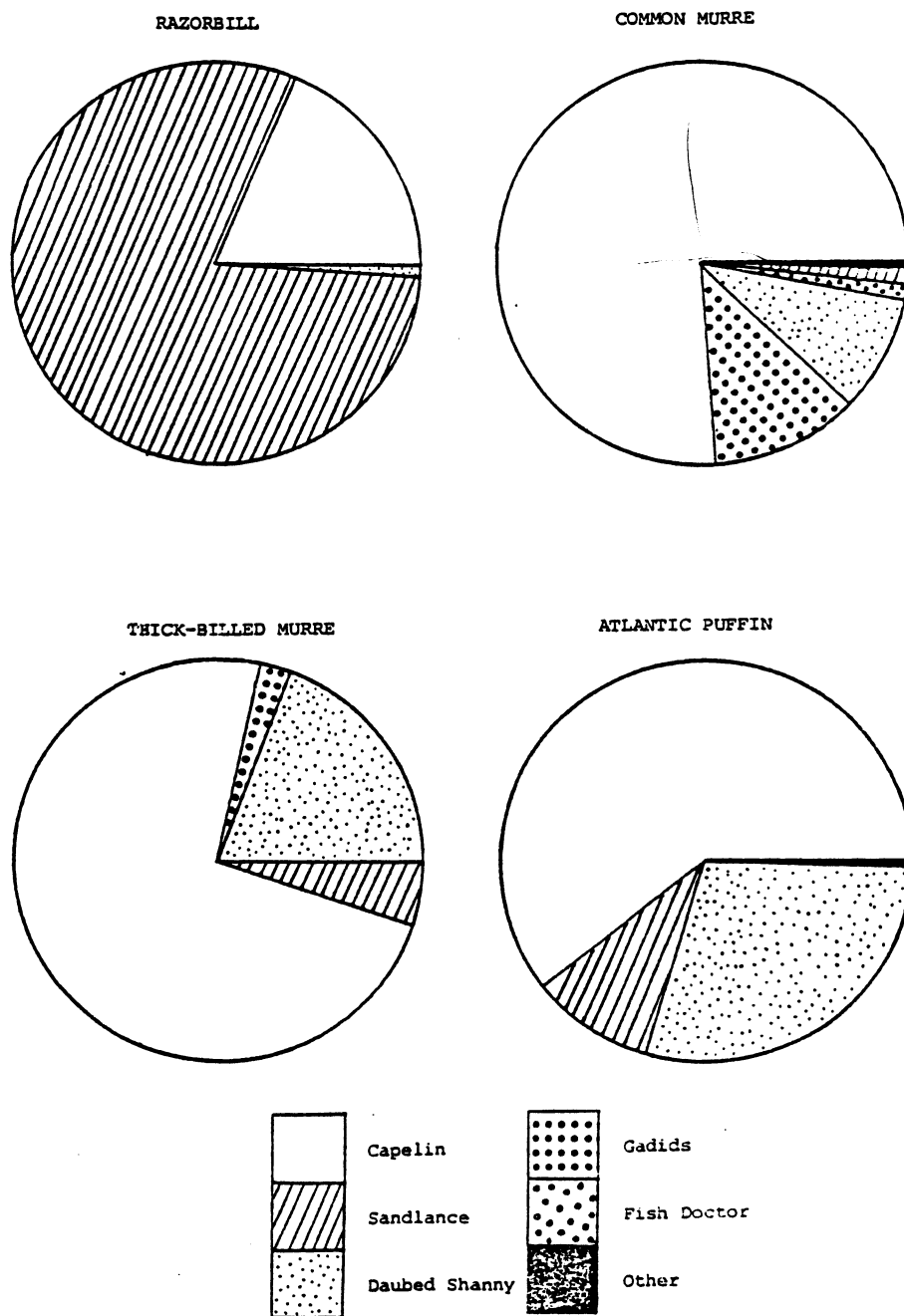


Figure 30. Percentages by number, composition of fish in alcid chick diets at the Gannet Clusters in 1982.

to produce Fig. 13, which shows the relative importance of prey species by weight. All species depended on Capelin but to different extents. For Common Murres the most important prey brought to chicks were Capelin (88%) together with blennies (8%) and gadids (5%). For Thick-billed Murres the main fish were blennies (73%) and Capelin (26.3%), for Razorbills, sandlance (62%) and Capelin (38%) and Atlantic Puffin, Capelin (72%), sandlance (20%) and gadids (8%).

The two murre species always brought a single prey to feed their chicks, so mean prey size is the same as mean chick size. In Atlantic Puffin and Razorbills, each meal comprised several fish. For Atlantic Puffin, meal sizes are summarised in Table 21 and did not differ significantly through the season. Mean meal sizes for the three periods varied from 13.5 to 17.6g, considerably larger than those recorded in most other studies (Table 22). The only area in which meal sizes were similar was at Great Island, Newfoundland. It is not clear why this difference between North East and North West Atlantic Puffin colonies should exist. One possibility is that the prey species and size classes of prey differ between the two areas. However, the main difference between the two areas is mainly in the size of loads, rather than in individual fish (Harris & Hislop 1978). The size of loads carried by Atlantic Puffin may reflect the distance which they must travel to obtain them. Data from the Gannet Clusters and Great Island, Newfoundland suggest that Atlantic Puffins may travel considerably further than birds at North East Atlantic colonies.

There is also some evidence that Razorbills brought relatively heavy meals to their chicks compared with murres. Single fish meals of Capelin were relatively heavy, averaging 17 grams. However, it was not possible to obtain complete Razorbill meals as we did for Atlantic Puffin so we can

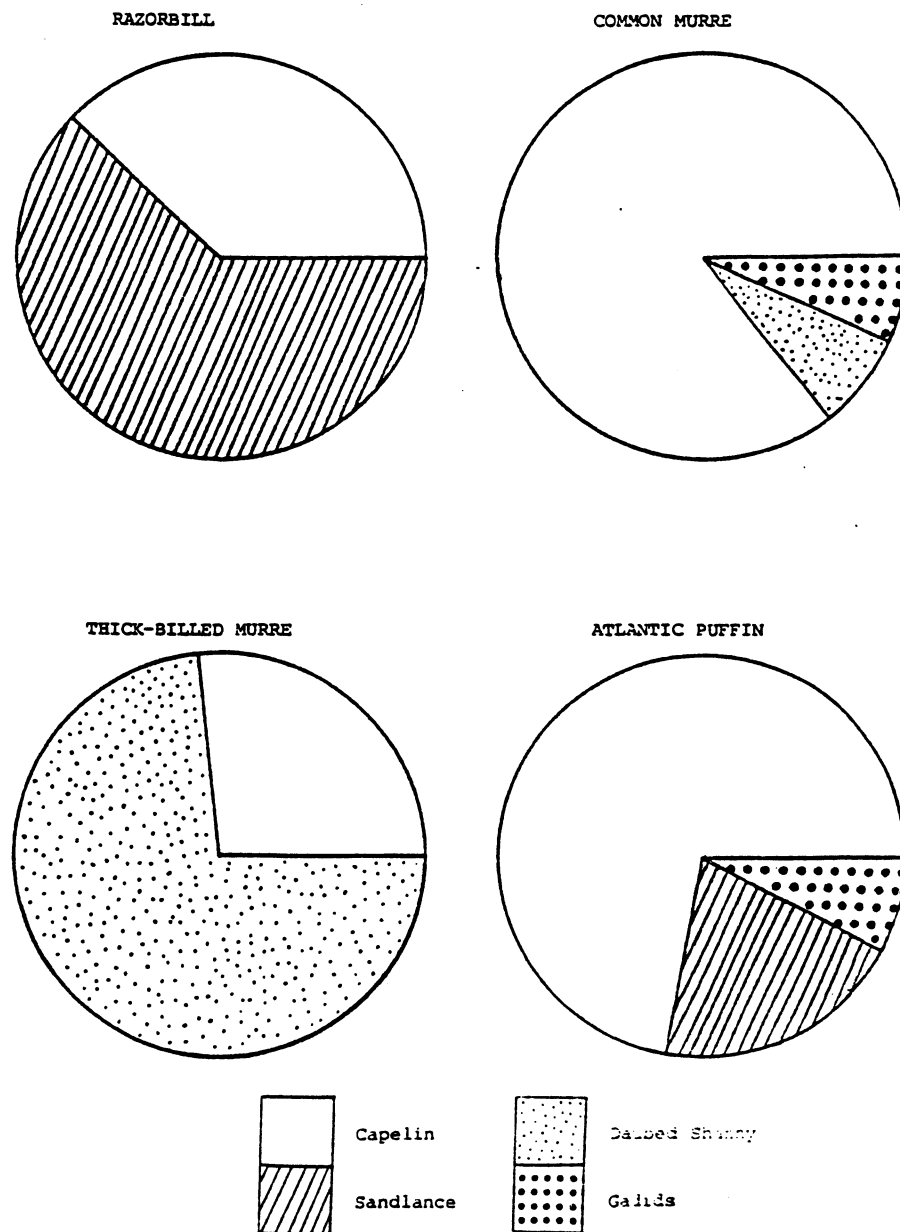


Figure 31. Percentage by weight, composition of fish in alcid chick diets at the Gannet Clusters in 1982.

provide only a relatively crude estimate of meal size. Individual Sandlance brought by Razorbills weighed 6 grams on average (Table 20). and the mean number carried per load was 2.9 ± 1.50 ($n = 39$), suggesting a mean meal weight of 17.4 grams. Our confidence in this value is increased because it is very close to the size of single Capelin meals.

Within the 1982 season there was some evidence for a change in the relative importance of different prey species among different alcids. Among Razorbills the proportion of Capelin decreased towards the end of the chick-rearing period. Similarly among Common Murre, the proportion of Capelin fell from 70-90% during the early and mid chick-rearing period, to 40% by the end of chick-rearing. In Atlantic Puffin, the prey composition in meals is shown in Table 23, which indicates that the proportion of meals containing Capelin increased significantly ($p < 0.05$) through the season, while the proportion of Sandlance decreased. There were no clear cut changes in prey size, within any species, through the season. Overall, Capelin averaged about 10g, sandlance about 5g and gadids 7g. The overall composition of Atlantic Puffin chick diet, by weight is presented in Fig. 31. Capelin was the most important species, both in terms of numbers (61%) and weight (72%), followed by sandlance (29% and 20%), and gadids (10% and 8%).

Table 24 compares some aspects of Atlantic Puffin feeding ecology between 1981 and 1982. In 1981 feeding rates were obtained only for the middle part of the chick-rearing period and gave slightly higher values (4.5 meals/day) than in 1982 (3.0 meals/day). Multiplying these mean daily feeding rates by the mean meal size gives an average daily food intake per chick of 68g in 1981 and 54g in 1982. However, since there was no difference in the growth rate of chicks in the two years (see below) it seems likely that the 1981 data on feeding rates are insufficient to make detailed inter-year comparisons. In addition, the variation in

TABLE 24. Composition of Atlantic Puffin chick diet: comparison
between 1981 and 1982.

		Capelin	Sandlance	Gadid	Notes	n
% meals containing:	1981	82.1	26.8	23.2		56 meals
	1982	77.3	13.6	15.9	χ^2 N.S.	
% composition by wt:	1981	85.6	8.1	6.3		199 fish
	1982	71.7	20.4	7.9		
% composition by total n:	1981	37.7	26.8	23.2		199 fish
	1982	60.96	28.88	9.6	χ^2 p < 0.01	

TABLE 25. Comparison of chick diets (% by numbers) for
Razorbill, Common Murre and Thick-billed Murre at
the Gannet Clusters in 1981 and 1982.

Fish Type	Razorbill		Common Murre		Thick-billed Murre	
	1981	1982	1981	1982	1981	1982
Capelin	10	20	78	76	45	20
Sandlance	80	81	7	1	20	5
Blennies	0	<0.5	14	10	33	73
Gadids	-	0	1	11	2	0
Other	9	-	-	-	-	-

NOTE: 1981 data from Birkhead & Nettleship (1982a).

feeding rates (Table 22) between the early, middle and late periods in 1982 further confound the difficulty of comparing the limited 1981 data with the more extensive material from 1982.

Prey composition differed between years and in 1981 both sandlance and gadids comprised a greater proportion of Atlantic Puffin chick diet than they did in 1982. In 1981 the proportion of Capelin, sandlance and gadid were similar, whereas in 1982 Capelin were twice as numerous as sandlance which were three times as numerous as gadids. This difference may have been related to the difference in the timing of breeding in Atlantic Puffin in the two years.

The relative importance of fish species (by number) among the four alcid species was almost identical in both 1981 and 1982 (Table 25).

(c) Food Intake of Chicks

Table 26 gives the mean weight of chick meals, the daily feeding rate and the daily food intake of chicks, averaged over the entire nesting period, for all species of alcid.

CHICK GROWTH

Murres

Because of disturbance it was not possible to obtain reliable measures of chick growth for murres.

Razorbills

The growth curve for all Razorbill chicks weighed regularly in 1982 is presented in Fig. 32a. The mean weight of chicks at day 2 was $73.75 \text{ g} \pm 8.62 \text{ S.D.}$ ($n = 32$). Peak weights were achieved close to fledging

TABLE 26. Food intake of alcid chicks at the Gannet Clusters in 1982.

Alcid	\bar{x} meal weight (g)	\bar{x} feeding rate/day	\bar{x} g/intake/ day
Razorbill	17	2.19	37.23
Common Murre	10	4.32	43.20
Thick- billed Murre	10	4.50	45.00
Atlantic Puffin	16	2.12	33.9

and, as in 1981, there was no weight recession prior to fledging. Maximum weights ($\bar{x} = 207.0 \text{ g} \pm 18.83 \text{ S.D.}$ ($n = 24$)) were similar to fledging weights ($\bar{x} = 202.85 \text{ g} \pm 17.39 \text{ S.D.}$) ($n = 33$) ($t = 1.09$, 65 df, NS). Mean fledging weights are 26.7% of mean adult weight. The pattern of growth in terms of weight increments is shown in Fig. 33, and this shows that over the first ten days of life the mean weight increment was in the order of 10 - 11 grams per day.

Hatching dates and day 2 weights were not correlated ($r = 0.192$, 31 df, NS) and this agrees with the lack of any marked seasonal change in egg size (see Fig. 16). There was a seasonal decline in growth rate, with day 10, maximum and fledging weights all showing a negative relationship with hatching date (Table 27). However, these effects are relatively weak. Chick weights at day 2 and day 10 were positively correlated, as were day 10 weights and fledging weights, but again the effects were not particularly pronounced. Chick fledging weights varied from 15 - 26 days, with a mean of 19.33 days $\pm 2.12 \text{ S.D.}$ ($n = 33$), which was not significantly different from the values obtained in 1981 ($t = 1.61$, 111 df, NS). Hatching date and fledging age were negatively correlated ($r = -0.349$, 32 df, $P < 0.05$), an effect which was not observed in 1981 (Birkhead & Nettleship 1982a).

Comparing growth parameters between 1981 and 1982, we found the following differences. Overall the growth rate in 1982 appeared to be higher than in 1981, with chicks of a given age consistently heavier than 1981. Table 28 summarizes the major difference, comparing weights at day two, ten, maximum weights, fledging weights and fledging ages. There were no significant differences between day 10 weights nor fledging

TABLE 27. Relationships between hatching date and growth parameters in Razorbills.

Relationship between hatching date and	r	df	P
1 Wt. at day 10	-0.018	32	>0.1
2 Maximum weight	-0.375	32	<0.05
3 Fledging weight	-0.227	32	>0.1
4 Wt at day 2 and day 10	+0.304	31	<0.1
5 Wt at day 10 and fledging	+0.307	31	<0.1

TABLE 28. Razorbill chick growth: 1981 and 1982 comparison.

Comparison	1981			1982			t	df	P
	\bar{x}	S.D.	n	\bar{x}	S.D.	n			
Day 2 wt.	68.80	10.27	61	73.75	8.62	32	2.46	91	<0.01
Day 10 wt.	156.78	21.51	21	161.25	19.48	34	0.78	53	N.S.
Max. wt.	199.60	23.82	80	207.70	18.83	34	1.93	112	<0.1
Fledge wt.	194.01	24.33	80	202.85	17.39	33	2.17	111	<0.05
Fledge Age	18.67	1.60	80	19.33	2.12	33	1.61	111	>0.1

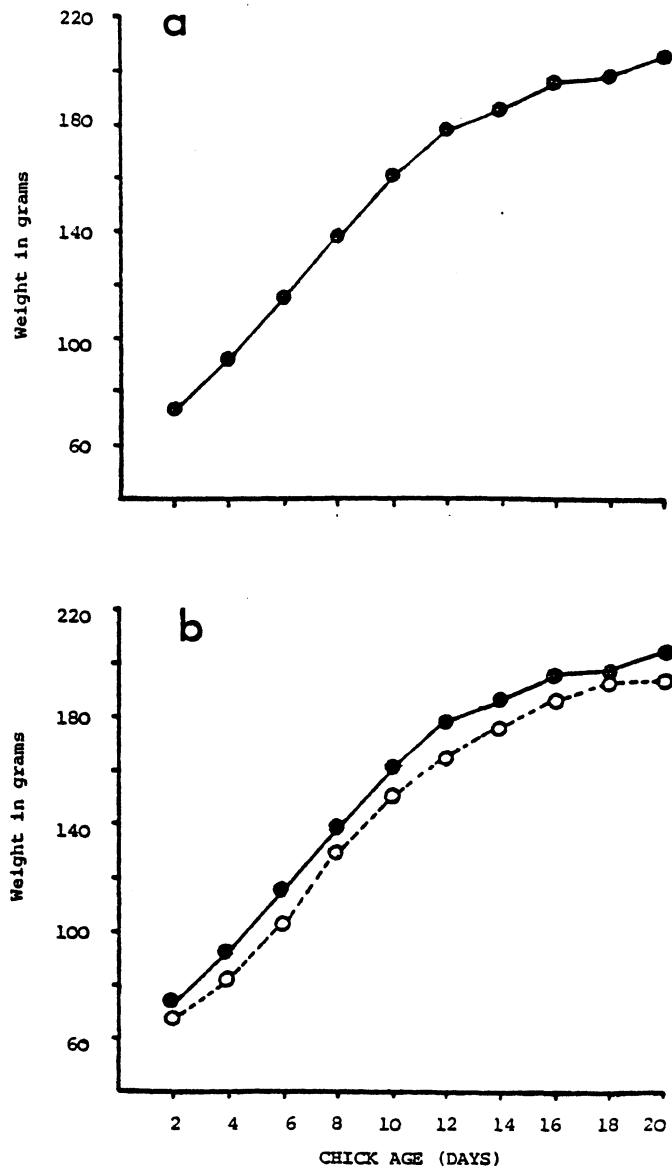


Figure 32. (a) Growth (weight) of Razorbill chicks at the Gannet Cluste in 1982. (b) Comparison of growth curves for Razorbills in 1982 (solid symbols) and 1981 (open symbols).

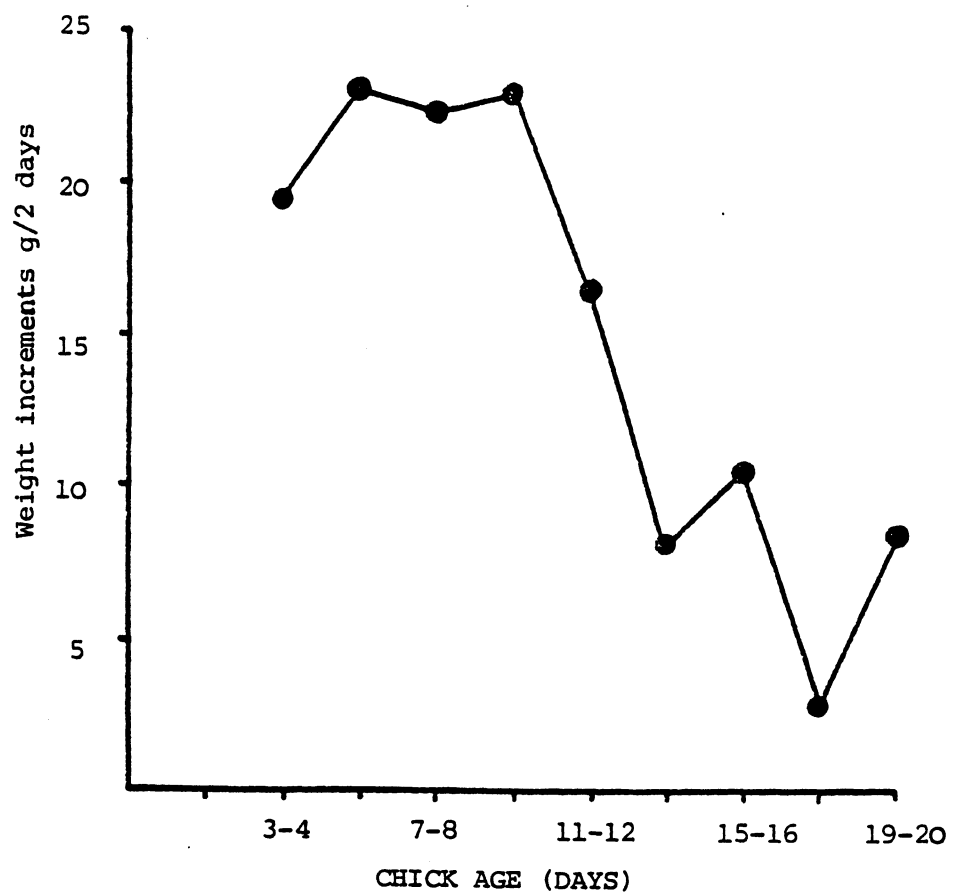


Figure 33. Weight increments in two day periods for Razorbill chicks at the Gannet Clusters in 1982.

age, but other differences were significant (Table 28). Comparing weight increments at 2 day intervals (Fig. 33) also shows that chicks in 1982 had greater weight increments over the first half of the chick-rearing period than they did in 1981. This is particularly true for the periods day 2 - 4, where the 1981 value was 16 g/2 day period versus 19 g/2 day period in 1982. The differences between 1981 and 1982 are shown graphically in Fig. 32b. Rather surprisingly, fledging weights between the two years did not differ significantly.

In both 1981 and 1982 there was a weak tendency for later hatched chicks to fledge at lower weights than early hatched ones. However, in neither year were these effects particularly marked. In 1982 the fledging age of chicks was negatively correlated with hatching date, just as we found for Common Murre and Thick-billed Murre in 1981. Among Razorbills through 1981 there was no tendency for later hatched chicks to fledge at younger ages ($r = 0.156$, 78 df, NS). It is possible that the later season in 1982 may account for this difference, since late hatching in 1982 may have resulted in greater pressure for late hatched chicks to fledge at younger ages.

We compared growth rates of chicks visited regularly with those visited only once and found no evidence that regularly visited chicks experienced lower growth rates than undisturbed chicks. Table 29 presents results for 70 chicks visited once to record their weight and wing-length. Chicks were assigned to wing-length size classes and compared with a sample of 65 weight and wing-length measurements taken at random from the sample of 34 chicks measured every two days during the chick-rearing period. There were no significant differences in weights between

TABLE 29. Comparison of weight in relation to wing-length for Razorbill chicks visited only once and those visited regularly.

Wing-length categories	Weighed once			Weighed regularly					
	\bar{x}	S.D.	n	\bar{x}	S.D.	n	t	df	P
25-29 mm	72.89	11.47	9	73.00	12.54	10	0.02	17	N.S.
30-39 mm	100.54	13.41	13	109.00	16.29	10	1.33	21	N.S.
40-49 mm	157.00	16.92	13	150.50	19.45	10	0.84	21	N.S.
50-59 mm	173.92	15.19	12	177.40	18.67	10	0.47	20	N.S.
60-69 mm	201.30	17.22	10	191.0	12.61	10	1.53	20	N.S.
70-79 mm	196.43	26.22	7	207.30	13.98	10	1.00	15	N.S.
80-89 mm	217.40	6.91	5	215.40	11.86	5	0.33	8	N.S.

wing-length classes for the two groups of chicks.

Some of the differences in growth patterns between years may be attributable to a difference in the timing of breeding (see above) and its consequences. Another possibility is that adult Razorbill responded to our presence differently in 1982 than in 1981. Our breeding success data suggest that this may be so. If, as the breeding success data suggest, adult Razorbill in 1982 were more tolerant of the presence of observers and returned to brood their chicks sooner on average than in 1981, this may account in part at least for some of the differences in the growth patterns observed. An additional possibility is that the weather conditions in 1982 were better on average, with fewer cold and foggy days than in 1981. The combination of better weather and more tolerant adult Razorbills could account for higher growth rates of chicks recorded in 1982.

Atlantic Puffin

The growth (weight and wing length) curves for Atlantic Puffins are shown in Figs. 34 and 35. The mean weight of 1 - 2 day old chicks was $50.74 \text{ g} \pm 6.72 \text{ S.D.}$ ($n = 31$), and peak weight was reached at an age of 33 - 34 days. The weight at the last weighing in before fledging was $361.85 \text{ g} \pm 37.29 \text{ S.D.}$ ($n = 79$). The mean age at fledging was determined as the mid point between two successive visits, when the chick had left the colony on the second visit. The mean age at fledging was $41.15 \text{ days} \pm 2.74 \text{ S.D.}$ ($n = 26$), for chicks of known age. The wing length of a further 53 chicks at fledging was known. Using the relationship between age and mean wing length for the 26 chicks of known age we calculated the age at fledging for the sample of 53 chicks, which was 37.62 days. However, the wing length values upon which this is based

were derived from the last measurements made on chicks prior to fledging. Since there was a mean difference of 1.6 days between their last being seen in the burrow and their estimated fledging date then the true value should be $37.62 \text{ days} \pm 1.6 = 39.22 \text{ days} \pm 2.1 \text{ S.D.}$ ($n = 53$). This is similar to the value for known-age chicks, but still significantly lower ($t = 3.17$, 77df , $p < 0.001$).

Fledging weights showed a significant seasonal decline ($r = -0.338$, 77df , $p < 0.01$; regression equation $y = 4.27x + 439.37$).

The fledging weights of chicks as a percentage of adult weight varied according to which adult weight was used. As in the other alcids we examined adult body weight decreased from the incubation period through to the chick-rearing period. Consequently chick fledging weight as a percentage of adult weight during the incubation period was 72.6%, but for the chick-rearing period it was 78.9% (see also Harris 1979).

In Table 30 we have compared Atlantic Puffin fledging weights as a percentage of adult weight for different colonies. The lowest values are for Great Island, Newfoundland where fledging weight was 56.7% of adult weight. However, these data may be biased because adult weights were recorded early in the season and may be relatively high, compared with values for the Gannet Clusters. However, even if we reduce the Great Island Atlantic Puffin weight value by 8% (the same difference as exists between incubation and chick-rearing in the Gannet Clusters 1982 data), i.e. to 423g, fledging weights of chicks are still extremely low, at 61% adult weight. We can also compare the data from the Gannet Clusters with two British colonies, one in which food was scarce, at least in some years, St Kilda, and the other, the Isle of May, where food may have been particularly abundant. At St Kilda fledging weights were recorded over 8 years, and varied between 60 - 72% adult weight. At the Isle of May values were higher, with puffins fledging at 72-75% adult weight. The

TABLE 30. A comparison of fledging weights of Atlantic Puffin
at the Gannet Clusters and other colonies.

Location	Fledging wt (g)	Adult wt (g)	Fledging wt as % of adult wt.	Reference
Gannet Clusters	361.8	498	72.6	This study
Great Island, Nfld.	261.8	468	56.7	Nettleship 1972
Funk & Small Islands	351.3	468(?)	75.1	Nettleship 1972
St Kilda	225-269	374.1	60.2-71.9	Harris & Hislop 1979
Isle of May	289-303	397.3	71.6-75.1	Harris 1978, 1979
Skomer Island	287-297	373.1	78	Ashcroft 1979
Skomer Island	284	382	74	Corkhill 1972
Lovunden, Norway	283	440	64	Myrbyrget 1962, 1963
Murmansk, USSR	330-370	500	66-74	Kartashev 1960
Barents Sea, USSR	295	490	60	Belopol'skii 1957

TABLE 31. Relationship between chick weight and wing-length
for Atlantic Puffin in 1981 and 1982..

Parameter	1981	1982
Data points	595	402
r	0.947	0.945
Intercepts	-0.608	-2.75
Slopes	2.89	2.89

NOTE: $t = 0.199$, 995 df , $P > 0.1$

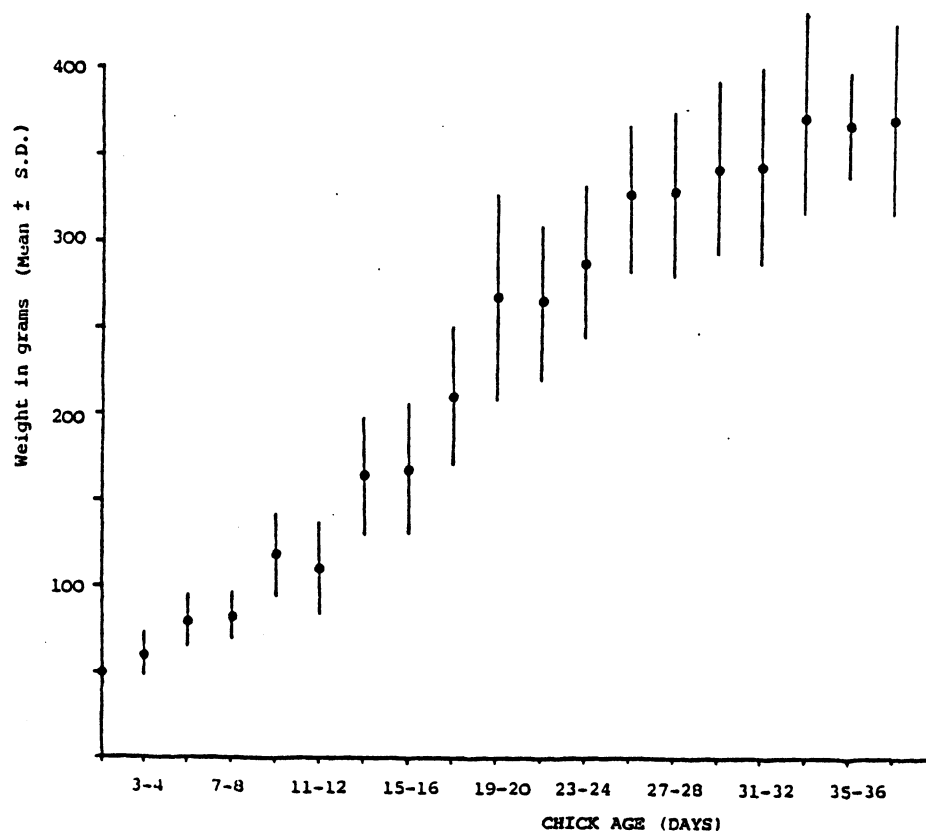


Figure 34. Growth (weight) of Atlantic Puffin chicks at the Gannet Clusters in 1982.

Original underweight chicks
by 11-6d (band 10) and
hatching date 10-10-82

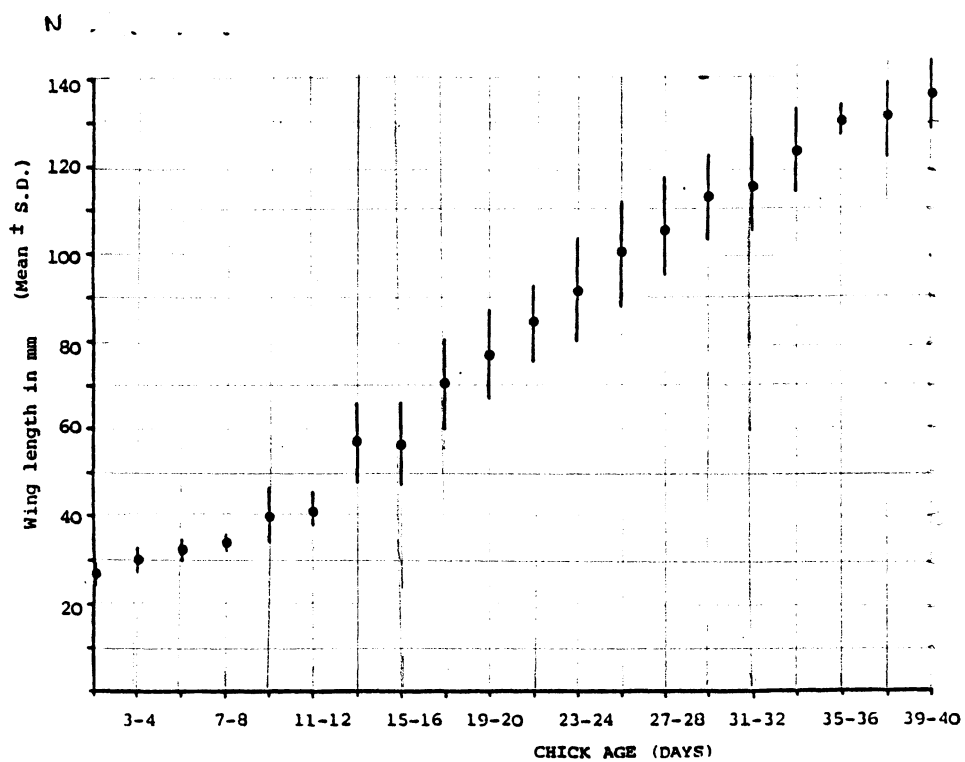


Figure 35. Growth (wing length) of Atlantic Puffin chicks at the Gannet Clusters in 1982.

highest values were obtained from Skomer Island, Wales, where puffins fledged at 74-78% adult weight. The value of 72.6% for the Gannet Clusters in 1982, is in the upper half of the values given in Table 30, indicating that puffins were not short of food during the chick rearing period.

The 1982 season at the Gannet Clusters was a late one, compared with 1981, and since there was a seasonal decline in fledging weight within the 1982 season, we might expect 1982 fledging weights to be lower than those in 1981. Unfortunately, we do not have comparable fledging weights for 1981. However, we used the following technique to compare the growth rates of puffins in 1981 and 1982. Wing length is closely correlated with age in Atlantic Puffins (see Fig.35). We therefore compared the slopes of the relationships between wing length and weight for all measurements of all chicks in 1981 and 1982. As Table 31 shows the slopes and the intercepts of the relationships in the two years were identical, suggesting that despite 1982 being a late season, growth rates, and (presumably) fledging weights, were similar in each year.

DISCUSSION AND CONCLUSIONS

Adult Biometrics

There were no significant differences in adult body weights between 1981 and 1982, at similar stages of the breeding season. In 1981 it was not possible to obtain body weights of alcidids during the pre-laying period so we are not able to say whether our values for Razorbill and Common Murre obtained in 1982 are high or low for that stage of the breeding cycle. However, because 1982 was a relatively late season (see below) we might expect adult body weights to have been relatively low. Low temperatures and ice-cover presumably prevented females from accumulating reserves necessary for breeding at the 'normal' time. However, the body weights for Razorbills and Common Murres in Table 2 may be biased in two ways. First, the Razorbill sample

was obtained only 1-3 days before the first eggs were laid, so body weights of any females in the sample would be relatively high. Unfortunately it is not possible to sex either Razorbills or murres, from their external appearance, so we cannot correct for this. From our observations of Common Murre on study plots we know that the sex ratio is male-biased during the pre-laying period, and males may be larger than females (Threlfall & Mahoney 1980). This too may bias the pre-laying adult body weight values upwards.

A small sample of Thick-billed Murre weighed during the incubation periods of both 1981 and 1982 were significantly heavier in 1982 than in 1981. The difference in body weights between 1981 and 1982 for the entire sample bordered on significance ($P < 0.1 > 0.05$). This fact together with the lack of difference in body weights of other species between years and lack of difference in egg volume indices between years indicates that once the ice moved out, food rapidly increased for all species of alcids.

Timing of Breeding

When observations began on 24 May 1982, the vicinity of the Gannet Clusters had approximately 9/10 ice cover (see Fig. 2) and it was not until about 6 June that extensive areas of open water became available around the colony. Our observations on replacement eggs indicate that it takes 14-16 days for alcids to produce an egg (see above) and in 1982 the first eggs were laid approximately 14-16 days after the sea became largely ice-free around the colony. In other words it appears that birds may have begun to accumulate reserves for egg laying as soon as the sea became ice-free. However, because in 1982 air temperatures were significantly lower and ice-cover more extensive during early May and June of 1982, compared with 1981, the start of breeding was delayed in 1982.

The rank order of egg laying in 1982 was very similar to that in 1981, despite 1982 being a late season. It is not clear why this should have occurred if all species started to form eggs at the same time (and since all species have similar replacement intervals). There are a number of possibilities: (a) During the prelaying period alcid species utilized different prey and differences in prey abundance or quality resulted in birds being ready to breed at different times.

(b) Birds may time their breeding so that they have young to feed at the nest-site at the peak of food availability.

(c) Birds may time their breeding so that there is abundant food for newly fledged young.

(d) A fourth possibility is that interspecific competition for food during the chick-rearing period forces different species to breed at different times, such that the temporal overlap in food requirements is minimal.

Of these ideas, it is not yet clear which is most likely, but we can eliminate some:

(a) If this were true, then we might have expected birds to attempt to breed as soon as possible (Birkhead & Nettleship 1982b), and had they done this, it may have been reflected in reduced mean egg size, but there was no evidence for this.

(b) We have shown that alcids at the Gannet Clusters feed their chicks on different prey species to a large extent. If the rank order of seasonal abundance or availability of these species remained unchanged despite the late start to the spring, then this could explain the timing of breeding.

(c) We have insufficient information for alcids to know whether the timing of breeding has evolved so that any peak in food availability coincides with chick-rearing at the breeding site or post-fledging.

However, since the energetic cost of commuting between feeding areas and the breeding site may be high, birds might be expected to time their breeding so that food was most abundant or closest to the colony, during the time chicks were to the breeding site.

(d) Inter-specific competition may explain the difference in food selected during the chick-rearing period. Two species, the Common Murre and Atlantic Puffin take mainly capelin, but competition may be reduced because these two species are the earliest and latest to breed, respectively. Moreover since the Atlantic Puffin has the longer incubation period and chick-rearing period, the temporal overlap in the period when each species has chicks at the colony is reduced still further.

Razorbill and Thick-billed Murre take different prey, from each other and from Common Murre and Atlantic Puffin; if prey species differ in their temporal availability this may explain the differences in timing of breeding we observed. Different alcid species may take predominantly different prey species because of competition in the past.

The concept of temporal peaks in food availability as discussed above requires some further comment. For Capelin, such peaks occur, in that this species moves into inshore waters to spawn at specific, predictable times of the year (Jangaard 1974), and there is abundant circumstantial evidence that many seabirds time their breeding (specifically, hatching) to coincide with the spawning of capelin. However, the 15 day differences in the chick-rearing periods of Common Murre and Atlantic Puffin appears somewhat paradoxical. One possible explanation is that Common Murres exploit Capelin relatively early, while they are inshore, whereas Atlantic Puffins exploit them later, after spawning when they have moved further offshore. The decrease in the proportion of Capelin in Common Murre chick diet after 11 August

(together with an overall reduction in the chick-feeding rate) provide some support for this idea. Whether the difference in timing of breeding has occurred because of competition is difficult to evaluate, but it seems possible for the following reasons: Common Murre feeding rates were higher than Atlantic Puffin, and by exploiting pre-spawning Capelin rather than post-spawning ones, may have had (a) a more accessible/closer food source (unfortunately we do not have feeding trip durations for Atlantic Puffin) and (b) a better quality food source. Common Murres are twice as heavy as Atlantic Puffins and in most inter-specific interactions, the larger of two organisms is dominant, so of the two species we would predict that Common Murre would dominate Atlantic Puffin. The size difference in Capelin brought by Common and Atlantic Puffin was small, (Table 20) and both alcid species are probably capable of handling and carrying prey of similar sizes, despite the difference in body size. However, there is another aspect to this; if Atlantic Puffin are forced to forage further from the colony, then central place foraging models (Orians and Pearson 1979) predict that they should bring relatively large loads back to their chicks. This is exactly what appeared to be happening (see Table 22).

Although we have only two years of quantitative data on the timing of breeding for alcids at the Gannet Clusters, there is now qualitative information for several years. When Tuck (1953) visited the Gannet Clusters in 1952, the season was relatively late, with the first chick being recorded on 17 July. In 1978, the season was also late, whereas in 1979 and 1981 it appeared to be earlier (Birkhead & Nettleship 1982a). In 1982 the season was relatively late. Although these results provide only an approximate idea of timing, they do indicate that the timing of breeding may be particularly variable in Labrador compared with areas further north (e.g. Gaston & Nettleship, 1981) and in boreal

regions (Birkhead 1980). Since environmental conditions at the end of the season do not appear to deteriorate as rapidly in Labrador as they do further north, alcids in Labrador may have more flexibility in the timing of their breeding season than birds breeding in high Arctic areas.

Egg Size and Composition

Contrary to expectations (because the 1982 breeding season was late) mean egg volumes did not differ between years for any species except Razorbill. In Razorbill egg volume indices were 1.3% smaller in 1982 compared to 1981 ($P < 0.05$). However, a comparison of eggs laid at the same site in both years showed no significant differences (paired $t = 0.85$, 163 df, NS). Similarly for Atlantic Puffin, a comparison of eggs laid in the same burrow in 1981 and 1982 did not differ in size. These results suggest, either that food became abundant very rapidly after the ice moved out allowing females to produce 'normal' size eggs, despite the late season, or that volume indices in 1981 were relatively low for some reason.

A comparison of first and replacement eggs for Razorbill, Common Murre and Atlantic Puffin confirmed results obtained in 1981; a positive correlation existed between the volumes of first and second eggs in all species, and replacement eggs being significantly smaller than first eggs. Replacement eggs in Razorbills were approximately 9% smaller than first eggs, whereas Common Murre replacement eggs were about 6% smaller.

Replacement intervals did not differ between years for Razorbills or Common Murres. Nor did the replacement intervals differ between Razorbills and Common Murres in 1982. The replacement intervals for Common Murre eggs on the undisturbed study plots were not significantly different from those on sites visited daily, so regular disturbance of the site did not appear to affect the replacement interval. Detailed observations of sexed B-N pairs prior to egg-laying on study plots indicated that female Common Murres spent very little time at the breeding site (and colony?) prior to egg-laying, so these results are probably not unexpected.

Comparison of first and replacement eggs provides some measure of the variance in egg size which is accounted for by a female effect. A comparison of eggs between years should also do the same for species with high survival rates, like alcids. However, because a few sites will inevitably be occupied by new females each year, the correlation between volume index between years will tend to be lower than between first and replacement eggs laid in the same year. For Razorbills the correlation between years was $r = 0.641$, and for Atlantic Puffins, $r = 0.597$ (both $P < 0.001$). However, in Atlantic Puffin the slope of the relationship did not differ significantly from 1, yet in Razorbills the slope was markedly lower than 1: 0.66 ($t = 5.46$, 16ldf , $P < 0.001$). This indicates that females which laid small eggs in 1981, produced larger eggs in 1982, while females which produced large eggs in 1981 laid smaller ones in 1982. These results suggest that a simple comparison of mean egg volumes between years may not provide the most accurate or meaningful picture of inter-year differences in egg-size.

Most studies of egg composition have assumed that the relative amounts of yolk and albumin are species-specific and do not vary between years. However, our results have shown that for both Common Murre and Razorbill the relative amounts of yolk may differ significantly between years for birds breeding at the same colony. In addition a comparison of Atlantic Puffin eggs for the Isle of May, Scotland (see Birkhead and Nettleship, 1982a) and the Gannet Clusters in 1982, showed that the proportion of yolk in eggs for the Gannet Clusters was significantly less than in eggs for the Isle of May. Clearly, egg composition is not species specific and may vary between years at the same colony.

Breeding Success

Our results from Razorbill control plots indicate that the regular visiting of breeding sites significantly reduces hatching success in this species. Most studies have recorded a fledging success in the order of 90-95% for Razorbills, so together with our values of 80-90% hatching success (Table 6) this indicates that breeding success among Razorbills at the Gannet Clusters was in the order of 72-84%. It is difficult to compare our values of Razorbill breeding success with published information since other workers (e.g. Bianki 1967, Lloyd 1979, Hudson 1982) visited breeding sites regularly to monitor breeding success. An additional problem concerns the tolerance of Razorbills to disturbance. At some colonies regularly visited by humans but where no hunting occurs, Razorbills may habituate (to some extent) to the presence of observers (e.g. Skokholm and Skomer, Lloyd 1979, Hudson 1982). Indeed, in the present study, breeding success at the same plots with the same degrees of disturbance in each year was significantly higher in 1982 compared with 1981 (Table 7). This difference was apparently due in part to birds being more tolerant of our presence at the colony in 1982.

Breeding success of murre in 1982 was similar to that recorded in 1981, with Common Murre more successful than Thick-billed Murre. However, measuring breeding success up to the time the chick leaves the colony will inevitably over-estimate the success rate. Moreover, in a year when food appeared to become scarce towards the end of the season (Figs. 20, 21 and 22) then post-fledging survival may be reduced. As in 1981 replacement eggs had significantly lower success than first eggs, indicating that birds breeding late in the season may have been particularly vulnerable to a reduction in food availability towards the end of the season. However, despite the decrease in success within a season, there was no evidence that success was lower in 1982, when breeding was late, compared to 1981.

Compared with Razorbills and murre, breeding success of Atlantic Puffins appeared relatively low, but this may have been due to disturbance by observers, and is unlikely to accurately reflect the breeding performance of this species.

Feeding Ecology

The information presented in the Results section is still fairly preliminary, since for a complete evaluation of the feeding ecology of the alcid species we need (a) specific identification of prey species (currently in progress), and (b) calorific values of prey species. In addition, the calorific value of different categories of prey within a particular species should be examined. For example the calorific values of prey at different stages in the reproductive cycle, at different ages and of different sexes may vary. However, although our analyses of alcid prey are still in progress, we can draw some conclusions. The results obtained in 1982 confirm data collected in 1981, that there exist fairly clear-cut differences in chick diets between species, and for the two species with the greatest overlap (Common Murre and Atlantic Puffin) there exist the greatest temporal difference in the timing of breeding.

Chick Growth

The rate of chick growth in Razorbills in 1982 was higher than in 1981. In addition weight increments, particularly early in the chick rearing period, were greater than in 1981. This suggest that food may have been particularly abundant relatively early in the chick-rearing period. However, as chicks got older the rate of feeding decreased (see below) and this may explain why Razorbill fledging weights did not differ between years, despite the differences in other aspects of growth.

The growth rates of Atlantic Puffin were higher than those in Newfoundland, and were about average compared with studies made elsewhere. However, as we have pointed out above, precise comparisons are difficult because adult body size varies between colonies, and this

must be taken into account in order to make inter-colony comparisons of chick weights. Adult body weights also vary within a season and the part of the season which adult body weights are taken to obtain chick weights as a percentage of adult body weights, have not been standardized between studies.

Comparison of Atlantic Puffin fledging weights at the Gannet Clusters between 1981 and 1982, was not possible because fledging weights were not obtained in 1981. However, a comparison of weight and wing-length relationships between years, indicate no difference in growth rates. Again, this is somewhat contrary to expectations since 1982 was a relatively late breeding season. There is some evidence that the number of days over which fledging occurred (14 days) in Atlantic Puffin was shorter than the period over which eggs were laid (18 days), but because we have no data for 1981 we are unable to say whether the relatively short fledging period in 1982 was associated with the lateness of the season.

Recommendations

The basic structure of the study will remain similar in 1983, with some observers being present at the colony prior to egg-laying, as in 1982. We will continue to monitor study plots for all species to record timing of breeding, breeding success, census counts and k values. Our results for Razorbill control plots in 1982 indicate that the intensity of observations of Razorbills in 1983 can be reduced without any decrease in the quality or quantity of information obtained: Razorbill breeding success will be monitored by a smaller number of visits to a number of control plots. In 1982 the presence of observers at the colony prior to egg-laying may have caused disturbance in some parts of the colony, so in 1983 Zodiac traffic between islands before and during egg-laying will be kept to a minimum. One of the main advantages of continuation for a third year will be to obtain detailed information on inter-year variability in all breeding

parameters. Our observations to date indicate that inter-year variability in the onset of breeding may be particularly high; it is especially important to evaluate the effect which the timing of reproduction has on other aspects of alcid reproductive biology.

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APPENDIX 1

Common and scientific names of fish species mentioned in the text.

<u>Common Name</u>	<u>Scientific Name</u>
Capelin	<u>Mallotus villosus</u>
Sandlance	<u>Ammodytes</u> sp.
Arctic Cod	<u>Boreogadus saida</u>
Atlantic Cod	<u>Gadus morhua</u>
Daubded Shanny	<u>Lumpenus maculatus</u>
Fish Doctor	<u>Gymnelis viridis</u>